

MAIZE GENETICS COOPERATION

NEWS LETTER

37

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April 15, 1963

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Bloomington, Indiana



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I. FOREWORD

Once again the onerous task of editing and assembling the News Letter has been most capably performed by Miss Ellen Dempsey. I am sure that I speak for all maize geneticists when I say that her invaluable services are greatly appreciated.

You will be interested in knowing that the current News Letter will be sent to 450 individuals and libraries. The demand increases by approximately ten percent each year.

A portion of the expense incurred in connection with cutting stencils, mimeographing, and binding was met by a grant from the National Science Foundation.

M. M. Rhoades

## II. REPORTS FROM COOPERATORS

AGRICULTURAL ALUMNI SEED IMPROVEMENT ASSOCIATION, INC.  
West Lafayette, Indiana

1. Preliminary indications of an Rf suppressor.

Observations from two sources during the past season indicate an unusual reaction of CI.44 when used as the pollen parent on lines carrying Texas sterile cytoplasm and restorer genes. The single cross Oh45 T Rf Rf x CI.44 was completely sterile until its silks started to dry and then it shed a little pollen.

In a program of backcrossing CI.44 on T Rf, difficulty has been experienced in "loosing" the Rf gene. This summer two of four backcross progenies of CI.44 on plants known to be of the composition T Rf rf yielded all sterile plants.

This peculiar reaction of CI.44 seems to indicate it carries a gene, or genes, which suppress the Rf gene. To our knowledge no such gene has been reported but it is entirely within the realm of possibility that such a gene does exist. Numerous additional crosses have been made to further investigate these unusual reactions. These crosses will be observed in Florida this winter and in Indiana next summer.

Merle T. Jenkins

ANDHRA UNIVERSITY  
Waltair, India  
Department of Botany

1. Numerical non-disjunction of chromosome 6 in an autotetraploid maize.

Numerical non-disjunction of chromosome 6 in a colchicine induced autotetraploid maize was studied by observing the number of nucleoli contained in the nuclei of the four spores in the pollen quartets in which the spores have not yet become free from each other. In maize, they remain together for a time after the completion of meiosis and it is also possible to distinguish the two division planes, since a cell division follows the first meiotic division. Usually each of the four microspore cells of the pollen quartet contains two nucleoli in the early stages organized by the two chromosomes 6 contained in their nuclei. These become fused together in the later stages. In each of five out of 207 pollen quartets examined at the early stages with

unfused nucleoli in the spore nuclei, three nucleoli were seen in each of two of the spore nuclei and only one in each of the other two. This distribution implies that non-disjunction occurred at division I. The pollen quartets in which a 3 : 1 distribution of nucleoli was observed comprise 2.42 percent of the total examined and can be taken to represent the percentage numerical non-disjunction of quadrivalents formed by chromosome 6. This value derived from the cytological data is close to the value obtained by Welch (1942) for chromosome 2 from genetical evidence. (See Welch, G. 1942 Linkage in autotetraploid maize. Ph.D. thesis, Cornell University.)

J. Venkateswarlu

BLANDY EXPERIMENTAL FARM  
University of Virginia  
Boyce, Virginia

1. Two recessive genes necessary for white seedlings.

Several different genes for white seedlings in maize are known. These are caused by monogenic recessives. Ten different rows segregating white seedlings were grown in 1962. Nine of these showed a monogenic segregation. It is not certain which genetic white seedling this is. Counts for these nine rows were: Green 690, white 228, compared with an expected ratio of 688.5 to 229.5, almost a perfect ratio. The other row showed a definite dihybrid ratio of 299 green : 20 white, almost a perfect 15:1 ratio. Here apparently two genes must be homozygous recessive to produce white seedlings. Seed is limited because of a drought in 1962 that killed all plants before pollen shedding. Reserve seed will be planted and plants selfed. Approximately 1/4 should be segregating for the two genes for white seedling, while another 1/4 should give monogenic ratios of 3:1. Has anyone observed a similar occurrence?

W. Ralph Singleton

2. Mutation CI to c:

In 1959 a plant which was  $\underline{B A_1 A_2 Pr Y Pl CI Sh Bz Wx R Og}$  was radiated at the rate of 94 r/day for the period 29 to 15 days before the pollen was collected for pollination onto a stock which was  $\underline{A_1 A_2 pr y C sh bz wx R og}$ . Among the resulting 12,000 seeds was one with a purple flinty endosperm. This was grown in 1960 and produced a plant which was  $\underline{B A_1 Pl Og}$ . Pollen examination indicated 97.5% good pollen. The resulting ear had a full seed set and segregated  $\underline{+/y +/pr C/c +/sh +/bz +/wx}$ . The colorless seeds were linked to the

Sh endosperms. In 1961 fifty of the colorless flinty seeds were planted. Forty-one of the resulting plants were Bz, with two bz. Most of these plants were also B, Pl and Og. Forty of the plants were tested for c and Cl. Thirty-two were cc, with two +c and six not tested on cc stock. Thirty-six were tested on CC stock with no evidence of the presence of Cl. It was evident that the purple seed in 1959 was the result of a mutation from Cl to c. In 1962, 10 of the 40 plants selfed in 1961 were tested for the response of the cc mutant to the action of Blotched. All ten of the lines tested blotched and were colorless when tested by c. As with the spontaneous Cl → c mutant tested by Coe (Genetics 47: #6, p. 779 - 783, 1962), this mutant acted like normal recessive c. In 1960 two, and in 1961 three more mutants which appear to be mutations from Cl to c were recovered from radiation experiments.

Alan Caspar

### 3. Summary of recovered endosperm mutations.

We have been attempting since 1952 to induce mutations of the endosperm genes in chromosome 9 of maize. Below is a summary of the mutants which have proved to be inherited without detectable sterility into the  $R_2$  generation. In experiments where more than one dose of radiation was used or in which more than one stage of microsporogenesis was radiated the populations are bulked as too few mutants are found at any one dose or stage to determine rates. In the stage experiments no populations are included which were radiated earlier than 13 days before pollen shedding. We have yet to prove a mutant from these stages because of the lack of coincidence between the embryo and endosperm.

These data do not indicate that the spontaneous mutation rate in the male is any different from those recovered for mutants recovered in the female. Therefore it would seem that radiation can induce mutations in maize which are in all ways similar to those which occur naturally at rates which are at least ten times greater than the control.



<u>Year</u>	<u>Experiment</u>	<u>R<sup>1</sup> Seeds</u>	<u>Proved Mutants</u>	<u>Rate 10<sup>6</sup></u>
1952	Chronic ♂ Radiation 5 r/d to 415 r/d	295,000	7 Sh→sh 1 Wx→wx	24
1952	Chronic ♀ Radiation 5 r/d to 415 r/d	30,000	1 Sh→sh	33
1953	20 hrs. 1320 r 13-20 days before anthesis	16,000	1 Sh→sh	63
1955	40 hrs. 2000 r 13-35 days before anthesis	18,000	3 Sh→sh	167
1958	23.5 hrs. 1880 r 14-35 days before anthesis	65,000	1 Sh→sh	15
1959	Chronic ♂ Radiation 29-14 days before anthesis	123,000	2 Sh→sh 2 Wx→wx 1 CI→c	16 16 8
1960	12 r/d to 129 r/d 23.5 hrs. 1080 r 13-28 days before anthesis	94,000	5 Sh→sh 2 CI→c	53 21
1961	23.5 hrs. 16-35 days before anthesis	987 r 83,000 705 r 69,000 517 r 79,000 270 r 97,000	2 CI→c 1 Sh→sh 2 Sh→sh 1 CI→c	24 14 25 10
	Total	328,000	3 Sh→sh 3 CI→c	9 9

## Control Populations Mutation in Male:

<u>Year</u>	<u>R<sup>1</sup> Seeds</u>	<u>Mutants</u>	<u>Rate 10<sup>6</sup></u>
1958	38,000	0	
1959	37,000	0	
1960	150,000	0	
1961	24,000	1 CI→c	
Total	249,000	1 CI→c	4.0
1953, 58-61	148,000	1 Wx→wx	7.0

## 1952-1961 Control Populations Mutations in Female:

	<u>R<sup>1</sup> Seeds</u>	<u>Mutants</u>	<u>Rate 10<sup>6</sup></u>
	4,089,000	0 CI→c	-
	6,598,000	6 Sh→sh	0.9
	6,180,000	14 Wx→wx	2.3
Coe (Genetics 47:779-783)	2,390,000	1 CI→c	0.4

BOSTON COLLEGE  
Chestnut Hill 67, Massachusetts  
Department of Biology

1. A new chlorophyll-deficiency mutant.

Among the progeny of a cross between an inbred sweet corn and a strain of South American maize, a chlorophyll-deficiency plant was found. Its leaves and stalk were light green. When this plant grew to two months old, yellow and white stripes appeared on the leaves. These characteristics became more pronounced as the stage of growth advanced. The plant was later in maturing than its sibs.

For a test of the inheritance of this variegated character, this plant was crossed on a standard inbred strain of Wilbur's flint possessing green leaves and stalk. The  $F_1$  plants from this cross were all green. In contrast, plants in the selfed progeny of the mutant showed the similar leaf and stalk characteristics as those of the parent, even though the degree of variegation varied from plant to plant. The  $F_2$  plants from selfing the  $F_1$  of the cross were classified as follows: 5 chlorophyll deficient plants: 77 green. This ratio fits well the  $F_2$  ratio expected for a pair of duplicate genes. A study of the chromosome constitution of this mutant is being carried on.

Y. C. Ting

2. A preliminary report on the fourth chromosome male gametophyte factor in teosintes.

The fourth chromosome male gametophyte factor (alleles  $ga_1$ ,  $Ga_1$ ,  $Ga_1^S$ ) in maize has been extensively studied but its occurrence in teosintes has not been reported. This factor has assumed an important role in evolution, because it acts as an isolating barrier between individuals or between populations of plants. During the last few years it was noted that a crossing barrier exists between maize and some of the teosintes. When pollen from an inbred strain of Wilbur's flint was applied to the silks of the teosintes, seed set was scant. It seemed possible that the crossing barrier between maize and these teosintes might well be the fourth chromosome male gametophyte factor. During the last two years a preliminary test on this factor in teosintes was made. Three varieties of Guatemalan teosinte and six varieties of Mexican teosinte were employed. From three to five plants of each variety were crossed by the maize tester of genotype  $ga_1/ga_1$ . Pollen of each teosinte was crossed to two plants of the maize tester having genotype  $Ga_1^S/Ga_1^S$ . The number of female gametes tested for each teosinte variety varied from 42 to 154. Even though these numbers used do not seem large enough to provide adequate evidence for any definite conclusion, they do disclose certain indications concerning

the genetic constitution of these teosintes. Maize testers of the genotypes  $ga_1/ga_1$  and  $Ga_1^S/Ga_1^S$  were kindly provided by Dr. O. E. Nelson of Purdue University. Seeds of teosintes were obtained from Professor P. C. Mangelsdorf of Harvard University. It was found that all of the teosintes (except Chilpancingo) possessed  $Ga_1$  (Table 1). Its strength in Florida, Lake Retene, Huixta, Arcelia, Chalco and Xochimilco teosintes appeared stronger than ordinary  $Ga_1$ , and it was subsequently designated as  $Ga_1^S$ .

Table 1. Results of the tests on the fourth chromosome gametophyte factors in Guatemalan (1-3) and Mexican teosintes ("x" indicates full seed set).

Teosinte	% seed set in X $ga_1/ga_1$	On $Ga_1^S/Ga_1^S$	Probable allele
1. Florida	0	x	$Ga_1^S$
2. Lake Retene	2	x	$Ga_1^S$
3. Huixta	0	x	$Ga_1^S$
4. Chilpancingo	0 (one plant set seed well)	x	$Ga_1$
5. Arcelia	0	x	$Ga_1^S$
6. Chalco	1.8	x	$Ga_1^S$
7. Xochimilco	7	x	$Ga_1^S$
8. Chapingo	24	x	$Ga_1$
9. Nobogame	25	x	$Ga_1$

Y. C. Ting

### 3. Meiosis in a haploid $Ga_1^S$ tester plant.

In a test for the fourth chromosome male gametophyte factor in different varieties of teosinte, a haploid tester plant was identified among a total of 47 plants homozygous for  $Ga_1^S$ . At pachytene of the microsporocyte divisions of this haploid plant, univalents like those in the haploid maize - teosinte hybrid (M. G. N. L. 30: 21), always folded back on themselves. Pairing between heterologous chromosomes and univalents unpaired throughout their entire length were seldom observed. At diakinesis, most of the chromosomes remained as univalents. It appears that the amount of duplication for various segments among maize chromosomes is not large, if any.

At metaphase I, a total of 538 randomly chosen sporocytes was studied in polar view. The most frequently observed type of chromosome

association in a single cell was 10 univalents, which represented 44 percent of the total. The less frequently observed type of association was eight univalents plus one bivalent, which represented 41 percent of the total. The third type of association was six univalents plus two bivalents, which made up 15 percent. From metaphase I to anaphase I, unusual features of chromosome behaviour were as follows: (1) The spindles often appeared crescent-shaped and univalent chromosomes were often distributed over the entire cell area. Hence it seemed difficult to distinguish metaphase I from anaphase I. (2) If all of the 10 chromosomes by chance oriented at the equatorial plate, it was found that they were likely to split. (3) In some cells the univalent chromosomes did not split and they were randomly distributed to the two poles. The distributions of 1-9, 2-8, 3-7, 4-6, 5-5, were all observed. As expected, the latter two were the most frequently observed ways of distribution. However, 0-10 type of distribution was not found in a limited number of sporocytes studied. (4) The 10 chromosomes of certain sporocytes were no longer distinct but divided into several conglomerate chromatin masses. These masses scattered along the spindle. After telophase I, cytokinesis in many primary sporocytes was incomplete.

At the second meiotic division, the unsplit chromosomes from the previous division divided in the normal manner, while halves of the previous split chromosomes did not. The undividing chromosomes usually failed to congress at the equator at metaphase II. On the other hand, the dividing chromosomes tended to do so. Attenuated chromatin masses were sometimes formed at anaphase II. At tetrad stage, the phenomenon of multispory consistently appeared. Micronuclei were always present.

For a test of ovule fertility the first ear of this haploid plant was pollinated by a sib. About 15 percent of the female gametes were fertile and set well developed seeds, which is much higher than expected. This high fertility is probably due to the high frequency of natural chromosome doubling in the ovules.

Y. C. Ting

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Department of Biology

1. Further studies of perennialism in derivatives of Zea.

A. Tetraploids:

Studies carried on since 1956 indicate that the prosaic breeding procedure of sibbing among the most perennial segregates in the hybrid

\*Research carried out at Brookhaven National Laboratory under the auspices of the U.S. Atomic Energy Commission.



of  $4n$  maize x  $4n$  perennial teosinte quickly restores perennialism to 50% maize tetraploids through increasing the expression of the rhizomatous habit under selection pressure. Similarly, only two generations of selection at the 75% maize level have resulted in a progressive recovery of the perennial expression. A high degree of maize-likeness therefore appears to be compatible with the perennial expression at the  $4n$  level.

#### B. Diploids:

Diploid derivatives of maize and perennial teosinte have been produced by making the triploid hybrid  $4n$  perennial teosinte x  $2n$  maize, then backcrossing this  $30$  chromosome hybrid back to  $2n$  maize, and then intercrossing among the resulting array of aneuploids and euploids. Selection for perennialism is practiced in the post-triploid generations.

If the triploid is used as the female in the backcross to maize, the chromosome numbers in the progeny are:

<u>First Post-Triploid Generation</u>		<u>Second Post-Triploid Generation, Obtained by Sibling First</u>	
<u>Chromosome No.</u>	<u>No. Plants</u>	<u>Chromosome No.</u>	<u>No. Plants</u>
20	1	20	35
21	3	21	12
22	7	22	9
23	8	23	3
24	9	24	3
25	10	25	0
26	11	26	0
27	5	27	1
28	6	28	0
29	3	29	0
30	0	30	0

If the triploid is used as the male in the backcross to maize, the chromosome numbers in the progeny are:

<u>First Post-Triploid Generation</u>		<u>Second Post-Triploid Generation, Obtained by Sibling First</u>	
<u>Chromosome No.</u>	<u>No. Plants</u>	<u>Chromosome No.</u>	<u>No. Plants</u>
20	8	20	41
21	3	21	8
22	1	22	4
23	0	23	2
24	1	24	1
25	1	25	0
26	0	26	0
27	2	27	0
28	3	28	0
29	2	29	0
30	3	30	0

As these data indicate, there is a rapid shift to euploidy in the second post-triploid generation obtained by sibbing among the euploids and aneuploids of the first. In the third post-triploid generation, nearly all are 20 chromosome euploids, except for a few rare trisomics.

Study of univalency at AI and of segregation of genetic markers in the triploid interspecific hybrid indicates that 20 chromosome plants found in the first post-triploid generation should have about 42% teosinte chromatin and about 58% maize chromatin. Pachytene analysis of such plants reveals several regions of pairing failure or apparent failure, including at least one large internal region and several smaller terminal regions. Failure to form bivalents, however, is rare.

Percentage of good pollen in 10 euploid plants of the first post-triploid generation ranged from 18% to 82%. Among 20 chromosome plants in the second post-triploid generation the proportion of good pollen ranged from 69% to 97%, and in the third post-triploid generation from 80% to 96%.

Twenty-one percent of the seedlings of the second post-triploid generation prove to carry lethal factors, and 10% of the seedlings in the third post-triploid generation likewise carry lethals.

The study of both pollen abortion and lethality of offspring indicates that perennial teosinte carries genetic lesions which act as diploid-lethals, but which are apparently functionally viable at the 4n level. Pachytene analysis indicates considerable non-homology between the genomes of maize and perennial teosinte. Since even in spite of very strong selection for teosinte characters, especially perennialism, in the post-triploid generations, these derivatives are still maize-like in morphology, it is probable that there is a strong tendency to eliminate teosinte chromatin at the 20 chromosome level, presumably in conjunction with the elimination of diploid-lethal factors.

Even though one must concede that we have as yet no good measure of how much teosinte chromatin may persist in advanced generation 20 chromosome plants, it is a clear result that we have not been able to demonstrate perennialism in any 20 chromosome plant. This is even true of the first post-triploid generation 20 chromosome plants which must carry large amounts of teosinte chromatin since these cannot have yet suffered post-triploid elimination of teosinte segments. It has also been impossible to demonstrate perennialism among the whole gamut of aneuploids found in the first or later post-triploid generations. A few of these are able to regrow a new generation of culms after maturing seed, thus appearing perennial (Maize News Letter 36:5) for a time. However, totipotency is lost among the axillary buds of the second generation culms, and the plants die.

Only recently, one 21 chromosome plant has been found which appears to be truly perennial, and has been cloned to 15 propagules. It is now producing fourth generation branches from third generation culms. It is hoped that this plant or clone, which cytogenetically undoubtedly represents the simplest form in which perennialism in *Zea* has yet been observed, will furnish a beginning point for definitive studies of the cytological, genetic, and biochemical basis of perennialism in *Zea*.

Donald L. Shaver

2. Further studies of the inheritance of two interspecific traits in derivatives of maize and teosinte.

Distichy of ears and photoperiodism are two traits which are considered to be taxonomically useful in distinguishing maize from teosinte. Both of these traits have been found in maize as well as in teosinte. That photoperiodism in maize can be inherited as a monogenic trait is not doubted. The inheritance of distichy, however, has been variously reported to be monogenic and polygenic.

It is suggested that very close taxonomic affinities of the two forms would be indicated if both traits were inherited in maize and teosinte as expressions of the same loci.

The inheritance of distichy was studied in selfed backcrosses of (eight-rowed Longfellow Flint x Fla. teosinte)xLongfellow Flint. If Florida Teosinte carries a locus which can confer distichy in a 75% maize background, then 1/2 of the selfed backcross progenies should segregate 3:1 for the presumed recessive distichous trait:

<u>Progeny No.</u>	<u>Distichous plants</u>	<u>Polystichous plants</u>
557	0	16
558	5	8
559	10	0
560	7	8
561	11	1
562	6	7
564	5	10
565	0	3
566	6	5

It is obvious that the expression of distichy in this 75% maize background is not monogenic. Moreover, there was no evidence of the expression of the type of photoperiodism conferred by the id locus in pure maize.

In the same manner, the inheritance of photoperiodism in selfed backcrosses of (Inb. Kys x Fla. Teosinte) x Kys was studied in 11 progenies totaling 107 plants. Photoperiodism of the type found in adjacent plants of pure maize carrying the id locus was not found at all. Whereas the pure maize plants segregating for id fell into two sharply separate classes of determinant and photoperiodic-indeterminant, the maize-teosinte derivatives showed a continuous range of flowering times, none, however, as late as pure maize homozygous id/id. No distichous plants at all were found in this selfed population of 75% Kys, 25% Florida teosinte plants.

One must concede that this study has failed to reveal the existence of teosinte loci which can confer either distichy or the id type of photoperiodism in a 75% maize background as single gene expressions.

A year ago the writer reported that 3 plants of the hybrid between teosinte and Andean maize which has been reported to be homozygous id/id were indeterminant-photoperiodic in growth habit. This appeared to be true in greenhouse culture. However, the observation could not be repeated out of doors in 1962, since this hybrid flowered about a month before either pure teosinte or maize homozygous id/id. Moreover, there has been no indication of a single gene segregation for photoperiodism in selfed hybrids of the Andean maize and corn belt inbreds. Therefore, there is no evidence in these studies that the Andean maize carries the classical id/id locus.

Donald L. Shaver

### 3. Further studies of linkage and preferential segregation in allotetraploids of Zea.

Data from a new region, gl<sub>6</sub> - lg<sub>2</sub> have been obtained from both autotetraploids and allotetraploids of Zea. Testcross data from the two types of coupling duplexes were as follows:

	... "Phenotype of Gametes"....				Total	Constitution of Duplex tested	
	<u>G1<sub>6</sub>Lg<sub>2</sub></u>	<u>G1<sub>6</sub>lg<sub>2</sub></u>	<u>gl<sub>6</sub>Lg<sub>2</sub></u>	<u>gl<sub>6</sub>lg<sub>2</sub></u>		<u>G1<sub>6</sub></u>	<u>Lg<sub>2</sub></u>
allotetraploid percent	1165 86.2	25 1.8	36 2.7	126 9.3	1352	<u>G1<sub>6</sub></u>	<u>Lg<sub>2</sub></u>
autotetraploid percent	524 70.7	84 11.3	54 7.3	79 10.7	741	<u>G1<sub>6</sub></u>	<u>Lg<sub>2</sub></u>
						<u>gl<sub>6</sub></u>	<u>lg<sub>2</sub></u>
						<u>gl<sub>6</sub></u>	<u>lg<sub>2</sub></u>



Coefficient of linkage in allotetraploid,  $B = .782 + .036$   
 Coefficient of linkage in autotetraploid,  $B = .419 \pm .110$   
 Coefficient of preferential segregation in allotetraploid for  $gl_6 = .333$   
 Coefficient of preferential segregation in allotetraploid for  $lg_2 = .496$

These data are in agreement with the range of results reported for other segments in previous work with these types of polyploids (Maize News Letter 34 : 56-59).

Donald L. Shaver

4. Further studies of trivalent frequencies in the interspecific triploid hybrid of perennial teosinte x annual teosinte.

A year ago (Maize News Letter 36: 4-5) it was reported that the frequency of trivalents in the triploid hybrid between perennial and annual teosinte was only about 0.36. This seemed surprising since this indicated less homology between the chromosomes of the two teosinte species than between the chromosomes of maize and perennial teosinte, where the trivalent frequency at diakinesis was about 0.65.

Since the first value was taken from the study of only one plant, two additional plants of  $4n$  teosinte x  $2n$  annual teosinte were studied. In one, the trivalent frequency among 1000 sets of homologues at diakinesis was  $0.269 + .1210$ . In the other, the trivalent frequency among 300 sets of homologues was  $0.397 + .1795$ . These additional data reconfirm the results reported a year ago. However, when univalents at MI-AI in the second plant were scored, in 200 cells, an average of  $8.89 + .0723$  was found. Hence it appears that over  $1/2$  of the diakinesis figures scored as trivalents were actually bivalent-plus-associated-univalent configurations. This indicates that caution must be used in interpreting diakinesis associations in this triploid. It seems likely that in the maize-teosinte triploids studied last year, many diakinesis figures scored as trivalents were also bivalent-plus-associated-univalent configurations.

The simplest interpretation of these results is that there is a high degree of preferential pairing and segregation in the teosinte inter-specific triploid, perhaps even more than in the teosinte-maize inter-specific triploid. However, since there are no genetic markers to follow in the teosinte triploid hybrid, it is still only a supposition that the preference for pairing is perennial teosinte chromosome with perennial teosinte chromosome. A clarification of this point could be made by inserting markers into annual teosinte from maize, and then determining the degree of genetic preferential segregation in the teosinte triploid.

Donald L. Shaver

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Los Angeles 24, California

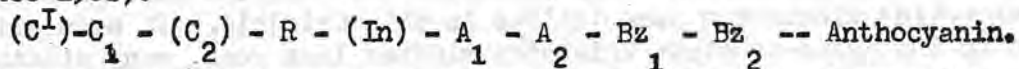
1. The effects of anthocyanin (cyanidin di-glucoside) on root growth.

Synthetic anthocyanidins, especially 3,7,4 trihydroxy 2-phenyl benzopyrylium chloride and 7,4 dihydroxy 2-phenyl benzopyrylium chloride, have been reported to stimulate the growth of wheat roots (Stenlid, *Physiol. Plant.* 15: 1962). To determine whether or not anthocyanin is also a growth stimulator, cyanidin di-glucoside was extracted from 'cy' husks of maize, and tested for biological activity on seedling roots of wheat, oats, and maize; all three types of roots showed a statistically significant increase in length over the controls. The maize seedlings used for assay were homozygous for the  $a_1$  gene. These data are being extended to include relative activities of pure preparations of cyanin, chrysanthemine and the aglycone, cyanidin. Responses to exogenous anthocyanin are also being determined for maize seedlings homozygous for  $a_1$  and seedlings homozygous for  $A_1$ .

G. M. Reddy  
M. Katsumi  
B. O. Phinney

2. Leucoanthocyanidin accumulation by maize.

Inter-tissue complementation studies with fresh aleurone tissue have suggested the following gene action sequence for the control of steps along a pathway leading to anthocyanin synthesis (Reddy and Coe, *Science* 1962):



In this sequence the homozygous  $a_2$  mutant accumulates a leucoanthocyanidin which can be converted to anthocyanidin by heating with acidified-alcohol (Coe, *Genetics* 1955). If the gene order is true, mutants which block steps prior to the  $a_2$  gene should lack leucoanthocyanidin when in combination with  $a_1$ . Those which block steps after the  $a_2$  gene should have leucoanthocyanidin when in combination with  $a_2$ . Homozygous double mutant stocks in several combinations were kindly supplied by Dr. Coe. Extracts of the aleurone were tested for the presence or absence of leucoanthocyanidin. Pericarps were peeled from 10-30 mature seed of each genotype after soaking in water for one hour. The exposed endosperms were then extracted with acidified-alcohol for 24-48 hours at room temperature. Each extract was heated 2-5 minutes to detect visible evidence of conversion to pigment. All tests turned out as predicted (Table 1). Recessive intensifier (in) increased the

amount of leucoanthocyanidin about five times. The purple pigments obtained by heating extracts from aleurone homozygous for  $\underline{in\ a_2}$ ,  $\underline{a_2\ bz_1}$ ,  $\underline{a_2\ bz_2}$ , and  $\underline{a_2}$ , had absorption spectra identical to cyanidin.

Pigmentation could be visibly observed from the heated extract of a single  $\underline{a_2}$  mutant.

Table 1. Presence (+) or absence (-) of leucoanthocyanidin based on visible appearance of pigment, two to five minutes after heating an acidic-alcoholic extract of aleurone.

Mutant combination	$C^I\ a_2$	$c_1\ a_2$	$c_2\ a_2$	$r\ a_2$	$\underline{in\ a_2}$	$a_1\ a_2$	$a_2$	$a_2\ bz_1$	$a_2\ bz_2$	$A_2\ bz_1$
Color	-	-	-	-	+	-	+	+	+	-

G. M. Reddy

### 3. Double mutants for dwarfing genes of Zea mays.

Four of the five gibberellin-responding dwarf mutants of maize have been intercrossed in all possible combinations and the  $F_1$  selfed to give  $F_2$ 's which segregate for the double mutant. These presumptive double mutants can be identified in the early seedling stage in some cases, or in other cases as the plants become older. The  $\underline{d_1 - an_1}$  double mutant has been backcrossed to both  $\underline{d_1}$  and  $\underline{an_1}$  plants; all progeny were dwarf, confirming the presumptive genotype of the double mutant. All presumptive double mutants (seven different combinations tested) respond to exogenous gibberellin by increased growth to give a phenotype which approached that of the normals.

Bernard Phinney.

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Research Department

1. Local evaluation of daylength sensitive exotic germplasm.

A much needed beginning has been made toward a systematized method of evaluating exotic germplasm for use in the Corn Belt. Fortunately, this has included considerations of yield and general agronomic excellence as well as the usual search for specific qualitative traits. Of especial interest to the practical temperate zone breeder are investigations which deal with material from short-day areas. It is very difficult to locally evaluate such introductions due, of course, to their tangled overgrowth under our field conditions. One must rely heavily, with some justification, upon native performance records. Since, however, the  $F_1$  crosses of such germplasm with early Corn Belt material are generally adapted to the Central Corn Belt, one would be interested in comparing their relative performance in such crosses with (1) their behavior in the overgrowth condition, and (2) the contribution given by the exotics after incorporation. The data reported here are concerned only with the first comparison.

In 1959, five exotics (one variety, one double cross, and three single crosses), representing various degrees of maturity and overgrowth response, were crossed in common to a very early Corn Belt dent inbred, A509. Attempts at crossing to a second early inbred, A340, failed. The two heterogeneous exotic populations were each represented by a sample of 28 plants crossed individually to A509 and bulked in equal proportions for this study. Each sample of 28 plants constituted the earliest segregates out of populations of 200 plants (San Juan) and 400 plants (H309). To this extent, these samples were not fully representative of the populations. The exotics, exotic x inbred crosses, the early inbred tester, two adapted single crosses, and an adapted synthetic variety were grown at Grinnell in 1960 in a replicated study involving six replications. Subplots were single 19 plant rows. Considerable care was taken to border the weak inbred tester and the excessively vigorous exotic populations with material of comparable vigor and maturity. Individual plant data were taken for a number of quantitative traits.

Subplot size was not adequate for a variance study in several of the traits. The study suffered further in the absence of additional testcross series to other early testers. In consideration, too, that the  $F_1$  rather than the  $F_2$  generation had to be used for the three exotic single crosses, it seemed wise not to attempt a close interpretation of the data. The average performance in each population for each of seven traits is offered for the reader's own consideration.



	<u>Midl/ Silk</u>	<u>Plant Ht. (in.)</u>	<u>Ear Node Ht. (in.)</u>	<u>Ear Lgt. (in.)</u>	<u>Kernel Row Number</u>	<u>Dry Weight Shelled Seed per Plant (grams)</u>	<u>% Prolific- acy<sup>2/</sup></u>
A509	22.0	54.0	12.4	4.48	15.6	47	0
Wf9 x Oh43	22.9	102.7	31.2	7.77	19.3	254	6
M44 x 187-2	24.5	100.7	34.7	9.57	15.8	271	0
Minnesota Synthetic 2	25.4	100.4	36.1	8.37	16.8	223	12
A509 x(Mp305xMp307)	27.5	106.3	44.3	7.54	15.2	238	38
x(Nc218xNc222)	27.9	106.3	41.0	7.72	16.1	233	11
x San Juan	28.5	107.9	44.9	7.85	16.5	219	2
x H309	30.3	108.3	42.5	7.93	16.9	198	2
x(Mp414xMp428)	33.0	108.3	41.3	7.79	16.2	231	40
Mp305 x Mp307 <sup>4/</sup>	39.8	123.1	63.9	7.98	12.8	301	91
Nc218 x Nc222 <sup>5/</sup>	46.3	109.2	57.8	7.28	16.6	217	11
San Juan <sup>6/</sup>	57.3	132.1	82.8	6.88	14.9	111	9
H309	65.1 <sup>3/</sup>	140.6	94.0 <sup>3/</sup>	--	--	--	--
Mp414 x Mp428 <sup>8/</sup>	49.4	116.9	50.7	6.74	13.7	142	69

<sup>1/</sup> Number of days after July 1

<sup>2/</sup> Based on number of plants bearing second ear 50% or more the size of first ear

<sup>3/</sup> A downward estimate as only the early portion (45%) of the population silked

<sup>4/</sup> Mississippi white dent single cross

<sup>5/</sup> North Carolina yellow dent single cross

<sup>6/</sup> Mexican white dent variety, race Vandeno

<sup>7/</sup> Mexican white dent double cross, race Celaya

<sup>8/</sup> Mississippi yellow dent single cross

E. E. Gerrish

## 2. Wild maize undone by domesticated forms?

A recent concept of wild maize, 6,000 BC, seems to be that of a branch of the Maydeae in a particularly precarious position due to (1) over specialization in the lateral, pistillate branches and, (2) confinement to a narrow ecological niche (low natural population). Is it in the realm of possibility that the wild forms were carried to extinction by the constant introgression of the more numerous, but even less fitted types developing under man's protection?

E. E. Gerrish

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1. C<sup>14</sup>- assimilations study.

Maize inbred lines, D-16, W37-A, and N-40 and one single cross hybrid F<sub>1</sub> (D-16 x W37-A) were tested for their respective capabilities in carbon assimilation. Three week old seedlings in lots of three were exposed to C<sup>14</sup>O<sub>2</sub> for 10 minutes for each entry and the seedlings were quickly killed by submerging into liquid nitrogen.

Subsequent extractions were carried out with Ethanol, Chloroform, and each extract was tested for its radioactivity and dry weight. The residue was finely homogenized in a glass tissue-homogenizer and suspended in water for homogeneous dispersion so that samples of uniform thickness without substantial self-absorptions could be prepared from residues for radioactivity determinations.

Radioactivity (cpm, count per minute) and the specific activity (cpm/mg of solute) are presented in tables 1 and 2 and dry weights of each extract fraction in table 3. There were varietal differences among the inbreds and differences between the F<sub>1</sub> and its parental inbreds (D-16, W37A) in each extract fraction. The total carbon assimilated rates highest for the F<sub>1</sub> hybrid (table 1). However, in terms of specific activity (table 2), the F<sub>1</sub> hybrid gave a count of 21,834 cpm/mg, which is lower than either of its parental inbreds. This seems, at first, to indicate that the highest total carbon assimilated by the F<sub>1</sub> hybrid was due to its larger leaf area but probably not due to an elevated chloroplast activity by "heterosis of chloroplasts". However, when one examines the residue fractions in table 2 column 3, it is noticed that the F<sub>1</sub> gives a specific activity (3,822 cpm/mg) higher than either parent activity. Since the ethanol and CHCl<sub>3</sub> would extract most of the free sugars, amino acids, and fatty materials etc. from the samples, the residue fraction would consist of cellulose and high molecular weight polymers. This seems to indicate that the F<sub>1</sub> hybrid exhibited a high degree of efficiency in translocation as well as transformations from immediate low molecular weight photosynthetic products to higher polymers of plant constituents, as evidenced by its higher specific activity in the residue fractions (table 2). It is also noticed that the hybrid F<sub>1</sub> accumulated in its residue 9.5% of the total C<sup>14</sup> assimilated during a 10 minute exposure, which is twice as much as the amount of C<sup>14</sup> accumulated by either of its parents in their residue fractions, respectively.

Since the total dry weight consists of all of the constituents in the tested plants, it would be premature to make any definite conclusions as to the hybrid chloroplast activity until the isolated chloroplasts are examined and compared against those of their parental inbreds.

Table 1 Radioactivity of Samples (CPM)

Sample	Ethanol Extraction CPM	%	CHCl <sub>3</sub> Extractions CPM	%	Residue CPM	%	Total CPM
D-16	3,695,642	93.28	96,000	2.42	170,068	4.29	3,961,710
W37A	3,594,992	90.33	153,025	3.84	231,856	5.83	3,979,874
F <sub>1</sub> (D-16xW37A)	4,915,195	85.63	282,481	4.92	542,356	9.45	5,740,032
N-40	5,067,208	90.24	149,855	2.67	397,403	7.08	5,615,466

Table 2 Specific Activity of C<sup>14</sup> in Samples (count/min./mg.)

Sample	Ethanol Extract	Chloroform Extract	Residue in H <sub>2</sub> O	*Pooled Specific Activity
D-16	115,489	8,000	1,966	30,357
W37-A	76,489	5,668	2,482	23,775
F <sub>1</sub> (D-16xW37A)	59,941	7,243	3,822	21,834
N-40	103,412	3,405	5,504	33,991

Each figure is average of 3 determinations

\*Pooled specific activity is obtained by:

$$\frac{(\text{SP}) (\text{DWS}) \text{ ETOH} + (\text{SP}) (\text{DWS}) \text{ CHCl}_3 + (\text{SP}) (\text{DWS}) \text{ Res.}}{\text{Total dry weight}} = \text{Pooled SP}$$

SP = Specific activity (Table 1)

ETOH = Ethanol

Res = Residue

DWS = Dry weight of the solute (Table 3)

CHCl<sub>3</sub> = Chloroform

Table 3 Dry Weight of Sample (MG)

Sample	Ethanol Extraction	%	CHCl <sub>3</sub> Extraction	%	Residue	%	Total Dry Weight
D-16	32 mg.	24.5	12 mg.	9.19	86.5 mg.	66.28	130.5 mg.
W37A	47	28.08	27	16.13	93.4	55.79	167.4
F <sub>1</sub> (D-16xW37A)	82	31.19	39	14.83	141.9	53.97	262.9
N-40	49	29.66	44	26.63	72.2	43.70	165.2

## 2. Brachytic-2 dwarf hybrids.

Hybrids of brachytic single crosses and normal single crosses have been obtained. The brachytic gene causes a shortening of stalk internodes, especially those below the ear. Other parts of the plant are usually not reduced. In the past three years, many hybrid combinations have been measured for ear and plant height, grain yield, and in some cases for culm diameter and silage yield.

A preliminary analysis of the performance is summarized in the accompanying table (No. 1). The means representing normal, semi, and full dwarf hybrids show an obvious trend. The brachytic-2 gene has partial dominance which is enhanced in specific genetic backgrounds. In addition, there is evidence that reciprocal semi-dwarfs respond differently. The degree of expression of the brachytic gene in identical nuclear backgrounds is not always equal in dwarf and normal cytoplasms.

Table 1 Dwarf-Normal comparative means by years:

	<u>1960</u>			<u>1961</u>			<u>1962</u>				
	Grain yield bu/A	Plant height inches	Culm dia- meter inches	Grain yield bu/A	Plant height inches	Ear height inches	Culm dia- meter inches	Grain yield bu/A	Silage yield lbs DM/A	Plant height inches	Ear height inches
Normal	90.2	88.0	0.98	100.9	94.6	37.6	0.81	90.3	8726.4	84.7	31.9
Semi-dwarf	86.0	81.6	1.05	101.1	92.5	35.1	0.82	86.4	8870.0	80.3	28.7
Dwarf	-	-	-	97.2	90.1	34.0	0.83	61.3	5749.9	57.1	13.6

J. C. Thompson and H. L. Everett

## 3. Chromosome knobs.

Dr. Albert Longley in a report to the Rockefeller Foundation Mexican Program ("Chromosome Knobs of Maize from the Latin Americas" by Albert Longley and Angel Kato Y. 1961) described the origin of large masses of heterochromatic material in several diverse collections of the race Nal-Tel. Plants used in Longley's studies were sacrificed. Seed samples (5 kernels) of collections reported to show unusual heterochromatic accumulations were planted in the greenhouse in winter 1962 and microspore mother cells were collected for chromosome observations.



These eleven collections were sampled: Guatemala 207, Guatemala 269, Guerrero 174, Panama 5P, Panama 12P, Panama 39P, Costa Rica 45, Nicaragua 3432, Nicaragua 3406, Costa Rica 400, and Guatemala 835. A total of 27 plants were characterized successfully for chromosome morphology. One plant in each of three collections (Guatemala 269, Panama 5P, and Panama 39P) showed a heterochromatic block similar to that terminating abnormal chromosome 10L terminating 9S. The abnormal 10 condition was seen in four other plants.

Due to poor plant growth and lack of adaptation to Ithaca conditions, it was not possible to obtain selfed lines. Crosses were made to other plants, however, and stocks carrying the unusual chromosome 9 have been obtained.

H. L. Everett and  
Margaret Emmerling Thompson

#### 4. Iojap and teosinte cytoplasm.

Mazoti (1950) has reported that the expression of the iojap gene is greatly reduced or entirely lacking in homozygous ij ij plants which contain teosinte cytoplasm. Several years ago Mazoti (kindly) gave us seed of two of his iojap stocks. One was a standard gl gl ij ij line with maize cytoplasm, and the other a stock derived from the first line by backcrossing it as male parent for 8 generations to teosinte cytoplasm. The second line with teosinte cytoplasm was thus also presumably gl gl ij ij. The two lines, however, clearly differed in the degree of chlorophyll variegation. The strain with teosinte cytoplasm has shown few striped plants in the four seasons it has been grown, and the few striped plants that did appear usually contained only one or a few short white stripes. The stock carrying maize cytoplasm has given all variegated plants which typically have a moderate number of relatively narrow stripes. That the stock with teosinte cytoplasm is homozygous ij ij has been confirmed by crossing it as male parent to standard ij ij and + ij female parents with maize cytoplasm. We have continued the backcrossing for three more generations with no change in the expression of the iojap phenotypes in the two lines.

The strain with teosinte cytoplasm was also crossed as female parent with two of our standard iojap stocks (obtained originally from the Coop. and maintained by selfing). The  $F_1$  families, all ij ij in teosinte cytoplasm, were vigorous. At maturity both progenies contained more striped plants than were present in the ij ij teosinte cytoplasm female parent. Each family also had solid green plants (4 green, 15 striped in one family, 8 green, 12 striped in the second family).

Green plants in the  $F_1$  families were backcrossed as seed parents by the standard iojap stocks. One backcross progeny contained 7 green or slightly striped plants and 7 plants with a moderate number of stripes. The second backcross progeny had 2 green, 2 slightly striped plants and 7 plants judged to be typical iojap like the recurrent male parent. A second backcross generation stemming from both green and striped female parents consisted of 6 families all of which contained only striped plants. The intensity of variegation in the BC2 progenies was not obviously correlated with the degree of variegation of the BC1 females (pollen from the same plant was used in making all backcrosses), all 6 BC2 progenies showing about the same degree of variegation whether derived from green or striped seed parents.

The expression of the iojap phenotype in the BC2 families was much more pronounced than in the original ij ij, teosinte cytoplasm stock from Mazoti, but was probably somewhat less pronounced than in the standard ij ij recurrent parents. The teosinte cytoplasm may thus be interacting with the ij genotype in our stocks, but if so the resultant modification of the iojap phenotype is less dramatic than in Mazoti's stocks. If one rules out pollen transmission of maize plastids and cytoplasm, the results to date might suggest, among other things, differences in iojap alleles or differences in modifiers of the iojap gene in the different stocks. Our standard iojap stocks (with maize cytoplasm) are considerably more variegated than the standard stocks received from Mazoti, and it appears that these differences are also manifest by the degree of expression of the two genotypes in teosinte cytoplasm.

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1. Conversion of inbreds to Texas-sterile cytoplasm by androgenesis in a tetraploid-diploid cross.

A Texas-sterile cytoplasm, tetraploid version of the "Emerson Brown" marker, a B P1, was used as the female parent in a cross by the Purdue inbred H52. Among the progeny, there was one individual, diploid and paternal in phenotype. This individual was partially fertile and set some seed upon self pollination. In the second generation, field grown, most individuals were completely sterile; a few were partially fertile; all were phenotypically indistinguishable in other characteristics from normal H52. Apparently an unreduced gamete from the male functioned androgenetically and, as expected, acquired the cytoplasm of the female parent. This gamete, presumably, was heterozygous for partial fertility; or, possibly, the greenhouse environment in which the androgenetic individual was grown favored pollen formation.



A number of other inbred lines were used as males on the tetraploid cyto-sterile marker stock last summer. Among the progeny now in the seedling stage a number of paternal monoploids and several diploids have been recognized. The expectation is that these individuals carry the Texas-sterile type of cytoplasm. (See Goodsell: Crop Science Vol. 1, No. 3, p. 227, 1962)

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1. Associations between chromosome knobs and plant characters.

Cytological and morphological analyses of a Maiz chapalote population has revealed statistically significant associations between specific chromosome segments marked by knobs and certain plant characters. Six knobs (positions 1L, 4S, 4L, 6a, 6b, and 8L) were segregating in the population to the extent that their presence or absence could be compared with 21 commonly-used plant characters. Only knobs 4L and 6b showed significant association with any of the characters used. These associations are listed in the following table:

Table 1

Knob--plant character association	Knob condition	N	X	S <sup>2</sup>	P value
Small stem diameter and knob 4L (mm.)	KK and KO	13	24.7	2.20	.05
	OO	5	26.9	4.25	
Many tillers and knob 4L	KK	9	2.7	0.50	.001
	OO	5	1.4	0.30	
	KO	4	2.0	0.66	
	OO	5	1.4	0.30	
Late pollen shedding and knob 6b (days)	KK and KO	27	71.14	11.97	.01
	OO	3	64.33	6.33	
Many stem internodes and knob 6b	KK and KO	27	14.14	1.20	.02
	OO	3	12.33	1.33	
Narrow leaves and knob 6b	KK and KO	27	9.27	0.71	.02
	OO	3	10.50	0.00	

Genetic experiments are now in progress to validate cytological observation and to possibly reveal the existence of knob-linked genes having some control on the expression of quantitative plant characters.

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1. Fatty acid composition of corn oil of certain inbred lines and their  $F_1$  hybrids.

Two groups of inbred lines (selected for high oil content in the kernel) were grown at Experiment, Georgia, in 1961. One group (I) of inbred lines which had been developed by a number of experiment stations was selected from the breeding nursery at the Georgia Experiment Station. A second group (II) of inbred lines was selected from inbreds developed at the Pee Dee Agricultural Experiment Station, Florence, South Carolina. Selfed seed of these inbred lines were analyzed for oil content and fatty acid distribution. All possible single crosses within groups I and II were also made in 1961. During the winter of 1961-62, these single crosses were grown in Florida and 5 to 7 selfs were made in each cross. Fatty acid analyses were made on the selfed seed of  $F_1$  progeny from crosses of inbreds of high x high, high x low, and low x low composition for each of the five important fatty acids in corn oil. The results of fatty acid analyses of the inbred parents and their  $F_1$  hybrid single crosses are given in Table 1.

