TABLE OF CONTENTS

Page

I. Foreword 1

II. Reports from Cooperators

Arizona, University of 2

Boston College 2

Brookhaven National Laboratory 7

Brookhaven National Laboratory and Texas A and M 18

Butler University 26

Cargill, Incorporated 29

Carnegie Institution of Washington . . . 42

Central Potato Research Institute, Simla, India 51

Defiance College 56

DeKalb Agricultural Association 59

Georgia Experiment Station 64

Harvard University 68

Harvard University and University of Massachusetts 75

Hawaii, University of 78

Illinois, University of 81

Indiana University 88

Iowa State University 102

Istituto di Genetica Vegetale, Universita' Cattolica, Piacenza, Italy 109

Istituto di Genetica, Universita' di Milano, Milan, Italy 114

Macdonald College of McGill University, Province of Quebec, Canada 118

Page

Marquette University 119

Maryland, University of 125

Minnesota, University of 129

Missouri, University of 134

Missouri, University of, and United States Department of Agriculture . . . 137

North Carolina State University 142

Pennsylvania State University 146

Pretoria, University of, Pretoria, Republic of South Africa 147

Purdue University 150

Texas, University of 158

Tufts University 160

United States Department of Agriculture 162

United States Department of Agriculture and South Dakota State University . . 165

Western Ontario, University of, London, Ontario, Canada 166

Wisconsin, University of 171

Addendum:

Agricultural Sciences, University of, Gödöllő, Hungary 180

Andhra University, Waltair, India . . . 182

Central Maize Research Station, Yousafwala, West Pakistan 186

III. Stocks Available and Wanted 188

IV. Report on Maize Cooperative 189

V. Recent Maize Publications 200

I. FOREWORD

This volume of the Maize Genetics Cooperation News Letter is the tenth which has been published by this laboratory. Beginning with the first issues, the onerous task of editing, assembling, and supervising the News Letter was largely in the hands of Miss Ellen Dempsey, and in succeeding years it has been solely in her capable hands. All of us who profit from these research reports owe her a debt of gratitude for faithful and efficient services. It is a pleasure to acknowledge our thanks for a job well done. The voluntary assistance of Karl Rinehart, John Mottinger, David Weber, Earle Doerschug, Andrew Snope and Wayne Carlson in reading proof is gratefully appreciated.

While great care is taken in transcribing the reports, it is inevitable that some mistakes will be made. If you find any errors in your report which should be corrected, please inform us and we will issue an Errata for general distribution.

M. M. Rhoades

II. REPORTS FROM COOPERATORS

UNIVERSITY OF ARIZONA
Tucson, Arizona

1. Studies on a stature mutant of maize, petite-one.

Measurements of the embryonic coleoptile length and embryo length of dwarf petite-1 are significantly less than those of the normal sib. Determination of cell number and cell size of the epidermis and cortical regions of the coleoptile and mesocotyl of the dwarf indicate the mutant has shorter cells but an equal number of cells as compared to the normal. The amount of ether extractable and diffusible auxin in four-day old coleoptiles of the dwarf is less than half of the amount obtainable from the normal sib. Differences in auxin content and cell size between the dwarf and normal seedlings can not be related to auxin inactivators, auxin inhibitors, gibberellins, amino acids or vitamins.

William O'Donald
Robert L. Hall
Robert M. Harris

BOSTON COLLEGE
Chestnut Hill 67, Massachusetts
Department of Biology

1. Further studies of Guatemalan teosinte chromosomes.

Monajil of northern Guatemala. Microsporocytes of four plants of open-fertilized Monajil teosinte were cytologically examined. At pachytene, the chromosomes were in general well spread. Identifications of the gross structural characteristics of the chromosomes were made practically without any difficulty. The terminal knobs on the short arms of chromosomes 1, 3, and 7 were large in size. The terminal knobs on the short arms of chromosomes 9 and 8 were medium-sized. The long arms of chromosomes 4, 5, and 6 had a large terminal knob, but the short arms of these were knobless. The terminal knobs on the short arm of chromosome 2, and on the long arms of chromosomes 8 and 10 were small. The long arms of chromosomes 1,2,3,7,and 9,and the short arm of chromosome 10 were without any knobs. All of these.knobs were homozygous and

none of them were intercalarily located. Furthermore the distal portion of the long arm of bivalent chromosome 3 was several times found to be asynaptic in about one-third of the total length of this arm. Whether this was caused by the presence of an inversion is uncertain, since there was no anaphasic bridge found among a limited number of sporocytes studied. A study of the F_1 hybrids of this teosinte and an inbred maize strain is in progress.

Y. C. Ting

2. Effect of x-rays on variegated leaf character.

In the summer of 1963, pollen of plants homozygous for a set of duplicate genes for variegated leaf, (vl_1 vl_1, vl_2 vl_2), was irradiated with x-rays. Three doses of x-rays 1000r, 2000r, and 3000r were applied. In about one hour after irradiation the pollen was crossed to the sib plants which were of the same genetic background. Pollen from each treatment was used on five different plants. In general, the seed sets were good for all the crosses. Seeds (kernels) from these crosses were planted in the summer of 1964. There were 527 fully grown plants obtained from treatment-1 (1000r); 555 plants, from treatment-2 (2000r); 362 plants, from treatment-3 (3000r). Frequent examinations of the vegetative characters, with special attention to the vl gene, were conducted during the whole growth period. No single plant was mutated back to the wild type. Leaves of all the plants appeared the same as those of the parental plants. Hence, it seems reasonable to conclude that x-rays are not effective in inducing reversion or inhibition of the vl gene in maize.

Y. C. Ting
E. Dancewicz

3. Additional studies of haploid maize.

Last summer a haploid was found among the progeny of an inbred maize strain, Coe-stock-6, which was provided by Dr. E. H. Coe, Jr., of the University of Missouri. This plant was earlier in tasselling than the sibs, and its stalk was shorter. Since the chromosomes of the sib plants of this haploid were well spread at pachytene, it was anticipated that chromosomes of the haploid would also be well spread at the corresponding stage. Furthermore, much more information concerning the meiotic chromosome behavior, such as pairing between heterologous chromosomes indicative of duplication, in haploid maize is needed. Hence, microsporocyte divisions of this haploid were investigated.

At pachytene, the 10 chromosomes, like those of the other haploid maize previously reported by the author (M. G. Newsletter, 1963), were always entangled and formed

nonhomologous associations, predominantly fold backs. Pairing between heterologous chromosomes and chromosomes unpaired throughout their entire length were infrequent.

Table 1
Chromosome Associations At Diakinesis Of Haploid Maize

	Type of Association				
Class	Univalent	Bivalent	Trivalent	Total	%
1.	10	0	0	226	56
2.	8	1	0	133	33
3.	6	2	0	26	6
4.	5	1	1	8	2
5.	7	0	1	11	3
				404	

From diakinesis to metaphase I, chromosomes in over 50 percent of the sporocytes remained as univalents. As is shown by Table 1, among a total of 404 randomly selected cells, 56 percent, or 226 of them were found to have 10 well defined univalents; 33 percent, or 133 of them, eight univalents plus one bivalent; six percent, or 26 of them, six univalents plus two bivalents; two percent, or eight of them, five univalents plus one bivalent and one trivalent; three percent, or 11 of them, seven univalents plus one trivalent. Most of these bivalents and trivalents showed affinity by only end-to-end or rod-shaped pairings. No ring-shaped configurations were observed among the limited number of cells studied. Furthermore, these pairings were not limited to certain chromosomes.

From metaphase II to anaphase II, the phenomenon of multispindle was found in a few diads. The extra spindles appeared when only one or two strayed chromosomes were present in the cytoplasm of the diads. These spindle regions were clear in the better stained cells.

This plant was completely sterile when it was pollinated by the sib plant. No anthesis was observed.

Since bivalents varying from one to three in number were observed in less than 50% of the microsporocytes examined, it appears reasonable to conclude that duplicate factors in maize are intra-chromosomal. Coincidentally, among about 15 reported cases of duplicate factor inheritance in maize,

three of the four better known sets were proved to be intrachromosomal. Apparently those genetic findings support the present cytological observations.

As stated in the foregoing paragraph, the phenomonon of multispindle was seen from metaphase II and anaphase II, the extra spindles being organized where only one or two strayed chromosomes were present. It is conceivable that the centromeres of the chromosomes, instead of the centrosomes of the cytoplasm, are responsible for the organization of the spindle. Therefore, the mitotic spindle is of nuclear origin. The classic theory stating that the mitotic spindle is originated in the centrosomes should be rejected.

Y. C. Ting
Francine Torres
E. Dancewicz

4. Spontaneous reciprocal translocation in a maize tester plant.

An interchange between the long arm of chromosome 6 and the short arm of chromosome 9 was identified in a plant of the progeny of an inbred maize tester strain. The genotype of this strain was Y/y, sh bz/ sh bz. By averaging five separate measurements, it was found that the length of the interchanged segment on the long arm of chromosome 6 occupied about 87 percent of the length of this arm, while that on the short arm of chromosome 9 included about 75 percent of this arm. This translocation was tentatively designated as T6-9a of our material. Since the exact locations of the previously reported translocations between the long arm of chromosome 6 and the short arm of chromosome 9 from other laboratories are not available, it is impossible to ascertain if this interchange has been published. However, it is certain that this did not come from an outcross.

At diakinesis it was observed that in a total of 309 randomly selected cells, 98 percent, or 303 of them formed chain-configurations involving chromosomes 6 and 9. A little more than one percent, or four of them formed ring-configurations, and only less than one percent, or two of them formed separate bivalents of these interchanged chromosomes. This unusually high frequency of the occurrence of chain-configurations might be caused by the frequent formation of non-homologous associations between the interchanged segment from the short arm of chromosome 9 and the long arm of the normal chromosome 6. This was actually observed at pachytene. These non-homologous associations could be a manifestation of duplication including the long arm of chromosome 6 and the short arm of chromosome 9.

Table 2
Percent Of Sterile Ovules And Kernels With Yellow Endosperm Obtained By Selfing And Outcrossing The Plant Having T6-9a (64-14-6).

Selfing and Crosses	% Sterile Ovules	% Yellow Endosperm
64-14-6⊗	40	48
64-14-6 x Wilbur's Flint	7	42.2
Wilbur's Flint x 64-14-6	---	36

Through a study of the percent of seed set after selfing and outcrossing this T6-9a plant the following results were obtained: The average ovule sterility, 23.5 percent, was much less than expected (Table 2). This is probably due to the fact that most of the egg nuclei carrying deficient or duplicate segments could function normally in fertilization and hence could transmit these abnormal segments to the next generation. In addition, it is clear that the Y locus was located in the long arm of chromosome 6, and it was included in the interchanged segment. If it were not so, the segregation for Y and y endosperms should be at a ratio of 1:1 in the two crosses with Wilbur's Flint (y/y). Furthermore, the smaller than expected percentage of Y endosperms recovered in the progenies of the crosses and selfing might be accounted for by the elimination of Y locus due to deficiency or duplication produced by crossovers within the interchanged segment.

Y. C. Ting
Francine Torres
E. Dancewicz

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1. Mutations induced by ethyl methanesulfonate (EMS).

The work reported here involves the use of endosperm marker genes on the short arm of chromosome 9 as a system for testing the mutagenicity of EMS and comparing its effects with those of ionizing radiations in producing chromosome breaks and gene mutations.

