E. G. Anderson

MAIZE GENETICS COOPERATION

NEWS LETTER

32

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Urbana, Illinois

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I. ACKNOWLEDGEMENT

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To the following companies we express our thanks:

DeKalb Agricultural Association, Inc.
Pioneer Hi-Bred Corn Co.
Bear Hybrid Corn Co., Inc.
Ainsworth Seed Co.
Coker's Pedigree Seed Co.
Crow's Hybrid Corn Co.
Greenwood Seed Co.
Pfister Associated Growers, Inc.
Clyde Black and Son
Funk Bros. Seed Co.
Eastern States Farmers' Exchange
Moews Seed Co.
American Maize-Products Co.
Cargill, Inc.
Earl May Seed Co.
Ferris Watson Seed Co.
Green Giant Co.

M. M. Rhoades

II. FREDERICK DAVID RICHEY
1884-1955

F. D. Richey, born in St. Louis, Missouri, was the son of an eminent lawyer. He graduated from the University of Missouri in 1909, and in 1949 the honorary degree of D. Sc. was conferred upon him by his Alma Mater. He joined the U. S. Department of Agriculture in 1911, and in 1922 was appointed Agronomist in Charge of Corn Investigations in the Bureau of Plant Industry. He was promoted to the position of Associate Chief of the Bureau in 1933 and held the post of Bureau Chief from 1934 to 1938. He resigned in 1938 to develop his own business of supplying single cross seed stocks of corn to seedsmen throughout the Midwest. In 1943 he returned to the Department of Agriculture as leader of the U. S. D. A. cooperative corn breeding work in the Southern Region, a position he held for eleven years. From 1954 until his retirement, he was Agronomist at the University of Tennessee Agricultural Experiment Station.

Richey was a Fellow of the AAAS and of the American Society of Agronomy, President of the Agronomy Society in 1937, and was elected Vice-President of the Genetics Society of America in 1932.

On taking charge of the Federal corn research program in 1922 he led in developing cooperative research between the State Experiment Stations and the U. S. D. A. He promoted cooperation between corn breeders, including both those who had formal cooperation with the Federal corn research program and others not formally cooperating with this program.

Richey's enthusiasm and leadership are well known to all with whom he came in contact. The informal cooperation previously mentioned led to the placing of hybrid corn research on a cooperative basis in 1925 under the Purnell Act by the Experiment Station Directors of the North Central Region. Richey was a member of the committee that drew up a plan for cooperation.

It was always a pleasure to attend a meeting of corn breeding research workers when Richey was present. He had very unusual ability to stimulate discussion of basic principles of corn breeding, and of problems of genetics, and he seems to the writer to have had an excellent grasp of plant breeding methodologies with sound basic viewpoints.

To review in a few words his many accomplishments in corn breeding is no easy task. A paper in 1922 was a masterly review of early studies of corn breeding prior to the days of hybrid corn. In 1925 he presented one of the first proofs of the fact that some inbreds had high combining ability in crosses with most other inbreds. This seems a new idea. His

paper with Garrison on the effect of continuous selection for ear type was almost a classic. Any close selection to ear type led to a reduction in yield. Richey developed the moving average as a means of correcting for soil heterogeneity and contributed in various ways to the development of sound methods of field experimentation prior to the present-day knowledge of methods of experimental design. In 1927 he proposed convergent improvement as a means of testing the Mendelian explanation of heterosis on the basis of dominant linked growth factors and presented further studies relating to similar methods. His clear presentation of the results of backcrossing, with mathematical expectations, helped materially to crystallize the idea of the backcross method. In 1945 he emphasized the correctness of Bruce's 1910 explanation of heterosis on a Mendelian basis. Also in 1945 and later Richey presented a reanalysis of Jenkins' (1935) data on combining ability after successive generations of inbreeding. He questioned the stability of combining ability in early generations of selfing. It may be of some interest that the late F. R. Immer, at the writer's suggestion, made a similar unpublished analysis and reached similar conclusions. It is apparent today that early testing is a valuable tool for many corn breeding problems; however, the writer is in agreement with the viewpoint of Richey that combining ability in early generations often is only relatively stable and by no means is as stable as one might be led to conclude from Jenkins' early conclusion. The discussion is presented here as an indication of Richey's methods of analysis. In another research paper Richey reanalyzed evidence, using data of Jenkins and Brunson, showing that the characters of inbreds are about as closely related to combining ability of their crosses as are different methods of testing for the character of combining ability. Several papers of Richey of a more popular nature helped materially in an understanding of the basic principles and great potentialities of hybrid corn.

It seems evident to the writer that Richey was an outstanding leader, and as Dr. Eckhardt has said in reference to Richey, he, "encouraged a whole generation of plant research men, especially those in corn breeding, to strive for greater heights in productive research."

Richey had definite viewpoints on controversial problems and often expressed his ideas in a definite and often in a blunt manner. To his friends these characteristics were appreciated and enjoyed. His somewhat dogmatic viewpoints were not so pleasing to those who disagreed with him. At the time that Richey received the distinguished service award from the United States Department of Agriculture, Dr. Robert M. Salter, at that time Chief of the Bureau of Plant Industry, Soils and Agricultural Engineering, made the following statement, "Because of the vast economic benefits that have derived from this (Federal-State Cooperative Research) program, and the part Dr. Richey played in it, I believe it safe to say that his contribution to the economic welfare of American Agriculture exceeds that of any other individual past or present."

H. K. Hayes

III. REPORTS FROM COOPERATORS

ALABAMA POLYTECHNIC INSTITUTE
Auburn, Alabama
Department of Botany and Plant Pathology

1. Production of linkage testers and translocation stocks adapted to the South.

A program has been initiated to incorporate certain linkage testers and translocations into lines which are adapted to the South. Linkage testers have been selected to mark each of the ten chromosomes and translocations have been selected to mark each arm of every chromosome. Most of this material was obtained from Dr. C. R. Burnham. The lines which are being used are Alabama 17, a white, early midseason line and Alabama 18, a yellow, late midseason line.

2. Relative maturity of certain inbreds compared with Alabama lines.

Inbred	First pollen
W23	6/30
A188	7/3
W22	7/6
Ab20	7/8 - early Alabama line
CC5	7/9
KYS	7/15
Ab12	7/15 - late midseason Alabama line
Ab2	7/19 - late Alabama line

Edward M. Clark

BEAR HYBRID CORN COMPANY
Decatur, Illinois

High seed set and low seed set selections from the elongate-produced tetraploid "synthetic A" were crossed in reciprocal combinations so that the direct effect of the pollen parent could be studied. The results are shown on the next page.

The high by high crosses show a significantly higher seed set than do the low by low crosses. The reciprocal crosses between the two levels of seed set gave the same average and are intermediate to the high by high and low by low.

Cross		Percent Seed Set						
		Replication						
Female	Male	1	2	3	4	5	6	Ave.
High Seed Set x High Seed Set		63.4	58.8	53.3	56.3	62.3	56.7	58.5
Low Seed Set x High Seed Set		49.3	55.2	54.7	51.7	48.7	52.4	52.0
High Seed Set x Low Seed Set		57.3	51.9	51.1	54.9	51.9	49.9	52.8
Low Seed Set x Low Seed Set		50.3	40.4	48.9	53.4	53.9	40.0	47.8

This data indicates that both the pollinator and the ear parent have an effect upon the seed set percentages expressed by the ear parent. Both appear to have equal or near equal effects in determining the percent of the ovules laid down by the female parent that can develop into normal kernels.

T. C. Warfield, Jr.

BLANDY EXPERIMENTAL FARM
University of Virginia
Charlottesville, Virginia

1. Blandy Radiation Field.

The Blandy Radiation Field was put into operation in July 1957. The field is a paved circle 30 feet in diameter embedded in the side of a hill with a Co^{60} source of 125 curies in the center. Doses as high as 1800 r can be given in a 24 hour period, sufficient to produce abundant "mutations" in corn. Current research work is devoted to ascertaining the nature of mutations induced at different stages in the life cycle of the corn plant. Present indications are that changes induced after meiosis are largely chromosomal while the recoverable mutants induced prior to meiosis resemble intragenic mutations. All plants exposed to radiation in the Blandy field are grown in 12-quart pails and moved in for a limited period of radiation.

2. Blandy Experimental Farm Graduate Fellowships.

A few graduate fellowships of $1200 each are available for students wishing to do graduate work at the Blandy Experimental Farm. Blandy Fellows are exempt tuition and fees at the University. About one half of the year is spent at the Blandy Farm, the remainder of the year in Charlottesville. While at the Farm students are supplied rooms at no cost, and board is on a cost basis, rarely as much as $30 a month. So

the $1200 fellowship has more purchasing power than in many places. Students interested in radiation research, especially with maize, may wish to apply. The deadline for applications is February 28, and awards are announced soon after April 1.

W. Ralph Singleton

UNIVERSITY OF CALIFORNIA
Los Angeles 24, California

1. Single gene dwarf mutants of maize and their differential growth response to gibberellins and to gibberellin-like substances.

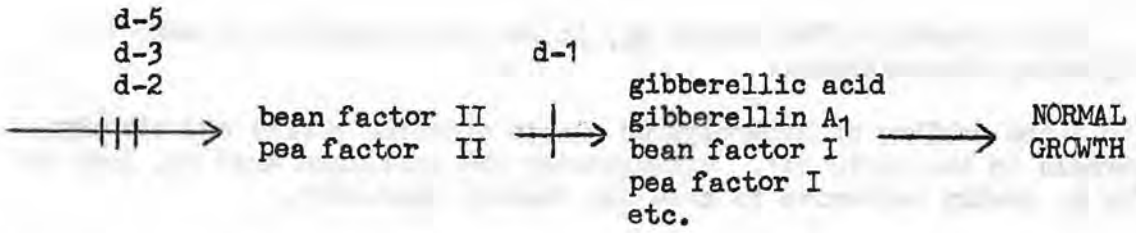
The 4 mutants, d-1, d-2, d-3, and d-5, respond by normal growth to microgram amounts of the gibberellins produced by the fungus Gibberella fujikuroi. Gibberellic acid (gibberellin A_3) has about twice the activity of gibberellin A_1. This relative activity is the same for the 4 mutants. Of the numerous gibberellin-like substances from flowering plants that produce a similar growth response with these 4 mutants, bean factor I has been isolated in crystalline form from young bean seeds (Phaseolus vulgaris). It has the same infrared spectrum and the same biological activity as gibberellin A_1. (British workers have recently reported the isolation of gibberellin A_1 from runner beans.)

Using the maize dwarfs for bioassay, additional gibberellin-like substances have been obtained from beans (Phaseolus vulgaris) and peas (Pisum sativum) that have biological properties different from the substances indicated above. These properties are as follows:

1. Bean factor II. Material has been isolated by chromatography and prepared in crystalline form. Thus the activity can be expressed relative to gibberellic acid. On this basis, activity is in the order of 130% that of gibberellic acid for the mutants, d-2, d-3, and d-5. However, activity is less than 10% that of gibberellic acid for the mutant, d-1. At low levels, d-1 seedlings show no growth response to bean factor II, while d-2, d-3, and d-5 seedlings respond at these levels by normal growth.

2. Pea factor II. Material has been purified, but is not crystalline. As yet, d-1 seedlings have shown no growth response to this factor, while d-2, d-3, and d-5 seedlings respond by normal growth.

These data are useful in determining the relative order of the dwarfing genes that presumably block different steps in a metabolic pathway concerned with gibberellin production in Zea mays. The data suggest that the d-1 gene is terminal for this series of mutants.



Bernard Phinney
Charles West
Peter Neely

2. The effect of gibberellins on the frequency of mitotic figures in a dwarf mutant of maize.

The parenchyma cells of the mature first leaf sheath of d-1 seedlings are both shorter and fewer in number than those of normals. Treatment of seedlings with gibberellins results in an increase in both length and number of these parenchyma cells. At a time when the first leaf blade has unfolded (8 days following soaking of seed), there are some 60% fewer mitotic figures in d-1 leaf sheaths than in normals. However, if d-1 seedlings have been treated with 10 micrograms/plant twenty hours prior to this period, the basal meristem of the first leaf sheath shows a frequency of mitotic figures very similar to normals (non-treated d-1 = 27 mitotic figures/leaf sheath; treated d-1 = 70 mitotic figures/leaf sheath; non-treated normals = 71 mitotic figures/leaf sheath.)

Kenneth Skjegstad

CENTRE DE RECHERCHES AGRONOMIQUES
Rabat (Morocco)

1. A new (?) gene affecting the structure of the endosperm.

In the flint inbred MR 368 the action of a recessive gene has been revealed, the effects of which on the structure of the endosperm are analogous to those described in connection with the genes h (soft starch, Mumm 1929), o_1 and o_2 (opaque endosperm, Singleton and Jones). This gene appearing in inbred MR 368 has proved different from the genes h, o_1, o_2, fl_1, fl_2 deriving from Dr. H. H. Kramer's gene stocks; the F_1 seeds from crosses of stock 368 with Kramer's stocks have all been quite normal.

Pending a possible further identification, it is proposed to call this gene h_2, while reserving the term h_1 for the first gene of this type found by Mumm in 1929.

With regard to the factor $\underline{h}_2$, it has been possible to make the following observations:

(1) - The selfing of heterozygous plants produces normal and starchy kernels in the ratio 3:1. Consequently the endosperm must be, just as for $\underline{h}$, trebly recessive to show the starchy character.

(2) - Apart from its action on the structure of the endosperm (entirely starchy and slightly reduced), the factor $\underline{h}_2$ has, at least within strain MR 368, an effect on the germination of the kernels: their germinating capacity is reduced (20-80% on filter-paper in the laboratory at 20°C., 1-30% in the field); germination is slower and the root system of the seedlings very rudimentary.

(3) - The $\underline{h}_2/\underline{h}_2$ plants that survive till flowering mature normally and their height, ear size and leaf number are similar or slightly inferior to those of normal plants. The various specific characters of the strain, the flowering and maturity dates are unaffected.

(4) - Hybrids between MR 368 $\underline{h}_2/\underline{h}_2$ and other inbreds (flint or dent) with normal kernels have been obtained as well as back-crosses of this hybrid to the original doubly recessive stock. In the ears from these back-crosses starchy kernels have been observed but always in a ratio inferior to 50% and sometimes very low (5%); on the other hand the germinating capacity and the weight of the starchy kernels proceeding from these back-crosses are equal or slightly inferior to those of the normal kernels of the same ears.

Consequently, in the inbreds used for the hybridizations there are dominant factors (in the recessive state with inbred MR 368) which, even in the presence of genotype $\underline{h}_2/\underline{h}_2$, mask the phenotype $\underline{h}_2$, and other ones that weaken the effects of the gene.

A study of the descendants of these back-crosses, now in progress, should lead to more accurate information about the number and the mode of action of these inhibiting or modifying factors.

2. Distribution of the effect of heterosis on some vegetative or agronomic characters of maize.

A series of 34 single hybrids created with flint or dent inbreds have been studied from the viewpoint of the effect of heterosis. On 40 plants for each hybrid and on 15 plants for each inbred, the following characters have been measured: interval from emergence to flowering (number of days from emergence date to male flowering date), ear height and total plant height (in centimeters), total leaf number, ear length (in cm.), relative ear height (percentage of total plant height), number of rows, average weight of kernel, and yield (quintals/hectare at 12% moisture). In each case the "heterotic deviation" has

been calculated, defined as the difference between the value of the hybrid and the average of the two parental values:

$$D = H - \frac{P_1 + P_2}{2}$$

For each character 34 deviations are thus obtained (one for each hybrid); their average m is calculated as well as the standard error of their distribution and the relation m/s in absolute value which reflects both intensity and regularity of the effect of heterosis. Moreover, the average relative deviation has been calculated (as percentage of the average value of the parental inbreds).

Character	Average m	Standard error s	m/s	Relative deviation
Interval emergence-flowering	- 6.7	1.4	<u>4.9</u>	- 9.5
Ear height	+ 27	11	<u>2.5</u>	+ 46
Total height	+ 51	14	<u>3.6</u>	+ 38
Relative ear height	+ 1.9	2.9	0.7	+ 4.3
Leaf number	- 0.8	0.7	1.1	- 4.4
Ear length	+ 3.5	1.1	<u>3.2</u>	+ 27
Number of rows	+ 0.3	0.7	0.5	+ 2.5
Ear number per plant	+ 0.23	0.32	0.7	+ 13.1
Kernel weight	+ 58	35	1.7	+ 26
Yield	+ 28	9.2	<u>3.1</u>	+ 147

The effect of heterosis is significant (5% level, m/s values underlined) for interval emergence-flowering (precocity), total height, ear length, yield and ear height. The most marked effect of heterosis is observed on flowering precocity (m/s = 4.9); the hybrids flower an average of 6-7 days before the parental strains; next comes total height (m/s = 3.6), the hybrids being an average of half a meter (m = + 51) taller than the parents. The number of rows of the ear is generally but little affected by heterosis (lowest m/s value: 0.5).

Finally, the effect of heterosis on yield, although the most important (147%) with regard to the yield of the strains, has been in these trials less constant (m/s = 3.1) than on earliness, height or length of the ear.

3. <u>Heredity of male sterility (Texas and U.S.D.A. types) in hybrids of dent x flint</u>.

In order to obtain some information on the behavior of Moroccan flint inbreds in crosses with male-sterile stocks of the cytoplasmic

type, a first hybridization program was carried out in 1955, with the American male-sterile lines W F_9^T, W F_9^S, W 22^T and W 22^S (all originated at the University of Wisconsin). In 1956, 20 single hybrids were studied with regard to pollen fertility. The following results were obtained:

Ear Parent (male sterile line)

Pollen Parent	W F_9^T	W 22^T	W F_9^S	W 22^S
21	-	-	fertile	-
32	-	sterile	fertile	-
224	sterile	sterile	-	sterile
228	-	-	fertile	-
250	sterile	-	fertile	sterile
255	sterile	sterile	-	-
346	-	sterile	-	-
368	-	-	½ sterile	sterile
386	fertile	-	-	-
612	sterile	-	-	sterile
623	sterile	-	-	-
628	-	-	-	½ sterile

Remarks

(1) - Strain 386 is the only inbred that gives a male sterile hybrid with the male sterile strains of Texas type.

(2) - Some inbreds give different results according to the type of sterility (250), or whether the female parent was WF_9 or WF_{22} (250 and 368).

(3) - There are two hybrids of intermediate type: WF_9^S x 368 and W_{22}^S x 628, which produce a variable ratio of viable pollen grains without ever being either completely fertile or completely sterile.

A. Cornu

CENTRO DI GENETICA DEL C.N.R.
University of Pavia, Italy
and
ISTITUTO DI GENETICA VEGETALE, FACOLTA' DI AGRARIA
University of Piacenza, Italy

1. Defective endosperm factors from maize-teosinte derivatives.

Data obtained during the past year suggest a revision of statements made in the 1956 Maize News Letter on defective endosperm factors in derivatives of the controlled introgression of teosinte in the inbred A158. Many of the defective factors are turning out to be identical or allelic. So far allelism has been well established for the following groups of factors:

a) $\underline{de}^{t4}$, $\underline{de}^{t5}$, $\underline{de}^{t10}$, $\underline{de}^{t11}$, $\underline{de}^{t17}$, $\underline{de}^{t18}$, $\underline{de}^{t19}$, $\underline{de}^{t23}$, $\underline{de}^{t24}$

b) $\underline{de}^{t14}$, $\underline{de}^{t15}$, $\underline{de}^{t20}$

Allelism is possibly true for the groups:

c) $\underline{de}^{t2}$, $\underline{de}^{t3}$

d) $\underline{de}^{t13}$, $\underline{de}^{t22}$, $\underline{de}^{t26}$, $\underline{de}^{t27}$, $\underline{de}^{t29}$

2. Ga factors in maize-teosinte derivatives.

The Ga factor, strongly linked to wx-locus, previously described (MNL, 1957), when crossed on and by strains provided by Dr. Schwartz, turned out to be identical or allelic to Gag described by him (MNL 25: 30).

3. Mendelian characters in Italian maize varieties.

To detect genetic mutants in Italian varieties of maize, self-pollination has been carried out in a few plants grown from seed collected throughout Italy. The selfed ears were examined and scored first for kernel characters. Subsequently 30-40 kernels from every ear were germinated in the greenhouse and classified for seedling mutants. Plant characters have not been observed as yet.

With the exception of color character, the segregation was often very close to 3:1; in a few cases the ratio was close to 15:1.

The following mutants have been obtained in a total of 186 selfed ears belonging to 103 different samples of open-pollinated populations:

Character	No. of ears in which found
Defective seeds	12
Sugary endosperm	1
Albino seedling	8
Luteus seedling	9
Virescent seedling	21
Yellow-green seedling	2
Pale-green	2
Glossy seedling	8
Liguleless	3
Striped leaves	4
Abnormal growth	6
Booster color	7

Several "papyrescent" glume types have also been collected, especially in the populations from middle and southern Italy. It may be of interest, also, to note that out of the 12 defective seeds observed only one is from northern Italy, which contributed about 2/3 of the studied samples.

Angelo Bianchi

4. Knobs in open-pollinated maize populations in Italy.

According to the results obtained by most of the maize cytologists up to date, knobs are found in 24 different positions of the chromosome set, but the actual existence of the knobs in such positions depends on the strain one is dealing with.

Since the knob endowment of the different varieties is becoming more and more a part of varietal descriptions, to designate the different knobs, it is here suggested adopting a practice similar to that largely used by salivary gland dipterian cytologists and, in order to avoid confusion, to modify slightly the Rhoades proposal (MNL 1957). For instance in chromosome 1, the knobs are as follows: 1S1, 1S2, 1L1; in chromosome 6 the symbols would be 6S1, 6L1, 6L2, 6L3, etc. If new positions are discovered a change would be necessary, according to the location of the new knobs. In every case the numeration would start from the left in the short arm and from the centromere in the long arm.

Samples of open-pollinated maize populations, collected throughout Italy, have been grown in Pavia, Piacenza and Rieti. At the appropriate stage, two or three tassels have been fixed and cytological observations were made.

So far 79 populations have been studied with the following results:

Origin	No. of Knobs				
	0	1	2	3	4
Northern Italy	10	11	15	13	3
Middle Italy	2	4	7	5	1
Southern Italy	2	1	2	3	0
Italy	14	16	24	21	4

As one can see the average knob number is quite low and in any case does not exceed 4.

The specific identification of the knobs has been possible in many cases. In the following table are summarized the results of the samples where all the knobs have been identified or no knob has been found.

Origin	Position of Knobs								B Chromosomes	Total samples
	1S2	3L1	4L1	5L1	6L3	7L1	8L1	9S1		
Northern Italy	1	1	1	2	2	7	4	5	2	25
Middle Italy	0	0	1	1	1	0	2	1	0	6
Southern Italy	0	1	1	0	1	1	0	0	0	4
Italy	1	2	3	3	4	8	6	6	2	35

It may be added that: a) no abnormal chromosome 10 has been observed in any case; b) the heteropycnotic region close to the centromere in the long arm of chromosome 7 is often very difficult to find; c) a prominent chromomere may be observed following the 8L1 knob, in position much closer to it than is detectable in American strains.

In several cases incomplete synapsis or precocious desynapsis was present in the pachytene chromosomes. In two cases, metaphases I showed few bivalents and several univalents. A paracentric inversion was possibly present in a plant.

Randolph's scale (Amer. J. Bot. 44: 129) has been adopted to evaluate differences in pachytene chromosome configuration, which range from the rating of 2 to 4. Clumped types of pachytene configurations have not yet been found in Italian varieties. Staining quality was, however, quite variable.

Few samples showed clear centromeres, possibly, as a result of the not very deeply staining quality of the heteropycnotic adjacent regions.

Angelo Bianchi
Anna M. Moa
Antonia Mariani

5. T Cytoplasm male-sterility in Italy.

To valuate the environmental influence on the T type cytoplasmic male sterility the following inbred strains obtained from Dr. D. F. Jones, have been carefully scrutinized during the flowering period in Piacenza, Italy.

Inbred	No. of plants
WF 9T	40
WF 22T	36
A 158T	46
Multiple tester for chromosome 2	10

The male sterility was complete in all the plants, since no pollen shedding has been observed, and the tassel usually showed no exserted anthers.

Angelo Bianchi
Giuseppe Marchesi

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION
New Haven 4, Connecticut

1. Separation of S and T pollen restoring genes.

In previous publications it was reported that S sterile inbreds restored to normal pollen production by crossing and backcrossing with Ky21 and selfing gave good restoration when tested on a number of S sterile lines but did not restore T sterile inbreds in all crosses. The same inbreds sterilized by T cytoplasm and restored to normal pollen production by restoring genes from the same Ky21 source have now been tested on both T and S sterile lines. In every case these T sterile lines restored to normal fertility give good restoration in some plants of all T sterile lines tested but fail to restore some S sterile inbreds of the same genotypes. This is further evidence that the fertility restoring genes in Ky21 are different for S and T cytoplasm and can be separated and fixed in the homozygous condition in different lines.

It has been shown that I153 and W22 can also be used to differentiate S and T cytoplasm. When I153 was crossed on to five other sources of cytoplasmic sterility, differing from the S and T sources, but all converted by backcrossing to the same inbred genotype, all of the progenies were either completely sterile or showed only a few anthers with little or no normal pollen. When crossed by W22 more pollen was produced but none were completely restored. This would indicate that none of these new sources of sterile cytoplasm are the T type. Some of them may be of the S type but the evidence is not conclusive. These five sources and several additional new sources are being put into the same genotypes by backcrossing and will be tested further.

2. Inhibitors of pollen restoring genes.

Previously all crosses of I153 and related lines (W153R, A344, A293) on T sterile inbreds have given completely normal pollen production on all plants in the F_1 hybrids. Last year a few combinations on HyT and W22T were either completely sterile or segregated into fertile and sterile plants. Pollen from the same I153 line on other T sterile lines produced all normally fertile plants. This is an indication that there may be pollen inhibitors that operate only in T sterile cytoplasm but not in normal cytoplasm to prevent the action of T restoring genes. This may account for some of the variable results with pollen restoring inbreds.

3. Universal seed parents.

These inhibitors of pollen restoration may also make possible sterile seed parents that can be used with non-restoring pollinators to give adequate pollen production in the final hybrids. This will be brought about by the normal segregation of restoring genes and inhibitors brought in solely from the seed parent. Such sterile universal seed parents could be produced and maintained with little more difficulty than present sterile seed parents and would be available for use with any pollinator, not carrying inhibitors, without incorporating pollen restoring genes.

D. F. Jones

4. Non-segregation in restoration of cytoplasmic male sterility.

A number of cases have been found where cytoplasmic male sterile (S type) plants crossed by plants carrying sterile cytoplasm and heterozygous for fertility restoring genes have given all-fertile progenies (S x SF → all SF). (The nomenclature is that proposed by the Northeastern Corn Conference [Maize News Letter 31: 2]). All of

the cases which shall be discussed here have occurred in pedigrees which received the fertility restorer genes in 1949 from a line of Ky21.

Most of the progenies consisted of 12 to 18 plants; however, as few as five and as many as eighty plants were observed in other progenies.

Pedigrees with M14 as the residual genotype: M14S4 (4 backcrosses with M14 after the first cross on to S) when pollinated by a hybrid of Ky21 and M14 gave rise to plants all of which were fertile. Since M14 will not restore S, the restorer(s) from Ky21 should have been segregating, and the progeny composed of both steriles and fertiles. Plants from this non-segregating progeny were crossed with M14S4 and M14S5. Both of these crosses yielded non-segregating progenies. This backcrossing was continued for 4 more generations; the last cross was M14S9 x M14SF5 (5 backcrosses after being restored to fertility) yielding M14SF6. A total of ten crosses of the type M14S x M14SF have been made; each gave rise to only fertile plants.

When these restored steriles were used as females in crosses with the inbred (M14) segregation resulted. Two such crosses were made; in each case an equal number of steriles and fertiles were produced.

Selfing plants heterozygous for the restorers presents a similar picture to that of a cross of the type S x SF. Four such selfs have been made. They were made in different years and with different progenies. Three of these produced only fertile plants; the fourth produced a progeny in which half the plants were sterile and half were only slightly fertile.

Pedigrees with A158 or P39 as the residual genotype: A158S4 was pollinated by (Ky21 x A158); this gave rise to seven fertile and five sterile plants. When one of these fertiles was put on A158S5 all the resulting plants were fertile. Plants from this non-segregating progeny were then crossed on to A158S6 and P39S6; both of these produced fertile non-segregating progenies. In each of these cases backcrossing to the respective steriles was continued for several generations. Many crosses of the types S x SF, SF selfed, and SF x inbred were made. The breeding behavior in all these crosses was similar to that exhibited with the M14 genotype.

The following is a summary of the results from all crosses involving the above pedigrees: Of 26 crosses of the type S x SF, 25 gave rise to non-segregating progenies; the other produced only one sterile plant in the entire progeny. Seven crosses of the type SF x inbred were made; each of these progenies exhibited normal segregation. From nine self-fertilizations of plants heterozygous for the restoring gene(s), seven did not segregate. One of the two which segregated was mentioned above; the other gave 17 fertile and 3 sterile plants. Since one of the three sterile plants was definitely off type, these three may have been outcrosses.

These data suggest the operation of a type of male gametophytic selection which insures fertilization by pollen grains carrying the restoring allele. At present it is not possible to determine whether this selection is a function of the S restoring gene(s), another gene closely linked to an S restorer, an interaction of an S restorer and a non-linked factor, or an interaction between any of these and the female; however, all these possibilities shall be investigated. Apparently no similar selection (at least not to such a degree) exists in the female, for in crosses of the SF x inbred type segregation appears to be normal.

In all of the above cases where no segregation occurred the male parent had S type sterile cytoplasm. It is of interest to know if this selection mechanism manifests its effect when the restorer gene(s) is not in S type cytoplasm. Two cases exist which suggest that it can. The crosses M14S4 x (Ky21 x M14) and M14S5 x ((Ky21 x M14) x M14) both yielded all-fertile progenies. This would be expected only if selection pressure were being exerted in the male (or male gametophyte) which had no sterile cytoplasm. If this is indeed the case, the result of the cross A158S4 x (Ky21 x A158) mentioned above cannot be resolved unless the selection factor(s) did not exist as such until the following generation.

This selection mechanism does not appear to function in T type sterile cytoplasm. A158T was crossed by A158SF4, and two of the progeny were selfed (the male parent also carried a T restorer). A few of the offspring from each of the two selfs were then crossed on to several S steriles. Since in both cases some of the S sterile lines were not restored, the S restoring gene(s) must have segregated while in T type cytoplasm.

No definite conclusions will be drawn until this phenomenon has been investigated further.

5. The application of non-segregating restorers to seed production.

If inbreds carrying restorers are to be utilized in the production of hybrid pollen parents, in most cases it will be necessary to convert the inbred by incorporating the restoring gene(s) into the inbred genotype by the cross-and-backcross method. Converting an inbred to the restorer version theoretically cannot be accomplished as quickly as conversion to the sterile counterpart. One reason for this is that crossing over must take place close to each gene involved in restoration so that only this genetic material is changed in the inbred. Another is that the converted inbred must be homozygous for the restorer(s) so that all the F_1 plants (hybrid pollen parent) will be fertile. To get the plants homozygous for the restoring genes several generations are required for selfing, testing progeny and multiplying the seed. Because of the first reason mentioned, slight combining ability

differences may persist for many generations. Such differences may be extremely slight and not readily perceptible by ordinary testing of hybrids produced with them. But when they are selfed to attain homozygosity of the genes involved in restoration, these slight differences can be multiplied; for while the differences can segregate in favor of the inbred genotype, they can also segregate and become homozygous for the type of the line from which the restorer genes came. While selection can be practiced, it is difficult to select for combining ability without extensive testing.

The possibility of utilizing the non-segregating restorer(s) (described in the preceding article) to eliminate the necessity of attaining homozygosity of restorers in converted inbred lines is being investigated. This would speed up the conversion by several generations. Not only would this eliminate selfing but also by eliminating selfing prevent the reversion to off-types which could result from selfing too soon. Further, since, with segregating restorers, one can only use the fertile plants for selecting those closest to type for propagation in a conversion program, about half of the land, labor, and costs are spent on sterile plants which will not be used. If the non-segregating restorer lines can be used to start the conversion program, the program could be continued more efficiently.

To date these non-segregating restorers have successfully functioned on M14S, M14DS, A73S, A374S, A158S, and P39S. It is unfortunate that this may only be practical when using the S type cytoplasm.

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1. A bio-assay for corn pollen viability.

A preliminary report (MNL Vol. 31) on the corn pollen longevity studies underway in this department mentioned the use of kernel-set as an assay for pollen viability. The number of kernels present on an ear is influenced by two major factors: a) the number of mature egg cells available for fertilization and b) the number of viable pollen grains available to fertilize them. If factor a) contributes to the variability of the numbers of kernels per ear per treatment, this contribution can be corrected by transforming the data by arc $\sin\sqrt{K/P}$, where K = the number of kernels per ear and P = the number of egg cells present on an ear. Obviously if factor a) does not contribute to the variability in the observed K, the above transformation need not be involved and the data are analyzed in the form K or $\sqrt{K}$. Hence, through the use of

a standard pollination technique, experimental design and subsequent statistical analysis of the data (K), the contribution of the number of mature egg cells per ear to the variability in the numbers of kernels per ear per treatment can be discounted. Thus a bio-assay for viable corn pollen can be developed that possesses only a few restrictions and provides several advantages over existing assays: e.g. germination of pollen on agar. Foremost among the advantages is the production of the succeeding generation. An obvious disadvantage for the application of this bio-assay in some studies is the time required to obtain the data and the infrequency with which the assay can be used. However, in contrast with the other assays available for testing pollen viability, this bio-assay provides a continuity to the research program.

Using this bio-assay, the study of pollen longevity was continued in 1957. The summarized results from these experiments will not be available until a later date. Of interest, however, was an experiment involving the cooperation of Dr. Patterson at Urbana, Illinois, and Drs. Jones and Stinson at New Haven, Connecticut. Pollen, some of which was previously held at -10°C., was shipped to these cooperators and was used successfully in effecting pollinations on the female Oh51A^{T} x B8. Similar pollinations were made in Ithaca. The seed yield from these three locations will be tested in a yield trial in New York in 1958.

H. L. Everett
D. B. Walden

2. Diepoxybutane as a chemical mutagen in maize.

Experiments were conducted for three seasons to determine the possible mutagenic effects of diepoxybutane, $CH_2 - CH - CH - CH_2$ (with O bridging the CH_2–CH and CH–CH_2 pairs), on pollen of Zea mays. (The term "mutation" unless otherwise specified includes both chromosome breaks and so-called "point" mutations.) Two methods of treatment were used. In one method the cut ends of newly shedding tassels were taken from homozygous multiple dominant stocks and were placed in 0.2 per cent solutions of the chemical for 18 hours. Pollinations were made on homozygous multiple recessive stocks immediately following the treatment. The other method of treatment involved boring a hole in the corn stalk about four inches below the lowest tassel branch. A one dram vial containing 4.5 cc. of 0.2 per cent diepoxybutane (DEB) solution was attached to the stalk and a piece of woven glass wicking was used to introduce the solution into the plants. Pollinations were made for five successive days from each treated and control tassel.

Losses of dominant marker genes in the endosperm of the resulting kernels were used to evaluate the mutagenicity of the DEB. All of the experiments utilized multiple recessive stocks having the chromosome

nine markers c sh wx or C sh bz wx, all of which affect the endosperm. These linked genes were used as material well-suited to investigate the problem of whether the appearance of the recessive characters involved chromosomal deficiency or gene mutation. Since the relative order of marked loci distal to the centromere in chromosome nine is known to be Wx, Bz, Sh, and I, the position and proportionate number of breaks within marked regions of the chromosome arm can be determined from the phenotypic appearance of the endosperm. Breakage-fusion-bridge cycles as well as interstitial deletions and end losses were induced frequently by the treatment. The type and frequency of endosperm deficiencies observed are presented in Tables 1 and 2.