The  $F_1$  hybrids had less palmitic acid than the average of the parents for all types of crosses in groups I and II. The cross of two inbred lines low in palmitic acid resulted in  $F_1$  hybrids with less palmitic acid than the low parent. The  $F_1$  hybrids were lower in stearic acid than the average of the parents in crosses of high x high and low x high. Crosses of low x low resulted in a slight increase of stearic acid in the  $F_1$  as compared to the average of the parents. For oleic acid, the high x high cross gave  $F_1$  hybrids with less oleic acid and the low x low cross had more oleic acid as compared to the parental averages. The low x high cross had less oleic acid in  $F_1$  hybrids of group I and more in group II as compared to the average of the parents. Linoleic acid content of the  $F_1$  hybrids was slightly increased over the parental average in the high x high cross, moderately increased in the high x low cross, and considerably increased in the low x low cross.  $F_1$  hybrids had lower linolenic acid contents than the average of the parents in all types of crosses except the low x low cross in group II.



Additional crosses of high x high, high x low, and low x low for each of the fatty acids are being made to substantiate the results obtained so far. Segregation in the F<sub>2</sub> generation will also be studied for each of the fatty acids.

This study was made possible by the cooperation of several individuals. The South Carolina inbred lines were made available by Dr. Alfred Manwiller. Oil analyses were determined by the Clinton Corn Processing Company, a division of Standard Brands, Inc., Clinton, Iowa. Fatty acid distributions were determined at the Blue Bonnet Division of Standard Brands, Inc., Indianapolis, Indiana. The oil and fatty acid analyses were made possible by grants from the Corn Industries Research Foundation to the Clinton Corn Processing Company and the Blue Bonnet Laboratories.

Table 1. Fatty acid distribution in seed of F<sub>1</sub> progeny (single crosses) of inbred lines of high x high, high x low, and low x low composition of the five important fatty acids in corn oil.

Fatty acid and pedigree	Group and type of cross	Percent on total fatty acid basis <sup>1</sup>				
		Female parent	Male parent	Average of parents	F <sub>1</sub> Single cross	Diff.*
<b>Palmitic</b>						
<u>Group I</u>						
Mp468 x Mp428	H x H	18.3	16.5	17.4	16.7	-0.7
Mp468 x GE84	H x L	18.3	11.9	15.1	13.1	-2.0
GE84 x GE72	L x L	11.9	12.0	12.0	11.3	-0.7
<u>Group II</u>						
SC246C x SC138-28	H x H	17.0	16.6	16.8	16.2	-0.6
SC246C x SC212D	H x L	17.0	13.0	15.0	13.6	-1.4
SC313 x SC212D	L x L	13.1	13.0	13.1	12.3	-0.8
Average		15.9	13.8	14.9	13.9	-1.0
<b>Stearic</b>						
<u>Group I</u>						
P121 x GE72	H x H	4.48	4.21	4.35	4.16	-0.19
Mp428 x GE72	L x H	2.25	4.21	3.23	2.66	-0.57
Tx203 x Mp428	L x L	2.44	2.25	2.35	2.45	+0.10
<u>Group II</u>						
SC260E x SC138-28	H x H	3.30	4.17	3.74	2.41	-1.33
SC313 x SC138-28	L x H	1.67	4.17	2.92	2.64	-0.28
SC313 x SC212D	L x L	1.67	2.16	1.92	2.06	+0.14
Average		2.64	3.53	3.08	2.73	-0.35

Fatty acid and pedigree	Group and type of cross	Percent on total fatty acid basis <sup>1</sup>				
		Female parent	Male parent	Average of parents	F <sub>1</sub> Single cross	Diff.*
<u>Oleic</u>		<u>Group I</u>				
T202 x GE72	H x H	46.5	45.8	46.2	39.4	-6.8
Mpl428 x T202	L x H	31.0	46.5	38.8	36.8	-2.0
Tx39-16 x Mpl428	L x L	32.7	31.0	31.9	33.1	+1.2
		<u>Group II</u>				
SC260C x SC138-2	H x H	43.8	44.4	44.1	40.4	-3.7
SC313 x SC138-2	L x H	24.3	44.4	34.4	36.7	+2.3
SC313 x SC311A	L x L	24.3	37.4	30.9	33.6	+2.7
Average		33.8	41.6	37.7	36.7	-1.0
<u>Linoleic</u>		<u>Group I</u>				
Mpl428 x GE84	H x H	49.0	47.6	48.3	49.2	+0.9
Mpl428 x T202	H x L	49.0	35.1	42.1	45.8	+3.7
T202 x GE72	L x L	35.1	37.3	36.2	44.0	+7.8
		<u>Group II</u>				
SC313 x SC211E	H x H	59.7	45.3	52.5	52.8	+0.3
SC313 x SC260C	H x L	59.7	35.7	47.7	49.3	+1.6
SC260C x SC138-2	L x L	35.7	36.5	36.1	40.0	+3.9
Average		48.0	40.0	43.8	46.9	+3.1
<u>Linolenic</u>		<u>Group I</u>				
T202 x P121	H x H	1.61	1.46	1.54	1.10	-0.44
T202 x GE72	H x L	1.61	0.82	1.22	1.11	-0.11
GE80 x GE72	L x L	1.04	0.82	0.93	0.00	-0.93
		<u>Group II</u>				
SC313 x SC311A	H x H	1.39	1.37	1.38	0.98	-0.40
SC313 x SC138-28	H x L	1.39	0.79	1.09	Trace	-1.09
SC246C x SC138-28	L x L	0.99	0.79	0.89	0.94	+0.05
Average		1.34	1.01	1.17	0.69	-0.48

<sup>1</sup>Average of two fatty acid analyses.

\* Difference of the F<sub>1</sub> single cross compared to the average of the two inbred parents.

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1. Prehistoric wild and cultivated maize from Tehuacan Valley in Mexico.

We have recently made a detailed study of all of the prehistoric maize from four caves in the Valley of Tehuacan in southern Puebla, Mexico, uncovered by MacNeish and his associates. These prehistoric specimens number more than 10,000 and include all parts of the plant: roots, stalk, sheaths, leaves, husks, prophylls, shanks, cobs, kernels, tassel fragments, and anthers. Together they provide a fairly complete picture of corn's wild progenitor and furnish abundant evidence of an evolutionary sequence from wild maize to modern cultivated maize.

The most numerous prehistoric specimens are those of cobs. The earliest cobs from two of the caves, San Marcos and Coxcatlan, most of which are well preserved, dated by radio-carbon determinations of associated wood at about 5000 B.C., are almost certainly those of wild maize since they are quite uniform and there is no evidence from other species that the practice of agriculture had become established. These cobs are small and slender, about two centimeters in length and taper at both ends. The kernel row number is usually eight but a few cobs are four-rowed and distichous. The rows bear six to eight spikelets - the average number of spikelets on intact cobs is 55. The spikelets are uniformly paired. The glumes are long in relation to the rachis diameter and are approximately like the glumes of half tunicate associated with minus modifiers. Tissues of both rachis and glumes are soft - not indurated like those of teosinte and *Tripsacum*. Many of the cobs have slender stumps, presumably of staminate tips which have been broken off in handling.

The specimens of lower stalk internodes with attached roots show that the seminal root system was well developed - probably an adaptation to somewhat droughty conditions. There is no evidence of tillers. The leaf sheaths are predominately completely glabrous. One intact husk covering from an early zone consists of only two husks: a thick outer one and a much thinner inner one. The low husk number and the short shank suggests that the ear was born in a high position on the stalk. The leaves are wide in relation to their length and the leaf veins are closely spaced as in teosinte and *Tripsacum*.

At about 4000 B. C. cobs somewhat larger in size but having the same botanical characteristics as the wild maize make their appearance in the two caves. Since by this time there is evidence of cultivation of beans, squashes, and chili peppers, we assume that the slightly longer cobs are those of early cultivated maize.

At about 1000 B.C. a completely different maize with tripsacoid characteristics, presumably the product of hybridization with teosinte or *Tripsacum*, makes its first appearance. Since neither teosinte nor *Tripsacum* is known in Tehuacan Valley today and since no archaeological remains of either species have been uncovered in the caves although the remains of other indigenous grasses are abundant, we assume that the tripsacoid maize has been introduced from elsewhere.

The hybridization of the introduced tripsacoid maize with the early cultivated maize of Tehuacan Valley gave rise to types resembling two living Mexican races: Chapalote and Nal-Tel, the former now found in northwestern Mexico, the latter in southern Mexico. The two races are closely related, differing primarily in pericarp color, Chapalote having brown and Nal-Tel orange pericarp. Since both colors occur among the prehistoric kernels in the Tehuacan caves there is no way of distinguishing Chapalote from Nal-Tel in the prehistoric cobs - both are obviously components of the same complex.

It now seems probable that wild maize, though perhaps never abundant in any part of Mexico, was widely distributed geographically. Fossil pollen from deep drill cores from the Valley of Mexico, identified by Barghoorn et al., show that wild maize once grew there. The appearance of a tripsacoid maize in the Tehuacan Valley suggests that adjoining regions also had maize. The popcorn race from the Valley of Toluca, Palomero Toluqueño, differs from the Chapalote-Nal-Tel complex of the Tehuacan Valley in having pilose leaf sheaths and pointed kernels and it may represent the descendant of a fourth distinct geographical race.

P. C. Mangelsdorf  
R. S. MacNeish  
W. C. Galinat

## 2. Further data on the components of the tunicate locus.

In previous News Letters (35, 36) we reported that the two components of the Tu locus which had been separated by crossing over appeared to have slightly different effects. After an additional backcross to the inbred A158 which produced lines which are theoretically 61/64 or 95.3 percent A158 there is now no doubt that this is true. The differences are apparent in a number of characteristics. Lines heterozygous for the locus  $tu^{h-d}$  have more prominent central spikes, longer staminate glumes, and longer, thicker pistillate glumes than lines heterozygous for  $tu^{h-1}$ . Although the kernels are not completely enclosed in either group of lines they are shelled off with difficulty from the  $tu^{h-d}$  lines and more easily from the  $tu^{h-1}$  lines.



There is still a possibility that the differences are due to modifying genes linked with the loci in question rather than to the loci themselves. This possibility now seems somewhat remote since increasing isogenicity has served to differentiate the components instead of increasing the similarity between them as would be expected if they were actually identical.

As pointed out previously, a difference in the two components of the Tu locus suggests that (a) the wild locus was Tu or (b) that there were two wild loci,  $tu^{h-d}$  and  $tu^{h-1}$  which through unequal crossing over sometime during domestication were brought together to produce the present Tu locus. The fact that all early prehistoric corn so far studied is similar to half tunicate rather than to full tunicate favors the latter possibility.

Crosses were made in 1961 between plants heterozygous for the two components. In 1962 plants heterozygous for both (+/-+), a modified trans form in which the two +'s represent different "wild" loci) were backcrossed to  $tu\ tu$ . A backcross population is now being grown in Florida to determine whether the Tu locus can be resynthesized by restoring its separate components to their original positions on the same chromosome.

P. C. Mangelsdorf

### 3. Combining extracted chromosomes with tripsacoid effects - its bearing on convergent improvement.

In last year's News Letter I reported the results of intercrossing lines of A158 which had been modified by incorporating into them chromosomes with tripsacoid effects extracted from varieties of maize from the countries of Latin America. During the past summer highly tripsacoid segregates from  $F_2$  populations of such crosses were grown for the purpose of establishing new lines of A158 carrying extracted chromosomes from both parental lines. In virtually all lines some plants were completely barren, producing no ears - in some lines virtually all plants were barren. This confirms the conclusion reached last year that there is a limit to the amount of tripsacoid germplasm which can be introduced in a homozygous state into an inbred strain.

These results have an important bearing on the method of convergent improvement in maize which assumes that inbred strains and their single crosses can be improved by backcrossing an  $F_1$  hybrid to each of its parental lines followed by selfing. If heterosis is due in some instances to blocks of genes originally from teosinte or *Tripsacum* then convergent improvement will not in such cases be successful because these blocks of genes tend to have deleterious effects when homozygous.

A survey of the published data on convergent improvement shows that results are, as expected, conflicting and the method has been unsuccessful more often than not. The data showing lack of improvement are of particular interest here. Of 54 single crosses of second cycle recovered lines of B2 and K4 tested by Sprague et al. (1959) not a single one was equal in yield to the original single cross. Of 40 single crosses involving recovered lines of Wf9 and 38-11 tested by Lonquist (1960) not one was equal in yield to the original single cross.

When blocks of teosinte or *Tripsacum* genes are involved in heterosis convergent improvement is obviously not a valid test to distinguish between dominance, overdominance, and epistasis as the principal factor in heterosis. Practiced for a sufficient number of cycles on inbred strains carrying blocks of teosinte or *Tripsacum* genes, convergent "improvement" will almost certainly lead to eventual extinction of the lines.

P. C. Mangelsdorf

#### 4. Linkage relations of the gene for pointed kernels.

An indication previously reported (MNL No. 35) that pointed kernels, characteristic of certain varieties of popcorn, may be a simple Mendelian character exhibiting incomplete dominance and having its locus on chromosome 4 has been substantially confirmed by additional data obtained in 1962. F<sub>2</sub> populations of crosses of round and pointed kernels segregated as follows:

	279A	279B	660		Total
			Su su	su su	
Pointed	45	36	104	18	203
Intermediate	96	86	177	56	415
Round	31	32	66	36	165
	172	154	347	110	783

The data fit a 1:2:1 ratio with reasonable closeness and in this respect differ from those of Hayes and East, 1915, which indicate that two factors are involved in the inheritance of pointed kernel shape. The consistent deficiency of round genotypes is probably due to the effect of the fourth chromosome *Ga* factor carried by the pointed-kernel stock. Evidence of linkage with *Su*, another chromosome 4 gene, is furnished by the data from family 660 in which 19 percent of the ears originating from starchy seeds were roundkerneled compared to 31 percent among those originating from sugary seeds.

Family 660 was also segregating for Ts<sub>5</sub>. The segregation for this character among the three classes for kernel shape was as follows: pointed, 63:59; intermediate, 129:104; round, 57:45. There is no indication in these data of linkage between Ts<sub>5</sub> and kernel shape. Therefore if kernel shape is indeed linked with the Su-su and Ga-ga loci as the other data indicate the sequence of genes must be Pt Ga Su Ts<sub>5</sub>. Additional tests involving backcrosses are being made to determine whether this conclusion is correct.

There is some indication of linkage between kernel shape and development of a staminate tip on the ear. Segregation for presence and absence of a staminate tip among the three classes for kernel shape was in one population as follows: pointed, 8:13; intermediate, 26:20; round, 13:2. If this indication is confirmed by further tests one more primitive character will be added to the list of those, Tu, Ga, Pt, and possibly Ts<sub>5</sub>, which have their loci on chromosome 4.

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W. C. Galinat

#### 5. Low penetrance of mutant dwarfs arising in teosinte derivatives.

We have repeated the experiments reported earlier (MNL 35) in which mutant dwarfs occurring in teosinte derivatives failed to segregate normally in F<sub>2</sub> populations of crosses with various inbred strains. The data on segregation of dwarfs obtained in 1962 are similar to those previously reported but are now explicable. The ears in F<sub>2</sub> populations in which the parental mutant dwarfs failed to reappear could be classified with respect to their ears into normal, intermediate, and tripsacoid. In 14 F<sub>2</sub> populations in which the dwarfs failed to appear or occurred in low frequencies, the ears were classified as follows: normal, 152; intermediate, 330; tripsacoid, 165.

These data show that the segregation for the tripsacoid condition is approximately normal. In some populations the tripsacoid condition of the ear is accompanied by conspicuous dwarfing of the plants, in other populations it is not.

P. C. Mangelsdorf  
W. C. Galinat

#### 6. The tripsacoid nature of variable mutants.

Because the mutants arising in maize-teosinte derivatives are often variable and difficult to classify, it occurred to us that some of the variable mutants arising spontaneously in maize or appearing after inbreeding might have arisen in the same manner and may be tripsacoid

in their characteristics. Accordingly we selected from the characters described in Emerson, Beadle, and Fraser a number of those described as "variable" or "difficult to classify." These were grown in 1962 and the ears were scored with respect to tripsacoid effects, especially the induration of the rachis and lower glumes of the cobs. The following characters proved to be associated with tripsacoid cobs: albescent, brevis, narrow leaf-1, pale green seedling-2, rootless, silky-1, zebra-1, zebra-2, zebra-3, and zebra-4. In several segregating populations the mutants were tripsacoid and normal plants not. Only one character of those studied in 1962, adherent-1, was not associated with tripsacoid effects.

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W. C. Galinat

#### 7. Segregation of genetically marked chromosomes in maize-Tripsacum hybrids.

We have for some years been attempting to produce a hybrid of Tripsacum dactyloides with our WMT stock which has recessive marker genes on seven chromosomes (1, 2, 3, 4, 7, 8, 9). The principal purposes of making this cross were (1) to determine whether Tripsacum carries dominant alleles of the maize recessives; (2) to determine whether Tripsacum, having almost twice as many chromosomes as maize, carries the dominant alleles in duplicate in some cases; (3) to identify cytologically the Tripsacum chromosomes which carry the dominant alleles.

A hybrid plant obtained by employing embryo culture exhibited none of the recessive characters introduced from maize but proved to be completely sterile, probably because of the greater amount of chromosome pairing than had previously been reported in maize-Tripsacum hybrids. The chromosome number of this hybrid was doubled through colchicine treatment (MNL 35). Backcrosses to the multiple recessive maize stock produced 32 triploid hybrids having 20 maize and usually 18 Tripsacum chromosomes. These, like the F<sub>1</sub> hybrids, showed no maize recessive characters with three exceptions: one plant each was bm<sub>2</sub>, a and j indicating that one or more Tripsacum chromosomes had in each case been lost. The cytological studies of the triploid which exhibited j showed that three Tripsacum chromosomes were absent.

The triploid hybrid proved to be highly sterile (1.7% fertile) when backcrossed by the multiple recessive stock. Ninety-two plants of the segregating backcross population were obtained. The frequencies of dominants in this population were as follows:

	Maize Chromosome						
	1	2	3	4	7	8	9
Dominant from <u>Tripsacum</u>	Bm <sub>2</sub>	Lg <sub>1</sub>	K <sub>1</sub>	Su <sub>1</sub>	Gl <sub>1</sub>	J <sub>1</sub>	Wx
Frequency of Dominants	34.5	23.9	31.6	28.2	38.0	60.5	37.0



If the *Tripsacum* chromosomes segregate at random at meiosis and if there is no selective gametic or zygotic elimination then there should be 50 percent of dominants for those loci for which *Tripsacum* carries one dominant allele and 75 percent dominants for loci for which *Tripsacum* carries two alleles. The data fit neither of these theoretical expectations, probably because the high degree of gametic elimination is selective against extra *Tripsacum* chromosomes. It may be significant, however, that six of the seven frequencies are similar to each other (average 32.2 percent dominants) while the seventh,  $J_1$ , has almost exactly twice this frequency. This may suggest that *Tripsacum* carries only one allele for the maize markers,  $bm_2$ ,  $lg_1$ ,  $a$ ,  $su$ ,  $gl_1$ , and  $wx$ , but carries two for  $j_1$ . The final answer will depend upon the cytological identification of the *Tripsacum* chromosomes carrying the dominant alleles in  $2n+1$  plants. If the presence of a particular dominant allele is always associated with a particular *Tripsacum* chromosome, it may be assumed that *Tripsacum* carries only one dominant locus for the character in question.

One *Tripsacum* chromosome has so far been identified both genetically and cytologically; the chromosome carrying the allele of  $wx$ . This is the satellite chromosome of *Tripsacum* which among the 18 *Tripsacum* chromosomes is the sixteenth longest in length. In one plant with better than average pachytene spreading this chromosome frequently associated with chromosome 9 of maize in a peculiar configuration. This chromosome has a median centromere and two terminal knobs. Its two arms fold back on each other, their terminal knobs fusing. This large fused knob may then fuse with the terminal knob of chromosome 9 of maize. In this plant the satellite chromosome of *Tripsacum* never becomes attached to the nucleolus although it did so at times in the  $F_1$  hybrid producing configurations in which two satellite chromosomes were attached to the nucleolus.

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#### 8. Effects of *Tripsacum floridanum* chromosomes on the meiosis of maize.

During the summer of 1961-62 a large population (about 650 plants) was grown of the progeny of the triploid hybrid of corn and *Tripsacum floridanum* (produced by Dr. Galinat by backcrossing the  $F_1$  corn-*Tripsacum* hybrid twice by corn, MNL 35, 36). Young tassel material was collected for the following types of cytological study: (1) frequencies of the numbers of extra *Tripsacum* chromosomes transmitted by the triploid hybrid; (2) identification of the *Tripsacum* chromosome carrying the dominant allele for  $gl_3$  when this is covered; (3) affinities of maize and *Tripsacum* chromosomes within themselves when they are present as parts of the haploid complement and in different combinations;

(4) effects of *Tripsacum* chromosomes on the synapsis and other aspects of the meiosis of maize when present singly and in various combinations. The following report concerns the fourth aspect mentioned above.

In some of the segregates a very interesting behavior was observed in the maize chromosomes themselves apparently under the influence of the *Tripsacum* chromosomes. This was in the form of interruption and breakdown of the normal course of the meiotic process at various stages of the division cycle and total degeneration of the microspores. The most common abnormality was pachytene pairing failure. The extent of this was highly variable ranging from small segments of the pachytene bivalents showing nonpairing but with good diakinesis and metaphase pairing (apparently chiasma formation unaffected) to a high degree of asynapsis including entire chromosomes leading to highly reduced bivalent formation at diakinesis and metaphase. As an example, in the following table are given the frequencies of chromosome associations at metaphase I in six segregates.

Plant No.	No. of Extra <i>Tripsacum</i> Chromosomes	Mean Association per Cell			No. of Cells Analysed
		Trivalent	Bivalent	Univalent	
575-3	2	0.32	5.28	10.48	25
575-8	2	-	10.00	2.00	20
575-11	3	0.20	9.90	2.60	21
575-15	3	0.15	6.00	10.55	20
573-5	12	0.13	11.13	9.33	15
575-10	10	-	2.75	24.50	16

A second class of aberrations include disturbances in the spindle. In these the anaphase is disorganized and the chromosomes are scattered all over the cell. They undergo divisions and fragmentations resulting in cells with large numbers of chromosomes which eventually degenerate. A variation on this is the clumping of the bivalents on the metaphase plate unaccompanied by division or fragmentation and final degeneration of the chromosomes.

A third type of aberration was exhibited by the plant 575-11, carrying six extra *Tripsacum* chromosomes. In this plant there is good pairing (average 11.83 bivalents and 2.33 univalents at metaphase I). But widespread degeneration takes place at almost all stages of meiosis prior to metaphase. The cells rarely get beyond metaphase I. In the table below are presented the frequencies of normal and degenerating cells in two anthers from the same spikelet.

	Pachytene	Diplotene	Diakinesis	Metaphase I
No. of cells normal	1	7	7	35
No. of cells degenerating	21	14	8	27
				(Total = 120)

The wall of the microsporocyte very early starts going through a morphogenetic development similar to that of the pollen grains. Thus frequently one comes across cells looking like pollen grains but containing degenerating meiotic figures from pachytene to metaphase.

A fourth type of aberration observed was translocation. So far two plants were observed which were heterozygous for a reciprocal translocation each in the maize chromosomes.

These effects resemble abnormalities of meiosis due to genetic causes (eg. asynapsis) and due to the action of chemical and physical agencies. It appears that the *Tripsacum* chromosomes act in disrupting the balance of genetic and physico-chemical factors at several points which together make meiosis and the subsequent events in the microspore an integrated system.

Further studies are in progress along these lines for a fuller understanding of these phenomena.

Raju S. K. Chaganti

#### 9. Northern flint-like characters derived from *Tripsacum*.

Certain plants in our maize populations segregating *T. dactyloides* and *T. floridanum* chromosomes had acquired from *Tripsacum* several characteristics which resemble those of the northern flints including the early flowering habit, tillering habit, flag leaf development, and long internodes above the ear position. The genes for earliness from *Tripsacum* may be hidden by the perennial character in this grass. But once the perennial plants are well established, these genes may serve to speed early flowering in the spring. The identification of northern flint-like characters with *Tripsacum* germplasm agrees with other evidence that the northern flints are tripsacoid.

W. C. Galinat

#### 10. Teosinte introgression and fasciation.

Origin of fasciation. Fasciation, a sort of incipient branching which flattens the ear while it increases the number of kernel rows, has an ancient history in maize, perhaps as a mechanism to concentrate the grain under short protective husks. Although obvious fasciation is rare in modern maize, it does occur in extreme form in certain relic races, which are now restricted to high elevations, such as Palomero Toluqueño in Mexico and Confite Puneño in Peru as well as in a race which is maintained as a novelty type in the United States, Strawberry popcorn. Experimental evidence now indicates that genetic factors for

fasciation are common in modern maize but their expression is controlled or modified by teosinte introgression.

Effect of teosinte germplasm on fasciation. Our teosinte chromosome 9 stock causes a complete submersion of any phenotypic effects of heterozygous fasciation in its hybrids with Strawberry popcorn and with a fasciated sweet corn inbred, Iowa 5125. All teosinte chromosomes tested (1, 3, 4) caused some reduction in both fasciation and kernel row number as well as an increase in ear length in such hybrids. The teosinte chromosomes entered the hybrids from an isogenic background (A158). The data for the Strawberry popcorn hybrid follow:

Strawberry pop crossed by	Aver. Kernel Row No.	Aver. Ear Length Cm.	Type of Fasciation
A158 (control)	21.0	15.0	medium at butt
A158-Fla. 1	20.6	16.0	slight at butt
A158-Fla. 3	20.5	15.3	medium at butt
A158-Fla. 4	20.0	15.4	slight at butt
A158-Fla. 9	18.0	17.5	none

Inheritance of fasciation. In the absence of teosinte introgression, fasciation segregates as a single factor showing incomplete dominance as found in the F<sub>2</sub> generation from a cross between strawberry popcorn (fasciated) and Argentine popcorn (non-fasciated). In 200 plants, 23% showed the extreme "bears paw" type of fasciation derived from the strawberry popcorn parent; 55%, the apparent heterozygotes, had butt fasciation in which there is much drop-rowing as the ear tapers sharply to the tip; the remaining 22% had the cylindrical non-fasciated type of ear originating from the Argentine popcorn grandparent.

W. C. Galinat

#### 11. Morphological and heterotic components of teosinte and "Tripsacum" introgression in maize.

Morphological components. On the basis of morphological effects described in a previous News Letter (35), it has been possible to identify four components of introgressed germplasm in teosinte derivative stocks of A158. For convenience, these are designated by numbers 1, 3, 4 and 9 which are probably the chromosomes responsible in whole or part for the various tripsacoid features.

The information obtained from the study of teosinte derivatives was applied to gain insight of the "Tripsacum" derivatives which were developed by introducing into A158, chromosomes or chromosomal segments extracted from tripsacoid races of maize which are not in sympatric



range with teosinte. It was found that some of the "Tripsacum" derivatives could be matched for certain components from teosinte derivatives. In other derivatives the dilute effect of one or more segments was apparent but in still others, the situation seemed to be more complex. It is assumed that tripsacoid components in South American tripsacoid races are derived from some species of Tripsacum as teosinte is unknown in South America. Tripsacoid features in "Tripsacum" derivatives could have been contributed by any of the chromosomes of Tripsacum which possesses the genes controlling these features. It is, however, remarkable that "Tripsacum" germplasm has quite similar although not completely identical effects at least on the internal morphology of the cob.

Heterotic components. A group of 16 teosinte and "Tripsacum" derivatives in addition to the control A158 were crossed in all possible combinations. Out of 136 combinations thus produced, 109 were included in the test. The  $F_1$  plants were grown in the summer of 1961 and heterosis was measured in terms of (1) yield; (2) height of the plant from the ground level to the base of the central spike; (3) days to anthesis; and (4) length of the central spike.

Table I. Results of crosses between inbred A158, teosinte, and "Tripsacum" derivatives expressed on per plant basis as percent of control A158.

	Yield	Height	Days to Anthesis	Central Spike	No. of Crosses
Control A158	100.0	100.0	100.0	100.0	
Maize (A158) x Teosinte derivatives	116.4	102.4	98.5	102.8	6
Maize (A158) x "Tripsacum" derivatives	87.9	100.8	100.2	107.6	8
Teosinte derivatives x Teosinte derivatives	117.6	103.9	98.3	108.9	22
"Tripsacum" derivatives x "Tripsacum" derivatives	98.9	101.2	97.7	112.5	24
Teosinte derivatives x "Tripsacum" derivatives	108.1	101.1	97.4	112.1	49

It is obvious from the results given in Table I that: (1) Introgressed germplasm from teosinte produces heterotic effects for all the characters used as measures of heterosis in these studies. In various intercrosses the introduced teosinte chromosomes not only showed interaction with each other, but also with maize (A158) and "Tripsacum" components. Furthermore, there was indication of an additive effect of the components in some crosses and dominance in the others. (2) The "Tripsacum" derivatives, in crosses with A158, have shown heterosis only for central spike. In crosses among each other, improvement is observed for height, days to anthesis, and central spike. Some of the intercrosses, however, showed significant heterosis for all the characters suggesting the presence of some heterotic "Tripsacum" components. There was

indication of inter-component interaction in many crosses.

Heterosis in maize. The two principal hypotheses which have been advanced to explain the genetic basis of heterosis are dominance and overdominance. The available information on these seems to suggest that the two hypotheses are not mutually exclusive. Present studies definitely suggest that this situation would be expected if it is assumed that there are, in the genetic complex of maize, small heterotic segments of "Tripsacum" and teosinte, which confer selective advantage to the heterozygote, but are somewhat deleterious in homozygous condition. The pseudo-over-dominant effect of these segments may be due to any of the models of gene action. Some of the segments may show additive effect, others epistatic, and still others dominance. If this assumption is valid, as the experimental results described above indicate, then to compartmentalize the observed vigor to one or the other hypotheses, at least for a complex hybrid like maize, is a basic fallacy.

S. M. Sehgal

## 12. Field studies on teosinte in Mexico.

Guerrero Teosinte. Teosinte was studied on the mountains (700 m to 1650 m) that surround the Balsas Basin where it behaves as a weed on open sites. Teosinte is extremely common on road cuts, erosion gullies and forms dense local populations on sites where there is available more moisture than on the surrounding hillsides. There is widespread evidence that the natural vegetation has been cleared in the past and abandoned hillsides have returned to a dry semi-arid scrub forest. In some areas the cultivation of maize has been only sporadic, but in areas accessible by road, cultivation of maize is of an intensive milpa, shifting-field form, except where prohibited by excessively steep slopes. Collections were made of teosinte expressing all degrees of vigor depending primarily on the population density and quality of the site. Under intense competition from other grasses the plants were often less than a meter high with one or two tassel branches. The other phenotypic extreme were plants in or adjacent to maize fields which developed thrifty stalks of 3 meters. Locally teosinte is definitely one of the dominant grasses on slopes that have obviously been cleared in the past but have not been cultivated for several years. Natural hybrids are not common but they have been collected from a majority of the populations studied to date. Also included here as Guerrero teosinte are collections from the drainage of the Rio Papagayo (Mazatlán, Guerrero).

Chalco Teosinte. A detailed study was made of teosinte in the Chalco area. Observations were conducted over the entire growing season in almost every part of the valley and under a wide variety of cultivation practices. In direct contrast to the situation studied in Guerrero, teosinte is limited to cultivated fields as a weed where it mimics maize. Field to field inspection indicated considerable variation in the number of teosinte plants, but essentially fields were of two types: either teosinte was absent (less than 1% of the plants in the field), or teosinte was present (more than 3%, usually between 5 and 15% of the plants in the field). The two classes were almost equally frequent. At the end of the season three selected representative fields were harvested and every plant was scored. The results are presented below:

Field	Total No. of Plants in the Field	Maize x teosinte Hybrids	% of Teosinte Plants in the Field*
Los Reyes	17,511 (acre)	38	4%
Chalco	17,574 (acre)	39	9%
Amecameca	9,121 (1/2 acre)	44	5%

\*Based on sample counts of 3600 to 4000 plants at the time of pollination.

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#### 1. Estimates of spontaneous non-reduction in diploid inbreds.

Three to thirteen plants in each of 121 dent inbreds were pollinated by Synthetic B, a tetraploid variety. Plump and presumably tetraploid kernels were counted, as well as the shriveled triploids on each ear. The following year, plump kernels were planted and the resulting plants were pollinated by a diploid. At maturity, each plant was scored for its ploidal nature on the basis of seed set.

The frequency of diploid eggs, presumably arising largely from non-reduction varied widely from inbred to inbred. Eighty five percent of the inbreds produced no verified tetraploids in as many as 3,500 fertilizations. However, the frequency of tetraploidy in the WF9 crosses was high.

Frequencies of tetraploid and triploid progeny from diploid-tetraploid crosses.

Seed parent	Total no. fertilizations	Total no. verified progeny		Frequency per 10,000 fertilizations	
		4n	3n	4n	3n
WF9	230	8	0	348	0
R205	870	15	0	172	0
B46	2100	17	1	81	5
38-11	320	2	0	62	0
R107	320	2	0	62	0
B10	900	4	0	44	0
R211	870	0	10	0	115
R81	2720	0	9	0	33

The quality of triploid seed varies widely. All triploids cited in the table survived field planting and in all cases were plump and indistinguishable from tetraploid or diploid kernels.

An unusual ear was found in inbred B10 pollinated by the 4n male. The ear bore the usual shriveled triploid kernels on one side and plump kernels on the opposite side. Further, the frequency of triploids among the plump kernels was very low. Subsequent examination of stomata of seedlings from plump kernels revealed that they were 4n. The sector bearing plump kernels presumably was tetraploid. Estimates of spontaneous non-reduction, based on unmarked 2n x 4n crosses, are likely to be too high since tetraploids arising from sectorial chimeras cannot be distinguished from those arising from meiotic accidents.

D. E. Alexander

2. 4n corn by 4n sorghum hybridization attempts.

Attempts have been made for several years to cross autotetraploid sorghum and autotetraploid corn. The effort has primarily been made using corn as female although male sterile tetraploid sorghum has also been used as female on occasion.

In 1962, approximately 80 putative hybrids were dissected from kernels exhibiting varying degrees of stimulation and transferred to sterile media. Many failed to differentiate normally; others slowly developed and were transferred to pots. All those showing near-normal growth have turned out to be parthenogens, or contaminants.



Several interesting growth patterns have been observed in some of the dissected embryos. One produced 10-12 plumule-like green projections on a sphere of undifferentiated tissue. Another produced a near-normal epicotyl that grew into the medium and maintained its green color for a time.

Clint Magill  
D. E. Alexander

### 3. Corn x Tripsacum hybrids.

The relationship of corn and Tripsacum has long been recognized. Forty-six European varieties and 82 corn belt inbred lines of corn were crossed with a clone of Tripsacum dactyloides having  $2n=36$  chromosomes. Corn was used as a female parent and two ears of each line were pollinated with Tripsacum pollen by the method outlined by Mangelsdorf and Reeves (1939). Immature embryos were excised under sterile conditions 12 to 28 days after pollination and were grown in nutrient media (White, 1943) in small 3 1/2" vials. Best growth was observed in embryos cultured 18 to 20 days after pollination; however, younger and older embryos failed to grow in vitro.

In general, Tripsacum crosses with open-pollinated European corns were more successful than when corn belt inbred lines were used. Fifteen of the 46 European varieties produced viable embryos when crossed with Tripsacum. Of the 82 corn belt inbred lines, only 12 were able to hybridize with Tripsacum. Reciprocal crosses using Tripsacum as female parent were also attempted, but in almost all cases, plants produced from the embryos are like Tripsacum and are probably apomictic. Further studies on the chromosomal relationships in the hybrids are in progress.

Satish C. Anand  
Earl R. Leng

### 4. Location of brachytic-2 dwarf.

Mung(unpublished) found the possible location of brachytic-2 as chromosomes 1, 3 or 6. An attempt was made to locate this gene, with A-B translocations, on the above mentioned chromosomes. Dwarf type plants occurred in the  $F_1$  cross ( $\underline{br}_2/\underline{br}_2$  x TB-1a)(break in 1L .2). but because of the reduced vigor of the hypoploid individuals it was impossible to classify the plants as dwarf or normal. Therefore, the  $F_1$  hypoploid plants were backcrossed to the following three genotypes:  $\underline{Br}_2/\underline{Br}_2$ ;  $\underline{Br}_2/\underline{br}_2$ ;  $\underline{br}_2/\underline{br}_2$ . The data for the backcross progeny, presented in table 1, indicate that brachytic-2 is located in the long arm of chromosome 1.

Table 1

	Backcross	Br <sub>2</sub> /-	br <sub>2</sub> /br <sub>2</sub>	Total
1.	Br <sub>2</sub> /Br <sub>2</sub> x (br <sub>2</sub> /br <sub>2</sub> x TB-1a)(hypoploid plant)	26	0	26
2.	Br <sub>2</sub> /br <sub>2</sub> x " " "	37	28	65
3.	br <sub>2</sub> /br <sub>2</sub> x " " "	0	278	278*

\*combined data from several families

The testcross data in table 2 were obtained by the use of reciprocal translocation stocks involving chromosome 1.

Table 2.

Translocation	Break Point	XY	xY	Xy	xy	Total	% Recomb.
1. T1-8	1S .39 8L .07	137	84	71	133	425	36.47
2. T1-6c	1S .25 6L .27	175	54	80	146	455	29.45**
3. T1-3	1 cent. 3 cent.	134	48	28	127	337	22.55**
4. T1-9	1L .19 9S .20	117	16	3	133	269	7.06**
5. T1-8	1L .22 8L .78	172	22	12	146	352	9.66**

X=translocation heterozygote;x=normal;Y=normal ht.;y=brachytic-2

\*\* X<sup>2</sup> for independence P > .01

The data in table 2 again indicate that brachytic-2 is located in the long arm of chromosome 1.

Brachytic-1 dwarf is also located in the long arm of chromosome 1. The test for allelism of these two dwarf mutants is negative. The F<sub>2</sub> of these two dwarf mutants segregated 228 normal: 184 dwarf (X<sup>2</sup> for 9:7 ratio = .1368; P=.75-.50). Brachytic 1 and 2 should therefore be over 50 cross-over units apart in the long arm of chromosome 1.

R. J. Lambert

##### 5. Frequency of seed set in an F<sub>1</sub> hybrid of *Tripsacum* and corn.

Well-established clonal divisions of the F<sub>1</sub> hybrid of *T. dactyloides* (3n=54) x *Zea mays* var. Puño (originally produced by Lois Farquharson) were allowed to open-pollinate in the nursery. Out of a total of 417 spikelets, 25 produced well developed seeds (6.0% seed-set). In hand pollinations, using corn as the male parent, 6 seeds were obtained from a total of 50 spikelets pollinated (12% seed-set). Nine of the 31 seeds germinated and two of these produced twin seedlings. The occurrence of twins indicates that the polyembryony of the *Tripsacum* parent was transmitted to the hybrid. The open-pollinated seedlings could be backcrosses to corn or *Tripsacum*, selfs, or apomicts. Cytological analysis of the plants is necessary to determine their chromosomal

constitution. If some of the seedlings are found to be backcrosses to corn, it may be possible to transfer Tripsacum germplasm to corn without developing amphiploids to obtain fertility.

R. J. Lambert

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1. Monogenic resistance to northern corn leaf blight, *Helminthosporium turcicum* Pass.

A type of resistance to *Helminthosporium turcicum* unlike that previously recognized and used in corn breeding programs has been observed in inbred GE440, Ladyfinger popcorn, inbred W37A, and a few other corn selections. This resistance, instead of being expressed only as a reduction in lesion number, is manifested by a different lesion type. The lesions on homozygous or heterozygous resistant plants are characterized by chlorosis, reduction in size, absence of wilting in the lesion, delay of leaf killing, and almost complete inhibition of fungus reproduction. The centers of lesions eventually die but a light green border always persists around the tan center until late in the season. This resistance is also expressed in the seedling stage.

The inheritance of resistance was studied in the F<sub>2</sub> and/or back-cross populations involving the 3 sources of resistance and several susceptible inbreds. The following data indicate that resistance is due to a single dominant gene in each of the 3 sources:

Cross	No. of plants observed		Expected ratio	P value
	Res.	Susc.		
	(Greenhouse data)			
B14 x GE440 F <sub>2</sub>	176	65	3:1	0.30-0.50
(B14 x GE440) x B14	52	62	1:1	0.30-0.50
187-2 x GE440 F <sub>2</sub>	93	24	3:1	0.20-0.30
(187-2 x GE440) x 187-2	61	53	1:1	0.30-0.50
W22R x LP <sub>2</sub> F <sub>2</sub>	83	26	3:1	0.70-0.80
(W22R x LP) x W22R	54	55	1:1	0.90-0.95
W64A x LP F <sub>2</sub>	81	29	3:1	0.70-0.80

Cross	No. of plants observed		Expected ratio	P value
	Res.	Susc.		
(W64A x LP) x W64A	30	29	1:1	0.80-0.90
Tx 325 x W37A F <sub>2</sub>	147	46	3:1	0.70-0.80
NC13 x W37A F <sub>2</sub>	150	45	3:1	0.50-0.70
(Field Data)				
B10 x GE440 F <sub>2</sub>	202	60	3:1	0.30-0.50
Oh41 x GE440 F <sub>2</sub>	187	68	3:1	0.50-0.70
B10 x LP F <sub>2</sub>	157	54	3:1	0.80-0.90
Oh41 x LP F <sub>2</sub>	186	63	3:1	0.90-0.95
(Oh07A x GE440) x Oh07A	92	97	1:1	0.70-0.80
(W22R x GE440) x W22R	97	110	1:1	0.30-0.50
(Oh07A x LP) x Oh07A	96	87	1:1	0.50-0.70
(W22R x LP) x W22R	102	98	1:1	0.70-0.80

a/ LP = Ladyfinger popcorn

To determine the relationship of the genes for resistance in the 3 resistant sources, the cross W37A x GE440 was advanced to the F<sub>2</sub> generation and the cross GE440 x Ladyfinger popcorn was crossed reciprocally with the susceptible hybrids Hy2 x Oh07 and WF9 x W22R as well as advanced to the F<sub>2</sub> generation. The genes in the 3 resistant sources appear to be identical, alleles, or very closely linked as indicated by the following data:

Cross	Number of plants in the greenhouse		Number of plants in the field	
	Res.	Susc.	Res.	Susc.
W37A x GE440	300	0		
GE440 x LP <sup>a/</sup> F <sub>2</sub>	110	0	297	0
(GE440 x LP) x (Hy2 x Oh07)	113	0	233	0
(Hy2 x Oh07) x (GE440 x LP)	112	0	240	0
(GE440 x LP) x (WF9 x W22R)	424	0	210	0
(WF9 x W22R) x (GE440 x LP)	109	0	229	0

a/ LP = Ladyfinger popcorn



It is suggested that the symbol Ht be used to designate the dominant gene in inbred GE<sub>440</sub> for chlorotic-lesion resistance to Helminthosporium turcicum. Up to this time, the genes in GE<sub>440</sub>, W37A, and Ladyfinger popcorn cannot be distinguished genetically or by disease tests.

A. L. Hooker

2. Location of a dominant gene in maize for resistance to Helminthosporium turcicum.

Homozygous resistant selections of GE<sub>440</sub> and Ladyfinger were crossed to a series of chromosome rearrangements marked with closely-linked endosperm or seedling traits. The F<sub>1</sub>'s (all resistant) were then testcrossed to susceptible stocks recessive for the appropriate genetic markers.

Classification of the testcross progenies is being carried out in the greenhouse this winter. Seed are planted in soil in flats, and the seedlings are artificially inoculated about three weeks after planting. Plants are scored for disease reaction at about five weeks of age.

In two series of plantings which have been run, tests have been made of 2<sub>4</sub> rearrangements, which together mark one or more regions in each of the ten chromosomes. In all cases, evidence for linkage has been negative or inconclusive, with the exception of Inv 2a, which gave the following results:

$\frac{gl_2 \text{ Inv } 2a \text{ ht}}{+ \quad + \quad Ht}$	X	$gl_2 \text{ ht}$	
<u>Classes</u>		<u>Number</u>	
$gl_2 \text{ ht}$		300	
$gl_2 \text{ Ht}$		56	
+ ht		63	Recombination = 119/709 = 16.8%
+ Ht		290	
Total		709	

Additional testcross progenies involving Inv 2a, T 2-6b, and T 2-10b are now being grown to provide further linkage data.

It is planned that homozygous resistant selections will be crossed to Chromosome 2 genetic testers in the current winter greenhouse generation as the first step in mapping the gene for resistance.

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1. Distribution and analysis of *Tripsacum dactyloides* in Illinois.

A survey of the distribution of *T. dactyloides* (L.) L. in Illinois has been in progress for 2 years. Using herbarium records and published reports as a guide to "car window" surveying, the authors have collected material from 26 different sites in 14 counties in central and southern Illinois. Seventeen of these sites had been previously reported and 9 new sites have been found.

The ploidy level of the different colonies is being investigated. From preliminary observations, it appears that both diploid ( $2n = 36$ ) and tetraploid ( $2n = 72$ ) races are present. Mixed colonies of varying ploidy levels may also occur. An attempt is being made to correlate certain characters with ploidy level in order to facilitate analysis of the distribution of the diploid and tetraploid races in the state.

Individuals from each site are being tested for ability to hybridize with corn. By pollinating shortened corn silks, it has been possible to produce 19 hybrids without resort to embryo culture. Seven of these hybrids were obtained from only 18 ears pollinated by a clone from near Sandoval in Marion County.

Efforts are being made to hybridize *T. dactyloides* with a set of chromosome marker stocks of maize. If a complete set of such hybrids can be produced, the contributions of particular *Tripsacum* chromosomes or chromosomal segments will be assessed by backcrossing to the proper marker stock.

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1. Some estimates of double reduction in autotetraploid maize.

The coefficient of double reduction ( $\alpha$ ) was determined for eight loci in autotetraploid maize (Table 1). Alpha values were derived from duplex backcross data. Two estimates of alpha appear for each locus. The first is based upon the assumption of no numerical non-disjunction ( $x = 0$ ) while the second alpha value is corrected for a numerical non-disjunction of 0.0258 per chromosome ( $x = 0.0258$ ). The occurrence of numerical non-disjunction results in an over estimation of alpha; therefore, correction for numerical non-disjunction decreases the size of alpha.

Formulas for estimation of the parameter alpha and its standard error were derived by the log likelihood method. The formula for alpha and its standard error are:

$$\alpha = \frac{12z - x - 2}{4 - 3x},$$

and,

$$S_{\alpha} = \frac{12}{4 - 3x} \sqrt{\frac{z(1 - z)}{n}},$$

where  $z$  is the proportion of recessive phenotypes in the population,  $x$  is the frequency of numerical non-disjunction and  $n$  is the total number in the population.