Stocks of multiple dominant homozygotes (I Sh Wx) were treated and crossed, as male or female parent, with a corresponding multiple recessive stock (C sh wx). In order to obtain large mutant areas, and to facilitate the establishment of sufficient seed stocks of the induced mutants for further study, EMS and radiation treatments were applied mostly to seed embryos or very young seedlings.

Since EMS becomes hydrolyzed in water over a period of time, and since its chromosome-breaking ability is influenced by impurities in the aqueous solvent, the following precautions were used in preparing EMS solutions. All treatments were begun within an hour after preparation of the solutions. The water used in all experimental procedures was distilled and deionized in order to provide conditions which minimize the production of chromosomal aberrations.

Three methods of treatment with EMS were used:
1) Seed soaking. The surface of the seeds was first disinfected with a mixture of equal portions of 95% ethyl alcohol and 3% hydrogen peroxide. The seeds were then soaked in deionized water at 27° C and bubbled continuously with oxygen for 24 hours. They were then soaked in 0.05 M or 0.025 M aqueous solution of EMS for either 5 hours at 27° C or for 2 to 5 days at 3° C. The rationale for the latter treatments, i.e., for prolonged applications at a cold temperature, was to ensure thorough penetration without chemical disintegration of the mutagen. This was followed by post-incubation in water. In this preliminary report the results of all seed soaking treatments are combined, since no conclusive evidence of significant differences attributable to different methods of soaking is yet available.

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

2) Root cutting. Seeds were prepared in the same manner as for the seed soaking treatment, then placed on slanted moist filter paper to ensure growth of straight roots. When the young roots reached 2 to 5 cm in length, the tips were cut off about 0.5 cm from the end. These young seedlings were then put in glass vials so that the root was immersed in a solution of 0.01M EMS, while the seed and shoot remained in air for normal respiration. This treatment was continued for 24 hours at about 24° C and under ordinary room illumination. The purpose of the cut root method was to ensure rapid uptake of the mutagenic solution, and subsequent transport through vascular tissue to the apical stem meristem of the young plant.

3) Injection. Injections of 5 to 10 ml of 0.005 to 0.05 M EMS solutions were made into the lower part of the tassel of young plants with a hypodermic needle and syringe. Test injections with dyes indicated an even distribution of the solution among florets. A few mutants were obtained with EMS by this method; however, treatment of the seed or very young seedlings was found to be more convenient and effective for the purposes of these experiments.

For radiation treatments seeds were exposed to x-rays after the same presoaking procedure as described above for EMS; dry seeds were irradiated with reactor-generated fast neutrons. The x-ray treatments were made with a G. E. Maxitron apparatus operated at 250 kVp, 30 ma, 1.0 mm Al filter, and 30 cm target distance. The soaked seeds were kept moist in a petri dish, placed on a turntable and exposed to 1 and 2 kr of x-rays at a dose rate of 1272 r/min. Fast neutron irradiations were carried out in the thermal column of the Brookhaven Graphite Reactor by using a U-235 converter plate. Dosages of 1 and 2 krads were delivered to dry seeds at a rate of 138.5 rads/min.

The results of treatments with EMS and with radiation, as observed in F_1 kernels, are summarized in Table 1. The data are grouped according to whether the treatment was applied early, i.e., to seeds or young seedlings; or late, i.e., applied to the tassel or pollen. If applications were made at an early stage of embryo or plant development, most mutations appeared in large sectors. This was shown by: 1) the appearance of large chlorophyll deficient sectors in treated plants, particularly in Yg_2/yg_2 heterozygotes; 2) in female reproductive tissue by the appearance of areas of mutant kernels on ears of treated plants pollinated with a recessive tester; and 3) in male reproductive tissue, by large chlorophyll deficient sectors in the tassel of treated plants as well as by a high frequency of mutant endosperm kernels of the same type on ears of recessive tester plants fertilized with

pollen from the tassel of treated plants. Therefore, the ear or tassel as a whole was taken as the unit for scoring frequency of mutations produced; each cluster of the same mutation was equated to a single mutation. On the other hand, when treatments were made at later stages, by injection of EMS into young tassels or by x irradiation of mature pollen, each single mutated kernel among the total number of kernels scored was considered to be an independently induced mutation.

Table 1
Mutations Induced by Ethyl Methanesulfonate and Radiation in Maize

Mutagen	Method or material	Total number of:	No. mutations			
			Single			Multiple
			C	sh	wx	
Seed or seedling treatment						
		Ears &/or tassels				
Fast neutrons	dry seed	193	3	1	1	0
X ray	wet seed	228	0	0	0	0
EMS	soaking	1158	18	20	24	1*
	root cut	149	3	5	2	0
Control	soaking	502	1†	0	0	0
	root cut	58	0	0	0	0
Tassel or pollen treatment						
		Kernels				
X ray	pollen	1004	1	1	1	6
EMS	tassel injection	4994	0	2	3‡	0
Control	pollen	181	0	0	0	0
	tassel injection	471	0	0	0	1§

* sh wx, but only wx appeared in next generation.

† The plant grown from this was weak and produced no seed.

‡ Two of these kernels came from the same tassel treated.

§ C sh wx, but only wx appeared in next generation.

The combined scoring of early EMS treatments yielded 5.4% (62 out of 1158) single mutations from soaked seed and 6.7% (10 out of 149) by the cut root method. A few cases of exceptionally high incidence of single locus mutations from early treatments were observed. In one, 4 out of 16 ears, and in another 8 out of 27 ears, had a mutation in one of the three loci scored. One multiple locus mutation (sh wx) was obtained from EMS treatment and, in the progeny test, only the wx mutation was transmitted. The high incidence of single locus mutations from early EMS treatments may be due in part to consequences of severe screening of large chromosomal deletions during development of the plant tissue (diploidal elimination) or in reproductive stages (haploidal elimination). However, no multiple locus mutations were obtained from tassel injections with EMS.

The mutations listed in Table 1 were all induced in 1963 and a representative sample (1 to 5) of mutant kernels, with the exception of those induced by x-ray treatment of pollen, were sown in 1964 to confirm the mutations by testing their transmission (Table 2). Of the 24 colored (non-I) mutations from treated material, all germinated and 16 or 17 were confirmed as c-type mutations. Of the 28 sh mutations tested, 24 germinated and 19 were confirmed as transmissible. One of those not transmitted was from a tassel injection treatment and may have been due to noncorrespondence between two generative nuclei that divided prior to the mutation event. Of the 31 wx mutations tested, all germinated, and all but two were transmitted to the next generation. One of these was induced by fast neutrons and was accompanied by loss of all other markers on half the kernel. The other was from late EMS injection and may have been due to noncorrespondence of mutation in the two generative nuclei as noted above.

Pollen fertility in the F_1 of the 29 transmissible wx mutations induced by EMS was checked under low magnification after staining with I_2-KI. More than 90% fertility was found in 22 of these wx mutants. Of the 18 sh mutations produced by EMS treatment 17 were tested for pollen fertility and 16 were found to be more than 90% fertile. Of the 14 definitely confirmed c mutations produced by EMS, all were tested and 13 showed more than 90% pollen fertility. In the I Wx→c Wx mutant, which was of low fertility in the F_1 with the C sh wx tester, the cause of pollen abortion appeared to be independent of chromosome 9 since the ratio of Wx (black) to wx (brown) grains was approximately normal.

Table 2
Progeny Test Confirmation of Induced Mutations

Treatment	No. mutations observed	No. tested mutations germinated	No. mutations confirmed
wx mutations			
Fast Neutrons	1	1	0
Early EMS appl.	27	27	27
EMS injection	3	3	2
sh mutations			
Fast neutrons	1	1	1
Early EMS appl.	25	21	17
EMS injection	2	2	1
c mutations			
Fast neutrons	3	3	2
Early EMS appl.	21	21	14(15)
EMS injection	0	-	-

The interpretation that true gene mutations, free of major change in chromosome structure, may be produced in Zea mays by EMS is encouraged by: 1) induction almost exclusively of single locus mutations; 2) the high fertility of most mutants and normal segregation of chromosome 9 markers in some; 3) alternative explanations to deletion for the I⟶c mutations; and 4) preliminary evidence of recombination among induced wx mutants.

E. Amano
H. H. Smith

2. Mechanisms of genetic recombination.

In 1928 Stadler irradiated maize plants in meiosis and reported no significant effect on intergenic recombinations. Since O. E. Nelson has demonstrated intragenic recombination at the waxy locus in maize an opportunity is provided to determine the effects of irradiation on intragenic recombination.

Table 3
Parents and Heteroallelic Material. The Irradiated Values Are From One Plant, The Control Values From Several Plants.

	Estimated no. microspores x 10^3	$\bar{X}$ no. Wx x 10^{-5} $\pm$ $s_{\bar{x}}$	Z value
Irradiated			
wx^C	162	3.70 ± 1.51	
wx^{90}	217	2.77 ± 1.13	
wx^C x wx^{90}-1	66	22.55 ± 5.82	-8.4441*
-2	61	57.49 ± 9.72	-2.7318*
-3	87	89.74 ± 10.16	0.2121
-4	50	52.21 ± 10.24	-3.0841*
-5	94	84.43 ± 9.50	-0.2706
-6	112	41.01 ± 6.04	-5.9058*
-7	69	66.22 ± 9.76	-1.9262†
-8	64	122.33 ± 13.84	2.3776†
-9	48	53.73 ± 10.53	-2.8829*
-10	49	60.73 ± 11.08	-2.1886†
-11	40	103.19 ± 16.11	0.9399
-12	42	50.38 ± 10.99	-3.0606†
Control			
wx^C	166	2.42 ± 1.21	
wx^{90}	395	0.76 ± 0.44	
wx^C x wx^{90}	362	85.69 ± 4.86	

* Exceeds .1% (.001) level of significance.

† Exceeds 5% (.05) level of significance.

Some of this work and the details of analysis have been reported by Briggs and Smith in MNL 38 (pp. 25-27). The $\underline{wx}^{C}$ x $\underline{wx}^{90}$ heteroallelic cross received 200 r of x-rays in meiosis. An effect on intragenic recombination is noted in that x-rays increase and decrease genetic recombination as compared to unirradiated plants (Table 3). A rough extrapolation of Stadler's data provides an estimate that he used doses of x irradiation up to approximately twenty times higher than those used here. His doses ranged from about 250 to 4000 r.

Maize and other organisms may have two mechanisms of genetic recombination, i.e., one for intergenic and one for intragenic recombination. If there are two mechanisms of genetic recombination in maize, the mechanism involved in intragenic recombination appears to be affected by irradiation, whereas the mechanism involved in intergenic recombination does not appear to be affected. Therefore, on the basis of an indirect comparison, there is some indication that there may be two mechanisms of genetic recombination in maize.

R. W. Briggs

3. Chemical mutagens on maize: Myleran.

In an experiment designed to investigate the mutagenicity of chemical mutagens on several endosperm genes on the short arm of chromosome 9, the agent Myleran (di-methane-sulphonyloxy-butane) was used. Myleran (m. w. 246.31) was investigated because its molecular relationship to ethyl methanesulfonate (m. w. 124.16) is essentially that of two EMS molecules joined together, and it is bifunctional. Effects of this agent have been reported in the literature, particularly by the Moutschen-Dahmens and Michaelis and Rieger. This experiment was performed to determine the most efficient treatment procedures for using this agent.