The extent of dominant marker loss varied from a tiny spot to the entire endosperm, with all intermediate types occurring. Losses occupying less than 1/8 of the kernel were not scored since they are both difficult to classify and are not markedly increased by the treatment.

A summary of the results and conclusions follows:

1. Diepoxybutane is a powerful inducer of mutant endosperm sectors in maize. The number of kernels showing single or multiple gene losses was either 10 or 14 per cent in the F_1 kernels, depending on the method of treatment. This frequency is approximately equivalent to that obtained from treatment of maize pollen with 1500 r of X-rays in similar stocks. The frequency of mutation induced by DEB is not influenced by the year of treatment or stock used. However, the cut tassel method of treatment resulted in a significantly higher rate of mutant kernels than the wick method. The wick method has the advantage that a greater number of mutant kernels is obtained per ear owing to increased seed set.

2. There appears to be no differential sensitivity of maize pollen to DEB treatment on any of the five days preceding pollen shedding.

3. The two stocks differ significantly in the number of breaks observed distal to C or I as well as the number observed between Wx and the centromere. It is suggested that this may be due either to sampling error or to differential sensitivity of some chromosomal regions to breakage.

4. The distance between marked loci in the short arm of chromosome nine as determined by the relative frequency of breaks occurring between these loci is very similar to the cytological distances as determined at pachytene. This is considered evidence that breakage resulting from DEB treatment is induced approximately at random along the chromosome arm.

5. About twice as many kernels had sectors of mutant tissue as had exclusively mutant tissue in the endosperm. This frequency of

Table 1. Type and frequency of mutant endosperms induced by 0.2 per cent DEB treatment of maize pollen in C sh bz wx x I Sh Bz Wx by the cut tassel method.

Treat.	Year	B.-F.-B. cycles starting in				Interstitial Losses		End Losses				More Complex	All Affected	Total Examined	Per cent
		E-I	I-Sh	Sh-Bz	Bz-Wx	ShWx	Wx	I	ISh	IShBz	IShBzWx				
0.2% DEB	1956	117	4	4	28	3	6	15	2	8	163	7	357	3314	10.8
	1957	44	1	1	10	-	1	3	1	2	57	3	123	920	13.4
	Total	161	5	5	38	3	7	18	3	10	220	10	480	4234	11.3
Control	1956	2	2	-	-	-		1		-	9	1	15	6377	0.2
	1957	1	-	-	-	-		-		-	-	-	1	874	0.1
	Total	3	2	-	-	-		1		-	9	1	16	7251	0.2

Table 2. Type and frequency of mutant endosperms induced by 0.2 per cent DEB treatment of maize pollen in c sh wx x C Sh Wx.

Treat.	Method	Year	B.-F.-B. cycles starting in			Interstitial Losses		End Losses			More Complex	All Affected	Total Examined	Per cent
			E-C	C-Sh	Sh-Wx	ShWx	Wx	C	CSh	CShWx				
0.2% DEB	Cut	1956	74	7	26	-	3	6	17	153	3	289	2436	11.9
	Tassel	1957	44	0	23	1	1	4	3	85	1	162	1145	14.2
		Total	118	7	49	1	4	10	20	238	4	451	3581	12.6
	Wick	1957	273	20	85	0	16	26	34	606	9	1069	10862	9.8
	Grand	Total	391	27	134	1	20	36	54	844	13	1520	14443	10.5
Control	Cut	1956	5	-	1	-	-	1	-	2	-	9	4338	0.2
	Tassel	1957	-	-	-	-	-	2	-	-	-	2	1548	0.1
	Wick	1957	5	1	-	-	-	5	-	2	-	13	5711	0.2
		Total	10	1	1	-	-	8	-	4	-	24	11597	0.2

sectoring is similar to that obtained following ultraviolet treatment of pollen and is in contrast to the results following X-ray treatment of pollen in which sectoring is rarely observed. The ratio of fractional to entire endosperm effects following DEB treatment was not influenced by the year of experimentation, the stock used, or the method of treatment. The size of mutant sectors forms a nearly normal frequency distribution about the center value of one-half the endosperm. The following factors may be involved in sectoring: (a) If the chromosome has effectively two strands at the time of treatment, breaks in chromatids rather than whole chromosomes would result in sectoring. (b) If breaks are entirely chromosomal but the centric and acentric portions are held together by the matrix until division occurs, a sector would result if following division, one acentric chromatid restitutes while the other is lost. (c) Chromosomal instability induced by the treatment may be involved in sectoring.

6. There is no evidence that DEB markedly increases the frequency of gene mutation in maize, although the loss of single loci may include some gene mutations. Furthermore, the treatment of maize pollen with DEB has little or no effect on the F_1 plant generation. This is similar to results following ultraviolet treatment of maize pollen and is in contrast to the results following X-ray treatment in which there is a close correlation between the frequency of mutation in the embryo and endosperm. The absence of any effect on the F_1 plant generation suggests that DEB will be of little value in the production of mutations in maize for plant breeding purposes using the above methods of treatment. However, since DEB is extremely effective as an inducer of gene mutation in the Neurospora back mutation test and of chromosomal deficiencies in Drosophila, there is the possibility that it may be effective in increasing the mutation rate in other organisms or in maize embryos under different conditions.

Jean D. Kreizinger

CROW'S HYBRID CORN COMPANY
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1. Dwarf prolific corn.

We have been doing some preliminary work since 1950 on a new type of corn that could be harvested with a combine. In order to get a heavy set of ears, we have crossed our inbred lines with teosinte and have backcrossed once to corn, then started a selfing program. We crossed about a hundred lines with teosinte this year to broaden the program. We have also crossed it with all our dwarf types, and with male sterile and male restorer. We believe that this project has merit, and we are going to make every effort to produce an acceptable

dwarf prolific corn. See the December 6, 1957 issue of Seed World, pp. 16-17, for a more complete discussion of the project.

2. Twin-shoot.

In 1956, we made a number of complementary crosses between twin-shoot and Inbred Hy, a single eared strain. We used single plants in each case for closer control. We needed to know whether any cytoplasmic inheritance was involved. However, the F_1 plants were all single-eared, regardless of the way the cross was made. F_1 ears were selfed to check F_2 ratios.

We had five ear rows of twin-shoot, numbering 194 plants, that were entirely homozygous for the character.

3. Siberian corn.

The strain of Siberian corn we mentioned in our last report seems to be quite dominant for earliness. The strain itself was producing silks and tassels this year 43 days after the seed was planted. The crosses we had made between Siberian corn and some of our regular early lines like M14 and Oh51A were from a week to 10 days earlier than the lines themselves. The Siberian corn is quite susceptible to bacterial wilt, and we have had a considerable amount of it in our breeding field the past two years. Lack of time kept us from following up on some indication of self-sterility in this corn. The pollinations we made to continue the strain were all sib-pollinations.

W. J. Mumm

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Kenya Colony, East Africa

1. Genetics of resistance to Puccinia polysora Underw.

F_1 families from crossing lines homozygous for $\underline{Rpp}_1$ and $\underline{Rpp}_2$ reacted uniformly against infection by P. polysora.

(a) Against Race EA.1 - typical hypersensitive lesions (class "01") characteristic of $\underline{Rpp}_1$. No effect of $\underline{Rpp}_2$ was detectable.

(b) Against Race EA.2 (against which $\underline{Rpp}_1$ confers no resistance) - typical necrotic lesions (class "1") characteristic of $\underline{Rpp}_2$ alone.

From studies of derivatives from this cross, the conclusion was reached that $\underline{Rpp}_1$ and $\underline{Rpp}_2$ are linked. Three separate estimates of

crossover probability were 0.09, 0.12 and 0.16. From the F_3 generation from selfing crosses of ($\underline{Rpp}_1$ X $\underline{Rpp}_2$) X susceptibles, lines were selected that were pure for both genes together.

2. Field breeding for resistance to P. polysora.

Colleagues on field stations in East Africa, using our pure resistant lines crossed and back-crossed to adapted local maizes, have developed, and brought into production, lines homozygous for either $\underline{Rpp}_1$ or $\underline{Rpp}_2$. In general these new lines are as productive as the old in the absence of P. polysora and greatly superior in its presence.

No evidence has as yet been obtained that any race of P. polysora other than EA.1 is prevalent in the field; consequently genes $\underline{Rpp}_1$ and $\underline{Rpp}_2$ are proving equally effective (although $\underline{Rpp}_1$ would become ineffective if EA.2 appeared).

H. H. Storey
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1. Preliminary observations of three types of leaf necrosis which appear to be simply inherited.

a. The field corn inbred line Q83 consistently exhibits a characteristic interveinal leaf necrosis. This condition has been observed on all plants of the line at many locations in the Northeast and in southern Florida for many years. F_1 progeny of Q83 x + do not show the condition.

b. The sweet corn inbred Iowa 5125B consistently exhibits a characteristic large circular necrotic area on the leaves, several times the size of typical H. turcicum lesions. All plants of the line are affected; the condition has been observed for a number of years in many locations across the northern United States.

During the course of routine selfing of Iowa 5125B two sister lines, differing by only two generations, were evolved. One of these, R43-9-1-2-1-2-1-1 has proved free of the leaf necrosis, while the other R43-9-1-2-1-2-2-2 remains typical of the original line. F_1 progeny of Iowa 5125B x + do not show the condition. The cross between the sister lines was made last year.

c. In 1957 several inbreds and some early breeding material were observed to top fire. All plants of the line 213-12(S5)9-1-1, planted at several locations within the nursery at Feeding Hills, Massachusetts, top fired. Segregation for this character was observed among twelve S_2 sister lines drawn out of a local Massachusetts open pollinated variety. No clear cut top firing was observed among plants from open pollinated seed of this variety. Plant populations of the S_2 lines were small. No consistent phenotypic ratio obtained.

Surface sterilized isolates made during 1957 suggest that Gibberella zea, or a very similar fungus, is associated with all of the symptoms described. The same fungus, however, was observed among some isolates taken from apparently normal leaves of lines which at no time exhibited any of the symptoms described.

These preliminary observations suggest that a single recessive gene may be involved in the cases of Q83 and Iowa 5125B and may possibly be involved in the top firing symptoms of 213-12(S5)9-1-1. Seed of the material described is available.

David L. Matthews

ESCUELA NACIONAL DE AGRICULTURA
La Molina, Lima, Peru

1. Presence of B chromosomes in Andean maize.

B chromosomes were determined to be present in at least three collections from the Peruvian highlands, in a preliminary examination made by Dr. Barbara McClintock at this institution. The maximum number of B's found per cell was three. This is the first report of B chromosomes from the Andean area of adaptation.

2. Frequencies of knobs in chromosomes of three races of the Peruvian coast.

Representative collections of the races of maize from Peru are being studied in order to determine the relative frequencies of presence of knobs in each chromosome, and in each arm of the respective chromosome. These studies were started under the guidance of Dr. Barbara McClintock, and this report deals with preliminary observations on the lowland races Perla (tropical flint), Alazan (floury, red pericarp, of high altitude origin), and Arizona (a Tuxpeño derivative introduced a good number of years ago). Relatively good data are available for the race Perla, while for the other two there are not yet enough observations to make results definite.

Pooling the frequencies for all three races, the following distribution is obtained:

Chromosome No. and arm

1		2		3		4		5		6		7		8		9		10	
S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L
.31	.16	.38	.46	.27	.27	0	.77	.07	.23	0	1.0	.23	.85	0	.61	.61	.69	0	.07

Each figure shows the frequency of presence of each knob (not considering the fact that there is more than one knob per arm in some chromosomes) per chromosome arm in percent of all collections studied; i.e.: .38 for chromosome 2 short arm, means that 38 percent of all collections studied for presence of knobs in that position showed a knob there.

A comparison of the three races discloses that there is a consistent high frequency of presence of knobs at chromosome 4 Long arm, 6 Long arm, 7 Long arm, 8 Long arm, and 9 both Short and Long arm. A good differential between races may prove to be chromosome 3 Short arm, with a frequency of knobs of .47 for Perla and zero for both Alazan and Arizona.

Extremely low frequencies of knob presence were found up to now for chromosome 4 Short arm, 5 Short arm, and 10 Long arm, where knob presence has been previously reported elsewhere.

Ulises Moreno
Alexander Grobman

3. Test for sugary endosperm gene in Chullpi, Andean sweet corn.

Two ear selections of the Andean sweet corn race Chullpi were crossed to Pajimaca, a tropical sweet corn from Cuba, originated by transfer of su_1 (sugary endosperm - 1 in chromosome 4) from North American varieties. All F_1 ears in both crosses showed sugary kernels, indicating that Chullpi carries at least su_1 prevalent in North American sweet corn.

A secondary observation made on the ears of the F_1 plants indicated the presence of a variegated pericarp pattern, which is known to be entirely absent in either parent. This would indicate the presence of a Controlling element (such as McClintock's Activator) introduced in the cross from one of the parents. Tests for presence and origin of this Controlling element will be made.

4. A leaf growth pattern index for differentiating strains of maize.

For the past few years we have been testing several methods of differentiating such a complex function as leaf growth in several races of maize. One such method that may prove to be valuable for this purpose and also for differentiation of inbred lines is based on transforming the successive length/width ratio of the leaves of maize to a relative percentage index value. The procedure of transformation goes stepwise as follows:

1) Plot in succession log length of leaf in the abscissa axis against log width in the ordinate axis, for each leaf (or mean values of leaf positions for several plants selected from the most frequent leaf number class in the population), on squared paper.

2) Draw lines that go in order from the first leaf point on the plane between both axes, to the second, and from this one to the third, and so on, ending by uniting the point for the last leaf with the first one.

3) Fix an arbitrary reference point on each axis and draw a line perpendicular to each axis at each point. Points may be selected so that the area limited by the coordinate system will be divided into four quadrants about equal in area. The two reference lines will make the four characterizing quadrants: I - upper left, indexing short, wide leaves; II - upper right, indexing long, wide leaves; III - lower left, indexing short, narrow leaves, and IV - lower right, indexing long, narrow leaves.

4) Determine by addition of squares or with an Amsler planimeter the area of the irregular shaped figure obtained at the end of step 2. Determine next the area of the sections of this figure that fall within each of the four quadrants, and express them in percent of the total area.

As an example, a comparison between single crosses and their S_1 line parents, is shown in the next table:

Pedigree	Quadrant			
	I	II	III	IV
C.P. -117	14.37	36.11	35.92	13.61
C.P. -117 x NS 54 -223	11.67	57.81	10.42	20.10
NS 54 -223	9.15	56.64	6.36	27.84
P.C. -79	13.66	81.49	0.58	4.25
P.C. -79 x NS 54 -52	3.28	70.79	3.50	22.43
NS 54 -52	10.49	56.00	21.87	11.63
HIM -40	11.94	71.97	0.25	15.83
HIM -40 x P.C. -37	0.0	90.66	0.0	9.34
P.C. -37	26.99	52.91	20.09	0.01

Among several conclusions that may be drawn from the comparisons shown above, referring to the II Quadrant, where most of the leaves from the middle of the plant fall, we may see that in the first single cross, the line NS 54 -223 is dominant over C.P. -117 in determining long, wide leaves. In the second single cross, an intermediate value is found between the indexes for both parents. In the third single cross, HLM -40 x P.C. -37, there is a higher value 90.66 than the index for either parent, pointing to marked heterosis for length and width of leaf.

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1. Anthranilic acid incorporation in Bf-1 and normal seedling leaves.

Bf-1 seedlings and anthers are known to accumulate several substances that fluoresce blue in ultraviolet light (Proc. Nat. Acad. Sci. 37: 645-649 and MGCNL 24: 12). One of these substances was identified as anthranilic acid (AA) and two others were found to have microbiological activity as AA. In order to obtain evidence on the relationship of AA to the other fluorescent AA-containing substances, radiocarbon labeled AA was employed. Normal bf-1/bf-1 and mutant Bf-1/Bf-1 seedling leaf slices were incubated in pH 6.5 phosphate buffer containing 2 microM uniformly labeled (biosynthesized) AA containing ca. 2×10^6 cpm. Parallel normal and mutant leaf slices heated at 100° C for 5 minutes in buffer before incubation with AA were used as controls. After 6 hours incubation the leaf slices were ground, centrifuged, and the supernatants taken for paper chromatography in butanol-acetic acid solvent. Fluorescent spots were marked and some chromatograms cut into strips for direct counting and radioautograms prepared from others. It was found that (a) normal (boiled or unheated) seedling leaves did not convert AA to the two major blue fluorescent substances as indicated by fluorescence or radioactivity, and (b) mutant (unboiled but not boiled) seedling leaf slices incorporated AA into one of the major fluorescent materials and probably the other. Thus, the mutant accumulated AA and AA-like materials, and also contains a thermolabile system for conversion of AA to AA-like substances; normal leaves do neither. Unless the AA-converting system is adaptive over a longer time than 6 hours, it appears that the Bf-1 gene does not operate simply by causing the accumulation of AA which is convertible to AA-complexes by processes common to both normal and mutant seedling leaves.

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1. Effect of cytoplasm on agronomic characters in maize.

The cytoplasm in a double-cross corn hybrid is obtained from one inbred line, the female inbred in the seed parent of the double cross. The same genotypic yellow double, GAC 0211, was made with the four following sources of cytoplasm:

Female		Male
(GA 172 x GA 199)	x	(CI 21 x GT 112)
(GA 199 x GA 172)	x	(CI 21 x GT 112)
(CI 21 x GT 112)	x	(GA 172 x GA 199)
(GT 112 x CI 21)	x	(GA 172 x GA 199)

This investigation was made to determine if the cytoplasm affects agronomic characters such as yield, lodging, plant and ear heights, and date of silking. Paired one-row plots (15 hills in length) for the six possible cytoplasmic comparisons were used in a randomized blocks design with ten replications in 1957. Some preliminary results were obtained in 1952 and 1953 under extreme stress of drought.

The 1957 results show the following: Significant differences were obtained between the yields of GA 199 and GT 112 cytoplasms with 89.7 bushels and 82.7 bushels per acre, respectively. GA 172 had more erect plants than CI 21 and GT 112. GA 199 silked earlier than GT 112. CI 21 produced taller plants and higher ears than GA 172.

These results indicate a cytoplasmic effect on the inheritance of the agronomic characters--yield, erect plants, date of silking, plant and ear heights--in the double cross, (GA 172 x GA 199) x (CI 21 x GT 112).

A. A. Fleming
G. M. Kozelnicky
E. B. Browne
Julian W. Crews

2. Heterofertilization and pleiotropism.

Several progenies of GT 112 are being maintained which show a 3 yellow to 1 "lemonade" endosperm color segregation. "Lemonade" kernels produce albino seedlings, except for a percentage of 1.45 which produce green seedlings. No albino seedlings from yellow kernels have been obtained. Thirty-six "lemonade" kernel-green seedling plants

produced ears segregating in the 3:1 ratio indicating that they are the result of heterofertilization. No ears homozygous for "lemonade" have been obtained.

The theory of close linkage of genes (two) is not supported in Chi-square tests of 29 families over a two-year period. Results indicate that the condition is of a monohybrid nature. "Lemonade" is due to a single pleiotropic recessive gene which also affects chlorophyll development. The absence of a yellow kernel-albino seedling class may be due to selective heterofertilization caused by a lethal condition induced by this gene or some other gene, such that albinism would not be expressed in the presence of heterozygous endosperm.

The percent of heterofertilization was calculated on the basis of 2897 seedlings grown from "lemonade" kernels. Theoretically, it would be 2.9 percent, or 1 out of 34, instead of 1.45 percent if two classes were obtained from heterofertilization instead of one.

G. M. Kozelnicky
A. A. Fleming

3. Attraction of insects by corn.

For three generations a number of sublines from some leaf-blight resistant inbreds have exhibited a peculiar attraction to insects. These inbreds were developed from material originally obtained from Dr. C. C. Werhnam of Pennsylvania State University. The insects are of both types; sucking and chewing. The attraction occurs approximately two weeks after pollination and appears to be dependent on the age of the plant. The period of attractiveness on each individual plant lasts from one to two weeks.

The insects are apparently drawn to the leaf surface where they appear to be feeding. Minute areas have been observed which may be punctures or globules of a liquid. Determinations are being made of the substance or substances which are attracting the insects. It is hoped that these will lead to a study of the inheritance of this character.

Potential value of this material may be that of luring insects to traps as a control measure or even more specifically, its use as a trap crop for an especially damaging corn insect.

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1. Mutation rates in maize-teosinte derivatives.

Certain derivatives of maize-teosinte hybrids which have mutated once continue to mutate at a fantastic rate. For example, a stock in which chromosome 4 from new teosinte had been introduced first mutated to dwarf. This same stock has subsequently mutated to defective seeds (eight times), albinos, virescents, two other types of chlorophyll deficiencies, and a gametophyte factor which affects Mendelian ratios. During the years in which these fourteen mutations occurred, the total number of plants grown did not exceed 195 (based on perfect stands) consequently more than seven percent of the plants grown produced mutations.

A similar situation has occurred in a stock in which chromosome 4 from Florida teosinte was introduced. In a population of not more than 85 plants, there have been four mutations to defective seeds, one to dwarf, one to virescent, one to yellow-green seedlings, and one to a gametophyte factor. A total of 9.4% of the plants have mutated.

2. The nature of the unstable mutants in maize-teosinte derivatives.

Many of the mutations which occur in derivatives of maize-teosinte hybrids are, as has been previously reported (MNL, 1956), unstable and the genetic nature of this instability has now been determined for one of these, a defective seed, and a similar situation is suggested for two others: a dwarf and a gametophyte factor.

The unstable defective seed, de^{t5}, is linked with c or r as is indicated by ears grown in 1955 and 1956 which were segregating for both c and r as well as de.

Year	No. Ears	De color	De not	de color	de not	Total
1956	10	1322	832	265	460	2879
1955	3	265	180	46	60	551

Similar ears which were also segregating for wx indicate that it is chromosome 9 and therefore the c factor which is involved in the linkage shown above. Following are the data from three ears:

Row	No. Ears	De Wx	De wx	de Wx	de wx	Total
56-66ff	3	763	198	185	20	1166

Three-point backcross tests are now being made to determine the sequence of the factors and the amount of crossing over between them. In the meantime the data already available indicate that the chromosome involved is probably 9.

It now appears probable that $\underline{de}^{t5}$ is not a single gene but a block of genes from teosinte. In the F_2 endosperm generation of a cross between a noncolored cc rr stock of $\underline{de}^{t5}$ and a colored normal stock the defective seeds with aleurone color (crossovers) are less defective and consequently weigh more than the colorless defective seeds (a mixture of noncrossovers and undetectable crossovers).

The average weights of the two classes of defectives from 28 segregating ears follows:

	No. of Kernels	Weight in Grams	
		Total	Average
Noncolored de	1121	31.84	.028
Colored de	814	35.47	.044

The colored seeds are 57.0% heavier than the noncolored.

The results indicate that the size of the teosinte segment is reduced through crossing over with a corresponding reduction in its deleterious effect upon the development of the endosperm.

This conclusion is supported by differences in the lignification of the glumes of different genotypes. Even small blocks of teosinte genes can affect the nature of the glumes causing them to be stiff and horny. In population of some 200 ears segregating for $\underline{de}^{t5}$ the segregating ears were generally more lignified than the nonsegregating and those segregating an extreme defective had on the average more lignified glumes than those segregating a partial defective.

Since an entire teosinte chromosome can be introduced into the inbred strain A158 without producing defective endosperm, this unstable defective probably represents either a particular block of genes which does not function well in the absence of the remainder of the chromosome or a block of genes which has been transposed from one chromosome to another.

The latter explanation seems the more plausible because these mutations are occurring in strains which have been inbred from five to seven generations and which are presumed to be homozygous for certain teosinte chromosomes and in which crossing over would therefore have no genetic results. The transposition of blocks of genes from one chromosome to another would, of course, be quite a different process and would be expected to produce genetic results.

A similar situation exists with respect to a homozygous genotype of the extreme form of $\underline{de}^{t5}$. If this extreme condition is due to the block of genes from teosinte being present in its entirety, then once the genotype is homozygous for the block of genes crossing over between the homologous chromosomes should have no effect and the mutant might be expected to be, in this state, quite stable. On the contrary it reverts to normal and near-normal at a very substantial rate. These reversions could be accounted for by the transposition of the block of teosinte genes back to its original chromosome.

There is some question whether the unstable defective endosperm described here and similar types which have appeared repeatedly in our maize-teosinte derivatives should actually be called mutants. Perhaps "pseudomutants" would be a better term. The defective endosperm appears actually to be a case of imperfect development resulting from a block of teosinte genes which does not function well in this particular intracellular environment. Bianchi has found that this defective endosperm as well as others of the same general type disappear when outcrossed to certain stocks. In other words, what is being inherited here is not a lesion in the chromosome which produces the defective endosperm whenever it is in the homozygous condition but a certain intracellular environment characteristic of this particular inbred strain. In this particular intracellular environment this particular block of teosinte genes does not function well enough to produce a completely normal endosperm.

3. An unstable mutant dwarf in a maize-teosinte derivative.

A number of mutant dwarfs have occurred in various maize-teosinte derivatives involving the inbred A158 in which one or more chromosomes of maize have been replaced by their homologs from varieties of teosinte. Until recently we have not undertaken a special study of these dwarfs. However, in the summer of 1957 a progeny of a teosinte derivative proved to be segregating for a highly variable dwarf. This derivative involved chromosomes (or parts of chromosomes) 1, 7, and 9 of Durango teosinte and had been selfed for five generations when the mutant dwarf first appeared.

The instability of the mutant dwarf is illustrated by comparison of its frequency distribution with respect to height with that of normal plants in the same progeny. The dwarfs vary from 30-149 cms.

in height, the normal plants from 142-196 cms. The higher variability of the dwarfs as compared to the normal plants is a close counterpart of the variability of the unstable defective endosperm mutant described above as compared to normal seeds on the same ear.

The majority of the dwarfs do not produce ears but some ears were obtained from plants throughout the range of variation with respect to height. The cobs of the dwarfs were on the average more lignified than the ears of the normal plants and those of the short dwarfs were more lignified than those of the tall dwarfs. The extreme variant in ear type, an ear produced by a short dwarf, was flattened and almost distichous and had prominent, highly lignified glumes.

These characteristics suggest that the unstable dwarfs, like the unstable defective seeds are the product of a block of teosinte genes which has been transposed to a new position in which it has a deleterious effect upon development and which is variable as result of crossing over. The fact that the cobs of the dwarfs are more lignified on the average than the normal plants suggests that this possibly transposed block of genes is an addition to, rather than a substitution for, the previous complement of teosinte genes in the genom.

4. An unstable gametophyte mutant involving preferential segregation.

In one of the stocks mentioned above in which there had been 14 recognizable mutations in the population not exceeding 195 plants, a gametophyte factor affecting the Mendelian ratios has been studied and has proved to be unstable.

This mutant was first discovered in 1954 in an ear segregating for sugary endosperm which had only 15% of sugary seeds instead of the 25% theoretically expected. Among the progeny of this ear, one ear was obtained which segregated normally (22.2% sugary) and five were low sugary ranging from 9.2% to 18.9% sugary. The five low-sugary ears combined had an average of 14.2% sugary in a total of 963 seeds.

When the original stock was crossed with an unrelated sugary inbred the starchy seeds when selfed produced nine normal sugary ears (25.8% sugary in 1552 seeds of six of these ears) and two high sugary ears (37.4% sugary in 447 seeds). These results indicate that the original low sugary ears were the product of aberrant segregation resulting from a deleterious gametophyte factor linked with sugary. The normal sugary ears in the progeny of the original ear (1 in 6) and the high sugary ears in the crosses (2 in 11) are crossovers and represent 18% of the ears tested.

Heterozygous sugary plants producing low sugary selfed ears, when backcrossed on homozygous sugary, produce 26.1% of sugary seeds (total

of 721); when backcrossed reciprocally by sugary they produced 49.4% sugary seeds (total of 987). These data prove that the aberrant segregation is largely if not completely confined to the male gametophyte.

In backcross experiments with the stock of low sugary which had been outcrossed to a second unrelated sugary inbred, eight normal sugary ears (48.9% sugary in 2415) and two high sugary ears (55.3% sugary in 653) were obtained. The deviation from normal segregation in these two high sugary ears is so much less than that found in previous selfs and backcrosses that a change of "state" was suspected. Consequently in 1957 a comparison was made between two high sugary stocks, one called "strong" high sugary (35.4% sugary seeds in selfed ear) the other called "weak" high sugary (55.6% sugary in the backcross which is equivalent to 27.8% in the self). Both stocks were selfed and backcrossed to row 274, an F_1 sweet corn hybrid. In addition the "strong" high sugary was backcrossed to row 270 which was planted to sugary seeds from a high sugary ear.

Six facts emerge from the data set forth in the accompanying table.

(1) Self-pollinations in the two stocks yield approximately the same results: 26.0 and 25.9% respectively of sugary seeds. However two of the eight ears in the "strong" stock deviate significantly from normal segregation while all of the nine ears in the "weak" stock are within the normal range.

(2) The backcrosses on 274 from the "strong" high sugary stock have a significantly higher percentage (55.4%) of sugary seeds than the backcrosses (49.3%) from the "weak" high sugary stock.

(3) The backcrosses to row 270 have a significantly higher percentage of sugary seeds (66.0%) than the backcrosses to row 274 (55.4%). This indicates that the behavior of the male gametophyte is influenced by the genetic constitution of the styles.

(4) Omitting the backcross involving Plant 273-2 which is clearly exceptional (71.1% sugary) the average percentage of sugary seeds in the backcrosses is 47.8 which is significantly lower than the 50% expected from random segregation. This suggests that the factor which in this stock is linked with Su is now conferring an advantage rather than a disadvantage on the gametophytes which carry it.

(5) The backcross involving 273-2 with 71.1% sugary seeds is significantly different from all of the other backcrosses in this population and is apparently a reversion to the "strong" high sugary state characteristic of the original stock as exemplified by the plants in row 272.

Selfed and Backcrossed Progenies of "Strong" (272) and "Weak" (273) High Sugary Ears

	Selfs			Backcrosses on 274			Backcrosses on 270		
Plant	Total	No. su	% su	Total	No. su	% su	Total	No. su	% su
272-1	149	26	17.4	218	126	57.8	286	168	58.7
2	416	111	26.7				269	161	59.9
3	332	70	21.1	27	16	59.2	178	134	75.3
4	no selfed ear			429	254	59.2	340	263	77.4
6	281	68	24.2	285	128	44.9	442	262	59.3
8	411	130	31.6	216	135	62.5			
9	226	44	19.5	199	117	58.8	299	180	60.2
10	393	106	27.0	39	26	66.7	304	253	83.2
11	265	87	32.8	178	79	44.5	368	221	60.0
Totals	2473	642	26.0	1591	881	55.4	2486	1642	66.0
273-1	309	89	28.8	349	159	45.6			
2	no selfed ear			349	248	71.1			
3	341	87	25.5	407	185	45.5			
4	310	85	27.4	349	152	43.6			
5	231	49	21.2	424	198	46.7			
6	271	73	26.9	831	394	47.4			
7	no selfed ear			322	160	49.7			
8	282	71	25.2	284	160	56.3			
9	339	84	24.8	432	202	46.8			
10	de linked with su			679	347	51.1			
11	311	87	28.0	373	178	47.7			
12	426	105	24.6	730	342	46.8			
Totals	2820	730	25.9	5529	2725	49.3			

(6) Although the data in the table do not themselves reveal it, it can be said that this gametophyte factor is associated with a block of genes from teosinte which affects the lignification of the glumes. Cobs of the two high sugary ears in 1956 were more lignified than those of the 9 normal sugary ears. The cobs of row 272, the "strong" high sugary stock, were more lignified on the average than the stocks of the "weak" high sugary ears in row 273 with the exception of the plant 273-2 which had a very strongly lignified cob and which, as already noted, had a very marked deviation from normal segregation. Thus it appears that the variations in the expression of this gametophyte factor, like that of the defective endosperm and dwarf plant described above, are due to the effect of crossing over within a block of teosinte genes.

5. The extraction of "teosinte" chromosomes from present-day maize varieties.

In a survey made several years ago of varieties of maize of this hemisphere for the presence of weak alleles of a tunicate, a number of plants were found whose ears had prominent lignified glumes. When this characteristic was introduced into the inbred strain, A158, through repeated backcrossing followed by selfing the final product in several cases was a modified strain of A158 similar in its characteristics to some of the modified strains which are produced by substituting a chromosome of teosinte for a chromosome of maize.

Chromosomes which have the same general effect as teosinte chromosomes have now been extracted from varieties from Mexico, Honduras, Nicaragua, Venezuela, Brazil, Paraguay, Argentina, Bolivia, and Cuba.

Not only do these extracted chromosomes produce phenotypic effects similar to those of teosinte chromosomes but like the latter, they also increase mutability. Furthermore at least some of the mutations are genetically identical to those produced by teosinte chromosomes. An unstable defective seed mutant which is genetically identical or "allelic" to *de*^{t5} described above has been produced by chromosomes extracted from varieties from Mexico, Honduras and Paraguay.

Since teosinte is not known in South America, two explanations for the occurrence of "teosinte" chromosomes in South American maize suggest themselves: (1) that the admixture of maize and teosinte which has occurred and is still occurring in Central America and Mexico has become widely distributed throughout this hemisphere; (2) that these extracted chromosomes in South American varieties are derived originally, not from teosinte but, from Tripsacum.

Since some of the South American races from which these chromosomes were extracted have no counterparts in Central America and Mexico and no obvious relationship to races of that region, and since we now know that Tripsacum is much more common and more diverse in South America than had previously been supposed, the second explanation seems at the moment to be the more plausible.

Whether these chromosomes come from teosinte or from Tripsacum, serious consideration must be given to the fact that the modern maize plant is a complex hybrid involving not only numberous once-distinct races but also the introduction of genes and blocks of genes from teosinte or Tripsacum or both. These general conclusions, which are supported by both archaeological remains and genetic evidence, are important not only for corn improvement but also for theoretical genetics. It may well be that many of the genetic phenomena observed in maize have significance only for this species.

6. Resemblance of maize-teosinte mutants to those occurring in long-inbred strains.

It now appears probable that many, if not the majority, of mutations occurring in long-inbred strains of maize are the result of some phenomenon involving blocks of teosinte genes. There is little doubt that the majority of maize varieties of Central America, Mexico, and the United States have at some time in their history undergone teosinte introgression or that the majority of inbred strains derived from these contain some teosinte genes. Strains such as Oh28, for example, have cobs as highly lignified as some of our maize-teosinte derivatives in which teosinte chromosomes have been introduced.

The mutants reported by Singleton are particularly interesting in this connection. When the mutant dwarf which he found in an inbred line of sweet corn was crossed with another inbred new variations such as germless seeds, brittle seeds, and virescent seedlings were observed. This situation is similar to that reported above where one mutation was followed by a series of others. Also all of these mutations reported by Singleton have occurred in our maize-teosinte derivatives, as have also the narrow leaf, male-sterile dwarfs, and small seeds reported by Schuler.

The transposition of a block of genes from one chromosome to another could produce heterozygosity in long-inbred, apparently homozygous strains and this process could account for the residual heterozygosity which Schuler found in several inbred mutants.

If the majority of mutants in long-inbred strains are the product of transposition of blocks of genes, they are of doubtful value in experiments designed to measure the heterosis resulting from heterozygosity at a single locus.

7. Possible relationship of maize-teosinte mutants to previously described mutation systems.

We have long suspected that the mutation systems described by McClintock and by Brink owe their origin to teosinte genes introduced into maize chromosomes. It has not yet been possible to prove this but it is significant that the controlled introgression of teosinte into maize produces mutability; that some of the mutants are unstable and involve a number of "states"; that defective seeds are common; that disturbance of Mendelian ratios often occurs; and that there appears to be "transposition" in both kinds of systems.