Crude estimates of a gene's location with respect to the centromere can be ascertained from the magnitude of alpha. Genes in close proximity to the centromere have small alpha values while genes more distal to the centromere have larger alpha values. The alpha values for the  $a_1$  and  $lg_1$  loci are not significantly different from alpha values expected from random chromatid segregation. Since the genes,  $a_1$  and  $lg_1$  are known to be more than 50 map units from the centromere, these alpha values are in general agreement with the known location of the loci with respect to their centromeres. The loci,  $r$ ,  $g_1$ ,  $vg_2$ ,  $su_1$  and  $y_1$ , have alpha values which are significantly different from those expected of random chromatid segregation, complete equational separation and chromosomal segregation. Alpha values of this magnitude are

expected of genes which are less than 50 units from the centromere but not completely linked to the centromere. Four of the five loci,  $r_1$ ,  $g_1$ ,  $su_1$  and  $y_1$ , have alpha values in agreement with their location with respect to the centromere. The fifth,  $yg_2$ , has an alpha value which is too small, since  $yg_2$  is known to be located more than 50 units from the centromere. The gene  $wx_1$  has an alpha value which is not significantly different from that expected of chromosomal segregation. There is a difference of opinion as to the distance between the  $wx_1$  locus and its centromere. It has been estimated by Anderson and Randolph to be between 2.0 and 3.6 units away from the centromere. The alpha value obtained for the  $wx_1$  locus indicates very close linkage of the gene and its centromere. With one exception, therefore, the magnitude of alpha was reliable in giving a rough estimate of the gene's location with respect to the centromere.

Table 1      Alpha and its standard error when numerical non-disjunction is zero and 0.0258.

Locus	Standard error		Standard error	
	$\alpha$	$x = 0$	$\alpha$	$x = 0.0258$
$a_1$	.1693	$\pm .0380$	.1661	$\pm .0387$
$r_1$	.0526	$\pm .0153$	.0471	$\pm .0156$
$lg_1$	.1066	$\pm .0201$	.1021	$\pm .0204$
$g_1$	.0514	$\pm .0146$	.04858	$\pm .0149$
$yg_2$	.0988	$\pm .0482$	.0942	$\pm .0389$
$wx_1$	.0097	$\pm .0341$	.0033	$\pm .0348$
$su_1$	.0478	$\pm .0080$	.0422	$\pm .0082$
$y_1$	.0385	$\pm .0066$	.0327	$\pm .0067$

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1. Survival of tetraploids in mixed 2n-4n plantings.

Four mixtures of varying proportions of tetraploid Synthetic B and diploid Ill. 1996 were grown in isolation in 1959. The plots were allowed to open-pollinate to provide free competition between pollen of diploids and tetraploids. After harvest, shriveled triploids were screened out, leaving a mixture of plump diploid and tetraploid kernels. A random seed sample from each of the four plots was planted the following year, again in isolated blocks.

Random seed samples of each of the four mixtures harvested from the plots in 1959 and in 1960 were planted and all plants detasseled. Interplanted diploid hybrids provided pollen. Tetraploids were identified at maturity by the presence of triploid kernels.

Survival of tetraploids was unexpectedly poor. In populations involving as little as a 10% admixture of diploids, virtually all tetraploids would be expected to disappear after three generations of competition.

Survival of tetraploids in mixed 2n-4n plantings.

	Initial population*							
	90:10		80:20		60:40		40:60	
Gen. of open-pollination	1	2	1	2	1	2	1	2
No. plants observed (2n and 4n)	745	763	798	840	827	840	846	842
% 4n plants	65	31	32	12	16	4	1	0

\*4n percentage listed first.

The rapid decline in 4n's was primarily brought about by more rapid growth of haploid pollen and/or its establishment than in the case of diploid pollen. A series of pollinations involving 4n females x unrelated 4n pollen parents, followed 3 1/2 hours later by application of haploid pollen, were made. Even with the long delay, haploid pollen tubes were able to effect fertilization at a high frequency. Genotype of pollen of the tetraploids appears to be of importance in establishment and/or pollen tube growth rate, in diploid or tetraploid styles.

Summary of  $4n$  seed set in  $4n \times 4n$  pollinations, followed  
3 1/2 hours later by pollination from a diploid source.

Pedigree (1)	No. pollinations	% $4n$ kernels (mean)	Duncan's multiple range test (2)
A. F. x "W8" (+2n ♂)	74	46	a b
A. F. x "W26" (+2n ♂)	63	34	a c
A. F. x "Oh51A" (+2n ♂)	53	37	b c
"W8" x A. F. (+2n ♂)	72	59	d
"W26" x A. F. (+2n ♂)	22	53	a d

- (1) First named member was seed parent. A. F. = Argentine Flint.  
(2) Means followed by same letter are not significantly different from each other (5% level).

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1. The use of hypoploids in identifying naturally occurring duplications.

We have commenced using various hypoploids in an arm by arm search for naturally occurring duplications in the maize genome. Assuming that such duplications are not uncommon, it is argued that during meiosis in the hypoploid individual, the chromosome arm, or part thereof, that is in haplo condition should synapse occasionally with segments of other chromosomes representing duplications of chromatin in the haplo arm. Crossing over in such "illegitimately" paired regions should yield gametes carrying reciprocal interchanges; the identification and analysis of translocations originating in this way might be expected to reveal the nature and extent of naturally occurring duplications.

D. E. Alexander presented preliminary reports (see M.G.C.N.L. 1954 and 1956) on a study which suggests that "crossing over had occurred between non-homologs during megasporogenesis of haploid maize plants." He suggests that cytological analysis of semisterile progeny of monoploid maize plants should lead to inferences concerning duplication in the genome. The use of hypoploids, as suggested here, should afford greater precision in searching for these duplications. Moreover, even though the hypoploid individual, as a result of gross deficiency, customarily

exhibits abortion of 50% of its germinal elements, the deficient chromosome does not transmit through pollen or egg, and therefore is not expected to occur among the progeny of the hypoploid plant.

In our scheme, hypoploid individuals among the progeny of pollen parents carrying an A-B translocation are used as pollen (or egg) parents in crosses with vigorous single-crosses. The progeny of such crosses are grown on a large scale and at harvest time are searched for the occurrence of scatter-grain ears. These are routinely analyzed to confirm the presence of an aberration and to identify it cytologically.

Our results at this stage are preliminary but perhaps worthy of mention. Four reciprocal translocations were found among the progeny of TB-9b hypoploids (haplo condition for the short arm of chromosome 9). One of these appears to involve an interchange between 9S and another as yet unidentified arm. Two others involve 6L and 8L, and 5S and 8L. The fourth is not identified.

Among the progeny of TB-9a hypoploids (haplo condition for the long arm of chromosome 9), five individuals were found, on the basis of aborted pollen, to carry aberrations. One of these is unanalyzed but reciprocal translocations were found in the remaining four cases. One of the latter appears to involve 5S and 9L; another apparently involves chromosome 9 but in this case the other member of the interchange has not yet been identified. The two remaining interchanges appear to involve 2L and 6L, and 8L and 10L.

It should be emphasized that these identifications are tentative. If they are confirmed it would seem that there is a tendency for the chromosome arm that is in haplo condition in the hypoploid to be involved in interchanges; to the extent that there is such a preferential involvement we may expect that the method suggested here has application in identifying duplication segments. On the other hand, it seems clear that the haplo arm is not always involved in the interchange, but even in these cases there is a suggestion that certain arms may be involved more frequently than others. It may be that the haplo arm in the hypoploid plant leads to more complicated or secondary "illegitimate" associations, or that chromosomes are more prone to break in hypoploids and that in this respect some regions are more unstable than others.

We are extending these studies and have included other hypoploids in the analysis. Tentative estimates would place the frequency of interchanges among gametes of hypoploid plants at about five to twenty per ten thousand. It appears, however, that this frequency varies considerably depending on the particular hypoploid involved.

John R. Laughnan  
W. H. Murdy

2. An attempt to localize the lethal effects of  $A_1$  deficiencies.

The lethality of the homozygous deficiencies  $\underline{a-x_1}$  and  $\underline{a-x_3}$  may be due to inviable endosperm and/or inviable embryo. Analysis of hypoploid endosperms and embryos produced by a pollen parent carrying the TB-3a translocation provides an opportunity to localize the lethal effects of Df  $\underline{a-x_1}$  and Df  $\underline{a-x_3}$ . When, for example, an egg parent heterozygous for the  $\underline{a-x_1}$  deficiency is crossed by a TB-3a pollen parent, the resulting hypoploid endosperm,  $3(\underline{a-x_1})/3(\underline{a-x_1})/3^B$ , is associated with hyperploid embryo,  $3(\underline{a-x_1})/3^B/B^3/B^3$ ; and hyperploid endosperm,  $3(\underline{a-x_1})/3(\underline{a-x_1})/3^B/B^3/B^3$ , is associated with hypoploid embryo,  $3(\underline{a-x_1})/3^B$ .

In the studies reported here a single TB-3a pollen parent, hyperploid for the  $B^3$  chromosome, was used as the TB-3a source. The following tables show the results of various crosses undertaken to study TB-3a hypoploid endosperm and embryo involving Df  $\underline{a-x_1}$  and Df  $\underline{a-x_3}$ .

Table 1

Frequencies of endosperm types on four ears from the cross:

$$3(a\ sh)/3(a\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$$

	Endosperm phenotypes			
	<u>A Sh</u>	<u>A sh</u>	<u>a Sh</u>	<u>a sh</u>
Number of kernels	429	0	406	319
Frequency(%)	37.1	0	35.2	27.7

Table 2

Megaspore transmission of Df  $\underline{a-x_1}$ \* in the cross:

$$3(\underline{a-x_1})/3(A\ sh) \times 3(a\ sh)/3(a\ sh) \quad (7\ ears)$$

	Endosperm phenotypes	
	<u>A sh</u>	<u>a sh</u>
Number of kernels	1289	1380
Frequency(%)	48.3	51.7

\*Df  $\underline{a-x_1}$  and Df  $\underline{a-x_3}$  are known to be deficient for both  $\underline{A_1}$  and  $\underline{Sh_2}$ . Both are lethal to the sporophyte when homozygous. Hemizygotes with  $\underline{a}$  and  $\underline{sh}$  are viable and exhibit the recessive phenotypes.



Table 3

Frequencies of endosperm types on six ears from the cross:

$$3(a-x_1)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$$

	Endosperm phenotypes			
	<u>A Sh</u>	<u>A sh</u>	<u>a Sh</u>	<u>a sh</u>
Number of kernels	1022	248	355	2
Frequency(%)	62.9	15.2	21.8	0.1
Expected frequency(%)*	54.1	13.4	18.2	14.3

\*Calculated below from data on egg and pollen transmission in Tables 1 and 2:

$$\begin{aligned} 0.541 &= 0.371 + (0.352 \times 0.483) \\ 0.134 &= 0.277 \times 0.483 \\ 0.182 &= 0.352 \times 0.517 \\ 0.143 &= 0.277 \times 0.517 \end{aligned}$$

The two colorless, shrunken kernels registered in Table 3 have not been analyzed further. They represent either  $3(a-x_1)/3(a-x_1)/3^B$  hypoploid endosperms, or  $3(a-x_1)/3(a-x_1)/3(a\ sh)$  endosperms resulting from contamination involving a sh pollen. The frequency of colorless, shrunken kernels (hypoploid endosperms) involving Df a-x<sub>1</sub> (Table 3, last column) is much lower than expected. Since kernels in this class should have hypoploid endosperms in which Df a-x<sub>1</sub> is uncovered, but should possess hyperploid embryos in which the deficiency is not uncovered, the frequency of this class is expected to be normal if the lethal effect of this deficiency resides in the embryo but not in the endosperm. These results suggest, therefore, that Df a-x<sub>1</sub> is lethal for endosperm tissue.

Kernels from the cross represented in Table 3 were not planted to study hypoploid plants, namely  $3(a-x_1)/3^B$  and  $3(A\ sh)/3^B$ . Instead, sample counts of normal and germless kernels were made on the assumption that even if the hypoploid embryo involving the deficiency is lethal, the associated hyperploid endosperm would develop normally resulting in a germless kernel. The results of this study are given in Table 4 where, for convenience, "Gm" refers to normal, and "gm" to germless kernels, as scored visually.

The increase in frequency of germless kernels when an egg parent heterozygous for the deficiency is crossed by the TB-3a pollen parent suggests that the hypoploid embryo involving the deficiency is inviable. It would appear then that Df a-x<sub>1</sub> is lethal in the sporophyte as well as in the endosperm but that the lethal effect of such embryos does not extend to the associated hyperploid embryos.

Table 4

Sample counts of normal (Gm) and germless (gm) kernels from the indicated crosses.

Cross	Kernel phenotypes							
	A sh		a sh					
	Gm	gm	Gm	gm				
$3(a-x_1)/3(A\ sh) \times 3(a\ sh)/3(a\ sh)$	181	0	179	0				
$3(a-x_1)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$	Kernel phenotypes							
	A Sh		A sh		a Sh		a sh	
	Gm	gm	Gm	gm	Gm	gm	Gm	gm
	296	35	75	1	120	29	0	0

Analyses similar to those involving Df  $a-x_1$  were undertaken with Df  $a-x_3$ . As Stadler and Roman pointed out, the latter deficiency is more drastic in its effects as it shows much reduced transmission through the female gametophyte and fails altogether to transmit through the male gametophyte. Essentially the same kind of analyses of Df  $a-x_3$  are presented in Tables 5 and 6 as are given for Df  $a-x_1$  in Tables 2 and 3.

Table 5

Megaspore transmission of Df  $a-x_3$  in the cross:

$3(a-x_3)/3(A\ sh) \times 3(a\ sh)/3(a\ sh)$  (7 ears)

	Endosperm phenotypes	
	A sh	a sh
Number of kernels	1245	519
Frequency (%)	70.6	29.4

The absence of colorless, shrunken endosperms among the progeny of the cross in Table 6, where over 200 would be expected, indicates that  $3(a-x_3)/3(a-x_3)/3^B$  hypoploid endosperm is inviable, and that Df  $a-x_3$ , like Df  $a-x_1$ , is lethal to endosperm tissue.

Table 6

Frequencies of endosperm types on 14 ears from the cross:

$$3(a-x_3)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$$

	Endosperm phenotypes			
	<u>A Sh</u>	<u>A sh</u>	<u>a Sh</u>	<u>a sh</u>
Number of kernels	1732	552	223	0
Frequency(%)	69.1	22.0	8.9	0
Expected frequency(%)*	62.0	19.6	10.3	8.1

\*Calculated below from data on egg and pollen transmission in Tables 1 and 5:

$$\begin{aligned} 0.620 &= 0.371 + (0.352 \times 0.706) \\ 0.196 &= 0.277 \times 0.706 \\ 0.103 &= 0.352 \times 0.294 \\ 0.081 &= 0.277 \times 0.294 \end{aligned}$$

Additional information on the viability of hypoploid endosperm and embryo involving Df a-x<sub>3</sub> is available from a different cross. Colorless, shrunken endosperms from the cross  $3(a-x_3)/3(A\ Sh) \times 3(a\ sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$  are expected to be mainly

$3(a-x_3)/3(a-x_3)/3(a\ sh)$  and  $3(a-x_3)/3(a-x_3)/3^B$  in constitution.

The former endosperm type should be associated with a  $3(a-x_3)/3(a\ sh)$  sporophyte. The latter endosperm type, if viable, should be associated with a  $3(a-x_3)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$  sporophyte. These two types of sporophytes can be identified easily by crossing with  $3(a\ sh)/3(a\ sh)$  plants. Nine out of twenty-nine colorless, shrunken kernels planted were analyzable. All nine individuals turned out to be  $3(a-x_3)/3(a\ sh)$  plants, suggesting that the  $3(a-x_3)/3(a-x_3)/3^B$  hypoploid endosperm is inviable. Purple, non-shrunken kernels from the same cross were also analyzed. Among sixty-three sporophytes tested, there were twenty-eight nonhypoploids, thirty-three  $3(A\ sh)/3^B$  hypoploids and one unanalyzable hypoploid. No  $3(a-x_3)/3^B$  hypoploid individuals were found. If no lethality is involved we expect (Table 5) 70.6% of the hypoploid sporophytes to be  $3(A\ sh)/3^B$ , and 29.4% to be  $3(a-x_3)/3^B$  in constitution. The absence of the latter type of hypoploid sporophyte indicates that this constitution is inviable.

These data indicate that hypoploid endosperm and embryo involving the A<sub>1</sub> deficiencies are inviable, that is, that Df a-x<sub>1</sub> and Df a-x<sub>3</sub> are lethal to both the endosperm and the embryo.

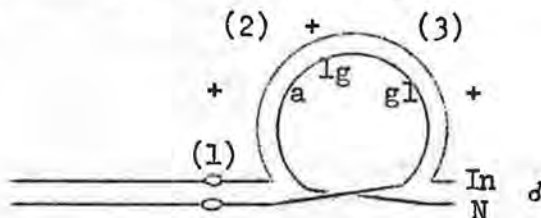
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1. Cytogenetic studies with Inversion 3c.

Inversion 3c, found by Rosalind Morris, is a paracentric inversion in the long arm of chromosome 3. A precise determination of the breakpoints cannot be made until pachynema of homozygous plants is studied but the proximal breakpoint is very close to the centromere and the distal break near the end of the long arm--i.e., almost all of the long arm is inverted. When plants heterozygous for the inversion with the normal alleles G1, Lg, A in the inverted homologue and the recessive alleles in the structurally normal chromosome were used as the pollen parent in testcrosses the following data were obtained:

Families 25083-94

gl lg a ♀ X



(0)	G1	Lg	A	In	631	(2-3)	G1	lg	A	In	37
(0)	gl	lg	a	N	643	(2-3)	gl	Lg	a	N	24
(1-2)	G1	Lg	a	In	3	(2-4)	gl	lg	A	In	0
(1-2)	gl	lg	A	N	6	(2-4)	G1	Lg	a	N	5
(1-3)	G1	lg	a	In	7	(3-4)	gl	Lg	A	In	2
(1-3)	gl	Lg	A	N	2	(3-4)	G1	lg	a	N	6
(1-4)	gl	lg	a	In	4						
(1-4)	G1	Lg	A	N	4						

In addition to the above classes the following individuals were found in the backcross progeny:

G1	Lg	A	high pollen sterility	5
G1	lg	A	" " "	1
gl	lg	a	In with two sizes of starch filled grains	2
gl	lg	a	high pollen sterility	4
gl	lg	a	N with two sizes of starch filled grains	2

At the time of pollen classification in the field the nature of the exceptional plants was uncertain and it was not until later in the season that it was realized that they contained deficient-duplicate chromatids arising from a bridge-breakage-fusion cycle following crossing over within the inversion loop to form a dicentric chromatid. The occasional transmission of these Df-Dp chromosomes through the pollen suggests that the distal breakpoint in In 3c is nearer the end



than the distal break in the In 3a since no functioning of Df-Dp chromosomes coming from crossing over in In 3a heterozygotes was found through the pollen.

It is quite likely that some plants scored as carrying the In actually possessed a Df-Dp chromosome with the normal order. The abortion of some of the Df-Dp pollen simulates the sterility arising from inversion crossing over. Further, some plants scored as carrying the In chromosome undoubtedly had a Df-Dp chromosome with the inverted order.

The reciprocal cross gave the following results: Families 25095-112

(0)	G1 Lg A In	877	(2-3)	G1 lg A In	24
(0)	gl lg a N	621	(2-3)	gl Lg a N	37
(1-2)	G1 Lg a In	8	(2-4)	gl lg A In	16
(1-2)	gl lg A N	30	(2-4)	G1 Lg a N	1
(1-3)	G1 lg a In	3	(3-4)	gl Lg A In	3
(1-3)	gl Lg A N	5	(3-4)	G1 lg a N	1
(1-4)	gl lg a In	10			
(1-4)	G1 Lg A N	4			
	G1 Lg A	high pollen sterility			10
	G1 lg A	" " "			1
	gl lg a	In with two sizes of starch filled grains			1*
	gl lg a	N with two sizes of starch filled grains			2**
	gl lg a	high pollen sterility			7
	gl lg A	" " "			2
	gl lg A	N with two sizes of starch filled grains			2**

\* one chromosome is In Df-Dp and the other normal.

\*\* one chromosome is N Df-Dp and the other normal.

The more frequent transmission of Df-Dp chromosomes through the megaspores is clearly evidenced by the unequal complementary cross-over classes in the (1-2) doubles, the (1-4) doubles and the (2-4) doubles. For example, the ratio of 30 gl lg A N to 8 G1 Lg a In, presumed to arise from (1-2) doubles, is actually due in part to the recovery of gl lg A Df-Dp chromosomes with a N order and producing no or little pollen abortion. These would be classified as gl lg A N. Chromosomes of this constitution could arise following single exchanges in region (2). Breaks in the dicentric chromatid near one centromere would yield a functioning gl lg A N Df-Dp strand while a break near the other centromere would produce a gl lg A In Df-Dp chromatid. The two kinds should occur in equal numbers; hence an excess of the gl lg A In class over the complementary G1 Lg a N class should be found. The observed ratio was 16:1.

Plants homozygous (Families 25127, 130 and 132) for In 3c and heterozygous for the  $\underline{gl}_6$ ,  $\underline{lg}_2$ ,  $\underline{a}_1$  loci were testcrossed as the egg parent to give the following data:

(0)	a	Lg	G1	962	(2)	a	Lg	gl	323
(0)	A	lg	gl	1005	(2)	A	lg	G1	330
(1)	a	lg	gl	619	(1-2)	a	lg	G1	104
(1)	A	Lg	G1	633	(1-2)	A	Lg	gl	124

$\Sigma = 4100$

A-Lg = 36.1%

Lg-G1 = 23.9%

It is clear that all three loci lie within the inverted segment. This is expected from what is known of the cytological position of these genes. The  $\underline{A}_1$  locus lies distal to point .75 (In 3b) and proximal to point .95 (In 3a). The  $\underline{gl}_6$  locus is proximal to point .25 (In 3b) and distal to .05 (In 3c). (As we stated earlier, the proximal break in In 3c has not been exactly determined but it is very near the centromere.) The crossover values from homozygous In 3c plants permit a study of the effect of the centromere on crossing over in adjacent regions. The Drosophila data indicate that distal regions brought near to a centromere have a greatly reduced frequency of crossing over. In the present study the  $\underline{Lg-A}$  region normally out in the distal portion of the long arm of 3 is placed close to the centromere and the proximal  $\underline{G1-Lg}$  region is far removed from the centromere. However, the crossover values in homozygous In 3c plants for the  $\underline{G1-Lg}$  and  $\underline{Lg-A}$  regions do not differ significantly from those in plants with structurally normal chromosomes 3. The data in maize, therefore, do not agree with those from Drosophila and emphasize the danger of generalizing about centric effects on crossing over from experiments with one organism.

M. M. Rhoades

## 2. Recombination values between the centromere and three loci in the short arm of chromosome 2.

In the 1956 News Letter data were presented which indicated that the unreduced eggs produced by homozygous  $\underline{el}$  plants arose by the failure of the second meiotic division. It was further argued that for a locus very near the centromere the percentage of diploid eggs homozygous for the recessive allele would be 50 and that the frequency of homozygosis could be used to measure the recombination value between a given locus and its centromere. The percent of recombination was determined in this way for the  $\underline{wx}$  and  $\underline{sh}$  loci in chromosome 9 and for the  $\underline{lg}_2$  and  $\underline{A}_1$  loci in chromosome 3. However, it seemed desirable to test the method by studying the homozygosis percentages for three loci, all of which were located in the same chromosome arm. Accordingly, plants homozygous for  $\underline{el}$  and heterozygous for the  $\underline{ws}_3$ ,  $\underline{lg}_1$ , and  $\underline{gl}_2$  markers, all known to reside in the short arm of chromosome 2, were used as the female parent

in testcrosses. The triploid offspring coming from these crosses were scored for the three marked loci.

el el    ws lg gl ♀    X    ws lg gl ♂  
           +    +    +

Triploid Progeny

+ + +	371	10.9% ws <sub>3</sub>	ws <sub>3</sub> -centromere	39.1% recombination
ws lg gl	28			
ws + +	10	13.3% lg <sub>1</sub>	lg <sub>1</sub> -centromere	36.7% "
ws lg +	12			
ws + gl	2	17.5% gl <sub>2</sub>	gl <sub>2</sub> -centromere	32.5% "
+ lg +	0			
+ + gl	30			
+ lg gl	23			
	<u>475</u>			

The recombination values are in the anticipated order and indicate that the method, although laborious, has some merit. It should be pointed out that although the homozygosis percentages were obtained from triploid plants, not all of them had 30 chromosomes. A few of the plants with 29 chromosomes could have arisen from 19 chromosome eggs having only one chromosome 2.

M. M. Rhoades

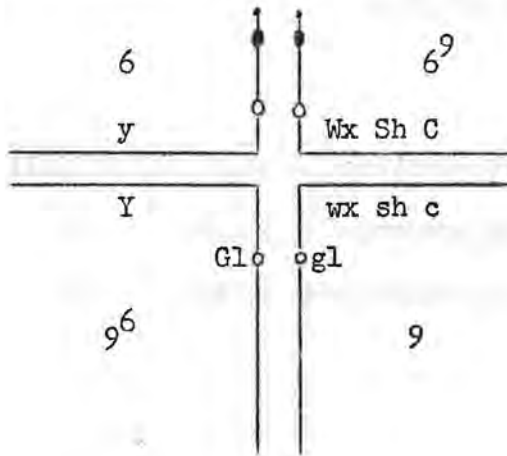
### 3. Further studies with T6-9b.

Genetic studies with T6-9b (breaks 6L.10-9S.37) reported in previous News Letters have shown that the frequency of recovery of T chromosomes from backcrossed T/N plants is 50% when the heterozygote is used as male parent, but only 31.5% when used as female parent. This observation was confirmed by crossing the translocation stock to five unrelated stocks and testing transmission rates in different backgrounds (Table 1).

Table 1. Transmission frequencies and recombination in T/N pistillate parents carrying N chromosomes from five different sources.

Female parent in B.C.	% T marker	% C-Wx recombination
T/ chr 3 tester	31.3	5.1
T/ chr 9 tester	31.5	2.8
B1 Mex/ T	33.9	5.2
chr 10 tester/ T	34.3	3.8
chr 6 tester/ T	40.2	12.4

Cytological studies of T/N plants have shown a high frequency of chains of four and trivalents due to absence of chiasmata in the  $6^9$  chromosome (see diagram).



In spite of the low recovery of T-bearing spores, there is no increase in ear abortion; the expected 50% frequency of aborted ovules was observed.

In order to explain the differences in ♂ and ♀ transmission of gametes with translocated chromosomes, the following sequence of events is proposed:

<u>Diakinesis configuration</u>	<u>MI orientation</u>	<u>Constitution of microspores</u>	<u>Constitution of megaspores</u>
Rings or chains	1/2 alternate	1/4 T	1/4 T
	1/2 adjacent	1/4 N	1/4 N
		1/2 aborted	1/2 aborted
Trivalent and univalent $6^9$	all alternate	1/4 T	1/2 N
		1/4 N	1/2 aborted
		1/2 aborted	

The difference in the array of ♂ and ♀ gametes on this scheme is attributed to the behavior of cells with trivalents and univalents. It is assumed that the univalent  $6^9$  chromosome undergoes a delayed equational division at AI and the resulting chromatids are oriented toward the inner poles of the two AII spindles in megasporogenesis. The basal megaspore would then receive either  $9 + 6$  or  $9^6$ ; the former is viable but the latter would abort. In microsporogenesis, four potentially functional spores are produced of constitution  $6 + 9$ ,  $6^9 + 9^6$ ,  $9^6$ , and  $6 + 9 + 6^9$ . The latter two will abort in most cases although occasional transmission of  $6 + 9 + 6^9$  occurs in the male gametes. The former two spores, one carrying normal chromosomes and one carrying translocated chromosomes would be produced in equal frequencies unlike the corresponding megaspores. Two cytological



observations support this scheme. First the orientation of trivalents at MI in microsporogenesis is almost entirely of the alternate type. Secondly, in sections of developing ears, only the basal megaspore gives rise to the embryo sac. Thus, spore substitution is ruled out. The behavior of the univalent  $6^9$  chromosome in meiosis has not been carefully followed cytologically. It probably is not lost from the nucleus since pollen from tertiary trisomes carrying  $6^9 \underline{Wx}/ 9 \underline{wx}/ 9 \underline{wx}$  shows about 43% Wx grains.

A trivalent frequency of 40% (32% was observed at microsporogenesis) would lead to 50% ovule abortion and a 30:70 ratio of translocated to normal chromosomes. Since the amount of crossing over in 9S will influence the trivalent frequency, there should be a low C-Wx recombination in plants with the distorted backcross ratio. This is seen to be true in Table 1. In the past few years, some ears have been noted which have 1:1 ratios for the translocated and normal chromosomes. These occur regularly in plants carrying abnormal chromosome 10 (see MNL 33: 55) but also arise occasionally in plants with N 10. One would expect to find a low frequency of trivalents and higher recombination values in such plants.

Last summer backcrosses of  $T/N \times N/N$  were planted and classified for T. Plants carrying the T were backcrossed again and ears were scored for aberrant segregations and 1:1 ratios. The plants bearing ears with normal ratios more often than not had been derived from a crossover in one of the arms of the T in the previous generation. The distribution of crossover and non crossover parent plants in the two classes of ears is as follows:

132 ears with aberrant ratios	{	125 non crossovers
		4 T-G1 crossovers
		3 Sh-Wx crossovers
19 ears with normal ratios	{	7 non crossovers
		2 T-G1 crossovers
		7 Sh-Wx crossovers
		3 C-Sh crossovers

Eleven of the 19 ears had markers allowing a test of crossing over in 9S. Table 2 shows the % Wx (Wx marks the T) and the Sh-Wx recombination in these eleven plants as well as in two plants with 1:1 ratios from the 1961 season. With 3 exceptions there is a good correspondence of the normal segregation with a high Sh-Wx recombination. The two plants from the 1961 crop were tested again in 1962 and the 1:1 ratios and high crossing over were maintained.

Table 2. Transmission frequencies and recombination in T/N pistillate parents having approximately normal backcross ratios.

	<u>Σ</u>	<u>% Wx (T marker)</u>	<u>% Sh-Wx Recombination</u>	<u>Phenotype of plant</u>
25212	183	47.0	15.8	C Sh Wx gl Y
	125	56.0	25.6	C Sh Wx Gl Y
	130	48.5	3.1	C Sh Wx Gl Y
25225	158	50.6	21.5	C Sh Wx Gl Y
	158	45.6	13.9	C Sh Wx Gl Y
	165	49.1	22.4	C Sh Wx gl Y
25228	209	55.5	25.8	c Sh Wx Gl Y
	184	50.0	22.3	c Sh Wx Gl Y
25232	127	53.5	18.9	C Sh Wx Gl Y
	156	53.8	3.2	C Sh Wx Gl Y
25235	108	41.7	26.0	c Sh Wx Gl Y
24435	190	52.6	22.1	C Sh Wx Gl Y
24450	164	44.5	20.1	C Sh Wx gl Y

A random sample of 12 noncrossover plants from the aberrant ratio class gave a total of 1832 seeds, a Wx frequency of 33.6% and Sh-Wx recombination of 3.8%.

The occurrence of plants with normal backcross ratios in the female is often associated with a crossover in one arm of the T. This may lead to a closer homology of the arms in question, although no striking difference in homology has been observed between the T and N chromosomes. The result, at any rate, is a higher crossing over in 9S, leading to a lower trivalent frequency (not yet confirmed cytologically) and to normal recovery of T and N chromosomes.

Ellen Dempsey

#### 4. Du-Oy linkage.

Some preliminary data from a selfed ear of Du oy/du Oy constitution gave the following classes:

<u>Du Oy</u>	<u>Du oy</u>	<u>du Oy</u>	<u>du oy</u>	<u>Σ</u>
176	75	62	2	315

This indicates a value of 18-19% recombination as based on Immer's Tables. Backcross data should be available next year.

Ellen Dempsey

5. A possible convertor at the Pl locus.

In a family of 36 dark purple plants, presumed to be homozygous B Pl, a single lighter-pigmented plant appeared. This exceptional plant was self-pollinated and also crossed as male parent with dark purple individuals from the same line and from a second, not closely related line. All the progeny (350) from these crosses were light-colored. Nor was there any segregation of dark purple color in the next generation when the  $F_1$ 's were selfed or backcrossed to dark purple.

This behavior parallels that described for conversion at the B locus. Except for anther color, however, these plants resemble sun reds in phenotype. Linkage tests are being made to determine whether the Pl locus or B are involved in this case.

Crosses with other lines and other genotypes have produced interesting results. The progeny from a cross with a line homozygous B Pl obtained from the Co-op were all dark purple. A line homozygous b pl also gave dark purple  $F_1$ 's whereas the progeny from a cross with b Pl were all sun red. Two lines of sun red plants (B pl) gave opposite results; one yielded only dark purple plants whereas the other produced only sun reds.

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1. Location of fl<sub>2</sub>.

The study of the progenies of the backcrosses (see News Letter, 36, p. 91) confirmed the linkage between genes la and fl<sub>2</sub>, and Tu and fl<sub>2</sub>. The results obtained were as follows:

<u>Genes</u>	<u>Parental</u>		<u>Non-parental</u>		<u>Total</u>	<u>Percent recom- bination</u>
fl <sub>2</sub> la	252	234	9	6	501	3
	(fl <sub>2</sub> +)	(+ la)	(+ +)	(fl <sub>2</sub> la)		
fl <sub>2</sub> Tu	97	88	38	42	265	30
	(fl <sub>2</sub> +)	(+ Tu)	(+ +)	(fl <sub>2</sub> Tu)		

Thus gene fl<sub>2</sub> appears really to be located on the short arm of chromosome IV, very near to la.

A. Cornu

2. Location of rp<sub>x</sub> (sensitivity to Puccinia Sorghi).

The study of the progenies of the backcrosses comprising genes rp<sub>x</sub>, ws<sub>3</sub> and lg<sub>1</sub>, provides the possibility of defining accurately the situation of the locus rp<sub>x</sub> on chromosome II (see News Letter 35, p. 134).

The backcrosses with ws<sub>3</sub>, rp<sub>x</sub> resulted in a progeny of 934 plants, of which 196, or 21%, were recombinant.

The three-point test (ws<sub>3</sub>, lg<sub>1</sub>, rp<sub>x</sub>) provided a progeny of 332 plants, among which were counted:

65	recombinants	between	<u>ws<sub>3</sub></u>	and	<u>rp<sub>x</sub></u> ,	or 19.5	per cent
40	"	"	<u>lg<sub>1</sub></u>	and	<u>rp<sub>x</sub></u> ,	or 12	" "
25	"	"	<u>ws<sub>3</sub></u>	and	<u>lg<sub>1</sub></u> ,	or 7.5	" "
2	double recombinant	plants,				or 0.6	" "

Thus it seems possible to locate the locus rp<sub>x</sub> on the short arm of chromosome II, between genes lg<sub>1</sub> and gl<sub>2</sub> and more or less at the same distance from both.

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1. The survey of maize factors.

The world literature dealing with the genetics and with the breeding of maize is very extensive (our private card-register alone contains more than 11,300 citations). Of this large quantity approximately 2/5 (according to our experience) deal directly with the problem of the genes. In spite of the great extent of the world literature on the factors and genes of maize, we can point out only a few works dealing with the working out of catalogues of factors and genes and with their description for their accurate determination. One of the first attempts at a systematic survey of genes was that carried out by R. A. Emerson et al (1935) and M. M. Chadžinov (1935). Of the later works we should like to point out the work published by L. M. Jones (1958, 1959). To the most detailed attempts belong the studies performed by J. Weiĵer (1952) and L. Řiman (1961). This short survey of the pertaining literature, however, only emphasizes the lack of synthetic works on the factors and genes of maize, which works, at the present situation of research work, we consider a very important component part of the total investigation of the problem of the genes of maize.

We have attempted to compile a comprehensive collection of the factors of maize, which we submit to our colleagues for their kind consideration:

Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
1	a, A	anthocyanin	5	65
2	ac, Ac	activator	1	
3	ad	adherent	7	2
4	ae	amylose extender	1	
5	ag, Ag	susceptible (resistant) to grasshoppers and locusts	1	
6	al	albescens	3	
7	am, Am	ameiotic	1	
8	an	anther ear	3	6
9	ar	argentina	1	1
10		argostripe	1	
11	as	asynaptic	1	
12	at	antherless	1	
13	au	aurea	2	
14	b, B	plant colour booster	1	4
15	ba	barren stalk	2	1
16	bd	branched silkless	7	

Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
17	be	blanched ear	1	
18	bf, Bf	blue fluorescent	2	
19	bh, Bh	blotched aleurone	1	
20	bk	brittle stalk	2	1
21	bl	blotched leaf	7	
22	bm	brown midrib	6	1
23	bn, Bn	brown aleurone	2	
24	bp	brown pericarp	1	
25	br	brachytic	3	
26	bs	barren sterile	1	
27	bt, Bt	brittle endosperm	4	3
28	bu		1	
29	bv	brevis	2	
30	bz, Bz	bronze	2	2
31	c, C	aleurone colour	2	2
32	cb	chloroblotch	1	
33	Ce		2	
34	Cg	<b>corn grass</b>	1	
35	cl, Cl	modifier of chlorophyll	3	
36	club	club	1	
37	co	coherent tassel	1	1
38		corn borer susceptible(resistant)	1	
39	cr	crinkly leaf	4	
40	ct	compact	1	
41	cz	cuzcoid	1	
42	d, D	dwarf plant	10	19
43	da, Da	dilute aleurone	2	1
44	de	defective endosperm	19	1
45	Df	diffuse	1	
46	di	disintegrated endosperm	1	
47	dl	dull brown endosperm blotch	1	
48	dm	dead leaf margins	2	
49	Ds		1	
50	dt, Dt	dotted aleurone	3	2
51	du	dull endosperm	2	
52	dv	divergent	1	
53	dy	desynaptic	1	
54	E	euchlaena	1	5
55	el		1	
56	En	enhancer	1	
57	et	etched endosperm	1	
58	f	fine stripe	3	2
59	fi	fine streaked	1	1
60	fl	floury endosperm	2	

Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
61	fn		1	
62	fr	frayed	2	
63	fs	fasciated	1	
64	fu	fused tassel branched	1	
65	fz		1	
66	g	golden	4	1
67	ga, Ga	gametophyte	8	1
68	gc		1	
69	ge	germinating seeds	15	
70	gi		1	
71	gl	glossy seedling	17	10
72	gm	germless	4	3
73	gs	green striped	3	1
74	h	soft starch	2	
75	ha		2	1
76	hc, Hc	hornlike coleoptile	1	
77	hf	hermaphroditic flowers	1	
78	hm, Hm	susceptible (resistant) to Helminthosporium carbonum leaf blight	2	
79		susceptible (resistant) to Helminthosporium turcicum leaf blight	1	
80	Hs	hairy sheath	2	
81	ch, Ch	chocolate pericarp	1	
82	I	inhibitor of aleurone colour	1	
83	id	indeterminate flowering	1	
84	ij	iojap striping	1	
85	in, In	intensifier of aleurone colour	3	2
86	it	intensifier of yellow endosperm	1	
87	j	japonica	4	1
88	Kn	knotted leaf	1	
89	l, L	luteus	11	8
90	la	lazy plant	2	1
91	le	lemon endosperm	1	
92	lg, Lg	liguleless leaf	3	
93	li	lineate	2	
94	lo	lethal ovule	2	
95	lp	pollen lethal	1	
96	lw	lemon white	4	
97	m, M	yellow white seedling	2	1
98	ma	maculate leaf	1	
99	mc	micropyle colour	1	
100	Md	midcob colour	1	

Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
101	me	mealy endosperm	1	
102	mg	miniature germ	1	
103	mi	midget	1	2
104	mn	miniature seed	1	
105	Mp		2	2
106	mr	midrib	1	
107	ms, Ms	male sterile	22	5
108	Mt	mottled aleurone	1	
109	na	nana	2	
110	nc		1	
111	nl	narrow leaf	2	1
112		necrotic	2	
113		new starchy	1	
114	o, O	opaque endosperm	3	1
115	og, Og	old gold stripe	1	1
116	or, Or		2	
117		orobanche seedling	1	
118	oy	oil yellow	2	
119	P	pericarp and cob colour	32	1
120	pa	pollen abortion	1	
121	pb, Pb	piebald	5	1
122	Pc	purple coleorhiza	4	
123	pd		1	
124	pe	pubescens hairy sheath	1	
125	pg, Pg	pale green seedling	12	5
126	Ph		1	
127	pi	development of secondary pistillate florets	2	
128	pk	polkadot leaves	1	
129	pl, Pl	purple plant colour	1	
130	pm	pale midrib	1	
131	pn, Pn	papyrescent glume	1	
132	po, Po	polymitotic	1	
133	Pp		1	
134	pr, Pr	red aleurone	2	
135	ps	panicula specialis	1	
136		pink scutellum	1	
137	pt, Pt	polytypic	1	
138	Pu	purple plumule	2	
139	py, Py	pigmy	2	
140	r, R	aleurone and plant colour	18	6
141		ragged seedling	1	
142	ra, Ra	ramosa ear	3	



Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
143	rd	reduced plant	1	1
144	re	reduced endosperm	4	
145	rf, Rf	fertility restoration	2	
146	rg, Rg	ragged leaf	2	1
147	rl	red leaf tip	1	
148	ro	rolled leaves	1	
149	rp, Rp	rust susceptible (resistant)	3	2
150	rpp, Rpp	susceptible (resistant) to Puccinia polysora Underw	2	
151	rs, Rs	rough sheath	2	
152	rt	rootless	1	
153	S	coloured scutellum	5	
154	sa	striped auricle	2	
155	sb	slit blade	1	
156	sc	scarred endosperm	2	3
157		semisterility	7	
158	sd, Sd		1	
159	sf	stiff leaves	1	
160	sh	shrunken endosperm	5	1
161		sienna	2	
162	sk	silkless	1	
163	si, Si	silky ear	3	
164	sl	slashed leaves	1	
165	sm, Sm	salmon silk	1	
166	sn	siamensis	1	
167	so	orange scutellum	2	
168	sp, Sp	small pollen	2	1
169	sr	striate	2	
170	st	sticky chromosome	1	1
171	su, Su	sugary endosperm	4	2
172	sy	yellow scutellum	1	
173	ta	tan cob	1	
174	tb	teosinte branched	1	
175	th	threaded	1	
176	tn	tinged plant	1	
177	tp	teopod	2	
178	tr	two ranked ear	1	1
179	ts, Ts	tassel seed	8	
180	tu, Tu	tunicate ear	1	6
181	tw	twisted seedling	3	4
182	v, V	virescent seedling	22	11
183	va	variable sterile	2	
184	Vg	vestigial glume	1	

Numerical order	Mark	Denomination	Number of genes	Number of non-included symbols
185	vp	vivipary	9	
186	w, W	white seedling	12	22
187		white	2	
188	wa	warty anthers	1	
189		waseca stripe	1	
190	Wc	white capped endosperm	1	
191	wd, Wd		1	
192	Wh	white endosperm	1	
193	wi	wilted	1	
194	wl	white leaf base	4	
195	ws	white sheath	3	
196	wt	wheat tassel	1	
197	wx, Wx	waxy endosperm	1	8
198	xn	xantha seedling	2	
199	y, Y	yellow endosperm	8	7
200	yd	yellow dwarf	1	
201	yf	yellow flecked seedling	1	
202	yg	yellow green	13	2
203	Yp	pale yellow endosperm	1	
204	ys	yellow stripe	3	1
205	yt	yellow top	1	
206	z		1	
207	zb	zebra striped	6	5
208	zg	zigzag culm	3	
209	zl	zygotic lethal	2	
210	zn	zebra necrosis	1	
210	Summary		591	254

We are of the opinion that it is essential that by far more careful attention should be paid to these studies than has been the case hitherto, as the number of papers and studies on the genes of maize increases rapidly every year, and a number of symbols are falling into oblivion or changing their original meaning, etc., all of which tends to cause a certain obscurity.

We have attempted to compile a comprehensive collection of the factors of maize, which we submit to our colleagues for their kind consideration.

Supplements and amendments will be published.

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1. Some effects of semi-sterility.

In making up several popcorn double-cross and 3-way hybrids, several single-cross hybrids were used which were semi-sterile because of a reciprocal translocation. In routine testing of 24 such hybrids, separate measurements were made on grain from plants bearing semi-sterile and normal appearing ears. Differences between semi-sterile and normal were highly significant in all cases. Some of the measurements are given below.

Ear type	Ears per plot	Equilibrium Grain Moisture at 70% R.H.	Popping popped raw	Expansion Cu. in. per lb.	100 kernel weight (gms)	100 c.c. weight (gms)
Normal	27	13.9	33.8	930	12.17	156
Semi-sterile	36	13.3	36.0	1010	13.31	153

Since grain was not crowded on the semi-sterile ears, the larger kernels and lower test weight were not surprising. However, based on other work, we expected that kernels from the normal ears with heavier test weight would expand more in popping than the grain from the semi-sterile ears. Also, the smaller kernels of the normal ears came to equilibrium in a constant humidity chamber at a higher per cent grain moisture than the larger kernels from the semi-sterile ears. This factor alone could have been responsible for the difference in popping expansion. However, when both types were brought to the same grain moisture level, the differences became slightly larger. The magnitude of this difference and the fact that it was in the opposite direction expected from physical measurements in other data suggest the possibility of position effect, or different endosperm/embryo or endosperm/pericarp ratios.

Two lines are now being used in a back-crossing program in an effort to obtain genetically identical lines with different chromosome structure in order to study this effect in more detail.

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## 2. The relation of Enhancer (En) to Spm.

Tests have now been completed that show a relation between the action of En (reports of this system in previous MGCNL) and that of Spm. In crosses of Dr. McClintock's Spm tester allele,  $\underline{a}_1^{m-1}$  (pale and stable) with an En stock, the kernels,  $\underline{a}_1^{m-1}/\underline{a}_1^{dt}$ , are characterized by mutant purple areas on a colorless background. In a further test-cross of these mutable kernels stable pale segregants typical of the  $\underline{a}_1^{m-1}$  expression were recovered and this is correlated with the absence of En in these kernels.

These tests show that En can both suppress the action, the pale coloration, of this allele and also induce this allele to mutate to higher levels of pigmentation. The principal difference in the En system is the occurrence of a colorless allele,  $\underline{a}_1^{m(r)}$ , that becomes mutable in the presence of En. This is in contrast to the pale coloration of McClintock's  $\underline{a}_1^{m-1}$  allele.