The Myleran used was obtained from Burroughs Wellcome and Co., Tuckahoe, New York. Its solubility presents a problem which, under current experimental procedures, seems to be even more difficult than has been reported. Methods for increasing solubility have been investigated by varying temperature, time and organic solvents. To date the maximum treatment time has been 24 hours and

the maximum temperature 35° C. A 7% ethyl alcohol solution has been used in attempting to increase solubility. The various combinations of treatments are shown in Table 4.

Seed treatments were used with this agent. In all cases the seeds were presoaked for 24 hours at 25° C. The treatments were administered in an aqueous phosphate buffer (0.02 M, pH 7.5). The genotype of the treated stock was C^I Sh Bz Wx. The tester stock, which was generously supplied by A. L. Caspar of Blandy Farm, had the genotype of A_1 A_2 R C sh bz wx^C v_1. Two field replications were used and each plot consisted of 50 seeds except that the controls C and D had 25. The treated stock was detasseled and used as the female parent, with the tester stock as the male. The field planting was arranged so that there was a male, then two females, then a male. This procedure gave a tester male alongside each row of treated females. With this arrangement an ample amount of pollen and good seed set was produced. An abundance of material was available for observing mutants, so that 1363 ears were examined in the entire experiment, an average of 3.04 ears per plant (tillering stock). Also, the treated stock, except for some treatments, produced 200-250 kernels per ear based on a conservative estimate. This material was grown in an isolated field which allowed the use of the open-pollinated crossing procedure.

From a nonmutated event the triploid genotype of the aleurone tissue should be C^I C^I C. If the C^I mutated to C the cross should be C C C or produce "fully colored" aleurone tissue. If C^I mutated to c, the cross c c C should be "pale with frequent colorless patches." The phenotypes and genotypes of the crosses are quoted from the work of E. H. Coe (Genetics 47: 779, 1962). All except one of the aleurone color mutants may be mutations of C^I to c, since they were not fully colored and fitted quite closely to the above description of the c c C genotype. However, other explanations of some of these mutants may be possible since waxy sectors were detected in some kernels. These kernels may have been caused by a phenomenon related to the breakage-fusion-bridge cycle. Also, several of these kernels occurred in the controls, and may, therefore, have little bearing on evaluating the effectiveness of the treatments. For purposes of classification in the table they were designated as c mutants. One full color kernel was produced; this may possibly represent a mutation of C^I to C. This mutant occurred in a control; therefore, it represents a spontaneous mutant.

During the growing season and before anthesis (ca. 10 leaf stage) the leaves were scored in the field for chlorophyll sectors. The classes were arbitrarily called "yellow-green" and "other." The "yellow-green" class is merely descriptive and may or may not be associated with the known locus on chromosome 9. All other chlorophyll abnormalities were included in the "other" class, except albino sectors. These have been noted following ethyl methanesulfonate treatments (Briggs, unpubl.), but not after Myleran.

The sector data were not taken completely quantitatively in that: 1) each leaf was not scored separately, and 2) if there were sectors on several leaves which appeared to come from one event, they were considered as one. The data as presented can be used to assess the relative effect of the treatments. Twenty plants per replication were used whenever available.

The treatments with .003 and .005 molarity for 12 hours at 35° C, seem to be quite effective in producing leaf sectors. However, very few plants were available for analysis. Also, treatments with .003 M for 24 hours at 25° C seemed rather effective in producing sectors.

The .002, .003 and .004 M treatments for 10 hours at 25° C and .003 M for 24 hours at 25° C appeared to be the most effective for affecting the aleurone and endosperm. It cannot be concluded that Myleran was responsible for the production of the waxy mutant, since one also occurred in a control containing alcohol, and the other occurred with Myleran and alcohol. Therefore, there is some indication that the alcohol was mutagenic.

Plant height, from ground level to tip of top leaf, was measured during the season, before and after anthesis. All treatments seemed to reduce plant height compared to the control. The most reduction was with the .003 and .005 M treatments for 12 hours at 35° C. However, the numbers of plants were also reduced with these treatments.

Silking date was taken as the time when 50% of the plants in a plot were 50% silked out and was recorded as the number of days after July 1. Little difference was noted in silking date except with the .003 and .005 M treatments for 12 hours at 35° C, but again there were few plants in these treatments.

The number of plants was also reduced with the higher molarity treatments for 12 hours at 35° C and no plants survived longer treatment periods. Also the .003 M treatment for 24 hours at 25° C considerably reduced the stand.

Insolubility, is defined here, as when Myleran was observed in the buffer at the end of the treatment time. Some Myleran was seen in all of the treatment containers after treatment. Since full solubility had apparently not been attained, the concentrations or molarity noted may not be too meaningful. That is, "higher molarity" treatments may give the same effect as lower ones. However, this apparently is not entirely true as far as physiological effects are concerned, cf. Table 4. Ostensibly, the Myleran was soluble enough to reduce stands when .003 and .005 M treatments for 12 hours at 35° C were used, and caused essentially complete killing when .002, .003 and .004 M treatments for 24 hours at 35° C were used.

The .003 and .005 M treatment for 12 hours at 35° C had a drastic physiological effect. However, the treatments with .002, .003 and .004 M for 10 hours at 25° C with alcohol had essentially no physiological effect. Therefore, it appears that heat is more effective than alcohol in causing a physiological effect with Myleran. However, based on mutations produced, the alcohol seemed to give better results.

The treatments for 24 hours at 35°C were too drastic and left essentially no plants for analysis. However, treatment at 24 hours and 25° C with alcohol appeared to be effective in sector production, but did not cause such a drastic physiological effect. It was also rather effective in producing aleurone color mutations. This treatment seemed to be the best used in this experiment.

The maximum treatment temperature which will permit some viability of seeds has not yet been determined in this laboratory. However, 24 hours at 35° C (no Myleran) reduced survival to about half, but essentially nothing else was affected. Therefore, higher temperatures and longer treatments may be used and still permit a reasonable survival rate. However, the data indicate that exceeding 12 hours at 35° C with the Myleran doses used here is not feasible.

Table 4

Treatment specifications, Plant Data and Mutations with Myleran

Control designation	Molarity	Time hours	Temperature °C	Alcohol*	No. of plants ($\bar{X}$)	Silking date	Plant height (cm) Early	Plant height (cm) Late	Leaf sectors "yellow green"	Leaf sectors "other"	Mutants
					Treatment--Myleran						
	.002	24	35								
	.003	24	35								
	.004	24	35		0.5†		38.0‡	-§			
	.003	12	35		2.0	32.0	31.3	119.3	200.0	75.0	
	.005	12	35		0.5†	37.0	20.5‡	90.0‡	100.0	0.0	
	.002	10	25	*	32.5	24.5	75.2	171.7	7.5	5.0	3 c
	.003	10	25	*	28.5	25.5	72.2	166.8	10.0	7.5	2 c
	.004	10	25	*	32.0	26.0	70.7	167.1	5.0	5.0	4 c, 1 wx
	.005	10	25	*	26.0	27.5	74.8	161.7	10.0	15.0	
	.003	24	25	*	9.5	28.0	59.7	143.5	26.6	37.8	5 c
					Control--Buffer						
A		10	25		35.0	25.0	81.8	175.6	20.0	7.5	3 c, 1 C
B		10	25	*	39.5	25.0	76.1	176.4	10.0	20.0	4 c
C□		24	35		14.0	25.0	78.4	174.6	7.0	21.4	
D□		24	25	*	22.0	29.0	67.6	157.3	0.0	20.0	1 wx

* 7% ethyl alcohol added to Myleran and buffer.

† Only one plant in one replication survived this treatment.

‡ Actual value for one plant, no average.

§ The plant did not survive to postanthesis.

□ One replication, see text for details.

This experiment was performed to determine efficient treatment procedures with Myleran based on physiological and genetic effects (detected from leaf sector analysis and mutants obtained). Apparent mutations have been obtained; however they have not met the criteria of Stadler (1946), nor have they been checked for correspondence or contamination. However, contamination should not be a problem, since the field was isolated from other maize and the treated stock was dominant for the genes that were analyzed.

Apparently Myleran is not nearly as efficient as ethyl methanesulfonate in producing mutations (Amano and Smith, in manuscript). Solubility may be a factor affecting its mutagenic efficiency. However, certain treatments are rather effective in producing leaf sectors and aleurone color mutations. Also, these data indicate that still more effective treatments can be devised.

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1. Further progress in perennialism of Zea.

A. Diploids. A continuation of the work of selective breeding in the Clone A family of perennial clones (MNL 38: 17-21) has resulted in the production of several 20 chromosome derivatives which can be cloned and apparently maintained indefinitely with careful handling. While they do not breed true for perennialism upon selfing, they are much more fertile than the parental Clone A. Moreover, it is the first time that factors needed for a minimal expression of perennialism have been shown to be transmitted by near diploids (though this transmission of course occurs rather readily by triploids). This indicates

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

that progress is being made in incorporating needed genes into gametophyte-viable chromosomes. Since these derived 20 chromosome perennials are maize-like, resembling maize-teosinte derivatives having more than 75% maize heredity, and produce polystichous ears, it seems fair to describe them as prototype perennial maize. Unlike Clone A, ear production does occur on long days, but on such a regime, ear formation is delayed and the organ is suppressed in size, but is competent to produce seed. Perennialism is maintained because basal branches retain totipotency. Propagation is facilitated by the production of an annulus of adventitious roots by each branch near the point of attachment to the parental plant.

Further study of Clone A derivatives partially confirms the idea that this group of material, as proposed previously (MNL 38: 17-21) is homozygous recessive for a major perennialism locus. When two "late" white maize inbreds were outcrossed to Clone A, backcrossed, and selfed, "clean" segregations were noted for the Clone A long-day phenotype, namely delayed tassel formation, and a failure of, or abortive, ear formation. This confirms the idea that Clone A has derived by means of an event whereby a major perennial teosinte locus has been successfully diploidized and is normally transmissable when inserted into 2n maize. However, this expression of the factor, provisionally named the "pe" gene, could not be identified when inserted into a white sweet corn, among five BC_1 S_1 progenies. Hence the locus is either background-dependent, or a 3% chance has "come off." Since none of the maize progenies displaying the "pe" phenotype were perennial, because they lacked basal branching, it seems possible to support the working hypothesis that perennialism displayed by the Clone A family is attributable to a major gene plus an unknown number of loci which confer basal branching and a favorable "background." Additional work has been initiated to gain further information on the nature and background dependency of "pe". It is recognized that "pe" may represent a close linkage rather than a "point" gene. It would obviously be difficult to locate its map position if available genetic stocks did not supply an effective "background."

Many massive experiments failed to produce perennial near-diploids (Genetics 50: 393-406 and unpublished results). Even though in this disappointing work derivatives often showed high degrees of branching once the first culms became florally induced, all succeeding basal branches lost totipotency, as in

pure maize. The entire Clone A family, which finally lead to success in isolating 20 chromosome perennials, was derived from a single exceptional plant. This plant and its Clone A derivatives differed markedly from all previous material in that once a basal branch was produced, it remained totipotent; hence most Clone A family near-diploids were perennial.