The maize-teosinte derivatives do not, as such, appear to carry the Ac factor of the McClintock system but they may in some manner give rise to it. In 1954 five different maize-teosinte derivatives produced 1.4, 1.2, 1.2, 0.7, and 2.0 percent of mosaic seeds involving the c locus when crossed with the Ac tester. Another derivative, one which

had previously mutated to defective seeds and which, following outcrossing, gave rise to other mutants, had 18.1 percent of mosaic seeds when crossed with the Ac tester. Several generations of selection have increased this percentage to 100. The stock now resembles some of McClintock's supresser-mutator stocks.

Paul C. Mangelsdorf

8. The characteristics of Huixta, Durango, and Nobogame teosinte chromosomes.

Since the summer of 1956 three teosinte varieties, Huixta from northern Guatemala, Durango and Nobogame from northern Mexico, have been studied cytologically in F_1 hybrids with an inbred strain of maize, Wilbur's flint. This strain of maize is characterized by practically knobless chromosomes and by imparting good spreading quality to pachytene chromosomes. Whenever it was possible, an inbred maize strain, Conn. P39, was also used in crosses in order to confirm the findings. Both of these strains of maize were previously studied in many crosses and no chromosome inversions or any other rearrangement were observed. Cytological observations on these teosinte varieties are as follows:

Huixta teosinte showed no inversions in hybrids with maize. It differs from other Guatemalan teosintes previously studied in having the majority of its knobs located internally. Of 585 F_1 microsporocytes examined at diakinesis, 12.3 percent had two univalents, 0.8 percent, four univalents.

The F_1 hybrids of maize and Durango teosinte were heterozygous for two inversions. Since the maize strain employed in the cross did not have any chromosome inversions, the inversions must have been introduced by the teosinte parent. These inversions are located on the short arms of chromosome 8 and 9 and are practically terminal. They represent 59 and 56 percent respectively of the short arms of these chromosomes (Tables 1 and 2). In the microsporocytes of these F_1 hybrids dicentric bridges and acentric fragments were found at both anaphase 1 and anaphase 2. At diakinesis, 0.8 percent of the microsporocytes had two univalents, but microsporocytes having more than two univalents were not observed among 514 cells studied.

Two previously unreported knob positions were found in Durango teosinte; one on the long arm of chromosome 8, the other on the long arm of chromosome 9.

The F_1 hybrids of maize and Nobogame teosinte were heterozygous for three inversions contributed by the teosinte parent. Two of these inversions are practically terminal. One is on the short arm of chromosome 8, the other previously reported (MNL 1957) on the short arm of chromosome 9. The In 8 represents 62 percent of the short arm; while the In 9 represents 59 percent of the short arm (Tables 3 and 4).

Table 1. Length of inversion in chromosome 8 of Durango teosinte.

Cell No.	Length in Microns		Percent of Short Arm
	Short Arm	Inversion	
1	14.0	7.6	54.0
2	16.4	8.8	53.0
3	12.5	9.0	72.0
4	14.2	9.2	64.0
5	9.2	5.0	54.0
Average	13.3	7.9	59.0

Table 2. Length of inversion in chromosome 9 of Durango teosinte.

Cell No.	Length in Microns		Percent of Short Arm
	Short Arm	Inversion	
1	19.6	11.9	60.0
2	16.8	10.8	64.0
3	17.2	9.4	54.0
4	18.8	8.1	43.0
5	14.5	9.0	62.0
Average	17.4	9.8	56.0

Table 3. Length of inversion in chromosome 8 of Nobogame teosinte.

Cell No.	Length in Microns		Percent of Short Arm
	Short Arm	Inversion	
1	16.5	9.2	56.0
2	15.4	9.6	62.0
3	16.5	10.3	62.0
4	14.2	8.8	62.0
5	18.8	13.0	69.0
Average	16.3	10.2	62.0

The third inversion is paracentric and it is on the long arm of chromosome 5. The length of this inversion is equivalent to about one half of the length of the long arm. At both anaphase 1 and anaphase 2, dicentric bridges and acentric fragments were found in the microsporocyte divisions of these F_1 hybrids. At diakinesis, among 514 cells examined, 11.8 percent of them had two univalents, 0.4 percent of them, four univalents.

Table 4. Length of inversion in chromosome 9 of Nobogame teosinte.

Cell No.	Length in Microns		Percent of Short Arm
	Short Arm	Inversion	
1	19.6	14.2	72.0
2	19.6	11.6	59.0
3	19.0	11.1	58.0
4	22.7	11.0	48.0
Average	20.2	11.9	59.0

The chromosomes of Nobogame teosinte have only a few knobs. Chromosome 7 has a large terminal knob on the short arm. Internal knobs of medium size occur on the long arms of chromosomes 2 and 4. A small internal knob is present on the short arm of chromosome 1 and a small terminal knob on the short arm of chromosome 6.

9. Spontaneous reciprocal translocations.

In a maize strain used as cytogenetic marker in a cross with a progeny of Durango teosinte-maize derivatives which was homozygous for In 8 a case of spontaneous reciprocal translocation was observed. This translocation is designated as T2-8. At diakinesis of the T2-8 heterozygotes 1.0 percent of the sporocytes showed regular behavior for both bivalents 2 and 8, 54.5 percent of them demonstrated a ring of four chromosomes, 12.5 percent of them demonstrated a chain of four chromosomes, and 31.8 percent of them showed other types of irregular behavior. The points of exchange between the long arms of chromosomes 2 and 8 are shown in Table 5.

Table 5. Chromosomes and the points of exchange of the arms involved in two translocation heterozygotes.

Progeny No.	Chromosomes	Chromosomal Designation	
56-68	6 - 7	6L . 17	7L . 23
56-528, 529	2 - 8	2L . 87	8L . 42

Among fourteen plants of selfed progenies of T2-8 heterozygotes six plants were normal in fertility, eight plants were semi-sterile.

A second case of spontaneous reciprocal translocation was found in a progeny of maize-Florida teosinte derivatives. In this translocation, the long arms of chromosomes 6 and 7 were involved. It is designated as T6-7. The points of exchange between the arms are shown in Table 5. Among the eight plants of the selfed progenies of T6-7 heterozygotes, four plants were normal in fertility, four plants were semi-sterile.

A study of the other aspects of the above two reciprocal translocations is in progress.

10. The origin of abnormal chromosome 10 in maize.

During the year 1956 a cytological study was made of a number of F_1 crosses of maize varieties collected from Latin America with inbred strains from the United States. In these F_1 crosses Mangelsdorf had previously found high percentages of aborted pollen and chromosome irregularities were therefore suspected.

At pachytene, B-chromosomes varying from one to six in number were observed in 25 plants from nine crosses. No B-chromosomes were found in eighteen plants from six crosses. In one additional cross not included in the above categories, involving a Peruvian variety as one parent, a B-chromosome was found in two plants, while a third plant in the same progeny lacked the B-chromosome, but was heterozygous for an abnormal chromosome 10.

It was further found that the entire extra piece of heterochromatin attached to the chromosome 10 resembled closely the terminal one third of the B-chromosome found in the two sister plants. This extra piece involved the pycnotic or knob-like region and its adjacent regions on both sides including the terminal spindle fiber attachment region which was often not apparent.

At metaphase 1 of the microsporocyte divisions in the plant heterozygous for this abnormal chromosome 10, secondary centric regions on more than one bivalent were observed in many sporocytes. The number of these secondary centric regions varied from one to four on a single bivalent. At anaphase 1 the continuation of the secondary centric regions was found. Dyads carrying one or more secondary centric regions tended to lead the way poleward in the chromosome movement. The other dyads which did not carry the secondary centric regions showed no aberrant configurations.

At metaphase 2, the secondary centric regions on certain dyads showed precocious poleward movement, and sometimes the arms of these dyads were extensively attenuated. At anaphase 2, the secondary centric regions often imparted a V-shaped configuration to the monads, with the primary centric regions lying toward the equatorial plane.

These unusual features found at meiotic divisions in the plant heterozygous for this abnormal chromosome 10 were about the same as those previously found in the other materials either heterozygous or homozygous for an abnormal chromosome 10.

In 1957 twelve additional plants of this same cross were studied cytologically with the following results: One plant was heterozygous for an abnormal chromosome 10; it had no B-chromosome. One plant had a trivalent of B-chromosomes, while the other chromosomes were normal. Six plants had a single B-chromosome and the remaining chromosomes in these plants were normal. The remaining four plants had an unusual chromosome 9 and they lacked the B-chromosome. In these four plants one of the chromosomes 9 had an extra piece of heterochromatin, resembling the bulging pycnotic region of the regular B-chromosome, attached to the distal end of its short arm. At pachytene this extra piece of heterochromatin appeared like a large terminal knob. However, unlike the effect of abnormal chromosome 10, precocious movement of dyads and secondary centric regions on the bivalents, dyads, and monads were not observed in the sporocytes possessing the unusual chromosome 9.

The above observations suggest that the extra piece of heterochromatin of the abnormal chromosome 10 came from a B-chromosome by simple translocation, and that the chromosome 9 with a terminal large piece of heterochromatin on the short arm originated in a similar way. This piece of heterochromatin often appeared like a large terminal knob.

Y. C. Ting

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11. The blotching system involving the c locus.

In the previous reports it has been stated that there are four genes involved in the blotching system which causes blotches of color to develop in the aleurone in cc genotypes. This conclusion was based on six ears which appeared to be segregating in a ratio of 243:781 (MNL, 1955) and which were therefore assumed to be heterozygous for four Bh loci as well as the R locus.

In subsequent experiments we have isolated testers for three Bh loci but have not been able to find a stock which is recessive for a fourth Bh gene. It now appears that there are only three Bh genes involved in the system and that the ratios reported earlier which seemed to indicate the existence of four genes resulted either from

misclassification or from some form of preferential segregation affecting the ratios.

Preliminary three-point linkage tests of the Bh gene on chromosome 9 have yielded the following data:

Ears	Genes	Number of Individuals				
		XY	Xy	xY	xy	Totals
297-1&4	Bh wx	411	167	188	49	815
297-1&4	Bh sh	420	158	188	49	815
297-2&3	Bh wx	411	156	394	91	1052
297-2&3	Bh sh	392	175	372	113	1052

In both 3:1 and 9:7 progenies, Bh shows slightly closer linkage with wx than with sh. Since the crossing over between Bh and wx is high (about 45%) the data so far available suggest that the sequence is sh, wx, Bh and that Bh has its locus on the long arm of chromosome 9. Backcross tests with sh and wx and tests with other genes on chromosome 9 are in progress.

12. A new blotching system affecting the r locus.

A very striking piebald color pattern, commonly found in high-altitude Peruvian flour corn, proves to be a blotching system affecting the r locus. At least two Bh genes are involved in the system since the ratio of Bh to bh is 27:37 when the C locus is also heterozygous. One of these genes is probably linked with y on chromosome 6 as the following data indicate:

Row	Number of Individuals				
	Bh Y	Bh y	bh Y	bh y	Total
56-623	215	95	387	115	803

The percentage of y kernels, 30.6%, among the Bh individuals differs significantly from the percentage, 23.3, among the bh individuals. Further tests to determine more precisely the degree of linkage are in progress.

The expression of blotching in this system is inhibited in crosses with the inbred, Indiana P39. In this respect this system differs

from that previously reported which affects the r locus which is inhibited by Conn. P39 but not by Ind. P39.

13. Utilization of Bh genes in the classification of maize.

In last year's News Letter, it was suggested that the genes in the two blotching systems then described might prove to be useful in the classification of maize. A preliminary experiment was conducted during the past season to test this possibility. The results are shown in the accompanying table.

When inbreds carrying the gene C are crossed with testers for the Bh genes, all of which are cc and RR, the F_1 seeds are self colored and do not provide an immediate test for blotching genes. However, the F_2 seeds should show whether or not the inbreds carried such genes.

These preliminary data, although too few to reveal clear-cut relationships, do show the possibilities of this method of approach which is a close counterpart of testing for the blood groups in man. Here is an excellent Ph.D. thesis problem. We shall be glad to provide, to anyone interested, seed of the tester stocks so far available as well as materials from which additional tester stocks can be isolated.

Tests of Inbred Strains for Presence of Blotching Genes

Inbred	Bh genes affecting c			Affecting r		Color genes	
	1	2	3	1	2	C	R
Hy	+	-	+	+	-	-	-
Oh7	-	-	-	-	-	-	-
Oh28	CC		CC	-	-	+	-
Wf9	-	-	-	+	-	-	-
38-11	CC	CC		-	-	+	-
Oh43	-	-	-	-	-	-	-
Oh45	+	+	+	+	-	-	-
Pa70	-		-	-	-	-	-
C103	-	-	-	-	-	-	-
C20	-	-	-	-	-	-	-
C21	-	-	-	-	-	-	-
R2	CC	CC		-	-	+	-
M14	-	-	-		-	-	-
Os420	-	-	-	-	-	-	-
Il1A	-	-	-	-	-	-	-
W23	-	-	-	-	-	-	-
B10	CC	CC	CC	+	-	+	-
NY16	-	-	-	+	-	-	-
A158	+	-	+	+	-	-	-

14. The inhibitor of tunicate.

The inhibitor of tu^h reported in last year's News Letter also affects the expression of the Tu gene as it was assumed that it would. The genotype Tu tu in the presence of the inhibitor is similar to the genotype tu^h tu without the inhibitor.

The inhibitor is apparently linked with Y on chromosome 6 as the following data from the progeny of a selfed ear heterozygous for both genes indicate:

	Weak tu^h	Intermediate tu^h	Strong tu^h
Yellow seeds	20	35	12
White seeds	3	14	7

A second test involving backcrosses instead of selfs produced the following results:

Rows	Yellow seeds		White seeds		Total	Cross-overs
	Weak tu^h	Strong tu^h	Weak tu^h	Strong tu^h		
57-553-54	33	16	24	28	101	40
57-555-56	25	23	18	30	96	41
Total	58	39	42	58	197	81

Although not one of the three tests shows highly significant deviations from independent inheritance, they are consistent in showing some association between the inhibitor and Y which came into the cross with it. Further tests are needed to verify this indication of linkage and to determine more precisely the amount of crossing over involved.

The interaction of the Tu gene with the inhibitor follows expectations quite closely. A population segregating for both genes would be expected to have one-fourth of its plants homozygous tunicate and three-fourths of these or three-sixteenths of the total to be an inhibited form of tunicate. In a population of 118 plants, 27 plants were Tu Tu and 20 of these were inhibited. Theoretical numbers are 30 and 22 respectively.

The fact that the inhibitor acts upon the expression of the Tu gene has made it possible to obtain fertile homozygous Tu Tu plants in

a great variety of stocks. These in turn are exhibiting a number of characteristics which may be regarded as primitive and which may provide clues as to the nature of wild corn and to some of the changes which must have occurred in the course of corn's evolution under domestication. For example, practically all Tu Tu plants bear their ears high on the stalk, the uppermost ear sometimes occurring at the node below the tassel. Since the upper part of the stalk is slender, this means that only small ears can be borne in this region. If wild corn was of this nature, then one of the most important changes occurring during domestication has been a shift in the position of the ear to a lower, thicker region of the stalk which is capable of bearing larger ears.

Since the number of husks surrounding an ear is directly correlated with the number of internodes between the tassel and the ear these small ears borne on the uppermost nodes of Tu Tu plants have only a few husks and these sometimes open up at maturity. This explains a previously puzzling situation: why an ear of pod corn should be twice protected, once with glumes surrounding the seeds and a second time with husks surrounding the ear. It is now possible to imagine the husks as a protective device primarily for the tender young female inflorescence and the glumes a protective device for the ripening kernel.

Paul C. Mangelsdorf

15. The widespread distribution of Chapalote maize in prehistoric times.

The present-day Mexican race of maize called "Chapalote" was one of the basic races in North America in prehistoric times. A re-examination of the actual cobs, photographs or descriptive literature covering 14 sites in northwestern Mexico and southwestern United States suggests that the archaeological maize from this area was either pre-Chapalote, Chapalote or a more evolved and more tripsacoid derivative called "Basket-maker" corn. The Mexican states with prehistoric Chapalote are Michoacan (lava impressions), Sonora (Dark Cave) and Chihuahua (Swallow Cave, Slab Cave, Tau Cave, Olla Cave). In the region now the U.S., Chapalote occurred in Arizona (Richards Cave, Tonto Cave, Painted Cave), Colorado (Cottonwood Cave, Lo Dais Ka Cave) and New Mexico (Bat Cave, Tularosa Cave, Cebollita Cave).

16. Archaeological evidence of the effect of teosinte introgression on maize evolution.

A large stratified collection of archaeological cobs from Cebollita Cave, New Mexico is being studied. Identification of the original maize (level-5) as Chapalote is possible because the cobs and kernels from this level are perfectly preserved by carbonization. In the next level up (level-4), which was not carbonized, there was sudden teosinte

introgression. Some of these cobs from this level are exact counterparts of modern F_1 hybrids between maize and teosinte and many others resemble teosinte derivatives in being small with highly indurated glumes. A few cobs have soft-glumes and resemble the carbonized ones from the previous level. In level-3 there is some recovery, on the average, from the marked effects of teosinte introgression as well as a tremendous increase in variability. Finally, in levels-2 and -1, the variation initiated by teosinte hybridization, includes a type of maize that has larger cobs and was presumably more productive than the original Chapalote race. Some of the larger cobs resemble those of the present day flour corns of the semi-arid regions in the Southwest. The introgression from teosinte which may initially have been detrimental proved to be beneficial in the long run, after new balanced polygene systems had become established.

17. Homozygous corn-grass.

For the first time we have obtained homozygous corn grass lines which approach the original "grassy" extreme reported by Singleton. Cg Cg plants of the grass extreme suddenly appeared in a line which was though to be homozygous minus-modified corn grass but which so closely approached normal corn that identification was usually impossible. These new Cg Cg stocks are uniform and breed true. They are much more profusely tillered than teopod and yet are more amenable to hand pollination. The breeding behavior of the new Cg Cg suggests a change at the Cg locus to a new stable allele. These new Cg stocks will be studied further in regard to the development of a forage or ensilage-type of corn as a possible substitute for sudan grass.

18. Papyrescent (Pn) linkage data for long arm of chromosome - 7.

According to the data (see below), the sequence of genes linked to papyrescent glumes is gl_1 - ij - bd - Pn. The Pn gene is to the right of bd and separated from it by about 5 map units. The cross-over value between bd and Pn was measured as a difference in the linkage of each to either Gl or Ij. This value (5 units) was not obtained directly because of difficulty in scoring certain decayed branched-silkless (bd) ears for glume character.

The Pn character should be more useful as a marker gene than the other factors near it in the long arm of chromosome-7. Bn (brown aleurone) is often difficult to classify and bd (branched-silkless) must be maintained as a heterozygote because it usually has no silks. The Pn gene also extends the genetic coverage of the long arm of chromosome-7 by 5 units beyond that previously known.

F_2 Linkage Data from the Cross Pn bd x gl ij

Genes XY	XY	Xy	xY	xy	Total	Recombination %[1]	Map Units[2]
Gl Pn	192	62	60	23	337	47.6	79.0
Gl Bd	178	75	63	21	337	46.9	74.0
Gl Ij	234	19	24	60	337	13.8	14.5
Ij Pn	200	59	52	26	337	42.9	58.6
Ij Bd	177	81	64	15	337	40.7	54.0

[1]Product method from tables of Immer, 1930.
[2]Conversion from tables of Haldane, 1919.

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1. Correlations among 28 characteristics of 145 inbred lines of maize.

A group of 145 standard American inbred lines were compared in many locations in 1948 by members of the North Central Corn Improvement Conference of the United States. These lines were involved in most of the open-pedigree hybrids developed by the Corn Belt agricultural experiment stations and in use prior to 1948. Data were summarized in 1948 in a mimeographed report by Brunson, Ullstrup and Dicke. The 378 possible correlations involving 28 plant and ear characters of the 145 widely used inbred lines are shown in Table 1. Many of the correlations were statistically significant and should have some predictive value in maize breeding research. These 378 correlations were obtained quickly and easily on the University of Illinois Illiac electronic digital computer.

R. W. Jugenheimer

Table 1. Correlations among 28 characteristics of 145 inbred lines.

Code	Character	1	2	3	4	5	6	7
1.	Days to half pollen		+.934**	+.928**	+.731**	+.820**	-.542**	+.115
2.	Days to half silk	+.934**		+.896**	+.732**	+.805**	-.518**	+.101
3.	Days to maturity	+.928**	+.896**		+.718**	+.812**	-.491**	+.104
4.	Plant height, in.	+.731**	+.732**	+.718**		+.885**	-.344**	+.081
5.	Ear height, in.	+.820**	+.805**	+.812**	+.885**		-.426**	+.215*
6.	Root-lodged plants, %	-.542**	-.518**	-.491**	-.344**	-.426**		+.038
7.	Stalk-lodged plants, %	+.115	+.101	+.104	+.081	+.215*	+.038	
8.	Plot yield, lb.	+.025	+.023	+.077	+.215*	+.059	-.060	-.059
9.	Ears per plant, no.	-.049	-.009	-.062	+.031	+.001	-.038	+.216*
10.	Reaction to 2-4D, gr.	+.077	+.102	+.098	+.248**	+.204*	+.133	+.055
11.	Mg. deficiency, gr.	-.166	-.153	-.186*	-.218*	-.216*	+.132	-.059
12.	H. Turcicum, gr.	-.542**	-.534**	-.559**	-.396**	-.537**	+.255**	-.162
13.	H. Maydis, gr.	-.056	-.042	-.066	-.011	-.041	-.040	-.086
14.	Diplodia stalk rot, gr.	-.245**	-.222**	-.211*	-.152	-.139	+.260**	+.149
15.	Gibberella stalk rot, gr.	-.412**	-.394**	-.439**	-.322**	-.389**	+.198*	-.022
16.	Smutted plants, %	-.315**	-.294**	-.305**	-.244**	-.270**	+.339**	-.003
17.	Kernel rot, gr.	+.015	+.030	+.036	+.133	+.066	-.112	-.094
18.	Eur. borer oviposition, gr.	+.079	+.111	+.096	+.040	+.084	-.185*	+.160
19.	Eur. borer leaf feeding, gr.	-.323**	-.339**	-.279**	-.122	-.153	+.151	+.022
20.	Eur. borer plant injury, gr.	-.234**	-.274**	-.233**	-.256**	-.187*	+.154	+.090
21.	Eur. plant tolerance, gr.	-.275**	-.305**	-.282**	-.294**	-.239**	+.217*	+.120
22.	Corn ear worm, gr.	-.304**	-.265**	-.284**	-.160	-.234**	+.198*	-.028
23.	Leaf aphids, index	+.509**	+.512**	+.573**	+.373**	+.452**	-.227*	+.070
24.	Thrips, gr.	+.143	+.112	+.162	+.069	+.123	-.214*	+.002
25.	Weight per 1,000 seeds, gm.	+.501**	+.469**	+.571**	+.469**	+.478**	-.138	+.039
26.	Protein, %	-.279**	-.257**	-.299**	-.434**	-.331**	+.157	-.183*
27.	Alcohol soluble nitrogen, %	-.317**	-.305**	-.330**	-.492**	-.394**	+.153	-.163
28.	Oil, %	-.049	-.011	+.030	-.110	-.063	+.028	+.063
	Range, mean, and standard deviation of 145 inbred lines							
	Range Lowest	59	60	99	42	10	0	0
	Range Highest	93	97	148	95	49	88	66
	Mean	75.861	77.943	123.492	65.119	27.934	17.664	8.844
	Standard deviation	6.814	7.204	10.511	10.067	8.904	17.044	10.645

*Exceeds the 5 percent level of significance of .174.
**Exceeds the 1 percent level of significance of .228.

Table 1. Correlations among 28 characteristics of 145 inbred lines (Continued).

Code	Character	8	9	10	11	12	13	14
1.	Days to half pollen	+.025	-.049	+.077	-.166	-.542**	-.056	-.245**
2.	Days to half silk	+.023	-.009	+.102	-.153	-.534**	-.042	-.222**
3.	Days to maturity	+.077	-.062	+.098	-.186*	-.559	-.066	-.211*
4.	Plant height, in.	+.215*	+.031	+.248**	-.218*	-.396**	-.011	-.152
5.	Ear height, in.	+.059	+.001	+.204*	-.216*	-.537**	-.041	-.139
6.	Root-lodged plants, %	-.060	-.038	+.133	+.132	+.255**	-.040	+.260**
7.	Stalk-lodged plants, %	-.059	+.216*	+.055	-.059	-.162	-.086	+.149
8.	Plot yield, lb.		+.164	+.125	-.205*	+.250**	-.189*	-.292**
9.	Ears per plant, no.	+.164		+.025	-.112	+.137	-.029	-.061
10.	Reaction to 2-4D, gr.	+.125	+.025		-.012	-.111	-.150	-.064
11.	Mg. deficiency, gr.	-.205*	-.112	-.012		-.014	+.144	+.087
12.	H. Turcicum, gr.	+.250**	+.137	-.111	-.014		+.017	-.081
13.	H. Maydis, gr.	-.189*	-.029	-.150	+.114	+.017		+.001
14.	Diplodia stalk rot, gr.	-.292**	-.061	-.064	+.087	-.081	+.001	
15.	Gibberella stalk rot, gr.	-.200*	+.050	-.076	+.195*	+.091	+.036	+.267**
16.	Smutted plants, %	-.069	+.002	+.162	+.077	+.211*	+.028	+.186*
17.	Kernel rot, gr.	+.244**	+.003	-.074	-.049	+.122	+.080	-.128
18.	Eur. borer oviposition, gr.	-.037	-.029	-.201*	-.070	-.018	+.056	+.059
19.	Eur. borer leaf feeding, gr.	-.013	-.028	+.035	-.112	+.226*	-.048	+.168
20.	Eur. borer plant injury, gr.	-.265**	+.038	-.029	+.035	+.184*	+.147	+.123
21.	Eur. plant tolerance, gr.	-.351**	+.086	-.093	+.066	+.161	+.137	+.202*
22.	Corn ear worm, gr.	+.123	+.234**	-.072	-.022	+.245**	+.029	+.031
23.	Leaf aphids, index	+.106	-.127	+.077	-.064	-.297**	-.285**	-.144
24.	Thrips, gr.	-.158	-.151	-.070	+.084	-.169	+.155	+.002
25.	Weight per 1,000 seeds, gm.	+.031	-.102	+.112	-.097	-.308**	-.007	-.074
26.	Protein, %	-.522**	-.096	-.092	+.328**	-.007	+.019	+.329**
27.	Alcohol soluble nitrogen, %	-.427**	-.084	-.095	+.304**	+.040	-.079	+.283**
28.	Oil, %	+.051	+.121	-.126	+.014	+.038	+.106	-.047
	Range, mean, and standard deviation of 145 inbred lines							
	Range Desirable	14.2	1.92	2	0.5	1	0.5	1.6
	Range Undesirable	2.1	.65	5	5.5	5	5.0	5.0
	Mean	8.525	1.172	3.754	2.666	4.398	2.996	2.900
	Standard deviation	2.216	0.224	0.852	0.969	0.958	1.033	0.635

*Exceeds the 5 percent level of significance of .174.
**Exceeds the 1 percent level of significance of .228.

Table 1. Correlations among 28 characteristics of 145 inbred lines (Continued).

Code	Character	15	16	17	18	19	20	21
1.	Days to half pollen	-.412**	-.315**	+.015	+.079	-.323**	-.234**	-.275**
2.	Days to half silk	-.394**	-.294**	+.030	+.111	-.339**	-.274**	-.305**
3.	Days to maturity	-.439**	-.305**	+.036	+.096	-.279**	-.233**	-.282**
4.	Plant height, in.	-.322**	-.244**	+.133	+.040	-.122	-.256**	-.294**
5.	Ear height, in.	-.389**	-.270**	+.066	+.084	-.153	-.187*	-.239**
6.	Root-lodged plants, %	+.198*	+.339**	-.112	-.185*	+.151	+.154	+.217*
7.	Stalk-lodged plants, %	-.022	-.003	-.094	+.160	+.022	+.090	+.120
8.	Plot yield, lb.	-.200*	-.069	+.244**	-.037	-.013	-.265**	-.351**
9.	Ears per plant, no.	+.050	+.002	+.003	-.029	-.028	+.038	+.086
10.	Reaction to 2-4D, gr.	-.076	+.162	-.074	-.201*	+.035	-.029	-.093
11.	Mg. deficiency, gr.	+.195*	+.077	-.049	-.070	-.112	+.035	+.066
12.	H. Turcicum, gr.	+.091	+.211*	+.122	-.018	+.226*	+.184*	+.161
13.	H. Maydis, gr.	+.036	+.028	+.080	+.056	-.048	+.147	+.137
14.	Diplodia stalk rot, gr.	+.267**	+.186*	-.128	+.059	+.168	+.123	+.202*
15.	Gibberella stalk rot, gr.		+.104	-.051	+.019	+.036	+.225**	+.355**
16.	Smutted plants, %	+.104		-.039	-.143	+.302**	+.215*	+.166
17.	Kernel rot, gr.	-.051.	-.039		-.029	+.016	-.075	-.129
18.	Eur. borer oviposition, gr.	+.019	-.143	-.029		+.014	+.010	+.022
19.	Eur. borer leaf feeding, gr.	+.036	+.302**	+.016	+.014		+.344**	+.311**
20.	Eur. borer plant injury, gr.	+.225*	+.215*	-.075	+.010	+.344**		+.884**
21.	Eur. plant tolerance, gr.	+.355**	+.166	-.129	+.022	+.311**	+.884**	
22.	Corn ear worm, gr.	+.018	+.176*	+.268**	+.012	+.128	+.039	+.053
23.	Leaf aphids, index	-.200*	-.053	-.045	+.098	-.215*	-.111	-.164
24.	Thrips, gr.	+.026	+.008	+.026	-.005	+.081	+.049	+.076
25.	Weight per 1,000 seeds, gm.	-.202*	-.039	+.097	+.072	-.141	-.010	-.049
26.	Protein, %	+.207*	+.269**	-.271**	-.026	+.142	+.262**	+.317**
27.	Alcohol soluble nitrogen, %	+.206*	+.252**	-.211*	-.028	+.164	+.177*	+.214*
28.	Oil, %	-.109	+.062	-.039	+.074	-.063	-.001	+.011
	Range, mean, and standard deviation of 145 inbred lines							
	Range Desirable	1.0	0	1	1	1	1	1
	Range Undesirable	4.5	35	6	5	5	5	5
	Mean	3.089	6.770	2.115	3.008	3.000	3.205	3.074
	Standard deviation	0.747	7.293	1.249	0.707	0.830	0.949	1.018

*Exceeds the 5 percent level of significance of .174.
**Exceeds the 1 percent level of significance of .228.

Table 1. Correlations among 28 characteristics of 145 inbred lines (Concluded).

Code	Character	22	23	24	25	26	27	28
1.	Days to half pollen	-.304**	+.509**	+.143	+.501**	-.279**	-.317**	-.049
2.	Days to half silk	-.265**	+.512**	+.112	+.469**	-.257**	-.305**	-.011
3.	Days to maturity	-.284**	+.573**	+.162	+.571**	-.299**	-.330**	+.030
4.	Plant height, in.	-.160	+.373**	+.069	+.469**	-.434**	-.492**	-.110
5.	Ear height, in.	-.234**	+.452**	+.123	+.478**	-.331**	-.394**	-.063
6.	Root-lodged plants, %	+.198*	-.227*	-.214*	-.138	+.157	+.153	+.028
7.	Stalk-lodged plants, %	-.028	+.070	+.002	+.039	-.183*	-.163	+.063
8.	Plot yield, lb.	+.123	+.106	-.158	+.031	-.522**	-.427**	+.051
9.	Ears per plant, no.	+.234**	-.127	-.151	-.102	-.096	-.084	+.121
10.	Reaction to 2-4D, gr.	-.072	+.077	-.070	+.112	-.092	-.095	-.126
11.	Mg. deficiency, gr.	-.022	-.064	+.084	-.097	+.328**	+.304**	+.014
12.	H. Turcicum, gr.	+.245**	-.297**	-.169	-.308**	-.007	+.040	+.038
13.	H. Maydis, gr.	+.029	-.285**	+.155	-.007	+.019	-.079	+.106
14.	Diplodia stalk rot, gr.	+.031	-.144	+.002	-.074	+.329**	+.283**	-.047
15.	Gibberella stalk rot, gr.	+.018	-.200*	+.026	-.202*	+.207*	+.206*	-.109
16.	Smutted plants, %	+.176*	-.053	+.008	-.039	+.269**	+.252**	+.062
17.	Kernel rot, gr.	+.268**	-.045	+.026	+.097	-.271**	-.211*	-.039
18.	Eur. borer oviposition, gr.	+.012	+.098	-.005	+.072	-.026	-.028	+.074
19.	Eur. borer leaf feeding, gr.	+.128	-.215*	+.081	-.141	+.142	+.164	-.063
20.	Eur. borer plant injury, gr.	+.039	-.111	+.049	-.010	+.262**	+.177*	-.001
21.	Eur. plant tolerance, gr.	+.053	-.164	+.076	-.049	+.317**	+.214*	+.011
22.	Corn ear worm, gr.		-.269**	-.118	-.112	-.119	-.050	-.059
23.	Leaf aphids, index	-.269**		-.061	+.416**	-.126	-.140	+.074
24.	Thrips, gr.	-.118	-.061		+.160	-.076	-.042	+.014
25.	Weight per 1,000 seeds, gm.	-.112	+.416**	+.160		-.243**	-.306**	-.022
26.	Protein, %	-.119	-.126	-.076	-.243**		+.885**	+.042
27.	Alcohol soluble nitrogen, %	-.050	-.140	-.042	-.306**	+.885**		+.029
28.	Oil, %	-.059	+.074	+.014	-.022	+.042	+.029	
	Range, mean, and standard deviation of 145 inbred lines							
	Range Desirable	0.5	0	1	119	16.1	6.5	5.8
	Range Undesirable	4.1	191	5	370	9.7	1.7	2.7
	Mean	2.264	74.762	2.328	224.090	12.329	1.065	4.538
	Standard deviation	0.624	39.555	0.854	42.426	1.306	0.208	0.547

*Exceeds the 5 percent level of significance of .174.
**Exceeds the 1 percent level of significance of .228.

2. Genetic confirmation of chromosomes involved in reciprocal translocations.

During recent years a large number of reciprocal translocations in maize have been accumulated. The cytological positions of the interchange points of most of these have been investigated by Dr. A. E. Longley. In most cases, however, little or no information is available on their genetic relations or transmission. The present study was initiated to obtain genetic confirmation of the chromosomes involved in some of these translocations.

In the translocations which follow, recombination studies were confined to markers which can be classified either as kernel or as seedling traits in order to eliminate the need for growing plants to maturity. The selection of markers was restricted to immediately available combinations in which the markers can be accurately classified together.

The data are tabulated in a manner similar to the form used in the 1935 Maize Linkage Summary. The cytological determinations are those of Dr. Longley, most of which have been listed in past issues of the Maize News Letter. The linkage phases of the various crosses are indicated, together with a notation of whether the F_1 was used as male or female parent. Most of the data are from testcrosses either in coupling (CB) or repulsion (RB) phase. The designation "BS" indicates that the progeny represents a testcross for one marker and an F_2 for the other.

Unless otherwise indicated, the data are from plants heterozygous for a translocation. Several crosses involve homozygous translocations; these are indicated by the notation T/T. Linkage data from male-transmission involving duplicate-deficient plants (symbol DD in the table) have also been included. The locus of the deficiency (one interchange point) is indicated by the symbol Df. On the assumption that the deficiency is not male-transmitted, the transmission of a linked gene is a function of recombination between the gene locus and the deficiency.

Aneuploid complements are female-transmitted in numerous instances. In a few cases, the aneuploid types are known from cytological investigation of the progeny to be duplicate-deficients arising from adjacent-1 disjunction of the heterozygous translocation. In other cases, evidence for functioning of aneuploid eggs is provided by the variable transmission of parental alleles in various linkage phases and in reciprocal crosses, correlated with observations of abortive pollen types. It is probable that a second type of aneuploids, trisomics, is produced in some instances as a result of 3:1 disjunction of the translocation heterozygote. Many of the recombination values given in the table are undoubtedly distorted by such events. Some instances of unequal classes in the table are, however, related to differential survival, e.g., reduced germination of su kernels. Some of the data suggest that

Table 1. Recombination in plants carrying reciprocal translocations.