Peter A. Peterson

## 3. The effect of B-chromosomes on pollen size.

In an effort to evaluate the role of B-chromosomes, studies on the effect on pollen size were conducted. Measurements were made of pollen grain diameters. This experiment was based on the premise that the genotype of the pollen grain is reflected in a phenotypic character, in this case pollen size. Thus, a correlation was sought between pollen size and the absence or the presence of a variable number of B-chromosomes. Rather than use mean values in the comparison (since plants are highly subject to environmental variation), the variances ( $s^2$ ) of the measurements of individual plants were analyzed. It was found that in a comparison of non-B and B-containing plants there is a greater amount of variation (significant at the 10% level) in the plants with B-chromosomes.

Further experiments using the same comparison on additional data are now being evaluated.

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#### 4. Nucleolar-like droplets at pachytene.

In microsporocytes of maize plants heterozygous for 1, 2, 8, and 12 knobs, nucleolar-like droplets appeared at various locations in the cells. These included the ends of chromosomes, interstitially on the chromosomes, and free in the nucleoplasm.

One hundred pachytene cells were analyzed in each family; from this the average number of droplets per cell was calculated (Table 1).

Additional studies were made on plants which arose from a backcross of the 12 knob plant by Tama Knobless Flint. Observations of the offspring, which had 1 to 8 knobs (heterozygous), gave similar results (Table 2).

It appears evident that there is an inverse relationship between the number of nucleolar-like droplets and the number of knobs present.

Table 1.

No. of knobs	Ave. no. of droplets per cell
1	3.19
2	3.10
8	2.38
12	1.83

Table 2.

No. of knobs	Ave. no. of droplets
1	2.66
2	2.44
3	2.38
4	2.00
5	1.46
6	1.55
7	1.92
8	1.01

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5. Relation of multiple chromosome associations at diakinesis to knob number.

Previous studies (S. E. Zvingilas, MGCNL 35 and 36) indicated that the knob and centromere associations of non-homologous chromosomes observed at pachytene persist through metaphase.

Additional investigations were carried on with diakinesis cells of plants which arose from a backcross of the 12 knob heterozygote to the knobless parent. These results support the previous conclusion; there is a positive correlation between the number of chromosomes in multiple association at diakinesis and the number of knobs present (Table 1).

Table 1.

No. of knobs	Ave. no. of assoc. bivalents at diakinesis
1	1.46
2	1.75
3	1.48
4	1.94
5	2.15
6	2.38
7	3.12
8	3.15

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1. Allele studies involving  $\underline{Cl}_2$ ,  $\underline{Cl}_3$  and  $\underline{Cl}_4$ .

Dr. Everett in 1949 (Proc. Nat. Acad. Sci. 35: 628-634) described two dominant suppressors of the  $\underline{cl}_1$  locus,  $\underline{Cl}_2$  and  $\underline{Cl}_3$ , which partially or completely suppressed the albino phenotype of this mutant. Since the discovery of the two original suppressors, we have found a third one which has been designated  $\underline{Cl}_4$ . This suppressor was found in a stock in which a gene for albinism was segregating, designated  $\underline{cl}_p$ . This gene was found to be allelic to  $\underline{cl}_1$ . The action of the suppressors,  $\underline{Cl}_2$ ,  $\underline{Cl}_3$  and  $\underline{Cl}_4$  is summarized in Table I.

Table I. Phenotypes produced by the suppressors  $\underline{Cl}_2$ ,  $\underline{Cl}_3$  and  $\underline{Cl}_4$ .

Genotype	Endosperm Phenotype	Seedling and Mature plant phenotype
1. $cl_1 cl_1$	white or pale yellow	albino
2. $cl_1 cl_1 Cl_2 cl_2$	white or pale yellow	pale green (pastel) - lethal
3. $cl_1 cl_1 Cl_2 Cl_2$	white or pale yellow	pale green (pastel), on the average darker green than #2. - lethal
4. $cl_1 cl_1 Cl_3 cl_3$	white or pale yellow	green as seedling, mature plant pale green, often zebra
5. $cl_1 cl_1 Cl_3 Cl_3$	white or pale yellow	green as seedling, green as mature plant apparently as vigorous as normal siblings.
6. $cl_1 cl_1 Cl_4 cl_4$	white or pale yellow	green as seedlings - lethal
7. $cl_1 cl_1 Cl_4 Cl_4$	white or pale yellow	green as seedlings, green as mature plant but not as vigorous as normal siblings

While it was known that the suppressors were inherited independently of the  $cl_1$  locus, it was not known whether they occupied the same or independent loci. The following crosses were made to determine this.

1.  $\underline{cl}_1 \underline{cl}_1 \underline{Cl}_3 \underline{Cl}_3$  x  $\underline{cl}_1 \underline{Cl}_1 \underline{Cl}_2 \underline{Cl}_2$
2.  $\underline{cl}_1 \underline{Cl}_1 \underline{Cl}_2 \underline{cl}_2$  x  $\underline{cl}_p \underline{cl}_p \underline{Cl}_4 \underline{Cl}_4$
3.  $\underline{cl}_1 \underline{Cl}_1 \underline{Cl}_2 \underline{Cl}_2$  x  $\underline{cl}_p \underline{cl}_p \underline{Cl}_4 \underline{Cl}_4$
4.  $\underline{cl}_p \underline{cl}_p \underline{Cl}_4 \underline{Cl}_4$  x  $\underline{cl}_1 \underline{cl}_1 \underline{Cl}_3 \underline{Cl}_3$

Yellow and white or pale yellow seeds from the  $F_1$  ears were planted in the field. The plants from the white or pale yellow seeds of crosses #1 and #4 produced plants that survived to maturity and produced ears. Most of the plants from the white or pale yellow seeds of crosses #2 and #3 died at an early age and the few that did survive were pale green runts. All surviving plants were self pollinated and where possible, a sample of 50 white or pale yellow seeds was planted from each ear. If the suppressors are alleles, no albino seedlings should be observed in the  $F_2$ 's of crosses #1, #3 and #4. If the suppressors occupy independent loci, then a ratio of 15 non-albino : 1 albino seedling should be observed among the plants produced by the white or pale yellow seeds from such  $F_2$  ears. A lower frequency of albino seedlings would indicate that the

suppressors are non-allelic but linked. Half of the  $F_1$  plants from cross #2 will have  $cl_2$  and the white seeds produced when these plants are self pollinated, therefore, will be expected to segregate albino seedlings in a 3 green to 1 albino ratio but no pastel seedlings. This was observed to be the case. The albino segregating ears were not included in the totals given in Table II. The results of these tests which are summarized in Table II indicate that these three suppressor genes are allelic.

Table II. Summary of Data from Allele Tests Involving  $Cl_2$ ,  $Cl_3$  and  $Cl_4$ .

Segregating Alleles	Number of Seedlings Tested	Number of Albino Seedlings	Conclusions
$Cl_2$ and $Cl_3$	4277	0	Allelic
$Cl_2$ and $Cl_4$	3495	0	Allelic
$Cl_3$ and $Cl_4$	3604	0	Allelic

The absence of albino seedlings in these  $F_2$  populations also indicates that the  $cl_p$  gene for albinism (present in the original  $Cl_4$  stock) can also be suppressed by  $Cl_2$  and  $Cl_3$ .

Donald S. Robertson

## 2. Chromosomal segregation in hyperploid TB-9b plants used as females.

As a regular practice, we have been perpetuating several of our B translocation stocks by using hyperploid plants (e.g.,  $9\ 9^{BB}9^B$ ) as males in outcrosses to inbreds. Pollen examination is used to select hyperploid plants for outcrossing but since sterility is low (approximately 15% - 20%), it is not always possible to select these plants by this method. Therefore, each suspected hyperploid is also crossed to appropriate tester stocks carrying recessive genes that are found in the region of the chromosome translocated to the B centromere.

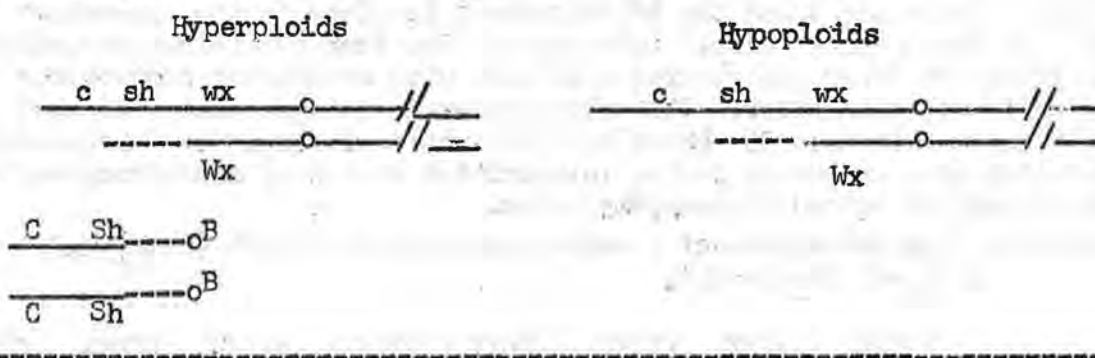
For TB-9b we have been using a  $c\ sh_1\ wx$  line as the tester stock. The break point in this translocation is about 40% of the distance out on the short arm of nine and the translocated piece includes the loci of  $c$  and  $sh_1$ . The  $wx$  locus is on the untranslocated portion of nine. When hyperploid plants are crossed as males to this tester stock, two classes of seeds are found on the ears, purple, starchy and colorless, shrunken. The latter class results when a deficient sperm ( $9^B$ ) unites with the polar fusion nucleus producing endosperm cells with the chromosomal constitution of  $9\ 9\ 9^B$ . The egg nucleus of such seeds will have been fertilized by the hyperploid sperm ( $9^{BB}9^B$ ) resulting in embryos with the chromosomal constitution of  $9\ 9^{BB}9^B$ . Some of the



purple, starchy seeds will be produced by the reciprocal fertilization and thus will have hypoploid embryos ( $9\ 9^B$ ) and hyperploid endosperms ( $9\ 9\ 9^B\ 9^B$ ). Plants from this latter class of seeds are semisterile. Figure one diagrams the genetic and cytological constitution of the embryos from both of these classes of seeds.

Figure 1

Genetic and cytological constitution of embryos hyperploid and hypoploid for TB-9b.



Plants from both of these classes of seeds have been testcrossed with a  $c\ sh_1\ wx$  stock. In the case of the seeds with hyperploid embryos, the crosses were made using the hyperploid plants as females while the hypoploid plants were crossed as both males and females.

Table 1 gives the results for the testcrosses of hyperploid plants. Classes  $C\ Sh_1\ Wx$  and  $C\ Sh_1\ wx$  are the most frequent and occur in equal frequency. These results would be expected if most of the time the normal chromosome nine paired with  $9^B$  and the two  $B^9$  chromosomes paired and if these two pairs then assorted independently of each other at meiosis I. The next most frequent class is  $c\ sh_1\ wx$ . This class would be expected if a gamete received only a normal chromosome 9 and could be the result of non-disjunction of the  $B^9$  centromere either in meiosis or during development of the female gametophyte. The latter possibility is not very likely since non-disjunction would have to occur in the two cell lineages giving rise to the two polar nuclei.

In order to get the  $c\ Sh_1\ Wx$  class, a  $B^9$  chromosome must have paired with a normal nine followed by crossing over between the  $c$  and  $sh_1$  loci which would produce a crossover chromatid of the  $B^9$  chromosome with the genotype  $c\ Sh_1$ . In order to account for the  $Wx$  allele, the  $9^B$  chromosome (carrying  $Wx$ ) must have ended up in the same cell as the  $B^9$  crossover chromatid. It will be noted that none of the reciprocal crossover classes occurred ( $C\ sh_1\ wx$ ) and that with the exception of one seed for which the shrunken classification was

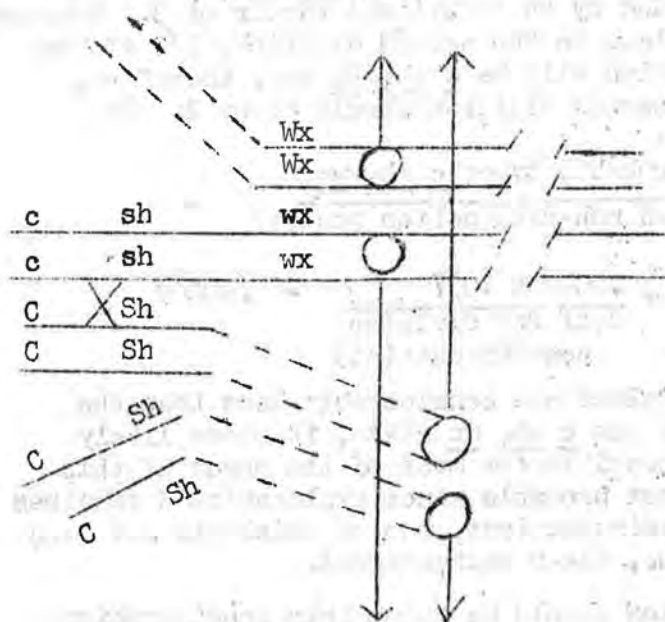
doubtful (a classification which was made and recorded prior to any attempt at interpreting the results), no seeds of the  $\underline{c} \underline{Sh}_1 \underline{wx}$  class were found. This class is theoretically possible if after the above crossover event, the  $B^9$  chromosome and the normal 9 chromosome went to the same pole and if after the second meiotic division, a microspore received the crossover  $B^9$  chromatid ( $\underline{c} \underline{Sh}_1$ ) and at the same time, the non-crossover 9 chromatid ( $\underline{c} \underline{sh}_1 \underline{wx}$ )\*. Since neither the  $\underline{C} \underline{sh}_1 \underline{wx}$  nor  $\underline{c} \underline{Sh}_1 \underline{wx}$  are found, the events which are responsible for them as outlined above must be extremely rare and some type of directed segregation must take place whenever a crossover takes place in the  $\underline{c} - \underline{sh}_1$  region. Figure 2 diagrams the pairing relationships and segregations necessary to explain the observed results. The results indicated that a crossover in the  $\underline{c} - \underline{sh}_1$  region determines that the normal chromosome 9 and the  $B^9$  chromosome involved in the crossover will go to opposite poles. This segregation then determines the poles to which the other centromeres will move with homologous centromeres going to opposite poles. This observation is in agreement with that of Burnham (Genetics 35: 446-481, 1950) where he found that chromosomes involved in a crossover in the interstitial region of a heterozygous translocation passed to opposite poles.

Table 1. Testcross data of plants hyperploid for TB-9b ( $\underline{c} \underline{sh}_1 \underline{wx}/\underline{C} \underline{Sh}_1 -/\underline{C} \underline{Sh}_1 -/--\underline{Wx}$ ).

	$\underline{CShwx}$	$\underline{cshwx}$	$\underline{Cshwx}$	$\underline{cShwx}$	$\underline{CShwx}$	$\underline{cshwx}$	$\underline{Cshwx}$	$\underline{cShwx}$
$\frac{5561-4}{4558-4}$	112	5	-	-	137	3	-	-
$\frac{5561-5}{4558-4}$	221	15	-	1	237	3	-	-
$\frac{5561-6}{4558-4}$	160	8	-	-	152	1	-	-
$\frac{5561-16}{4558-4}$	243	16	-	1	242	-	-	-
$\frac{4564-2}{4558-3}$	284	31	-	1	271	-	-	-
$\frac{4564-16}{4558-3}$	290	27	-	1	276	-	-	(1)
Totals	1310	102	-	4	1315	7	-	(1)
%	47.8%	3.7%	-	0.1%	48.0%	0.26%	-	(0.04%)

\*Theoretically, the  $\underline{c} \underline{Sh}_1 \underline{wx}$  class also could be produced by a double crossover between the normal 9 chromosome and the  $B^9$  chromosome which would move  $\underline{Sh}_1$  into a normal 9 chromatid. If the crossover were then followed by non-disjunction of the  $B^9$  chromosomes, some gametes of the  $\underline{c} \underline{Sh}_1 \underline{wx}$  would be expected. Since this would involve the simultaneous occurrence of two rare events (double crossover and non-disjunction), it is not likely that this genotype would be produced in this manner.

Figure 2. Probable pairing relationships and segregation responsible for the c sh<sub>1</sub> Wx class.



Three events could give rise to the c sh<sub>1</sub> Wx class. 1) A crossover could take place between the wx locus and the translocation point putting Wx on the 9 chromosome along with c sh<sub>1</sub> and this event accompanied by non-disjunction of the B centromeres, 2) A crossover could have taken place between the sh<sub>1</sub> locus and the translocation point putting c and sh<sub>1</sub> on the B<sup>9</sup> chromosome, which as the data from the c Sh<sub>1</sub> Wx class indicate would then segregate from chromosome 9, ending up in a cell with the 9<sup>B</sup> chromosome carrying Wx or 3) Non-disjunction of the 9 centromeres and B centromeres, in which the normal 9 and 9<sup>B</sup> chromosomes go to one pole and the two B<sup>9</sup> chromosomes to the other.

Table 2 gives the results of testcrosses of deficient plants. From these data, the amount of crossing over between the waxy locus and the translocation break point has been determined to be .48%. This information permits the elimination of one of the three explanations for the c sh<sub>1</sub> Wx class given above. If explanation 1 is responsible for this class, the frequency with which these seeds can be expected can be predicted. This predicted value should be equal to the probability of non-disjunction (=2 x .037, the frequency of the c sh<sub>1</sub> wx non-disjunctional class) times the probability of a crossover between the wx locus and the translocation break point (.0048). Since there are two ways the non-disjunctional chromosomes will segregate

with respect to the crossover products and only one will allow for the expression of the  $c\ sh_1\ Wx$  genotype, this product will have to be divided by 2. Further, if the desired non-disjunction takes place in the first division of meiosis, only three of the meiotic products will be functional and of these, only one will carry  $c\ sh_1\ Wx$ . This requires that the above product be divided by an additional factor of 3. However, if the non-disjunction takes place in the second division, 1/2 of the products following non-disjunction will be  $c\ sh_1\ Wx$  and, therefore, instead of dividing by 3, the second division should be by 2. To summarize, the formula will be:

$$\frac{(\text{Probability of C.O.}) \times 2 \times (\text{probability of } c\ sh_1\ wx)}{2 \times (3 \text{ or } 2) \text{ depending upon when non-disjunction occurs}} =$$

$$\frac{.0048 \times .037}{3(\text{if first division non-disjunction})} = .00006 \text{ or } \frac{.0048 \times .037}{2(\text{if 2nd division non-disjunction})} = .00009$$

Since both of these predicted values are considerably less than the observed frequency of .0026 for the  $c\ sh_1\ Wx$  class, it seems likely that explanation 2 or 3 is responsible for most of the seeds of this phenotype. Explanation 2 is most probable since explanation 3 requires the occurrence of two rare non-disjunctions, one of which has not been demonstrated to take place (i.e., the 9 centromeres).

The results of these studies should be taken into consideration in using B translocations, particularly if one is attempting to incorporate genes into the translocated piece. The likelihood of succeeding will be extremely low if this is attempted in a hyperploid. However, if a hyperploid is outcrossed as a female, approximately half of the offspring will then be heterozygous for the translocation (9<sup>BB9</sup>), a condition which would be more conducive to picking up the desired crossovers.

Table 2. Testcross data of plants hypoploid for TB-9b ( $c\ sh_1\ wx/--Wx$ ).

	cshWx	cshwx		cshWx	cshwx
$\frac{4558-8}{4893-9}$	1	174	$\frac{4894-2}{4893-3}$	0	207
$\frac{4558-13}{4893-9}$	0	97	$\frac{4894-5}{4893-3}$	0	217
$\frac{4893-2}{4894-3}$	0	130	$\frac{4894-8}{4893-9}$	1	216
$\frac{4893-2T}{4894-3}$	1	160	$\frac{4895-1}{4893-9}$	4	160
$\frac{4893-3}{4894-4}$	0	189	$\frac{4895-3}{4893-3}$	3	326
$\frac{4893-9}{4558-13}$	0	183	Total	10	2059
			% C. O.	.48%	



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1. Defective endosperm factors from maize-teosinte derivatives.\*

Additional allelism tests have been obtained on the defective endosperm types ( $de^t$  factors) in the derivatives of the controlled teosinte introgression in the inbred A158.

While no other case of allelism has been found, it is now well established that  $de^{t12}$ ,  $de^{t13}$  and  $de^{t25}$  are three different and independent factors. Moreover  $de^{t5}$  is not allelic to  $de^{t28}$ . When  $de^{t22}$  (an allele of  $de^{t13}$ ) is introduced in the background of the stock of the balanced lethal system  $de^{t1}/de^{t2}$ , although segregating regularly in its own original background, it "disappears" completely. In other words the genotype  $De^{t22}/de^{t22}$  behaves as though it were  $De^{t22}/De^{t22}$  in the new background. The same behaviour had been shown to hold for  $de^{t5}$  in the genetic background of a multiple tester developed by Dr. P. C. Mangelsdorf (W. M. T. r G). It should be noted that, while in the case of  $de^{t5}$  we are dealing with a factor affecting the endosperm mainly from a quantitative point of view, in the case of  $de^{t22}$  its effects are obviously also qualitative.

Angelo Bianchi

2. Mendelian characters in Italian maize.\*

Self pollination has been carried out in plants of over 200 samples of Italian maize provided by "Stazione di Maiscoltura di Bergamo".

The following mutants have been obtained in a total of 1500 selfed ears:

Character	No. of cases exhibiting a ratio of:		Character	No. of cases exhibiting a ratio of:	
	3:1	15:1		3:1	15:1

A. Seed Traits:

Defective	45	Floury	1
Opaque	4	Brittle	2
Lemon	2	Pink-yellow	2
White	2	Small	3
Waxy	3	Germless	2
Shrunken	4	Pregermination	1
Defective floury	1		

\*Work subsidized by The Rockefeller Foundation, New York.

Character	No. of cases exhibiting a ratio of:		Character	No. of cases exhibiting a ratio of:	
	3:1	15:1		3:1	15:1
<b>B. Seedling traits:</b>					
Albino	9	2	Fine stripe on pale green background	3	1
Dwarf	8	3	Fine stripe on virescent background	2	
Luteus	18	3	Japonica	9	3
Yellow green	26	1	Bifurcate coleoptile	4	3
Pale green	54	11	Green striped	2	1
Fine stripe	21	8	Oily spotted		1
Glossy	39	12	Luteus + glossy	1	
Abnormal growth	20	26	Leafy coleoptile	1	
Liguleless	1		Green mottled	3	1
Virescent	49	12	Allium type	4	4
Lutescent	22	5			
Booster color	63	8			
Pale luteus	6	3			
Fine stripe on yellow green background	7	1			

M. Pozzi  
A. Bianchi

### 3. New knob types in Italian maize.\*

The cytological survey of open pollinated Italian maize is in further progress. Among the findings dealing with knob characters, the following may be reported:

- a) The type of chromosome 8 possessing in its long arm a prominent chromomere distal to the large knob has been again found, in a few cases together with the standard but more distal large chromomere; this suggests that the new small knob position - exactly midway between the two standard ones - is really a new knob forming region, and not the result of a chromosome inversion involving the previously known types.
- b) A small knob has also been detected in the middle of the short arm of chromosome 8.
- c) In a few cases the distal prominent chromomere of the long arm of chromosome 6 has been found replaced by a large, long-shaped knob.

\*Work subsidized by The Rockefeller Foundation, New York.

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1. Recombination in the  $a_1sh_2$  region.

Backcross data on recombination rate in three different genetical backgrounds, having in common the "Texas" male sterile cytoplasm, are reported for  $a_1sh_2$  markers in coupling in the following table:

Genetical background	No. of ears	Total no. of seeds	$A_1sh_2$ seeds	$a_1Sh_2$ seeds	% of recombination
A158	36	21386	9	14	0.107
W22	33	9632	3	4	0.072
WF9	31	12215	8	6	0.114
Totals	100	43233	20	24	0.101

The crossover value is clearly lower than that previously reported (0.27%). However, it is undecided whether this is due to different environmental conditions (including the T type cytoplasm) or to a difference in nuclear genotypes, although the latter interpretation appears less likely because of the uniform behavior of the different backgrounds of the inbred lines used. It is interesting that this value is of the same order of magnitude as at least one intracistron recombination rate:  $wx^{90}/wx^C$  produces, according to our data, about 1%  $wx$  pollen grains, mainly as a result of the recombination process.

A. Bianchi  
G. Lapietra

2. Effect of storage on x-rayed pollen.

By applying Everett's technique it has been possible to prolong the pollen life-span and to study the effect of storage on x-rayed pollen (1750 roentgen in about 7').

The data appearing in the following table are roughly in agreement with those obtained with storage of dry irradiated seeds:

Temperature and relative humidity	Storage periods (in hours)	Chromosome and markers	Kernels scored	% of germless kernels	% of endosperm mutations
3° <u>±</u> 1° C 70-90%	1	3,5 a <sub>1</sub> sh <sub>2</sub> ,pr	988	9.6	14.6
	4		1130	16.6	19.6
	60		980	9.1	17.6
	121		498	13.2	13.6
20-30° C 60-70%	1	idem	663	11.7	10.2
	4		587	19.2	19.0
	22		153	17.9	22.2
	30		136	22.0	18.2
3° <u>±</u> 1° C 70-90%	1	idem*	716	15.5	13.7
	48		193	18.6	19.8
	78		340	19.1	11.9
	96 1/2		68	19.1	14.0
3° <u>±</u> 1° C 70-90%	148	9 C sh bz wx	217	23.9	16.4
	1 1/2		493	4.2	2.6
	52		558	6.6	4.3
	148		212	6.6	3.3

The data marked with an asterisk refer to a hybrid type, homozygous nevertheless for the appropriate markers involved: the radio-sensitivity of the hybrid appears somewhat greater as compared with that obtained from an inbred line.

The recovery following the initial increase of damage could partially be ascribed, either to the active metabolism of pollen and/or to aplontic selection. The types of mutations detected are of the kind common in maize, and interpretable as chromosomal deletions.

G. Gavazzi

### 3. Mutagenic activity of nebularine and ethyl methane sulphonate.

Mutagenic activity of such chemicals has been studied on the basis of endosperm mutations, following treatment of mature pollen. Solutions are administered with a vial applied to tassels newly shedding pollen 24 hours before a first pollination, which was, then, repeated for 2 more successive days.



Chemical	Concentration	Chromosome 9 markers		Chromosome 3 markers	
		No. of kernels scored	% of mutations	No. of kernels scored	% of mutations
Nebularine	control	838	0.1	518	0.4
	.25%	1873	0.5	343	2.6
	.5%	712	2.0	480	4.3
	1.0%	460	2.4	522	1.8
	2.0%	293	1.4	203	13.3
Ethyl methane sulphonate	control	167	0.6		
	0.25%	437	0.2		
	.5%	224	0.9		
	1.0%	117	3.4		
	2.0%	154	2.6		

Additional treatments, under the same experimental conditions, have been made with diethylsulphonate and curcume extracts with negative results.

The types of mutations detected in nebularine experiments are hardly to be interpreted as point mutations, at variance with data reported in other organisms, including barley. The activity of ethyl methane sulphonate appears not very strong especially if one considers its powerful action when applied to seeds.

Some data have been obtained also on the basis of seedling characters, making use of markers of the corresponding chromosome regions ( $yg_2$ , for chromosome 9, and  $a_1$  for chromosome 3). The mutation rate in such cases is greatly reduced, more or less, as already found with other chemicals (as diepoxibutane). Namely the chemicals used behave as good inducers of partial endosperm mutations (affecting only a part of the endosperm) but have a reduced or null effect on the sporophyte generation.

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1. "Curing" maize of its plasmids.

Plants infected with about 30 different viruses have been reported to be cured by exposure to high temperature. Various chemicals also have been reported to differentially inactivate viruses. It has been repeatedly suggested that cytoplasmic male sterility in maize may be due to the presence of an alien virus. A very crudely designed experiment in 1959 gave evidence that maize has been "cured" of its cytoplasmic male sterility by heat shock (MNL 35:83, 1961). In 1961 and 1962 this experiment was repeated using refined seed stocks and equipment and the heat shock treatment was extended to include maize carrying a variety of plasmids and/or episomes in an attempt to "cure" them of their "infection". In addition, lines of the same material were treated with streptomycin, dl-parafluorophenylalanine, and acriflavine which are known to kill, inactivate or induce mutations in viruses and other plasmids. Both mutant forms of the plasmids and the elimination of the plasmids from the cell line (cure) were sought in the treated material. No effect was detected as a result of any treatment. These experiments contribute no evidence in support of the idea that controlling elements are due to the presence in the cytoplasm of virus-like entities in so far as their reproduction may be inhibited by external agents without killing the host cell. A brief account of these experiments is presented here for the record.

Technique: The heat treatment procedures were previously described (MNL 35:83). In 1961 and 1962 a constant temperature water bath replaced the oven., and aluminum foil pans 6 3/4 x 4 1/4 x 1 3/4 inches replaced the cardboard dishes used in 1959-60. The seeds when planted were routinely maintained for 48 hours at 30°C and then treated for 12 hours at 46°C. Following treatment they were transferred to the greenhouse and subsequently the surviving young plants were transplanted into the field.

The chemical treatment consisted of soaking dry seed for 24 hours at 30°C in the dark. The chemicals used and the concentrations used were:  
streptomycin - 0.025% and 0.1% in water  
dl para fluorophenylalanine - 0.0125%, 0.025% and 0.1% in water  
acriflavine - 0.025% and 0.1% in water.  
The soaked seeds were planted directly in the field. No phytotoxicity was noted and in most cases nearly 100% survival was obtained.

### Cytoplasmic male sterility

A. Heat treatment: During 1960 an inbred line with the rare recessive leaf stripe gene -  $l_2$  - and carrying either "T" or "S" cytoplasm following 8 backcrosses was multiplied for use in a large scale experiment. In 1961, 15,600 seeds were heat treated and 2,750 seeds served as controls. Only "T" cytoplasm was used. At flowering time, in August, only 1,988 remained from the treated group and only 728 from the control group. No effect of treatment was noted.

The 1962 experiments were conducted on fewer seeds but a much higher survival rate following transplanting was achieved. Both "T" and "S" cytoplasm were used. 2,700 "T" cytoplasm treated seeds were represented by 1,263 field survivors in August and 450 untreated seeds following transplanting gave 441 plants in the field. "S" cytoplasm stocks consisted of 900 treated and 150 untreated with 273 plants flowering from the heat treated and 148 from the non treated. No plants shed pollen in 1962 in either of these experiments.

B. Chemical treatment: 134 seeds of the same inbred stock with "T" cytoplasm used in the heat treatment were treated with each concentration of each chemical while 268 seeds were soaked in water. None of the treated or water soaked seeds produced pollen shedding plants.

### Variiegated pericarp

A. Heat treatment: One experiment was conducted in 1961 using seed from the mating of homozygous variegated (inbred W9 background) x  $P^{WW}$  (inbred A171). The results obtained are tabulated in the table under "Homozygous Variegated".

In another experiment in 1961, 990 seeds from the mating medium variegated ( $P^{VV}/P^{WR}$ ) x inbred W9 ( $P^{WR}$ ) were treated in the water bath, while 150 seeds were germinated and transplanted as controls. The results obtained are shown in the table under "Heterozygous Variegated".

Pericarp phenotype	<u>Homozygous Variegated</u>				<u>Heterozygous Variegated</u>			
	<u>Control</u>		<u>Heat treated</u>		<u>Control</u>		<u>Heat treated</u>	
	Total number	%	Total number	%	Total number	%	Total number	%
medium variegated	61	83.6	108	87.8	45	36.3	245	36.3
light variegated	8	11.0	4	3.3	7	5.6	43	6.4
very light variegated	0	0	1	0.8	1	0.9	1	0.1
colorless pericarp	0	0	1	0.8	66	53.2	332	49.2
red	4	5.4	9	7.3	5	4.0	54	7.9
	<u>73</u>		<u>123</u>		<u>124</u>		<u>675</u>	

There does not seem to be any consistent effect of the treatment in the case of "Homozygous Variegated" although the numbers of survivors were too small to have much significance. A slight increase in the frequency of movement of  $M_p$  away from  $P^{IT}$  is noted in the heat treated "Heterozygous Variegated" (as indicated by the increased frequency of light variegated and reds). A larger control would have been necessary to establish the difference as real.

The seed used in the heat treatment experiments in 1962 all came from the pollination of many ears of inbred W9 with the pollen from one homozygous variegated plant (in W9 background). 3,600 seeds were treated in the water bath and 600 were transplanted without treatment. The results of the analysis of the ears are shown below:

	Controls		Heat treated	
	Number of ears	%	Number of ears	%
1. Pericarp class				
medium variegated	506	94.2	1,361	93.8
light variegated	23	4.3	40	2.8
very light variegated	0	0	2	0.1
orange variegated	0	0	3	0.2
red	9	1.7	42	2.9
$p^{WT}$	2	0.4	3	0.2
Total	537		1,451	
2. Number kernels per red spot (one kernel and larger)	3441/1526 = 2.26		8108/3871 = 2.09	
3. Number red spots (one kernel and larger) per med. var. ear	1526/506 = 3.02		3871/1361 = 2.85	
4. Estimated freq. per 1,000 kernels of red spots of kernel size:				
1 kernel	6.1986		5.4604	
2 kernels	0.3892		0.3743	
4 kernels	0.0795		0.0789	
8 kernels	0.0670		0.0418	
16 kernels	0.0167		0.0170	
32 kernels	0.0126		0.0139	
64 kernels	0.0084		0.0062	
128+ kernels	0.0126		0.0108	

Whereas there was a slight increase in the frequency of light variegated in 1961 following heat treatment, a decrease was observed in the 1962 group. And since very light variegated and orange variegated are rare phenotypes, their appearance in only the heat treated could be ascribed to chance. The number and size of red pericarp spots on the medium variegated ears do not differ enough to warrant drawing conclusions.



B. Chemical treatments: Variegated pericarp stocks in W9 background were treated with the same chemicals, concentrations and times as the cytoplasmic male sterile stocks. A total of 1,584 ears from these treatments were analysed in the same way as the heat treated variegated stocks. These extensive data show no striking departure from that in the heat treated material and so they will not be included here.

Bronze mutable: A small progeny from a homozygous  $bz_1^m sh$  ear which had been heat treated showed no striking difference from the untreated. Both heavily and lightly mottled and stable bronze ears were present in both groups in about equal numbers. No detailed analysis of the spotting frequency or distribution was undertaken.

Dotted: The only provocative observations involve the acriflavine treated progeny of a homozygous  $a_1 Dt$  ear in inbred W9 background. Among 230 selfed ears coming from one selfed ear, 209 were normally dotted, 6 were segregating 3 dotted: 1 non-dotted and 15 showed a few kernels without dots while other kernels on the same ear showed all gradations of dots up to the usual level in this line. Through an oversight in the field, the untreated control material was not hand pollinated so no conclusions can be drawn.

Robert I. Brawn

## 2. Dark variegated pericarp.

Last year it was reported that dark variegated pericarp occasioned a coarse (earlier) pattern of  $Ds$  breaks than the standard medium variegated when both were used as males on  $Ds$  testers. In 1962 similar crosses were made onto the progeny of one selfed ear of homozygous  $Ds$ . Again the visible pattern of  $Ds$  breakage was coarser when the male was dark variegated than when the male was medium variegated. The difference has not yet been scored qualitatively. These further observations support the hypothesis that the dark variegated phenotype results from a change of state of  $Mp$  in the direction of a lower dosage than that of the standard  $Mp$  of medium variegated.

Medium variegated ( $P^{VV}/P^{WX}$ ) when tested showed the expected  $1/2$  kernels with  $Ds$  breaks and  $1/2$  without breaks while homozygous medium variegated produced nearly all kernels with  $Ds$  breaks. However, homozygous dark variegated gave 20 to 30% kernels without  $Ds$  breaks. Likely the kernels on the  $Ds$  tester without breaks are the result of the loss of  $Mp$  from  $P^{XX}$ . This is consistent with the high frequency of red ears in the progeny of dark variegated reported last year. In

	1962 a further three progenies from dark variegated gave colored pericarp				colorless pericarp,	Total
	self red	dark var.	medium var.	light var.	red cob	
number	262	559	59	10	54	946
per cent	27.91	59.09	6.24	1.06	5.71	

Several anomalies are obvious in these observations. First, the change to medium variegated from dark variegated involves a change of state according to my hypothesis rather than a transposition of  $\underline{Mp}$  as in the change of medium variegated to light variegated. If so, this change is frequent. Transposition of the modified  $\underline{Mp}$  should occur in dark variegated to give a lighter pericarp class analogous to light variegated. As yet this class has not been identified. In scoring progeny from dark variegated a class phenotypically like medium variegated is observed, but its true nature is unknown.

Second, the frequency of reds in the progeny of dark variegated is high, consistent with the heavy striping of the pericarp. A corresponding lighter level of pericarp variegation occurs with low frequency. This is not what one would predict from the twin spot hypothesis of the movement of  $\underline{Mp}$ . Dark variegated ears with twin spots of red, and what looks like medium variegated, have been observed but remain to be grown out for progeny examination.

Finally in 1961, 4 ears out of 188 had colorless pericarp and in 1962, 54 ears out of 946 had colorless pericarp in the progeny of dark variegated. This is about 10 times more frequent than the occurrence of colorless pericarp progeny from medium variegated in the same inbred W9 background.

Robert I. Brawn

### 3. Indeterminate-growth in Gaspe Flint background.

An indeterminate growth segregate was found in 1958 which flowers only in short days. This new mutant has not been checked for allelism with Singleton's  $\underline{id}$ . In an effort to develop a growth chamber sized corn with the  $\underline{id}$ -like gene, the new mutant was crossed with the world's earliest and possibly smallest corn, Gaspe Flint. Following one back-cross to Gaspe Flint a few plants were selfed. Some of the progeny exhibited very peculiar flowering behavior. The main stalk came into flower just after Gaspe Flint in early July and resembled Gaspe except that it was a few inches taller. However, in September it was discovered that these same plants had indeterminate growth tillers from five to seven feet tall. By early October, just before frost, tassels were appearing on these tillers. Many plants in the row were ear bagged in July, but none of those which exhibited the abnormal behavior silked and so none were selfed.

Normal Gaspé Flint averages only 5 or 6 leaves on the main stalk. Tassels are visible in the leaf whorl two or three weeks after planting dry seed and pollen sheds in about one month. It has been suspected for some time that the growing point in the seed of Gaspé Flint has already been converted from the vegetative to the reproductive stage. Thus only the tassel would form after planting. Leaf number would be limited to those which have differentiated in the embryo of the seed while attached to the mother plant.

My working hypothesis to explain the early flowering main stalk and id-like tillers involves maternal genotype control of the growing point in the seed and autonomous genotype control in the tillers. That is, when id/id seed is produced on an +/id plant, the hormone pattern in the non-short day maternal plant may cause the embryo growing point to change from the vegetative to the reproductive stage as the seed matures. Growing points subsequently produced by the id/id plant in the form of tillers would be under the control of the plant's own genotype and would be indeterminate in growth.

Robert I. Brawn

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1. Further observations on the etched phenotype.

A. Lack of gene expression in the root. In order to determine whether or not the starchless sectors found in et/et/et endosperm were present in et/et roots, the following procedure was followed: ten 10 mm. roots (chosen because of strong etched expression in the endosperm) were hand sectioned and stained with iodine. If staining of the starch grains was initially poor, the section was washed with a drop of concentrated HCl and restained. No starchless sectors were found in any areas of the root exhibiting detectable starch concentrations. In addition measurements of starch grain number, size, and location in the roots of these etched plants were not significantly different from comparative measurements made on two different non-etched inbred types.

Since the effect of the et allele is manifested only early in the embryology of the endosperm and shoot (virescence) it was thought that the 10 mm. roots observed may have been "too old" for et expression. However, roots just emerging through the seed coat also were without detectable starch sectoring.

Observations on 9, 10, and 11 day old endosperms disclosed the same sectoring pattern seen previously in the mature kernel. These sectors of starchless cells are evident in the young endosperm as soon as enough starch develops to disclose their presence. This is interpreted to mean that starch is never formed in these sectors instead of being formed and then degraded after synthesis.

The etched allele, like sugary, affects nuclear control over the plastid in the endosperm tissue and is without corresponding effects on the same plastid in a different tissue--the root. It would be of interest to screen other known gene controlled plastid alterations (in the endosperm and shoot) to determine if any of these exhibit a comparable interaction with the root plastids.

B. Endosperm cultures. After finding cell lineages in the endosperm which do not store starch while other cells (the majority) do produce starch it was thought desirable to attempt an isolation of each type in tissue culture. The basic question we were interested in was whether the starch producing cells would give rise to starchless or vice versa. Pieces of endosperm were planted 9 and 10 days after pollination on unmodified Coe's media (MNL 1961). Serving as controls for starch synthesis patterns were other starchy inbred types (W22, W23, W8, 4Co63) and sugary Black Mexican sweet corn.

To date we have not been able to develop clones of callus which parallel the cell types in the organized endosperm.

We have found that the rapidly dividing cells at the periphery of the callus do not contain starch grains whereas the older cells (in from the clump surface and presumed not to be dividing) do show starch grains. The distribution of the starch containing cells in both etched and non-etched cultures appears scattered; that is, they are intermingled with the starchless cells. It is because of this lack of uniform starch synthesis that we are unable (as yet) to see any of the characteristic clearcut sectoring of the organized endosperm.

Unexpectedly the etched callus exhibits a growth rate that is greater than that of Black Mexican, a very fast grower. This contrasts strongly with the other starchy endosperm types which are growing very poorly--if at all. The relative growth responses by the different endosperms are as follows:

Very poor growth  
W22 and W23  
Poor to good growth  
W8, 4Co63  
Good growth  
Black Mexican  
Best growth  
Etched



Inbreds W22 and W23 have a much higher proportion of flint type starch than W8 or 4Co63--these being more floury. It appears that in tissue cultures cells having a shift away from full starch synthesis can divide at a higher rate than those cells committed to full starch production.

Irwin M. Greenblatt  
Ann L. Lewis.

## 2. Corn root callus cultures.

For the past nine months we have continuously cultured root callus of different inbred lines employing an unpublished technique originally developed by Nickell (formerly of the Pfizer Co.) and communicated to us by Dr. Phinney of U.C.L.A. The media used is a modified basic White's with 2-4D as a growth stimulating component. (We will gladly supply the exact recipe and procedure upon request by any interested party.)

The cut surfaces of the primary root and/or secondary and adventitious roots serve as donating cells for the callus.

Sub-cultures have been made repeatedly so we now have clumps of cells, mitotically active, which do not contain any differentiated elements from the parent root system.

The growth characteristics of these root calluses are very different from those exhibited by a fast growing tobacco callus (for example). The most striking feature is that under constant conditions of light, heat, and humidity these clumps of cells show very erratic growth phases. We have recorded some pieces suddenly doubling in size in a six day period and then just as suddenly coming to an apparent complete stop for over a month. Some clumps were scored as being dead, left alone, and five weeks later scored as having new growth developing. The growth, which is definitely an increase in cell number, does not occur uniformly over the surface of the callus. Instead, sites of growth develop and it is these cells that continue to grow forming a "knob" of cells extending from the body of the callus.

When the callus goes into a sporadic "dormant" phase it is characteristic to see cell enlargement taking place all along the surface. Such a callus then appears very glossy.

Controlled variations in light and temperature seem not to affect the callus growth. We have been growing these cultures under high continuous light. Sample cultures kept under open room conditions seem not to grow any differently.

Raising or lowering the amount of 2-4D in the media is without gross effect except at the null level. Without 2-4D a large number of cultures have been observed to generate small organized roots.

Irwin M. Greenblatt  
Ann L. Lewis

### 3. Gene expression in root tissue cultures.

Like the endosperm callus, the root callus exhibits pigmentation. To summarize our results to date:

<u>Genotype</u>	<u>Callus Phenotype</u>
W22 A C R <sup>r</sup> b pl df	Red
W22 A C R <sup>r</sup> b pl Df <sub>cl*</sub>	Colorless
W22 A C R <sup>ch</sup> B Pl	Dark purple
W23 A C R <sup>sc</sup> P <sup>WR</sup>	Colorless
W23 A c r <sup>g</sup> P <sup>RR</sup>	Colorless
W23 A C R <sup>ch</sup>	Purple

\*The state of the Diffuse allele here used is a very stable and strong pigment inhibitor.

Each of these callus phenotypes corresponds to what is seen in the organized root. Note that the red pericarp allele does not produce a detectable effect. R<sup>r</sup>, R<sup>ch</sup>, B, Pl, Df<sub>cl</sub>, all known to affect root color, are similarly active in the callus.

Those cultures scored as colorless are not strictly so. All the cultures have amber color (characteristic of most plant callus). The intensity of this amber coloring increases considerably with aging.

When pigment develops it does so on a cell to cell basis. That is, a cell is either completely pigmented or not at all. The placement of these pigmented cells with respect to each other appears almost at random--given a specific area in the callus. The older the area (in terms of how long ago it stopped dividing) the higher the frequency of pigmented cells.

Pigment from all of the colored cultures diffuses out into the media, sometimes producing a dark ring of pigment surrounding the clumps of callus.

Irwin M. Greenblatt  
Ann L. Lewis

UNIVERSITY OF MARYLAND  
College Park, Maryland

During 1962 an asynaptic monosomic was isolated from the  $X_1$  following irradiation of the pollen with 1000r. The loss of  $P^{WT}$  and the dominant alleles of  $zb_1$  and  $br_1$  disclosed that chromosome 1 from the pollen parent was absent in the microsporocytes of the  $X_1$  monosomic. Both asynapsis and regular first division association have previously been reported in monosomics not identified in regard to the missing chromosome (J. of Hered. 1929, 1956). Thus both monosomic 1 carrying the normal allele of the recessive  $as$  in chromosome 1 as well as asynaptic homozygotes exhibit irregular association. The above observation suggests a dosage relationship of a gene or genes in chromosome 1 with normal, orderly first division association of the complement.

R. L. Baker  
D. T. Morgan, Jr.

UNIVERSITY OF MINNESOTA  
St. Paul 1, Minnesota

1. All-arms tester set of interchanges.

The first few backcrosses to the A188 inbred were made here, the subsequent ones up to 8 and 10 backcrosses by M. T. Jenkins. For those with fewer than this number, the additional backcrosses are being made here.

Homozygous stocks are being established after the 8 to 10 backcrosses. These are then being checked for chromosome identification by cytological examination at diakinesis in crosses with the chromosome identification set. To date, 1-9b, 2-4b, 3-4(5156), and 5-7e are apparently correctly identified. The stock originally designated as 5-10(6061) is now a 2-10 stock. The others in the series will be checked.

C. R. Burnham

2. Sporocytes from crosses needed to check and identify the chromosomes in the multiple interchange stocks were collected, but cytological examination is still in progress.