On the assumption that pe acts to confer totipotency upon basal branches, this "gene" was combined with the gt gene discovered by E. G. Anderson. One hundred and thirty-three seedlings, expected to segregate 15:1 for the double recessive phenotype were seeded in the greenhouse in early April, and transplanted out-of-doors in early May. Grassy tiller segregates soon cut off the first generation of tillers which in most cases ended determinately in abnormal female inflorescences in maize-like fashion. In 8 of the 133 plants, however, the "grassy tillers" grew luxuriantly, and reached a size superior to that of the main stalk. Both the first culm and the first generation tillers produce normal, fertile tassels, and polystichous, fertile ears, though these were tassel-tipped and delayed in timing. First-rank tillers soon produced a new generation of tillers. Either first or second generation tillers could be removed and easily propagated by virtue of their production of adventitious roots near the point of attachment to the parental culm. Both continued to produce further tillers after such cloning. Unfortunately, however, the third and succeeding vegetative generations were no longer indeterminant, but showed a progressively suppressed and preinduced growth habit. As of early October, the fourth vegetative generation had been produced. Four of the most vigorous of these were lifted and brought to A & M where a long day regime was initiated in a futile attempt to restore normal growth aspect to the fifth vegetative generation. As of January, 1965, only one is still alive, now on its sixth vegetative generation, but is almost certainly now dying.

While these "two gene" gt/gt pe/pe clones of essentially pure maize were not perennial, at least under the conditions described, they were possibly more perennial-like than any maize observed thus far. As of early October, the double recessive segregates described above were perfectly green, including the first culms, bearing mature ears, while their sib mates were almost completely dead. It is possible that the progressive suppression of the third and succeeding vegetative generations may have related

to a short day effect imposed by the advancing fall season, and that these two-gene clones might be perennial in a continuous regime of long days. This possibility is being tested. Moreover, the unexpected production of near-normal ears by these clones may have related to an unfortunate choice of a maize background marginal for the expression of pe. This possibility is being tested by transferring the two-gene system into a maize background in which the expression of pe is "clean." Moreover, additional syntheses are being made in which other maize loci, such as id, which confer attributes of perennialism, are being added to the gt-pe combination. Nevertheless, it appears that gt-pe maize is unique. One obvious use for it would be as a near-perennial "base" recurrent parent from which to extract pure-breeding perennial diploids from perennial teosinte or from Clone A family derivatives. Another might be as a simple modification in a seed field pollen parent to delay and spread pollen production without delayed planting. Since both gene modifications are recessive, resulting seed production would have a normal phenotype. Another might be as an evergreen-proliferative type of maize where mature ears could be harvested from a field which would then serve as a source of succulent pasturage until freezing weather.

B. Tetraploids. Rapid progress continues in breeding for perennialism and maize-likeness at the 75% maize level. While most segregates produce four-rowed ears, the frequency of polystichous ears was greater in the fourth generation of mass selection than in the third. Moreover, the incidence of plants showing production of rhizomes during the juvenile growth phase has also increased markedly. The ease with which this level of results was obtained is greatly surprising, in view of the fact that the project was begun with the expectation that it would be a 20 to 50 year task. It appears rather that if the proper effort could be supported, practical 4n maize perennial varieties could be achieved within five years. The perennial expression in general is enhanced by environmental factors which induce vegetative vigor in maize, such as cool temperatures, long days, high light levels, adequate levels of plant food, and uncrowded growing space. The expression is depressed by the opposite conditions, which are often to be found in the greenhouse. In pot culture, polystichy is depressed, as in depauperate maize, and field-polystichous segregates are often distichous in pot culture. Ear formation is greatly depressed by long days, even though tassel formation

and dehiscence proceeds. There does not, however, appear to be set ear-inducing photoperiod, but rather the threshold appears to be intrinsically set differently in each plant by genetic factors. Thus at Brookhaven, ears harvested from perennial plants on October 7 ranged in maturity stage from complete maturity to only milk stage. Basal branch formation is inhibited by "age" after a juvenile flush of activity. This inhibition is relieved by further aging of the first culms, and renewed basal growth occurs at the time maturity of seed is reached on the first culms. In marginally perennial plants, such renewed growth is often preinduced, and the branchlets, usually subtended by their own annulus of adventitious roots, can be removed and cultured, and these propagules may then terminate in a fertile female inflorescence. Axillary buds of such propagules, however, may develop as fully indeterminant culms. Hence marginally perennial plants have often shown an alteration of totipotency among the axillary buds of successive vegetative generations. Basal activity can be stimulated at any time by removing older culms. The perennial expression thus appears to be intimately associated with auxin-level controlling factors and photoperiod responses.

C. Winter hardiness. A small population of 4n perennials is being observed for winter hardiness at College Station. A small fraction still persists as of late January. Hardiness appears to have several components: 1) "resistance" to preinduction during the long fall inducing photoperiod before frost, 2) resistance to the shock of hard freeze-backs, 3) maintenance of activity by deeply placed buds, and 4) resistance to freeze injury by rhizomes, and relative frost resistance of foliage. The appearance of marked differences in the overwintering population suggests that a great deal of selection progress could be made. The often observed frost resistance of maize plants having a high sugar content suggests incorporation of C1O3 genes into perennial material as another active approach. As of now, several plants have an excellent chance to survive the winter.

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2. Further experiments in mechanical induction of tetraploidy.

A definite relationship between pollen size and chromosome number of its gametes indicates that mechanical screening of pollen produced by triploids can be used to direct triploid maize progeny into the tetraploid chromosome number range (MNL 38: 20-21). Eight additional experiments were completely successful in inducing tetraploidy. Triploid embryos, produced upon a 4n female parent, grow very readily if the collapsed pericarp is removed. Sterile techniques are not needed. Fungicide-treated abscised embryos germinate vigorously on moist filter paper in petri dishes, and if transplanted promptly to small soil pots for further establishment and hardening-off before taking to the field, produce strong mature plants with ample pollen and vigorous ear production. Sib pollination of triploid plants with the 125 micron pollen fraction obtained by screening results in many viable, plump kernels per ear. These can be grown out in the normal manner, and again sib-pollinated. While this generation is almost entirely composed of hypo-tetraploid plants, gametophyte embryo selectivity shifts the population composition toward eutetraploidy (Can. J. Genet. Cytol. 4: 226-233). If desired, a second sib generation will result in a 4n population with normally distributed chromosome numbers from which genes or linkages introduced by the original diploid can be recovered, or from which desirable 4n plants can be selected for a second cycle of backcrossing to the original diploid, if more complete recovery of the diploid genome as a tetraploid is sought.

Actual counting of chromosomes is not necessary. 4n plants can readily be identified by visual examination, by test screening of pollen for the presence of 125 micron grains or by test crossing to an established tetraploid. The technique is therefore readily adaptable to ordinary maize breeding techniques since it requires a minimum of special equipment and skill. The technique appears to be by far the most rapid and easily applied method of inducing tetraploidy thus far proposed for maize. A natural application of the method would be to solve the difficult problem of establishing aleurone and plant color genetic 4n testers. For example, if a 4n stock "pure" for the $\underline{A_1}$ $\underline{A_2}$ $\underline{C}$ $\underline{R}$ $\underline{Pr}$ series were crossed to a 2n $\underline{r}$ tester, and the resulting triploids handled as described, any post-triploid 4n recovery having a colorless aleurone would be a newly-derived 4n $\underline{r}$ tester stock.

D. L. Shaver

3. A new maize monosomic.

In examining the somatic chromosome numbers of a population of more than 300 diploid highly maize-like derivatives of maize and perennial teosinte, six plants were noted having root tips with only 19 chromosomes. Two of these plants died while still juvenile. The remaining four were later examined from microspores. Two of these had a "germline" count of 20 chromosomes, while the last two were true monosomics. Analysis of pachynema revealed that one was monosomic for chromosome 6, and the other monosomic for chromosome 9. It appears that only monosomic 6 and 10 are previously reported. An obvious use for perennialism would be to dependably maintain such rare and highly useful stocks as these, once they are found.

D. L. Shaver

4. An apparent case of andromictic reproduction in maize.

A field corn single cross was pollinated by a sweet corn hybrid by applying sweet corn pollen to aged field corn silks. Among three derived ears, one sugary-type kernel was found. This exceptional kernel grew readily and produced a vigorous, fertile plant, which was selfed. The selfed progeny bore no trace of field corn ancestry in any phenotypic trait, and completely lacked any segregation of the field corn alleles for starchy kernels and red cob. There was, however, segregation for phenotypic traits within the "type" of the original heterotic sweet corn male parent, indicating that this was not a case of haploid apomictic androgenesis. It seems most likely that the exceptional plant derived by means of double pollen fertilization, followed by fusion of two male gametes. It is, of course, possible that the exceptional embryo derived by means of apomictic development of a functioning, exceptional 2n pollen grain from the sweet corn parent, but in view of the competitive disadvantage of 2n male gametophytes, this is considered a less likely alternative.

D. L. Shaver

5. Preliminary genetic evidence for "diploid lethals" in perennial teosinte.

Several lines of evidence indicate that the massive failures described several times by the writer (e.g. Genetics 50: 393-406) to recover perennialism or other teosinte traits in derived diploids most probably relate to genetic factors carried in teosinte chromosomes which are inviable in 1n gametophytes or as homozygous loci in 2n sporophytes. "Mangelsdorf tester" was used as a recurrent parent to derive diploid maize-teosinte derivatives. Selection in the post-triploid generations against Mangelsdorf marker genes was enforced to retain heterozygosity for the teosinte chromosome regions carrying the contrasting dominant alleles. Moreover, if the teosinte region were diploid-viable, it is to be expected that such selective reproduction would rapidly result in homozygosity of teosinte segments, as a piece-meal step toward "diploidizing" the perennial teosinte genome. It was found, however, that this more elegant genetic technique of selecting for "covering" teosinte segments during the post-triploid generations had two effects: 1) A bifurcation of ploidy levels in the population from a near-diploid level back to the tetraploid level, indicating that selection for teosinte genes resulted in selection for higher and higher chromosome numbers until tetraploidy (and perennialism) was reattained. This appears to be a demonstration that the necessary array of genes for perennialism is present in the first post-triploid generation, but is lost in later PTG's (Genetics 50: 393-406). 2) A high degree of sterility and inviability persisted among the diploid bifurcate of the population. The experiment has not been highly satisfactory because these causes of mortality have greatly reduced the population sizes that could be maintained during the PTG's. For example, a diploid population of only 18 persisted in the third PTG. Among these, two were incompetent to produce any inflorescence at all, while three were completely pollen and ear barren, and two were male sterile. This pattern was very different from that of other experiments where genetic markers were not selected. Among the 13 plants producing ears by sib pollination, all seed progenies segregated for all three seed markers introduced by the maize parent, *wx*, *su*, and *Y*, except for one ear having no *wx*, but this derived from a male-sterile plant. This experience is assumed to be positive evidence supporting the "diploid lethal" hypothesis. While it was possible to maintain teosinte chromatin in diploids "covering" all tested regions, it was not possible to

obtain viable plants homozygous for the three teosinte seed trait alleles. Further experiments have been started making use of maize recurrent parents having single, multiply-marked chromosome arms.

D. L. Shaver

6. A new meiotic mutant?

In observing the cytological properties of a population of pachytene synthetic plants, a plant was found in which cytokinesis after telophase II was greatly delayed by comparison with normal plants, in which cytokinesis begins at meiotic interphase. In the putative mutant, all microspores examined showed an apparent coenocytic condition after T II. Smears revealed no trace of the beginnings of cell wall formation in what appeared to be tetranucleate microspores, well after T II. Division, however, eventually occurred, and normal, fertile pollen was produced. Good seed sets were obtained both by selfing and outcrossing to another diploid. No large pollen grains were produced and only shriveled seeds resulted from outcrossing to a tetraploid.