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
2-4a	2L.29	su_1 gl_2	RB♀	209	251	202	154	816	363	44.5	su_1 3.3 T 14.0 Tu
	4L.16	lg_1 gl_2	CB♀	133	17	45	149	344	62	18.0	
2-4b	2L.88	lg_1 gl_2	CB♂	101	17	10	83	211	27	12.8	Tu 5.0 gl_3 15.2 T
	4L.54	"	CB♀	109	20	24	142	295	44	14.9	
		"	Total	210	37	34	225	506	71	14.0	
2-4c	2L.77	su_1 v_4	CB♀	99	29	17	42	187	46	24.6	su_1 9.2 T 30.8 Tu
	4S.09	lg_1 gl_2	CB♀	309	49	46	299	703	95	13.5	v_4 19.9 T
2-4d	2S.20	su_1 v_4	RB♀	16	32	18	10	76	26	34.2	B 18 T 6 v_4
	4L.25	"	CB♀	71	33	32	48	184	65	35.3	su_1 28.4 Tu 0.2 T
		"	Total					260	91	35.0	
2-4f	2L.78	su_1 v_4	RB♀	72	196	185	46	499	118	23.6	su_1 6.1 T 19.3 Tu
	4L.13	lg_1 gl_2	CB♀	529	89	74	545	1237	163	13.2	
2-4g	2L.13	su_1 v_4	CB♀	379	52	35	237	703	87	12.4	Ts_5 7.1 T 2.7 su_1
	4S.26	su_1 gl_2	CB♀	525	234	183	359	1301	417	32.1	
		gl_2 v_4	CB♀	270	119	144	170	703	263	37.4	
		lg_1 gl_2	CB♀	271	54	50	223	598	104	17.4	
2-4j	2S.19	su_1 v_4	RB♀	43	444	398	6	891	(49)	(5.5)	Functional aneuploid eggs apparently produced. An inversion probably involved.
	4L.30							404su	6	1.5	
		su_1 gl_2	RB♀	60	724	567	7	1358	(67)	(4.9)	
								574su	7	1.2	
		"	RB♂	3	183	150	4	340	(7)	(2.1)	
								154su	4	2.6	
		gl_2 v_4	CB♀	437	1	4	449	891	5	0.6	
		su_1 lg_1	RB♀	9	82	68	0	159	(9)	(5.7)	
								68su	0	0.0	
		lg_1 gl_2	CB♀	73	4	3	79	159	7	4.4	

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
2.4k	2L.12	su_1 v_4	RB♀	14	32	10	0	56	14	25.0	
	4L.18	"	RBS♀	46	33	29	0	108		8.0*	
		su_1 gl_2	RB♀	226	327	206	125	884	351	39.7	
		gl_2 " v_4	CB♀	17	6	7	26	56	13	23.2	
			CBS♀	46	11	29	22	108		29.0	
		lg_1 gl_2	CB♀	186	43	37	201	467	80	17.1	
2-41	2L.56	su_1 v_4	RB♀	16	28	10	2	56	18	32.1	
	4S.51	"	RBS♀	33	20	41	4	98		20.0	
		lg_1 gl_2	CB♀	58	13	14	69	154	27	17.5	
2-4m	2S.08	su_1 v_4	RB♀	4	20	26	13	63	17	27.0	Aneuploids may be transmitted
	4S.16	"	RB♂	5	110	107	0	222	5	2.3	
		"	Total	9	130	133	13	285	22	7.7	
		"	RBS♀	62	47	137	20	266		22.0	
		su_1 gl_2	RB♂	78	138	96	39	351	117	33.3	
		gl_2 " v_4	CB♀	45	45	37	75	202	82	40.6	
			CB♂	81	40	31	70	222	71	32.0	
		"	Total	126	85	68	145	424	153	36.1	
		lg_1 gl_2	CB♀	209	58	55	235	557	113	20.3	
2-4 4374-7	2L.15 4L.23	su_1 v_4	CB♀	204	192	206	178	780	398	51.0	Cytology probably wrong.
2-4 6266-7	2L.45 4L.20	su_1 v_4	CB♀	225	177	209	140	751	386	51.4	Cytology may be wrong.

*If one double recessive had occurred.

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
2-5a	2L.16	pr v_4	CBS♀	25	5	36	10	76		44.0	cent-T 7.3 v_4
	5L.18	"	CBS♂	165	25	133	75	398		27.0	
		"	Total	190	30	169	85	474		29.0	
2-5b	2L.02	pr v_4	CBS♀	52	15	61	11	139		59.0	
	5S.02										
2-5e	2S.12	lg_1 gl_2	CB♀	32	5	4	29	70	9	12.9	sk - T = 15.1
	5S.23	"	CB♂	45	12	12	42	111	24	21.6	T - v_4 = 2
		"	Total	77	17	16	71	181	33	18.2	
2-6b	2S.69	y gl_2	CB♀	50	34	35	43	162	69	42.6	Probable order:
	6L.49	lg_1 gl_2	CB♀	76	6	9	71	162	15	9.3	gl_2 - T - B
											Pl 7.7 sm 3.7 T
2-6c	2L.32	y gl_2	RB♀	387	488	449	313	1637	700	42.8	ts_1 12.3 T 1.7 v_4
	6L.20	lg_1 gl_2	CB♀	706	110	130	691	1637	240	14.7	T 5.0 Pl 6.0 sm
2-6d	2L.52	y v_4	CB♀	188	32	26	120	366	58	15.8	T - v_4 = 4.2
	6L.57	"	CB♂	142	6	2	112	262	8	3.1	T 5.2 Pl 6.9 sm
		"	Total	330	38	28	232	628	66	10.5	
		lg_1 gl_2	CB♀	79	7	9	64	159	16	10.1	
2-6e	2L.28	y gl_2	RB♀	6	48	47	12	113	18	15.9	gl_2-B-T; near B
	6L.22	y lg_1	RB♀	19	35	37	22	113	41	36.3	T 4.7 Y 5.2 Pl
		lg_1 gl_2	CB♀	42	14	11	46	113	25	22.1	T apparently in 2S

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
2-9a	2S.48	c wx	CB♀	161	55	44	143	403	99	24.6	wx 35.6 T
	9L.85	wx lg_1	RB♀	192	267	241	233	933	425	45.6	B 1.2 sk 1.2 T
		wx gl_2	RB♀	170	289	296	178	933	348	37.3	
		wx v_4	RBS♀	55	28	61	19	163		41.0	
		gl_2 v_4	CBS♀	67	15	49	32	163		31.0	
		lg_1 gl_2	CB♀	345	88	121	379	933	209	22.4	
2-9b	2S.12	wx v_4	CB♀	64	15	7	68	154	22	14.3	wx 7.5 T
	9L.12	wx gl_2	RB♀	76	135	115	72	398	148	37.2	ts_1 5.0 T 7.8 v_4
		gl_2 v_4	RB♀	26	50	45	33	154	59	38.3	
		lg_1 gl_2	CB♀	154	27	23	152	356	50	14.0	
2-9	2L.32	wx v_4	CBS♀	21	4	23	6	54		44.0	sh_1 11 wx 1.4 T
6656-1	9S.31	lg_1 gl_2	CB♀	175	39	39	168	421	78	18.5	
2-10a	2L.17	R gl_2	RB♀	45	58	50	32	185	77	41.6	T 1.8 g_1 8.1 R
	10L.53	lg_1 gl_2	CB♀	79	19	16	71	185	35	18.9	ts_1 13.5 T
											cent-T 6.5 v_4
2-10b	2S.45	R v_4	CB♀	239	140	97	134	610	237	38.9	Probable orders:
	10L.77							231r	97	42.0	gl_2 - T - B
		R gl_2	CB♀	311	68	41	190	610	109	17.9	cent - R - T
								231r	41	17.7	2 10^2 probably
								258gl	68	26.4	female-transmitted
		gl_2 v_4	CB♀	218	134	118	140	610	252	41.3	
								258gl	118	45.7	
4-5a	4L.19	su_1 pr	CB♀	173	82	*	*	255Su	82	32.2	
	5S.29										

*sugary kernels not classified

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
4-5d	4S.21 5L.19	su_1 pr	RB♀	4	58	49	2	113	6	5.3	su_1 3.4 T - cent bm_1 2.5 T su_1-bm_1 linked in T/T
4-5h	4L.30	su_1 pr	CB♀	325	66	--352--		391Su	66	16.9	T closer to su_1 than
	5L.08	su_1 pr	RB♀ T/T	110	384	379	112	985	222	22.5	to pr
4-5i	4L.10 5S.13	su_1 pr	CB♀	214	86	57	192	549	143	26.0	T closer to su_1 than to pr
4-6a	4L.33	su_1 y	RB♀	4	125	133	6	268	10	3.7	Ts_5 14.9 su_1 4.9 T
	6L.44	"	CB♀	492	19	24	475	1010	43	4.3	Y 1.3 T 5.3 Pl
		"	Total					1278	53	4.1	su_1 19.7 Pl in T/T
4-6b	4S.71	su_1 y	RB♀	150	354	603	26	380y	26	6.8	Ts_5 1.6 T 8.6 su_1
	6L.25	su_1 Df	CB♂ DD	---63--		--475--		538	63	11.7*	T 5.6 Y 9.3 Pl 4^6 6 female-transmitted
4-6c	4S.13 6S.86	su_1 y	CB♀	1347	127	58	820	878su	58	6.6	su_1 8.6 T 31.2 Tu T 8.4 Y 23.0 Pl 4 6^4 probably female-transmitted
4-6e	4S.60 6L.51	su_1 y	CB♀	168	101	100	135	504	201	39.9	
4-6 4341-5	4S.37 6S.81	su_1 y	RB♀	82	418	414	16	430su	16	3.7	4 6^4 probably female-transmitted

*If deficiency not male-transmitted

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
4-6 4461-2	4S.86 6L.17	su_1 y	CB♀	311	410	306	395	1422 617Y	716 306	50.4 49.6	If T in 4S: 4^6 6 probably female-transmitted. Probable order: T - su_1 - cent cent - Y - T
4-6 5227-5	4S.46 6S.84	su_1 y	CB♀	380	33	34	305	752 339su	67 34	8.9 10.0	4 6^4 probably female-transmitted. Order: su_1 - T - cent
4-7a	4S.27 7L.07	su_1 gl_1	CB♀	314	25	11	316	666	36	5.4	
4-7 4698-1	4L.08 7L.74	su_1 gl_1	CB♀	151	71	64	147	433	135	31.2	
4-9a	4L.18 9L.50	su_1 C	CB♀	169	89	92	160	509	181	35.6	su_1 9.8 T 14.1 Tu C wx 11.5 or 31.0 T su_1 2 or 21 T
4-9d	4L.14 9L.15	su_1 C	CB♀	1219	333	337	1136	3025	670	22.1	su_1 3.8 T 21.2 Tu
4-9e	4S.60 9L.24	su_1 C	CB♀	1085	409	442	1039	2975	851	28.6	
4-9g	4S.35 9L.42	su_1 C	RB♀	34	73	76	29	212	63	29.7	su_1 3.3 T 22.1 Tu
		"	CB♀	107	37	36	120	300	73	24.3	
		"	RB♂	129	310	365	131	935	260	27.8	
		"	Total					1447	396	27.4	

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
4-9 4373-2	4L.29 9L.39	su_1 C	CB♀	378	220	216	387	1201	436	36.3	
4-9 5657-2	4L.33 9S.25	su_1 C	RB♀	101	478	470	59	1108	160	14.4	C 12.4 wx 1.8 T
		"	CB♀	129	34	34	127	314	68	21.7	
		"	Total					1422	228	16.0	
		"	CB♂	111	75	71	118	375	146	38.9	
		C wx	RB♀ T/T	856	1540	1668	796	4860	1652	34.0	
		"	RB♂ T/T	847	1480	1671	756	4754	1603	33.7	
		"	Total	1703	3020	3339	1552	9614	3255	33.9	
4-9 5918-4	4S.24 9L.18	su_1 C	RB♀	21	49	51	18	139	39	28.1	
		"	RB♂	58	123	127	62	370	120	32.4	
		"	Total	79	172	178	80	509	159	31.2	
4-9 6222-1	4L.03 9S.68	su_1 C	RB♀	9	141	145	77	154C	9	5.8	C 3.3 T 0.3 sh_1 6.3 wx 4 94 female-transmitted. Order: su_1 - cent - T
4-10b	4L.18 10L.57	su_1 R	CB♂	71	8	17	84	180	25	13.9	Ts_5 15.0 su_1 4.0 T T 1.6 g_1; T 8.6 R; g_1 8.3 R
4-10e	4L.04 10L.01	su_1 R	RB♀	392	1395	1451	377	3615	769	21.3	T 22.8 R
		"	CB♀	318	80	77	354	829	157	18.9	
		"	RB♂	28	77	93	22	220	50	22.7	
		"	Total					4664	976	20.9	
		"	CB♀ T/T	184	51	48	190	473	99	20.9	
		"	CB♂ T/T	110	43	38	111	302	81	26.8	
		"	Total	294	94	86	301	775	180	23.2	

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
5-9d	5L.22 9L.15	pr wx	CB♀	138	11	16	127	292	27	9.2	
6-7a	6L.74 7L.61	y gl_1	CB♀	322	293	312	298	1225	605	49.4	
6-7 4545-5	6L.25 7S.75	y gl_1	CB♀	504	67	75	525	1171	142	12.1	
6-7 4573-2	6L.22 7L.27	y gl_1	CB♀	418	35	9	339	801	44	5.5	
		"	CB♂	148	6	11	181	346	17	4.9	
		"	Total	566	41	20	520	1147	61	5.3	
6-7 4594-10	6L.52 7S.67	y gl_1	CB♀	139	70	72	160	441	142	32.2	
		"	CB♂	61	33	29	75	198	62	31.3	
		"	Total	200	103	101	235	639	204	31.9	
6-7 5181-6	6S.79 7L.86	y gl_1	CB♀	252	171	138	200	761	309	40.6	
6-9a	6S.79 9L.40	y wx	CB♀	78	3	5	63	149	8	5.4	-- Plant 2489-1
		"	CB♀	70	6	6	80	162	12	7.4	-- Plant 2489-4
		"	Total	148	9	11	143	311	20	6.4	-- Family 2489
		"	CB♂	51	9	15	58	133	24	18.0	-- Plant 2489-4
		"	CB♀	349	34	34	362	780	68	8.7	-- Family 2490 (except- 17)
		"	CB♀	63	17	21	58	159	38	23.9	-- Plant 2490-17
		"	CB♀	57	7	5	65	134	12	9.0	-- Plant 2490-2
		"	CB♂	49	6	54	110	219	(60)	(27.4)	-- Plant 2490-2
								164y	54	32.9	
								55Y	6	10.9	
								103Wx	54	52.4	
								116wx	6	5.2	

Table 1. (Continued)

T	Cytol.	Genes	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
6-9a (Cont.)	6S.79 9L.40	y wx	CB♂	32	11	7	25	75	18	24.0	-- Plant 2490-12
		"	CB♂	74	11	9	110	204	(20)	(9.8)	-- Other 2490
								119y	9	7.6	Non-homologous pairing, much crossover suppression, unequal recombination in male and female transmission have been reported.**
								85Y	11	12.9	
								83Wx	9	10.8	
								121wx	11	9.1	
		y Df	CB♂ DD		7		401	408	7	1.7*	
6-9b	6L.13 9S.42	y wx	CB♀	726	12	5	681	1424	17	1.2	Y 1.4 T 5.5 Pl
		"	CB♂	110	2	4	101	217	6	2.8	wx 3.8 T
		"	Total	836	14	9	782	1641	23	1.4	
		C wx	CB♀	317	34	43	283	677	77	11.4	
		"	CB♂	395	90	78	380	943	168	17.8	
		"	Total	712	124	121	663	1620	245	15.1	
6-9d	6S.54 9L.76	y wx	CB♀	114	58	49	133	354	107	30.2	
		"	CB♂	109	19	25	105	258	44	17.1	
		"	Total	223	77	74	231	612	151	24.7	
6-9e	6L.17 9L.22	y wx	CB♀	1880	110	112	1869	3971	222	5.6	Y - T = 0.0
		"	CB♂	194	6	20	248	468	26	5.6	Probable order: cent - T - Y
		y C	CB♀	143	72	57	136	408	129	31.6	
		"	CB♂	238	170	115	339	862	285	33.1	
								353C	115	32.6	
		C wx	CB♀	161	54	44	149	408	98	24.0	
		"	CB♂	300	109	106	348	863	215	24.9	
		"	Total	461	163	150	497	1271	313	24.6	

*If the deficiency is not male transmitted.

**Previously reported recombination values: wx 11.6 T, T 4.9 Y (female transmission); T 17.3 Y (male transmission). It appears from the present study that 6^9 9 eggs function. Trisomic eggs (from 3:1 disjunction of the translocation heterozygote) are probably also produced. It is obvious that this translocation requires much more study, with special attention to verifying chromosome constitutions of parents and progeny.

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
6-9e (Cont.)	6L.17 9L.22	y wx	RB♀ T/T	9	294	302	9	614	18	2.9	
		C wx	CB♀ T/T	72	33	38	72	215	71	33.0	
		y C	RB♀ T/T	33	68	72	42	215	75	34.9	
6-9 4505-4	6L.13 9 near cent	y wx	CB♀	139	20	24	124	307	44	14.3	C 29.3 wx 2.9 T<1.6 Y
6-9 4778-9	6S.80 9L.30	y wx	CB♀	433	113	47	532	1125	160	14.2	6^9 9 female-transmitted
								480Wx	47	9.8	
		"	CB♂	425	14	18	471	928	32	3.4	
		y Df	CB♂ DD		48		325	373	48	12.9*	
		"	CB♂ DD		13		289	302	13	4.3*	
		"	Total		61		614	675	61	9.0*	
		y wx	RB T/T	398	382	367	348	1495	746	49.9	
		C wx	CB T/T	130	453	501	150	1234	280	22.7	
6-10b	6L.17 10L.14	y R	RB♀	108	548	537	111	1304	219	16.8	T 8.2 Pl 3.6 sm
		"	CB♀	252	49	35	250	586	84	14.3	T 2.5 g_1; T 18.6 R;
		"	Total					1890	303	16.0	g_1 15.8 R
		"	CB♀ T/T	473	108	105	445	1131	213	18.8	Probable order: Y - T - Pl
6-10d	6L.15 10L.06	y R	CB♀	560	94	106	557	1317	200	15.2	
6-10e	6L.21 10S.62	y R	RB♀	40	191	142	41	414	81	19.6	
		"	RB♀	14	56	50	17	137	31	22.6	
		"	Total	54	247	192	58	551	112	20.3	
7-9a	7L.27 9L.20	gl_1 wx	CB♀	302	81	92	297	772	173	22.4	wx - T = 0.3 (575 plants)

*If the deficiency is not male-transmitted.

Table 1. (Continued)

T	Cytol.	Genes XY	Linkage Phase	Number of Individuals XY	Xy	xY	xy	Total	Recombinants No.	%	Additional Information
7-9b	7S.92 9S.24	gl_1 wx	CB♀	282	50	60	235	627 285wx	110 50	17.5 17.5	wx <1 T - cent 7^9 9 female-transmitted
7-9c	7L.16 9L.18	gl_1 wx	CB♀	275	21	22	202	520	43	8.3	
7-9 4363-1	7 near cent 9 near cent	gl_1 wx " "	CB♀ CB♂ Total	291 230 521	16 11 27	26 14 40	256 180 436	589 435 1024	42 25 67	7.1 5.7 6.5	C 11.2 T 2.2 wx
7-9 5074-9	7S.48 9L.53	gl_1 wx " "	CB♀ CB♂ Total	154 82 236	48 15 63	41 15 56	172 64 236	415 176 591	89 30 119	21.4 17.0 20.1	
7-9 6225-2	7 near cent 9 near cent	gl_1 wx " "	CB♀ CB♂ Total	171 173 344	10 14 24	35 15 50	154 173 327	370 375 745	45 29 74	12.2 7.7 9.9	
9-10b	9S.11 10S.28	wx R " " " " " "	RB♀ CB♀ Total RB♀ T/T CB♀ T/T Total RB♂ T/T	44 52 31 71 464	75 24 94 26 971	71 32 81 24 944	30 57 38 72 594	220 165 385 244 193 437 2973 1408R 1565r 1435Wx 1538wx	74 56 130 69 50 119 1058 464 594 464 594	33.6 33.9 33.8 28.3 25.9 27.2 35.6 33.0 38.0 32.3 38.6	wx 5.7 T; T 16.3 g_1; T 23.7 R; g_1 8.9 R; T 8.8 g_1 T previously reported in 9L, 10L
9-10 5488-2	9L.57 10L.89	wx R	RB♂	65	121	116	60	362	125	34.5	Data from female transmission uncertain because of apparent transmission of aneuploids.

parental plants classified as being heterozygous for a translocation were in fact aneuploid. The indicated recombination values in these cases are obviously subject to correction.

Recombination values for markers in only one of the two translocated chromosomes have been included where relevant. Fairly extensive data on $\underline{lg_1}$-$\underline{gl_2}$ recombination were obtained and are presented to indicate the variability encountered. These data should serve as a caution in comparing recombination values obtained in tests lacking adequate controls.

The last column of the table includes additional information provided by published or unpublished work of others, or derived from this or other phases of the present study.

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1. A genetic analysis of a duplication and a deficiency involving chromosomes 9 and 3.

Some years ago I received an aberration identified by Frances Clark Beard as one in which a segment from the long arm of chromosome 3 had been inserted into the short arm of 9. Inasmuch as this constituted a type of aberration not previously subjected to genetic analysis, a number of tests have been performed. The chromosome 3 deficient for a segment in the long arm is designated as Df 3 and the chromosome 9 with this piece inserted into the short arm is called Dp 9. Heterozygous plants of Dp 9/ N 9 Df 3/ N 3 constitution produce the following four kinds of spores in equal numbers: Dp 9 Df 3, Dp 9 N 3, N 9 Df 3, N 9 N 3. The N 9 Df 3 class of megaspores and microspores aborts. Female transmission of the remaining three classes is normal. When heterozygous plants are used as the pollen parent, the Dp 9 N 3 class of pollen is handicapped and functions infrequently. From backcrosses of Dp 9 Wx/ N 9 wx; Df 3 A/ N 3 a plants used as the egg parent the following data were obtained:

A Wx	A wx	a Wx	a wx	
2618	431	2409	2262	Σ = 7720
33.9%	5.6%	31.2%	29.3%	

% A = 39.5 % a = 60.5
%Wx = 65.1 %wx = 34.9

Inasmuch as the A allele was in Df 3, a ratio of 1 A: 2 a would be expected if no crossing over occurred between A and the deficiency. The deviation from this ratio is due to crossing over between A and the deficiency. More specifically, the percentage of A wx kernels among the colored class is 1/2 the recombination value between A and the deficiency if the wx allele is invariably in N 9 and the Wx allele in Dp 9. Since there is a low percentage of crossing over between Wx and the Dp, the calculated recombination value of 11.2% between A and the Df is only a close approximation of the correct value.

A total of 142 plants from A Wx kernels was tested for the kind of chromosome 3 contributed by the heterozygous female parent. Of these, 127 had a Df 3 and 15, representing crossovers between A and the Df, possessed a N 3. This is a recombination value of 10.6 percent. Sixty a Wx kernels were similarly tested and only 6, or 10 percent, had a Df 3 arising from crossing over. The evidence is good, therefore, that in A Df 3/ a N 3 plants the A locus is 10-11 recombination units from the deficiency. That the A locus is not included in the piece of 3L inserted into 9S is evident from the approximate 1 A: 2 a backcross ratio. If it were so placed, the number of A kernels would be nearly twice as great as that of a kernels.

The location of the Df in 3L is revealed from the backcross of Dp 9/ N 9; + + Df +/ gl_6 lg_2 N a_1 plants. When these heterozygotes were used as the female parent, the data shown in item 1 of Table 1 were obtained. The marked reduction of crossing over in the Lg-A region strongly suggests that the Df includes a segment between these two loci. The recombination value for Gl-Lg is higher than normal and the 14 percent recombination found for the A-Et interval is also slightly higher than normal; the only reduction occurred in the Lg-A interval. When heterozygous plants of the same constitution were used as the pollen parent in backcross tests, the data shown in item 2, Table 1 were obtained. Again a reduction in crossing over is found in the Lg-A region, thus confirming the data from the female B.C. That the Df is nearer Lg than to A is evident from the analysis of the frequency of certain of the crossover classes.

If the Df is close to Lg, then the + + a crossover chromatids would possess the Df and the gl lg + chromatids would have a N chromosome 3. Since the Df 3 N 9 spores abort, a ratio of 1 + + a: 2 gl lg + would be expected. The observed ratio was 44: 83. Among the double crossover strands a ratio of 2 + lg + : 1 gl + a would be expected and the observed numbers were 32 : 19. The above calculations are based on the assumption that all crossing over between Lg and A occurs to the right of the deficiency. If the Df were very close to A, then the ratios of the single and double crossover classes would be the reverse of those given above. Equal amounts of crossing over between Lg-Df and Df-A would produce 1:1 ratios of the crossover classes. The unequal frequencies of the crossover classes indicate that the Df is much closer to Lg than to A. This conclusion is supported by the male B.C. data in

Table 1.

			(0) + + +	(0) gl lg a	(1) + lg a	(1) gl + +	(2) + + a	(2) gl lg +	(1-2) + lg +	(1-2) gl + a
1.	Dp 9 / N 9 ; + + Df + / gl lg N a	♀ B.C.	275	504	292	147	44	83	32	19
		Σ = 1396	Gl-Lg = 35.1%				Lg-A = 12.8%			
2.	Dp 9 / N 9 ; + + Df + / gl lg N a	♂ B.C.	176	368	151	83	51	112	27	13
		Σ = 981	Gl-Lg = 27.9%				Lg-A = 20.7%			
3.	Dp 9 / N 9 ; + + N + / gl lg N a	♀ B.C.	347	338	154	168	155	156	32	53
		Σ = 1403	Gl-Lg = 29.0%				Lg-A = 28.2%			
4.	Dp 9 / N 9 ; + + N + / gl lg N a	♂ B.C.	466	339	119	128	150	178	49	38
		Σ = 1467	Gl-Lg = 22.7%				Lg-A = 28.3%			
5.	N 9 / N 9 ; + + N + / gl lg N a	♀ B.C.	381	370	168	180	188	200	41	55
		Σ = 1583	Gl-Lg = 28.0%				Lg-A = 30.6%			
6.	N 9 / N 9 ; + + N + / gl lg N a	♂ B.C.	64	42	17	38	28	14	9	8
		Σ = 220	Gl-Lg = 32.7%				Lg-A = 26.8%			

which there were 51 + + a : 112 gl lg + single crossovers and 27 + lg + : 13 gl + a double crossovers. The data are consistent and place the Df between the Lg and A loci but much closer to Lg than to A.

Extensive data from Drosophila has demonstrated that a duplicated segment markedly reduces crossing over in the homologous segments of two structurally normal chromosomes. Since a comparable experiment has never been made with plants, it seemed desirable to test the effect of the piece of 3L inserted into 9S on crossing over in two normal chromosomes 3. The data listed in items 3, 4, 5, and 6 of Table 1, which are from full sibs of the Dp 9/ N 9 Df 3/ N 3 plants described above,

Table 2.

			(0) + + +	(0) sh bz wx	(1) + bz wx	(1) sh + +	(2) + + wx	(2) sh bz +	(1-2) + bz +	(1-2) sh + wx	Crossover percentages Sh-Bz	Bz-Wx	
1.	+ + Dp + / sh bz N wx	N 3 / N 3	♀ B.C.	5371	5391	8	6	103	95	1	0	0.14	1.8	Σ = 10975
2.	+ + Dp + / sh bz N wx	N 3 / N 3	♂ B.C.	687	2956	34 (26?)	5	5	68	2	0	0.39?	2.0	Σ = 3757
3.	+ + Dp + / sh bz N wx	Df 3 / N 3	♂ B.C.	2267	1817	7	15	34	18	0	0	0.5	1.3	Σ = 4158
4.	+ + Dp + / sh bz N wx	Df 3 / N 3	♀ B.C.	1808	921	3	5	60	27	0	0	0.3	3.1	Σ = 2824

Table 3.

			(0) + + +	(0) yg sh wx	(1) + sh wx	(1) yg + +	(2) + + wx	(2) yg sh +	(1-2) yg + wx	(1-2) + sh +	Crossover percentages Yg-Sh	Sh-Wx	
1.	+ + Dp + / yg sh N wx	N 3 / N 3	♀ B.C.	1174	1033	22	21	18	10	2	0	1.96	1.32	Σ = 2280

show that the presence of the duplicated piece of 3L in 9S caused no significant reduction in crossing over in either the Gl-Lg or Lg-A regions when the two chromosomes 3 are structurally normal.

Having located in 3L the original site of the transposed segment, we next turned our attention to the effect of the inserted piece on crossing over in 9S and to the determination of the place of insertion. Plants of Dp 9/ N 9 N 3/ N 3 constitution, with the Dp 9 carrying normal alleles of chromosome 9 markers and the N 9 possessing the recessive sh bz wx alleles, were used in backcrosses both as the female and male parent. The female B.C. data are given in line 1, Table 2. It is evident that crossing over in the two marked regions of 9S is greatly reduced. A similar reduction was found in female backcrosses of + + Dp +/ sh bz N wx/ Df 3/ N 3 plants as is shown in line 4 of Table 2.

When + + Dp +/ sh bz N wx Df 3/ N 3 plants were used as the male parents the data shown in line 3 were obtained. The data from backcrosses of + + Dp +/ sh bz N wx N 3/ N 3 plants as the pollen parents are given in line 2. There is some uncertainty about the recombination values of the Sh-Bz region in the latter cross because, in a number of kernels, classification for sh was difficult. Of the 34 + bz wx kernels, only 8 were proven to be + bz wx and the remainder could not be tested. A number of others that had been included in this class, later were shown to be sh bz wx. Therefore, the recombination percentage is uncertain from this cross.

In order to test the effect of the Dp on crossing over in the distal portion of 9S, backcrosses using + + Dp +/ yg sh N wx N 3/ N 3 plants as the female parents were made and the data in Table 3 were obtained.

The great reduction in crossing over throughout the length of 9S was wholly unexpected and is in contrast to the much smaller effect on crossing over found in chromosome 3 with the heterozygous Df. In both Dp 9/N 9 and Df 3/N 3 bivalents the size of the unpaired segment is precisely the same, yet a much greater reduction in crossing over took place in chromosome 9 than in chromosome 3. This may well be related to the more frequent occurrence of non-homologous pairing in Dp 9/N 9 bivalents than in Df 3/ N 3 bivalents.

The place of insertion of the 3L segment into 9S was determined to be between Bz and Wx. Among 85 crossovers between Bz and Wx which were analyzed for the presence or absence of the Dp, there occurred 3 to the left of the Dp and 82 to the right of the Dp. The Dp is therefore inserted between Bz and Wx but is much closer to Bz than to the Wx locus. Tests to determine which of the chromosome 3 loci are included in the transposed segment have been negative to date. The loci known not to be included are lg_2, pm, na, gl_6 and ts_4--all of which are proximal to A.

2. Relation of crossing over to preferential segregation.

Some years ago, I advanced the hypothesis that preferential segregation caused by abnormal 10 occurred only when a crossover (or crossovers) resulted in the formation of dyads composed of a knobbed and a knobless chromatid, and that the knobbed chromatid was preferentially segregated to the basal megaspore from which the embryo sac was derived. In the presence of abnormal 10, either heterozygous or homozygous, other chromosomes of the complement also undergo preferential segregation if one homologue is knobbed and the other knobless. The preferential segregation of heteromorphic homologues other than chromosome 10 was first demonstrated by Longley whose observations have been amply confirmed in this laboratory. According to the hypothesis that preferential segregation occurs only when heteromorphic dyads are produced, and it is the knobbed chromatid which segregates preferentially at anaphase II, those loci closer to the knob would undergo a higher degree of preferential segregation than would more distant loci. There is abundant evidence that this is so (for example, see Kikudome's report in this News Letter).

A test of the hypothesis that preferential segregation is dependent upon crossing over giving heteromorphic dyads was made possible by studying the ratios of genes in 9S from plants in which the amount of crossing over was greatly reduced compared to that in sibs in which recombination was normal. Such a test was made using the Dp9 chromosome described earlier in this report since it was demonstrated that the amount of crossing over in Dp9/N9 plants is greatly reduced in 9S. Sib plants of three classes, all heterozygous for abnormal 10, were obtained. One class was of Dp9/N9 constitution. The chromosome with the Dp had a small terminal knob (K^s) on 9S and carried the yg allele while the N9 had a much larger knob (K^m) and the Yg allele. The second class of plants was of N9/N9 constitution. One chromosome 9 had the prominent knob and the Yg allele; the other possessed the small knob and the yg allele. The third class had two N9's, one with the small knob and the yg allele, the other possessing the wd allele and wholly devoid of a knob. All three classes were heterozygous for abnormal 10 and had heteromorphic chromosomes 9. Preferential segregation takes place when the two chromosomes 9 differ in knob size (as convincingly demonstrated by Kikudome in this News Letter) so studies of preferential segregation were made. The first two classes were pollinated by yg plants and the ratio of Yg : yg plants obtained. The third class was pollinated by wd pollen and the yg : wd ratio determined. In back crosses of K^m Yg N/K^s yg Dp plants, in which crossing over is greatly reduced in 9S the Yg plants constituted 54.7% of the offspring. Plants of K^m Yg N/K^s yg N constitution with normal crossing over in 9S gave 65.2% of Yg plants. Individuals of K^s yg N/k wd N genotype, again with no reduction in crossing over, produced 60.4% yg seedlings. Data from K^s yg Dp/k wd N plants have not yet been obtained. Control data from closely related plants of K^s yg N/k wd N constitution and homozygous for N10 gave 50.2% yg plants. The data from the above crosses are

given below. The conclusion seems justified that preferential segregation is reduced when crossing over is also decreased. The data offer some support to the hypothesis that the formation of heterozygous dyads via crossing over is an essential antecedent to preferential segregation.

K^m Yg N/K^s yg Dp x yg ⟶ 1634 Yg : 1353 yg 54.7% Yg

K^m Yg N/K^s yg N x yg ⟶ 1331 Yg : 709 yg 65.2% Yg

K^s yg N/k wd N x yg ⟶ 1221 yg : 802 wd 60.4% yg

The female parents in the above three crosses were all heterozygous for abnormal 10.

K^s yg N/R wd N x wd ⟶ 499 yg : 494 wd 50.2% yg

The female parent used above was homozygous for N10.

M. M. Rhoades

3. Preferential pairing in structurally heterozygous tetraploids.

Structurally heterozygous tetraploids were obtained by crossing diploids homozygous for asynaptic and either homozygous or heterozygous for inversion 3a by tetraploids homozygous for normal chromosome 3. The In 3a chromosomes carried the $\underline{A}_1$ allele and the normal chromosomes carried the $\underline{a}_1$ allele. Thus the tetraploid progeny of these crosses was either simplex (In $\underline{A}$, N $\underline{a}$, N $\underline{a}$, N $\underline{a}$) or duplex (In $\underline{A}$, In $\underline{A}$, N $\underline{a}$, N $\underline{a}$).

The simplex backcrosses gave a total of 4253 colored kernels and 4653 colorless or 1 : 1.09. Control data is not yet available but it is not believed that the presence of only one inverted chromosome would affect the ratio very much.