3. A severe hailstorm almost eliminated early plantings, but later material in about the 2-leaf stage showed little permanent damage.

C. R. Burnham  
Paul Yagy

#### 4. Association test between interchanges and midribless leaf character.

In 1959 a selfed culture of Illinois High Oil produced several plants whose lower leaves had no midribs. The character is recessive and affects the first 2 to 5 leaves of the plant which hang limp from the stalk. A selfed ear culture was used as the source of the character for this study. By selection, selfing, and sibbing, plants have been obtained with no midribs in any of the leaves; however all these extreme types have been weak plants. The original trait appears to have no effect on vigor or viability. The expression of the character is most striking in the third to tenth leaf stage and thus may have some possibility as a seedling marker. Seed has been offered to Maize Cooperative Genetic Stocks.

The A 188 interchange series (developed by Burnham, Longley and Jenkins) was used to determine the location of the gene(s) controlling this character. The following is a portion of the data obtained in recent  $X^2$  tests of backcrosses involving the character and a series of chromosomal translocations.

Family	Translocation	NR	Tr	Nr	TR	Total	P
25076	3-4(5156)	17	28	61	36	142	.01
25081	4-7(7108)	17	34	46	42	139	.01
25106	4-8(6926)	22	23	51	69	165	.01
25079	3-7c	12	19	50	57	138	.01

N = normal; T = translocation-heterozygote; R = ribbed; r = midribless

Although further tests are required, it appears that a major factor is located on the long arm of chromosome 4 and possibly another on the long arm of chromosome 7.

Charles Laible

MISSISSIPPI STATE UNIVERSITY  
State College, Mississippi

#### 1. The cytology and morphology of male-sterile lines of corn.

Measurements of normal, male-sterile, and restored corn stalks showed that the internodes and tassel culms were shortened in the male-sterile version. Pre-anthesis plants showed shortening in the male-sterile version between 10 and 14 days after meiosis. The exact time depends upon the internode location in relation to the ear and when elongation occurs. Since pollen degeneration occurs about 5 days after meiosis, shortening does not appear to be the effect of the cytoplasm itself. Genetic male steriles also showed a shortening of the tassel culm and internodes above and below the ear. Shortening depended upon the line and internode location. Pollen breakdown preceded shortening by at least 5 days.

Patricia A. Sarvella  
C. O. Grogan



UNIVERSITY OF MISSOURI  
Columbia, Missouri

1. Preferential pairing in trisome 3 plants with two standard chromosomes 3 and a chromosome 3 from exotic strains of maize.

Data were presented in the 1962 News Letter which indicated that preferential pairing was active in trisome 3 plants which had two standard chromosomes 3 and a chromosome 3 from an exotic strain. Additional data have been collected on some of the exotic trisome hybrids used last year and also on some new ones. It has become apparent that there is considerable variability in the progeny ratios of different plants obtained from the same exotic source in some cases. This is to be expected as the exotic lines used are open pollinated varieties and the structure of their chromosomes 3 may not be homogeneous. Also there may be genic control of the trivalent frequency which may be variable. Therefore, the data must be presented giving the interaction  $X^2$ s between plants and any conclusions must be deferred until a thorough sampling is made. This finding does not invalidate the experiment but it does complicate it. It may be necessary to extract inbred lines from the exotic sources before any critical work can be done.

Table 1 presents data on the backcross progeny ratios of trisome 3 plants containing exotic material from twelve different strains. Eight of them exhibited preferential pairing. In the case of Argentine popcorn the percentage of A gametes was significantly higher than 1/3. No explanation can be offered at the present time. The interaction  $X^2$ 's were significant in seven cases.

TABLE 1

Gene Segregation of Trisome 3 Plants used as the Pollen Parent

Source of A Chromosome	No. of plants	No. of gametes	% A	$X^2$ (2a : 1A)	Inter. $X^2$ between pls.
Standard	8	13,984	32.75	2.11	2.31
Argentine popcorn	11	17,005	35.10	23.97**	28.31**
Gaspe flint	5	9,368	33.63	.34	22.09**
Nmura	2	2,001	33.58	.06	.08
Tepite	2	1,439	32.66	.32	.77
Maiz chapolote	6	9,583	31.25	18.58**	75.56**
Reventador	6	5,815	30.47	21.31**	10.49
Grande	4	2,737	30.14	12.45**	11.34**
Jala	4	3,455	30.13	16.04**	2.57
Papago flour	14	10,620	29.82	58.95**	19.28
Gourdseed	9	10,496	29.23	79.26**	39.22**
Zapaluta chica	12	16,824	27.18	290.10**	40.74**
Avati tupi	3	5,321	24.78	175.02**	14.58**

\*\*significant at .01 level

## 2. Preferential pairing in trisomic inversion heterozygotes.

Stocks of tetraploids and trisomes which are heterozygous for many different inversions are being synthesized and tested.

Preliminary data have been collected for a series of trisomes 3 which are heterozygous for one of five different inversions and will be presented here.

TABLE 2

Gene Segregation of Five Different Trisomic 3 Inversion Heterozygotes used as the Pollen Parent

Inversion	Breakage Points	No. of Plants	No. of Gametes	% $\underline{A}$	Interaction $X^2$ between plants
In 3a	3L.40-L.95	13	7543	22.0	11.98
In 3b	3L.25-L.75	5	2917	19.4	1.45
In 3c	3L.09-L.90+	3	2507	12.6	22.09**
In 3d	3S.72-L.42	3	5526	26.8	1.53
In 3h	3L.19-L.72	4	7532	14.4	27.28**

Additional data must be obtained before any conclusions or conjectures can be stated. It is apparent that different inversions give markedly different results.

G. G. Doyle

## 3. Preferential pairing in trisome 3 plants containing irradiated In 3a chromosomes.

In an attempt to produce and isolate chromosomes 3 with more than one inversion, pollen from homozygous In 3a plants was given 1000r and was placed on the silks of standard trisome 3 plants.

Forty-one of the trisome plants from this cross were backcrossed as the male to an  $a_1$  tester. The In 3a chromosome carried  $\underline{A}_1$ . The results are given in the table below.

TABLE 3

The Transmission Frequencies of Irradiated In 3a Chromosomes  
in Trisomic Pollen Parents

Plant no.	No. of gametes tested	% A	Plant no.	No. of gametes tested	% A	Plant no.	No. of gametes tested	% A
1	1027	25.2*	15	589	18.5*	28	2215	14.4**
2	1125	24.4	16	1279	18.1**	29	1546	14.3**
3	1370	24.2	17	2033	17.8**	30	1028	14.2**
4	1127	22.4	18	1547	17.6**	31	1256	13.9**
5	708	22.0	19	1101	17.5**	32	815	13.9**
6	1878	21.7	20	1515	17.4**	33	1579	13.5**
7	1435	21.4	21	1557	17.2**	34	1735	12.6**
8	2261	21.1	22	2052	17.2**	35	1516	11.7**
9	619	20.0	23	812	16.5**	36	1291	11.5**
10	1478	19.2**	24	619	16.5**	37	1799	10.2**
11	793	19.2	25	1653	15.9**	38	1663	10.0**
12	1375	19.0**	26	1163	15.8**	39	2199	8.8**
13	1635	18.9**	27	1003	15.6**	40	500	1.8**
14	364	18.7				41	1489	1.1**

\* significant at the .05 level

\*\*significant at the .01 level

Thirty or 73% of the forty-one plants tested had a percentage of A gametes which was significantly lower than 22%, the percentage found when unirradiated In 3a chromosomes are used. In these thirty cases it is believed that the In 3a chromosome has been structurally changed. There are four possibilities: an additional inversion large enough to be cytologically detectable, a translocation involving chromosome 3, small inversions, and deletions. The nature of these structural changes will be determined this summer. It is probable that a large number of the cases involve deletions in which case the A gene must crossover onto a normal chromosome if it is to be transmitted. Because of the presence of the inversion and of the incomplete pairing in a trisome this is rendered difficult.

In any event it appears that chromosomes are more liable to structural changes than is commonly believed. Preferential pairing has never been used before to detect induced structural changes.

Pollen from normal 2n plants (i.e. with all standard chromosomes) will be irradiated this spring and used in the greenhouse on standard trisomes. Here we can expect deviations from 33.3% in the transmission of the A gene. If stable transmissible structural changes are frequently induced then this provides a method for synthesizing a modified genome for use in a synthetic allotetraploid strain.

#### 4. The synthesis of artificial allotetraploid corn strains.

In the last issue of the News Letter three methods were presented which could be used in the synthesis of an allotetraploid corn. To produce this artificial strain of corn, a corn genome must be modified by chromosomal structural changes so that it loses most of its pairing affinity with the standard corn genome. It is possible theoretically to do this by:

a. Combining many separately induced inversions on the same chromosome by crossing over.

b. Producing chromosomes with many inversions by the repeated irradiation of chromosomes which have inversions to start with. These chromosomes could be isolated by their enhancement of the effect of preferential pairing.

c. Creating structurally modified chromosomes by the isolation and recombination of structural rearrangements already present in the species (notably in exotic lines).

It is now believed that serious technical difficulties limit the feasibility of using any of these methods for the production of agronomically successful allotetraploids. These three methods in addition to being very tedious virtually make it necessary to work on the chromosomes individually. After each of the ten chromosomes has been modified, they would have to be put together and made homozygous. In the process, which would require many growing seasons, it would be difficult to keep the modified chromosomes intact.

Furthermore, the use of these methods makes it almost impossible to obtain more than a few different modified genomes because of the labor involved. Any variability for adaptive purposes would have to come from the standard corn genome used with them in the allotetraploid. Also, the quality of the genetic material cannot be controlled very easily. In the case of method c it is highly probable that agronomically poor genes would be picked up along with the structural rearrangements. When inversions are used as in methods a and b the inversion must be induced in agronomically good material to start with, since an inversion virtually blocks the exchange of genetic material within it. Back-crossing would not be successful.

However, there seems to be a practical method for the synthesis of a large number of different artificial allotetraploids. This method is suggested by the data reported in the preceding section. The procedure is to irradiate a wide variety of inbred lines for several generations. Selection would be practiced to eliminate gross chromosomal structural changes and deleterious mutations. At intervals these inbred lines would be crossed with each other or with unirradiated inbred lines and the hybrid would be doubled to form a tetraploid. The gene segregation patterns, quadrivalent frequencies, and the fertility of these tetraploids would be determined. How rapid the approach to allotetraploidy would be is undeterminable at this time. This is somewhat of a blind



approach to the problem, as it would not be possible to analyze what has happened to the structure of the chromosomes after several generations of repeated irradiation.

G. G. Doyle

5. The duplication of specific chromosome segments by crossing translocations involving the same chromosomes.

The  $F_2$  and in some cases the  $F_3$  generations of translocation crosses for the duplication of the su<sub>1</sub>, ae, y and wx loci have been obtained. It is highly probable that all of these loci have been duplicated. Considerable work remains to be done to isolate plants which are homozygous for the duplication and to prove that the selected loci are included in the duplicated segment.

One of the questions to be answered is - how functional are the pollen grains which contain duplications in competition with normal pollen? If they cannot compete successfully then we could not get a homozygous duplication. However, it has been determined that the duplication pollen is functional in a few cases where one of the parental translocations carried the recessive gene and the other parental translocation carried the dominant allele. In the  $F_2$  generation the frequency of recessives should be  $1/6$  if the duplication pollen is not functional. In the case of the translocation cross of 9S.68-4L.03/9S.25-4L.33, the frequency of wx kernels was 15.27% which is significantly lower than 16.66%. If we let  $x$  equal the frequency of duplication pollen transmission and let  $r$  equal the frequency of recessive gametes then we can set up the formula:

$$r = 1/6 - 1/6x$$

$$\text{or, } x = 1 - 6r$$

In this example  $x$  equals 8.38%. This formula may be derived by a consideration of the diagram below. It is assumed that the deficient gametes are non-functional on both the male and female sides. It is assumed that the three kinds of gametes, the two parental translocations and the duplication type, function with equal frequency in the female.

♀ \ ♂	1/2(1-x)	1/2(1-x)	x	0
	Wxc 4 <sup>9</sup> a 9 <sup>4</sup> a	Wxc 4 <sup>9</sup> b 9 <sup>4</sup> b	Wxc Wxc 4 <sup>9</sup> a 9 <sup>4</sup> b	4 <sup>9</sup> b 9 <sup>4</sup> a
1/3 Wxc 4 <sup>9</sup> a 9 <sup>4</sup> a	Wxc	Wxc	Wxc	--
1/3 4 <sup>9</sup> b Wxc 9 <sup>4</sup> b	Wxc	Wxc	Wxc	--
1/3 Wxc 4 <sup>9</sup> a Wxc 9 <sup>4</sup> b	Wxc	Wxc	Wxc	--
0 4 <sup>9</sup> b 9 <sup>4</sup> a	--	--	--	--

G. G. Doyle

6. New sources of ae.

Two new sources of ae have been found in an exotic strain Bolivia 561, NRC No. 9815 and a South African open-pollinated variety, Potchefstroom Pearl, PI 221825.

M. S. Zuber

7. Mutants recovered in the selfed progeny of chemically and x-ray treated seeds.

In an earlier experiment (MNL 36, p. 57, 1962) Yg<sub>2</sub> yg<sub>2</sub> and Wd wd seeds were treated with ethyl methanesulfonate (EMS) and diethyl sulfate (DES). The frequent yellow-green and albino sectors on the leaves of the treated plants were regarded as phenotypic expressions of the mutation or loss of the dominant genes.

The purpose of the experiment reported here was to induce mutations in homozygous multiple dominant embryos using 5-bromouracil (5-BU) and maleic hydrazide (MH) in addition to the previously tested EMS and DES, and x-rays as a standard, to isolate the mutants through selfing, and subsequently to study the type and behavior of the mutants induced, thereby characterizing the genetic effects of the mutagens used.

Homozygous multiple dominant seeds were soaked with frequent stirring in the dilute solutions of chemicals (columns 1 and 2 in Table) for 8 hours at 25°C, and were rinsed before planting. For comparison a group of dry seeds were x-rayed with 10000 r. Only the EMS, DES and x-ray treated material showed moderate retardation of growth. In the EMS material frequent yellow-green and rare albino sectors, and in the x-rayed  $M_1$  plants a few yellow-green sectors, occurred.

The treated plants were selfed (column 3 in Table) and approximately 1/3 of the seeds were planted. The emerging seedlings and the resulting  $M_2$  plants were all normal in phenotype. However, some of the EMS and x-ray treated  $M_2$  plants had approximately 50% normal and 50% empty pollen (column 4 in Table). The  $M_2$  plants were selfed and after harvest the ears were examined for segregating endosperm mutants and for seedling mutants in the sand bench. All the endosperm and seedling mutants were recovered from one or more segregating ears with 3 normal : 1 mutant ratios, (columns 5 and 6 in Table). Two ears showed exceptional ratios. The segregating ear from the 5-BU treatment segregated 29 green : 42 albino : 4 green with albino sectors. One of the 3 segregating ears from the MH treatment yielded 5 green : 23 albino : 5 green with albino sectors. The green seedlings with albino sectors are not necessarily due to the treatments since such seedlings occurred in the  $M_2$  control and in the progeny of x-rays, DES, EMS treated plants also (column 7 in Table). Allelic and linkage studies are in progress to identify and place the recovered mutants.

In the progeny of one EMS-treated plant 9 of 26 plants showed pollen abnormality. 13 ears of the same 26 plants also segregated for pr. Six such segregating ears were from plants with abnormal pollen, but this frequency of correspondence is expected by chance alone. In the progeny of the other EMS-treated plant, and in one x-ray treated plant, no mutations were detected, although they showed pollen abnormalities indicating gross chromosome aberrations.

The experiment indicates the following: (1) Changes induced by EMS are either gross chromosome aberrations not transmitted through the male gametophyte (inferred from pollen abnormality) or less drastic chromosomal changes which have been transmitted through the pollen at least once and were recovered in the homozygous condition. It is indeed remarkable that in the progeny of 6 EMS-treated plants 8 different mutants occurred, while with x-rays only 2 different mutants

were recovered in the progeny of 9 treated plants. (2) DES in this experiment induced no pollen abnormalities and was at least as effective a mutagen as x-rays at optimum dose. (3) MH and 5-BU perhaps both induced mutations which at present are suspected to be -- as one possible interpretation -- dominant.

The effect of chemical and x-ray treatments  
on homozygous multiple dominant seeds.

1	2	3	4	5	6	7
Treat- ment	Conc. M/l or dose (r)	No. of M <sub>1</sub> selfed plants	No. of M <sub>2</sub> plants with abnormal pollen	No. of segre- gating M <sub>2</sub> ears	No. and type of different mutants recovered	Fr. of green seedlings with albino sectors per 10 <sup>4</sup> seedlings
DES	0.05	4	0/65	10/60	2 r, weak yellow green	41
EMS	0.075	6	11/155	42/138	8 *	3
5-BU	0.10	4	0/70	1/68	1 albino	7
MH	0.05	9	0/112	3/103	1 albino	32
x-rays	10000	9	6/74	2/78	2 albino	21
control		5	0/62	0/64	0	8

\* pr, su, gl, a or c, dilute with abnormal endosperm and inviable embryo, dilute with normal endosperm and inviable embryo, 2 different weak yellow-greens.

G. Ficsor

8. Analysis of fertilization in diploid x tetraploid crosses.

The different possibilities of abnormality in corn fertilization are being investigated in marked crosses of diploid x tetraploid. Diploid females heterozygous for one gene in each of the ten chromosomes (bm<sub>2</sub>, lg, a, su, pr, y, gl, j, wx, and g) were crossed by pr-tetraploid and Synthetic-B tetraploid males. The majority of seeds obtained were shrivelled and the germination was very poor. Seeds from 51 crossed ears were classified for size and endosperm markers and planted. Almost all of the shrivelled seeds failed to germinate. However, a good-sized population was obtained from the rest. 83 plants were tested by selfing and crossing to a multiple tester line.



No haploid plants appeared in the progeny, as judged by morphological traits, sterility and guard cell measurements. There were also no tetraploids. As expected, about 70% of the plants were either triploids or multiple trisomics, identified by high sterility, specific morphological properties, and characteristic ratios. The rest were diploids.

The mode of origin of diploids from such crosses can be traced by distribution of markers. Maternal diploids coming from unreduced eggs should be heterozygous at all the loci, whereas paternal diploids should be homozygous dominant at all loci. Diploids originating from fertilization of a normal egg by haploid pollen from tetraploid male should have at least one dominant at each locus. Doubling of reduced egg or fusion of any two haploid nuclei in the embryo-sac without fertilization should result in plants homozygous at all loci. Plants arising from megaspore fusion without male contribution could also be detected by statistical distribution of markers. Diploids originated from either self- or outside contamination could easily be categorized by following through the distribution of different markers. Progeny tests revealed that the diploid exceptions in this experiment came only from contaminations and none of the other possibilities mentioned above could be realized. Also, no case of noncorrespondence between endosperm and embryo was noticed.

From this investigation it appears that the occurrence of haploids, diploids and tetraploids from diploid x tetraploid crosses is infrequent. Studies are being continued, employing a larger population and the reciprocal cross using diploids as the male.

E. H. Coe, Jr.  
K. R. Sarkar

#### 9. Symbol index to the Newsletters.

Copies of the Symbol Index to volumes 12 through 35, prepared as an Appendix to volume 36, are available and will be sent on request (Curtis Hall, University of Missouri, Columbia, Missouri). Notes on errors will be appreciated. One error that has been found may be indicative of others, though an attempt was made to avoid these: On page 42 under ws, 32:80 and 34:88 belong under ws<sub>3</sub>.

E. H. Coe, Jr.

#### 10. Mutable glossy-1.

A mutable glossy allelic to gl<sub>1</sub> (designated gl<sup>m</sup>) has been found in an Ac-carrying line. Expression is excellent in sheaths of older plants; seedlings do not show clear sectors. As far as I am aware no mutability for the glossy character has been reported previously. Seed is available.

E. H. Coe, Jr.

11. Comparisons among plants with various constitutions for B, B', and b.

Advanced progenies on uniform backgrounds were available this year for a test of dosage, timing, and reciprocal effects in crosses of  $\underline{B'} \times \underline{B'}$ ,  $\underline{B'} \times \underline{b}$ ,  $\underline{B'} \times \underline{B}$ ,  $\underline{B} \times \underline{B'}$ ,  $\underline{b} \times \underline{B}$ , and  $\underline{B} \times \underline{B}$ . Respectively, 7, 4, 7, 4, 2, and 1 entries in three 15-seed replicates were coded and randomized, and planted in a linear, serpentine pattern. Plants were graded shortly after flowering, cobs indoors after harvesting, drying, and shelling.

Genotype egg/pollen	Plant Color Grade									Plants no.	Average Grade	
	0	1	2	3	4	5	6	7	8			9
$\underline{B'}/\underline{B'}$		30	153	31							215	2.00
$\underline{B'}/\underline{b}$		59	92	5							156	1.65
$\underline{B'}/\underline{B}$			14	174	71	5					262	3.26
$\underline{B}/\underline{B'}$			5	29	19	2					55	3.33
$\underline{b}/\underline{B}$							1	20	51		72	7.69
$\underline{B}/\underline{B}$							4	4	9	6	23	7.74

Genotype	Cob Color Grade					Plants no.	Average Grade			
	0	1	2	3	4					
$\underline{B'}/\underline{B'}$	56	98	26	15	3	198	1.05			
$\underline{B'}/\underline{b}$	13	115	15	3		146	1.05			
$\underline{B'}/\underline{B}$	8	101	83	63		255	1.79			
$\underline{B}/\underline{B'}$	3	21	13	16		53	1.79			
$\underline{b}/\underline{B}$						43	20	4	67	6.42
$\underline{B}/\underline{B}$							1	10	11	7.91

Since  $\underline{B'}/\underline{B}$  and  $\underline{B}/\underline{B'}$  do not differ, no reciprocal difference in transmission of the phenomenon exists; since  $\underline{B'}/\underline{B}$  and  $\underline{B}/\underline{B'}$  plants are darker than  $\underline{B'}/\underline{B'}$  and  $\underline{B'}/\underline{b}$ , the change from  $\underline{B}$  to  $\underline{B'}$  must not be completed immediately. These data are very difficult to harmonize with a plasmid model.

E. H. Coe, Jr.

12. Somatic mutation to B'.

Several sectored plants were observed last summer in  $\underline{B}$  lines derived from unstable sources. Progeny tests confirm mutation to  $\underline{B'}$  during development. The previously-published conclusion that mutation to  $\underline{B'}$  is meiotic is in error.

E. H. Coe, Jr.

UNIVERSITY OF NEBRASKA  
Lincoln, Nebraska  
Department of Agronomy

1. Development of trisomic stocks in maize.

Seventeen second generation progenies of colchicine-treated plants of the line CC5 were grown in the field in 1962. Pollen samples were taken from all the plants and microsporocyte samples in many cases. Preliminary cytological observations on 25 plants indicated that four were trisomic and seven were heterozygous for a translocation.

Other material included  $14_1$  progenies derived from ears, found in Dr. J. H. Lonquist's breeding material, which segregated for seeds of different sizes. Five progenies segregated for the trisomic condition. Chromosome 10 was involved in two cases; chromosomes 2, 4 and 5 were tentatively identified in the other cases.

Rosalind Morris  
Mustafa H. Isikan

2. Cytological study on maize inbred lines.

Seven inbred lines (N6, L289, N75, K41, SA24, M14 and KYS), which had been maintained by self pollination for from eight to  $14_1$  generations, were found to have an unusually high frequency of ears with sterility or defective seeds in 1961. Progenies from these abnormal ears and also from normal ears of each line were grown in 1962. One-fifth of the plants in progenies from normal ears and one-third of the plants in progenies from abnormal ears segregated for abnormal pollen. Observations on individual anthers of all plants in an L289 progeny gave wide variations in amounts of abnormal pollen among anthers of the same plant. The frequencies of ears with sterility or defective seeds were similar in progenies from normal and abnormal ears. Meiotic observations on 30 plants in progenies from abnormal ears showed no deviations in chromosome number and no definite structural changes. The early separation of members of one or more bivalents at diakinesis and metaphase I was observed in 18 out of the 30 plants and in all except one of the lines. Lagging univalents were observed at later stages of meiosis and micro-nuclei occurred in a small percentage of the quartets (See Table 1).

It is possible that pairing irregularities contributed to the ear abnormalities assuming that the same type of behavior occurred in the megasporocyte.

Table 1. Frequencies of cells with univalents at various stages of meiosis in five plants representing different inbred lines.

Inbred line and plant no.	% cells/univalents		% cells/lagging univalents		% quartets with micro-nuclei
	Diakinesis	Metaphase I	Anaphase - Telophase I	Anaphase - Telophase II	
L289-5	1.5 (400) <sup>1/</sup>	12.8 (117)	6.1 (82)	5.0 (317)	5.5 (201) <sup>2/</sup>
K41-3	19.0 (100)	33.7 (89)	17.5 (114)	7.3 (246)	5.1 (217)
SA24-3	10.9 (46)	24.2 (251)	4.0 (50)	10.1 (128)	4.1 (295)
ML4-2	22.2 (99)	4.7 (107)	2.0 (150)	6.1 (147)	4.5 (133)
KYS-2	2.6 (76)	23.6 (351)	12.5 (88)	8.4 (155)	10.7 (93)

<sup>1/</sup> Number of cells observed.

<sup>2/</sup> Number of quartets observed.

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### 3. Location and phenotypic expression of Hs (Hairy sheath).

Previous studies have placed Hs in chromosome 7, with recombination values of 32% between Hs and ra, 43% between Hs and gl<sub>1</sub> (Der Zuchter 3: 333-338. 1931). An Hs stock was crossed with T6-7S.73 also carrying gl<sub>1</sub>, and the F<sub>1</sub> Hs semisterile plants were testcrossed to gl<sub>1</sub>. From 71 testcross progeny plants classified in 1962, recombination values were obtained as follows: 50.7% for T to Hs, 49.3% for G1 to Hs and 4.2% for T to gl. These data would place Hs in the distal part of the long arm of chromosome 7.

The segregation of the three characters in the testcross progenies (Hs vs. normal, G1 vs. gl and T vs. normal) gave a good fit to a 1:1 ratio in each case although close to the borderline (.10 > P > .05). It was noticed that the expression of Hs in the F<sub>1</sub> plants was clear although not as pronounced as in the Hs stock. However, the expression of Hs in the testcross progenies was less distinct than in the F<sub>1</sub>. Often careful examination of various parts of the stem, leaf sheaths, and tassel stalks had to be made to decide if extra hairs were present.



Earlier work with Hs in crosses with four inbred lines (N6, L289, K41 and N75) had shown that the expression of Hairy sheath was intermediate in the  $F_1$  and became difficult to classify in the first back-cross progenies or in their selfed progenies. The Hs stock, grown at the same time as these various crosses, gave consistently good expression. Thus, it would appear that the expression of Hairy sheath is modified considerably by different genetic backgrounds. For this reason its effectiveness as a gene marker is reduced.

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1. Pa W 703 and W 703.

As the colorless pericarp yellow endosperm version of Q 703 (or W 703) has proven commercially useful in early (A.E.S. 100 to 300) hybrids, it has been of interest to speculate on the differences between the original and subline. Q 703 has red pericarp, white cob, and fairly strong stalks; Pa W 703 has colorless pericarp, red cob, and stalks that tend to dissolve after physiological maturity. The  $F_1$  hybrid has little or no hybrid vigor.

An attempt was made to collect data on an  $F_2$  population of W 703 x Pa W 703 in 1962. Weather conditions were not conducive to stalk rot, so that data were available only on pericarp and cob color.

Red Pericarp--Red Cob	196
Red Pericarp--White Cob	99
Colorless Pericarp--Red Cob	100
Colorless Pericarp--White Cob	6
Red Pericarp	295
Colorless Pericarp	106
Red Cob	296
White Cob	105
$X^2$ Pericarp Color (3:1)	.440
$X^2$ Cob Color (3:1)	.300
$X^2$ Pericarp and Cob Color (9:3:3:1)	34.107
$X^2$ Linkage	33.367
Linkage = $20.91 \pm 2.33\%$	
$X^2$ Fit with linkage	1.270

It thus seems probable that two linked genes are involved in differences between these sublimes as was suggested by Braun (N.L. 37, p. 50). Nevertheless, it is difficult to envisage a major change or chance outcross when very little or no heterosis between sublimes is manifested.

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1. Cyclic hydroxamate content of maize seedlings.

Segregation for the presence or absence of a cyclic hydroxamate or its 2-glucoside in maize seedlings has been reported previously (MNL 36: 71-72). The inheritance pattern of this character is being investigated using the waxy translocation stocks of Dr. Anderson.

In an attempt to find other sources of segregating material, at least 12 seedlings each of 1813 corn plant introductions of the U.S.D.A. collection have been scored visually. The test employed crushing the mesocotyl of 6-day-old dark-grown seedlings in an aqueous 0.1 M  $\text{FeCl}_3$  solution; presence of the cyclic hydroxamate was indicated by a blue color reaction. Qualitative ratings given to individual seedlings were: 0, no blue color observed; 1, slight blue color; 2, moderate blue color; 3, intense blue color reaction. The following data were obtained:

Visual Rating	Plant Introductions Scored
0 - 1	4
0 - 2	13
0 - 3	13
1	1
1 - 2	206
1 - 3	274
2	290
2 - 3	679
3	333

The low, high and possibly segregating lines have been selected for quantitative determinations and genetic analysis.

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1. Genetic control of carbohydrate type and quantity in maize kernels.

Culpepper and Magoon (1924, J. Agr. Res. 28:403-413), in a test of sweet corn (su<sub>1</sub>) and dent corn (Su<sub>1</sub>) varieties at 5-day intervals beginning at 5 days after pollination and ending at 30 days, observed that: (1) dry matter increased in both types with age; (2) total sugar increased up to the 15th day, followed by a decrease (sweet corn had about twice as much sugar as dent); (3) reducing sugars showed larger increases in su<sub>1</sub> than in Su<sub>1</sub> genotypes; (4) sucrose increased to the 15th day, followed by a decrease (su<sub>1</sub> had about twice as much sucrose as Su<sub>1</sub>); (5) water-soluble polysaccharides (WSP) increased rapidly in su<sub>1</sub> but remained very low in Su<sub>1</sub> (at 30 days su<sub>1</sub> had about 10 times as much WSP as dent); and (6) starch increased rapidly in both types, Su<sub>1</sub> having more starch than su<sub>1</sub>.

During recent years several other genes have been shown to alter carbohydrate type and quantity at maturity or during kernel development. The gene wx (Andrew et al, 1944 J. Agr. Res. 69:355-371) increases sugars and WSP on a percentage basis in a su<sub>1</sub> background and alone. The effects of bt<sub>1</sub> and bt<sub>2</sub> were reported by Cameron and Teas (1954, Amer. Journ. Bot. 41:50-55). Each brittle gene increased sugar and reduced starch content at mid-development and beyond. No increase in WSP was observed. Laughnan (1953, Genetics 38:485-499) reported similar effects at kernel maturity for the gene sh<sub>2</sub>. Su<sub>1</sub> sh<sub>2</sub> kernels contained a high percentage of sucrose and less starch than su<sub>1</sub>, but had very little WSP. The double recessive su<sub>1</sub> sh<sub>2</sub> had even higher sugar and less starch than su<sub>1</sub>. The WSP content was about the same as sh<sub>2</sub> alone (about 2%).

Mangelsdorf (1947, Genetics 32:448-458) and Cameron (1947, Genetics 32:80-81) reported that in mature kernels the gene du, when homozygous with su<sub>1</sub>, produced less starch, more WSP, and perhaps more sugars than su<sub>1</sub> alone. Horovitz et al (1941, Annal. Inst. Fitotec. Sta. Catalina 3:37-44) reported that su<sub>2</sub> su<sub>1</sub> produced about 14% sugar in mature kernels in contrast to about 5% for su<sub>1</sub> alone. Additional data by Dvonch et al (1951, Cereal Chem. 28:270-280) and Dunn et al (1953, Agron. Jour. 45:101-104) indicate that in mature kernels starch is lower and WSP is sometimes higher in su<sub>1</sub> du and su<sub>1</sub> su<sub>2</sub> than in su<sub>1</sub>.

The genes ae, su<sub>2</sub>, and du have been reported to alter the proportion of the two starch fractions, amylose and amylopectin (Kramer et al, 1949, Agron. Jour. 41:409-411, 1958, Agron. Jour. 50:207-210; Vineyard and Bear, 1952, Maize Genetics Coop. News Letter 26:5; Zuber et al, 1958 Agron. Jour. 50:9-12; and others). Amylose is a straight

chain molecule having 200-300 glucose units and stains blue with iodine. Amylopectin, which has a higher molecular weight than amylose, consists of branched chains with about 25 glucose units in each branch and stains red with iodine. Weatherwax (1922, *Genetics* 7:568-572) was the first to show that waxy (wx) corn starch stained red with iodine. Sprague et al (1943, *Agron. Jour.* 55:817-822) showed that the standard waxy endosperm contains no amylose but all amylopectin starch.

According to Zimmerman (1960, *Ann. Rev. Plant Physiol.* 11:167) and Porter (1962, *Ann. Rev. Plant Physiol.* 13:303-328) the main transport material in higher plants is sucrose, the first free sugar after photosynthesis. There is evidence that sucrose is the main glucose donor in the formation of polysaccharides which may become increasingly larger until starch is formed. It is thought by some that amylopectin is formed by the rearrangement of preformed amylose chains (Porter, 1962; Whistler and Young, 1960, *Cereal Chem.* 37:204). However, Erlander (1961, *Cereal Chem.* 37:81) claims that amylose arises from debranching of amylopectin and that the absence of amylose in waxy starch can be accounted for by the absence of the debranching enzyme. There seems to be insufficient evidence to conclude that either amylose or amylopectin is formed first (Porter, 1962).

Research at The Pennsylvania State University with genetic mutants affecting the properties of maize endosperm is being carried out with the following objectives in mind: (1) to determine the effects of specific genes and gene combinations on carbohydrate type and quantity at varying endosperm maturities; (2) to elucidate the pathway (or pathways) of carbohydrate synthesis and the "gene-enzyme" or "gene-enzyme component" relationships; and (3) the application of this knowledge, where feasible, in improving the quality of sweet corn or in the breeding of types for particular industrial purposes.

In 1961 thirty genetic lines were obtained from Dr. H. H. Kramer. The genotypes of these lines are shown in Table 1. They are single, double and triple recessives of *ae*, *du*, *sh<sub>2</sub>*, *su<sub>1</sub>*, *su<sub>2</sub>*, and *wx*. All these mutants were studied in a background related to the single cross, W23/L317, except Golden Cross Bantam sweet corn (*su<sub>1</sub>*). The backgrounds are not isogenic; therefore, possible background effects must be kept in mind. These lines were grown in a replicated trial in 1961 and fresh kernels samples of 50 grams were taken from 2 - 3 ears at 16, 20, 24, and 28 days after pollination and stored in 95% ethanol within 2 hours after removal from the plant.

Dry matter content was determined by weight of the alcohol insolubles plus the alcohol solubles. Chemical analyses were made for reducing sugars, sucrose (after Hassid, 1936, *Ind. and Eng. Chem.* 8: 138-140), water-soluble polysaccharides (after Cameron, 1959, *Agron. Jour.* 51:424-427), and starch (after Hixon, 1944, *Iowa A.E.S. Report*, Part II). Total carbohydrate content was calculated by summing the weights of the individual carbohydrates analyzed.



Very significant differences were noted for all carbohydrate and dry matter analyses between genotypes at all kernel maturities. Very significant differences were observed between maturities within genotypes for all characteristics measured. These data are presented in Table 1.

Dry Matter content. The dry matter content of normal increased from 15.7% at 16 days to 43.8% at 28 days after pollination. All the recessive genotypes, with the exception of su<sub>2</sub> and su<sub>2</sub> wx, tended to be significantly less than normal. The genotypes that were exceptionally low in dry matter were sh<sub>2</sub>, ae wx, du sh<sub>2</sub>, sh<sub>2</sub> su<sub>1</sub>, ae du su<sub>1</sub>, ae du wx, ae su<sub>1</sub> wx, and ae su<sub>2</sub> wx. The other genotypes were intermediate between these and normal. It is important to keep these dry matter differences between genotypes in mind when comparing the quantities of particular carbohydrates reported here as percentages of dry matter. Actual weights and percentages of fresh weights have been omitted here in interest of space.

Reducing sugars. The reducing sugars content of normal decreased from 9.4% at 16 days to 0.8% at 28 days after pollination. All other genotypes possessed approximately the same amount of reducing sugars as normal except sh<sub>2</sub>, su<sub>1</sub>, ae wx, du wx, sh<sub>2</sub> su<sub>1</sub>, ae du su<sub>1</sub>, ae du su<sub>2</sub>, and ae du wx. These appeared to be higher in reducing sugars than normal. Of these, sh<sub>2</sub> su<sub>1</sub>, ae du su<sub>1</sub>, and ae du su<sub>2</sub> appeared exceptionally high, especially at later kernel development.

Sucrose. Sucrose content in normal decreased from 8.2% at 16 days to 2.2% at 28 days after pollination. The genotypes sh<sub>2</sub>, du sh<sub>2</sub>, sh<sub>2</sub> su<sub>1</sub>, and ae du wx were exceptionally high in sucrose (7-10 times more than normal) at almost all kernel ages. The genotypes ae, du, su<sub>1</sub>, ae du, ae su<sub>1</sub>, ae su<sub>2</sub>, du su<sub>2</sub>, du wx, sh<sub>2</sub> su<sub>2</sub>, su<sub>1</sub> wx, ae su<sub>1</sub> su<sub>2</sub>, du su<sub>1</sub> wx, and du su<sub>2</sub> wx had 2 - 4 times as much as normal. The genotypes ae wx, su<sub>1</sub> su<sub>2</sub>, ae du su<sub>1</sub>, ae du su<sub>2</sub>, ae su<sub>1</sub> wx, ae su<sub>2</sub> wx, and su<sub>1</sub> su<sub>2</sub> wx had 5-6 times as much sucrose as normal. The gene su<sub>2</sub> appears to be epistatic over sh<sub>2</sub> and sh<sub>2</sub> seems to be partially epistatic over du and su<sub>1</sub>.

Water-soluble polysaccharides. The WSP content of normal appeared to decrease slightly from 3.7% at 16 days to 2.2% at 28 days. The decrease was not significant. Apparently, WSP was not accumulating with kernel development. A slight, but insignificant, increase over normal was noted for ae, sh<sub>2</sub>, ae du, ae wx, du sh<sub>2</sub>, du su<sub>2</sub>, du wx, sh<sub>2</sub> su<sub>1</sub>, ae du su<sub>2</sub>, ae du wx, ae su<sub>1</sub> wx, and ae su<sub>2</sub> wx. Significant increases over normal were noted for su<sub>1</sub>, du su<sub>1</sub>, sh<sub>2</sub> su<sub>2</sub>, su<sub>1</sub> su<sub>2</sub>, su<sub>1</sub> wx, ae du su<sub>1</sub>, ae su<sub>1</sub> su<sub>2</sub>, du su<sub>1</sub> su<sub>2</sub>, du su<sub>1</sub> wx, du su<sub>2</sub> wx, and su<sub>1</sub> su<sub>2</sub> wx. The gene su<sub>1</sub> is associated with a dramatic increase in WSP at all 4

stages of kernel development. The gene ae apparently is epistatic or partially epistatic over su<sub>1</sub>. The genes du and su<sub>2</sub> appear to intensify the accumulation of WSP in combination with the other genes.

Starch. The starch content in normal increased from 39.2% at 16 days to 73.4% at 28 days after pollination. Extreme starch reduction (approximately one-half or less of normal) was associated with the genotypes sh<sub>2</sub>, su<sub>1</sub>, ae su<sub>1</sub>, du su<sub>1</sub>, du sh<sub>2</sub>, sh<sub>2 su<sub>1</sub>, sh<sub>2 su<sub>2</sub>, su<sub>1 su<sub>2</sub>, su<sub>1 wx</sub>, ae du wx</sub>, du su<sub>1 su<sub>2</sub>, du su<sub>1 wx</sub>, and su<sub>1 su<sub>2 wx</sub>.</sub></sub></sub></sub>

Total sugar and total carbohydrates are also shown in Table 1. Total sugar content is the sum of the reducing sugars and sucrose contents. Total carbohydrates content is the sum of the contents of all the carbohydrates analysed. There seems to be a decrease in total sugar with kernel development in most instances. An increase in total carbohydrates with kernel development is indicated in all cases except those that are medium to high in sugar and low in WSP and starch.

Table 1. The quantities of various carbohydrates<sup>1/</sup> and total dry matter<sup>2/</sup> in entire kernels of thirty-one maize genotypes at four stages of maturity.<sup>3/</sup>

Code no.	Geno-type	Kernel age (days)	Reducing sugars %	Sucrose %	Total sugar %	WSP* %	Starch %	Total carbohydrates** %	Dry matter %
1	normal	16	9.4	8.2	17.6	3.7	39.2	60.5	15.7
		20	2.4	3.5	5.9	2.8	66.2	74.9	27.1
		24	1.6	2.6	4.8	2.8	69.2	76.1	37.2
		28	0.8	2.2	3.0	2.2	73.4	78.6	43.8
2	ae	16	8.6	21.9	30.6	5.7	20.8	57.2	18.4
		20	4.8	13.9	18.7	4.2	37.6	60.5	26.0
		24	3.1	8.3	11.4	3.7	48.9	64.0	34.0
		28	1.9	7.4	9.4	4.4	49.3	62.9	37.5
3	du	16	8.8	15.5	24.2	4.1	25.1	53.4	16.2
		20	4.8	10.5	15.3	2.7	44.6	62.6	25.6
		24	2.8	6.1	9.0	2.4	56.5	67.9	33.5
		28	1.3	6.7	8.0	1.9	59.9	69.8	38.9
4	sh <sub>2</sub>	16	6.9	21.4	28.3	5.6	22.3	56.1	16.8
		20	4.9	29.9	34.8	4.4	18.4	57.6	20.3
		24	4.4	24.9	29.4	2.4	19.6	51.4	22.9
		28	3.6	22.1	25.7	5.1	21.9	52.8	26.3

<sup>1/</sup>Percent of dry matter

<sup>2/</sup>Percent of fresh weight

<sup>3/</sup> Three replications

\*WSP = water-soluble polysaccharides

\*\*Sum of weights of reducing sugar, sucrose, WSP, and starch/dry matter weight.