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1. Light effect on d_1 locus.*

Differences in manifestations at the organ level under environmental manipulation for a genetically determined locus such as d_1 give us information about the factors that influence the locus. The experiments reported here investigate the influence of light on the aspects of cell growth in which the d_1 locus participates. Seeds segregating for d_1 were germinated in two control temperature rooms at 26° C, one room in continuous

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*The cost of the computation at the Computation Center at Stanford University was partially financed by NSF grant GP 948 to the Center.

light and the other in continuous dark for 8 days. The stock carrying d_1 was backcrossed for several generations to University of Minnesota station inbred A25 and then selfed. Seed was supplied through the courtesy of E. C. Abbe. Control temperature rooms at Stanford University were loaned by P. R. Ehrlich. Thomas Cornwall assisted in the experiments. Plants in the dark room were exposed to light 8 days after planting when growth of the first leaf was complete or nearly complete. Measurements of maximum length and width of the first leaf blade were made at maturity so that all measurements would be at comparable time of growth. The mean, standard deviation, standard error, and number for each population are in Table 1. Since difference between dwarf and normal sibs is an indication of locus effect, a method for comparison of proportionate values for quantitative differences of comparable morphological units, "mean comparative intensity difference" ($\bar{X}$CID) is also listed in Table 1.

Dark-grown dwarfs had significantly longer and wider first leaves than light-grown dwarfs, while the first leaves of dark-grown normals were slightly longer and wider than light-grown normals (Table 1). Since dark-grown dwarfs had shorter and wider first leaves than those of either the light-grown or dark-grown normals, they do not phenocopy the normals. While these results are of interest, they tell us nothing about the effect of light on the participation of the locus in normal growth. We can pinpoint this information to the locus, however, if we compare dwarf-normal organ differences in light and dark using the $\bar{X}$CID as an index. If we assume that the dwarf mutation alters instructions by the locus, the degree of change as manifested in organ growth is an indication of the degree of participation by the locus in normal cell growth. The $\bar{X}$CID is therefore a guide to the normal effect of the locus through the intensity of the dwarf-normal growth difference. On the basis of these assumptions, the higher the $\bar{X}$CID, the greater is the effect of the locus in normal growth. Using this analysis, we find that dark-grown dwarf and normal sibs differ considerably less than do light-grown dwarf and normal plants in length of the first leaf blade (Table 1, $\bar{X}$CID).

This analysis of difference suggests a possible role of light on the participation of the locus in normal cell growth. Previous studies of Phinney and his group (1956, 1958, 1961, and 1963) and my recent experiments currently being written for publication indicate that the d_1 locus contributes to control of rate of synthesis leading to a gibberellin-like substance, which influences cell growth. A time regulation mechanism for the locus

is suggested by these studies. Analysis of the present experiments indicates that this time regulation is influenced by light. The greater dwarf-normal difference in leaf blade length in light growth as compared to the dark-grown difference suggests that the locus contributes to cell growth to a greater extent in the presence of light. It is possible, then, that light influences the rate of synthesis controlled by the locus. This hypothesis could be tested by comparing dwarf-normal $\bar{X}$CID of organs grown at various light intensities.

Table 1
Statistical Analysis of d_1 and Normal First Leaf Differences in Light and Dark Growth.

Leaf 1	Dark-grown N	Dark-grown $\bar{X}$	Dark-grown SD	Dark-grown SE	Light-grown N	Light-grown $\bar{X}$	Light-grown SD	Light-grown SE
Normal Length	56	58.8	± 5.7	.7	11	56.0	± 3.9	1.1
Normal Width		11.7	± 0.7	.09		10.7	± 0.6	0.1
Dwarf Length	23	40.2	± 4.7	.9	16	28.4	± 4.0	1.0
Dwarf Width		15.5	± 1.2	.2		13.9	± 1.1	2.2
*$\bar{X}$CID N:D Length		.31				.49		
Width		.24				.23		

$$*\bar{X}CID = \frac{\bar{X}_1 - \bar{X}_2}{\bar{X}_1},$$ $\bar{X}_1$ and $\bar{X}_2$ are means of two populations with $\bar{X}_1$ the larger mean.

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1. Preliminary investigations in the development of a schematic model for yield heterosis in maize.

Simple diagramatic models have served traditionally in discussions of heterosis to illustrate gene action postulated for certain allelic and non-allelic situations. Inasmuch as the total number of genes involved has been very small, no schematic representation of the entire heterotic process has been possible. The value of such expanded diagrammatic treatments will be questioned on the basis of restrictions imposed on number of loci, level of dominance, type of epistasis, etc., and on their general inappropriateness in interpreting experimental data. In spite of these limitations, it would seem that those basic genetic concepts held important in yield heterosis should be expected to function well enough collectively in diagrammatic models to give recognizable facsimiles of known yield patterns. A model which meets these latter considerations should qualify to serve as illustrative material and to stimulate further development of schematic representations, should this be deemed worthwhile. This, rather than the presentation of critical conclusions, is the purpose of this investigation.

In holding to the most widely accepted views, allowance is made for a predominance of action by dominant, favorable genes. Inter-locus effects are predominately additive with certain allowance made for non-additivity. Allelic series are used to gain variability and to force a greater awareness of their presence. Yield is treated as the terminal result of the interplay of gene action on simpler component traits in the belief that this is valid, and that it will gain greater attention in the future.

Description of the model: For purposes of the model it is assumed that (1) a multiple allelic series exists at each locus, (2) within each series, dominance of favorable alleles over less favorable alleles is the general rule, the exception involving an occasional instance of intermediate dominance, (3) gene action among loci conditioning the same trait is additive except for occasional epistasis exhibited between certain non-alleles, (4) unfavorable epistatic combinations will have been minimized under selection, (5) the various component traits are independent, non-compensatory, and show strictly a multiplicative relationship, and (6) no linkage is present.

Eight loci are assigned letter designations of a through h. These eight loci are grouped into four pairs (a and b, c and d, e and f, g and h), each pair specific for one of four different yield components. For convenience of calculation, bushel per acre values of 0.4, 1.0, 1.6, 2.2, and 2.8 are assigned to the five alleles which form the allelic series at each locus. These are values found through trial and error to give realistic yields under conditions of the model. Within each series, the alleles 1.0 and 2.2 express a strict intermediate dominance relationship whose combined value is 1.6. Dominance is expressed in all other combinations.

Epistasis involves the allele designated 2.2 at the first locus of a pair. This allele, hereafter designated "suppressor" allele, is specific in its action against either of the two alleles designated 1.6 and 2.2 of the second locus. To be involved these alleles must be the dominant alleles at their respective loci. The effect is that of completely masking the contribution of the second locus. The relationship among non-alleles is otherwise additive.

The diagram on page 31 may help to clarify some of the relationships among alleles and non-alleles within a yield component.

Yield in bushels per acre for an individual genotype is the product of the four component traits, each of these component values being the sum value of the two loci. This is illustrated in Table 1 for three pairs of inbreds and F_1 hybrids. Various combinations of alleles have produced superparental, dominant, partially dominant, intermediate, partially recessive and sub-parental effects at the yield component level. A recessive effect is also possible but does not appear in these illustrations. A deliberate effort was made to include these more extreme component effects for the sake of illustration. Comparable inbred and single cross yields are more easily attained when the dominant and partially dominant component effects alone are used.

Backcross yields: Backcross yields are described in the literature as behaving as if conditioned by additive gene action and answer closely to the formula $BC = \frac{F1 + P}{2}$. Additivity in this reference covers both within and between loci effects, thus, in the case of within locus effects, to a predominance of action by genes showing incomplete dominance. The term additive is used only with reference to between loci effects in this model. Table 2 contains the formula and model values for the backcross populations of the three crosses illustrated in Table 1.

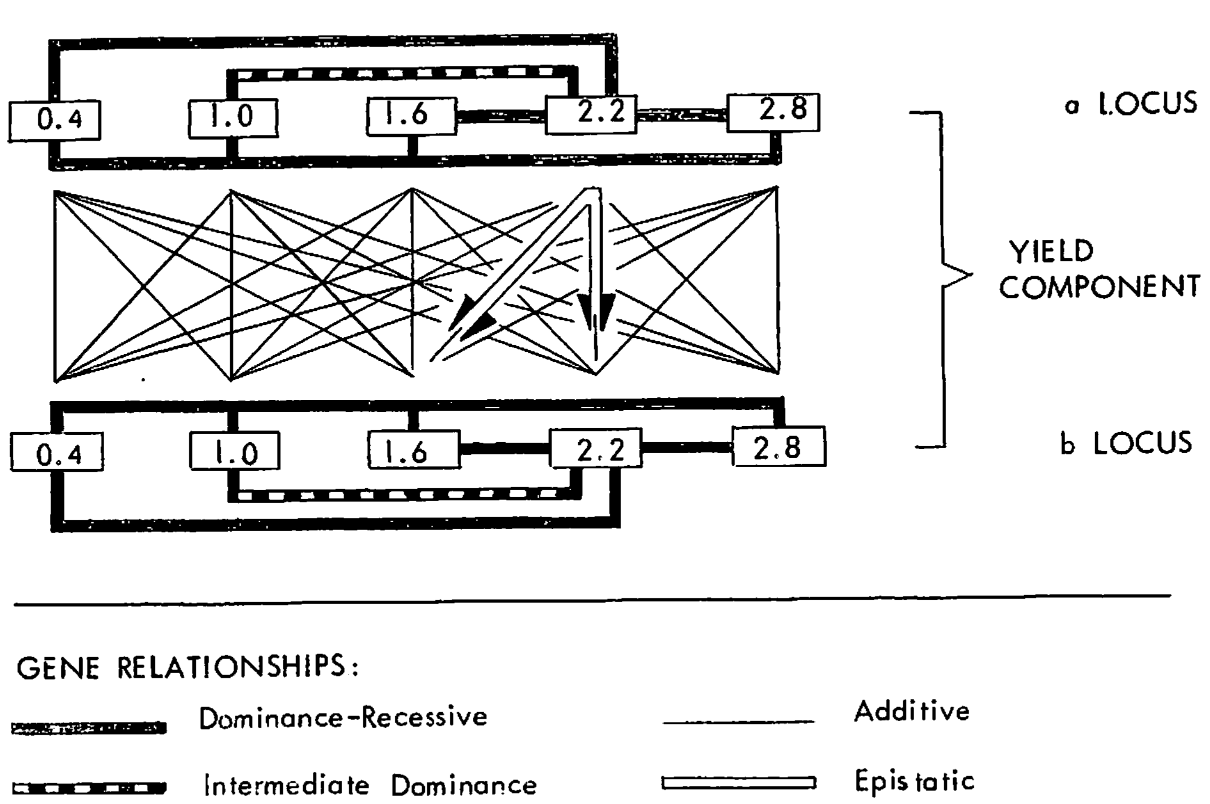
0.4
1.0
1.6
2.2
2.8
a LOCUS
YIELD COMPONENT
0.4
1.0
1.6
2.2
2.8
b LOCUS
GENE RELATIONSHIPS:
Dominance-Recessive
Additive
Intermediate Dominance
Epistatic