However, the backcrosses of the duplex heterozygotes as compared with those of the duplex normal give widely different ratios. When the duplex heterozygote is used as the seed parent the ratio is 2812 colored to 387 colorless or 7.26 : 1, and as the pollen parent 4700 colored to 670 colorless or 7.02 : 1. The control duplex as the seed parent gave a ratio of 1874 : 460 or 4.07 : 1 and the reciprocal crosses gave 2865 colored to 715 colorless or 4.01 : 1.

The above data clearly indicate that a considerable amount of preferential pairing takes place in the duplex heterozygote. The frequency (P) with which the structurally homologous segments pair with each other above the random amount (33.3%) can be determined by the use of the following formula which was obtained by modifying Mather's analysis of the gene segregation in normal tetraploids to include

factors to express the different frequencies of certain modes of pairing; thus $(1 - q)(1/3 + p)$ expresses the frequency that autosyndetic pairing occurs when two bivalents are formed. The details of the algebraic manipulations are too long to include here. The formula is as follows:

$$p = \frac{1/6 + 1/12\ aeq - R}{1/4 - 3/8aq + 1/8\ aeq}$$

where a = the frequency of adjacent disjunction of the quadrivalent, e = the frequency of equational orientation, q = the frequency of quadrivalent formation, and R = the frequency of the recessive class as found in a backcross.

The value aeq is equal to 2α, a mathematical term as used by Mather to express the frequency of double reduction, a phenomenon partly responsible for deviations from a 5:1 ratio. The value of α here can be estimated from the control ratio $4.03:1 = 5 - 2\alpha:1 + 2\alpha$ ($\alpha = .095$). However it seems inadvisable to substitute this value in the above formula since the value of q is probably lower in the structural heterozygote than in the control. Also the aq term causes some trouble. A rough estimate of the values of a and q can be made from cytological observations if we assume that all the groups of homologous chromosomes behave in about the same manner. The amount of equational separation (e) for the A locus can be derived for diploids from the data of Rhoades on the frequency of second division segregation in diploid eggs of el el plants. It is .74 (MGC News Letter 30, p. 40). If we assume that crossing over is the same frequency in the diploid and the tetraploid strains used, then this value may be taken as an estimate of "e".

In view of the fact that this study is as yet in a preliminary stage, the value of p cannot be estimated with any degree of accuracy until various things are known - the effect of crossing over within the inversion loop, amount of numerical nondisjunction (3 - 1 split of quadrivalent), etc. It is impossible to draw any definite conclusions as to some of the problems this work is endeavoring to answer such as: what magnitude of structural rearrangement is required to produce the autosyndetic pairing found in allotetraploids? However, the data presented here are in general agreement with those reported on structurally heterozygous triploids by Rhoades in the last issue and indicate that a substantial amount of preferential pairing does take place.

G. G. Doyle

4. Occurrence of crossover strands in the diploid gametes of as plants.

Asynaptic plants produce both haploid and diploid eggs as well as non-functional spores with unbalanced chromosomal complements. Haploid and diploid sperm are also produced, but zygotes coming from the functioning of 2n pollen grains are rare because of competition with 1n

grains. The crossover studies to be reported, therefore, involve only diploid eggs.

Asynaptic plants heterozygous for various linked markers were used as egg parents in backcrosses to diploid and tetraploid testers. When the pollen parents were diploid, the triploid progeny was analyzed for crossovers; when the pollen parents were tetraploid, the tetraploid progeny was dealt with. In most cases, a second backcross (or a self pollination) was necessary to determine the complete genotype of the original diploid gamete.

The kinds and frequencies of diploid eggs are given in the tables. The first sets of data, involving genes on chromosome 9, test crossing over in a single chromosome arm. The last set of data, involving chromosome 5 markers, tests regions on both sides of the centromere. The chromosome 9 studies shown in Tables 1 and 2 include both coupling and repulsion backcrosses. Table 1 gives the actual genotypes of the diploid gametes and their frequencies. In Table 2, this data has been re-arranged so that gametes coming from similar crossover events in the C.B. and R.B. tests may be summed, even though they are of different genotypes. Two crossover designations are given above each class; the first assumes doubling occurred at the first meiotic division, the second assumes doubling at the second division.

On the first hypothesis an equational first meiotic division followed by a failure of second division is postulated. Centromeres of sister chromatids pass into different nuclei. On the second hypothesis, the first division is completed normally and the dyads at each pole then disjoin into their component chromatids without a true second division, i.e., "sister" centromeres remain in the same nucleus. There is genetic evidence for the occurrence of both processes, but it is uncertain whether mixed events can occur in the same cell (equational division for some of the chromosomes and normal AI for others) or whether all the chromosomes of a cell behave in the same way. Cytological observations favor the former proposal.

Examination of the classes listed in Table 2 reveals that region (2) and (1-2) crossovers are far too frequent on hypothesis (1). Similarly the combined (2),(1-2) class of hypothesis (2) is larger than expected. Region (2) in both cases is the wx-centromere region which is only about 11 genetic units in length (Rhoades, MNL 30: 42). Thus neither hypothesis alone can fully account for the data, although hypothesis (2) is the better explanation in most cases.

Formation of a restitution nucleus at second division (hypothesis 2) will give all the types of diploid gametes obtained in the observed frequencies, with the exception of the (2), (1-2) class. Gametes in this questionable class possess one apparent non-crossover strand from each of the parental homologues. In order to learn more about the origin of this class, it was necessary to know whether or not such

Table 1.

			Type of diploid gamete									
			C Wx / c wx	C Wx / C Wx	C Wx / c Wx	C Wx / C wx	C wx / c Wx	C wx / C wx	C wx / c wx	c Wx / c Wx	c Wx / c wx	c wx / c wx
1.	C Wx / c wx	as/as X 4n c wx CB	73	19	15	2	3	1	18	0	0	35
		Σ = 166										
2.	C wx / c Wx	as/as X 4n c wx RB	0	0	8	3	60	25	11	23	2	0
		Σ = 132										
			Sh Wx / sh wx	Sh Wx / Sh Wx	Sh Wx / sh Wx	Sh Wx / Sh wx	Sh wx / sh Wx	Sh wx / Sh wx	Sh wx / sh wx	sh Wx / sh Wx	sh Wx / sh wx	sh wx / sh wx
1.	Sh Wx / sh wx	as/as X 2n sh wx CB	11	15	9	1	1	1	7	0	3	8
		Σ = 56										
2.	Sh wx / sh Wx	as/as X 2n sh wx RB	0	0	1	1	4	0	1	0	0	0
		Σ = 7										

Table 2.

Source of 2n gamete										
hypothesis 1:	(2)	(2)	(1-2)	(1-2)	(1-2),(0) (1),(2)	(1) (1-2)	(1) (1-2)	(1-1-2)	(1-1-2)	(1) (1-2)
hypothesis 2:	(0)	(0)	(1)	(1)	(2),(1-2)	(1-2)	(1-2)	(1-1)	(1-1)	(1-2)
$\frac{C\ ^{1}\ Wx\ ^{2}}{c\ \ wx}$ o $\frac{as}{as}$ X 4n c wx CB	19	35	15	18	73	2	0	0	1	3
$\frac{C\ ^{1}\ wx\ ^{2}}{c\ \ Wx}$ o $\frac{as}{as}$ X 4n c wx RB	23	25	8	11	60	3	2	0	0	0
	42	60	23	29	133	5	2	0	1	3
$\frac{Sh\ ^{1}\ Wx^{2}}{sh\ \ wx}$ o $\frac{as}{as}$ X 2n sh wx CB	15	8	9	7	11	1	3	0	1	1
$\frac{Sh\ ^{1}\ wx^{2}}{sh\ \ Wx}$ o $\frac{as}{as}$ X 2n sh wx RB	0	0	1	1	4	1	0	0	0	0
	15	8	10	8	15	2	3	0	1	1

strands had experienced crossing over in the other chromosome arm (not tested in the chromosome 9 studies) and also whether or not such strands carry "sister" centromeres or "homologous" centromeres. For this reason, compounds of $\frac{A}{a}$ — ○ $\frac{Bt}{bt}$ — $\frac{pr}{Pr}$ were used, in which crossing over can be detected in both arms and in which the centromere is marked by Bt.

When $\frac{A}{a}$ — ○ $\frac{Bt}{bt}$ — $\frac{pr}{Pr}$ as/as plants were pollinated with 4n a bt pr testers, the following kinds of seed were produced:

A Bt Pr	A Bt pr	A bt Pr	A bt pr	a Bt --	a bt --
432	352	35	2	4	450

Due to extremely poor germination of bt types, only a part of this population could be tested for genotype. At present 98 plants have been analyzed and the results are given in Table 3.

The exceptional class corresponding to the (2).(1-2) class in the previous table is listed under (1-2). In this case, region (2) is from the centromere to Bt, a distance of approximately 1%, making a (1-2) double highly unlikely. Therefore, the heterozygous condition for Bt indicates that homologous, rather than sister, centromeres are present. The strands in these gametes have not undergone crossing over in the regions tested, and have probably come from univalent chromosomes which separated equationally at the first meiotic division. Occasional recovery of two strands with homologous centromeres (Bt/bt) that have experienced crossing over is indicated by the (1-2-3) class, which is more easily interpreted as the result of a single in (3) followed by an equational first division.

Since the majority of the data on types of diploid gametes is accounted for on hypothesis (2) while the exceptional class can only be explained by hypothesis (1), it appears that both events must occur during formation of diploid eggs. Pollen mother cells have been seen which contain a mixture of bivalents and univalents at AI. The univalents sometimes divide equationally after the dyads have reached the poles. This leads to a mixture of dyads and monads in each nucleus. It is possible that, when a majority of monads is present, the sister centromeres of the dyads disjoin without a spindle mechanism, to give a total of 20 separate centromeres in each cell. Dowrick (Heredity 7: 219-226) suggests that the capacity of the centromeres for division determines the occurrence of the second meiotic division. In the present case, the single condition of the majority of centromeres might prevent a second division. Thus, a chromosome pair tested genetically would sometimes contribute 2 chromatids with sister centromeres to the diploid spore (bivalent MI, dyad PII = hypothesis 2) and sometimes it would contribute 2 chromatids with homologous centromeres (univalent MI, monad PII = hypothesis 1). Diploid eggs may arise, therefore, by a combination of doubling (or centromere separation) at AI and at PII.

Table 3.

$\frac{A\ ^{1}}{a}\ o\ \frac{^{2}\ Bt\ ^{3}\ pr}{bt\ \ Pr}\ \frac{as}{as}$ X 4n a bt pr RB

Source of 2n gamete											
Hypothesis 1:	(1-2)	(1-2)	(2)	(2)	(1)	(1)	(1-2-3)	(1-2-3)	(2), (3) (0), (1)	(3)	(1-2-3-3)
Hypothesis 2:	(0)	(0)	(1)	(1)	(2)	(2)	(3)	(3)	(1-2)	(1-2-3)	(3-3)
	A Bt pr | A Bt pr	a bt Pr | a bt Pr	A Bt pr | a Bt pr	a bt Pr | A bt Pr	A Bt pr | A bt Pr	a bt Pr | a Bt pr	A Bt pr | A Bt Pr	a bt Pr | a bt pr	A Bt pr | a bt Pr	A Bt Pr | a bt Pr	A Bt Pr | A Bt Pr
	41	--*	8?#	--	0	--	23	3	20	2	1

Σ = 98

* Blanks in the data represent failure of germination of seed.

\# Require further tests due to possible segregation of another aleurone factor. These may be A/A instead of A/a.

The fact that crossover chromosomes are found in diploid eggs of as plants (which was first reported in 1947 by Rhoades, Genetics 32: 101) would be surprising if these eggs came from EMC's with only univalents. It seems likely, however, that EMC's containing both univalents and bivalents give rise to diploid eggs and therefore a certain amount of crossing over would be expected.

A calculation of the percent of crossover strands among the total strand population gives 12.9% C-Wx recombination in the coupling backcross and 9.9% C-Wx recombination in the repulsion backcross. The value for the Sh-Wx region in the coupling data in Table 1 is 21.4%. The last value is based on a small population of only 56 gametes, since triploid plants are more difficult to obtain than tetraploid ones. Using only the phenotypically Bt classes, a value of 14.2% is obtained for the Bt-Pr region in the chromosome 5 test. Most of these values are less than the standard values. Because of the unusual events which occur during formation of diploid gametes, it is difficult to predict the expected rate of exchanges. However, if some univalent chromosomes are present in the cell at the time of crossing over, a reduction in the recombination values would be expected.

5. A duplicate factor ratio.

A chance segregation of pale green plants occurring in the F_2 of crosses between KYS and two tester stocks may represent another occurrence of the pg_{11} pg_{12} duplicate factors found by Rhoades. In F_2's segregating ws lg gl, 126 green: 12 pale green: 42 ws plants were found. This is close to the 15: 1 ratio of green: pale green expected if duplicate factors are involved. It seems likely that KYS is homozygous for or carries either pg_{11} or pg_{12} while the second factor of the pair is carried in the ws lg gl tester stock as well as in a Rg lg a et stock.

6. Further studies of KYS male sterility.

In the MNL 31: 81, mention was made of an aberrant F_2 from self pollination of Ms ms S s, which segregated male sterile plants. No male steriles (Ms ms s s) were expected since only S pollen functions in Ms ms S s heterozygotes. The Ms ms S s plant which was self pollinated came from a cross of as/KYS ♀ X KYS ♂ (Ms ms S s X ms ms s s). Two other Ms ms S s plants coming from the same cross (and the same ear) were selfed and gave no male steriles. Numerous other unrelated F_2's also gave only normal plants. The single aberrant population remains unexplained. Although as was segregating, asynaptic plants can easily be distinguished from the male steriles on the basis of ear sterility.

Thirteen genetic testers were checked for ms and s constitution. Nine were Ms Ms S S, two were ms ms S S, and two were Ms ms S S. Our stocks of Mangelsdorf tester are ms ms S S. Evidently the s allele is restricted in its occurrence, whereas the ms mutation is more widely distributed.

The S locus has been located on chromosome 2 at about 10 units beyond fl at position 78 (Prensky, MNL 31: 73). Data are given here which show linkage of S with B and ts.

		+:ws	+:gl	B:b	+:ts	Crossover percentages B-S	ts-S
1.	$\frac{Ms\ ws\ gl\ b\ S}{ms\ +\ +\ b\ s}$ ♀ X $\frac{Ms\ ws\ gl\ B\ S}{ms\ +\ +\ b\ s}$ ♂	66:22	62:26	64:24	---	27.3	---
2.	$\frac{Ms\ ws\ gl\ B\ ts\ S}{ms\ +\ +\ b\ +\ s}$ (X)	96:23	92:27	104:15	64:55	25	7.6
3.	$\frac{Ms\ ws\ gl\ B\ ts\ S}{ms\ +\ +\ b\ +\ s}$ (X)	92:38	92:38	116:14	69:55	21.5	11.3

Plants of $\frac{ts\ S}{+\ s}$ constitution produce two types of functional pollen--ts S and + S. The frequency of the latter type is the frequency of ts-S crossing over. The values obtained for the B-S and ts-S regions are in good agreement with Prensky's data and place the S locus close to the centromere of chromosome 2.

Ellen Dempsey

7. The influence of abnormal chromosome 10 (K 10) on the recombination frequency between r and sr_2.

Joachim and Burnham (MNL 29) reported that g-r-sr_2 appears to be the linear order of these genes on normal chromosome 10 (k 10). The recombination values obtained for the r-sr_2 region ranged from 21.4% to 31.0%. In MNL 30, Joachim confirmed the linear order and obtained recombination values ranging from 25.1% to 31.5%.

The experiment reported here was carried out to determine the effect of abnormal chromosome 10 (K 10) on the recombination frequency between r and sr_2. The backcross data shown below were obtained for sib plants segregating for abnormal chromosome 10.

	(0) g + +	(0) + r sr	(1) g r sr	(1) + + +	(2) g + sr	(2) + r +	(1-2) + + sr	(1-2) g r +	Σ
$\frac{g\ +\ +\ K}{+\ r\ sr\ k}$	564	196	33	87	3	5	0	0	888
$\frac{g\ +\ +\ k}{+\ r\ sr\ k}$	235	233	47	54	159	154	9	5	896

Recombination:

	K 10/k 10	k 10/k 10
g-r	13.5%	12.7%
r-sr_2	0.9%	36.4%
g-sr_2	14.4%	46.2%
Double crossovers	0.0%	1.6%

Percentage:

g	67.6*	49.8
R	73.6*	51.0
Sr	73.9*	50.0

* Statistically significant difference from a 1:1 ratio.

The data indicate that there is a drastic reduction in the recombination frequency between r and sr_2 in sibs having the abnormal chromosome 10. This reduction could be attributed to non-homology between abnormal 10 and normal 10 in the distal 1/6 segment of the long arm of normal 10. The absence of double crossovers in K 10/k 10 plants should not be surprising, since there is a great reduction in recombination between r and sr. (The frequency of expected double crossovers in the K 10/k 10 class is 1.2%.) The recombination value obtained for the r-sr region in k 10/k 10 sibs shows that there is considerable crossing over in the region distal to r. This is in agreement with crossing over data obtained by Joachim and Burnham.

In the g-r region, where there is homology between K 10 and k 10 chromatin, there exists no detectable difference between the recombination values obtained for the respective sib classes.

8. Preferential segregation in chromosome 9.

A. The effect of knob size.

(1) Heretofore it has been regarded that, in the presence of abnormal chromosome 10, preferential segregation of the other nine chromosomes occurs only when one homologue is knobbed and the other is knobless. When both homologues have the same sized knob there is no preferential segregation even when abnormal 10 is present. In a family segregating for K^L 9S + wx/ k 9S wd + and K^L 9S + wx/ K^M 9S + + plants (K^L = a large knob on chromosome 9 nearly the same length as the heterochromatin of abnormal 10; K^M = knob approximately 2/3 the size of K^L; K^S = knob size approximately that found for chromosome 9 in "KYS" strain), the Wx:wx ratio was checked in plants of the K^L/K^M constitution. Statistically the Wx:wx ratio was found not to be a 1:1 ratio. Since this locus is quite removed from the knob of the short arm, the following set-up was used to determine whether this finding was apparent or real.

$$\frac{K^M \; + \; + \; + \; +}{K^S \; yg \; c \; sh \; wx} \quad \frac{K\ 10}{k\ 10} \qquad X \qquad K^S \; yg \; c \; sh \; wx \; k \; 10$$

The results of the experiment are shown below:

(0)	(0)	(1)	(1)	(2)	(2)	(3)
+ + + +	yg c sh wx	+ c sh wx	yg + + +	+ + sh wx	yg c + +	+ + + wx
2224	1028	401	202	133	56	625

(3)	(1-2)	(1-2)	(1-3)	(1-3)	(2-3)	(2-3)
yg c sh +	+ c + +	yg + sh wx	+ c sh +	yg + + wx	+ + sh +	yg c + wx
230	8	4	14	11	10	4

Total population: 4950

% Yg = 69.0
% C = 64.8
% Sh = 63.2
% Wx = 55.4
% Doubles = 1.03

Recombination:

% yg-c = 12.9
% c-sh = 4.3
% sh-wx = 18.1
% yg-sh = 16.8
% c-wx = 21.8
% yg-wx = 33.3

The results prior to classification of the yg marker were:

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	
+ + +	c sh wx	+ sh wx	c + +	+ + wx	c sh +	+ sh +	c + wx	Σ
2440	1716	162	67	647	280	10	4	5336

Recombination:

% C = 61.1
% Sh = 59.0
% Wx - 52.2

% c-sh = 4.6
% sh-wx = 17.6
% c-wx = 21.7

The post-germination percentages for the loci C, Sh, Wx are not the same as the percentages gotten for these respective loci in the pre-germination data. Approximately 6% of the seeds failed to germinate and most of the seeds that failed to germinate were the "shrunken" ones. The data were further analyzed to determine whether this seed loss introduced a bias into certain of the classes or whether, in spite of the loss, the post germination values were accurate reflections of the pre-germination values. Firstly the following type of comparison was made between the pre- and post-germination values:

	(0) + + +	(0) c sh wx	(1) + sh wx	(1) c + +	(2) + + wx	(2) c sh +	(1-2) + sh +	(1-2) c + wx	Σ
Pre-germination	2440	1716	162	67	647	280	10	4	5336
Post-germination	2426	1429	137	64	636	244	10	4	4950

	Pre-Germination	Post-Germination	Difference
$\frac{+ + +}{(+ + +) + (c\ sh\ wx)}$	0.59	0.63	+ 0.04
$\frac{+ sh\ wx}{(+ sh\ wx) + (c + +)}$	0.71	0.68	- 0.03
$\frac{+ + wx}{(+ + wx) + (c\ sh +)}$	0.70	0.70	
$\frac{+ sh +}{(+ sh +) + (c + wx)}$	0.72	0.72	

This comparison shows that in the non-crossover and single crossover (c-sh) classes there is selection against "shrunken" and no apparent selection against "shrunken" in the other two crossover classes. This selection appears to be somewhat small. The 0.6-0.7-0.7-0.7 type of proportion is found in both the pre- and post-germination groups. When the recombination values for the c-sh, sh-wx, and c-wx regions are compared, they are very similar in the pre- and post-germination data.

	Pre-Germination	Post-Germination
% c-sh	4.6	4.3
% sh-wx	17.6	18.1
% c-wx	21.7	21.8

Since selection against "shrunken" has not seriously affected the relative proportions of Yg:C:Sh:Wx, the following correction procedure was taken to determine percentage of plants that would have had the Yg phenotype had all the seeds germinated.

	Post-Germination		Pre-Germination	
$\frac{\%\ Yg}{\%\ C}$	$\frac{69}{64.8}$	=	$\frac{x}{61.1}$	x = 65.1% Yg
$\frac{\%\ Yg}{\%\ Sh}$	$\frac{69}{63.2}$	=	$\frac{x}{59.0}$	x = 64.4% Yg
$\frac{\%\ Yg}{\%\ Wx}$	$\frac{69}{55.4}$	=	$\frac{x}{52.2}$	x = 65.0% Yg
				Av. x = 64.8% Yg

Had all the seeds germinated, approximately 65% of the plants would have been of the Yg phenotype. This corrected value is quite comparable to the percentage obtained for this phenotype in similar experiments where no selection against any particular class occurred. The ratios obtained for all of the loci studied were statistically significant deviations from a 1:1 ratio. These data definitely show that preferential segregation does occur even when both homologues are knobbed, but only when the knobs are of different sizes.

(2) In a family segregating for K^S 9/ k 9 and K^M 9/ K^S 9, the following backcross data were obtained:

		+ + +	c sh wx	+ sh wx	c + +	+ + wx	c sh +	+ +	c + wx
a.	$\frac{K^S \text{ c sh wx}}{\text{k + + +}}$ $\frac{K\ 10}{k\ 10}$	1157	1828	41	101	344	677	2	5
b.	$\frac{K^M + + +}{K^S \text{ c sh wx}}$ $\frac{K\ 10}{k\ 10}$	2286	1398	134	79	827	418	4	5

a. $\Sigma = 4155$

% c = 62.6*
% sh = 61.3*
% wx = 53.4*

Recombination:
% c-sh = 3.6
% sh-wx = 24.7
% c-wx = 28.0

b. $\Sigma = 5136$

% C = 63.3*
% Sh = 62.2*
% Wx = 54.3*

Recombination:
% c-sh = 4.3
% sh-wx = 24.4
% c-wx = 28.4

*Statistically a significant deviation from a 1:1 ratio.

In this sib comparison, the degree of preferential segregation obtained in both groups for the respective loci is similar, although it is slightly higher in the K^M/K^S group. Even the recombination values are of the same magnitude. It seems, then, that K^M/K^S is equivalent to K^S/k. This finding further substantiates the previous finding (8A-1) that when both homologues are differentially knobbed, preferential segregation occurs in favor of the larger knobbed chromosome. Comparison of the data of the above K^M/K^S group with those of the K^M/K^S group discussed previously (8A-1) shows that both the recombination values and the percentage values obtained for the loci involved are in agreement.

(3) The effect of knobs of three different sizes upon the degree of preferential segregation of the wd and wx loci was studied. "wd" is actually a small terminal deficiency in the short arm of chromosome 9 and is pseudoallelic to yg.

		++	+wx	wd +	wd wx	Σ	Percentage Wd	Wx	Recombination
$\frac{K^S + +}{k \ wd \ wx}$	$\frac{K\ 10}{k\ 10}$	1372	669	419	992	3452	59.1	51.9	31.5
$\frac{K^M + +}{k \ wd \ wx}$	$\frac{K\ 10}{k\ 10}$	3994	1543	757	2272	8566	64.6	55.5	26.9
$\frac{K^L + wx}{k \ wd \ +}$	$\frac{K\ 10}{k\ 10}$	1442	3463	1726	581	7212	68.0	56.1 (wx)	28.1

The precentage values shown for each locus are all statistically significant deviations from the 1:1 ratio one expects in normal (absence of abnormal 10) backcrosses. The source for each knob size is not the same, and the source of the small knob used here is different from that of the small knob used in the previous experiments. Statistical analyses were made to determine whether the percentage values obtained for the locus closer to the knob were truly an expression of the different levels of activity of the knob size, or whether knob size was inconsequential. It was found that K^L was different from K^M and K^S and that K^M was different from K^S. In other words, the larger the knob, the higher the degree of preferential segregation of the locus under study. Analyses have not been made for the Wx data as yet.

B. Comparisons were made of ratios obtained in the non-crossover classes and crossover classes for all knob combinations studied. The numerator in each instance is that reciprocal class containing the dominant marker nearest to the knob.

Examples: $\frac{+ + + +}{(+ + + +) + (yg\ c\ sh\ wx)}$; $\frac{+ + sh\ wx}{(+ + sh\ wx) + (yg\ c\ + +)}$

	(0)	(1)	(2)	(3)	(1-2)	(1-3)	(2-3)
$\frac{K^L + wx}{k \ wd \ +}$	0.67	0.71					
$\frac{K^M + +}{k \ wd \ wx}$	0.64	0.67					
$\frac{K^S + +}{k \ wd \ wx}$	0.58	0.62					
(Control)	(0.51)	(0.51)					
$\frac{K^S + + +}{k \ c \ sh \ wx}$	0.61	0.71	0.66	0.71			

	(0)	(1)	(2)	(3)	(1-2)	(1-3)	(2-3)
$\frac{K^M + + +}{K^S \text{ c sh wx}}$	0.62	0.63	0.66	0.56			
*$\frac{K^M + + + +}{K^S \text{ yg c sh wx}}$	0.68	0.66	0.70	0.73	0.67	0.56†	0.71
**$\frac{K^M + + + +}{K^S \text{ yg c sh wx}}$	0.70	0.62	0.67	0.73	0.71	0.63	0.25‡
**$\frac{K^M + + + +}{K^S \text{ yg c sh wx}}$	0.73	0.62	0.68	0.73	0.73	0.67	1.00#

*Post-germination data used here.

**Not summarized in this report since they show essentially the same results as the K^M + + + +/K^S yg c sh wx group.

†0.56 ratio: due to 14:11 ratio obtained for the reciprocal crossover classes.

‡0.25: only 2 + + sh + to 6 yg c + wx ratio obtained.

#1.00 ratio: due to 3:0 ratio obtained for the reciprocal crossover classes.

C. Evidence that abnormal 10 alters the recombination frequency in chromosome 9.

The following sib comparison (backcross) data were obtained involving a small knobbed strain. The data for the sibs heterozygous for abnormal 10 are the same data reported under 8A-3. The loci studied were wd and wx.

						Percentage		
	+ +	+ wx	wd +	wd wx	Σ	Wd	Wx	Recombination
$\frac{K^S + +}{k \text{ wd wx}}$ $\frac{K\ 10}{k\ 10}$	1372	669	419	992	3452	59.1*	51.9*	31.5
$\frac{K^S + +}{k \text{ wd wx}}$ $\frac{k\ 10}{k\ 10}$	2034	733	716	1947	5430	51.0	50.6	26.7

*Statistically significant deviations from a 1:1 ratio.

It seems that abnormal 10 has the capacity of increasing the recombination frequency between the two loci studied. The Wd and Wx ratios obtained were found to be significant deviations from a 1:1 ratio. Since 59% Wd is statistically different from 51% Wd, and also 51.9% Wx from 50.6% Wx, the 4.8% difference between the two mean recombination frequencies could be statistically a significant one. Analyses ("t" test) have shown that the two means are different, although the difference is a small one.

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1. The enhancer factor--a fourth location.

In a previous Maize News Letter (1953) it was reported that Enhancer, (En), the dominant mutator that causes pg^m-mutable pale green- to mutate to Pg-green - can be variously located. (Without En, pg is stable). It has been found (1) adjacent to pg (the autonomous mutable condition), (2) on the same chromosome and 36 units from pg, and (3) on an independent chromosome. En has recently been found at a 4th location, on another independently assorting chromosome. This new location appeared among some F_2 progenies of a series of crosses of a non-segregating En stock (Pg/Pg En/En) by pg^s (stable pale green). Ordinarily, the self of this F_1 (Pg/pg En/+) yields an F_2 with pale green seedlings segregating 3 pg^m : 1 pg^s. This ratio indicates that En is segregating (pg with En is mutable and pg without En is stable). In one particular series of crosses, 2 or the 10 segregating progenies gave only 6% pg^s among the pg class which is significantly lower than the expected frequency of stables (25%). The expected genotype of the parents, F_1 and the segregation of these exceptional F_2 progenies are as follows:

Pg/pg +/+ x Pg/Pg En/En —— F_1 Pg/pg En/+ (green)

Exceptional F_2 progenies			% pg^s
1956	443-10 ⊗	135 + : 35 pg (2 pg^s : 33 pg^m)	5.7%
1956	443-13 ⊗	145 + : 49 pg (3 pg^s : 46 pg^m)	6.1%

These results suggest that En must be in a heterozygous condition at two separate loci, each locus independent of pg. The F_1 of the above cross would then be Pg/pg En/+ En/+. Of the resulting F_2 progeny, only 1/16 of the pg genotypes would lack En. These would therefore be stable: chromosome linkage of En has not yet been established for either of the two independent locations.

This second independent location of En originated in the En stock which has been propagated since 1952.

2. a_1 mutable

In previous Maize News Letters (1953, 1956) it was reported that a new a_1 mutable (a_1^m) appeared in a culture of mutable pale green (pg^m). This mutable allele mutates from a_1 to A_1 (colorless to full color) and is characterized in the kernel by dots of dark anthocyanin pigment on a non-pigmented colorless background.

At least seven distinct patterns are recognizable: these range from kernels with a small dot pattern to other kernels with large areas of anthocyanin pigmentation. These patterns depend on the frequency and time of mutation events. Individual patterns are heritable as definite properties of the individual a_1^m allele and are not a result of segregating modifiers. This is evident from the results of continued outcrosses. In each case the parental pattern is recovered in all of the progeny except a few (± 1%) which possess new patterns that are in turn distinct and heritable. Such results indicate that control of the pattern is intrinsic to the mutable allele itself. Outcross tests show also that the control of mutability resides at the a_1 locus indicating that mutability is autonomously controlled.

Mutation to the colorless stable form: the most conspicuous change in the different patterns of a_1^m is the change to a stable, non-pigmented form, a_1^s. The rate of change to a_1^s varies in frequency, but in general the earlier occurring patterns mutate to a_1^s at a higher rate (± 6%) in testcrosses than do the finer dot-like patterns (1-2%). Thus, the different patterns can also be identified by their rate of mutability to the stable form.

A separable mutator: In several testcrosses (a^mSh/a^{dt}sh x a^{dt}sh/a^{dt}sh) of an a^m allele with a fine mutable pattern, half of the non-shrunken kernels were stable and half were mutable. The shrunken kernels were completely colorless. Such a result indicates that a mutator is segregating and when present causes the a_1^m allele to mutate. Half of the shrunken kernels should therefore contain the factor. Crosses were made between plants of stables and numerous sib shrunken kernels. In half of the crosses, half of the non-shrunken kernels on the ear were mutable. This verifies the presence of a separable factor controlling mutability. This independent controller of mutability arose from the autonomous type. The recovery of this independent controller of mutability is similar to the recovery of independent En in pg stocks containing the autonomous type of mutability control.

The colorless kernels that become mutable in the presence of the above described controller of mutability are unaffected by Dt or Ac. Similarly, a^{dt} and Ds-controlled loci do not mutate in the presence of

this independent mutator. Crosses are now in progress to determine whether this independent mutator will cause pg^s to become mutable.

Peter A. Peterson

3. Studies of the mutable system at the viviparous-2 locus.

There are three alleles known at the vp-2 locus on chromosome five, vp-2, w^{alb}-4889 and green mosaic. They all are characterized by pale yellow or white seeds that often are smaller than normal and frequently have a tendency to germinate prematurely producing albino seedlings. In addition to these traits the green mosaic allele shows frequent back mutation to normal in both the endosperm and seedling, resulting in a pale yellow endosperm with patches of yellow and in white seedlings with a mosaic of green tissue.

For the past couple of years an intensive study of the mutable green mosaic allele has been made. As mentioned in last year's News Letter five levels of mutability have been recognized (very strong, strong, light, light minus, and weak); in addition several stable white lines have been isolated. In all cases these stable white lines have been derived from ears that were segregating for weak mosaic or white as well as other mutable types. As a general rule it does not appear that lines segregating for only stable white seedlings can be derived from very strong or strong mosaic stocks in one step. An ear must first occur that is segregating one of the lower levels of mutability in addition to very strong or strong mosaic. From such an ear it is then possible in future generations to isolate stable white lines.

Additional intercrosses between stocks of the various levels of mutability have been made. The results are in agreement with the pattern of interaction reported last year. Crosses of very strong, strong, light mosaic and light minus mosaic to stable white lines result in seedlings that have lower levels of mutability than the mosaic parent. Usually the level of mutability is at least one class lighter. Similar crosses to the vp-2 and the w^{alb}-4889 alleles give the same results as crosses to stable white. Crosses between very strong and light, very strong and weak, and strong and light all have lower levels of mutability than the parent with the highest level.

By selfing it has been possible to establish lines at each of the various levels of mutability that consistently, although not invariably, give ears with only one class of mosaic seedlings. When such lines are outcrossed and the outcrosses selfed, three classes of segregating ears are produced: 1) those which segregate only mutant seedlings with the original level mutability, 2) those segregating both seedlings with the original level and some with the lower levels of mutability and 3) those segregating only seedlings with levels of mutability lower than the original parent. Of 105 such outcrosses tested this year the frequencies of the three classes were 26, 52, and 27 respectively.

Selfs of outcrosses of stable white lines that were derived from mutable stocks segregate only white seedlings provided the outcross parent has not been derived from green mosaic lines. However, selfs of crosses of such white lines to non-segregating ears from families that are heterozygous for green mosaic result in ears segregating for mutability. Two such selfs of crosses to a non-segregating ear in a strong mosaic family have produced ears with weak mosaic seedlings. Other selfs of outcrosses to normal ears from mosaic families of uncertain levels of mutability have produced ears with various combinations of light, light minus, weak and white seedlings. Additional crosses of this type have been made using stocks of the different known levels of mutability. In addition the vp-2 and w^{alb}-4889 alleles are being tested to see if crosses to non-segregating ears out of mosaic families will induce these alleles to become mutable.

Selfs of normal plants from F_1 ears of very strong and strong mosaic times stable white produced 5 ears, none of which have very strong or strong mosaic seedlings. Of the three ears tested involving very strong mosaic one segregated light minus, weak mosaic and white seedlings and the other two, weak mosaic and white seedlings. Of the two ears tested involving strong mosaic one gave weak mosaic and white seedlings and the other gave only one white seedling.

The above results are consistent with the hypothesis that mutability at the vp-2 locus is caused by a separable modifier. There is some indication that the modifier can be either linked or independent of the locus. Further tests are being planned to establish this, as well as, the relationship between the various levels of mutability.

4. Allele tests of white-albino mutants.

For the past several years allele tests have been carried out between known white-albino mutants (mutants with white or pale yellow endosperm that give albino or pale green seedlings) and those sent me by other workers with the following results:

Source	Allelic to	Chrom.
Dr. Everett, out of KyS	w-3	2
Dr. Everett, out of 2655 54	lw-2	5
Dr. Mumm #1, out of M14	vp-5	1
Dr. Mumm #2, out of Oh7 Dr. Braun, out of 182D	allelic to each other	?