Code no.	Geno-type	Kernel age (days)	Reducing sugars %	Sucrose %	Total Sugar %	WSP* %	Starch %	Total carbo-hydrates** %	Dry matter %
5	su <sub>1</sub>	16	9.2	16.5	25.7	14.3	23.3	65.3	19.9
		20	5.4	10.2	15.6	22.8	28.0	66.5	25.6
		24	3.6	9.5	13.1	28.5	29.2	70.8	30.5
		28	3.9	4.4	8.3	24.2	35.4	69.6	37.6
6	su <sub>2</sub>	16	7.4	10.5	16.7	3.6	39.3	59.6	17.5
		20	3.5	9.2	12.7	3.1	50.7	61.8	24.9
		24	1.9	2.6	4.5	2.5	63.9	70.9	34.9
		28	1.4	1.9	3.3	1.9	64.6	69.8	43.6
7	wx	16	10.1	9.6	19.7	3.5	34.1	57.2	14.9
		20	3.5	5.2	8.7	2.3	53.3	64.6	23.9
		24	2.5	4.5	7.0	2.8	61.9	71.5	33.1
		28	1.6	1.7	3.3	2.2	69.0	74.5	37.3
8	ae du	16	8.7	19.9	28.6	6.5	28.6	63.7	20.0
		20	7.3	10.4	17.7	7.1	43.5	68.4	24.6
		24	4.6	6.8	11.4	7.4	51.4	70.2	27.9
		28	2.8	5.9	8.8	5.7	55.5	69.9	33.7
9	ae su <sub>1</sub>	16	6.9	12.6	19.6	3.7	18.3	41.5	19.3
		20	3.7	8.3	12.0	3.6	29.3	44.9	24.8
		24	2.2	5.3	7.6	3.6	37.2	48.4	31.5
		28	2.1	5.3	7.4	3.2	34.4	45.1	33.9
10	ae su <sub>2</sub>	16	12.2	31.4	43.6	4.4	14.1	62.1	16.9
		20	5.6	16.3	21.9	4.5	35.2	61.6	24.3
		24	3.6	13.5	17.1	4.3	37.6	59.1	28.8
		28	2.4	8.9	11.3	3.2	48.2	62.8	35.4
11	ae wx	16	6.1	23.8	29.9	4.2	19.7	53.9	18.3
		20	3.8	23.2	27.0	4.6	26.6	58.2	23.5
		24	3.9	17.9	22.4	5.6	37.1	64.9	25.0
		28	3.2	12.3	15.4	4.6	39.5	59.5	28.3
12	du su <sub>1</sub>	16	5.3	17.6	22.9	13.3	21.5	57.7	18.5
		20	2.7	11.1	13.8	24.5	24.8	63.1	22.7
		24	2.5	7.3	9.8	29.5	23.6	62.8	26.9
		28	1.7	5.1	6.8	40.9	18.6	65.5	32.4

Code no.	Geno-type	Kernel age (days)	Reducing sugars %	Sucrose %	Total Sugar %	WSP* %	Starch %	Total carbohydrates** %	Dry matter %
13	du sh <sub>2</sub>	16	10.7	33.9	44.7	4.1	8.8	57.6	16.6
		20	4.0	33.4	37.8	3.8	16.3	58.0	23.2
		24	2.3	27.1	29.4	5.3	20.9	55.6	24.8
		28	2.9	19.9	22.8	6.4	24.6	53.7	27.7
14	du su <sub>2</sub>	16	5.1	21.7	26.8	3.3	27.1	57.2	19.5
		20	2.9	10.3	13.2	2.9	41.9	58.0	27.7
		24	1.8	6.8	8.6	3.4	47.1	59.0	32.9
		28	3.8	6.1	9.9	5.1	48.9	60.3	37.7
15	du wx	16	7.3	25.5	32.8	5.5	21.3	59.6	21.1
		20	4.1	15.8	19.9	12.2	34.3	66.4	25.7
		24	3.8	11.6	15.4	11.4	37.9	64.7	30.4
		28	3.0	9.5	12.5	11.6	45.4	69.5	34.8
16	sh <sub>2</sub> su <sub>1</sub>	16	8.9	24.1	33.1	5.0	7.2	47.3	20.5
		20	8.1	25.4	33.5	4.9	11.7	50.1	23.8
		24	7.1	19.1	27.8	4.6	14.4	46.9	25.2
		28	5.7	20.1	24.5	4.9	15.7	45.4	24.6
17	sh <sub>2</sub> su <sub>2</sub>	16	10.4	14.6	25.1	6.3	26.8	58.1	18.8
		20	4.0	8.5	12.6	9.5	38.3	60.3	28.3
		24	3.3	7.6	10.9	10.0	38.6	59.5	33.8
		28	2.5	6.8	9.3	13.6	35.1	57.9	38.3
18	su <sub>1</sub> su <sub>2</sub>	16	4.9	16.8	21.8	33.7	11.9	67.5	20.1
		20	2.8	11.2	14.1	31.5	20.1	65.6	28.5
		24	2.4	9.6	12.0	31.0	20.5	63.5	31.1
		28	2.5	10.4	12.8	36.9	18.9	68.6	35.4
19	su <sub>1</sub> wx	16	4.4	14.7	19.1	19.5	28.1	66.6	21.9
		20	3.4	11.1	14.4	26.4	29.9	70.9	29.5
		24	2.6	7.5	10.1	29.1	32.8	71.9	35.0
		28	3.0	5.7	8.7	30.3	32.5	71.5	37.3
20	su <sub>2</sub> wx	16	6.1	12.3	18.4	3.4	30.1	51.8	17.9
		20	3.2	9.7	12.9	4.4	44.0	61.3	25.7
		24	1.5	7.1	8.5	3.5	62.6	74.7	37.3
		28	0.9	3.5	4.4	3.3	66.3	73.9	42.5



Code no.	Geno- type	Kernel age (days)	Reducing sugars %	Sucrose %	Total Sugar %	WSP% %	Starch %	Total carbo- hydrates** %	Dry matter %
21	ae du su <sub>1</sub>	16	12.8	24.6	37.3	9.6	23.6	70.5	17.3
		20	9.2	18.0	27.2	12.4	30.9	70.5	22.6
		24	4.7	15.5	21.3	16.1	32.7	70.0	25.8
		28	4.6	10.6	15.3	18.2	38.0	71.5	27.6
22	ae du su <sub>2</sub>	16	7.7	21.7	29.4	7.6	30.8	69.9	22.4
		20	7.7	17.9	25.6	10.2	36.8	72.7	25.8
		24	6.8	10.4	17.2	10.2	45.0	72.4	31.7
		28	5.4	10.4	15.7	10.8	47.5	74.1	32.5
23	ae du wx	16	6.8	39.9	46.7	4.2	15.9	66.7	18.5
		20	4.1	34.6	38.7	3.6	26.6	68.9	24.6
		24	3.6	30.7	34.3	4.5	31.1	69.9	25.8
		28	4.4	23.7	28.1	4.9	32.0	65.1	24.5
24	ae su <sub>1</sub> su <sub>2</sub>	16	8.5	23.2	31.7	6.6	23.8	62.0	20.3
		20	3.5	9.7	13.2	10.4	41.6	65.3	27.1
		24	2.7	7.9	10.6	10.6	39.6	61.1	31.5
		28	2.4	8.6	11.0	11.0	41.0	65.9	34.1
25	ae su <sub>1</sub> wx	16	8.0	28.2	36.2	4.5	22.0	62.7	16.3
		20	5.2	21.9	27.0	8.4	30.7	66.0	21.7
		24	3.5	15.0	18.5	12.2	38.5	69.1	25.8
		28	2.8	11.1	13.9	12.4	38.3	64.5	26.2
26	ae su <sub>2</sub> wx	16	10.3	22.2	32.4	5.1	18.0	55.5	16.4
		20	7.9	17.1	25.1	5.9	40.3	71.3	19.4
		24	4.0	16.4	20.4	5.9	41.7	67.9	27.0
		28	3.2	12.6	15.8	5.0	49.6	70.4	28.4
27	du su <sub>1</sub> su <sub>2</sub>	16	7.3	16.4	26.9	21.8	19.4	68.1	20.7
		20	4.1	12.3	16.4	31.9	21.2	69.4	26.5
		24	2.9	7.3	10.2	34.9	24.9	70.1	31.6
		28	2.4	5.4	7.8	34.8	22.8	65.5	33.9
28	du su <sub>1</sub> wx	16	5.9	16.8	21.7	24.4	14.7	60.8	22.0
		20	3.2	10.2	13.4	36.1	21.4	70.9	27.9
		24	2.9	7.8	10.7	38.4	17.5	66.6	33.4
		28	2.3	6.7	9.0	47.5	15.9	72.3	35.3

Code no.	Geno- type	Kernel age (days)	Reducing sugars %	Sucrose %	Total Sugar %	WSP* %	Starch %	Total carbo- hydrates** %	Dry matter %
29	du su <sub>2</sub> wx	16	9.2	25.7	34.9	4.6	17.2	53.4	15.2
		20	5.2	19.5	24.7	14.8	24.7	64.2	20.8
		24	3.0	10.6	13.3	14.3	33.9	61.5	27.9
		28	2.7	8.9	11.6	16.7	38.1	64.5	30.7
30	su <sub>1</sub> su <sub>2</sub> wx	16	6.5	19.6	26.1	22.1	11.9	60.1	18.5
		20	3.4	15.1	18.5	33.9	13.8	66.2	24.8
		24	2.8	11.4	14.3	38.9	16.2	69.3	32.0
		28	2.1	10.6	12.7	40.1	18.2	71.0	34.6
31	Golden Cross Bantam(su <sub>1</sub> ) Sweet Corn	16	8.1	15.4	23.6	7.8	28.7	60.1	16.1
		20	3.2	5.5	8.7	27.0	35.5	71.3	26.8
		24	1.9	3.9	5.9	33.3	38.5	77.7	33.5
		28	1.6	1.9	3.6	34.8	33.9	72.3	37.0
LSD Genotypes within Ages									
		5%	3.2	10.4	10.9	10.4	14.2	15.3	2.9
		1%	4.2	13.9	14.5	13.9	18.8	20.4	3.9
LSD Ages within Genotypes									
		5%	2.4	6.0	5.8	4.8	7.6	7.5	2.9
		1%	3.2	7.9	7.7	6.3	10.1	9.9	3.8

A partial symmetric correlation matrix is presented in Table 2. All variables measured, percent dry matter, percent total sugar, percent reducing sugar, percent sucrose, and percent alcohol insolubles (AIS, not shown in Table 1) were either positively or negatively associated. Total sugar, reducing sugar, and sucrose contents were negatively correlated with dry matter content. AIS was positively associated with dry matter content. A correlation value of -0.81 between sucrose content and alcohol insoluble content indicates, as previous workers have shown, that one may obtain increases in sugar content by selecting for types with low AIS. AIS determinations are relatively inexpensive as compared with sugar determinations. This is of value in sweet corn breeding.

Table 2. Symmetric correlation matrix.

Variable	1	2	3	4
1. Dry matter %	-			
2. Total sugar %	-0.72**	-		
3. Reducing sugar %	-0.73**	0.69**	-	
4. Sucrose %	-0.62**	0.94**	0.50**	-
5. AIS %	0.76**	-0.86**	-0.62**	-0.81**

1/ AIS Alcohol insolubles (contains WSP, starch, and kernel residue)

\*\*Exceeds the 1% point ( $r > 0.15$ )

Sweet corn quality. Some of the most interesting genotypes showing promise for possible use in sweet corn quality improvement are ae su<sub>1</sub> wx, ae du wx, ae wx, and sh<sub>2</sub>. However, it must be pointed out that none of these genotypes, except sh<sub>2</sub>, have been evaluated for other factors that contribute to sweet corn quality besides carbohydrates.

Indicated areas of genetic control in carbohydrate synthesis. These data support the findings of previous workers that the gene su<sub>1</sub> apparently causes or is associated with a substantial block between WSP and starch. The gene sh<sub>2</sub>, as reported by Laughman and as these data indicate, apparently causes a substantial block between sucrose and WSP.

The genes ae, wx, su<sub>2</sub>, and du have been of interest for several years because of their effects on the proportions of amylose and amylopectin starch. Because of this, some have thought that perhaps these genes were operating within the starch fraction affecting the formation of straight and branched chain molecules. However, these data indicate that ae alone also causes a marked increase in sucrose and reduction in total starch. In addition, ae combined with wx and wx du causes a dramatic increase in sucrose. The amylose and amylopectin data (Kramer et al, 1958, and Vineyard and Bear, 1952) combined with the effects of ae and wx on sugar content as shown in Table 1, indicate that ae and wx are in separate pathways of starch synthesis. This is, of course, assuming that the mutants are associated with partial or complete blocks in the biosynthesis of starch. This leads us to propose that the mutant gene ae is associated with a partial block between sucrose and the branched chain polysaccharides which eventually form amylopectin starch, and the mutant gene wx is associated with a substantial block between sucrose and the straight chain polysaccharides which eventually form amylose starch. There is some indication that du and perhaps su<sub>2</sub> may be in a second amylopectin pathway. We have not taken space in this report to discuss all the apparent gene interactions. These will be discussed in detail in a later article.

Additional carbohydrate studies are planned with the gene mutations used in this study and additional mutants. Studies of the effects of these genes alone and in combinations on qualitative and quantitative changes in enzymes known to be associated with carbohydrate synthesis are being initiated. Studies to determine the types of carbohydrates produced in each genotype are presently underway.

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1. A case of cytoplasmic control of susceptibility to Helminthosporium leaf spot in corn.

In the 1962 issue of the News Letter, we reported a case of an apparent relationship between cytoplasmic male sterility involving the T plasmatype derived from FL4T and susceptibility to Helminthosporium leaf spot. A case of cytoplasmic control of susceptibility has been hypothesized in the light of the following observations: (1) the extreme susceptibility to the disease of cyto-sterile inbred lines, single crosses and double crosses in contrast with the apparent resistance of their normal counterparts, and (2) the extreme uniformity in the degree of infection of plants within the population of any line carrying the T-cytoplasm. To provide a more conclusive proof of this hypothesis further studies were conducted using populations of reciprocal crosses which differed only in the cytoplasmic background and this was made possible with the use of a "restored-cyto-sterile" parent. Inbred lines differing in the cytoplasmic background and/or in their genetic constitution for the fertility restoring factor were also included.

Each experiment was grown in three replications and the plants were subjected to very severe natural or artificially induced infestations of the disease. Disease reaction of individual plants in each entry were scored in numerical values ranging from 0 to 5, correspondingly from a very negligible infection to a very severe condition.



Table 1. Reaction to *Helminthosporium* leaf spot of early backcrosses differing in the cytoplasmic background.

Entries		Genotypic Composition of Population for Restoration	Av. Disease Rating	
Cytoplasm:	Pedigree		Factor	Veg- : Ma- etative:ture
Normal	(Ph15 N) x (Ph15 <sup>2</sup> TRf)	.5 Rf rf + .5 rf rf	0.0	0.0
Cyto-sterile	(Ph15 <sup>2</sup> TRf) x (Ph15 N)	.5 Rf rf + .5 rf rf	3.1	5.0
Normal	(Ph3N) x (Ph3 <sup>3</sup> TRf)	.5 Rf rf + .5 rf rf	0.2	0.2
Cyto-sterile	(Ph3 <sup>3</sup> TRf) x (Ph3N)	.5 Rf rf + .5 rf rf	2.9	5.0

Table 2. Disease reaction of three-way crosses differing in the cytoplasmic background.

Entries		Genotypic Composition of Population for Restoration	Av. Disease Rating	
Cytoplasm:	Pedigree		Factor	Veg- : Ma- etative:ture
Normal	(Ph3N)(Ph9T x Ph11Rf)	.5 Rf rf + .5 rf rf	0.0	0.0
Cyto-sterile	(Ph9T x Ph11Rf)(Ph3N)	.5 Rf rf + .5 rf rf	2.9	5.0
Normal	(Ph15N)(Ph9T x Ph11Rf)	.5 Rf rf + .5 rf rf	0.0	0.0
Cyto-sterile	(Ph9T x Ph11Rf)(Ph15N)	.5 Rf rf + .5 rf rf	3.2	5.0

Table 3. Disease reaction of F<sub>2</sub> self progeny of cyto-sterile and normal three-way crosses.

Entries		Genotypic Composition of Population for Restoration:	Av. Disease Rating	
Cytoplasm:	Pedigree	Factor	Veg-	Ma-
			etative	tature
Normal	(Ph3N)(Ph9T x Ph11Rf)	3/8 Rf <u>  </u> + 5/8 rf rf	0.9	1.5
Cyto-sterile	(Ph9T x Ph11Rf)(Ph3N)	3/4 Rf <u>  </u> + 1/4 rf rf	1.7	3.8
Normal	(Ph15N)(Ph9T x Ph11Rf)	3/8 Rf <u>  </u> + 5/8 rf rf	0.9	1.9
Cyto-sterile	(Ph9T x Ph11Rf)(Ph15N)	3/4 Rf <u>  </u> + 1/4 rf rf	2.0	4.5

Table 4. Disease reaction of sterile, restored-sterile and normal versions of five Philippine inbreds.

Entries	Average Disease Rating	
	Vegetative	Mature
Normal inbreds	0.0	2.3
Sterile versions	1.4	5.0
Restored-sterile versions	1.8	5.0

Table 5. Disease reaction of five normal inbreds and their respective sterile versions at different backcross generations.

Entries	Average Disease Rating	
	Vegetative	Mature
Normal inbreds	1.2	1.7
Sterile versions (BC <sub>4</sub> )	2.8	4.8
Sterile versions (BC <sub>5</sub> )	2.8	4.8
Sterile versions (BC <sub>6</sub> )	2.8	4.8

It is evident from the data just presented that the cyto-sterile lines were contrastingly much more infected with the disease than their normal counterparts. Infection was so severe that the plants of the cyto-sterile lines dried up prematurely. Utmost uniformity in reaction was repeatedly observed among the plants of the cyto-sterile populations. It is interesting to note that the normal Philippine inbreds involved, namely, Ph3, Ph9, Ph11 and Ph15, were remarkably resistant to the disease. It would have been difficult to demonstrate cytoplasmic control of susceptibility if the natural inbreds happened to be equally susceptible.

It could also be gleaned from the data that the fertility restoring gene does not have any influence on the expression of susceptibility.

It is hypothesized that the T-cytoplasm carries a factor which is responsible for the induction of extreme susceptibility to Helminthosporium leaf spot. Whether the expression is strictly cytoplasmic or partly controlled by genes, as is the case with cytoplasmic male sterility, is still unknown. With our available inbred lines and 52 open-pollinated varieties so far tested against Ph11T, no such "resistance restoring" gene has been found.

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2. The effect of the number of resistant parental inbreds on the reaction of the double cross hybrid to downy mildew disease.

An extensive survey of the reaction of corn inbred lines to downy mildew has shown that resistance can be found only among lines of local origin. All introduced lines, so far tested, were susceptible to the disease. Hybrids of diverse parentage, therefore, can not be produced from the resistant inbreds. If diversity were to be achieved some lines from the susceptible class must be used. Thus it became necessary to know the least number of resistant parental lines in order to produce resistant hybrids.

Several double crosses containing from zero to four resistant parental inbreds were produced in 1961. The reaction of these hybrids to downy mildew was evaluated in 1962 wet season under induced epiphytotics of the disease. The results are presented below.

Combinations	: Percentage: : Infection :	Total : Plants :	Number of Crosses
All lines resistant	22 $\pm$ 3.2	444	4
3 lines resistant	34 $\pm$ 2.9	365	5
2 lines resistant	42 $\pm$ 2.6	716	6
1 line resistant	57 $\pm$ 3.2	495	4
All lines susceptible	54 $\pm$ 3.7	280	3

The results strongly indicate a positive correlation between the degree of damage and the dose of susceptible inbreds involved in the hybrid. For every additional susceptible line, there was a corresponding increase in susceptibility of the double cross. If a highly resistant hybrid were to be produced, therefore, it is necessary to use only parental lines that are resistant to the disease.

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### 3. Inheritance of the reaction of corn to downy mildew disease.

Immediately after the screening of inbred lines for their reaction to downy mildew, crosses between resistant and susceptible lines, their  $F_2$ , and their backcrosses to both parents were produced. The reaction of these crosses together with that of the parents was tested in a replicated plot in 1962 wet season under epiphytotic of the disease. The results are presented below.

Entries	: Percentage : : Infection <u>1/</u> :	Total Plants Examined <u>2/</u>
Resistant parent (R)	33.7 $\pm$ 4.0	735
Susceptible parent (S)	84.3 $\pm$ 2.4	628
R x S	46.8 $\pm$ 2.2	1167
(R x S) Selfed ( $F_2$ )	41.5 $\pm$ 2.7	991
(R x S) R	24.3 $\pm$ 2.2	1024
(R x S) S	62.5 $\pm$ 2.8	924

1/ and 2/ - Each figure represents the average and total, respectively, of 44 plots representing 11 crosses each of which was replicated 4 times.



Disease epiphytotics in this test was more severe than that in the screening phase. An average infection of 50% was obtained compared to only 37% in the latter. This is probably the reason why the resistant lines which had infection counts of less than 10% in the screening nursery had a much higher infection in this test. Nevertheless, the susceptible inbreds had a much higher infection count than the resistant lines, thus maintaining a good distinction between the two classes.

Only two phenotypes were obtained in this experiment, the resistant and the susceptible classes. Probably this is inadequate to identify qualitative characters that are controlled by two or more factor pairs. The original plan was to count infected plants at two stages of growth so that more classes could be obtained, but strong winds and heavy rainfall destroyed the plants before the second reading. Nevertheless some interesting information can be obtained from the present results.

The most striking feature of the data is its pronounced trend towards the resistant parent. The  $F_1$  and  $F_2$  are much nearer the resistant than the susceptible parent. In the backcrosses, the resistant phenotype is much more easily recovered than the susceptible phenotype. This behavior can mean any one or both of the following: (1) that resistance is partially dominant over susceptibility, and (2) that the superiority of the crosses in terms of vigor and growth rate caused the "skewed behavior". If the former is true then it is a very good indication that only a few factor pairs control the reaction of corn plants to the disease. If the latter is present, which is very likely as shown by the "over recovery" of resistance even only at the first backcross, not much information can be obtained from the present data. It will be necessary in subsequent inheritance studies to use also single crosses between resistant inbreds and between susceptible inbreds as resistant and susceptible parents, respectively.

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#### 4. The frequency of restorer factors for A, B, S and T sterility inducing plasmatypes in inbred lines of corn in the Philippines.

The survey of pollen restorers for A, B, and S plasmatype was started when the T-cytoplasm was suspected to carry factors that induce susceptibility to some leaf diseases (see item No. 1). Crosses of all standard and promising lines to A158A, A158B, and A158S obtained from the Connecticut Experiment Station were made in the 1961-62 wet season and tested for pollen fertility and reaction to leaf diseases in the 1962 wet season. The percentages of fertile tassels in the  $F_1$  are presented in table 1.

Table 1: Percentage of male fertile plants in F<sub>1</sub> crosses of Philippine inbreds with A, B, S, and/or T sterility-inducing plasmatype.

Inbreds	Source of Sterility-Inducing Cytoplasm							
	FLMT1/		A158A		A158B		158S	
	:Fertile: :Tassel : %	Total : plants : examined	:Fertile: :Tassel : %	Total : plants : examined	:Fertile: :Tassel : %	Total : plants : examined	:Fertile: :Tassel : %	Total : plants : examined
Ph2	43	89	100	50	98	50	96	56
Ph4	100	120	41	54	10	60	53	66
Ph6	100	139	6	64	6	49	18	60
Ph8	100	72	95	37	98	56	91	47
Ph10	0	14	100	43	96	55	80	51
Ph12	2	79	100	44	100	44	100	26
L. 314	27	225	-	-	100	8	-	-
L. 315	26	196	-	-	100	31	-	-
L. 316	100	173	91	34	89	53	92	59
L. 317	100	152	84	31	-	-	-	-
Ph1	12	282	0	67	12	75	74	62
Ph3	20	313	100	77	100	63	100	74
Ph5	100	198	0	64	0	58	-	-
Ph7	100	233	96	48	-	-	-	-
Ph9	0.4	235	99	244	100	204	100	182
Ph11	100	713	0	28	0	28	-	-
Ph13	3	191	100	77	100	59	-	-
Ph15	71	170	100	31	-	-	-	-
Ph17	77	110	100	40	100	66	100	68
Ph19	100	201	100	24	-	-	-	-
Ph21	100	65	0	25	0	27	-	-
F44	4	171	100	12	100	25	100	10
Mean	58.4	188	70.6	55	67.2	56	83.7	64

The plasmatypes T, A, B, and S had an average sterilizing capacity of 41.6, 29.4, 32.8, and 16.3, per cent respectively. It seems that the T-type is more efficient in sterilizing Philippine inbreds or that the frequency of restorer factors for T in these inbreds is much less than those for any of A, B, or S. Also, there is a very striking similarity in the behavior of A, B, and S plasmatypes. Any line that is sterilizable by one is also sterilizable by the other two; and any line that is essentially a restorer for one is also a restorer for all. This could indicate that the same factors can restore the three cytoplasm and/or the three cytoplasm are essentially the same.

It can also be seen from the results that segregation of the restorer factors for A, B, or S within an inbred line occurs very rarely. An inbred is essentially either a restorer or a non-restorer. Very seldom will a sterile plant appear in a restorer line or a fertile plant in a non-restorer. This lack of variability is a disadvantage because one has to grow larger populations to obtain the less frequent desirable segregate.

There is however one big advantage for the A, B or S cytoplasm to warrant their utilization in spite of their apparent inferiority to T in some aspects. Not one had a tendency to increase leaf disease susceptibility in the F<sub>1</sub> progenies of their crosses. Under epiphytotics of Helminthosporium leaf spot, the crosses were definitely as resistant as their original normal inbred parent.

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#### 1. Environmental modification of rf<sub>2</sub> rf<sub>2</sub> sterility.

(ms<sub>1</sub>) Rf<sub>1</sub> rf<sub>2</sub> rf<sub>2</sub>\* appears not to be as completely sterile under all environmental conditions as (ms<sub>1</sub>) rf<sub>1</sub> rf<sub>1</sub> Rf<sub>2</sub>. Test crosses of plants segregating for both loci gave good sterile versus fertile segregations in Florida in 1961-62 for the test of segregating Rf<sub>1</sub> but gave partial fertiles versus full fertiles for the test of segregating Rf<sub>2</sub>. When the same populations were regrown in Iowa in 1962 both loci gave good sterile versus fertile segregations. In the winter of 1962-63 in Florida a similar test once again gave good sterile versus fertile segregations for test crosses of segregating Rf<sub>1</sub> but test crosses

\*(ms<sub>1</sub>) is used as symbol for Texas (T) cytoplasm.

of segregating  $Rf_2$  were almost entirely fully fertile. Further, a usually completely sterile line of the genotype ( $ms_1$ )  $Rf_1$   $Rf_1$   $rf_2$   $rf_2$  was partly fertile.

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## 2. Allelism of $Rf_1$ and partial-restorer genes.

The partial fertility restoration ability of several inbred lines has been found to be due in each case to a single dominant gene. A preliminary series of test crosses has indicated that the single gene is in every case allelic with  $Rf_1$ . That is, test cross populations of ( $ms_1$ )  $rf_1$   $rf_1$  x ( $Rf_1$   $Rf_1$  x partial restorer) gave segregations of approximately 1 full fertile to 1 partial fertile. The possibility that there is an allelic series of restorer genes at the  $Rf_1$  locus is being explored.

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## 3. $Ga^S$ $Ga^S$ in foreign cytoplasm.

The effect of  $Ga^S$   $Ga^S$  in Japanese Hulless popcorn apparently does not change in the presence of other cytoplasm. By recurrent back-crossing, the genotype of a Hulless inbred line was transferred to the cytoplasm of (1) Gourdseed Southern Dent, and (2) Argentine multiple eared popcorn. When these two new lines plus the original Hulless were pollinated as females by two corn belt inbred lines of  $ga$   $ga$  constitution, virtually no pollinations were effected on any of the three strains.

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## 1. Investigations on possible episomic nature of Modulator.

As reported in the 1962 Newsletter (p. 78-79) several experiments were undertaken to test for a possible cytoplasmic state of the controlling element, Modulator.



Firstly, a number of reciprocal crosses were made between a white inbred line (colorless pericarp,  $P_{WW}$ ) and plants heterozygous for light variegated pericarp ( $P^{rr}M_p + 1$  transposed  $M_p$ ) or very light variegated ( $P^{rr}M_p + 2$   $tr-M_p$ 's). If  $M_p$  is chromosomal, the expected results for such crosses is a ratio of 1 white ear to 1 colored ear. The colored class includes light variegated (1  $tr-M_p$ ), very light variegated (2  $tr-M_p$ 's), medium variegated (no  $tr-M_p$ 's) and red pericarp (no  $M_p$  at the P locus), the ratios of the various types varying with the position of the  $tr-M_p$  and the frequency of secondary transpositions of  $M_p$ . If  $M_p$  were capable of a cytoplasmic state in some cases, the expectation would be that the families resulting from crosses of a variegated female parent with a white male parent would still show a 1:1 ratio with the colored ears distributed as in the parental variegated while those in which the variegated plant was used as pollen parent would show a higher frequency of red ears (if the  $M_p$  at the P locus were lost in the cytoplasm) or a higher frequency of medium variegated ears (if the  $tr-M_p$ 's only were lost). Neither expectation was realized. The rather surprising result was a preponderance of white ears in the crosses where the variegated plant was used as pollen parent while the reciprocal cross (variegated plant used as female parent) gave the expected 1:1 ratio. The results were as follows:

female parent	Number of families giving			Total No. families	Total ears	
	more than 50% colored ears	less than 50% colored ears	exactly 50% colored ears		colored	white
lt. or very lt. var.	16	12	3	31	1302	1256
white	12	40	2	54	1229	796

Some pairs of reciprocal crosses showed very striking deviations from the expected ratios with the maternal transmission of variegated giving the expected results while the reciprocal cross gave no colored ears or one or two out of some fifty ears.

It would appear from these results that for some reason, either the chromosome carrying the color gene or the gene itself is discriminated against in pollen transmission. Brink some years ago reported normal transmission of variegated through both male and female gametes and this is still the case for some variegated lines in the present study. Brink and Wood showed that Modulator had no effect on pollen tube growth and Fradkin and Brink found no pollen sterility in plants carrying  $M_p$  even though endosperm mosaicism indicated that chromosome breaks were probably occurring in that tissue. Episomes in bacteria (e.g. transducing phages and the sex factor of *E. coli* in cases of sexduction) occasionally carry the gene or genes near to their point of chromosomal

attachment into the cytoplasm with them when they enter the cytoplasmic state. If such a phenomenon occurred with the Mp at the P locus and the red gene, results such as those obtained might be expected. Experiments are now under way to clarify the situation.

Secondly, experiments were carried out in which variegated kernels were given treatments (heat and acriflavine) known to cure cells of lower organisms of cytoplasmic particles. The heat treatment as outlined by Braun (MGCNL 35:83-84) had no effect on the phenotype of the resulting plants. Acriflavine treatment had no effect on a medium variegated but two strong treatments gave a higher ratio of medium variegateds to lights (69 and 61%) than either a weak treatment (42%) or three related untreated families grown in previous years (43, 36 and 43%). This is a shift in the direction expected if the treatment were destroying some of the transposed-Modulators. The acriflavine treatment and several other treatments having similar effects on microorganisms are being repeated on a larger scale during the current growing season.

Nancy van Schaik  
Department of Genetics

## 2. An acute molybdenum deficiency in maize.

A general yellowed and stunted appearance associated with yellow interveinal streakings which soon become necrotic resembling a kind of marginal leaf scorch was found to be the symptom of an acute molybdenum deficiency in maize.

This condition was particularly prevalent during the first 5 to 6 weeks after emergence of the plants. From this stage onwards, plants were found to recover from the acute symptoms. In many instances the plants recovered to such an extent that distinct symptoms were no longer visible. At this stage, affected plants could be recognized only by their smaller size when compared with the better growing plants in the same field.

Molybdenum deficiency symptoms in maize were found to occur on soil with a pH of 4.4 and lower but not on soils with a pH of 4.66 or higher, which indicates a critical pH level. A similar condition was found in a bean field where ten pH readings made from rhizosphere soil of 10 severely affected bean plants averaged 4.33, while readings from 10 symptomless plants growing in the near vicinity, averaged 4.52. The pH of the soil, therefore, had a very marked effect on the availability of molybdenum to plants. This was further proved by adding enough slate lime to the experimental soil to bring the pH from 4.03 and 4.37 to 4.67 and 4.77. In this experiment severe deficiency symptoms were found in maize plants grown at the lower pH values and none at the higher

values. In spite of the low pH of these soils, the molybdenum deficiency was easily diagnosed by planting maize seed soaked for one hour in a 0.5% solution of sodium molybdate between the yellow plants. Plants originating from the treated seed were green and grew like normal plants.

In addition to the severe molybdenum deficiency symptoms, very distinct phosphorus deficiency symptoms were also observed on the same plants in the plots with a soil pH of 4.0.

It appears, therefore, that it is of paramount importance to check soil pH regularly and to guard against abnormal acidification.

J. J. du Toit  
Plant Pathologist

### 3. Root disease of maize -- a request.

A serious root rot of maize, causing the rotting of all major roots as well as the newly formed thin roots, is found to occur in varying degrees through the whole Transvaal region of South Africa.

Organisms commonly associated with it are: three different *Fusaria*, two *Helminthosporia*, a *Trichoderma* and a nematode, *Pratylenchus zeae*. The production of a phytotoxic substance by one or more of the fungi, is another possibility.

Any information in this connection will be highly appreciated.

J. J. du Toit  
Plant Pathologist

### 4. Position effect as a factor in pollen tube competition in *Zea mays* L.?

Studies of pollen tube competition reported in previous years (M.N.L. 1958-1962) have indicated that many genes are probably involved in pollen tube growth. Since the male gametophyte is apparently very sensitive to gene action it is possible that position effect, resulting from reciprocal translocation, may be revealed in its effect on pollen tube competition. In the table below are tabulated the progenies of crosses between normal seed parents and reciprocal translocation heterozygotes as pollen parents, as recorded in column 1. Optimum growing conditions were available so that errors for classification of semi-sterility were negligible. The pollen tubes containing the T1-3i reciprocal translocation were significantly more efficient in competition than normal tubes as is apparent in the difference in the number of normal and sterile plants recorded in the progeny. This was also the case for T1-6c. However, in the case of T1-8i the normal class

predominated, whereas no significant differences were recorded in the progenies of T1-4a and T1-7b. It is of interest to note that although chromosome 1 was involved in all the reciprocal translocations studied, there was a marked difference in pollen tube competition recorded for the different progenies.

Chromosome Translocation Type	Crosses Normal X Semi-sterile		P Value
	P r o g e n y		
	Normal	Semi-sterile	
T1-3i	165	345	<0.01
T1-4a	83	83	>0.99
T1-6c	142	188	0.01-0.02
T1-7b	111	135	0.10-0.20
T1-8i	240	100	<0.01

J. D. J. Hofmeyr  
Department of Genetics

#### 5. Location of genes for ear-row number in Zea mays, L.

The different progenies recorded in the table of contribution No. 4 (above), showed a wide segregation for ear-row number, ranging from 8 to 16 rows. Of these only the first (T1-3i) showed a significant difference between the normal and semi-sterile ears with respect to ear-row number, and hence only these results are recorded in Table 1.

Table 1. Results of the cross: Normal X Semi-sterile  
Ear Row Number

	8	10	12	14	16	Average
Normal	1	10	85	62	8	12.8
Semi-sterile	3	66	227	49	-	11.9

Table 2. Factorial Analysis

Source	D.F.	S.S.	M.S.	F
Total	39	12551		
Replications	3	455	155	3.77*
Fertility(a)	1	801	801	17.4 **
Rows per ear (b)	4	5024	1256	27.3 **
Interaction: (a) X (b)	4	5029	1257	27.3 **
Error	27	1232	46	

\*\*Significant at P = 0.01, \* Significant at P = 0.05.  
Coeff. of Rank Correlation = 0.8 (significant).



The results show a clear association between ear-row number and semi-sterility when the T1-3i reciprocal translocation is employed, which was not the case for the other reciprocal translocations. Since chromosome 1 was employed in every case it would appear that the genes for ear-row number are concentrated mainly in Chromosome 3.

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#### 1. Radiation induced modification of paramutation expression.

Experiments were designed to determine whether the paramutation inducing process has a radiosensitivity similar to gene mutational events. The source inducing the paramutation change ( $R^{st}$  and  $R^{mb}$ ) and the site of action ( $R^r$ ) were each tested.

The experimental procedure was similar for all groups. Tassels were cut one day after they began to shed pollen and placed in flasks. They received 2000r from the gamma source and were then bagged for use the following day. The tassels were used to make individual crosses onto the appropriate tester (i.e.  $R^r$  for  $R^{st}$  tassel etc.). The hybrids were then crossed to  $r^g r^g$  stock, using the  $r^g r^g$  as female.

When the site for paramutation change was irradiated before crossing to  $R^{st}$  or  $R^{mb}$ , approximately 10% of the time (10 out of 107 ears) there is no apparent paramutation, (i.e. the testcross ears were 50% dark purple). In addition there is evidence that there is some alteration of the usual paramutation interaction in 15-20% of the rest of the ears. They appear to have either a reduced paramutational change or are segregating for paramutation alteration on the ear. Each ear traces back to a single irradiated pollen grain. Further tests are being conducted to determine more precisely which event has happened.

When the  $R^{st}$  stock was irradiated prior to crossing to  $R^r$  and then testcrossed, 64% of the time there was no apparent effect. There were no ears that were 50% dark purple (i.e. no paramutation). However 23% of the ears had light spotted and dark spotted seed predominantly with very few yellow and some dark purple kernels. There was a definite effect on the paramutation interaction but probably no instance of complete inactivation. The remainder of the ears are in a suspect category with light spotted predominant and some dark mottled or full purple seed, but very few yellow. The ears appear to be significantly different from the majority class which had predominantly light spotted and full yellow seeds.

The final group involved irradiation of the  $R^{mb}$  with subsequent testcrossing identical to  $R^{st}$ . Here there was 5% apparently complete inactivation of the paramutation interaction (i.e. ears were 50% dark purple). A reduced paramutation effect is more difficult to detect in the marbled induced change as the variability is greater. There was no effect on the paramutation interaction or perhaps some with reduced effect in 84% of the ears. The other 9% of the ears have what appears to be an increased paramutation expression. The seeds are predominantly yellow and light spotted with no very dark mottled and no full purple seed on the ears. The altered  $R^r$  seed appear very similar to the  $R^r$  from a  $R^{st}$  induced paramutation change. This would indicate that the  $R^{mb}$  source has some mechanism which inhibits full induction of the paramutation alteration.

These results indicate that paramutation has a radiosensitivity much greater than can be attributed to gene mutation changes. The effects seem more in line with an inactivation process. Further tests are being conducted to obtain additional information of the effects of radiation on paramutation.

D. B. Linden

2. Survey of some South American races with variegated aleurones for paramutation induction ability.

From the collection of 37 races with marbled and/or stippled like aleurones successful evaluation for paramutation like induction ability was completed for 17 and partially completed for 6 others. The results are as follows:

Collection	Race	Marbled type	Stippled type	Paramutation Induction
Bolivia 596	-	X	X	yes
Bolivia 648	-	X	X	yes
Bolivia 706	-	X	-	yes
Bolivia 733	-	X	-	yes
Bolivia 753	-	X	X	yes
Bolivia 646	-	X	X	yes
Bolivia 876	Huilcaparu	-	X	yes
Bolivia 320	Checchi	-	X	yes
Bolivia 833	Checchi	-	X	yes
Bolivia 967	-	X	X	yes
Peru 683	-	-	X	yes
Peru 1085	-	-	X	yes
Bolivia 617	-	X	X	yes?
Bolivia 771	Huilcaparu	X	X	yes?

Collection	Race	Marbled type	Stippled type	Paramutation Induction
Bolivia 928	Checchi	X	X	yes?
Bolivia 643	-	X	X	yes?
Bolivia 591	Huilcaparu	X	X	yes?
Bolivia 623	Huilcaparu Moteado	X	X	yes?
Bolivia 666	Huilcaparu Moteado	X	X	no
Bolivia 718	Paru	X	-	no
Bolivia 724	Paru	X	-	no
Bolivia 723	-	X	X	no
Bolivia 663	Altiplano	-	X	no

Some of the races tested appear to be segregating for paramutation induction ability. Within races, some testcross ears are 50% dark purple while others have no purple. Each tested  $F_1$  plant ( $R^{st} R^r$ ) was also either selfed or used as a female with  $r^g r^g$ .

In some races particularly Bolivia 967 the paramutation expression was very evident in the crosses using the  $F_1$  as female. This again is not a uniform expression within the race as some ears were 50% dark purple, others 25% dark purple 25% light purple, and still others with more complicated ratios or no dark purple.

The degree of paramutation alteration induced in  $R^r$  varied among the different races as well as within some races. Bolivia 320 appears to be as strong as and probably stronger than  $R^{st}$ . Others are similar to  $R^{mb}$  types while still others seem to be distinctly different from either of these two.

The portion of the paramutation interaction which induces the change in the  $R^r$  gene seems to have a considerable degree of variability. Further tests are underway to investigate the nature of this variability. The relationship between the various sources will be studied and interactions among them will be determined.

D. B. Linden

### 3. Fluorescent metabolites accumulated by a mutant of maize.

A mutant of maize obtained by exposure to high energy irradiation at the atomic bombs test site in Bikini was shown to accumulate blue fluorescent metabolites.

The homozygous segregated mutant accumulated fluorescent compounds in leaves during the first stage of plant growth and in the anthers of mature plant. Progeny from the heterozygous mutant accumulated the fluorescent metabolites in both the young leaves and the anthers or in anthers only, according to the gene dose. A single gene was suggested to be responsible for the accumulation of blue fluorescent material.



Separation of these materials by paper chromatography showed three main fluorescent spots called A, B and C in order of increased Rf. The blue fluorescent compound pertaining to the C spot was isolated and identified as anthranilic acid; the eluates from B and A spots showed anthranilic acid activity in biological assays. Incubation of uniformly  $C^{14}$ -labeled anthranilic acid with unboiled and boiled mutant and normal seedling leaf slices showed that unboiled mutant seedling slices incorporated radiocarbon into the B spot and presumably into that of lower Rf. Incorporation of AA into the succeeding compounds of the tryptophan cycle could not be demonstrated for either normal or mutant seedling slices, although coupling of indole with serine by tryptophan synthetase was demonstrated to occur in maize.

In the present study an attempt was made to isolate and identify the blue fluorescent material of the B spot. Chromatographic separation on paper showed that the B spot was a mixture of two compounds. Acid and alkaline hydrolysis of the whole B spot eluates gave rise to two compounds, one of which was a fluorescent compound identified as anthranilic acid by chromatography, electrophoresis and chemical test. The other compound that arose from hydrolysis was identified as a sugar by chromatography with control of pure sugars, chemical tests, and by preparation and identification of 2,4-dinitrophenylhydrazine derivatives by chromatographic methods. The experimental evidence suggested a six carbon aldose and it was tentatively identified as glucose.

The nature of the bonding between anthranilic acid and glucose was demonstrated to be a B-glucoside ester in one of the separated compounds called B<sub>1</sub>. This compound was insoluble in ether, migrated toward the cathode in electrophoresis with 0.1M phosphate pH 7.5 and was completely hydrolyzed by the enzyme B-glucosidase but not with maltase. In addition to the ester another compound apparently having a glucosylamine structure was found in the B spot eluates although the actual evidence do not permit to establish with certainty the origin of this compound or its physiological role.

The lack of transformation of AA into the succeeding compounds of the tryptophan cycle under genetic control of maize suggest there are internal metabolic regulatory systems for AA conversion to indole and tryptophan. Mutation can arise from alteration after irradiation of the gene responsible for this inhibition or by the activity of a new gene suppressor which in turn represses the one mentioned before.

A direct block in the pathway of AA is discarded since the available evidence shows that synthesis of this compound is not under genetic control. It is suggested that there is a detoxifying mechanism which permits the plant to store the accumulated AA as a B-glucosidic ester indefinitely or to discharge it in some adaptive metabolic pathway. The arrested production of AA after the development of the fourth leaf suggest that a feed back mechanism is involved and that some of the fluorescent compound or related substances cause the suppression of the system responsible for AA biosynthesis.

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1. Location of wilted (wi) on chromosome 6.

Crosses were made between a series of translocation stocks in which waxy (wx) was used as a marker for the chromosomal interchanges and a wilted (wi) Wx stock. These  $F_1$  plants were then selfed and the waxy kernels from the resulting progeny were planted.

Expected ratios (25%) of wilted were obtained with all translocations except T6-9b. Progenies involving T6-9b, which has break points on the short arm of chromosome 9 between the centromere and waxy (.37) and on the long arm of chromosome 6 near the Y locus (.10), gave 6% wilted plants. It is therefore apparent that wilted is located on chromosome 6 near the Y locus. Further testing will be carried out to establish the position of wilted in regard to other genes on chromosome 6.

Joseph Van Horn

2. Possibility of a new allele at the  $ga_1$  locus.

At the present date we have evidence of the presence of three alleles  $Ga^S$ , Ga and ga at the  $ga_1$  locus on chromosome 4. Plants Ga/Ga are fertilized by ga/ga. The advantage of  $Ga^S$  pollen over ga is almost 1 on  $Ga^S/ga$  silks.  $Ga^S$  and Ga do not have an advantage over ga on ga/ga silks.

Nelson (1952), in studies of several popcorns, found a percentage of sugary kernels ranging from 13.9 to 15.5 in  $F_2$  crosses of P51 (ga su/ga su) x the popcorns. In this experiment Schwartz D139 ( $Ga^S$ ) was included. He concluded that there is a possibility of different alleles of the same type as  $Ga^S$  in these popcorns.

The popcorns 845, 1001, 4524, 401, 4519, and 4541, the genetic stock Ga and Schwartz's D139 were used in this experiment. In order to have a common genetic background, they were backcrossed five times to the dent corn Hy. In each backcross generation a test for the presence of  $Ga^S$  was made. The recovered plants were crossed onto P51 (ga su/ga su); these  $F_1$ 's were selfed and intercrossed in all possible combinations, in pairs reciprocally. The results of these selfs and crosses are in table 1.

TABLE 1

The percentages of sugary kernels in the F<sub>2</sub>'s and paired reciprocal intercrossoes of F<sub>1</sub>'s that are obtained by crossing P51 (ga su/ga su) times derivatives of various popcorns or genetic stocks.

♀ ♂	D139	845	1001	4524	24	401	4519	4541	Ga	Total
N ears	13	4	2	2	1	1	6	1	2	32
D139 Kernels	4,655	1,719	756	883	483	524	2,605	477	896	12,998
% Sugar	13.83	14.36	11.50	14.84	12.84	15.46	14.94	13.63	13.73	14.24
845	2 998 16.53	18 7,769 13.89	2 884 13.57	2 988 13.87	2 1,061 14.89	3 1,088 14.34	4 1,453 17.34	2 1,026 12.38	2 877 12.77	37 16,144 14.38
1001	2 722 15.37	2 876 17.24	21 8,678 15.30	2 602 19.77	2 856 14.02	2 858 15.62	3 1,286 12.87	2 804 16.79	2 915 14.43	38 15,597 15.46
4524	2 821 12.91	2 951 13.67	2 740 12.70	18 6,246 15.26	2 887 14.21	2 819 15.02	4 1,252 20.26	3 1,390 14.03	2 829 13.27	37 13,935 14.37
24	3 1,285 13.23	2 683 14.79	2 942 15.81	2 856 18.22	18 7,709 15.40	2 904 14.38	4 1,271 17.16	3 1,330 13.76	4 1,796 15.37	38 16,293 15.38
401	3 1,070 14.02	3 1,139 16.07	2 733 14.87	2 930 16.02	2 905 16.80	13 5,585 18.28	3 1,371 15.17	2 851 19.39	2 776 16.75	32 13,360 16.19
4519	4 1,718 26.66	5 1,753 26.15	4 1,498 24.85	3 1,354 24.36	4 1,834 24.98	4 1,588 25.37	42 17,389 26.54	4 1,851 25.86	7 2,598 25.59	80 31,583 25.59
4541	2 845 14.20	2 839 15.38	1 353 16.15	2 905 13.03	1 314 17.52		3 1,404 15.49	18 7,355 14.26	2 853 14.77	31 12,868 14.75
Ga	1 190 16.32	2 1,008 13.59	2 852 15.73	2 857 16.92	2 767 16.56	2 812 15.27	4 1,862 15.06	3 1,297 14.03	21 9,270 14.11	39 16,835 15.33
Total	28 10,586 14.65	35 14,984 15.01	34 13,939 14.33	32 12,267 16.10	30 12,982 15.26	25 10,580 15.01	70 28,641 17.20	34 14,530 14.86	37 16,212 14.44	

All the crosses except the ones that involve 4519 had the expected reduction in sugary kernels, namely to about 15 percent when crossed as a male, female or selfed. When 4519 was used as a female or selfed the percentage of sugary kernels was 25 or more - no reduction. Used as a male, the percentage of sugary kernels was reduced to 15 as observed before.

Since 4519 derivatives in paired pollinations give 25 percent sugary when used as females, but 15 percent sugary when used as males, it suggests the presence of a new allele at this locus. This allele seems to be different from those known up to now since the action of this gametophyte factor is confined to the male gametophyte.

Another explanation of these results would be the existence of a fertility factor  $F$  closely linked to  $Ga$ , 4519 being  $F Ga$  and all the other popcorns  $f Ga$ . This  $F$  factor in dominant condition nullifies the action of the gametophyte factor, by removing the selectivity of the silks for  $Ga$  pollen. Then both  $ga$  and  $Ga$  pollen have the same chance of effecting fertilization. The inclusion of this fertility factor would give 25 percent sugary kernels when 4519 is used as a female. All the other popcorns would be carrying  $f$  and as a consequence  $Ga/ga$  silks will screen  $ga$  pollen and this would account for the 15 percent sugary kernels observed when 4519 was the male.

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Oliver E. Nelson

### 3. Association of recombination and mutation to colorless and near-colorless aleurone in plants heterozygous $R^r R^{st}$ .