Table 1
Yields of Three Pairs of Inbreds and F_1 Hybrids

Yield Component	Locus	1N	1N		1N	1N		1N	1N		Apparent Gene Action at Component Level
		Inbred A			A x B			Inbred B			
A	a	2.2	2.2	-3.2	2.2	1.0	-1.6	1.0	1.0	-2.6	Subparental
	b	1.0	1.0		1.0	1.6		1.6	1.6		
				x			x			x	
B	c	0.4	0.4	-3.2	0.4	2.8	-5.6	2.8	2.8	-3.2	Superparental
	d	2.8	2.8		2.8	0.4		0.4	0.4		
				x			x			x	
C	e	1.0	1.0	-1.4	1.0	1.6	-3.2	1.6	1.6	-3.2	Dominant
	f	0.4	0.4		0.4	1.6		1.6	1.6		
				x			x			x	
D	g	1.6	1.6	-2.0	1.6	0.4	-3.2	0.4	0.4	-2.0	Superparental
	h	0.4	0.4		0.4	1.6		1.6	1.6		
				28.7 Bu/Acre			91.8 Bu/Acre			53.2 Bu/Acre	
		Inbred C			C x D			Inbred D			
A	a	0.4	0.4	-2.0	0.4	2.2	-2.2	2.2	2.2	-2.6	Partially recessive
	b	1.6	1.6		1.6	0.4		0.4	0.4		
				x			x			x	
B	c	1.0	1.0	-3.2	1.0	1.6	-3.2	1.6	1.6	-2.6	Dominant
	d	2.2	2.2		2.2	1.0		1.0	1.0		
				x			x			x	
C	e	0.4	0.4	-3.2	0.4	1.0	-3.8	1.0	1.0	-1.4	Superparental
	f	2.8	2.8		2.8	0.4		0.4	0.4		
				x			x			x	
D	g	1.0	1.0	-1.4	1.0	0.4	-3.8	0.4	0.4	-3.2	Superparental
	h	0.4	0.4		0.4	2.8		2.8	2.8		
				28.7 Bu/Acre			101.7 Bu/Acre			30.3 Bu/Acre	
		Inbred E			E x F			Inbred F			
A	a	1.6	1.6	-2.0	1.6	0.4	-4.4	0.4	0.4	-3.2	Superparental
	b	0.4	0.4		0.4	2.8		2.8	2.8		
				x			x			x	
B	c	0.4	0.4	-3.2	0.4	1.0	-3.8	1.0	1.0	-1.4	Superparental
	d	2.8	2.8		2.8	0.4		0.4	0.4		
				x			x			x	
C	e	1.6	1.6	-3.8	1.6	0.4	-3.2	0.4	0.4	-1.4	Partially dominant
	f	2.2	2.2		2.2	1.0		1.0	1.0		
				x			x			x	
D	g	1.0	1.0	-2.0	1.0	1.0	-2.6	1.0	1.0	-3.2	Intermediate
	h	1.0	1.0		1.0	2.2		2.2	2.2		
				48.6 Bu/Acre			139.1 Bu/Acre			20.1 Bu/Acre	

Table 2
Backcross Yields for Crosses in Table 1 as Derived from Formula Based on Additive Gene Action and from the Model

Inbreds Involved	Backcross Values Derived from	P_1	BC_1	F_1	BC_2	P_2
A and B		28.7		91.8		53.2
	Formula		60.3		72.5	
	Model		63.9		76.9	
C and D		28.7		101.7		30.3
	Formula		65.2		66.0	
	Model		61.2		63.3	
E and F		48.6		139.1		20.1
	Formula		93.9		79.6	
	Model		90.2		65.9	

Model backcross values in these examples fall above and below those values derived from the formula by amounts ranging from 4.4 bushels to 13.7 bushels respectively. The closest single approach is 2.7 bushels. These are quite typical for this particular model, although closer and more distant approaches to the formula values are possible. Model values in excess of the F_1 appear among segregates of the backcross populations. This is inevitable under the assumptions already made for gene action. It seems reasonable to conclude, however, that such segregates would rarely appear in practice in the face of far greater numbers of loci, and the inevitable restrictions imposed by linkage and population size.

Variety crosses: Yields from variety crosses have ranged from levels below that of the midparent value to levels exceeding that of the better parent. In order to represent wide-based populations for this study, hypothetical frequency distributions had to be established for the alleles at each locus of the model. This has been done in Table 3 for four different populations identified as Alpha, Beta, Kappa, and Sigma. Frequency distributions are symmetrical and confined to three adjacent alleles. These features are necessary in maintaining simplicity

and uniformity. As a compromise, the three-class distribution exploits a portion of the variability of the allelic series, yet allows relatively sharp differences to be drawn between opposing frequency distributions.

Table 3
Frequency Distributions for Alleles of Alpha, Beta, Kappa and Sigma

ALPHA

Loci	Alleles 0.4	1.0	1.6	2.2	2.8
a			2	11	2
b	2	11	2		
c	4	7	4		
d		3	9	3	
e	4	7	4		
f			2	11	2
g		5	5	5	
h	1	13	1		

BETA

Loci	Alleles 0.4	1.0	1.6	2.2	2.8
a	5	5	5		
b		4	7	4	
c	2	11	2		
d			5	5	5
e	5	5	5		
f		1	13	1	
g	2	11	2		
h		1	13	1	

KAPPA

Loci	Alleles 0.4	1.0	1.6	2.2	2.8
a			3	9	3
b	1	13	1		
c		1	13	1	
d	2	11	2		
e	1	13	1		
f			5	5	5
g	5	5	5		
h	5	5	5		

SIGMA

Loci	Alleles 0.4	1.0	1.6	2.2	2.8
a			5	5	5
b	1	13	1		
c	2	11	2		
d		5	5	5	
e	1	13	1		
f			5	5	5
g	4	7	4		
h	2	11	2		

Any use of these populations requires that a reasonably small sample of gametes be selected which can adequately represent the much larger array of possible gametes. Five different symmetrical frequency distributions, each comprising 15 alleles, appear among the populations of Table 3. This establishes a sample size of 15 as the minimum number of gametes needed to satisfy each frequency distribution in a given population. Four symmetrical distributions could have been established with a gamete sample size of 12, or six symmetrical

distributions with a sample size of 18. A choice among five possible symmetrical distributions was felt to be adequate for the construction of the four populations. Two samples of 15 gametes each (designated A and B) are drawn from each population. These are shown in Table 4. Each sample of gametes satisfies the frequency distribution for the alleles at each locus of its respective population. This highly idealistic approach to sampling seemed the only one available at this level of investigation.

The yield for an individual population is the average performance of the 225 combinations involving the gametes of gamete sample A crossed with sample B for that particular population. The yield for the cross of two populations is the average performance of the 225 combinations involving the gametes of gamete samples A of the two populations in question. Yields of individual populations and population crosses involving Alpha crossed to Beta, Kappa and Sigma appear in Table 5. It will be seen that three levels of population hybrid response relative to the midparent value or the higher parent have been obtained.

The construction of a population poses no particular problem other than the choice of eight frequency distributions collectively capable of giving a realistic population yield. Population crosses, however, bring together dissimilar allele frequencies with the possibilities of distinct gains or losses at the yield component level. If epistasis is weak or absent, there is a gain relative to the midparent value where one or both frequency distributions of a component are unlike. If the more favorable allele frequencies come entirely from one parent, the component gain in hybrid combination cannot equal the better parent. If the more favorable allele frequencies enter reciprocally from each parent, gains exceeding the better parent are possible. In the face of increasingly powerful epistasis there is a loss at the component level from the near-midparent level to levels below that of the lesser parent.[1] Increases in the incidence of intermediate dominance act to lessen component gains, mildly in the absence of epistasis, but more strongly in its presence.[2]

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[1]It is because of the need to exploit this effect in population crosses that a minimum of epistasis was assumed within established populations.

[2]The suppressor allele within each yield component is itself reduced by entering into intermediate dominance relationships within its own allelic series.

Table 4
Gamete Samples Drawn from Varieties Alpha, Beta, Kappa and Sigma

Variety	Sample	Loci	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ALPHA	Sample A	a	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.8	1.6	2.2	2.2
		b	1.0	1.6	1.0	1.6	0.4	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0
		c	0.4	1.6	0.4	1.0	1.0	1.6	1.6	1.0	1.0	0.4	1.0	1.0	1.6	1.0	0.4
		d	1.0	1.0	1.0	2.2	1.6	1.6	1.6	1.6	1.6	1.6	1.6	2.2	1.6	1.6	2.2
		e	1.6	1.6	0.4	1.0	1.0	0.4	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.6	0.4
		f	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	2.8	1.6	2.2	2.2	2.2	2.2
		g	2.2	1.6	1.0	1.0	2.2	2.2	1.6	1.0	2.2	1.6	1.6	1.6	1.0	2.2	1.0
		h	1.0	0.4	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	Sample B	a	2.2	2.2	2.2	2.2	2.8	1.6	2.2	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.2
		b	0.4	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.6	1.0	1.0	1.0
		c	1.0	1.6	0.4	1.0	0.4	1.0	1.6	1.0	1.0	1.6	0.4	1.0	1.0	0.4	1.6
		d	1.6	1.6	1.0	1.6	1.6	2.2	1.0	1.6	1.6	2.2	1.0	1.6	2.2	1.6	1.6
		e	1.0	0.4	1.6	0.4	1.0	1.6	1.0	1.6	0.4	1.6	1.0	1.0	0.4	1.0	1.0
		f	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	2.2	2.2	1.6	2.2	2.8	2.2
		g	1.6	1.0	1.0	2.2	2.2	1.0	2.2	2.2	1.0	2.2	1.6	1.6	1.0	1.6	1.6
		h	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.0	1.0
BETA	Sample A	a	0.4	0.4	1.6	0.4	1.6	1.6	1.0	0.4	1.0	1.0	1.0	1.6	1.0	1.6	0.4
		b	1.6	2.2	1.6	1.0	1.6	2.2	1.0	2.2	1.6	1.6	1.6	2.2	1.0	1.0	1.6
		c	0.4	1.0	1.0	0.4	1.6	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
		d	2.2	2.8	2.2	2.2	1.6	1.6	1.6	2.8	2.8	2.8	2.2	1.6	2.8	2.2	1.6
		e	1.6	1.0	0.4	1.0	0.4	1.6	0.4	1.6	1.6	1.0	1.0	0.4	1.0	1.6	0.4
		f	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0
		g	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.6	0.4	1.0	1.0	1.0	1.0	0.4	1.0
		h	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 4 Continued

BETA

Loci (Sample B)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	1.0	1.6	0.4	0.4	1.6	0.4	1.0	1.6	1.0	1.0	1.6	1.0	0.4	0.4	1.6
b	2.2	2.2	1.6	2.2	1.6	1.6	1.6	1.0	1.0	1.0	1.6	1.0	1.6	1.6	2.2
c	1.0	1.0	1.0	1.0	1.0	0.4	0.4	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.6
d	2.2	2.2	2.8	2.8	1.6	1.6	1.6	1.6	2.8	2.2	2.8	2.2	2.8	1.6	2.2
e	1.0	0.4	1.6	1.0	1.0	1.6	0.4	0.4	0.4	1.6	1.0	1.6	0.4	1.0	1.6
f	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	0.4	1.0
g	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.6	1.0	1.6	1.0	1.0	1.0	0.4	1.0
h	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0

KAPPA

Loci (Sample A)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	2.2	2.8	1.6	2.8	2.2	2.2	2.8	2.2	2.2	2.2	2.2	1.6	2.2	2.2	1.6
b	0.4	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
c	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0
d	1.0	1.0	1.0	0.4	1.6	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	0.4	1.0
e	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	0.4	1.0
f	2.2	1.6	1.6	2.8	2.2	2.8	2.8	2.2	2.2	2.8	1.6	2.2	2.8	1.6	1.6
g	0.4	0.4	0.4	1.0	1.0	1.0	1.0	0.4	1.6	1.6	1.6	1.6	1.0	0.4	1.6
h	1.0	0.4	1.6	0.4	1.0	1.0	1.6	0.4	1.6	0.4	0.4	1.6	1.0	1.6	1.0