Crosses between w-3 and pastel-8686, both of which had been shown to be on chromosome two by linkage test, have established that these two mutants are allelic. The two mutants are quite distinct; w-3 has white seeds and pure white albino seedlings while pastel-8686 has white seeds and pale yellow-green seedlings. The F_1 between them is closer to w-3 than pastel-8686 in phenotype but this will need to be tested further since the seedling tests were performed during cloudy weather. It may be that high temperature and sunlight are necessary for the greening of pastel seedling. The fact that pastel-8686 seedlings were much paler than those observed in previous years grown under more favorable conditions would suggest that this is so.

Dr. Smith at Stanford has shown that w-3 seedlings when grown in the dark produce protochlorophyll that is converted to chlorophyll a when they are transferred to the light. Chlorophyll a on exposure to the light is destroyed so that the albino seedlings result. A study of chlorophyll synthesis in the pastel-8686 allele might prove very enlightening in view of what is already known about chlorophyll synthesis in w-3.

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1. West Indian maize.

There is support for Harland's hypothesis that West Indian maize strains are inbred lines that have also been selected for vigour. Comparison of the growth between sibs and once selfed lines has been made, although the number of lines tested has been limited owing to difficulties of seed setting. In Early Caribbean and Cuban Flint strains, the sibbed lines were no more vigorous than the selfed lines. Thus the drastic occurrence of inbreeding depression normally expected in outbreeding maize populations has not been demonstrated.

Most of the families produce seedlings differing from normal. These include small and narrow leaved ones, and various yellow leaved ones probably associated with the character "virescent". True albinos also occur and rapidly die. Comparison was made between the growth, flowering and ear formation of adult plants raised from normal and abnormal seedlings. The data were unable to establish that abnormal seedlings were severely handicapped, either in their early mortality or in their final heights and flowering times. A relationship was established between intensity of anthocyanin coloration of the seedling bases, and the frequency of small seedlings. There were no small seedlings with very dark red bases, 12% among those with very pale red bases, while all green seedlings were 65% small.

Meiosis was examined in normal plants of Cylindrical Dent, Cuban Flint, and Early Caribbean. Meiosis was normal in that 10 bivalents were formed; there was no indication of lagging chromosomes which might have accounted for aberrant seedlings. In one plant of Coastal Tropical Flint the anthers were very small and shrivelled but P.M.C.s were present, although divisions could not be seen. Mitoses have also been examined in abnormal seedlings of four families. The diploid count of 2n = 20 was obtained for seedlings that included albino, yellow-leafed, "virescent" and weakly seedlings, as well as normal controls.

Some plants produced viviparous growth in their tassels, the florets developing directly into young plants. It has been possible to vegetatively propagate these, and they form good roots. These propagules appear to make only limited growth and mortality has been heavy. This is believed to be the first record of this condition in cultivated maize, although it is known that Singleton's "corn-grass" mutant will vegetatively propagate. This character supports the view that West Indian maize has evolved along a differing path from North American corn.

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1. Test of Ga specificity.

Further genetic tests for specificity of the interaction between gametophyte factors in the style and those in the pollen were made. Five plants that were homozygous ga in 4 but heterozygous for a Ga factor in group 5 and for bt were self pollinated and also crossed as ♂ on two Bt Bt Su Su stocks: #1 which carries the Ga in 4 and the ga in 5 and #2 which carries the Ga in 5 and ga in 4. These crosses were grown in an open pollination plot with borders and scattered rows of bt bt and Bt bt plants as supplemental pollinators. When mature the number of ears segregating and not segregating bt were counted. The selfs of the five parents had 12% or less of bt seeds.

♂ parents	♀ = Ga in 5, ga in 4 Stock #2			♀ = ga in 5, Ga in 4 Stock #1		
	Bt Bt	Bt bt	% het.	Bt Bt	Bt bt	% het.
19875 - 2	65	2	3.0	46	18	28.1
19875 - 3	63	4	6.0	47	27	36.5
19875 - 7	20	1	4.8	61	15	19.7
19873 - 3	56	14	20.0	37	21	36.2
19873 - 5	42	31	42.5	43	21	32.8

If the Ga in 4 were specific in its effect, the cross with stock #1 should have given a ratio of 1 Bt Bt : 1 Bt bt. The tests indicate there was some effect of stock #1 on the ratio of Bt : bt through the pollen. This stock is known to carry the Ga in 4 and not the one in 5, suggesting a non-specific effect of the Ga in 4. Since stocks 1 and 2 are far from isogenic it is possible that the effect is due to some other factor, although there was no disturbance of the bt ratio when the test crosses of that stock were selfed.

The comparable data for the tests of plants homozygous for the ga in 5 but heterozygous for su and for the Ga in 4 were summarized in the Maize News Letter #28, p. 60. Stock #2 carrying the Ga in 5 had no effect on the Su : su ratio, indicating it had a specific effect.

2. Crossing over in ♂ vs ♀.

Tests of la - su - gl in crosses with maize chapaloti, Long eared Papago, Argentine pop, and Mexican Meal consistently showed higher recombination in the ♂ than in the ♀ in the la - su region but no difference in the su - gl region.

For region 1: 8.49 ± .66% as ♀, 11.01 ± 0.79% as ♂.

This difference is smaller than that found in tests with other stocks.

For region 2: 39.0 as ♀, 39.4 as ♂.

Tests of sh - wx with gourd seed, Tom Thumb pop, Maize chapaloti, Long eared Papago, and KYS, showed very little difference, except in occasional plants.

3. New characters.

"Expanded glumes" is a recessive in which at the time of anthesis and for a short time after that the glumes of the tassel are almost at right angles to the axis. Linkage was found with T5-7(5179):5L.64 - 7L.68 with a recombination value of 24.4 ± 3.2%; and with T5 - 10.(5688): 5L.78 - 10L.49 with a recombination value of 4.8 ± 0.6%. This gene must be located in the long arm of chromosome 5.

4. Tests for directed segregation in a Ω4 with short interstitial segments.

An earlier test with Argentine pop had given doubtful results. In a new test of the F_1 backcrossed to Argentine pop there was a ratio of 258 fertile : 211 partially sterile. The deviation from 1 : 1 is significant; but even if it is the result of directed segregation the effect is small.

5. Progress in producing stocks with several interchanges.

From the following crosses of translocations with one chromosome in common, a crossover has been obtained which combines the two translocations:

2 - 3d + 2 - 4b*, 4 - 8a + 2 - 4b*, 9 - 10b + 8 - 9b*,

5 - 7(5179) + 1 - 7(4405)*, 1 - 9b + 9 - 10b**, 5 - 7(5179) + 5 - 6c**.

* = homozygous stock, ** = plants with crossover identified. All have been crossed with standard normals and checked cytologically. 4 - 8(5339) has been substituted for 4 - 8a. In addition there are: (2 - 3d + 2 - 4b + 4 - 8a) - see succeeding note by Inman; and 1 - 5 - 6 - 7 - 8 (produced by successive irradiation).

The translocation labeled 3 - 6c gave 204 when crossed with 2 - 3d. It is probably a 4 - 6. Stocks of a new series of translocations selected by Inman for the purpose of building multiple translocation stocks for special uses have been furnished by E. G. Anderson. Crosses and backcrosses are ready for the selection of possible crossovers.

The two ideas worked out by Inman; 1) the proposal for avoiding high sterility as more translocations are added, i.e. during the building process and 2) the proposals for special uses have raised the hopes for producing the needed stocks. It does not appear to be necessary in corn to use Inman's proposal for the use of gene markers in the early stages as an aid in selecting the desired crossovers, but they may be needed in later stages. They are being used for that purpose in the barley translocations. The closely linked gene markers are introduced in the non-translocated chromosomes brought together to produce the 06.

6. Linkage in polyploids.

Fisher's papers on the analysis of linkage data in autopolyploids have been reviewed by Dr. C. E. Gates, our Experiment Station Statistician. Mimeographed material explaining the mathematics and the method is available.

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Assisted by: L. L. Inman
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J. Axtell

7. The production of large chromosome rings and a proposed use for studies of chromosome pairing relationships.

A method was proposed earlier (Maize News Letter #29, p. 55) for avoiding some of the high sterility encountered as the number of translocations in a stock is increased. One test has been completed. A homozygous stock which had combined translocations 2 - 4b and 4 - 8a was crossed with another that had combined 2 - 4b and 2 - 3d. As predicted, the F_1 had 2 rings of four chromosomes. Cytological examination of the progeny of this F_1 crossed with a normal indicated independent assortment of the "fertile" combinations from each of the two rings. One-fourth of the progeny had the desired ring of eight chromosomes (2 - 3d + 2 - 4b + 4 - 8a); one-half had a ring of six chromosomes (2 - 3d + 2 - 4b or 2 - 4b + 4 - 8a), and one-fourth had a ring of four chromosomes (2 - 4b). A stock homozygous for the three translocations can be isolated from the plant with the 08.

By using this method and by proper planning of the crosses of stocks with as many translocated chromosomes in common as possible, the predicted maximum pollen sterility should be about 75%. This is no greater for the production of a multiple translocation stock to produce a ring with all the chromosomes than for the production of the ring of eight.

8. Chromosome rings in which the homologous differential segments are in separate rings are theoretically possible.

In a species with an odd number of chromosome pairs, a single ring including all the chromosomes would be expected from a cross between a stock having a standard normal chromosome complement and a homozygous stock having a translocation on every arm of every chromosome of the complement. In a species with an even number of pairs of chromosomes it was demonstrated by diagrams that two rings of chromosomes are to be expected from such a cross and the corresponding homologous differential segments of each chromosome pair are in separate rings. The ten pairs of chromosomes of maize may be divided into two groups with an odd number of pairs of chromosomes. If a multiple translocation stock is produced with translocations restricted to chromosomal interchanges within the group and involving every arm, two rings of ten chromosomes with homologous centromeres in the same ring are expected in the pollen mother cells of the progeny from a cross with a stock having a normal arrangement of chromosomes. Comparisons between a multiple translocation stock that would produce progeny with two rings of ten chromosomes with homologous centromeres in the same ring, with a multiple translocation stock that would produce progeny with two rings of ten chromosomes with homologous centromeres in different rings, may reveal whether chromosome pairing during meiosis is more strongly governed by the mid-sections including the centromeres or by the distal portions of the chromosomes.

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9. Studies of chromosome pairing in crosses between translocations involving the same chromosomes.

A series of 2 - 6 translocations and a few others are being used. In combinations in which the break points are on opposite arms in both chromosomes 2 and 6, the pairing configuration in F_1 might be of two types, depending on whether homologous "between breaks" segments or homologous ends are paired. In T2-6a (2L.40; 6S.00 - 0.5) x T2-6b (2S.69; 6L.49), 81% of the spore-mother-cells had 10 pairs and 19% had a complex of four chromosomes. In T2-6a x T2-6 (6049)(2S.70; 6L.23), 58% had 10 bivalents and 42% had a complex of four.

At pachytene each of the two "bivalents" from the translocated chromosomes always includes the same chromosomes. In all configurations, whether "pairs" or a complex of 4, pairing in the terminal homologous regions is complete. In those with "bivalents" there are loops in the intercalary non-homologous regions, and unpaired centromeres. These observations suggest that pairing is initiated at the ends.

In T2-6b (2S.69; 6L.49) x T2-6c (2L.32; 6L.23), in which the two translocation breaks are on opposite arms in one chromosome, but in the same arm in the other chromosome, 6% of the P. M. C. at diakinesis had 10 "pairs" and 94% had an association of four. In all figures the homologous ends were paired. In the "complexes of four" the intercalary homologous "between breaks" segments are in reverse order with respect to each other but they remain unpaired.

In another combination of this type, T2-6c x T2-6(6049)(2S.70; 6L.23), an inversion loop was observed in the "between breaks" region in 5 of the 9 cells observed, while the other 4 showed non-homologous pairing.

All the observations indicate that pairing starts in the terminal regions, and then proceeds toward the centromere.

In T3-6a(3L.06; 6L.30) x T3-6b(3S.73; 6S. Sat.): in pachytene a cross-shaped configuration of four chromosomes is observed, in which the short terminal segments of chromosome 3 pair in many cases, thus resulting in a partly closed cross-configuration in which the distal end of the short arm of 3 is brought close to the nucleolus and paired with its homologous translocated segment. The translocated portion of the satellite was in no case paired with its partner.

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1. Ac-Ds induced high amylose mutants.

An experiment was designed to induce new high amylose mutants by the use of the Ac-Ds mutator system. Since Coe (News Letter 31: 140), found that high amylose produced by the genes ae and du is expressed clearly on a wx background this experiment was conducted with homozygous wx stocks. Crosses were made in both directions between C^i-wx-Ds/C-wx-Ds, one Ac and a number of waxy stocks. The F_1 obtained was selfed and the ears examined for segregation of endosperm mutants of all types but specifically for the collapsed endosperm type that is typical of the high amylose waxy phenotype.

The following types of cases were found among 2417 selfed ears examined.

(1) Two ears (from the same family and therefore possibly the same mutant) segregating 3:1 for a collapsed type closely resembling the typical high amylose waxy phenotype, except that the collapsing is quite irregular suggesting that the new mutant is frequently mutating to the original form. Seedlings grown from these seeds are pale green and therefore rather weak.

(2) Four ears segregating 3:1 for wrinkled kernels the expression of which is not yet understood. Most of these seeds failed to germinate.

(3) Six ears segregating for tarnished kernels. The poor expression of this type prevents accurate classification.

(4) Seven ears with various sizes of ear sectors (from 20-100 seeds). Within the borders of these sectors there is a segregation for collapsed, or shrunken seeds. Some of the seeds themselves appear to be sectored for normal vs. collapsed tissue.

(5) In addition there were 19 ears with 1 to 5 scattered seeds of a tarnished or translucent type. All of these but two failed to germinate.

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M. G. Nuffer

2. The effect of X-ray and UV on mutation in a doubled haploid line.

In an effort to determine whether X-rays can produce desirable genetic variability, plants of a supposedly homozygous (doubled haploid) line were self-pollinated with treated (1200 r) pollen and the resulting seeds were grown to observe the types of mutants produced. A small population from pollen subjected to UV as well as an adequate control were also included.

The kernels from 41 control, 77 X-ray and 14 UV-treated ears were planted and the resulting seedlings were noted at several stages of maturity.

Mutant types that appeared in the first generation are summarized in Table 1.

Table 1. Types and frequencies of mutants in S_1.

	No. of kernels planted	No. seedlings	Mutant types			
			chloro-phyll	Male sterile	dwarf	narrow leaf
Control	5632	4493 (79.7%)	12 (0.26%)	37 (0.83%)	92 (2.04%)	0
X-Ray 1200r	10813	5205 (48.1%)	46 (0.88%)*	319 (6.12%)	247 (4.74%)	14 (0.26%)
UV	706	410 (58.0%)	0	29 (7.07%)	16 (3.92%)	0

*Four yellow striped plants from one ear are included.

The effect of the treatments in producing types lethal under field conditions (column 3, Table 1) is quite striking and demonstrates the effectiveness of the treatment. The treatments were moderately efficient in producing other types listed in the table. No vigorous or more desirable types were found. All the mutant cases, except the male sterile plants, and about 1/3 of the normal plants were self-pollinated.

At least 40 kernels of each self-pollinated ear of the normal plants of the control and treated families were planted in a sand bench in the greenhouse. The seedlings from these (450 control, 202 X-ray and 160 UV treated) F_2 ears were checked for segregating mutant types. These are listed in Table 2.

Table 2. Types and frequencies of mutants in the seedling stage of S_2.

	No. of ears tested	No. of ears producing mutant seedlings			
		poor germination*	chlorophyll type**	narrow leaf	dwarf
Control	450	12 (2.66%)	10 (2.22%)	3 (0.66%)	1 (0.22%)
X-Ray	232	15 (6.46%)	21 (9.05%)	4 (1.72%)	3 (1.29%)
UV	160	9 (5.62%)	15 (9.37%)	3 (1.87%)	1 (0.62%)

*Germination below 50%. Normal is 83%.
**Both white and virescent seedlings are included.

Most of the mutants found did not give a clear 3:1 ratio, but instead had a deficiency of the recessive class. Again, in the F_2 there was a complete lack of vigorous seedling or desirable mutant types. It should be pointed out, however, that recognition of desirable types is a quite arbitrary choice.

T. Yabuno
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3. The effect of EDTA on the frequency of crossing over.

It is thought that the failure to obtain an increase in crossing over in corn that has been grown on calcium-deficient soil comparable to that obtained in Drosophila and other organisms that were treated with EDTA is due to the fact that corn has a very critical calcium requirement for growth, and therefore does not survive at a level low enough to affect crossing over. To overcome this a special treatment was devised to provide a very low concentration of metallic ions in the flowering parts of the plant during a short period of time just prior to meiosis.

Vigorous F_1 plants of the constitution $\underline{a}$ $\underline{a}$ $\underline{sh}/\underline{a}^m$ $\underline{Sh}$, $\underline{dt}$, no $\underline{Ac}$ were treated with a .001 molar solution of chelating compound, (ethylene dinitrilo tetracetic acid). The method of treatment consisted of feeding through the cut end of the sixth or the seventh leaf. The leaf was cut about four inches from the auricle and the cut end was placed in a vial containing the above solution for a period of twelve to twenty-four hours. The treatment was applied when the most advanced region of a tassel was just premeiotic. The plants were pollinated by $\underline{a}^s$ $\underline{sh}$, $\underline{Dt}$ and the ears were examined for crossovers between $\underline{a}$ and $\underline{sh}$. The results shown in the following table, though of a preliminary nature, clearly show significant increase in cross-over types in the treated material.

Frequency of crossovers from the cross a a sh/a^m Sh x a^s sh.

	Total No.	a a^m Sh	a a Sh	a-Sh	a^m sh or a sh	a^s sh	T co	%
Control	3628	0	0	0	2	0	2	.00055
EDTA	4035	0	4	3	3	3	13	.0032

4. Response of 2 alleles of an_1 to gibberellic acid.

Plants that are homozygous an_1 normally do not shed much pollen because the anthers remain encased in the glumes. Several an individuals were treated at a stage comparable to shedding in a normal plant, by rubbing a spot at the base of the tassel with a glass rod coated with a lanolin paste containing 1.25% gibberellic acid. Within less than twenty-four hours that portion of the tassel immediately above the region touched with the paste appeared as a sector of normally expressed anthers that shed normal pollen. The remainder of the tassel continued to have tightly-closed florets and produced no pollen. The effect of the treatment appeared to be that of lengthening of the filaments and opening of the glumes. Similar treatment was applied to plants that were homozygous for another allele an_{6923} (a radiation induced mutant associated with bz_2). The treated plants showed an elongation of tassel parts but failed to extrude any anthers. Careful examination showed that the anthers were empty and beginning to degenerate.

M. G. Nuffer

5. Chromosome 9 mapping.

Data has been accumulated for incompletely placed factors as follows:

Genes XY	Phase	XY	Xy	xY	xy	Total	Recombination
Ar Bk_2	RS	227	130	110	1	468	9
Ar Bm_4	RS	222	60	63	24	369	55
Ar Ms_2	RS	100	46	44	0	190	<15
Ar Wx	CS	477	32	41	121	671	12
Au Cr	CS	32	7	1	9	49	12
Bf Bk_2	RS	141	41	60	8	250	39
Bf Bm_4	RS	117	65	68	0	250	<11
Bf Ms_2	RS	157	55	46	7	265	38
Br Wx	CS	171	48	38	18	275	43
Bk Gl_{15}	RS	85	24	32	0	141	<22

Genes XY	Phase	XY	Xy	xY	xy	Total	Recombination
Bk Bm_4	CS	597	152	180	69	998	44
Bk Ms_2	RS	93	31	34	2	160	27
Bk V	RS	100	37	54	1	192	15
Bk Wx	RS	427	156	207	11	801	25
Bm_4 Ms_2	RS	99	27	28	6	160	47
Bm_4 V	RS	131	31	23	7	192	54
Bm_4 Wx	RS	351	96	87	27	561	52
Cr Sh	CS	30	3	11	5	49	30
D_3 Sh	CS	54	12	8	4	78	39
D_3 Wx	CS	66	0	3	9	78	< 6
Gl_{15} Wx	CB	171	11	13	188	383	7
Ms_2 Wx	RS	247	100	108	0	455	<11
V Wx	CS	167	7	10	38	222	8

The one backcross entry has complete four-point data as follows:

F_1	Parental	Region 1	Region 2	Region 3	1-2	1-3	2-3	1,2,3	Total
+ + + +	132 149	10 8	28 30	13 10	0 0	0 0	2 1	0 0	383
c sh wx gl_{15}	281	18	58	23	0	0	3	0	
		4.7%	15.1%	6.0%			0.8%		

c sh 4.7 sh wx 15.9 wx gl_{15} 6.8

It is now possible to designate a map, in a gross manner, with wx at 59, ar at about 71, bk_2 at about 80, and Bf_1 at about 119. The factors d_3, gl_{15}, au, v, and ms_2 are all clustered between wx and ar; cr is between ar and bk_2, and bm_4 is to the right of Bf. Using parentheses to designate uncertain relative position, the map may be drawn as follows:

wx (d_3, gl_{15}, pg_{12}, v, ms_2) ar (cr) bk_2	Bf_1 (bm_4)
59 71 80	119

A more adequate map must await resolution of the clustered and uncertain factors.

Notes: Allelism tests show the au_1 au_2 duplicate system to be allelic to pg_{11} pg_{12}. A crinkly type, probably cr_2 (considered lost),

has appeared in $\underline{au}_1$ $\underline{au}_2$ cultures; it is not easily classified. Pollen for backcrosses has been obtained from $\underline{d}_3$ plants by applying 1% gibberellins in lanolin to the sheaths about 3 weeks before tasselling. Independence of $\underline{gl}_{10}$ (Sprague's) with $\underline{wx}$ (48.5% in 979 plants) and $\underline{vg}$ (49.0% in 649 plants) agrees with Anderson's report (News Letter 30: 9) for chromosome 5 instead of 9. Independence for $\underline{ta}$ with $\underline{wx}$ (48.5% in 154 plants) has been found.

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M. G. Nuffer

6. High-haploid line.

The line which has about 3% haploids in self progenies (see previous two News Letters) is a haploid inducer when used as male. In crosses of $\underline{gl}_1$ egg parent by the line (stock 6) and a $\underline{R}^r$ line, maternal haploids have been found as follows:

Pollen	Haploids	Total	% Haploids
6	13	472	2.75
R^r	6	724	0.83

Additional tests on a larger scale and tests of crosses and backcrosses involving stock 6 are in the process of analysis, and are confirmatory.

No paternal haploids have occurred in the following tests:

Cross	Haploids	Total
R^r x 6	0	8,899
R^r x gl	0	1,989
6 x gl	0	[illegible]
Totals	0	11,534

7. A new recessive aleurone color factor.

A new colorless aleurone mutant which gives a good 3:1 and negative allelism tests with $\underline{a}_1$, $\underline{a}_2$, $\underline{c}$ and $\underline{r}$ testers has been found. It apparently segregates independently with $\underline{a}_2$, but no other information is available on location as yet. Recessive plants of sun-red type have been obtained, and the mutant apparently has a dosage effect similar to that of $\underline{c}$. It is tentatively designated $\underline{c}_2$.

8. Anti-inhibitor effect of bz_2.

Kernels of C^i C C Bz bz_2 bz_2 constitution have considerably more color than either homozygote for bronze-2. The color is at least as dark as that of A^d. Although further tests are needed, it presently appears that a single dose of C^i and one or two doses of bz_2 are necessary for the effect.

9. Intensely pigmented tissue cultures.

Successful cultures of young endosperms, doubling in size in 6 weeks, were obtained last Spring. Intense pigmentation was produced through the use of in. Tester lines (a_1, a_2, bz_1, c, C^i, r) converted to su in are now available in addition to ACR Pr su in, which is the type cultured. Sugary is required according to Straus and LaRue (Amer. Jour. Bot., 1954). The medium is the tomato juice one which they used:

White's mineral stock	100 cc
Ferric citrate solution, 0.25%	4 cc
Nitsch' trace elements	1 cc
Sucrose	30 gm
Agar	10 gm
Tomato juice (see below)	200 cc
Water (double distilled)	to 1 liter

The tomato juice is made with one can of dietetic tomatoes, blended, filtered, and adjusted to pH 6.5-6.8 with 0.2M NaOH. The medium is poured into small screw-cap bottles and autoclaved complete. Additives of kinetin (10 micrograms per liter) and corn milk were tried in all combinations with and without tomato, but tomato alone was as good as or better than any other. Inoculations made at 10 or 11 days post-pollination were successful, but not 9, 13, 14, 15, 16, 17, 19, or 21 days (inoculations were all made in one day, from greenhouse material). Pieces of ear were surface-sterilized 10-15 minutes in 20% Clorox, and whole endosperms were removed with a sterile scoop.

10. Test for doubleness at C locus.

For the population reported last year, all tests are complete, and no cases of crossing over within C^i have been obtained. For the four assumed structures, maximum map distances for C to I are:

I C: 0.00032 map units maximum.
C I: 0.00032 map units maximum.
I c: 0.064 map units maximum.
c I: 0.079 map units maximum.

Further tests will yield diminishing returns, since the last two structures result in an asymptotic relation of map distance to number tested. No further tests are planned.

11. Spontaneous mutation of C^i.

The tests of cases reported last year for 809,370 gametes are complete:

Endosperm	Number Obtained	Valid Cases	Deficiency for C^i	Terminal Deficiency	Non-Corresponding	Failed
Self-color	6	1 (c)	3	0	0	2
Variegated entire	85	0	0	32	31	22
Variegated sector	19	0	0	8	6	5
Colored pits	12	0	0	3	3	6
Colored scutellum	4	0	0	0	1 (haploid)	3
Diffuse color	4	0	0	0	3	1
Totals	130	1 (c)	3	43	44	39

Only one valid mutant, which is c, has been obtained. It has completely normal transmission and responds to Bh. This case was from one of the two full-sized self-color kernels reported last year. The other of these was a non-transmissible deficiency for C^i. Since the two which failed were small in size (one was germless), there is little doubt that only one valid mutant occurred in this population. Mutation of C^i to C has not been observed in 1,231,883 gametes; mutation of C^i to c has occurred once in 809,370.

The structure of C^i can be considered either as compound and c I or I c, with the two units quite close together, or as single and incapable of mutating to one of its two known lower alleles.

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1. Characteristics of maize races growing in the middle part of Japan.

Japanese races are composed of two types of flint corn. One type is the so-called "Tripsacoid" maize. It was introduced into Japan recently, probably after the establishment of the Agricultural Experiment Station in 1877, from the northwestern United States and Europe. At present, its races are distributed mainly over open fields in the northern part of Japan. On account of their lateness and susceptibility to frost damage, none of the old Japanese races are grown in such fields. The other type of flint corn is a group of old Japanese races belonging to the so-called "Caribbean" tropical flint (Sutô, 1956). It is said that a Portuguese introduced seeds of this type from Europe to Kyûshû in 1573. This maize has rapidly spread over the temperate uplands ranging from about 300 to 100 m in altitude. In accordance with adaptation to specific environments in such regions, a number of local races had been differentiated, without any contamination with other types, before 1877. As compared with the North American or European flints, they are characterized by the following characters: Plant mediate or tall in height, medium or late in maturity, highly resistant to humidity, lodging and leaf blight, well-adapted to barren soil; tillers and prop roots absent or few in number; leaves many in number and large in size, the longest leaf arising from a high position on the stalk; stalk thick in diameter, having many short internodes; tassel very long and pendent, having fewer long branches; paired spikelets very lax, shedding a small amount of pollen at anthesis; ear high in position, large in size, conical or occasionally cylindrical in shape, usually having an enlarged butt and about 12 to 16 kernel-rows; shank having enlarged nodes and a ribbed surface; husks short in length, but very abundant in number, having no flag-leaves; cob very large in diameter and soft in texture; kernels large, somewhat spherical in shape, orange in color and hard in texture, giving a good quality.

There are three centers of their distribution in the temperate regions of Japan; (1) the highland fields around Mt. Aso in Kyûshû, (2) the terraced fields at the mountain sides in Shikoku and (3) the upland fields at the foot of Mt. Fuji in Honshû. The 57 samples used in this work were collected from about 100 farmer's fields in 10 upland localities around Mt. Fuji and neighboring mountains at the central part of Japan. According to agronomical, genecological and cytogenetical viewpoints, the findings obtained are summarized as follows:

a) The 57 samples were identified as belonging to 19 races, of which the maturity was early in 2 races, medium in 4, late in 8 and extra-late in the remaining 5. Six of these, comprising 2 early, 2 medium, and 2 late races, were proved to be favorable as breeding material.

b. The 10 native localities examined were classified into 5 areas.

1) The eastern area consists of three localities, Tsukui (T), Dôshi (S) and Akiyama (A). The majority of corn fields were terraces of the mountain solitudes of Mt. Tanzawa situated at the eastern part of Mt. Fuji. The 6 races were distributed. They had a typically conical and short ear with large and spherical kernels and about 12 kernel-rows. Yields of both grain and stalks were usually low, and their quality was inferior to that in any area of this region. Characteristics of the races were not so particular, but of a primitive nature. All of them but one, largeness in kernel size, are considered unworthy for agronomical purposes. But, it is cytologically interesting that these races possessed many knobs, 9 to 10 on the average, and had no B chromosomes with the exception of one race in Dôshi.

2) The Kamigane area occupies the southern side of the mountain-range of Chichibu situated at the northern part of Mt. Fuji. Soils were fertile. Farmers were very careful in their management of corn fields and in their selection of the seed corn. There was a useful late race, besides an early one and a medium one. The cob was very large and soft, sometimes hollow in its center, making it easily possible to push kernels into the cob with the fingers. Kernels were spherical in shape and more yellowish in color. Races frequently had a B chromosome. The frequency of chromosome knobs was as high as that in the former area.

3) The northern area is composed of several localities, i.e. Funatsu (F), Narusawa (N), Yamanaka, Iwama and others. They are all situated at the northern foot of Mt. Fuji, which is the best place for corn production in this region. From old times, farmers have carefully grown corn as a staple food. The two races were distributed, one, which was found to be early, in Narusawa and Yamanaka, and the other, which was medium, in Funatsu and Iwama. Both are considered to be of some agronomic value. The ear was long-cylindrical, having a hard rod-like cob and about 8 to 12 kernel rows. Kernels were large in size, very good in quality, and their color was brilliant orange. The frequency of B chromosomes was high, as in the Kamigane area. The knob number was less, about 7 on the average.

4) The southern area occupies the southern foot of Mt. Fuji, containing such localities as Jûrigi (J), Suyama (S) and Itazuma (I), and represents another of the most productive corn growing areas. Five races were grown in these localities; an 8-rowed extra-early one was the most interesting. No B chromosomes were observed in any of these races. The number of chromosome knobs was about 8. In the extra-early race of the Jûrigi locality, the number of knobs was 5, this being the smallest number in this region.

Table 1. Frequency of occurrence of chromosome knobs in 51 maize races growing in Mt. Fuji and its neighboring districts.

Native place	No. of races		1		2		3		4		5		6		7		8		9		Subt.		
		B	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	Total
T	5	-	1	-	2	3	-	5	-	3	-	6	-	10	-	5	-	9	1	1	4	41	45
	av.	-	0.2	-	0.4	0.6	-	1.0	-	0.6	-	1.0	-	2.0	-	1.0	-	1.8	0.2	0.2	0.8	8.2	9.0
A	6	-	3	3	-	4	1	6	-	2	-	5	-	12	-	6	-	11	1	4	5	53	58
	av.	-	0.5	0.5	-	0.7	0.2	1.0	-	0.3	-	0.8	-	2.0	-	1.0	-	1.8	0.2	0.7	0.8	8.8	9.7
D	4	1	-	1	1	3	1	3	-	3	-	4	-	8	-	4	-	7	1	1	4	33	37
	av.	0.3	-	0.3	0.3	0.8	0.3	0.8	-	0.8	-	1.0	-	2.0	-	1.0	-	1.9	0.3	0.3	1.0	8.3	9.3
K	9	7	-	1	-	6	2	9	-	2	-	9	-	16	-	8	-	16	4	6	6	74	80
	av.	0.8	-	0.1	-	0.8	0.2	1.0	-	0.2	-	1.0	-	1.8	-	0.9	-	1.8	0.4	0.7	0.7	8.2	8.9
F	6	6	-	5	3	1	-	4	-	2	-	6	-	10	-	5	-	5	3	-	6	37	43
	av.	1.0	-	0.8	0.5	0.2	-	0.7	-	0.3	-	1.0	-	1.5	-	0.8	-	0.8	0.7	-	1.0	6.2	7.2
N	6	5	-	-	-	4	1	5	-	-	-	6	-	9	-	6	-	9	2	-	3	39	42
	av.	0.8	-	-	-	0.7	0.2	0.8	-	-	-	1.0	-	1.5	-	1.0	-	1.5	0.3	-	0.5	6.5	7.0
J	3	-	-	-	1	1	1	1	-	-	-	1	-	5	-	2	-	2	1	-	3	12	15
	av.	-	-	-	0.3	0.3	0.3	0.3	-	-	-	0.3	-	1.7	-	0.7	-	0.7	0.3	-	1.0	4.0	5.0
S	6	-	-	1	-	3	2	5	-	1	-	5	-	12	-	6	-	11	2	2	3	47	50
	av.	-	-	0.2	-	0.5	0.3	0.8	-	0.2	-	0.8	-	2.0	-	1.0	-	1.8	0.3	0.3	0.5	7.8	8.3
I	6	-	-	2	-	1	1	6	-	2	-	6	-	11	-	5	-	10	-	4	1	48	49
	av.	-	-	0.3	-	0.3	0.2	1.0	-	0.3	-	1.0	-	1.8	-	0.8	-	1.7	-	0.7	0.2	8.0	8.2
Total	51	19	4	13	7	28	9	44	-	15	-	47	-	92	-	47	-	80	15	18	35	384	419
	av.	0.4	0.1	0.3	0.1	0.5	0.2	0.9	-	0.3	-	0.9	-	1.8	-	0.9	-	1.5	0.3	0.4	0.7	7.5	8.2

The abbreviations under the 1st column, T, A, D, K, F, N, J, S and I, are the 1st letter of the local name, Tsukui, Akiyama, Dôshi, Kamigane, Funatsu, Narusawa, Jûrigi, Suyama and Itazuma, respectively. The letters in the 1st row, B, 1, 2, 3....9, S and L, correspond to B chromosomes, chromosomes 1, 2, 3....9, and the short and long arms of the chromosomes, respectively. One of the ten chromosome (no. 10) is not included in the table because of having no knobs.

5) The western area occupies the western foot of Mt. Fuji. Corn introduction to this area is comparatively recent. The growing area is not so wide. Corn growers are careless in corn management. There were three races. Plants and leaves were remarkably small. The ear was also small and conical, and had many kernel-rows containing small kernels, generally arising in a high position on the stalk. The variability of characters within a race was very conspicuous. It is assumed that repeated contaminations of the Caribbean corn with a primitive race of pop corn have occurred. Such a race has from old times been native to this region, essentially similar to the race "Lady Finger" grown in Latin America. No cytological examination was made on any races in this area.

2. A recessive mutant producing male sterility.

Two male sterile plants appeared in certain populations heterozygous for ra_1-gl_1-ij, a chromosome 7 linkage tester which has been preserved by sib-crosses in the breeding fields of our institute. One male sterile was called "A28" and the other "A29". These two mutants behaved similarly so far as the results of crossing experiments were concerned. In the present work, two stocks of different sources, a chromosome 7 linkage tester marked by ra_1-gl_1-ij and a multiple tester (Mangelsdorf's or Randolph's), were used as pollinators to be crossed with the male steriles. F_1 plants resulting from a cross with the multiple tester were all normal in a total of 1072, whereas two F_1 populations involving the chromosome 7 linkage tester were composed of a few male-sterile plants in addition to normal ones. One of these was an F_1 derived from the cross of a ms plant and consisted of 209 normal and 5 ms plants; the other F_1 was derived from a cross of a normal plant heterozygous for ms and gave 617 normal and 9 ms plants. The present sterile mutation, like that reported in 1950 by Prof. M. M. Rhoades in his paper on cytoplasmic male sterility, may also be induced by the genes, ra_1-gl_1-ij, especially ij.