It has been observed that in  $R^r R^{st}$  plants mutations occur to colorless and to near-colorless aleurone, and that some of the mutants carry both the red plant color characteristic of  $R^r$  and the paramutagenic action characteristic of  $R^{st}$  (Ashman, Genetics 45:19). This finding suggests that such mutants result from intragenic recombination at the  $R$  locus. To obtain information bearing on this possibility a second test was made utilizing genetic markers on either side of the  $R$  locus. The following cross was made in the latter test:

$$\begin{array}{c} + & R^r & + \\ \hline g & R^{st} & M^{st} \end{array} \times \begin{array}{c} g & r^g & + \\ \hline g & r^g & + \end{array}$$

Golden ( $g$ ) is 14 units proximal to  $R$ , and  $M^{st}$ , a modifier of the stippled phenotype, is 6 units distal to  $R$ . Ears from the above cross were scored for colorless and near-colorless kernels. The kernels selected were planted and the resulting plants were scored for golden and for plant color; the ears produced on the plants were pollinated

with pollen from plants heterozygous  $\underline{R}^r \underline{r}^g$ . The ears were harvested and examined for any non-mutants, which would be segregating either of the parental phenotypes,  $\underline{R}^r$  or  $\underline{R}^{st}$ ; however, no such ears were found. The kernels on the ears were examined and the mutants were tentatively classified for aleurone phenotype, i.e. colorless or near-colorless; the classification was verified in a later generation when the mutants were isolated in homozygous stock cultures. The distal marker,  $\underline{M}^{st}$ , was tested for by pollinating several  $\underline{r}(m)/\underline{r}^g$  plants of each mutant with  $\underline{R}^{st}$  pollen. The frequency of colored areas in the aleurone is much greater in  $\underline{r} \underline{M}^{st}/\underline{r} \underline{M}^{st}/\underline{R}^{st} \underline{M}^{st}$  kernels than in  $\underline{r} +/\underline{r} +/\underline{R}^{st} \underline{M}^{st}$  kernels; therefore, those mutants carrying  $\underline{M}^{st}$  could be identified.

A total of 262 ears was scored for seed color mutants, and the non-mutant  $\underline{R}^r$  and  $\underline{R}^{st}$  kernels totaled 50,515 and 49,446 respectively. Thirty-nine seed color mutants were obtained, and they have been characterized for aleurone phenotype, plant color, and proximal and distal genetic markers. These data are presented in Table 1.

Table 1 - Classification of the seed color mutants isolated from the cross  $+ \underline{R}^r +/g \underline{R}^{st} \underline{M}^{st} \times g \underline{r}^g +$  for aleurone pigment and plant color, and for the distribution of the proximal and distal genetic markers.

Plant color	Constitution of proximal and distal markers			
	Non-recombinants		Recombinants	
	$+$ $+$	$g \underline{M}^{st}$	$+$ $\underline{M}^{st}$	$g$ $+$
	Near-colorless aleurone			
Green	0	2	8	1
Red	0	0	13	0
	Colorless aleurone			
Green	0	1	0	0
Red	<u>1</u>	<u>1</u>	<u>11</u>	<u>1</u>
	1	4	32	2

The data show that 32 of the 39 mutants received the proximal marker from the  $\underline{R}^r$  parental chromosome and the distal marker from the  $\underline{R}^{st}$  parental chromosome. Also, these 32 mutants were not of a single class but included both those with colorless and near-colorless aleurone, and those with red and green plant color. The seven other mutants were comprised of one that carried both markers from the  $\underline{R}^r$  parental chromosome, four that carried both markers from the  $\underline{R}^{st}$  parental chromosome, and two that carried the proximal marker from the  $\underline{R}^{st}$  parental chromosome and the distal marker from the  $\underline{R}^r$  parental chromosome.



It is evident from the data that the majority of mutants, regardless of aleurone phenotype or plant color, are associated with a single crossover in the R locus region. A certain proportion, perhaps all, of the seven exceptional mutants could be explained as instances of a mutation producing crossover occurring coincidentally with recombination between the R locus and either the proximal or distal genetic marker. Such coincident crossovers, barring interference, would be expected to give  $0.14 \times 39$  or five mutants carrying g (six were obtained), and  $0.06 \times 39$  or two mutants not carrying M<sup>st</sup> (three were obtained). The observed number of mutants in these two classes is, therefore, no greater than would be expected from coincident crossing over.

The two mutants carrying g and not M<sup>st</sup> require the seemingly unlikely occurrence of three coincident crossovers in a 20 unit chromosome segment. The expected frequency of such multiple crossover mutants, again barring interference, can be calculated as  $(.14 \times .06) \times 39$  or 0.3 mutants. Triple crossing over would appear to be an inadequate explanation for the occurrence of these two mutants. However, this may be another instance of the "negative interference" phenomenon observed at other loci in maize and in other organisms.

The above data support a conclusion that most, and possibly all, mutations to colorless and near-colorless aleurone in R<sup>r</sup> R<sup>st</sup> heterozygotes are associated with recombination, the mutants being composed of that portion of the R<sup>r</sup> chromosome proximal to the R locus, and that portion of the R<sup>st</sup> chromosome distal to the R locus. In referring the results of these and previous tests to the fine structure of the parental R<sup>r</sup> and R<sup>st</sup> alleles, a reasonable hypothesis could assume that the phenotype characteristic of R<sup>st</sup> is dependent on the presence of two closely linked components, and that these two components are separable by conventional genetic recombination. Stadler and Emmerling have presented evidence that the R<sup>r</sup> allele is composed of two such closely linked components, a plant color component (P) and a seed color component (S). A two component structure for R<sup>st</sup> would assume that the stippled phenotype is lost when a crossover occurs that separates the two units, and in the heterozygous combination tested above, R<sup>r</sup> R<sup>st</sup>, the crossover strand carrying the colorless or near-colorless mutant may or may not also carry the plant color component (P) from R<sup>r</sup>. A more detailed hypothetical structure of the R<sup>st</sup> gene is deferred, pending a more complete characterization of the 39 mutants isolated in the above test. At least one of the mutants with near-colorless aleurone and green plant color has shown evidence of back mutations to self-colored aleurone, and several mutants originally isolated with green plant color have, in later generations, given evidence of mutating to red plant color. Also, the important characteristic of paramutagenic action, both qualitative and quantitative, is yet to be determined.

4. Frequency of mutation of  $R^{lst}$  to  $R^{sc}$  in plants heterozygous  $R^{lst}/r^r(I)$  and  $R^{lst}/r^g$ .

The frequency of germinally recoverable mutations of  $R^{st}$  or  $R^{lst}$ , which differ only in the presence of a linked modifier on the  $R^{st}$  chromosome, to  $R^{sc}$  (self-colored aleurone) has been observed by several investigators to be greater when  $R^{st}$ , or  $R^{lst}$ , is homozygous than when it is heterozygous with  $r^r$  or  $r^g$ . These findings suggest that a meiotic or premeiotic interaction takes place between two  $R^{st}$  genes that reciprocally increases their instability.

In further investigations of this phenomenon use was made of paramutagenic, near-colorless aleurone mutants with red plant color that were obtained from plants heterozygous  $R^r R^{st}$ . The mutants were designated  $r^r(I)$ , and similar mutants from a more recent test have been shown to be associated with recombination in the  $R$  locus region (see above). The "I" is used in the notation to indicate that the mutants are paramutagenic. A small population of kernels homozygous for several different  $r^r(I)$  mutants was examined and no mutations to self-colored aleurone were observed. Since the  $r^r(I)$  mutants carry the paramutagenicity characteristic of  $R^{st}$ , but were not observed to mutate to self-colored aleurone, as does  $R^{st}$ , a test to determine the effect of  $r^r(I)$  mutants on the stability of  $R^{st}$  seemed appropriate.

Stocks for the test were obtained by pollinating  $R^r/r^r(I)$  and  $R^r/r^g$  plants with  $R^{lst}$  pollen. The  $R^{lst}/r^r(I)$  and  $R^{lst}/r^g$  kernels from the matings were planted and the resulting ears were pollinated with  $r^g$  pollen; the  $R^{lst}/r^g$  heterozygous combination was used as a control. Two independently occurring  $r^r(I)$  mutants were used,  $r^r(I)^1$  and  $r^r(I)^3$ . The self-colored aleurone kernels were selected and grown out for verification of germinal  $R^{sc}$  mutations. The plants from the self-colored kernels were scored for plant color, with the thought in mind that if any of the  $R^{sc}$  mutants did arise from mutations of  $r^r(I)$  to self-colored aleurone these mutants would very likely have red plant color; however, all  $R^{sc}$  mutants had green plant color. The data from the test are presented in Table 2.

The data clearly show that  $R^{lst}$  mutates to  $R^{sc}$  more frequently when heterozygous with  $r^r(I)$  than when heterozygous with  $r^g$ . The rate of mutation obtained in  $R^{lst}/r^r(I)$  heterozygotes is comparable to that previously obtained in  $R^{st} R^{st}$  and  $R^{lst} R^{lst}$  homozygotes, which was found to be 17.0, 28.3, and 19.9  $\times 10^{-4}$  in three independent tests (Ashman, Genetics 45:19; McWhirter, MNL 1961). Therefore, even though the  $r^r(I)$  mutants have lost the stippled phenotype they still possess two properties of the  $R^{st}$  allele: paramutagenic action, and that of acting on  $R^{st}$  genes to increase their instability. These data offer additional evidence for the compound nature of the  $R^{st}$  gene.

Table 2. Frequency of mutations of  $R^{1st}$  to  $R^{sc}$  when heterozygous with  $r^r(I)$  and  $r^g$ .

Heterozygous combination	Pedigree number	No. of $R^{1st}$ kernels	No. of $R^{sc}$ mutants	Rate of mutation $\times 10^{-4}$
$R^{1st}/r^r(I)^1$	R56	7,179	17	23.7
$R^{1st}/r^r(I)^3$	R58	7,318	26	35.5
Pooled		14,497	43	29.7
$R^{1st}/r^g$	R57	3,366	4	11.9
$R^{1st}/r^g$	R59	4,532	1	2.2
Pooled		7,898	5	6.3

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### 1. Evidence of heterofertilization in maize.

From one of our projects of corn breeding one interesting finding regarding heterofertilization was accidentally obtained. As part of a project for obtaining a new white flint variety for this area (São Paulo State and neighboring), a planting was made in an isolated plot of white kernels from segregating  $F_2$  ears of a cross yellow  $\times$  white, involving the local Cateto variety and flints from Colombia. At harvest 61 ears were found to be segregating white and yellow kernels. These ears are considered to be the result of plants from heterofertilized kernels (white endosperm  $y y$  and embryo  $Y y$ ). It is estimated that the total population was about 60,000 plants. So we had roughly 0.1% of segregating ears due to heterofertilization. If we assume the same proportion of non detected heterofertilized ears (i.e. both embryo and endosperm being recessive white) we come out with an estimate of about 0.2% of heterofertilization in this material.

The proportion of white and yellow kernels in these 61 ears is expected to follow the 1:1 ratio, since the plants should be heterozygous  $Y y$  and the bulk of the 60,000 surrounding plants were homozygous recessive  $y y$ . This was in fact the case, except that two ears had a highly significant  $X^2$  (0.1% level) and one had a  $X^2$  significant at the 5% level. All the others did not deviate significantly from the

expected 1:1 ratio. Excluding the two highly significant ears, the sample was a rather uniform one as can be seen by the breakdown of the  $\chi^2$ :

	D.F.	$\chi^2$
Sum of 59 $\chi^2$	59	55.16
Pooled $\chi^2$	1	0.31
Heterogeneity	58	54.85

All three ears with significant  $\chi^2$  had an excess of yellow kernels. The two ears with a highly significant  $\chi^2$  gave a segregation of 0.59 yellow: 0.41 white. Since there is no reason to admit that these plants should have preferential crossing between them, this excess of yellow kernels must be due to some amount of selfing. It can be shown that in order to give that proportion of yellow and white kernels these two plants probably had about 36% of selfing.

E. Paterniani

## 2. Some preliminary results on the effect of inbreeding on viability and variability in corn.

Morton, Crow and Muller (1956) gave a method for estimating the number of deleterious equivalents carried by a zygote in a given population, and we started work with this method in maize making crosses and selfings within a population of the race Cateto, in order to obtain different levels of inbreeding. 52 plants were selfed ( $F = 0.5$ ) and at the same time outcrossed at random with individuals of the same population (control,  $F = 0.0$ ). Some preliminary results can be reported:

a) Effect on viability as measured by germination rate - About 89% of the progenies obtained by selfing showed a nearly perfect germination, as did all those obtained by outcrossing, and 11% showed a decrease in germination of about 13%, i.e. a germination rate of 87%.

### b) Effect on variability of seedling height

b.1) Seedling height (seedlings one week old) was measured in the greenhouse. In general, those progenies which showed decrease in germination rate, showed also a greater variability in height of the survivors. Thus it can be concluded preliminarily and for this material, that those genes, which act in increasing mortality of seedlings, are polygenes with a general deleterious effect on biological activity, showing cumulative effects.



b.2) The squared coefficient of variability (C.V.)<sup>2</sup> for height, within selfed progenies, ranged from 67.2 to 1444.0 while for the outcrossed the range was from 62.4 to 285.6.

b.3) As was shown by A. Robertson (1952), dominant genes act by increasing genotypic variability within inbred lines in the first generations of inbreeding (when compared to random mating conditions). Additive genes act decreasing the genotypic variance within inbred lines. In the present case it was observed that:

b.3.1) 26 progenies, obtained by selfing, showed a greater (CV)<sup>2</sup> than the respective "controls", which may be the result of the action of recessive genes in homozygous condition and also perhaps the result of homeostasis of the "controls".

b.3.2) 12 of these showed a significantly lower (CV)<sup>2</sup> than the "controls". This can be explained, if we assume that additive genes diminished the genotypic variability within inbred lines, in accordance with Robertson's argument.

b.3.3) 14 of the progenies obtained from selfing remained with the same variability as the "control" progenies. An equilibrium between dominant and additive genes can perhaps explain these observations.

The experiment will be repeated in order to obtain further supporting results.

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#### 1. Crossing over and disjunction in trivalent configurations containing corn-Tripsacum interchange chromosomes.

In a 21 chromosome stock in which a portion of the short arm of the distal region of chromosome 2 has been exchanged for a corresponding region of a *Tripsacum* chromosome, trivalent configurations are found in 95-98 percent of sporocytes at pachytene. These trivalent configurations

always or nearly always involve preferential pairing of the two homologous corn segments for the distal region of chromosome 2S. These trivalent configurations are frequently unpaired in the region of the interchange. Since crossover frequency in corn has been found to be markedly increased adjacent to regions of synaptic failure in certain heterozygous aberration configurations, the crossover frequency between the two homologous corn distal 2S segments in the trivalents described above was considered to be a matter of interest. Stocks were constructed to test this frequency in which recessive  $ws_3$   $lg_1$   $gl_2$  were carried only on the corn 2S segment attached to the *Tripsacum* centromere. Disjunction of the two corn centromeres from the *Tripsacum* centromere occurs with a frequency of only about 4 percent. From this type of disjunction gametes carrying the chromosome with the *Tripsacum* centromere are deficient for all of the long arm of chromosome 2 and about half of the short arm, and are inviable. From test crosses of 21 chromosome plants of the constructed stock, 20 chromosome recessive progeny arise only from crossing over between the two chromosome 2S distal homologues followed by disjunction at anaphase I of the two chromosomes involved in this chiasma, and 21 chromosome recessive progeny arise only from crossing over in this region followed by non-disjunction at anaphase I of the two chromosomes involved in this chiasma. Twenty-one chromosome progeny are easily identified because they are unfailingly pollen sterile while 20 chromosome progeny have completely normal pollen. These testcrosses are therefore a simple test not only of crossover frequency in distal 2S in these trivalent configurations but also of adjacent distribution from chiasmata.

Results were as follows: for the  $ws_3$ - $lg_2$  region 22/306 20 chromosome recombinants, 2/222 21 chromosome recombinants; for the  $lg_1$ - $gl_2$  region 42/306 20 chromosome recombinants, 3/222 21 chromosome recombinants; for the region proximal to  $gl_2$  51/306 20 chromosome recombinants, 1/222 21 chromosome recombinants. This is interpreted as 18 percent crossing over in the  $ws_3$ - $lg_1$  region (14 percent followed by disjunctive distribution, 4 percent non-disjunctive); 32 percent crossing over in the  $lg_1$ - $gl_2$  region (27 percent disjunctive, 5 percent non-disjunctive); 35 percent crossing over proximal to  $gl_2$  (33 percent disjunctive, 2 percent non-disjunctive). Total non-disjunction from a chiasma in this portion of the trivalent was about 14 percent (as compared to the 4 percent of non-disjunction which has been found for the corn centromeres).

Crossover frequency in the  $ws_3$ - $lg_1$  and  $lg_1$ - $gl_2$  regions did not differ significantly from standard expectation. A maximal estimate of the extent of the genetic map of chromosome 2S included in the interchanged segment is 54 units (based on unpublished data of Dr. E. B. Patterson and Dr. E. G. Anderson from genetic studies of translocations, and the cytological findings of Longley (1958). A maximal estimate of the probable extent of genetic map proximal to

$gl_2$  actually synapsed at pachytene and therefore available for crossing over (if this occurs at pachytene) based on 115 measurements of pachytene trivalent configurations is 114 units. The amount of recombination found proximal to  $gl_2$  in this experiment did not differ significantly at the 5 percent level from standard expectation based on these maximal estimates (chi square - 3.47 for 20 chromosome progeny, d.f. 1). Since all the estimates were intentionally maximized, the results are inconclusive, and it may be that crossover frequency was in fact increased somewhat in the region synapsed proximal to  $gl_2$ . In any event there does not seem to have been enough increase in crossover frequency in this region to compensate for the crossover suppression in the region at synaptic failure. Further tests are planned in which markers on both sides of the point of interchange may be utilized with progenies sufficiently large for studies of interference.

M. P. Maguire

## 2. Recombination inhibition and enhancement in disomic plants heterozygous for a substitution from *Tripsacum*.

In disomic plants which are heterozygous for a segment derived from a *Tripsacum* chromosome substituted for approximately the distal 60 percent of the short arm of chromosome 2, pachytene synapsis is usually normal throughout the complement. The *Tripsacum* segment has been shown to carry normal dominants for the chromosome 2S markers  $ws_3$   $lg_1$   $gl_2$ , but in test crosses crossing over rarely occurs between the *Tripsacum* and corn segments, a region estimated to contain 54 map units. Preliminary tests have indicated, however, that crossing over may be greatly increased elsewhere in chromosome 2 in plants of this constitution. Forty-four percent recombination (215/484) was found in the  $gl_2-v_1$  region although it is probable that only about 29 crossover units were available for crossing over in this region, 5 of these on the long arm side of the centromere. Tests are planned using additional marker loci to determine the degree and distribution of possible crossover frequency increases outside the region of crossover suppression. The extent of this region of crossover suppression may be varied by the use of rare recombinants between the *Tripsacum* and corn segments.

M. P. Maguire

## 3. Behavior of *Tripsacum* chromosomes added to the normal corn complement.

Studies are continuing on the genetic and synaptic homologies of *Tripsacum* chromosomes in the corn complement. A number of new stocks are currently available for tests. In one of these an extra chromosome from *Tripsacum*, having physical properties similar to chromosome 9 or 10



of corn, does not synapse with any of the corn chromosomes. Twenty-one chromosome plants are indistinguishable from 20 chromosome plants on the basis of gross morphology. Test crosses with multiple recessive stocks give normal disomic ratios for all markers tested with the possible exception of  $g_1$  for which classification was difficult and recessive progeny seemed to be deficient. Tests with chromosome 10 tester stocks are currently underway.

This *Tripsacum* chromosome is particularly interesting, however, because of the fact that it is transmitted by 21 chromosome plants through the egg to about 84 percent of its progeny. Twenty-one chromosome plants are highly pollen and ovule sterile. In microsporogenesis the *Tripsacum* chromosome lags in about 89 percent of anaphase I cells. It divides in about 54 percent of pollen mother cells and is apparently included in telophase I nuclei without having divided in most of the remainder. In those cases where the *Tripsacum* chromosome divides in the first division it lags at anaphase II and is sometimes excluded from telophase II nuclei so that it is present in about 30 percent of microspores. Scant data available from selfing are consistent with the interpretation that the *Tripsacum* chromosome actually is transmitted through the pollen with about the same frequency with which it occurs there. So far no anaphase configurations have been found at megasporogenesis, but the basal megaspore has been functional in all of the 44 ovules examined which were at the appropriate stage for such a determination. Genetic tests indicate that parthenogenesis cannot explain the high transmission frequency of the *Tripsacum* chromosome, and it is thought unlikely that it divides twice or has extra centric activity in megasporogenesis since neither of these seems to occur in microsporogenesis. The most likely explanation for the high transmission frequency at present appears to be that eggs or embryos not carrying the *Tripsacum* chromosome are strongly selected against in the maternal background in which this *Tripsacum* chromosome is present.

M. P. Maguire

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1. Teopod-2 and  $sr_2$  in relation to preferential segregation in chromosome 10.

In crosses of  $Tp_2$  with chromosome 10 stocks, it was found that  $R-Tp_2$  showed about 36% recombination, while  $g-Tp_2$  showed independence. This placed  $Tp_2$  distally to  $R$  in the long arm of chromosome 10. In a cross with T9-10b (break in short arm of chromosome 10),  $Tp_2$  showed independence to  $wx$ , and so, corroborated the location of  $Tp_2$  far distally on the long arm of chromosome 10.



Later we combined  $Tp_2$  with Rhoades's abnormal 10, and crossed it to  $sr_2$ . Abnormal 10 and  $sr_2$  came to us from Maize Genetic Coop. stocks. The one segregating  $sr_2$  and  $R:r$ , showed an  $R-sr_2$  recombination of 25%.

In the experiment presented in Table 1, which includes four points, several striking results are noticeable. The following brief comments are offered as tentative suggestions.

- a. - Locus  $sr_2$  is responsible for, or closely associated with, preferential segregation, (a neocentromeric locus?), as revealed by the asymmetrical frequencies in members of complementary classes.
- b. - The region distal to  $sr_2$  concentrates an enormous amount of crossingover. More than half of the total of contributed gametes originated as crossovers in the region between  $sr_2$  and  $Tp_2$ .
- c. - We did not make cytological verifications of the distribution of the abnormal piece of chromosome 10 among the progeny. But if we assume that the favored classes and the presence of abnormal 10 are correlated (as obtained by Rhoades), then the gametes ( $r-Sr_2-tp_2$ ) indicated in Table 1 as a product of single crossovers in region-2, must contain the abnormal 10 piece, being really double crossovers (2+3). Also, the complementary and less favored gametes ( $R-sr_2-Tp_2$ ) must be double crossovers (2+3) deprived of abnormal 10.
- d. - There is indication of incompatibility of the allele  $sr_2$  and the piece of abnormal 10 which prevents their inclusion in the same gamete. The combination  $sr_2$ -abnormal 10 in the same chromosome (as the single crossover in region 2) is believed to be inviable.
- e. - We may infer that the crossover activity in the region distal to  $Tp_2$  is as high as that in the region  $sr_2-Tp_2$ , the majority of effective gametes being double crossovers (2+3) as a result of a balanced mechanism.
- f. - Another, and altogether different interpretation of the data, would be that  $Tp_2$  is not located in chromosome 10, but exhibits a spurious association with it.

Table 1. Linkage Data from the Cross;  
(1)

$r^r + Tp_2$ abn.				$r^r sr_2 +$ N				X	$r^r sr_2 +$ N				Total	Ratio of R:r on ear
$R^G$	$sr_2$	$+$	N	$r^r$	$sr_2$	$+$	N		$r^r$	$sr_2$	$+$	N		
Constitution of chromosome 10 in maternal gametes														
(0)	(0)	(1)	(1)	(2) or (2+3)?	(2) or (2+3)?	(1+2)	(1+2)							
r	R	r	R	r	R	r	R							
$Sr_2$	$sr_2$	$sr_2$	$Sr_2$	$Sr_2$	$sr_2$	$sr_2$	$Sr_2$							
(+)(2)	(-)	(-)	(+)	(+)	(-)	(?)	(?)							
$Tp_2$	$tp_2$	$tp_2$	$Tp_2$	$tp_2$	$Tp_2$	$Tp_2$	$tp_2$							
53	23	2	6	67	18	0	0						49 R:146 r	
76		8		85		0						169	R = 25.1%	

(1) One ear obtained with 195 seeds.

(2) The signs (+) and (-) in this place indicate preferential segregation associated with the locus  $Sr_2$  as revealed by the asymmetrical frequencies of members of complementary classes.

R -  $sr_2$  recombination = 4.7% % R in total plants = 47/169 = 27.8%  
 R -  $Tp_2$  recombination = 55.0% %  $sr_2$  in total plants = 43/169 = 25.4%  
 $sr_2$  -  $Tp_2$  recombination = 50.9% %  $tp_2$  in total plants = 92/169 = 54.4%

% R in parental classes = 23/76 = 30.3%

% R in classes: non-crossover with  $sr_2$  locus = 41/161 = 25.4%  
 crossover with  $sr_2$  locus = 6/8 = 75%  
 % R in classes: non-crossover with  $tp_2$  locus = 23/76 = 30.3%  
 crossover with  $tp_2$  locus = 24/93 = 25.8%  
 %  $sr_2$  in classes: non-crossover with  $tp_2$  locus = 25/84 = 29.7%  
 crossover with  $tp_2$  locus = 18/85 = 21.2%  
 %  $sr_2$  in classes: non-crossover with R locus = 41/161 = 25.4%  
 crossover with R locus = 2/8 = 25%  
 %  $tp_2$  in classes: non-crossover with R locus = 23/76 = 30.3%  
 crossover with R locus = 69/93 = 74.2%  
 %  $tp_2$  in classes: non-crossover with  $sr_2$  locus = 25/84 = 29.7%  
 crossover with  $sr_2$  locus = 67/85 = 78.8%

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1. Genetics of tillering.

This past summer reciprocal crosses were made between translocation stocks and several stocks which are highly tillering in Massachusetts. These were Ladyfinger Pop, New York Flint, Golden Bantam Sweet Corn, Golden Cross Bantam Sweet Corn, a tillering stock obtained from Kermicle and another obtained from W. L. Brown. Backcrosses were also made from earlier Parker Flint-translocation  $F_1$ 's to each parental stock. Studies are continuing.

N. H. Nickerson

2. Responses of  $na_1/na_1$  to maleic hydrazide-indole butyric acid treatments.

Among a series of treatments on genetic forms involving several growth regulators and their combinations, a rather striking effect was noted. In a population segregating 1:1 for  $na_1/na_1$  and  $+/na_1$  a group of 17 plants which received MH one day and IBA the next throughout the growing season had no  $na$  plants manifested. The probability of these 17 plants being all  $+/na_1$  is .008 by one statistical approach; there is thus a significant indication that the effect is a real one. Backcrosses of most of these plants to  $na_1/na_1$  plants were obtained to verify their genetic constitutions in 1963. Studies will be continued further.

N. H. Nickerson  
M. T. Shealey

3. Other effects of maleic hydrazide on maize.

Differences noted between separate strains of Coop stocks were extremely marked. On the one hand, in such stocks as those carrying  $Vg$ , apparently no new mitoses would occur after treatment started; leaves subsequently produced became narrower from base to tip with the uppermost ones reduced to short bladeless midribs. On the other extreme, some stocks did not show any appreciable change from control plants, even though the dosage of MH was the same in all cases. MH suppressed expression of  $Kn$ , as did naphthalene acetic acid, but plants remained essentially as vigorous as controls.

N. H. Nickerson  
R. Colby

#### 4. Modification of expression of Vg.

Indole butyric acid caused a reduction in expression of Vg. In a population of 59 plants segregating 1:1 for Vg and normal, 1/4 plants, all receiving IBA, shed normal pollen and had glumes equal to +/+ control plants. Ligule growth, another manifestation of the Vg gene, was markedly less in 7 of the 1/4 plants, however. Under Massachusetts growing conditions, some pollen is formed by all Vg plants. Some homozygous Vg plants will be available to study this effect further in 1963. Plants heterozygous for Kn expressed the knotted condition under IBA treatments more strikingly than did controls.

N. H. Nickerson  
T. N. Emblar

#### 5. Response of milo and sorghum stocks to gibberellic acid.

A definite reduction in time of flowering varying from 10 days to two weeks compared to control plants has been obtained for three-dwarf, two-dwarf and one-dwarf stocks of sorghum. Milo maize of six different maturity gene combinations showed varying responses. Those with the shortest time of maturity (38 and 44 days) were drastically affected by GA; most plants died. As genetically-controlled time lengths to maturity increased, time from planting to anthesis (compared to controls of each group) shortened under GA treatments, as indicated.

50-day plants-----	7 days earlier than controls			
60-day plants-----	10 days	"	"	"
90-day plants-----	13 days	"	"	"
100-day plants-----	16 days	"	"	"

It should be emphasized that under Massachusetts growing conditions 50-day plants take nearly 80 days to reach anthesis. It has been suggested (and data have been obtained) by Dr. Lane at Beltsville that the maturity genes are photoperiod-sensitive genes.

N. H. Nickerson  
P. R. Kremer

#### 6. Increase in dry weight upon treatment with a naturally-occurring growth substance.

In 5-plant samples of 38-day and 44-day milo treated daily with a growth substance recently isolated from some members of the cabbage family, increases in dry weight were obtained which were two to three times greater than dry weights of controls. Studies are continuing to determine whether the effect is repeatable with this and other closely allied substances, whether it can be achieved with less frequent treatments, and how effective treatment is when begun at specific plant ages. Studies also are being run on mice to determine carcinogenic properties of these substances.

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1. A test for a cytoplasmic component of the R paramutation system.

The stippled allele ( $\underline{R}^{st}$ , spotted aleurone, green seedling) seemingly is unaltered in either aleurone expression or paramutagenic action in  $\underline{R}^r \underline{R}^{st}$  plants, in which  $\underline{R}^r$  (colored aleurone, red seedling) invariably is changed to a weakly pigmenting, paramutant form,  $\underline{R}^{r'}$ . (The tests made, however, would not have disclosed small changes in  $\underline{R}^{st}$  action.)

One possible explanation for this stability of stippled in  $\underline{R}^r \underline{R}^{st}$  heterozygotes is that  $\underline{R}^{st}$  produces and releases into the cytoplasm a specific product which then mediates the regularly observed change in  $\underline{R}^r$  in the homologous chromosome. The following tests, with W22 inbred stocks, for the occurrence of such a cytoplasmic intermediate substance have given negative results.

Table 1 (See footnotes)

Mating	No. ♂♂ tested on paired ♀♀	Av. color score of $\underline{R}^g \underline{r}^r \underline{r}^r$ kernels only
(1) $\underline{r}^r \underline{r}^r \text{ ♀} \times \underline{R}_4^g \underline{R}_4^g \text{ ♂}$ (control)	14	6.04
(2) $\underline{R}^{st} \underline{r}^r \text{ ♀} \times \underline{R}_4^g \underline{R}_4^g \text{ ♂}$	14	6.19
Difference		0.15

$$t = 2.206 \quad (t_{.05} = 2.160) \quad \text{Doubtfully significant}$$

<sup>1</sup>  $\underline{r}^r$  = colorless aleurone, red seedling (non-paramutagenic)

<sup>2</sup>  $\underline{R}_4^g$  = colored aleurone, green seedling, a highly paramutable (in  $\underline{R}^g \underline{R}^{st}$ ) mutant from standard  $\underline{R}^r$ .

<sup>3</sup>  $\underline{R}_4^g \underline{R}^{st} \underline{R}^{st}$  and  $\underline{R}_4^g \underline{r}^r \underline{r}^r$  kernels yield green and red seedlings, respectively, on sprouting, and so are readily separable following scoring for aleurone color.

<sup>4</sup> Kernel color was scored on a scale in which 1 represents colorless and 7 complete pigmentation.

The rationale of the test made is that if  $\underline{R}^{st}$  forms a cytoplasmic element of the kind in question then the female gametophytes involved in mating (2), in Table 1, and the derived endosperm, will carry the factor, whereas those concerned in mating (1) will lack it. Accordingly, if the cytoplasmic element promotes paramutation of  $\underline{R}^g$  in the endosperm, the  $\underline{R}_4^g \underline{r}^r \underline{r}^r$  kernels from mating (2) will have a lower average color score than those from mating (1). The data in Table 1 show that this is not the result observed. In fact, there is a small, but doubtfully significant difference in the opposite direction, the possible meaning of which will be considered later.

The second experiment, the results of which are summarized in Table 2, was of the same design as the first but the male parents used in pollinating paired ?? in this case were  $\underline{R}_6^g \underline{R}_6^g$  plants.  $\underline{R}_6^g$  is a comparatively stable paramutant form (extracted initially from  $\underline{R}_6^g \underline{R}^{st}$ ) of  $\underline{R}_6^g$ , another green seedling mutant from standard  $\underline{R}^r$ . The aleurone pigmenting value of  $\underline{R}_6^g$ , when tested in the conventional way, is about half that of  $\underline{R}_6^g$  (or  $\underline{R}_4^g$ ) on the 1-7 scale. It was thought that  $\underline{R}_6^g$ , by virtue of its known paramutability and inherently much weaker pigmenting action, might be a more sensitive tester for a paramutagenic cytoplasmic element than the  $\underline{R}_4^g$  allele used in the first experiment.

Table 2

Mating	No. ♂ tested on paired ??	Av. color score of $\underline{R}_6^g \underline{r}^r \underline{r}^r$ kernels only
(3) $\underline{r}^r \underline{r}^r \text{ ♀} \times \underline{R}_6^g \underline{R}_6^g \text{ ♂}$ (control)	15	2.81
(4) $\underline{R}^{st} \underline{r}^r \text{ ♀} \times \underline{R}_6^g \underline{R}_6^g \text{ ♂}$	15	3.38
Difference		0.57

$$t = 5.072^{**} \quad (t_{(.001)} = 4.140) \quad \text{Very highly significant}$$

Again the ( $\underline{R}_6^g \underline{r}^r \underline{r}^r$ ) kernels from the matings in which  $\underline{R}^{st} \underline{r}^r \text{ ♀♀}$  are involved are not less pigmented than kernels of the same genotype from mating (3). On the contrary, they are more darkly colored, on the average, by an amount about equal to one-half class interval on the 1-7 scale. Furthermore, the difference in this case is very highly significant statistically.

Neither experiment (1) nor experiment (2), therefore, affords any evidence that the  $r^r$  allele derived from  $R^{st}r^r$  plants is accompanied by a cytoplasmic element that depresses the pigment-producing action of a paramutable  $R$  gene introduced into the endosperm through the pollen.

The observed small excess in score of  $R_4^g r^r r^r$  seeds from  $R^{st}r^r \text{ } \text{ } \times R_4^g R_4^g$  crosses over that from the  $r^r r^r \text{ } \text{ } \times R_4^g R_4^g$  matings in experiment 1, and the more pronounced difference in the same direction in experiment 2 appear to be meaningful.

A few years ago it was observed that if plants homozygous for one or another  $R$ -pale allele (conditioning very dilute aleurone color) were pollinated with  $R^{st} R^{st}$  the background color on the resulting kernels (i.e., in the areas between the solidly pigmented spots conditioned by  $R^{st}$ ) often was enhanced, as compared with that of  $R$ -pale selfed. The enhancement was not inherited, and so was adjudged not to be due to paramutation of the  $R$ -pale gene. The probable explanation of the phenomenon appeared to be that under the action of stippled (considered as an inhibited self-color gene that mutates frequently in the endosperm to the active form) anthocyanin precursors were accumulated in the  $R^{st}/R$ -pale/ $R$ -pale aleurone cells in amounts above the level characteristic of homozygous  $R$ -pale. Additional pigment was then synthesized by  $R$ -pale from the added supply of precursors.

The observed intracellular enhancement of aleurone pigment formation by  $R^{st}$ , as just described, raised the question whether the phenomenon was expressed in grosser form also as an interaction between stippled kernels and a second class of seeds, on the same ear. This issue was directly relevant to the present experiments because the comparison being made was between  $r^r$ -carrying kernels borne on  $R^{st}r^r$  and  $r^r r^r$  plants, respectively. Evidence has now been obtained that there is, in fact, such a kernel interaction.

Mixtures of pollen were prepared from  $R_6^g R_6^g$  and  $R^{st} R^{st}$  plants which were then applied to  $r^r r^r$  individuals. The resulting  $R_6^g r^r r^r$  kernels were found to be darker, on the average, by a value of 0.27 class intervals on the 1-7 color scale, than  $R_6^g r^r r^r$  seeds from  $r^r r^r \text{ } \text{ } \times R_6^g R_6^g$  control matings. The difference was highly significant statistically. It is possibly meaningful also that, whereas the effect of kernels carrying  $R^{st}$  in single dose was to raise the color score of the accompanying class of seeds by 0.27 class intervals, the action of the allele in double dose was to increase the corresponding value to 0.57, or about twice as much (Table 2).

This pigment-enhancing "side-effect" of stippled tends, of course, to vitiate the present test for a cytoplasmic component in the  $\underline{R}$  paramutation system. If a cytoplasmic element that depresses  $\underline{R}$  aleurone pigmentation is present in the  $\underline{r}^{\text{st}}$  segregates from  $\underline{R}^{\text{st}}\underline{r}^{\text{st}}$  ♀♀, its effect is exceeded by the oppositely directed inter-kernel action of stippled.

R. A. Brink

2. Relative paramutagenic capacities of the paramutant forms of  $\underline{R}^{\text{G}}$  mutants derived from the standard  $\underline{R}^{\text{r}}$  allele.

It has been found that the standard  $\underline{R}^{\text{r}}$  allele and its  $\underline{R}^{\text{G}}$  mutant derivatives not only become heritably reduced in pigmenting action when passed through a heterozygote with the stippled ( $\underline{R}^{\text{st}}$ ) allele but that they also acquire the capacity to promote a similar, though smaller, reduction in pigmenting action when combined with other paramutable genes (Brown and Brink, Genetics 45:1313-1316, 1960). The data reported here indicate that ten  $\underline{R}^{\text{G}}$  alleles independently derived by mutation from standard  $\underline{R}^{\text{r}}$  are indistinguishable from one another with regard to the level of paramutagenic activity acquired in heterozygotes with  $\underline{R}^{\text{st}}$ .

Pollen from each of twelve  $\underline{R}^{\text{r}}\underline{R}^{\text{r}}$  plants was applied to silks of  $\underline{R}^{\text{G}}\underline{R}^{\text{st}}$  plants representing the ten  $\underline{R}^{\text{G}}$  alleles. Progeny from a total of 111 successful pollinations of this type were grown in the following season, and two randomly selected  $\underline{R}^{\text{r}}\underline{R}^{\text{G}}$  plants from each family were testcrossed to  $\underline{r}^{\text{G}}\underline{r}^{\text{G}}$  pistillate parents. In this way,  $\underline{R}^{\text{G}}$  genes derived from nine to twelve  $\underline{R}^{\text{G}}\underline{R}^{\text{st}}$  plants in the case of each  $\underline{R}^{\text{G}}$  allele were combined with standard  $\underline{R}^{\text{r}}$  genes from a common source. Differences in paramutagenic competence among the paramutant forms of the various  $\underline{R}^{\text{G}}$  alleles should be reflected in this test as differences in the level of pigmenting action of  $\underline{R}^{\text{r}}$  genes in the corresponding groups of  $\underline{R}^{\text{r}}\underline{R}^{\text{G}}$  plants.

Forty-two  $\underline{R}^{\text{r}}\underline{r}^{\text{G}}$  kernels from each  $\underline{r}^{\text{G}}\underline{r}^{\text{G}}$  ♀ x  $\underline{R}^{\text{r}}\underline{R}^{\text{G}}$  ♂ test mating were scored against a standard set of kernels defining seven pigmentation classes. The mean  $\underline{R}^{\text{r}}\underline{r}^{\text{G}}$  scores from testcrosses of two  $\underline{R}^{\text{r}}\underline{R}^{\text{G}}$  plants from each of the 111  $\underline{R}^{\text{G}}\underline{R}^{\text{st}}$  x  $\underline{R}^{\text{r}}\underline{R}^{\text{r}}$  matings are shown in Table 1.

An analysis of variance performed on the data in Table 1 revealed no differences among the mean scores attributable to the  $\underline{R}^{\text{G}}$  alleles involved in the respective pedigrees ( $F = .751, P > .1$ ). The overall mean  $\underline{R}^{\text{r}}\underline{r}^{\text{G}}$  scores from testcrosses of  $\underline{R}^{\text{r}}\underline{R}^{\text{G}}$  plants involving individual  $\underline{R}^{\text{G}}$  alleles are all within the range 5.21 to 5.34. These results show that the ten  $\underline{R}^{\text{G}}$  mutants from standard  $\underline{R}^{\text{r}}$  are indistinguishable from one another with regard to the level of paramutagenic action acquired in heterozygotes with  $\underline{R}^{\text{st}}$ .



Table 1

Mean scores for  $\underline{R}^r \underline{R}^g$  kernels from testcrosses to  $\underline{r}^g \underline{r}^g$  pistillate parents of  $\underline{R}^r \underline{R}^g$  offspring of  $\underline{R}^r \underline{R}^{st} \text{♀} \times \underline{R}^r \underline{R}^r \text{♂}$  matings. Each entry represents the pooled tests of two  $\underline{R}^r \underline{R}^g$  plants.

$\underline{R}^r \underline{R}^r \text{♂}$ parent no.	$\underline{R}^g$ allele number									
	1	2	3	4	5	6	7	8	9	10
1	5.10	5.26	5.29	5.48	5.38	5.50	5.57	---	5.28	5.01
2	4.73	5.26	5.32	5.32	5.01	5.32	5.27	5.32	5.07	5.18
3	5.43	5.32	5.11	5.30	4.98	5.25	5.48	5.41	5.18	5.19
4	5.35	5.28	5.12	5.29	5.41	5.00	5.27	5.20	5.53	5.43
5	5.34	5.07	4.87	5.43	5.16	5.37	5.11	5.02	5.22	5.43
6	5.31	5.12	5.43	---	5.49	5.22	5.43	5.11	5.84	4.99
7	5.24	5.41	5.31	5.40	5.41	5.32	5.29	5.36	5.08	5.08
8	5.42	5.31	5.40	---	---	5.29	5.20	5.31	5.03	4.81
9	5.20	5.46	5.26	5.10	5.19	5.48	---	5.30	5.27	5.68
10	5.55	5.63	5.03	5.17	5.28	5.29	5.44	5.19	5.45	5.08
11	5.29	---	4.92	5.43	---	5.38	---	5.51	5.10	5.40
12	5.24	5.28	5.42	5.06	4.97	---	---	5.10	5.43	---
Mean	5.27	5.31	5.21	5.30	5.23	5.31	5.34	5.26	5.29	5.21

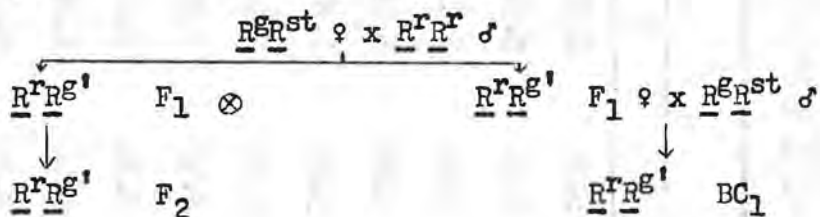
Previous studies (Brink, Brown, Kermicle and Weyers; Genetics 45:1297-1312, 1960) established that the pigmenting capacities of  $\underline{R}^r$  and eight of its  $\underline{R}^g$  mutant derivatives are reduced to a similar extent in heterozygotes with  $\underline{R}^{st}$ . Testcrosses to  $\underline{r}^g \underline{r}^g$  pistillate parents of  $\underline{R}^r \underline{R}^{st}$  and  $\underline{R}^g \underline{R}^{st}$  sib progeny from  $\underline{R}^r \underline{R}^g \times \underline{R}^{st} \underline{R}^{st}$  matings have confirmed that the  $\underline{R}^r$  and  $\underline{R}^g$  alleles are equally sensitive to the paramutagenic stimulus of  $\underline{R}^{st}$  when measured in terms of aleurone pigmenting action. The present test does not provide for an assessment of the relative paramutagenic potencies of paramutant  $\underline{R}^r$  and paramutant  $\underline{R}^g$ . The observation that ten  $\underline{R}^g$  mutants of independent origin do not differ in level of paramutagenic action acquired in heterozygotes with  $\underline{R}^{st}$ , however, agrees with the conclusion, implied by the results of tests of  $\underline{R}^r \underline{R}^{st}$  and  $\underline{R}^g \underline{R}^{st}$  plants, that the mutational events underlying the origin of the  $\underline{R}^g$  alleles involved in these studies have not altered the chromosomal elements concerned with paramutation.

Douglas F. Brown

### 3. Progressive secondary paramutation.

The reduction in the pigmenting action of paramutable R alleles which is induced by paramutant R' genes is slight when compared with that incited by  $\underline{R}^{st}$  (Brown and Brink, Genetics 45:1313-1316). Tests of  $\underline{R}^r \underline{R}^g$  and  $\underline{R}^r \underline{R}^g$  plants in F<sub>1</sub>, F<sub>2</sub>, and backcross 1 generations, which are described here, reveal that the extent of impairment in the pigmenting action of  $\underline{R}^g$  or  $\underline{R}^r$  is cumulative when the paramutant allele acts in two successive sporophytic generations.

$\underline{R}^r \underline{R}^g$  staminate testcross parents were produced according to the following mating plan:



Four lines, each containing a different  $\underline{R}^g$  allele, were established from single  $\underline{R}^g \underline{R}^{st} \text{ ♀ } \times \underline{R}^r \underline{R}^r \text{ ♂}$  pollinations. A single  $\underline{R}^r \underline{R}^g$  offspring from each  $\underline{R}^g \underline{R}^{st} \times \underline{R}^r \underline{R}^r$  mating was selfed to produce  $\underline{R}^r \underline{R}^g$  F<sub>2</sub> plants, and another was crossed to  $\underline{R}^g \underline{R}^{st}$  to produce  $\underline{R}^r \underline{R}^g$  backcross 1 (BC<sub>1</sub>) plants. The two  $\underline{R}^g \underline{R}^{st}$  plants in each pedigree were sibs grown from the same parental ear.

Table 1

Mean scores for  $\underline{R^r r^g r^g}$  kernels from testcrosses of control  $\underline{R^r R^g}$ ,  $\underline{R^r R^g}$  F<sub>1</sub>,  $\underline{R^r R^g}$  F<sub>2</sub>, and  $\underline{R^r R^g}$  BC<sub>1</sub> plants (first four lines of figures), and for  $\underline{R^g r^g r^g}$  kernels from testcrosses of control  $\underline{R^r R^g}$ ,  $\underline{R^r R^g}$  F<sub>1</sub>,  $\underline{R^r R^g}$  F<sub>2</sub>, and  $\underline{R^r R^g}$  BC<sub>1</sub> plants (last four lines of figures). The number of plants tested is given in parentheses following each mean score.