Loci (Sample B)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	1.6	1.6	2.2	2.2	2.8	2.8	2.8	2.2	2.2	1.6	2.2	2.2	2.2	2.2	2.2
b	1.0	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0
c	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4
d	1.0	1.6	1.0	1.0	1.0	1.0	1.0	0.4	1.0	0.4	1.0	1.0	1.0	1.6	1.0
e	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6
f	2.8	1.6	2.2	2.8	2.2	2.8	2.2	2.6	1.6	2.2	1.6	2.8	1.6	1.6	2.2
g	1.6	1.6	1.0	0.4	0.4	0.4	0.4	0.4	1.0	1.0	1.6	1.6	1.0	1.6	1.0
h	1.0	1.6	1.0	1.6	1.6	1.0	0.4	1.6	0.4	0.4	0.4	0.4	1.0	1.0	1.6

Table 4 Continued

SIGMA

Sample	Loci	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sample A	a	2.2	2.8	1.6	1.6	2.2	2.2	2.8	2.8	2.2	2.8	1.6	2.2	1.6	2.8	1.6
	b	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0
	c	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	0.4	1.0	0.4	1.0	1.6	1.0
	d	1.6	2.2	2.2	1.0	1.0	1.6	2.2	1.6	1.6	2.2	1.0	1.0	1.6	2.2	1.0
	e	1.6	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	f	2.2	2.2	1.6	1.6	1.6	2.8	1.6	1.6	2.2	2.8	2.8	2.8	2.2	2.2	2.8
	g	0.4	0.4	1.6	1.6	1.0	0.4	1.0	1.6	1.0	1.6	0.4	1.0	1.0	1.0	1.0
	h	1.0	1.0	1.0	1.0	0.4	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.6	0.4	1.0
Sample B	a	2.8	1.6	2.2	2.2	2.2	1.6	1.6	1.6	2.8	2.2	2.8	2.8	2.2	1.6	2.8
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.6	0.4	1.0	1.0	1.0
	c	1.0	1.0	1.0	0.4	1.0	1.0	1.0	0.4	1.0	1.0	1.6	1.6	1.0	1.0	1.0
	d	2.2	1.0	1.6	2.2	2.2	1.0	1.6	1.0	2.2	1.6	1.0	2.2	1.6	1.6	1.0
	e	1.0	1.0	1.0	1.0	1.0	1.0	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4
	f	2.2	2.2	1.6	1.6	2.8	2.2	1.6	2.8	2.2	1.6	2.8	1.6	2.8	2.8	2.2
	g	0.4	1.6	1.0	1.0	1.0	1.0	1.6	0.4	1.0	1.6	0.4	1.0	0.4	1.6	1.0
	h	1.0	1.0	0.4	1.0	1.0	1.6	1.6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.4

Table 5
Yields of Individual Populations and of Population Crosses Alpha x Beta, Alpha x Kappa and Alpha x Sigma.

Population	Yield		
	Parental	F_1	Midparental Value
Alpha	91.3	..	
Beta	55.9		
Kappa	66.6		
Sigma	83.9		
Alpha x Beta		68.2	(73.6)
x Kappa		84.0	(79.0)
x Sigma		92.4	(87.6)

Component gains and losses are present in each population cross in the strengths necessary to give the level of population hybrid yield sought. In jockeying these effects to obtain the ascending order of population hybrid performance shown in Table 5, a strong association of population with population hybrid becomes evident. This is in accord with actual field results. The attempt to align the internal structure of population Alpha with those of the three other populations to give three specific levels of hybrid response was especially difficult. This was not possible until a detailed study was made of individual component contributions under many combinations of opposing allele frequencies. The construction of populations could then proceed in a stepwise manner. The results indicate what would be required of the internal arrangement of opposing varieties or composites under conditions imposed by the model.

Association of inbred and topcross yields: In general, the literature reports a significant positive association between the yields in inbred and topcross condition. For purposes of the model the gametes from gamete sample A of Alpha are considered as a group of inbreds from a common source population crossed in common to three broad-based testers, Beta, Kappa and Sigma. The topcross yield for each inbred is the average performance of the 15 combinations involving the respective Alpha gamete crossed with the 15 gametes representing each of the other three populations. The yield of each inbred, the topcross yields on each tester and average topcross yield on the three testers appear in Table 6. The

association of inbred yield with average topcross yield is significant beyond the 1% level.

Table 6
Inbred and Topcross Performance for Inbreds (gametes) from Alpha

Inbred		Topcross Yields			
Designation	Yield	Beta	Kappa	Sigma	Average
A1	54.5	59.3	73.9	90.4	74.5
A2	50.3	80.8	79.3	101.1	87.1
A3	23.3	35.4	56.4	60.2	50.7
A4	58.6	53.6	69.9	87.1	70.2
A5	69.2	58.3	79.9	92.9	77.0
A6	85.2	65.6	97.6	109.4	90.9
A7	69.2	63.4	97.1	98.0	86.2
A8	43.3	42.5	72.1	73.0	62.5
A9	69.2	80.6	78.3	90.8	83.2
A10	63.2	76.0	94.0	95.9	88.6
A11	66.8	102.0	91.6	95.9	96.7
A12	85.2	116.1	102.1	107.8	108.7
A13	63.2	79.7	98.4	98.5	92.2
A14	101.2	65.8	94.0	109.5	89.8
A15	43.3	43.5	74.8	75.3	64.5

Inbred yield vs. average topcross yield r = 0.79**

<u>Yield performance in diallel of high and low general combiners</u>: Among inbreds classified as high and low general combiners on common testers, the single crosses among high combiners have distinctly outyielded the single crosses among low combiners. The average performance of single crosses between high and low combiners has, in general, exceeded the midpoint between high and low groups, but has not equalled the average of the high group. For the model two diallel series of crosses were made involving the two highest and the two lowest performing inbreds based upon two evaluation schemes, average topcross performance and inbred performance per se. One inbred was common to the two high groups and the same two inbreds were involved in the two low groups. The group averages for high x high, high x low and low x low combinations appear in Table 7. In each case the average yield for the H x H and L x L groups are distinctly different. Where the initial selection

of inbreds was based upon topcross performance, the average for H x L clearly exceeds the mid-group value and, where selection was based upon inbred performance per se, the average for H x L is close to the mid-group value. This is in line with recent findings which suggest that inbred performance per se is based primarily upon additive effects whereas performance in topcross combination involves heterotic effects as well.

Table 7
Average Yields for Groups of Inbreds within Two Diallel Series Involving Two High and Two Low Performing Inbreds Selected on the Basis of Topcross and Inbred Performance. (Mid-group values in parenthesis.)

Basis of Inbred Selection	Mean Yields of Indicated Groups			Inbreds Involved Under Individual Classifications	
	H x H	H x L	L x L	High	Low
Topcross Performance	101.2	86.9 (72.3)	43.3	A11 A12	A3 A8
Inbred Performance per se	147.9	91.7 (95.6)	43.3	A12 A14	A3 A8

Summary statements: By assigning values to the alleles of an eight-locus model, it was possible to simulate rather closely the type of yield responses encountered in a typical maize breeding effort. Simulated yields were obtained for inbreds, single crosses, first back-cross generations, varieties, F_1 varietal crosses, topcrosses, and diallels among inbreds of high and low general combining ability. Salient features of the model are the use of yield components within which the members of allelic series, in non-allelic combinations, exhibit additive and non-additive relationships. Dominance, strict intermediate dominance and recessiveness are expressed among the alleles within each multiple allelic series. Yield components themselves exhibit a multiplicative relationship.

The obvious oversimplification in some features, the over-frequency in the use of other features and the uniformity of action in all features throughout the model are conditions imposed by the very limited size

of the model, and the need for simplicity and ease of manipulation. No suggestion is intended that allelic series are in fact present at all loci, or that such series are consistent in any attribute other than having more than two alleles. Furthermore, not every locus can be expected to be involved in epistasis, nor would every instance of epistasis necessarily involve only two loci. Certainly, too, one would expect to find few component traits conditioned by as few as two loci. The writer believes, however, that most features of the model, aside from those which exclude linkage and the possibilities of relationships among component traits, reflect genetic views favored by a majority of maize breeders. Even were this opinion incorrect, it would still appear that enough agreement was found between simulated and known yield behavior patterns to warrant further consideration of this approach, if only for illustrative purposes. Such schematic representations as may result can, in the writer's opinion, aid in a better understanding of the dynamics of yield heterosis.

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1. Restoration of A_1 gene action by crossing over.

Neuffer has undertaken an extensive study of a_1^{m-3} and a_1^{m-4}, two independent inceptions of control of A_1 gene action by the Ac system, to determine whether a controlling element, presumed to be associated with the A_1 gene in each case, could be removed by crossing over, thereby restoring A_1 gene action. His results were negative as are those that I have obtained during the course of studies of a_1^{m-3} and a_1^{m-4}. My data, however, are limited. My studies of a_1^{m-2}, on the other hand, have given quite different results. Restoration of A_1 gene action appears to arise from a crossover event which occurs relatively frequently with some states of a_1^{m-2} but infrequently, if at all, with others.

Nelson (personal communication) has shown that by means of a crossover, Wx gene action may be restored in tests conducted with wx^{m-1} and wx^{m-6}, two independent inceptions of control of action of the Wx gene by the Ac system, and also with wx^{m-8}, controlled by the Spm system. His method of analysis is precise in that it

allows placement of the component that is removed by the crossover.

Gene action at the a_1^{m-2} locus is under the control of the Spm system. Initially, Spm was associated with this locus. Later, it was possible to isolate a number of instances in which no evidence was given of the presence of Spm at the a_1^{m-2} locus. Action of the A_1 gene, nevertheless, remained under the control of the Spm system. States 7977B and 7995, Table 1, are instances of this. Many studies of a_1^{m-2} are conducted with plants that are a_1^{m-2} Sh_2/a_1 sh_2 in constitution and many such plants have been crossed with plants that are homozygous for a_1 and sh_2. The a_1 mutant utilized in these studies is the standard recessive that responds to Dt but not to Ac or Spm. The majority of the testcrosses that produced the data given in line 1 to 6 of Table 1 utilized the heterozygote as the ear parent. This table was constructed mainly to illustrate the frequency of appearance of the A_1 phenotype in the sh_2 class of kernels in some types of cross and their absence in this class in others. It should be stated that these data were obtained from crosses made in years in which no plants were present in the field that had A_1 and sh_2 in chromosome 3.

The data in line 1 of Table 1 were obtained from tests of A_1 mutants of a_1^{m-2}. These mutations occurred in a chromosome carrying a_1^{m-2} and Sh_2 and in plants that had an Spm whose transposition-inducing component acts early in plant development. All of these A_1 mutants were stable in the presence of Spm. Line 2 is constructed from data obtained from tests of plants carrying a stable mottled mutant of a_1^{m-2}. (This phenotype is described in Carnegie Institution of Washington Year Book No. 61, 1962.) These mutants do not produce a typical A_1 phenotype. However, in the testcrosses, 2 sh_2 kernels expressing a typical A_1 phenotype appeared. The data in line 3 came from testcrosses of plants that had Spm associated with the A_1 locus but the transposition-inducing component of this Spm acts late in plant and kernel development and, in this regard, it is very stable. (Kernels with this Spm are illustrated in B, Plate I of my report appearing in the Carnegie Institution Year Book No. 63, 1964.) It does not allow any germinal mutations to occur at a_1^{m-2} nor at a_1^{m-1} or wx^{m-8} which have been tested for this. Nevertheless, 5 sh_2 kernels with very clearly expressed A_1 phenotypes appeared on the ears that contributed the data in line 3 in the table. None appeared in the Sh_2 class. In contrast to this, no kernels with this phenotype appeared in tests of plants having an inactive Spm associated with the a_1^{m-2} locus, either in the Sh_2 or sh_2 class.