From the data obtained on F_2 and backcross segregations, it seems highly probable that the present sterility is controlled by a single recessive allele. However, a significant discrepancy from the expected ratio of 3:1 or 1:1 was frequently encountered between (1) sterile stocks (A28 and A29), (2) different fields planted, (3) generations of sterility induced, and (4) different pollinators. At present the genetical cause is unknown. Out crosses were all made using the male sterile as the female parent. The cytoplasm in all crossing progenies should therefore have been transmitted from the sterile parent only. Whether the discrepancy is caused by such a cytoplasmic effect or not will be further studied.

At any rate, it may be assumed from the data in Table 2 and 3 that a gene governing the present case of male sterility is located on chromosome 4 with approximately 40% of recombination with su_1.

Table 2. F_2 data on the linkage detection of male sterility (x) in the repulsion phase of segregation.[1)]

Chr. no.	Marker gene (y)	Families	F_2 Individuals					X^2	P
			XY	Xy	xY	xy	Total		
1	bm_2	37	3476	936	1688	499	6588	2.7904	0.10*
2	lg_1	37	3469	934	1695	490	6588	1.2678	0.3-0.2
3	A_1	11	716	735	314	303	2068[2)]	0.4139	0.7-0.5
4	su_1	36	2973	1336	1756	422	6487	99.0611**	0.01
5	pr	6	290	136	132	50	1719	1.1905	0.3-0.2
6	Y_1	3	332	114	247	105	798	1.7944	0.2-0.1
7	ra_1	1	64	21	27	9	121	0.0012	0.95-0.99
8	j_1	37	3698	693	1816	331	6538	0.1458	0.8-0.7
9	wx	34	1896	1009	1157	549	4611	3.1305	0.10-0.05
10	g_1	37	3321	1080	1637	550	6588	0.2907	0.5-0.3

1) Nine of the F_2 populations listed above came from a cross of male-sterile hybrids with two multiple linkage testers, Mangelsdorf's and Randolph's, and the one involving linkage group 7 was from a cross with a single linkage tester marked by the three well-known genes, $\underline{ra}_1$-$\underline{gl}_1$-$\underline{ij}$.

2) This is the total of two F_2 progenies, one of which was heterozygous for three aleurone color genes, $\underline{A}_1$ $\underline{a}_1$, $\underline{C}$ $\underline{c}$ and $\underline{R}$ $\underline{r}$, all resulting from crosses with Mangelsdorf's tester, while the other was heterozygous for the alleles, $\underline{A}_1$ $\underline{a}_1$ and $\underline{C}$ $\underline{c}$, from Randolph's tester.

Table 3. Linkage relation of male sterility to the gene, su_1, in the repulsion phase of 36 F_2 families.

Pedigree used	Fam.	F_2 segregation					X^2 for linkage			Recombination value
		+	su	ms	su.ms	Total	Total	Deviation(1)	Heterogeneity	
1. A29-234	16	1125	558	860	222	2765	58.0738(16)**	50.4246**	7.6492(15)	40.84±1.59%
2. A29-236	15	1458	566	659	154	2837	54.7261(15)**	0.2224	54.5047(14)**	42.86±1.54%
3. A29-239	5	390	212	237	46	885	34.0094 (5)**	15.9749**	18.0345 (4)**	35.49±2.92%
Total	36	2973	1336	1756	422	6487	146.8094(36)**	99.0611**	47.7483(35)*	41.21±1.02%
1 + 3	21	1515	770	1097	268	3650	92.0832(21)**	83.0576**	9.0256(20)	39.74±1.39%

Numerals given in parentheses are the number of the "Degrees of Freedom (DF)" for X^2.

3. The source of pollen degeneration in a cytoplasmic male sterile.

A stock of unknown origin of cytoplasmic male sterility was furnished by Dr. D. F. Jones to Dr. H. Terao about fifteen years ago. This sterility has been maintained by crosses with the American sweet corn "Country Gentleman" in our breeding field. In the summer of 1956, Prof. G. F. Sprague and Dr. M. T. Jenkins visited our fields, and they said that the sterility may be of the T type. The pollen restoration in its F_1 hybrids was remarkably different in races of the two different origins, Japanese old flint and U. S. Corn-belt dent. The majority of flint races native to Japan were found to restore pollen production with a high frequency, whereas most of the races from the U. S. Corn-belt gave completely sterile F_1's though a few of them restored fertility with a low frequency.

The source of pollen degeneration in microsporogenesis of the male sterile plant was examined by anatomical pictures of the cross or longitudinal sections of young anthers cut at 15 μ and stained with Heidenhain's iron-alum haematoxylin method. Meiosis was normal, liberating the young microspores from the tetrads. Soon after this stage, an abnormal growth of the tapetal cells occurred. Owing to such an abnormality of the tapetum, the supply of nutrients to the microspores apparently became impossible. The microspores progressively underwent chromatolysis, resulting in a degeneration of pollen grains. In extreme cases of abnormal development of the tapetum, plasmodial masses were sometimes met within the anther cavity. These varied in shape as well as in size. Usually, it is said that the cytoplasm in the tapetal cells strongly indicates a metabolic reaction, and that the nutrients produced in the cytoplasm are then utilized by the developing microspores. The tapetal cells in the male sterile plants became abnormally enlarged, probably due to an accumulation of nutrients which are not supplied to the microspores. The plasmodial masses were apparently formed by evolving such an excessive protoplasm from the enlarged tapetum. In appearance, these plasmodial masses seemed to digest the microspores through covering them with a lengthened pseudopodial cytoplasm. At last, no pollen grains were found to exist in such an anther cavity. The flowers with such anthers never exserted their anthers. The plant was completely male sterile. It may therefore be concluded that the male sterility is conditioned by the abnormal behavior of the tapetum

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1. Estimates of genetic variance components in two open-pollinated varieties and populations derived from the cross between them.

Estimates of the genetic variance components based on two years data have been obtained for the F_2 generation of the cross of the Jarvis and Indian Chief open-pollinated varieties of corn. These estimates and those made earlier on the parent varieties and F_1 of the variety cross are given below.

Estimates of Genetic Variances 1956-1957

Population	Male	Female	Mean Yield lbs./plot
Intra-variety			
Jarvis	.00101	.00093	.520
Indian Chief	.00057	.00082	
Inter-variety			
Jarvis x Indian Chief	.00036	.00078	.587
Indian Chief x Jarvis	.00038	.00052	
Advanced Generation Variety Cross			
(Jarvis x Indian Chief) F_2			
1956	.0021	.0013	.540
1957	.0014	.0016	

Although the variance estimates for the different populations were obtained in different years, it is not likely that the differences in the genetic variances of the three kinds of populations are due to environmental differences. The genetic variance of the F_1 cross between the varieties is less than the intra-variety estimates, which is compatible with the partial to complete dominance hypothesis for the explanation of gene action conditioning the expression of yield.

The estimate of the genetic variance of the (Jarvis x Indian Chief) F_2 is considerably greater than any of the other estimates. In fact, the estimates of the male component for this population is the highest estimate obtained to date from populations involving these varieties. This suggests that a 20% increase in yield is possible by selecting and intercrossing the superior 5% of the (Jarvis x Indian Chief) F_2

progenies. The relatively high genetic variance and mean yield of this population provides indications that such material may have potential value that has not been exploited in the breeding programs.

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1. Brown spot resistance in corn.

Individual inbred, F_1, F_2, B_1 and B_2, corn plants were inoculated with brown spot (Physoderma maydis Miyabe) and rated for disease symptoms in three environments (i.e., one location in 1956 and two locations in 1957). Double cross plants were also grown and rated.

Three groups were studied. Group 06 consisted of six inbreds and all possible sub-populations (15 F_1, F_2, B_1 and B_2 combinations). Group 08 consisted of eight inbreds (six common to group 06) and all possible sub-populations (28 F_1, F_2, B_1 and B_2 combinations). Group 11 consisted of eleven inbreds (six common to group 08 and four common to both 06 and 08) and all possible F_1's.

The following mean number of plants were observed for each combination in each indicated sub-population in each group:

Group	Inbreds	F_1	F_2	B_1	B_2
Group 06	83	92	166	87	88
Group 08	61	64	123	62	62
Group 11	80	87	-	-	-

For example in group 06, 83 plants were rated of each of the six inbreds, and 92 F_1 plants were rated of each of the 15 possible F_1's.

The following conclusions were drawn:

1) F_1 plants were found to be approximately 13 percent more susceptible than inbred plants when compared on the same rating scale.

2) In 98 comparisons of F_1's with inbred parents, ten were more resistant than either inbred parent and 43 were more susceptible.

3) Significant and positive correlations were found between mid-parent and F_1 means (.7526, .4214 and .5711).

4) Significant and positive correlations were found between inbred means and "general inbred means" in two groups (.8665 and .6551) and nonsignificant but positive in a third group (.5274). "General inbred mean" is mean performance of an inbred in F_1 crosses.

5) Predicted double cross performance was correlated with actual performance. Three prediction methods were used: Jenkins' methods B and C and inbred method E. Method C gave the highest correlations and inbred method E, in general, gave the poorest.

6) Components of variance were estimated from F_1 data in diallel cross analysis. General combining ability was found to be approximately twice the size of specific combining ability in two groups and equal in size in a third group. Additive variance (assuming no epistasis) was found to exceed dominance variance by 1.60, 4.68 and 5.38 times in three groups, respectively. Partial dominance was indicated in two groups and over dominance in a third group. The diallel procedure was used as developed by Matzinger and Kempthorne (Genetics 41: 822-833. 1956). The inbred lines in each group were not random lines from a random mating population, an assumption required by the analysis. It seemed worthwhile, however, to complete the analysis and to interpret the estimates with caution.

7) Constant parent regression analysis as proposed by Hull gave results indicating partial dominance.

8) Heritabilities estimated from F_2 and backcross data ranged up to 66.8 percent; however, only 60 percent of the estimates were positive. Mean heritability was approximately 21 percent when the negative estimates were assumed to be zero.

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1. Temperature mutant.

A new allele of the st gene has been found, which manifests its mutant effect only in the endosperm. This allele, designated st^e,

[1]Operated by Union Carbide Corporation for the United States Atomic Energy Commission.

shows dominance over st. When st^e/st^e plants are grown in the field in the summer and selfed, every kernel shows the mutant phenotype, i.e., scarring and variegation for those endosperm markers that are present in the heterozygous condition. However, when sib plants are grown in the greenhouse in the winter, the kernels produced are completely normal in phenotype. If these normal appearing kernels are planted in the field the following summer, the extreme mutant phenotype is again expressed. Plants homozygous for st^e were grown in a light chamber that simulated the long day conditions of the field (16 hr. day) and the low temperature of the greenhouse (70°F), to distinguish between an effect of temperature and length of day. The kernels produced were completely normal. A sib plant was grown in the light chamber under the same conditions except that, after pollination, a heating pad was wrapped around the ear shoot, which raised the daytime temperature in that region of the plant to approximately 90°F. The progeny kernels of this plant showed the mutant phenotype. These experiments indicate that this allele is temperature sensitive with the mutant phenotype expressed only at the high temperatures.

2. A new mutable allele at the c locus.

In recent years (M.N.L. 30) we have studied a spontaneously occurring mutational system at the c locus. This highly mutable recessive gene, c^m, mutates to both C and to a stable c. The mutations occur at many stages in the development of the plant, in the sporophyte and gametophyte, as well as in the endosperm. The size of the mutated areas varies from only a few cells on a kernel to large sectors on the ear, which include a large number of kernels. Mutations to c are about four times as frequent as those to C. The germinal changes to both C and c are completely stable in subsequent crosses. The mutations are not associated with chromosomal aberrations. No aberrations are found in the progeny of mutated kernels and there is an absence of variegation within the mutated areas on the kernels for either C itself or any other markers more proximally placed on the short arm of chromosome 9. Linkage relationships indicate that the mutability of c^m is autonomously controlled. It is completely independent of the Ac-Ds system.

The c^m gene is stable in the zygote. This condition persists until some time during ontogeny when the gene becomes unstable and free to mutate. At fertilization, those genes in the zygotes that had not as yet mutated to either C or to the stable c revert to the stable condition and the cycle is repeated. However, the unstable condition persists in the endosperm resulting in frequent somatic mutations.

Three states of the c^m gene are found regarding the stage in ontogeny at which time the gene becomes unstable.

A. A late state where mutations occur only after fertilization.

B. An intermediate state where the $\underline{c}^m$ gene becomes unstable some time around meiosis. Up to about 10% of the kernels in the colored class are self-colored, occurring singly on the ears.

C. An early state where this gene becomes unstable in the young sporophyte. While the majority of the colored kernels on such ears are self-colored, arising in sectors, both singly occurring self-colored kernels and variegated kernels are found indicating late mutations of genes that had not mutated earlier.

Of the three, the late mutating stage is the most stable showing only infrequent shifts to one of the other states.

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1. Segregation absence.

An aberrant of C 103 with darker leaf color and without the typical faint longitudinal striping common in sections of this state with this inbred is now known as Pa C 103 g (g for green). In 1956, in an extremely small population, a few plants had the upper leaves failing to unroll from around the tassel. The single-cross C 103 x Pa C 103g in 1956 and 1957 exhibited a small amount of vigor, but this vigor in no way approached expected, probably eliminating the possibility of an outcross.

The single-cross, F_2, and BC_1 generations in both directions (with reciprocals) were hand planted in unthinned observation populations of from 400 to 600 individuals at Hershey (Pa.) in 1957 along with the two lines. Observations were periodic until after silking in this dry year.

Pedigree	Leaf Observations
C 103	100% light green color, slight longitudinal striping
Pa C 103g	100% dark green color, striping absent
C 103 x Pa C 103g	100% similar to Pa C 103g
Pa C 103g x C 103	100% similar to Pa C 103g

Pedigree	Leaf Observations
(C 103 x Pa C 103g) selfed once	100% similar to Pa C 103g
(Pa C 103g x C 103) selfed once	100% similar to Pa C 103g
(C 103 x Pa C 103g)C 103	100% similar to Pa C 103g
C 103 (C 103 x Pa C 103g)	100% similar to Pa C 103g
(C 103 x Pa C 103g)Pa C 103g	100% similar to Pa C 103g
Pa C 103g (C 103 x Pa C 103g)	100% similar to Pa C 103g

It has been suggested for numerous reasons that the leaf color and striping of C 103 in this area is possibly due to low magnesium nutrition. Due to the location of this observation area on a subsoil area with better magnesium supply, it is suggested that the results are not conclusive.

2. Preliminary tests to detect non-allelic gene interaction (Epistasis) in four-way and eight-way hybrids.

Using the method L. F. Bauman described at the 1956 Annual Meeting of the American Society of Agronomy in which the deviation of a single-cross X tester from the average of the two inbreds X tester is a measure of the amount of epistasis present in the single-cross, appropriate crosses were made with material of current commercial interest in this state.

Two tester inbreds (A 158 and W 153R) were used with the single-crosses (Pa 54 x Pa 11), (Pa 32 x Pa 33), (Ind Wf 9 x Oh 51A), (Ill A x W 22), and (Oh 43 x Oh 45); the four-way hybrids Pa 444 (Pa 54 x Pa 11) (Pa 32 x Pa 33), Pa 602 (Ind Wf 9 x Oh 51A) (Ill A x W 22), and Oh W 64 (Ind Wf 9 x Oh 51A) (Oh 43 x Oh 45); and the eight-way hybrids (Pa 444 x Pa 602) and (Pa 444 x Oh W 64). Testing was at three locations representing extremes in soil and ecology within the appropriate maturity range in this state. The 1957 testing year was extremely dry on two of the three locations.

Tester parent was found to exhibit a profound effect on the measurement of epistatic deviations. Major location effects both as to extent and direction of the epistatic deviation were found in some cases; in others the epistatic deviations were remarkably uniform in size and direction from location to location. Every four-way and eight-way hybrid showed significant epistatic deviation for one or more characters with one or both testers. The characters and hybrids in combined total exhibited significant epistatic deviations in 25% of the four-way hybrid cases and 69% of the eight-way hybrid cases. Disregarding direction, the extent of the average epistatic deviation was uniformly greater with fewer lines involved, with the exception of ear length. (See table 1 on following page.)

G. W. Gorsline

Table 1. Summary of epistatic deviations at Centre Hall, Mifflenburg, and Towanda during the 1957 season in Pennsylvania.

	Yield	% H_2O	Plant Height	Ear Node Height	Ear Height Ratio	Ear Length	Ear Diameter	Ear Length-Diameter Ratio
Tester Parent A 158								
Pa 444	- .8	+ .8	- 1.0	+ .6	+ 2.2*	- .10	+ .02	- .12
Pa 602	+ 6.5*	- .3	- 1.1	- 2.8*	- 2.0*	- .02	+ .02	- .02
Oh W 64	.0	+ .6	+ 1.2	+ 2.0*	+ 1.4	- .07	- .02	+ .01
Pa 444 x Pa 602	+ 1.7	- .2	+ .8	+ .2	- .1	+ .08	- .01	+ .06
Pa 444 x Oh W 64	- 1.4	- .9*	- .7	- 2.6*	- 3.1*	- .30*	- .02	- .16*
Tester Parent W 153R								
Pa 444	- 4.6	+ .5	+ .2	+ .2	+ 1.1	- .02	- .02	+ .02
Pa 602	+ 1.2	- .4	+ 1.4	+ .1	+ 1.0	+ .03	- .03*	+ .08
Oh W 64	- 2.4	+ .3	+ .2	.0	+ .2	+ .06	+ .02	+ .04
Pa 444 x Pa 602	+ 1.8	+ 1.2*	- 3.7*	- 2.0*	- 2.2*	+ .08	+ .03*	- .02
Pa 444 x Oh W 64	- 1.3	- 1.1*	.0	+ .3	- .3	- .26*	- .03*	- .08
Error Factors								
L.S.D. (.05)	4.9	.9	2.4	1.9	2.0	.22	.03	.13
H.S.D. (.05)	8.9	1.6	4.5	3.4	3.7	.40	.06	.24
Average Weighted Deviations disregarding signs								
Four-Way Hybrids	2.61	1.05	1.58	1.62	2.80	.105	.042	.108
Eight-Way Hybrids	1.55	.85	1.30	1.28	1.42	.180	.022	.085
Difference in Favor of Four-Way's	1.06	.20	.28	.34	1.38	.075	.020	.023

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1. Corn breeding report from the Philippines.[1]

a. Philippine Hybrids - Four locally developed hybrids, three yellow flint and one white flint were approved by the Philippine Seed Board for distribution to Filipino farmers in 1956. These hybrids outyielded significantly the best open-pollinated variety in the country by about 30% or yielding on the average 60 to 70 cavans per hectare. Last year two farmer cooperators were approved by the Seed Board to produce commercially hybrid corn seed for distribution.

Five new outstanding experimental yellow flint hybrids will be recommended soon to the Philippine Seed Board. The results of four seasons of regional tests indicated a highly significant difference when compared with the best open-pollinated yellow flint variety (College Yellow Flint).

b. The Search for Downy Mildew Resistant Lines - Downy mildew, a fungus disease caused by two species of Sclerospora of the family Peronosporaceae is causing serious damage to corn crops in some regions of the Philippines. It decreases considerably corn yields and in many cases virtually wipes out corn fields. The morphological characteristics and pathogenecity of the organism has been studied thoroughly but no successful control measure has been found effective in combating the disease.

All of the available inbred lines, single crosses and double crosses of yellow and white flint corn of the College of Agriculture were tested for resistance to downy mildew (Sclerospora philippinensis Weston for Luzon Island and S. spontanea Weston for the Visayan Islands) in the wet season of 1956. Artificial inoculation was done to supplement the natural infestation of the fungus. Two replications were used.

Disease observations were arbitrarily classified into seven groups, namely:

Group	Description	Per cent infection
I	Totally free	0
II	Very slightly infected	1 - 9
III	Slightly infected	10 - 29

[1] The corn breeding program is being undertaken with the assistance of the Cornell visiting professor at the College of Agriculture, University of the Philippines.

Group	Description	Per cent infection
IV	Moderately infected	30 - 69
V	Highly infected	70 - 89
VI	Very highly infected	90 - 99
VII	Totally infected	100

Six inbred lines (five white flint inbreds and one yellow flint inbred) were found totally free from downy mildew infection. Similar results were obtained for two seasons. It seems that "near immunity" is easier to get among white-endosperm lines than among yellow-endosperm inbred lines.

The test for specific combining ability of the resistant lines is the next step to be undertaken. This season these inbred lines will be crossed with the high combining parental single crosses that are involved in the Philippine hybrids.

Crosses between resistant and susceptible inbred lines were being made this season to study the mode of inheritance of resistance to downy mildew.

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1. Characterization of sterility-inducing cytoplasms.

The WF9 genotype has been transferred by backcrossing to 12 separate isolations of sterile cytoplasm. WF9 is sterile, or nearly so, in all of these cytoplasms. Each type of sterile WF9 was crossed to 4 inbred lines: BH2, CE1, F5DD1 and C25-13. Pollen fertility of these F_1 hybrids at Johnston, Iowa in 1957 is shown in the table on the next page.

On the basis of these results it would seem that each of the new sources of sterile cytoplasm is identical either to the USDA or to the Texas type of sterile cytoplasm. It is possible, of course, that crosses with some other inbred may differentiate some of these cytoplasms from the type with which they now seem to be identical. If they cannot be so differentiated, however, it would seem that (1) only two possible types of "mutation" of normal cytoplasm to a sterility inducing type have been found, among 12 separate isolations, or (2) the two types of sterile cytoplasm trace back to two separate introductions of foreign cytoplasm (as from closely related species) into the maize genotype.

Cytoplasm	Male Parent				Origin of Cytoplasm
	BH2	CE1	F5DD1	C25-13	
	Pollen Fertility				
USDA (Jones)	F*	F	S	S	Teopod x iojap
Texas (Jones)	F	S	F	S	Golden June
Texas (Rogers)	F	S	F	S	Golden June
No. 4	F	F	S	S	ERF Composite (Pioneer)
No. 5	F	F	S	S	Honey June
No. 6	-**	F	S	S	BRC Composite (Pioneer)
No. 7	F	F	S	S	BRC
No. 8	F	F	S	S	BRC
No. 9	-	S	F	-	BRC
No. 10	F	F	S	S	BRC
No. 11	-	S	F	-	BRC
No. 12	F	S	F	S	BRC
No. 13	-	F	S	-	BRC

*F - fertile, S - sterile
** Cross not grown

Donald N. Duvick

2. An extreme nuclear-cytoplasmic interaction.

In a set of some twenty pop corn F_1 hybrids grown in yield test in Ohio in 1955 it was observed that each of two hybrids resulted in zero yield while the average yield of the remaining hybrids in the test was approximately 65 bushels per acre. To those accustomed to expect heterosis in F_1 crosses of unrelated lines, this is an exceptional phenomenon. These two crosses had one inbred line (P2-5-1-X) in common and in both crosses P2-5-1-X was used as the maternal parent. The following year P2-5-1-X was crossed reciprocally with four unrelated lines, two of which were dents and two pops. The resulting hybrids were compared in observation plantings in 1957. In all cases, hybrids involving P2-5-1-X as a seed parent were completely devoid of vigor, i.e., they exhibited less vigor than the weaker of the inbred parents; the leaves were characterized by an abnormal striping (resembling somewhat certain virus effects) and most of the plants were partially pollen sterile. Reciprocal crosses, on the other hand, exhibited normal hybrid vigor and phenotype. Thus, on the basis of these limited data, it would seem that P2-5-1-X is characterized by cytoplasm which is highly incompatible with nuclei of the strains with which it has been tested. It is, therefore, another example of cytoplasmic inheritance but one with drastic

phenotypic effect. It is interesting to note that P2-5-1-X itself shows some leaf striping abnormality but it is much less pronounced in the line than in its crosses in which P2-5-1-X is used as seed parent. P2-5-1-X possesses as much vigor as might be expected from most relatively homozygous lines.

Several similar cases of maternally inherited loss of vigor characterized by similar phenotypic alterations have been found in WF9, $WF9^S$, $WF9^T$ and in several hybrids or segregating populations of hybrids of WF9, $WF9^S$ and $WF9^T$ with other inbreds. Some of these types have been extremely variable in expression, but it has not yet been possible to determine whether this variability is due to a "mutability" of the cytoplasm or whether it is due to segregation of "resistant" and "susceptible" genotypes, with respect to the cytoplasm. One strain of this type has been backcrossed, as male, to a normal appearing strain of WF9 for two generations; the backcrossed plants as yet show no sign of the vigor reduction or striping characteristic of the male parent.

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1. Embryo transplantation in corn.

Hall reported in Hereditas (1954) that crossability between wheat and rye could be increased if the wheat plants used for the crosses grew from embryos which were transplanted onto rye endosperm. The wheat transplanted onto rye endosperm and pollinated with rye pollen produced about 5 times as many hybrid kernels as the wheat transplanted on wheat endosperm. This result encouraged me to investigate the effect of embryo transplantation on crossability between a dent-sterile popcorn and a dent corn inbred. The relative ease of controlled pollination, the large number of seeds on a single ear of corn, the large seed and ease in grafting would make this investigation easier than the wheat and rye experiment.

A technique was developed for transplanting an embryo from one seed to another. The seed is soaked in water until the embryo and the endosperm can be separated with the least damage. The length of time of soaking depends on the corn variety. In this experiment, 149-5AA was soaked for 15 hours and L317 for 12 hours. Corn starch paste, a rubber band, and a splint were used to hold the grafted seed together. The grafted seeds were planted in sterilized soil in small pots in the greenhouse within one hour after grafting.

L317, a dent inbred, and 149-5AA, a dent-sterile popcorn, were used. The former is ga/ga in genotype and the latter Ga^s/Ga^s. None or few seeds are produced when 149-5AA is used as a seed parent and pollinated by L 317. Full seed set results when L317 as the female is pollinated by 149-5AA.

The following transplantations were made:

1) L317 grafted on 149-5AA endosperm (D/P)
2) 149-5AA grafted on 149-5AA endosperm (P/P)
3) 149-5AA grafted on L317 endosperm (P/D)

For ease in further discussion the symbols listed above will be used to refer to the various grafted types.

The rate of germination in grafted seeds is slower than non-grafted seeds. The grafted seeds germinated within 7-10 days while the non-grafted germinated 3-4 days after planting.

The P/P grafts have a high percentage of viable plants while the P/D grafts have a very low percentage, indicating a certain kind of inhibition or incompatability between the embryo and the endosperm of the two different varieties. The inhibition is only in one direction because the D/P group showed a much higher percentage of viable plants (See table 1). The cause of the unilateral inhibition is not yet known.

It is interesting to note that the dent-sterile popcorn which will not set seed with dent corn pollen produces few viable plants when its embryos are grafted onto dent corn endosperms. Whether this inhibition has any relationship to the constitution of the plants at the Ga^s/ga locus is a matter for speculation. Experiments are in progress to attempt to gain evidence on this point.

Table 1. Viable plants resulting from grafted seeds.

Kind of Grafting	No. of Grafted Seeds	Viable Plants	% of Viable Plants
D/P	36	21	58.3
D/P	30	14	46.7
D/P	45	25	55.5
D/P	45	28	62.2
P/P	90	52	57.8
P/P	105	99	94.3
P/D	100	6	6.0
P/D	108	8	7.4

Table 3. Number of seed set in the crosses specified below:

Date of Pollination (August)	Pollen Parent											
	L 317 grafted on 149-5AA						L 317					
	Female Parent						Female Parent					
	149-5AA grafted on 149-5AA		149-5AA		149-5AA grafted on L317		149-5AA grafted on 149-5AA		149-5AA		149-5AA grafted on L317	
	No. X's	Total Seed Set	No. X's	Total Seed Set	No. X's	Total Seed Set	No. X's	Total Seed Set	No. X's	Total Seed Set	No. X's	Total Seed Set
15	4	24	5	1	-	-	6	11	5	4	-	-
16	4	2	3	11	-	-	2	9	3	15	-	-
20	1	7	-	-	-	-	1	13	-	-	-	-
21	1	28	4	120	-	-	1	9	3	76	-	-
22	2	9	6	90	-	-	2	21	3	28	-	-
23	2	88	3	75	-	-	2	51	3	149	-	-
25	3	46	2	11	1	15	3	25	2	17	1	8
26	2	55	3	105	2	7	2	70	3	106	1	6
27	-	-	1	15	-	-	-	-	1	3	-	-
29	-	-	-	-	1	4	-	-	-	-	1	15
Total	19	259	27	428	4	26	19	209	23	398	3	29
Mean		13.6		15.8		6.5		11		17.3		9.7

Another interesting observation is the height of plants from the P/P and P/D grafts. The rate of growth of the two types was significantly different from early seedling stage until before maturity. However, the difference is not significant at maturity (See Table 2). The few P/D grafts that grew to maturity showed a much slower early growth rate than the P/P grafts, indicating possibly a lingering of the effect responsible for the low rate of germination. At seedling stage, the P/D grafts were about one-half of the height of P/P grafts and about the same height at maturity. Thus the factor responsible for the slow early growth of plants from the P/D grafts does not affect the later stages.

Table 2. Plant heights in cms. of P/P and P/D at various time intervals after plantings.

Number of Days After Planting	P/D	P/P	t-test
12	5.55	13.40	10.97**
19	16.10	34.19	8.87**
33	40.25	64.75	6.12**
47	50.75	75.25	6.45**
58	79.25	105.87	6.85**
67	109.87	116.25	1.91-
86	160.75	163.62	.52-

\- not significant at 5% level.
** significant at 1% level.

Crosses were made using D/P (L317 on 149-5AA) and non-grafted L317 as pollen parents on grafted and ungrafted 149-5AA. Equal numbers of crosses of these pollen parents on 149-5AA were made at the same time to eliminate environmental influence in comparing the effect of the two pollen parents. The total average difference is not significant in any cross (See Table 3). Thus, the embryo transplantation didn't result in any increase in crossability between 149-5AA and L317.

Virgilio R. Carangal

2. The effect of Pt on tassel development.

In reporting on Pt (A.J.B., 1954, Vol. 41), it was remarked that Pt surprisingly did not apparently affect tassel development in spite of its extreme effect on ear development. Since that time it has been found that in certain genetic backgrounds, the tassels of Pt plants may be drastically altered. The commonest effect within a spikelet is a proliferation of pistillate tissue produced by the meristem cutting off new rings of tissue successively at its periphery. Each ring may

produce a silk although not necessarily. This is analogous to the commonest effect produced in Pt ears.

When both tassel and ear are affected, there is general agreement between the severity of the effect on both. And when the phenotype of the ear is "inhibited" as is the case with many Pt/Pt plants, then the tassel also shows some degree of inhibition, i.e. restricted spikelet development.

The genetic background in which the effects of Pt are extended to the tassel has not been characterized although it is probably not complex. The best source was the linkage tester for Chr. 8 carrying i, v_{16}, ms_8 which was obtained from the Coop (50-55).

Oliver E. Nelson, Jr.

3. Double mutants in the chromosomal vicinity of a mutable locus.

The mutable allele a^{Pm} produces a high rate of mutation at the A_1 locus (News Letter 30: 111). This allele mutates both somatically and germinally so that deep, pale, light pale and colorless levels of anthocyanin pigmentation are expressed in the aleurone tissue. The alleles produced by germinal mutation vary in stability from stable (a^{P5}, no mutants in 30,000 tested gametes) to moderate stability (a^{b1}, 1 mutant per 13,000 gametes) to moderate mutability (A^1, 1 mutant per 4,000 gametes) to instability as marked as that in the parent allele.

Four of these new deep alleles, six new pale alleles, and four of the colorless alleles were examined for rates of mutation to stable alleles giving different levels of aleurone pigmentation. The results are given in Table 1. Two cases of coincident mutations at two loci occurred among the 158 mutants. In these cases the deep (A^4) and the pale (a^{a1}) alleles mutated to alleles expressing the colorless level while the adjacent dominant shrunken-2 allele assumed the recessive form. These mutants will be designated $\frac{1}{a\ sh_2}$ and $\frac{2}{a\ sh_2}$ respectively. One of these mutants, $\frac{1}{a\ sh_2}$, has been tested further and has been shown to behave in a manner similar to that of the a-X1 mutant of Stadler and Roman.

Although there is no visible indication of pollen abnormality in plants heterozygous for the double mutant ($\frac{a\ sh_2}{a\ sh_2}/\frac{1}{}$), the transmission of the microgametophyte carrying $\frac{1}{a\ sh_2}$ is reduced. Table 2 shows a good deal of variation in the degree of transmission among the different cultures. The average per cent of normal transmission for these five cultures is 44.

Table 1. Rates of mutation in alleles derived from $\underline{a}^{Pm}$.

Allele tested	Gametes tested	Stable Mutants	Rate of Mutation
a^{P5}	30,538	0	-
a^{5}	29,527	0	-
a^{P1}	16,152	0	-
A^{2}	4,007	0	-
a^{P2}	2,096	0	-
a^{4}	24,010	1	1 per 24,010
a^{P3}	42,392	2	1 per 21,196
a^{b1}	26,540	2	1 per 13,270
A^{1}	36,379	8	1 per 4,547
a^{b2}	15,103	5	1 per 3,051
A^{4}	172,146	77	1 per 2,238
A^{R}	14,470	7	1 per 2,064
a^{P4}	22,525	15	1 per 1,501
a^{a1}	36,762	41	1 per 897

Table 2. Male transmission of $\frac{1}{\underline{a}\ \underline{sh_2}}$ in competition with $\underline{a}^{b1}\ \underline{Sh_2}$ as measured by percentage of normal transmission.

Cross	Total kernels	Sh_2	sh_2	% of sh_2	% of normal transmission
$A^{d}sh_2/A^{d}sh_2 \times a^{b1}Sh_2/\frac{1}{a\ sh_2}$	1722	1343	379	22	28
$A\ sh_2/A\ sh_2 \times a^{b1}Sh_2/\frac{1}{a\ sh_2}$	911	679	232	26	34
$A\ sh_2/A\ sh_2 \times a^{b1}Sh_2/\frac{1}{a\ sh_2}$	1128	762	366	32	48
$a\ sh_2/a\ sh_2 \times a^{b1}Sh_2/\frac{1}{a\ sh_2}$	3048	2667	381	12	14
$a\ sh_2/a\ sh_2 \times a^{b1}Sh_2/\frac{1}{a\ sh_2}$	1998	1634	364	18	23

Transmission of $\frac{1}{a\ sh_2}$ through the megagametophyte was found to be normal. Data on this point are available by making use of the inability of the double mutant to dot in the presence of the gene Dt. Five ears resulting from the cross $\frac{1}{a\ sh_2}/a\ sh_2 dt/dt \times a^{b_1} Sh_2/a^{b_1} Sh_2 Dt/Dt$ produced 1084 kernels, 402 of which had dots. Independent data from closely related material show that only 70% of the endosperms of the constitution $a\ sh_2/a\ sh_2/a^{b_1} Sh_2$, Dt/dt/dt actually dot. If the 402 dotted kernels make up 70% of the $a\ sh_2$ gametes, then the total number of kernels carrying $a\ sh_2$ is 574. Hence the $a\ sh_2/a\ sh_2/a^{b_1} Sh_2$, Dt/dt/dt endosperms make up 52.8% of the total, and the $\frac{1}{a\ sh_2}$ carrying gametes make up 47.2% of the total functional gametes.

The similarities between $\frac{1}{a\ sh_2}$ and a-X1 may be summarized as follows:

1) Both have reduced male transmission.