Allele tested	Staminate testcross parent class			
	Control	F <sub>1</sub>	F <sub>2</sub>	BC <sub>1</sub>
R <sup>r</sup>	9.05 (6)	8.27 (10)	7.65 (10)	7.36 (10)
R <sup>r</sup>	9.26 (6)	8.03 (7)	---	7.29 (7)
R <sup>r</sup>	9.05 (6)	8.44 (10)	7.71 (9)	7.65 (10)
R <sup>r</sup>	9.31 (6)	8.06 (10)	7.41 (10)	7.16 (10)
R <sup>g</sup> <sub>1</sub>	9.47 (6)	8.67 (10)	7.84 (10)	7.05 (10)
R <sup>g</sup> <sub>3</sub>	9.32 (6)	9.38 (10)	8.06 (5)	8.01 (10)
R <sup>g</sup> <sub>4</sub>	9.20 (6)	8.36 (10)	7.45 (10)	8.57 (10)
R <sup>g</sup> <sub>5</sub>	9.37 (6)	8.31 (9)	7.87 (4)	7.67 (10)
Mean	9.25	8.44	7.71	7.60
P*	<div style="display: flex; justify-content: space-around; align-items: center;"> <span>&lt; .001</span> <span>&lt; .001</span> <span>&lt; .001</span> </div>			

\* The probability under the null hypothesis determined by an analysis of variance.

$R^x R^g$  staminate testcross parents were derived by a similar scheme. In this case, four  $R^x R^g$  lines differing in the  $R^g$  allele involved were established each from a single  $R^g r^x \text{♀} \times R^x R^{st} \text{♂}$  pollination. One  $R^x R^g$  plant in each line was selfed and another was pollinated by an  $R^x R^{st}$  plant to produce  $R^x R^g F_2$  and  $R^x R^g BC_1$  offspring, respectively.

The progenies of the three matings in each line, along with control  $R^x R^g$  plants from  $R^g r^x \text{♀} \times R^x R^x \text{♂}$  crosses, were grown and testcrossed to  $r^g r^g \text{♀♀}$  in the same season. Samples of kernels from the testcross ears were first scored for aleurone pigmentation according to an eleven class scale, and then identified as to genotype by seedling test ( $R^x r^g r^g$  or  $R^x r^g r^g$  kernels produce red seedlings when germinated;  $R^g r^g r^g$  or  $R^g r^g r^g$  kernels produce green seedlings).

The mean scores for  $R^x r^g r^g$  kernels from testcrosses of control  $R^x R^g$ ,  $R^x R^g F_1$ ,  $R^x R^g F_2$ , and  $R^x R^g BC_1$  plants, and for  $R^g r^g r^g$  kernels from testcrosses of control  $R^x R^g$ ,  $R^x R^g F_1$ ,  $R^x R^g F_2$ , and  $R^x R^g BC_1$  plants are presented in Table 1. The scores in column 2 of the table represent the non-paramutant level of expression of the various  $R^x$  and  $R^g$  alleles; those in column 3 represent the level of pigmenting action of the same alleles following one generation of heterozygosity with a paramutant factor. It may be seen that the latter values are significantly lower on the average than the former, indicating that, as expected, secondary paramutation has taken place in the  $F_1$  generation  $R^x R^g$  and  $R^x R^g$  families as a whole.

The mean scores entered in columns 4 and 5 of Table 1, which were obtained from testcrosses of  $F_2$  and  $BC_1$   $R^x R^g$  and  $R^x R^g$  plants, indicate the pigmenting capacity of the several  $R^x$  and  $R^g$  alleles after a second generation in combination with a paramutant homologue. Comparisons between the scores in columns 4 and 5 on one hand and those in column 3 on the other, then, provide a test for progressive secondary paramutation in two sporophytic generations. The results are clear. The mean scores obtained by testcrosses of  $F_2$  and  $BC_1$  plants are significantly lower than those obtained by testcrosses of the related  $F_1$  plants. The paramutagenic effects of paramutant  $R^x$  genes, therefore, are persistent and cumulative through at least two successive sporophytic generations.

Douglas F. Brown



#### 4. Mutation rate of paramutant $R^r$ .

The mutation rate to  $r^r$  of paramutant  $R^r$  genes ( $R^{r'}$ ) has been measured in  $R^{r'}R^{r'}$  plants (obtained by selfing  $R^rR^{st}$  plants) and compared with that of the standard non-paramutant form of  $\bar{R}^r$  (see table).

There is a significant difference between the two rates ( $x^2 = 31.04$ ,  $p < .001$ ), that of the paramutant being about 60% of the non-paramutant rate. Reductions of a similar magnitude have been observed also with a series of paramutant and non-paramutant  $R^g$  alleles.

$R^r$ form	Putative mutants	No. tested	Verified as $r^r$ mutants	Corrected population size	Rate of mutation
Non-paramutant	292	233	232	182353	$12.72 \times 10^{-4}$
Paramutant	200	195	192	258325	$7.43 \times 10^{-4}$

R. A. Bray

## III. STOCKS AVAILABLE AND WANTED

## A. Wanted:

W. D. Bell, Pennsylvania State University

Unclassified chlorophyll-deficient mutants, particularly yellow-stripes, green-stripes, pale green or yellow seedlings.

R. G. Creech, Pennsylvania State University

All mutants showing positive allele tests with ae (amylose extender on chromosome 5) for genetic fine structure studies.

All mutants affecting carbohydrate synthesis in the corn kernel (phenotypic changes in endosperm). Please state genetic background, i.e. dent, floury, etc.

## B. Available:

E. H. Coe, Jr., Curtis Hall, University of Missouri

Glossy-1 mutable.

E. H. Coe, Jr. or M. G. Neuffer, Curtis Hall, University of Missouri

Purple-seeded translocation set, wx-marked for each chromosome. Useful in locating factors affecting aleurone color.

A. L. Hooker, 242 Davenport Hall, University of Illinois

Genetic stocks homozygous for a dominant gene (Ht) conditioning resistance to Helminthosporium turcicum. Two stocks are available: Source A resistance from GE440 and Source B from Ladyfinger popcorn. Each is a mixture of S<sub>3</sub> lines from crosses between the resistant sources and corn belt inbreds. Silking data is similar to WF9.

## D. L. Shaver, Biology Division, Brookhaven National Laboratory

The following tetraploid genetic stocks are available.  
In some cases it is not certain that all loci are  
"pure for the aleurone and plant color series":

A <sub>1</sub> A <sub>2</sub> C R P <sup>r</sup> et	a <sub>1</sub> A <sub>2</sub> C R P <sup>r</sup> B Pl	y-sm tester
ij Y seg. su	a <sub>2</sub> bt	b-lg <sub>1</sub> tester
A <sub>1</sub> A <sub>2</sub> B Pl C R P <sup>r</sup>	a <sub>1</sub> Dt A <sub>2</sub> C R P <sup>r</sup>	B lg <sub>1</sub> su
g Y seg. su	a <sub>2</sub> bt g	sh <sub>1</sub> wx
yg <sub>2</sub> sh <sub>1</sub> wx	y-pl tester	lg <sub>2</sub> gl <sub>6</sub>
C wx PVV	a <sub>1</sub> -lg <sub>2</sub> tester	

## H. G. Wilkes, Harvard University

Seed is available for research purposes to anyone  
interested from the following bulk collection sites.

Guerrero: Teosinte seed from Cerro de Los Chivos, Pochote,  
Zacatlancillo, and Mazatlán.

Valley of Mexico	Teosinte	Hybrids
Los Reyes	X	X
Chalco	X	X
Amecameca	X	X

There are also available seed envelopes from single  
teosinte plants which may be used for progeny test by  
those interested in the high level of hybridization  
found in the Valley of Mexico.

## IV. CHROMOSOME 1 LINKAGE DATA

(Compiled by D. R. Knott\*, University of Wisconsin)

## Linkage Group 1

Genes known to be in linkage group 1 are:

ad <sub>1</sub>	- adherent-1
ag	- grasshopper resistance
an <sub>1</sub>	- anther ear-1
as	- asynaptic
bm <sub>2</sub>	- brown midrib-2
br	- brachytic
f <sub>1</sub>	- fine stripe-1
Ga <sub>4</sub>	- gametophyte factor-4
ga <sub>6</sub>	- gametophyte factor-6
gl <sub>10</sub>	- glossy seedling-10
gs <sub>1</sub>	- green striped-1
hm	- helminthosporium resistance
Kn	- Knotted
ms <sub>17</sub>	- male sterile-17
P	- pericarp and cob color
pa	- pollen abortion
sr	- striate
ts <sub>2</sub>	- tassel seed-2
Ts <sub>3</sub>	- tassel seed-3
Ts <sub>6</sub>	- tassel seed-6
v <sub>19</sub>	- virescent seedling-19
Vg	- vestigial glumes
vp <sub>5</sub>	- vivipary-5
zb <sub>4</sub>	- zebra striped-4
zg <sub>2</sub>	- zigzag culm-2
z1	- zygote lethal

\*Present address: Department of Field Husbandry, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.



sr-0  
 ga<sub>6</sub>-15  
 zb<sub>4</sub>-19  
 ms<sub>17</sub>-23  
 ts<sub>2</sub>-24  
 P-26  
 z1-28  
 as-56  
 hm-64  
 br-81  
 Vg-85  
 f1-86  
 an<sub>1</sub>-104  
 Ts<sub>3</sub>-119  
 Kn-127  
 gs<sub>1</sub>-135  
 Ts<sub>6</sub>-158  
 bm<sub>2</sub>-161

## Possible locations:

ag - 12 (could be 39)  
 Ga<sub>4</sub> - 16  
 pa - 54 (near as, possibly  
 between P - as)  
 ad<sub>1</sub> - four units from an  
 (100 or 108)  
 Centromere - probably between 47  
 and 68, possibly  
 between as and br.

The distance from P to br is  
 problematical. Rhoades (J. of  
 Heredity 1950) lists it as 47 units,  
 presumably based on three point tests  
 with a translocation as the marker  
 between P and br. The best of Beadle's  
 data on three point tests with P-as-br  
 gives 55 units. Anderson's data  
 (Genetics 1941) with translocations  
 also gave about 55 units. Burnham  
 lists pa as being 30 units from P  
 and 34 units from br, or a total of  
 64. The distance here is listed as  
 55 - an average figure.

## LINKAGE DATA ON CHROMOSOME 1

Taken from the Maize Genetics Cooperation News Letters 1935-1951.

Phase	XY	Xy	xY	Two-Point Tests		Recom- bina- tions	%	Authority and year of newsletter
				xy	Total			
ad <sub>1</sub> an <sub>1</sub>	CB	247	7	10	199	463	17	
	RB	4	36	31	1	72	5	
						535	22	4.1 Emerson '38
Kn Ts <sub>3</sub>	RB	3	9	16	2	30	5	16.7 Emerson '40
Kn Ts <sub>3</sub>	RB	2	78	68	5	153	7	4.6 Murray '44
Kn Ts <sub>6</sub>	RB	8	27	47	13	95	21	22.1 Emerson '40
Ts <sub>6</sub> f <sub>1</sub>	CB	21	17	20	32	90	37	41.1 Lindstrom '40
Ts <sub>6</sub> gs <sub>1</sub>	CB	128	37	46	113	324	83	25.6 Lindstrom '37
v <sub>19</sub> bm <sub>2</sub>	RS	102	58	67	6	223		16.0 Emerson '41
zb <sub>4</sub> bm <sub>2</sub>	RS	487	103	144	23	757		46.0 Hayes '37
zb <sub>4</sub> br <sub>2</sub>	RS	448	142	152	12	754		31.1 Hayes '37
zb <sub>4</sub> f <sub>1</sub>	RS	455	135	158	9	757		28.0 Hayes '37
zb <sub>4</sub> P <sup>1</sup>	CS	266	24	5	64	359		6.9 Hayes '37
	CS	63	30	2	24	119		6.7 Hayes '37
	CB	67	6	3	67	143	9	6.3 Hayes '39

## Two-Point Data

From three-point tests with a translocation as a marker at one end

br an <sub>1</sub>	CB	39	6	8	43	96	14	14.6	Emerson '40
	CB	103	25	18	107	253	43	17.0	Emerson '40
br bm <sub>2</sub>	CB	27	10	15	37	89	25	28.2	Emerson '40
	ms <sub>17</sub> P	RB	5	41	38	3	87	8	9.1
sr P	RB	2	61	38	0	101	2	2.0	Emerson '38
	RB	3	181	189	9	381	12	3.0	Emerson '38
	RB					375	109	29.0	Anderson '37
	RB					230	78	34.0	Anderson '37
ts <sub>2</sub> P	RB					228	45	19.8	Anderson and Emerson, '37
	RB					129	27	20.9	Emerson '37
	RB	24	38	37	18	117	42	35.9	Emerson '38
	RB	20	64	54	20	158	40	25.3	Emerson '40
	CB	100	17	24	117	258	41	15.9	Emerson '40
	RB	31	67	52	20	170	51	30.0	Emerson '40
	RB					592	6	1.0	Emerson '37
ts <sub>2</sub> P	RB	1	93	115	2	211	3	1.4	Emerson '38
	CB	206	2	1	167	377	3	.8	Emerson '38
	RB	3	254	325	1	583	4	.7	Emerson '38
	RB	3	135	176	1	315	4	1.3	Emerson '38

Three Point Tests Where a Translocation was the Middle Marker

Region	Recombinations			Percent (P to br)	Total Plants	Authority
	1	2	1 & 2			
P br	71	108	28	52.1	449	Anderson '37
P br	60	58	19	47.0	332	Anderson '37
P br	5	29	0	40.0	85	Emerson '40
P br	19	34	10	37.1	170	Emerson '40

Three Point Tests  
Recombinations

Genes	0		1		2		1 & 2		Total	Authority
1. $\frac{+ + Kn}{ts_2 f_1 +}$	171	125	101	161	94	31	29	71	783	Bryan '37
		296		262		125		100		
				33.5%		16.0%		12.8%		
2. $\frac{+ Ts_3 +}{an + gs}$	62	70	17	0	5	22	7	0	183	Emerson '40
		132		17		27		7		
				9.3%		14.8%		3.8%		
3. $\frac{+ + Ts_6}{an gs +}$	58	37	16	6	13	7	10	5	152	Emerson '40
		95		22		20		15		
				14.4%		13.2%		9.9%		
4. $\frac{+ Ts_3 +}{an + bm_2}$	59	26	10	1	18	24	2	1	141	Emerson '40
		85		11		42		3		
				7.8%		29.8%		2.1%		
5. $\frac{+ + Ts_6}{an bm_2 +}$	81	41	23	4	5	0	0	0	154	Emerson '40
		122		27		5		0		
				17.5%		3.3%				
6. $\frac{+ Kn +}{an + gs}$	49	32	9	14	0	8	2	1	115	Emerson '40
		81		23		8		3		
				20.0%		7.0%		2.6%		

(2, 3, 4, 5, - segregations are very irregular)

Genes	Three Point Tests								Total	Authority
	Recombinations									
	0	1	2	1 & 2						
7. $\frac{+ Kn +}{an + bm_2}$	56 100	44	26 33 18.6%	7	24	14	7 7 3.9%	0	178	Emerson '40
8. $\frac{+ + +}{br f an}$	347		22 4.8%		77 17.0%		7 1.6%		453	Emerson '40
(data only from plants clearly $f_1$ )										
9. $\frac{+ + Ts_6}{br bm_2 +}$	93 176	83	94 153 46.1%	59	1	1 .6%	0 1 .3%	1	332	Lindstrom '40
10. $\frac{br f an}{+ + +}$	512 888	367	26 51 4.4%	25	78	125 203 17.5%	12 15 1.3%	3	1157	Emerson '41
11. $\frac{br f an}{+ + +}$	1109 1962	853	26 70 3.2%	44	92	73 165 7.5%	7 9 .4%	2	2206	Emerson '41
(Crossing over reduced by translocations)										
12. $\frac{ag P pa}{+ p +}$	65 149	84	8 18 7.8%	10	23	26 49 21.3%	6 14 6.1%	8	230	Horovitz and Marchioni '48
13. $\frac{Vg + +}{+ br bm_2}$	70 146	76	1 2 .8%	1	53	50 103 40.1%	5 6 2.3%	1	257	Sprague Journal Heredity 30: 143-145 '39
14. $\frac{+ Kn +}{an + gs}$	96		29 21.8%		7	5.3%	1 .8%		133	Emerson '41
15. $\frac{+ Kn +}{an + bm_2}$	146		47 18.4%		43	16.8%	20 7.8%		256	Emerson '41
16. $\frac{+ + +}{br f an}$	507		12 2.2%		4	.7%	17 3.1%		540	Emerson '41 (probable inversion)



Four Point Tests

	Recombinations										Total						
	0	1		2		3		1 & 2		1 & 3		2 & 3		1, 2 & 3			
$\frac{+ + Kn +}{br f_1 + bm_2}$	162	182	14	4	50	50	47	52	7	10	1	2	16	32	6	2	640
	347		18		100		99		17		3		48		8		
			2.8%		15.6%		15.5%		2.7%		.5%		7.5%		1.3%		
	Recombinations br-f <sub>1</sub> = 7.2% f <sub>1</sub> -Kn = 27.0% Kn-bm <sub>2</sub> = 24.1%																
	Authority: Bryan '38																
$\frac{hm + + +}{+ br f bm_2}$	897		75	134	14	60	327	435	49	15	60	73	13	78			2230
			209		74		762		64		133		91				
			9.4%		3.3%		34.2%		2.9%		6.0%		4.1%				
	Recombinations hm-br = 18.3% br-f = 10.3% f-bm <sub>2</sub> = 44.3%																
	Authority: Ullstrup and Brunson '45																
$\frac{+ + + Ts_3}{br f an +}$	104		11		22		19		4		1		5		4		170
	Recombinations br-f = 11.9% f-an = 20.6% an-Ts <sub>3</sub> = 17.1%																
	Authority: Emerson '41																
$\frac{+ + Ts_6 +}{an gs + bm_2}$	152		56		35		11		16		1		0		0		271
	Recombinations an-gs = 26.9% gs-Ts <sub>6</sub> = 19.2% Ts <sub>6</sub> -bm <sub>2</sub> = 4.4%																
	Authority: Emerson '41																

Four Point Tests - data derived from five point tests where a translocation was one end marker

$\frac{+ + + +}{br f an bm_2}$	167	6	35	118	3	6	17	352
	br-f = 4.2% f-an = 15.6% an-bm <sub>2</sub> = 40.1%							
	Authority: Emerson '41							
$\frac{* + + +}{br f an gs}$	123	2	16	60	3	1	2	207
	br-f = 2.9% f-an = 10.1% an-gs = 30.4%							
	Authority: Emerson '41							
$\frac{+ + + +}{br f an bm_2}$	81	1	23	52	3	10	1	171
	br-f = 8.2% f-an = 15.8% an-bm <sub>2</sub> = 36.8%							
	Authority: Emerson '41							
$\frac{+ + + +}{br f an gs}$	97	4	3	19	0	2	1	126
	br-f = 4.8% f-an = 4.8% an-gs = 17.5%							
	Authority: Emerson '41							
$\frac{+ + + +}{br f an bm_2}$	113	0	7	59				179
	br-f = 0% f-an = 3.9% an-bm <sub>2</sub> = 33.0%							
	Authority: Emerson '41							
$\frac{+ + + +}{br f an gs}$	161	12	4	26	1	2	1	207
	br-f = 7.2% f-an = 2.9% an-gs = 14.0%							
	Authority: Emerson '41							

Five Point Tests

Emerson 1941

	+   br +   f T1-5a + +   an +   bm <sub>2</sub>	+   br +   f +   an T1-3d + +   gs	+   br +   f +   an T1-3d + +   bm <sub>2</sub>	+   br +   f +   an T1-4 + +   bm <sub>2</sub>
0	142	119	59	185
1	5	5	2	4
2	6	4	4	4
3		1		4
4	72	9	36	125
1-2				
1-3	1			
1-4	5	1	1	3
2-3	1			1
2-4	3	1	1	3
3-4	2	1	2	8
1-2-3				
1-2-4				
1-3-4				1
2-3-4			1	
	<u>237</u>	<u>141</u>	<u>106</u>	<u>338</u>
	br-f=4.6%	br-f=4.2%	br-f=2.8%	br-f=2.4%
	f-T=4.2%	f-an=3.5%	f-an=5.7%	f-an=2.4%
	T-an=1.7%	an-T=1.4%	an-T=2.8%	an-T=4.1%
	an-bm <sub>2</sub> =34.6%	T-gs=8.5%	T-bm <sub>2</sub> =38.7%	T-bm <sub>2</sub> =41.4%

Five Point Tests (con't)

Emerson - 1941

	+ + + Ts <sub>3</sub> +	br f an + gs	+ + + Ts <sub>3</sub> +	br f an + bm <sub>2</sub>	+ + + Ts <sub>6</sub> +	br f an + gs +	+ + + Ts <sub>6</sub> +	br f an + bm <sub>2</sub>	+ Vg + + + +	br + f an bm <sub>2</sub>
0	88		68		82		26		164	
1	4		7		6		2		5	
2	21		15		32		12		1	
3	21		14		35		22		42	
4	33		30		31		1		103	
1-2					1		1			
1-3					5				4	
1-4			2		2				2	
2-3					3		3			
2-4	3		9		16				1	
3-4	16		5		19				15	
1-2-3										
1-2-4					1					
1-3-4					1					
2-3-4	2		1		1					
1-2-3-4										
	<u>188</u>		<u>151</u>		<u>235</u>		<u>67</u>		<u>337</u>	
br-f=	2.1%	br-f=	5.9%	br-f=	6.8%	br-f=	4.5%	br-Vg=	3.3%	
f-an=	13.7%	f-an=	16.6%	f-an=	23.0%	f-an=	23.9%	Vg-f=	6%	
an-Ts <sub>3</sub> =	21.3%	an-Ts <sub>3</sub> =	13.3%	an-gs=	27.2%	an-Ts <sub>6</sub> =	37.3%	f-an=	18.1%	
Ts <sub>3</sub> -gs=	28.7%	Ts <sub>3</sub> -bm <sub>2</sub> =	31.2%	gs-Ts <sub>6</sub> =	30.2%	Ts <sub>6</sub> -bm <sub>2</sub> =	1.5%	an-bm <sub>2</sub> =	35.9%	

Data giving only map distances:

p - 30 - pa - 34 - br Burnham - 1941

sr ms<sub>17</sub> - 1.7 - ts<sub>2</sub> - 1.3 - P - 1.5 - z1 br Emerson - 1943

sr Ga<sub>4</sub> - 10 - ms<sub>17</sub> - 3 - P br Emerson - 1946

Centromere is between 21.2 units to the right of P and 13 units to the left of

br Anderson - 1945

vp<sub>5</sub> is in the short arm of chromosome 1 Robertson - 1949

D. R. Knott



## V. REPORT ON MAIZE COOPERATIVE

During the past summer a large series of andromonoecious dwarfs was grown and each stock was tested for allelism with  $d_1$ ,  $d_2$ ,  $d_3$ ,  $d_5$ , and  $an_1$ . The results have not yet been fully summarized, but most of the newly-acquired traits represent alleles at one of the five tested loci. Each of the stocks is being extracted in more uniform background to determine whether some stocks may represent distinct alleles at a particular locus.

Considerable confusion has developed in the labelling of some of the glossies. In several instances, stocks from different sources carrying the same designation have proved to be non-allelic. During the past season all of the known glossies, together with new and unidentified glossies, were grown and intercrossed to eliminate duplication of stocks and permit simplifying records. Some of the glossies were also crossed to wx-marked translocations or to genetic testers to determine or confirm chromosomal locations.

Stocks of brachyotics, reduced, compact, and miscellaneous other mature plant dwarfs were increased and allele tested among themselves. In some cases, crosses were made to genetic or chromosomal testers to determine their chromosome locations.

About 900 families of permanently-lettered reciprocal translocations were grown to obtain fresh seed. Included were consecutive translocations from 1-2b to 4-9b. Crosses were made to obtain known homozygotes and heterozygotes and to preserve closely-linked genetic markers. All were outcrossed to adapted lines to increase vigor and standardize the maturity range. This material has not yet been catalogued for distribution.

Several hundred families of untested new chlorophyll traits from Dr. E. G. Anderson's collection were increased. Most of these have now been seedling tested for final evaluation. Some of the best traits, particularly those which survived as homozygotes in the field, were crossed to wx-marked translocations to determine chromosome locations. Most of the  $F_1$ 's were selfed or testcrossed in the current Florida generation.

The stock collection was moved this winter to improved laboratory facilities provided by the Botany Department. A 45° cold room with capacity for storage of a considerable quantity of seed samples is now in operation.

During 1962, 1932 seed samples were supplied in response to 100 letters of request. Both figures represent an all-time high. Distribution of seed samples was about thirty-five percent higher than in the previous peak year.

The following listing of available stocks is a supplement to those listed last year. Requests for stocks or for copies of stock lists should be sent to the Botany Department, University of Illinois, Urbana, Illinois.

Chromosome 1

ad<sub>1</sub> an<sub>1</sub> bm<sub>2</sub>  
 an<sub>1</sub> Kn bm<sub>2</sub>  
 as  
 br<sub>1</sub> Vg  
 Kn  
 Kn Ts<sub>6</sub>  
 lw<sub>1</sub>  
 pCR  
 PCW  
 P<sup>MO</sup>  
 P<sup>RR</sup> ad<sub>1</sub> an<sub>1</sub>  
 P<sup>RR</sup> ad<sub>1</sub> bm<sub>2</sub>  
 P<sup>RR</sup> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>  
 P<sup>RR</sup> br<sub>1</sub> f<sub>1</sub> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>  
 P<sup>VV</sup>  
 P<sup>WR</sup> bm<sub>2</sub>  
 P<sup>WR</sup> gs<sub>1</sub> bm<sub>2</sub>  
 P<sup>WW</sup> br<sub>1</sub> f<sub>1</sub> bm<sub>2</sub>  
 P<sup>WW</sup> br<sub>1</sub> f<sub>1</sub> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>  
 P<sup>WW</sup> hm br<sub>1</sub> f<sub>1</sub>  
 sr<sub>1</sub>

Chromosome 1 (continued)

sr<sub>1</sub> P<sup>WR</sup> an<sub>1</sub> bm<sub>2</sub>  
 sr<sub>1</sub> P<sup>WR</sup> bm<sub>2</sub>  
 sr<sub>1</sub> P<sup>WR</sup> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>  
 sr<sub>1</sub> zb<sub>4</sub> P<sup>WW</sup>  
 ts<sub>2</sub> P<sup>WW</sup> br<sub>1</sub> bm<sub>2</sub>  
 Ts<sub>6</sub>  
 v<sub>19</sub> bm<sub>2</sub>  
 Vg  
 Vg an<sub>1</sub> bm<sub>2</sub>  
 vp<sub>5</sub>  
 vp<sub>8</sub>  
 zb<sub>4</sub> ms<sub>17</sub> P<sup>WW</sup>  
 zb<sub>4</sub> P<sup>WW</sup> bm<sub>2</sub>  
 zb<sub>4</sub> P<sup>WW</sup> br<sub>1</sub>  
 zb<sub>4</sub> ts<sub>2</sub> P<sup>WW</sup>  
 an<sub>6923</sub>-bz<sub>2</sub> (includes locus of  
an<sub>1</sub>)  
 necrotic 8147-31

Chromosome 2

al lg<sub>1</sub> gl<sub>2</sub> B sk  
 al lg<sub>1</sub> gl<sub>2</sub> b sk  
 ba<sub>2</sub>

Chromosome 2 (continued)

$fl_1$   
 $lg_1 gl_2 B$   
 $lg_1 gl_2 b$   
 $lg_1 gl_2 b fl_1 v_4$   
 $lg_1 gl_2 b fl_1 v_4 Ch$   
 $lg_1 gl_2 B gs_2$   
 $lg_1 gl_2 b gs_2 sk$   
 $lg_1 gl_2 b gs_2 v_4$   
 $lg_1 gl_2 b gs_2 v_4 Ch$   
 $lg_1 gl_2 B sk v_4$   
 $lg_1 gl_2 b sk v_4$   
 $lg_1 gl_2 b sk fl_1 v_4$   
 $lg_1 gl_2 B v_4$   
 $lg_1 gl_2 b v_4$   
 $lg_1 gl_2 b v_4 Ch$   
 $lg_1 gs_2 b v_4$   
 $ws_3 lg_1 gl_2 B$   
 $ws_3 lg_1 gl_2 b$   
 $ws_3 lg_1 gl_2 b fl_1 v_4$   
 $ws_3 lg_1 gl_2 B sk$   
 $ws_3 lg_1 gl_2 b sk$

Chromosome 3

$A_1 ga_7; A_2 C R$   
 $A_1 sh_2; A_2 C R$

Chromosome 3 (continued)

$A^d-31; A_2 C R$   
 $a^p et; A_2 C R Dt_1$   
 $a_1; A_2 C R B Pl dt_1$   
 $a_1 et; A_2 C R Dt_1$   
 $a_1 sh_2; A_2 C R Dt_1$   
 $a_1 sh_2; A_2 C R dt_1$   
 $a_1^{st} sh_2; A_2 C R Dt_1$   
 $a_1^{st} et; A_2 C R Dt_1$   
 $a_{x-1}; A_2 C R$   
 $a_{x-3}; A_2 C R$   
 $ba_1$   
 $Cg$   
 $cr_1$   
 $d_1$   
 $d_1 gl_6$   
 $d_1 Lg_3$   
 $d_1 Rg$   
 $d_1 rt$   
 $d_1 ts_4 lg_2$   
 $d_1 ts_4 lg_2 a_1; A_2 C R Dt_1$   
 $d_2$   
 $gl_6$   
 $gl_6 lg_2 a_1 et; A_2 C R Dt_1$   
 $gl_6 Lg_3$

Chromosome 3 (continued)

gl<sub>6</sub> Rg  
 gl<sub>6</sub> v<sub>17</sub>  
 gl<sub>7</sub>  
 lg<sub>2</sub> A<sub>1</sub><sup>b</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 lg<sub>2</sub> a<sub>1</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 lg<sub>2</sub> a<sub>1</sub> et; A<sub>2</sub> C R dt<sub>1</sub>  
 lg<sub>2</sub> a<sub>1</sub> sh<sub>2</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 lg<sub>2</sub> a<sub>1</sub><sup>st</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 lg<sub>2</sub> a<sub>1</sub><sup>st</sup> sh<sub>2</sub>; A<sub>2</sub> C R Dt<sub>1</sub>  
 lg<sub>2</sub> pm  
 Lg<sub>3</sub>  
 Lg<sub>3</sub> Rg  
 na<sub>1</sub>  
 pg<sub>2</sub>  
 pm  
 ra<sub>2</sub>  
 ra<sub>2</sub> gl<sub>6</sub> lg<sub>2</sub>  
 ra<sub>2</sub> lg<sub>2</sub> pm  
 ra<sub>2</sub> Rg  
 Rg  
 rt; A<sub>1</sub> A<sub>2</sub> C R  
 ts<sub>4</sub> na<sub>1</sub>  
 v<sub>17</sub>  
 vp<sub>1</sub>  
 Primary trisomic 3

Chromosome 4

bm<sub>3</sub>  
 bt<sub>2</sub>  
 bt<sub>2</sub> gl<sub>4</sub>  
 de (1 or 16?)  
 Ga<sub>1</sub> Su<sub>1</sub>  
 ga<sub>1</sub> su<sub>1</sub>  
 gl<sub>3</sub>  
 j<sub>2</sub>  
 j<sub>2</sub> gl<sub>3</sub>  
 la su<sub>1</sub> gl<sub>3</sub>  
 la su<sub>1</sub> Tu gl<sub>3</sub>  
 lw<sub>4</sub>; lw<sub>3</sub>  
 o<sub>1</sub>  
 st  
 su<sub>1</sub> bm<sub>3</sub>  
 su<sub>1</sub> gl<sub>3</sub>  
 su<sub>1</sub> gl<sub>4</sub>  
 su<sub>1</sub> gl<sub>4</sub> Tu  
 su<sub>1</sub> j<sub>2</sub> gl<sub>3</sub>  
 su<sub>1</sub> o<sub>1</sub>  
 su<sub>1</sub> ra<sub>3</sub>  
 su<sub>1</sub> Tu  
 su<sub>1</sub> Tu gl<sub>3</sub>  
 su<sub>1</sub> zb<sub>6</sub>  
 su<sub>1</sub> zb<sub>6</sub> gl<sub>3</sub>



Chromosome 4 (continued)su<sub>1</sub> zb<sub>6</sub> Tusu<sub>1</sub><sup>am</sup>Ts<sub>5</sub>Ts<sub>5</sub> su<sub>1</sub>Tu gl<sub>3</sub>v<sub>8</sub>Chromosome 5a<sub>2</sub>; A<sub>1</sub> C Ra<sub>2</sub> bm<sub>1</sub> bt<sub>1</sub> bv<sub>1</sub> pr; A<sub>1</sub> C Ra<sub>2</sub> bm<sub>1</sub> bt<sub>1</sub> pr; A<sub>1</sub> C Ra<sub>2</sub> bm<sub>1</sub> pr v<sub>2</sub>; A<sub>1</sub> C Ra<sub>2</sub> bm<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> C Ra<sub>2</sub> bt<sub>1</sub> pr; A<sub>1</sub> C Ra<sub>2</sub> bt<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> C Ra<sub>2</sub> pr; A<sub>1</sub> C R

ae

bm<sub>1</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr v<sub>2</sub>; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr ys<sub>1</sub> v<sub>2</sub>; A<sub>1</sub> A<sub>2</sub> C Rbt<sub>1</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rgl<sub>5</sub>gl<sub>8</sub>Chromosome 5 (continued)gl<sub>17</sub> bt<sub>1</sub>gl<sub>17</sub> v<sub>2</sub>lw<sub>2</sub>lw<sub>3</sub>; lw<sub>4</sub>na<sub>2</sub>na<sub>2</sub> prpr; A<sub>1</sub> A<sub>2</sub> C Rpr ys<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C Rsh<sup>fl</sup> = "sh<sub>4</sub>""sh<sub>3</sub>" = allele of bt<sub>1</sub>v<sub>3</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rv<sub>12</sub>vp<sub>2</sub> gl<sub>8</sub>vp<sub>2</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rvp<sub>7</sub>vp<sub>7</sub> pr; A<sub>1</sub> A<sub>2</sub> C R

Primary trisomic 5

Chromosome 6at = allele of si<sub>1</sub>po Y<sub>1</sub> pl

Pt

si<sub>1</sub> Y<sub>1</sub> Plsi<sub>1</sub> Y<sub>1</sub> pl

Chromosome 6 (continued)

$si_1$  y pl  
 $y_1$  l<sub>10</sub>  
 $y_1$  ms(1?)  
 $Y_1$  pb<sub>4</sub> pl  
 $Y_1$  pG<sub>11</sub>; wx pG<sub>12</sub>  
 $y_1$  pG<sub>11</sub>; wx pG<sub>12</sub>  
 $y_1$  Pl Bh  
 $y_1$  pl Bh  
 $Y_1$  Pl sm py; A<sub>1</sub> A<sub>2</sub> b P<sup>RR</sup>  
 $Y_1$  pl su<sub>2</sub>  
 $y_1$  pl su<sub>2</sub>  
 $Y_1$  Pl; seg w<sub>1</sub>  
 $Y_1$  pl; seg w<sub>1</sub>  
 $y_1$  Pl; seg w<sub>1</sub>  
 $y_1$  pl; seg w<sub>1</sub>  
 l<sub>4920</sub>  
 "male sterile-silky" =  
     allele of si<sub>1</sub>  
 "orobanche" (seedling)  
 "ragged" (seedling)  
 "white 8896" (seedling)

Chromosome 7

bd  
 E<sub>2</sub>

Chromosome 7 (continued)

$gl_1$  ij bd  
 $gl_1$  sl  
 Hs  
 ij  
 in; pr A<sub>1</sub> A<sub>2</sub> C R  
 o<sub>2</sub>  
 o<sub>2</sub> gl<sub>1</sub> sl  
 o<sub>2</sub> ra<sub>1</sub> gl<sub>1</sub>  
 o<sub>2</sub> ra<sub>1</sub> gl<sub>1</sub> ij  
 o<sub>2</sub> ra<sub>1</sub> gl<sub>1</sub> Tp  
 o<sub>2</sub> v<sub>5</sub> gl<sub>1</sub>; seg ra<sub>1</sub>  
 o<sub>2</sub> v<sub>5</sub> ra<sub>1</sub> gl<sub>1</sub>  
 o<sub>2</sub> v<sub>5</sub> ra<sub>1</sub> gl<sub>1</sub> Hs  
 o<sub>2</sub> v<sub>5</sub> ra<sub>1</sub> gl<sub>1</sub> Tp<sub>1</sub>  
 Tp<sub>1</sub>  
 va<sub>1</sub>  
 vp<sub>9</sub> gl<sub>1</sub>; wx

Chromosome 8

v<sub>16</sub> j<sub>1</sub>  
 v<sub>16</sub> ms<sub>8</sub> j<sub>1</sub>  
 v<sub>16</sub> ms<sub>8</sub> j<sub>1</sub>; l<sub>1</sub>  
 "necrotic 6697" (seedling)  
 "sienna 7748" (seedling)

Chromosome 9

Bf<sub>1</sub>  
 bm<sub>4</sub>  
 bp Wx; pRR  
 C Ds wx  
 C sh<sub>1</sub> Wx; A<sub>1</sub> A<sub>2</sub> R  
 C sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 c sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 C wx; A<sub>1</sub> A<sub>2</sub> R  
 c Wx; A<sub>1</sub> A<sub>2</sub> R  
 c wx; A<sub>1</sub> A<sub>2</sub> R  
 Dt<sub>1</sub> (See chromosome 3 stocks)  
 gl<sub>15</sub> Bf<sub>1</sub>  
 gl<sub>15</sub> bm<sub>4</sub>  
 I Ds Wx  
 I wx; A<sub>1</sub> A<sub>2</sub> R B pl  
 K<sub>9</sub><sup>L</sup> C sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 l<sub>6</sub>  
 l<sub>7</sub>  
 ms<sub>2</sub>  
 ms<sub>2</sub> sh<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C R  
 ms<sub>20</sub>  
 sh<sub>1</sub> wx gl<sub>15</sub>  
 sh<sub>1</sub> wx l<sub>7</sub>  
 sh<sub>1</sub> wx v<sub>1</sub>

Chromosome 9 (continued)

wx Bf<sub>1</sub>  
 wx Bf<sub>1</sub> bm<sub>4</sub>  
 wx bk<sub>2</sub>  
 wx bk<sub>2</sub> bm<sub>4</sub>  
 wx d<sub>3</sub>  
 wx l<sub>6</sub>  
 Wx pg<sub>12</sub>; Y<sub>1</sub> pg<sub>11</sub>  
 wx pg<sub>12</sub>; Y<sub>1</sub> pg<sub>11</sub> pl  
 wx pg<sub>12</sub>; Y<sub>1</sub> pg<sub>11</sub>  
 wx<sup>a</sup>  
 yg<sub>2</sub> c sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 yg<sub>2</sub> C sh<sub>1</sub> bz wx; A<sub>1</sub> A<sub>2</sub> R

Chromosome 10

a<sub>3</sub>  
 a<sub>3</sub> g<sub>1</sub>  
 bf<sub>2</sub>  
 du<sub>1</sub>  
 du<sub>1</sub>; wx  
 g<sub>1</sub>  
 g<sub>1</sub> r<sup>g</sup>; A<sub>1</sub> A<sub>2</sub> C  
 g<sub>1</sub> r<sup>ch</sup>  
 g<sub>1</sub> r; A<sub>1</sub> A<sub>2</sub> C wx  
 g<sub>1</sub> R sr<sub>2</sub>

<u>Chromosome 10 (continued)</u>	<u>Unplaced genes</u>
$g_1 r sr_2$	$br_2$
$gl_9$	ct
$l_1$	el
$l_1; seg w_1$	$fl_2$
$li g_1 R; A_1 A_2 C$	$gl_{11}$
$li g_1 r; A_1 A_2 C$	$gl_{12}$
$nl_1 g_1 R; A_1 A_2 C$	$gl_{14}$
$Og R; A_1 A_2 C B Pl$	$gl_{16}$
$r^r; A_1 A_2 C$	$gl_g$
$r$ abnormal 10; $A_1 A_2 C$	h
$R^S sr_2; A_1 A_2 C$	$l_3$
$r^r sr_2; A_1 A_2 C$	$l_4$
$r^S wx; A_1 A_2 C$	mn
$R^r$ : Boone; $A_1 A_2 C$	$ms_5$
$R^{mb}; A_1 A_2 C$	$ms_6$
$R^{nj}; A_1 A_2 C$	$ms_7$
$R^{st}; A_1 A_2 C$	$ms_9$
$v_{18}$	$ms_{10}$
$w_2$	$ms_{11}$
$w_2 l_1$	$ms_{12}$
zn	$ms_{13}$
"oil yellow" (seedling and plant)	$ms_{14}$
Primary trisomic 10	Mt



Unplaced genes (continued)

rd  
 Rs<sub>1</sub>  
 rs<sub>2</sub>  
 "sh<sub>5</sub>"  
 v<sub>13</sub>  
 va<sub>2</sub>  
 w<sub>11</sub>  
 wi  
 ws<sub>1</sub> ws<sub>2</sub>  
 zb<sub>1</sub>  
 zb<sub>2</sub>  
 zb<sub>3</sub>  
 "luteus 4923" (seedling)  
 "necrotic 8376" (seedling)  
 "white 8657" (seedling)

Multiple gene stocks

A<sub>1</sub> A<sub>2</sub> C R<sup>r</sup> Pr B Pl  
 A<sub>1</sub> A<sub>2</sub> C R<sup>g</sup> Pr B Pl  
 A<sub>1</sub> A<sub>2</sub> C R<sup>g</sup> Pr B pl lg<sub>1</sub> y<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R Pr  
 A<sub>1</sub> A<sub>2</sub> C R Pr wx  
 A<sub>1</sub> A<sub>2</sub> C R Pr wx gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R Pr wx y<sub>1</sub>

Multiple gene stocks(continued)

A<sub>1</sub> A<sub>2</sub> C R pr  
 A<sub>1</sub> A<sub>2</sub> C R pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R pr su<sub>1</sub> y wx  
 A<sub>1</sub> A<sub>2</sub> C R pr y<sub>1</sub> gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R pr y<sub>1</sub> wx  
 A<sub>1</sub> A<sub>2</sub> C R pr y<sub>1</sub> wx gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> c R Pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> c R Pr y<sub>1</sub> wx  
 A<sub>1</sub> A<sub>2</sub> c R Pr y<sub>1</sub> sh<sub>1</sub> wx  
 A<sub>1</sub> A<sub>2</sub> C r Pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C r Pr su<sub>1</sub> y<sub>1</sub> g<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C r Pr y<sub>1</sub> wx  
 A<sub>1</sub> A<sub>2</sub> C r Pr y<sub>1</sub> sh<sub>1</sub> wx  
 bm<sub>2</sub> lg<sub>1</sub> a<sub>1</sub> su<sub>1</sub> pr y<sub>1</sub> gl<sub>1</sub> j<sub>1</sub>  
 wx g<sub>1</sub>  
 colored scutellum  
 lg<sub>1</sub> su<sub>1</sub> bm<sub>2</sub> y<sub>1</sub> gl<sub>1</sub> j<sub>1</sub>  
 su<sub>1</sub> y<sub>1</sub> wx a<sub>1</sub> A<sub>2</sub> C R<sup>g</sup> pr  
 y<sub>1</sub> wx gl<sub>1</sub>

Popcorns

Amber Pearl  
 Argentine  
 Black Beauty

Popcorns (continued)

Hulless  
Ladyfinger  
Ohio Yellow  
Red  
South American  
Strawberry  
Supergold  
Tom Thumb  
White Rice

Exotics and Varieties

Black Mexican Sweet Corn  
(with B-chromosomes)  
Black Mexican Sweet Corn  
(without B-chromosomes)  
Gourdseed  
Maiz chapolote  
Papago Flour Corn  
Parker's Flint  
Tama Flint  
Zapaluta chica

Chromosome rearrangements

The following rearrangements are being maintained primarily for use in determining the chromosome locations of new traits. All are marked with closely-linked endosperm or seedling traits.

The cytological positions of Inv 2a were determined by Dr. Morgan; those of Inv 9a were determined by Dr. Li. The indicated interchange points of the reciprocal translocations are taken from published work of Dr. Longley.

Inversions

lg <sub>1</sub> or gl <sub>2</sub> Inv 2a (also available with Ch)	2S.7; 2L.8
wx Inv 9a	9S.7; 9L.9

Reciprocal translocations

wx 1-9c	1S.48; 9L.22
wx 1-9 4995	1L.19; 9S.20
wx 1-9 8389	1L.74; 9L.13
wx 2-9b	2S.18; 9L.22
wx 3-9c	3L.09; 9L.12
wx 3-9 5775	3L.09; 9S.24
wx 4-9b	4L.90; 9L.29
wx 4-9 5657	4L.33; 9S.25
wx 4-9g	4S.27; 9L.27
wx 5-9a	5L.69; 9S.17
wx 5-9c	5S.07; 9L.10
wx 5-9 4817	5L.06; 9S.07
wx 6-9a	6S.79; 9L.40
wx, y 6-9b	6L.10; 9S.37
wx 6-9 4505	6L.13; 9 cent

Reciprocal translocations (continued)

wx 6-9 4778	6S.80; 9L.30
wx 7-9a	7L.63; 9S.07
wx or gl <sub>1</sub> 7-9 4363	7 cent; 9 cent
wx 8-9d	8L.09; 9S.16
wx 8-9 6673	8L.35; 9S.31
wx 9-10b	9S.13; 10S.40
su <sub>1</sub> 1-4a (also available with P <sup>RR</sup> )	1L.51; 4S.69
su <sub>1</sub> 1-4d (also available with P <sup>RR</sup> )	1L.27; 4L.30
su <sub>1</sub> 4-5j	4L.21; 5L.36
su <sub>1</sub> y 4-6a	4L.37; 6L.43
su <sub>1</sub> 4-8a	4S.59; 8L.19
su <sub>1</sub> , R 4-10b	4L.15; 10L.60
y 1-6c (also available with P <sup>RR</sup> )	1S.25; 6L.27
gl <sub>2</sub> 2-3c	2S.46; 3S.52
gl <sub>2</sub> 2-3 5304	2S.62; 3L.29
gl <sub>2</sub> 2-6b	2S.69; 6L.49
gl <sub>2</sub> , R 2-10b	2S.50; 10L.75
gl <sub>1</sub> 6-7 4545	6L.25; 7S.73

Stocks of A-B chromosome translocations

B-1a	1L.2	Proximal to <u>Hm</u>
B-1b	1S.05	
B-3a	3L.1	
B-4a	4S.25	Proximal to <u>su<sub>1</sub></u>
B-7b	7L.3	Proximal to <u>ra<sub>1</sub></u>
B-9a	9L.5	Proximal to <u>Bf<sub>1</sub></u>
B-9b	9S.4	Between <u>C</u> and <u>wx</u> ; close to <u>wx</u>
B-10a	10L.35	Proximal to <u>g<sub>1</sub></u>

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