2) Different stocks give rise to wide differences in degree of reduction of male transmission.

3) Both have normal egg transmission.

4) Both are unable to dot in the presence of Dt.

5) In both cases homozygotes are lethal.

6) The A_1 and Sh_2 loci are included in both cases.

The question arises whether these mutations are actually deficiencies as in the case of a-X1 or whether they are regions inactivated by the adjacent mutable locus. No conclusive evidence on this point is available, but small scale tests have failed to reveal reverse mutations at either the A_1 or Sh_2 locus.

Double mutants of this type are expected under the following hypothetical model for the structure of a^{Pm}. In this scheme the components of a^{Pm} are: β, the deep pigment producing factor, α, the unit responsible for pale pigmentation, P^b, the dominant brown pericarp factor, and M, the mutability factor. These components are arranged in the following order:

----Centromere-----β-----M-----α-----P^b-----Sh_2-----.

It is assumed that the mutability factor involved here, like others more thoroughly studied, is capable of inhibition of adjacent loci, and that this capacity to inhibit may spread along the chromosome in either direction. Further it is assumed that when two genes are inhibited in

this manner, all loci between them on the chromosome will also be inactivated.

The possible effects that various types of inhibition by M might produce are:

Inactivation of	Mutant Produced	Frequency of this Mutation
M	Stable, pale, dominant brown pericarp, Sh_2	Frequent
β M	Stable, pale, dominant brown pericarp, Sh_2	
M α	Stable, deep, dominant brown pericarp, Sh_2	No occurrence. (In very similar material, M. G. Nuffer has found this type of mutant which, however, is somewhat mutable.)
M α P^b	Stable, deep red pericarp, Sh_2	Nine cases
M α P^b Sh_2	Stable, deep, red pericarp, sh_2	Several deep sh_2 kernels arose in crosses of a^{pm} sh_2/a sh_2 x a sh_2/a sh_2 but were discarded as probable contaminations. (No analysis of pericarp constitution.)
β M α	Stable, colorless, dominant brown pericarp, Sh_2	Seven cases
β M α P^b	Stable, colorless, recessive brown pericarp, Sh_2	Common
β M α P^b Sh_2	Stable, colorless, recessive brown pericarp, sh_2	Two cases (Not yet analyzed for pericarp constitution.)

Critical types of mutation which could not be explained by this hypothesis are:

Mutant Type	Requires Inactivation of	Intermediate Components Unaffected
Stable, pale, recessive brown pericarp, Sh_2	β M - P^b	α
Stable, deep, dominant brown pericarp, sh_2	M α - Sh_2	P^b
Stable, pale, dominant brown pericarp, sh_2	β M - - Sh_2	α P^b
Stable, pale, recessive brown pericarp, sh_2	β M - P^b Sh_2	α
Stable, colorless, dominant brown pericarp, sh_2	β M α - sh_2	P^b

None of these critical types have been found as yet, but an extensive program for their detection is underway.

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1. Competitive growth of pollen tubes in maize.

In this preliminary investigation the possibility was considered whether there is a relation between combining ability and pollen tube growth.

The experimental procedure was to mix equal quantities of pollen of yellow and white seeded inbreds obtained from 15-20 plants in each case and to use this mixture to pollinate different white seeded inbreds and the white seeded variety Potchefstroom Pearl. The sources of pollen were the well known American inbreds K 64, 33-16 and Hy and the South African inbred A 413, all known for their good combining ability. In addition five local yellow inbreds and a white inbred P 697 all of unknown combining ability, and the white inbreds F60 and E58 of known weak combining ability were used as pollen parents. The maternal parents were the inbreds K64, 33-16, E58 and F60 all of known combining ability and 20 other white inbreds of unknown combining ability. Pollen mixtures of the good white combiner K64 with different yellow

inbreds of unknown combining ability or with the yellow good combiner Hy were used to pollinate the white maternal parents named above. A consistent and significant excess of white seed was obtained throughout where equal numbers of yellow and white kernels were expected. Similar results were observed where Hy (yellow seeded) was used in pollen mixtures with the weak combiners F60 and E58, but in these cases there were consistent and significant excesses of yellow seed. The combination however of Hy with P697 using the same pollen sample on 7 different white inbreds in four cases yielded a distinct superiority of Hy and in three cases a slight superiority of P697 depending on the maternal parent used in the crosses.

In crosses where the yellow inbreds Hy and A413, known for their superior combining ability, were used in pollen mixtures with the variety Potchefstroom Pearl, the varietal pollen proved to be significantly superior as was reflected by the far greater number of white seeds formed. Since varietal pollen is composed of a great diversity of genetic types, there was an opportunity for gametic selection which could explain its apparent superiority.

Where the weak white combiners F60 and E58 were used in pollen mixtures with the yellow inbreds of unknown combining ability, some combinations gave a significant preponderance of white seeds and other combinations of preponderance of yellow seed with similar maternal parents. This would suggest that F60 and E58 are superior to some of these yellow inbreds and inferior to the others tested.

If unequal pollen mixtures had caused the deviations from an expected equality of the numbers of yellow and white seeds a consistency in the results would have been expected when the same sample of pollen was used in different crosses. A wide variation, however, was obtained, differing characteristically according to the maternal inbred used indicating that a deficiency in the pollen mixture could not have been the sole cause, and that other factors are involved.

The good white combiner 33-16 reacts the same as K64 when used as the maternal parent, but shows a striking exception when used as a pollen parent. Six different pollen mixtures of 33-16 and yellow inbreds of good, weak and unknown combining ability used to pollinate 18 different white inbreds yielded a consistent and significant deficiency of white seed. On these ears the ratio of yellow to white differed widely from equality, ranging from 3:1 to as much as 32:1. This could not have been due to pollen sterility since in the absence of competition with pollen from other sources 33-16 pollen produced well filled ears. Josephson and Jenkins (J. of Agron 40: 267-274, 1948) reported that 33-16, when used in crosses, transmitted male sterility to its progeny maternally through its cytoplasm but apparently not through its pollen. It seems likely that 33-16 cytoplasm present in its pollen tubes is responsible for the apparent deficient growth of such pollen tubes as is indicated by the deficiency of white seed in the crosses

reported above. Since seed of reciprocal crosses is available it should be possible to test the genic or cytoplasmic nature of this phenomenon.

Although the results suggest that there may be a relation between combining ability and pollen tube growth, final conclusions must await the results of actual yield tests of the crosses made. Such results should become available during the present season. If such a relation exists it should be a great help in the evaluation of inbred lines for combining ability on an extensive scale and thus help materially to speed up the Hybrid Maize Program.

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1. Effects of gibberellic acid on maize plants homozygous for the recessive gene (la).

A compound of interest to both geneticists and physiologists is gibberellic acid. Reports indicate it differs physiologically from most other auxins in that it is usually much less active in assays based on response of isolated plant parts, but stimulates growth of intact plants much more than most other auxins, as evidenced by increases in height, fresh weight, and dry weight. It has been shown to produce responses on known gene controlled auxin characteristics in maize. The present study was undertaken to determine if gibberellic acid would affect a genetically controlled auxin factor where bending of the stem from perpendicular to horizontal is concerned. The gene in question (la in maize), when in the homozygous condition causes an auxin differential between sides of the stem resulting in a horizontal growth form. The redistribution of auxins in lazy stems is reversed from normal horizontal stems, so that about 55 percent of the auxin moves in the upper half (Shafer, J., Botanical Gazette 101: 68 (1939).

Gibberellic acid was applied by three types of application and at three stages of growth. (1) a .5 percent gibberellic acid - lanolin paste was applied to the cotyledonary node and coleoptile of the embryo at the time the coleoptile broke through the pericarp during germination, (2) an aqueous solution of gibberellic acid at the concentration of .01, .1 and 1.0 ug. was injected into the stem by use of an ordinary hypodermic needle or sprayed on the leaf surface by using a small atomizer to previously untreated plants beginning at the fifth leaf stage of growth and repeating treatments at weekly intervals for a four week period, (3) a .5 percent gibberellic acid-lanolin paste was applied to previously untreated plants on the under side of the curvature as soon as bending of the internodes started. This was done by removing a

small section of the leaf sheath and applying the paste directly to the base of the internode. Check plants were maintained for all trials. The study showed that gibberellic acid would not overcome the unequal balance of auxin concentration at the base of internodes just above the soil surface in lazy corn, even though the acid was applied to the side having the lower natural auxin concentration during the bending stage. A possible explanation of this may lie in the rapid lateral transport of gibberellic acid to the higher auxin side. The basis for this explanation would have to be further investigated.

It was shown, however, that leaf and internode tissue of lazy corn elongate excessively when gibberellic acid is applied. There was indication that very small amounts of the acid, .04 ug./plant are as effective in bringing this elongation about as are higher concentrations, 4 ug./plant, and that there may not be an inhibitory effect by higher concentrations as is often evidenced by many auxins.

Treatments numbers 1 and 2 brought about excessive elongation of those internodes in corn that normally remain short and below the soil surface. Normally the second through the fourth or fifth internodes fail to elongate sufficiently to cause this portion of the corn stem to be above the soil surface. It was found that all internodes above the second in treated plants had elongated. Some were found to be eight or nine times the normal length.

Measurements were made of several internodes. Table 1 presents the analysis of data on measurements of the fourth internode following injection or spray treatment.

Table 1. Length of the fourth internode in cm. following treatment with gibberellic acid by injection or spray. Treatments started at fifth leaf stage and repeated at weekly intervals on same plant for 4 weeks.

Treatment	Concentration in ug./plant/ treatment	Total amount applied to each plant	Length of 4th Internode in cm. Plants 1	2	3	S	Mean
Injection	0.01	0.04	1.4	1.3	2.5	5.2	1.73
	0.1	0.4	1.5	3.5	2.5	7.5	2.50
	1.0	4.0	2.5	3.2	5.1	10.8	3.6
Spray	0.01	0.04	4.0	2.6	2.0	8.7	2.87
	0.1	0.4	1.7	2.0	1.2	4.9	1.63
	1.0	4.0	.9	2.3	2.5	5.7	1.90
Check	0	0	1.0	.9	1	2.9	.97

Table 1. Continued.

Analysis of Variance			
Source of Variation	d.f.	s.s	M.S.
Total	20	24.383	
Between treatments	6	13.916	2.319*
Error	14	10.467	.748

*Significant at the .05 level.

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1. Maize-Tripsacum hybrids.

Hybrids between Texas inbred 203 and diploid Tripsacum dactyloides backcrossed to inbred 203 for five generations are under study, and the results obtained thus far are different in certain respects from any yet reported. Two related groups of the hybrid derivatives may be recognized on the ground that the phenotypic differences between them are significant for certain characters. One peculiar feature of both groups is that, in spite of their being fifth generation backcrosses, above 99 percent of the plants are completely pollen sterile and about 90 percent ovule sterile.

Although most of the work done to date is genetical in nature, cytological examinations have been made on about half of the nearly sterile B_3 plants of each group, and every plant examined was found to have an extra chromosome. Many of them also showed a chromatin tie and occasionally other irregularities. The plants of inbred 203 used in the work contained no B-chromosomes, and the Tripsacum had only the usual 18 pairs, characteristic of the diploid forms. Much additional cytological work is needed, but a tentative conclusion that most or all of the nearly sterile plants are 2n+1 is justified.

2. Characters of hybrid derivatives having only inbred 203 in their maize ancestry.

In 1955, 45 B_3 plants which had inbred 203 as their only source of maize ancestry were grown to maturity; in 1956, 290 B_4 plants; in 1957, 84 B_5 plants. Of these 419 plants only three had fertility approaching normal. These three plants produced pollen in abundance, and their ears were approximately filled with grains. However, their pollen,

including that of the S_1 progeny of two of them, was from 25 to 50 percent defective.

Most of the nearly sterile plants have less vigor than inbred 203, but they are strong enough that with only standard nursery care there is little or no danger of losing the stocks. Data have been recorded on 17 characters by which comparisons can be made in all combinations between inbred 203, S_1 progenies of two of the almost normally fertile hybrid derivatives and the two groups of nearly sterile hybrid derivatives. Both the hybrid derivatives and their Tripsacum ancestor are smaller plants than inbred 203, and most of the measurements taken on them result in lower values. But there is a mere possibility that this tendency in the nearly sterile derivatives is simply a component of their general lack of vigor, attributable to the 2n+1 condition rather than to particular genes on the extra chromosome. For the time being, therefore, the data to be presented will be restricted to a few selected characters which would not be expected to respond, as they have done, to a mere decrease in vigor. Before presenting the data, a few notes of explanation are needed on the pedigree numbers in use.

Inbred 203. Isolated about 25 years ago for agronomic use; contains but little genetic variability.

11a and 11b. The two main groups of nearly sterile derivatives of a 203-Tripsacum cross, backcrossed to 203 five times prior to 1957; completely pollen sterile and about 90 percent ovule sterile.

5601. An almost normally fertile sib of 11a; few, if any, of the S_1 plants with an extra chromosome; ears normally filled with grains, but pollen 25 to 50 percent defective.

5602. Similar to 5601, except that it is a sib of 11b.

Nerve indices shown in the tables are numbers of nerves in the leaf blade per inch of width, with the measurements taken to the nearest 1/8 of an inch.

Mean values for three plant characters of Inbred 203 and of two sterile derivatives of inbred 203 x Tripsacum dactyloides (2n), third and fourth backcrosses to inbred 203; all combinations compared.

Pedigree	No. rows alicoles		Leaf length/width		Days to maturity	
	B_3	B_4	B_3	B_4	B_3	B_4
203	6.48**	6.36**	7.65	7.83**	119[1] **	106[1] **
11a	4.38	4.13	7.60	8.97	132 1.9	120 2.0
203	6.48**	6.36**	7.65**	7.83**	119[1] **	106[1] **
11b	4.38	4.18	9.58	9.48	126 0.4	122 0.5

** Differences between means significant at the .01 level.

[1] Age at which all plants of inbred 203 were mature.

Table continued.

Pedigree	No. rows alicoles		Leaf length/width		Days to maturity	
	B_3	B_4	B_3	B_4	B_3	B_4
11a	4.38	4.13	7.60**	8.97*	132*	120**
11b	4.38	4.18	9.58	9.48	126	122

** Differences between means significant at the .01 level.
* Differences between means significant at the .05 level.

Mean values for four plant characters of inbred 203, of two almost normally fertile derivatives of (inbred 203 x Tripsacum dactyloides-2n) x 203_4, and of two nearly sterile derivatives of (inbred 203 x Tripsacum dactyloides-2n) x 203_5.

Pedigree	No. rows alicoles	Leaf length/width	Nerve index	Days to maturity
203	5.96*	7.36	5.41	105**
5601	6.30	7.52	5.59	108
203	5.96	7.36**	5.41*	105
5602	5.81	8.64	5.78	107
203	5.96**	7.36**	5.41**	105**
11a	4.19	10.45	6.98	119
203	5.96**	7.36**	5.41**	105**
11b	3.91	9.52	6.52	110
5601	6.30**	7.52**	5.59	108
5602	5.81	8.64	5.78	107
5601	6.30**	7.52**	5.59**	108**
11a	4.19	10.45	6.98	119
5601	6.30**	7.52**	5.59**	108
11b	3.91	9.52	6.52	110
5602	5.81**	8.64**	5.78**	107**
11a	4.19	10.45	6.98	119
5602	5.81**	8.64	5.78**	107
11b	3.91	9.52	6.52	110
11a	4.19	10.45*	6.98*	119**
11b	3.91	9.52	6.52	110

** Differences between means significant at the .01 level.
* Differences between means significant at the .05 level.

The results shown above are regarded as conclusive evidence that the differences between the 11a, 11b classes and inbred 203 are real. Although no comparable data are given for the Tripsacum parent of these derivatives, it is common knowledge that their deviations from inbred 203, as shown, are consistently in the direction of diploid Tripsacum dactyloides.

Also, the deviations of 5601 and 5602 from inbred 203 are statistically significant for certain characters, but the significance is less pronounced. In all such instances except one, these deviations are again in the direction of Tripsacum. The exception is number of rows of alicoles, 203 vs. 5601, B_5, which is undoubtedly explainable by the known fact that inbred 203 contains a little genetic variation for this character.

3. Occurrence of genes for sugary and white cob among the hybrid derivatives.

The endosperm of inbred 203 is starchy and the cob is red. The endosperm of Tripsacum also is starchy in phenotype, and the rachis might be classed as white (at least without red pigment).

In 1955, one ear of each of 31 multiple-eared B_3 plants of 11a and 11b was outcrossed to homozygous su_1 maize stocks, and five plants distributed among the two groups produced a total of 29 grains classified as starchy and 31 classified as sugary. The two types of grains were extremely difficult to classify, however, because most of them which showed any similarity to sugary had lobes of starch, and many which finally were classified as sugary were primarily starchy with a minute area of sugary endosperm at the apex only one to two millimeters in diameter.

The su pollen applied to six of the 11a and seven of the 11b plants was also pure for white cob. The offspring of six of the 11b plants segregated for white cob, but none of the 11a offspring segregated. In 1957, several hundred F_1 plants resulting from outcrosses of 11a with a white-cob stock were grown, and no white-cob plants were among them. It may be concluded, therefore, that the gene for white cob was present in 11b but not in 11a.

Before making any attempt to explain the origin of the genes for sugary and white cob in these stocks, the chance that they entered by accidental contamination should be dealt with. The probability of contamination is reduced to nil by the following facts: These hybrid derivatives did not produce silks until very late in the season; the F_1 and the first two backcross generations, in particular, never produced their first silks until the other maize stocks had finished shedding pollen. The sweet corns planted in this area are even earlier than the other types, and they were approaching maturity when silks of

these F_1 to B_2 hybrids made their first appearance. Special late plantings of inbred 203 had to be made to provide pollen for these early generation hybrids. Regardless of this, better than ordinary precautions were always taken to protect the hybrids from possible contamination. None of the early generation hybrid derivatives have shown any character, except sugary and white cob, to suggest parentage other than inbred 203 and Tripsacum, and it has not been found possible to recognize the heterozygotes for sugary and white cob in any generation by phenotype. None of the early generation hybrids showed special vigor, such as to indicate hybrid vigor, although rogues did rarely occur in the B_4 and B_5 generations and were destroyed.

The explanation of the occurrence in these plants of genes for sugary and white cob probably is either (a) mutations induced by the original species hybridization or (b) the exchange of genes from Tripsacum chromosomes to maize chromosomes in an early generation after the original hybridization, followed by a loss of the Tripsacum chromosomes bearing the maize alleles. This last suggestion may seem bold, especially as applied to the su gene. Although the endosperm of Tripsacum is starchy in phenotype, Mangelsdorf and Reeves showed in 1939 that Tripsacum has a gene allelic with su_1 in maize, which is not completely dominant to the maize su_1 allele. The difficulty found here in classification also paralleles that reported in 1939.

For the observed frequencies of five heterozygous and 26 homozygous plants, neither the hypothesis of a 1:4 nor that of a 1:7 ratio need be rejected. This makes difficult any attempt to estimate which generation, if any, after the initial hybridization was entirely heterozygous. Added to the difficulty are the recorded facts that all of the hybrid derivatives are descendants of one B_1 plant and that 11a and 11b each descended from one offspring of that B_1 plant. It is a reasonable estimate that each of the B_2 plants produced 12.5 to 25 percent of su gametes.

The observed frequencies of six plants heterozygous for white cob to one homozygous red, among the 11b B_3 plants, serve only to create doubt that the gene for white cob is similar in behavior to that for sugary.

In any event, complete pedigrees have been kept of all plants of 11a and 11b, and this will continue to be done. The seeds of the segregating plants originating from them are being recorded separately, so that if the necessity arises of treating them as a separate group from the non-heterozygotes, this can be done conveniently.

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1. Crossover data for chromosome 4.

$$\frac{Su\ Gl_4\ Tu}{su\ gl_4\ tu} \times su\ gl_4\ tu$$

(o)	(o)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	Total
95	111	14	19	2	12	1	2	225

Recombinations $Su\text{-}Gl_4 = 16.0$
$Gl_4\text{-}Tu = 7.6$

2. Tan cob color.

Two mutations affecting cob color have been found in breeding material. One of these, giving a brown color, was found to be an a allele. The second, characterized by a pale brown or tan coloration, on the basis of data now available, appears to act as a specific modifier of the P alleles.

P^{rr} x ta

P^{rr} Ta 156 P^{rr} ta 43 P^{rw} Ta 31 P^{rw} ta 10

P^{ww} x ta

P^{rw} Ta 137 P^{rw} ta 45 P^{ww} Ta & ta 52

Plants of the genotype P^{rr} ta have a tan pericarp as well as cob color.

3. Frequency of triploids.

In years past triploid ears have been found with some regularity while harvesting our experimental yield trials. This year it was decided to get proximate figures on frequency of occurrence. This was done by keeping a record of the number of triploid ears and assuming that all plots had a perfect stand with each plant bearing a single ear. Records were made at three different locations and at each location the frequency was approximately 1 per 1000.

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1. A gene for resistance to Puccinia sorghi in the variety Blacks Yellow Dent.

Studies reported in the 1955 and 1956 Maize Genetics News Letters have shown that the strains B38, K148, Cuzco, and GG208 each have a dominant gene for resistance to leaf rust. Furthermore, these genes appear to be in an allelic series.

A rust resistant early generation inbred line has been established from the variety Blacks Yellow Dent. This inbred line differs genetically from the previously reported sources of resistance as indicated by the differential rust reactions shown in the following table:

Reactions to five cultures of Puccinia sorghi

Source of resistance	901a	908R	921a	927R	930R
B38	0;	0;	0;	3	0;
K148	1-	3	1-	3	1-
GG208	1-	1-	0;	1-	3
Cuzco	0;	0;	0;	0;	0;
Blacks Y.D.	0;	3	3	3	0;

Inheritance of resistance was studied in the F_3 from the cross Blacks Y.D. x B14 (a susceptible inbred). Progenies of 102 F_2 plants were evaluated separately with 6 cultures of P. sorghi. Twenty seedlings from each ear were classified for reaction to each rust culture. The following table shows the results obtained:

Rust culture	Parent Reactions		F_3 Reactions			Expected ratio	X^2 Value	P Value
	Blacks Y.D.	B14	Res.	Seg.	Susc.			
901ab	Res.	Susc.	24	51	27	1:2:1	0.176	0.95-0.90
917a	Res.	Susc.	24	51	27	1:2:1	0.176	0.95-0.90
928b	Res.	Susc.	24	51	26	1:2:1	0.089	0.98-0.95
929d	Res.	Susc.	24	51	27	1:2:1	0.176	0.95-0.90
904d	Susc.	Susc.	0	0	102	All susc.		
921b	Susc.	Susc.	0	0	102	All susc.		

Each F_3 progeny reacted the same to cultures 901ab, 917a, 928b, and 929d. All seedlings were susceptible to cultures 904d and 921b. The segregating F_3 progenies gave a satisfactory fit to a 3:1 ratio (X^2 = 0.931, P = .50-.30).

The preceding data indicates that a single dominant gene for resistance to P. sorghi is present in the Blacks Y. D. inbred line. Differential rust reactions indicate that this gene is different from those previously identified. Appropriate crosses have been made to determine its allelic relationship to the known genes for rust resistance.

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1. Diffuse.

Diffuse (Df), a dominant inhibitor partially epistatic to red pericarp (P^{rr}) pigmentation, was reported in 1954 (Jour. Hered. 45: 47-50) as giving about five per cent recombination with T2-4b (2L.81 4L.53, from 1956 revised list of Anderson & Longley, M.G.C. News Letter No. 30). Df assorted independently of T1-4a, T2-4l, and T2-7c. These data excluded the mid-regions of the long arm of chromosome 2 and the short arm of chromosome 4 as possible sites of Df. They did not permit a decision between the two possible locations of Df indicated by the close linkage with T2-4b.

Subsequent tests (see table) show that Df gives about 2.8 per cent recombination with T1-4b, and also is closely linked with T4-9b and T4-5f. It assorts independently of two different translocations marking the long arm of chromosome 2. Thus the site of Df appears to be near, and proximal to, the point on chromosome 4 marked by T1-4b.

Three families gave aberrant recombination ratios on the hypothesis that Df is located on the distal portion of the long arm of chromosome 4. Linkage with T2-5f (2L.91 5L.10) was indicated in one family. Df assorted at random in two other families segregating T4-5b (4L.76 5L.68). Mislabeling of the reciprocal translocation stocks may be involved in these three cases; or possibly, Df is a transposable element.

As noted in 1954, kernels from a relatively large patch which was colorless or near-colorless as the result of Df action in P^{rr} plants gave the same kind of progeny as typical dark diffuse kernels from the

same ear. It was concluded from this result that the light colored area did not represent a mutation of the Df gene, but was a "pattern" effect. A family grown in 1957 from a similar colorless area, however, gave colorless offspring; whereas plants grown from typical Df kernels on the same ear gave typical Df offspring. The reason for these contradictory results remains to be found.

Family	Mating	Marker locations (Longley & Anderson)	Number of offspring: Semisterile Df	Semisterile df	Normal Df	Normal df	Per cent Recombination
12-465	Df/T1-4b x df	1S.55 4L.83	1	62	62	1	
-466	"		1	78	69	2	
-480	"		3	80	70	4	
Total			5	220	201	7	2.8
12-467	Df/T4-9b x df	4L.90 9L.29	6	75	61	20	
-468	"		4	55	41	7	
-469	"		2	41	58	2	
-481	"		9	88	97	10	
-482	"		5	28	30	1	
-483	"		2	78	76	12	
-484	"		1	30	59	7	
-485	"		2	63	106	4	
Total			31	458	528	63	8.7
12-470	Df/T4-5f x df	4L.50 5L.80	12	93	84	17	
-471	"		12	91	89	16	
-486	"		21	131	100	15	
-487	"		15	92	91	12	
Total			60	407	364	60	13.5
12-472	Df/T2-5f x df	2L.91 5L.10	41	61	50	41	
-488	"		61	63	62	51	
-489	"		60	70	46	58	
Total			162	194	158	150	47.0
12-474	Df/T2-3d x df	2L.67 3L.48	55	70	45	47	
-475	"		39	43	42	44	
-490	"		46	61	51	46	
Total			140	174	138	137	47.0

Irwin M. Greenblatt

2. Transallelic action of self-colored mutants from stippled (R^{st}) in heterozygotes with self-colored aleurone (R^r).

As previously reported, standard R^r is changed invariably to a weakly pigmenting form, termed $R^{r:st}$ in plants heterozygous for stippled

($\underline{R}^{r}\underline{R}^{st}$) (Genetics 41: 872). Marbled ($\underline{R}^{mb}$) has a similar, but not the same, effect on standard $\underline{R}^{r}$ in $\underline{R}^{r}\underline{R}^{mb}$ heterozygotes (PNAS 43: 1053). No evidence has been obtained to date proving that the action of stippled is altered in $\underline{R}^{r}\underline{R}^{st}$ heterozygotes. That is, the transallelic effect appears to be non-reciprocal.

Germinally transmissible mutations of stippled to self-colored aleurone (termed $\underline{R}^{sc}$ here, for convenience) occur in our standard stippled strain (inbred W22 background) with a frequency of about 2 per 1000 gametes (R. B. Ashman data).

All such $\underline{R}^{sc}$ mutants from $\underline{R}^{st}$ thus far tested have proved stable in $\underline{R}^{sc}\underline{R}^{st}$ heterozygotes. That is, they are refractory to the kind of genetic change which standard $\underline{R}^{r}$ invariably undergoes in $\underline{R}^{r}\underline{R}^{st}$ plants. It appeared earlier, on the basis of the results of a limited test, that these $\underline{R}^{sc}$ mutants from stippled likewise were incapable of "inducing" a heritable change in $\underline{R}^{r}$ in $\underline{R}^{r}\underline{R}^{sc}$ heterozygotes. (M.G.C.N.L., No. 31). This is known now to be incorrect. More extensive tests carried out in 1957 show that some self-colored mutants from stippled promote a marked change in color determining action of standard $\underline{R}^{r}$ in $\underline{R}^{r}\underline{R}^{sc}$ heterozygotes, and that others are either inactive in this respect, or only weakly active. Thus when stippled mutates to self-colored aleurone the capacity shown by the parent $\underline{R}^{st}$ allele to induce a genetic change in standard $\underline{R}^{r}$ in $\underline{R}^{r}\underline{R}^{st}$ heterozygotes, may or may not change also.

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1. Mutation spectrum of variegated pericarp.

A progeny test involving more than twenty-five thousand plants, was used to study the mutation rate of a common variegated pericarp allele ($\underline{P}^{vv}$) in homozygous ($\underline{P}^{vv}/\underline{P}^{vv}$) and heterozygous ($\underline{P}^{vv}/\underline{P}^{wr}$) maize plants in two otherwise near-isogenic stocks corresponding to inbred lines W22 and W23. The results were first reported in the 1956 News Letter (30: 137-138). Additional mutant types were observed in the study which were not relevant to the main problem and so were not included in the initial report. Data on the spectrum of mutation of a specific allele are rare in comparison with reports on the frequency of mutation, and it is now proposed to place in the record the complete data bearing on this point.

The $\underline{P}^{vv}$ allele common to all of the stocks used in this study exhibits a spectrum of mutation comprising six types. In addition to the medium variegated parental type, the frequencies of light variegateds, very light variegateds, orange variegateds, self reds, near selfs, and colorless pericarp and cobbed offspring are listed in the accompanying table according to the two inbred backgrounds in which the $\underline{P}^{vv}$ allele was tested. About half the offspring from heterozygous $\underline{P}^{vv}/\underline{p}^{wr}$ plants, of course, had colorless pericarp, red cobs. They are entered separately in the table.

	W22				W23			
	Homozygous		Heterozygous		Homozygous		Heterozygous	
Pericarp Class	No. of Plants	Per Cent	No. of Plants	Per Cent	No. of Plants	Per Cent	No. of Plants	Per Cent
Med. var.	4325	94.546	2137	95.487	6114	90.097	3293	81.269
Lt. var.	101	2.208	48	2.145	330	4.863	314	7.749
V. lt. var.	7	0.153	0	0	7	0.103	15	0.370
Orange var.	2	0.044	0	0	4	0.059	4	0.099
Self red	125	2.732	46	2.055	257	3.787	390	9.625
Near-self	7	0.153	6	0.268	45	0.633	21	0.518
pww	8	0.175	1	0.045	29	0.427	15	0.370
pwr	(0)		(2433)		(0)		(4018)	
Total of colored	4575		2238		6786		4052	

The abbreviated table in the 1956 News Letter showed that (1) mutation of the variegated pericarp allele to red and light variegated is much lower in homozygous $\underline{P}^{vv}/\underline{P}^{vv}$ than in heterozygous $\underline{P}^{vv}/\underline{P}^{wr}$ plants in the W23 but not in the W22 background, and (2) the rate of change to both red and light variegated was markedly lower in the W22 than in the W23 background.

Unequivocal conclusions cannot be drawn from the data in the present table on the relationship of heterozygosity or homozygosity and W22 or W23 background to the rate of mutation to very light variegated, orange variegated and near-self reds. The pattern, however, probably parallels that noted for mutation to red and to light variegated. This leads to the conclusion that all the mutants arise following some event which is subject to the already known Modulator dosage effect. Valentine (N. L. 31: 129-171, 1957) has interpreted orange variegated, however, as due to a mutation of the Mp component of the $\underline{P}^{vv}$ allele.

Colorless pericarp and cob mutants do not show an effect of heterozygosity on rate of origin from medium variegated. Furthermore, they occur with approximately the same frequency as very light variegateds, which would not be true if they arose by a further multiplication

and transposition of tr-Mp in very light variegateds. This relatively high frequency of occurrence, together with the observation that occasional medium variegated ears have a sizeable patch of mutant P^{ww} tissue, leads to the tentative conclusion that these colorless pericarp types do not involve a detectable transposition event. This conclusion is supported by Brink's observations that a P^{ww} mutant derived in a single step from P^{vv} produced the same Ds chromosome breakage pattern as the parent medium variegated.

Several additional points may be noted about the rarer mutants in the mutation spectrum here reported for P^{vv}: (1) two phenotypes, very light variegated and colorless pericarp and cob, were recorded among the offspring of variegated plants which were not expected as primary mutant types (Brink, Genetics 39: 724-740, 1954), (2) two phenotypically distinct classes of reds were obvious, but as yet the relationship of near-selfs to self reds is not clearly understood, and (3) a consideration of all the data indicates that orange variegated is the rarest of the P^{vv} mutational spectrum yet recognized.

Finally, one ear in this study had a large patch of dark variegated pericarp, a phenotype not previously reported in the pericarp work. This phenotype is transmissible, and is being studied further.

2. Transallelic change at the C locus.

An invariable transallelic change of the kind reported by Brink for R^{st} and R^{mb} in heterozygotes with R^{r} was not found at the C^{I} - C locus when a particular C^{I} allele was used in a mating scheme similar to that developed by Brink (see Genetics 41: 872-889, 1956).

The C^{I} allele used has been in the genetic cultures at Macdonald College for many years. It is distinguished from the typical C^{I} allele by the phenotypes it produces in $C^{I}C^{I}C$ and $C^{I}CC$ aleurones. Selfed ears on $C^{I}C$ plants carrying the Macdonald C^{I} allele contain four equal and rather distinct phenotypes: (1) entirely colorless, (2) near colorless background (?) but with a few spots of deep pigment, (3) heavily flushed with pigment over the entire kernel and with numerous distinct small spots of deep pigment clearly visible through the flush of pigment, and (4) deeply pigmented overall.

It was thought that the apparent mutable nature of this C^{I} allele might be affected by the C allele in heterozygotes. However, C^{I} alleles from $C^{I}C^{I}$ homozygotes and C^{I} alleles from $C^{I}C$ heterozygotes produce the same phenotype when placed on homozygous A C R pr silks in Wisconsin inbred 22 background.

The effect of this C^{I} allele on various C alleles extracted from heterozygotes with it remains to be tested.

R. I. Brawn

IV. REPORT ON MAIZE COOPERATIVE

During the past season, a large number of intercrosses of chromosome testers were made with a view to extracting new combinations of traits and determining map positions. It will be some time, however, before many of these new combinations have been extracted and are available for distribution. If anyone desires specific combinations of traits not yet listed in the catalog of available stocks, it is quite likely that stocks can be furnished from which such combinations may be readily derived.

Stocks of about 150 reciprocal translocations were increased last summer. Many of these have closely-linked markers. In each instance, pollen examinations were made to confirm the presence of the complete translocation. Crosses were made to the inbred lines M14, W23, and Oh51A and, when necessary, to appropriate genetic testers to determine their positions on the linkage maps. Most were also crossed to the inbred line Kys to provide material more suitable for cytological studies. Inventory of these stocks has not yet been completed.

The stocks which follow represent traits or combinations supplementary to those listed in last year's News Letter. Additional copies of the previous catalog of stocks are available upon request. Requests should be sent to the Botany Department, University of Illinois, Urbana, Illinois. Newly-available stocks are as follows:

Chromosome 1

sr_1 p^{WR} an_1 gs_1 bm_2

Chromosome 2

lg_1 gl_2 b sk v_4; carries fl_1
ws_3 lg_1 gl_2 B sk

Chromosome 3

a_1; A_2 C R B Pl dt_1
A_1 sh_2; A_2 C R
$a_1{}^{st}$ et; Dt_1
$a_1{}^{st}$ sh_2; Dt_1
gl_7
lg_2 $a_1{}^{st}$ et; Dt_1
lg_2 a_1 sh_2 et; carries Dt_1
lg_2 pm

Chromosome 5

a_2 bt_1 pr; seg bm_1 bv_1; may seg v_2; A_1 C R

Chromosome 6

po Y_1 pl
y_1 pb_4 Pl
Y_1 pb_4 pl
y_1 Pl Bh

Chromosome 7

bd

Chromosome 9

bk_2 ms_{20}
wx bk_2
wx d_3
yg_2 c sh_1 wx; A_1 A_2 R

Chromosome 10

R^g sr_2
r^r sr_2

E. B. Patterson

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