Table 1

Phenotypes of Kernels on Ears Produced by Crosses of Plants That Were Homozygous for a_1 and sh_2 with Plants That Had a_1 sh_2 in One Chromosome 3 and Sh_2 and the Markers Given in Column 1 in the Homologue

Constitution of Sh_2 chromosome	Phenotypes of Kernels					
	Sh_2			sh_2		
		A_1	Colorless		A_1	Colorless
1. A_1; mutant of a_1^{m-2}		8,959	13		12	8,906
2. Mottled: mutant of a_1^{m-2}	Mottled 10,498	0	8	Mottled 15	2	10,399
3. Spm^w a_1^{m-2}	Spm^w a_1^{m-2} 12,138	0	7	Spm^w a_1^{m-2} 10	5	12,131
4. Inactive Spm a_1^{m-2}	(see text)				0	10,843*
5. State 7977B a_1^{m-2}	" "				5	16,033*
6. State 7995 a_1^{m-2}	" "				5	8,780*
7. Spm^w a_1^{m-5} (♀ in cross)	Spm^w a_1^{m-5} 3,757	0	3	Spm^w a_1^{m-5} 6	0	3,626
8. " " (♂ in cross)	4,370	2	5	0	0	3,930

* A few of these kernels received a crossover chromatid with a_1^{m-2} but its presence in most such kernels cannot be detected visually.

The phenotypes of the Sh2 class in this cross, line 4, and in those in lines 5 and 6, have been omitted from the table because there are a number of different types and these would be difficult to arrange in this table. None of these, however, is A_1 in phenotype. States 7977B and 7995, lines 5 and 6, also produced some A_1 sh_2 kernels on the testcross ears. An active Spm was not present in the heterozygous parents. In some crosses, it was introduced into many kernels by the a_1 sh_2 pollen parent that also was homozygous for wx. Some of the plants in lines 5 and 6 had wx^{m-8} in one chromosome 9. Three of the 10 A_1 sh_2 kernels in lines 5 and 6 received wx^{m-8} from the ear parent and Spm from the pollen parent. The A_1 expression in these three kernels was completely stable but that of the wx gene was not. wx^{m-8} responded to the introduced active Spm by producing a number of endosperm sectors exhibiting various levels of Wx gene action.

Lines 7 and 8 of Table 1 are included to illustrate that no A_1 sh_2 kernels appeared in testcrosses conducted with a state of a_1^{m-5} having an Spm^w associated with it. This Spm^w undergoes frequent mutation to a state that allows early occurring transposition and thus early occurring mutations to high alleles of A_1.

Whether or not a controlling element may be removed from a locus by crossing over may well depend on the "state of the locus", as suggested by the data in Table 1, and also upon the organization of components in the comparable region of the homologue.

Two other studies aimed at removing a controlling element from the vicinity of the genes it can affect are reported below.

B. McClintock

2. Attempts to separate Ds from neighboring gene loci.

Early in the study of transposition of Ds to various locations within the short arm of chromosome 9, two instances of its insertion just distal to Sh_1 were found, the first instance in 1948 and the second instance in 1949. In both instances, Ds remained in this location thereafter. Although it did not transpose away from this location, it responded to Ac by producing dicentric chromatids and also a series of changes affecting the genes located to either side of it. The types of change were described in the Carnegie Institution of

Washington Year Books Nos. 51 to 55 covering the years 1952 to 1956. In the presence of Ac, one of these changes induced a modification affecting the adjacent proximal chromosome segment carrying the genes Sh_1 and Bz_1. Gene expression of Sh and Bz was nullified. In the presence of Ac, however, return to high levels of Bz gene action occurred but no changes to Sh expression were ever noted. Tests indicated that the segment Ds sh bz^m was inherited as a unit, as illustrated by the data given in Table 2. It may be mentioned that the presence of this unit has a strong influence on crossing over in the chromosome segment proximal to it. Studies of this were made, initially, with 10 sister plants. Five of these were Ds sh bz^m Wx/Sh bz wx; no Ac in constitution, and five had normal chromosomes 9 with the markers sh bz Wx and Sh bz wx. The ears of these plants received pollen from plants that were homozygous for C, sh, bz, and wx. Crossing over between Sh and Wx amounted to 24.6% (3,332 kernels) in the former plants and 12.6% (3,423 kernels) in the latter plants. Crossing over between the Ds sh bz^m unit and C was near normal, amounting to 4.1% in a total of 5,470 kernels on testcross ears.

Altogether 16 plants were examined, each derived from a kernel that had received a germinal Bz mutant. These Bz kernels appeared on ears produced by crosses similar to those shown in Table 2. Tests were conducted with these 16 plants and extended tests were conducted with the progeny of four of them. These tests indicated that in each case, the mutation to Bz was not accompanied by removal of Ds nor did the responsible event alter the unit of inheritance which now was Ds sh Bz. In the presence of Ac, dicentric chromatid formations occurred just distal to the locus of Bz. Return to bz^m expression also occurred in all well examined cases although the frequency of this varied with the different mutants. In the absence of Ac, however, Bz gene expression was completely stable. The Bz mutants differed from one another and from the original Bz in strength of Bz gene expression. Crossing over between the Ds sh Bz unit and Wx again was very high, amounting to approximately 25% in backcross tests using the heterozygote as an ear parent, and approaching 30% when the heterozygote was used as a pollen parent.

In order to determine whether or not Ds could be removed from the vicinity of the mutant Bz locus by crossing over, tests were conducted with plants that were C Ds sh Bz Wx/C Sh bz wx and had no Ac. These were used as ear parents in crosses with plants that were homozygous for C, sh, bz, and wx and had no Ac. Among a total of 16,578 kernels this cross produced, the

Table 2

Phenotypes of Kernels on Ears of Plants That Were C Sh bz/C Ds sh bz^{m-4} in Constitution and Had 1 Ac, Not Linked with These Markers, Produced by the Cross with Plants That Were Homozygous for C, sh, bz, and wx, and Had No Ac

	Pigment in Aleurone Layer		
	Totally Bz	Spots of Bz in a bz Background	Totally bz
Sh_1	0	0	9,177
sh_1	9	4,291	4,656

Table 3

Phenotypes of Kernels on Ears Produced by Reciprocal Crosses Between Plants That Were C Sh Bz Wx/C sh bz wx in Constitution and Had No Ac With Plants That Were Homozygous For C, sh, bz, and wx and Had No Ac or Were Homozygous for c, sh, bz, and wx and Had One or More Ac

Parentage of hetero-zygote	Phenotypes of Kernels								
	Sh Bz		Sh bz		sh Bz		sh bz		Total
	Wx	wx	Wx	wx	Wx	wx	Wx	wx	
case I									
Ear	1,201	318	1	13	17	0	332	1,185	3,067
Pollen	1,546	527	2	15	23	2	606	1,401	4,122
case II									
Ear	91	24	0	2	2	0	23	101	243
Pollen	397	157	0	7	8	1	149	356	1,075

following phenotypes appeared: 8,337 sh Bz : 1 sh bz : 2 Sh Bz : 8,238 Sh bz. The one sh bz kernel was wx and the two Sh Bz kernels were Wx. Plants were grown from each of the latter two kernels. Both plants were C Sh Bz Wx/C sh bz wx in constitution and had no Ac. Thus, contamination was excluded as the reason for the phenotype of the kernel producing each of these plants. Both plants, and also the progeny of one of them (case I, Table 3), were crossed reciprocally with plants that were homozygous for C, sh, bz, and wx, and had no Ac and with other plants that were homozygous for c, sh, bz, and wx, and had one or more Ac. No evidence was given in the latter cross of the presence of Ds in the C Sh Bz Wx chromosomes. The phenotypes of the kernels that appeared on the ears produced by these crosses is given in Table 3. Transmission of the C Sh Bz Wx chromosomes is normal through pollen and egg and crossing over between the marked intervals conforms with that expected to occur between two normal chromosomes 9. It is evident from this series of tests that removal of Ds, or its effects, has restored normal crossover potentials between the loci of Sh and Bz.

That crossing over may have removed Ds in the above described cases is supported by a much more extensive series of studies that were conducted with selected progeny of plants carrying I Ds Sh Bz in this order in both chromosomes 9 and also Ac. Seven independent instances of Ds-induced nullification of gene action in the chromosome segment immediately distal to Ds, and including the I locus, were isolated and each examined extensively. (Descriptions of these cases are given in the previously mentioned Carnegie Institution Year Books.) The events responsible for these nullifications did not remove Ds. It remained just distal to Sh. The null segment in each case behaved as if it were a deficiency although no evidence of deficiency was given by the meiotic prophase chromosomes. It was decided to use these 7 cases in order to determine if crossing over could occur between the nullified region and Ds or between Ds and Sh. These tests were conducted in 1955 and 1956 but were not reported earlier because a part of the study was never completed.

Plants with no Ac that had a chromosome 9 with the null region and also the markers Ds Sh Bz Wx, and a normal homologue with the markers C sh bz wx, were used as ear parents in crosses with plants that were homozygous for c, sh, bz, and wx, and had no Ac. The resulting ears were examined for kernels in the Sh class that were Bz pigmented and for kernels in the sh class that were colorless. These were the kernels of importance to this study. The results of these tests are given in

summary form in Table 4. The percent crossing over between Sh and Bz (region 2) and Bz and Wx (region 3) observed in these tests is also given for reference. In the three cases where the same testcross was conducted both in 1955 and 1956 (cases 1, 4, and 7 in the table) a striking degree of consistency was noted with each case in the amount of crossing over that occurred in both years within each of the three tested regions.

Plants were grown in the summer of 1956 from the types of kernels indicated in the last three columns of Table 4. Tests conducted with the plants derived from the C Sh Bz Wx kernels, and continued with their progeny, were aimed at determining the following: presence or absence of Ds in the C carrying chromosome, percent crossing over between C and Sh, degree of transmission of the C Sh Bz Wx chromosome through the pollen, and the phenotype of the seedlings that are homozygous for this chromosome. Because the number of C Sh Bz kernels was significantly larger than the number of colorless, sh kernels in cases 3, 4, and 7, either contamination or some other cause was suspected to be the reason for this. Apparently, this is true. Three of the plants derived from the 20 selected C Sh Bz Wx kernels (1 from case 4 and 2 from case 7) had the same constitution as the ear parent plant. Another kernel produced a plant that had the null segment and Ds Sh Bz Wx in one chromosome 9 and c sh bz wx in the homologue. The Bz phenotype in the kernel producing this plant probably resulted from the action of blotched on the c gene as blotched segregated in one of the tested ears of this plant. A strong expression of blotched appears occasionally and unexpectedly in the cultures. The phenotype of the remaining 16 kernels did not result from contamination or misclassification. Each had received a chromosome 9 from the heterozygous parent with the markers C Sh Bz Wx. No evidence was given of the presence of Ds in any one of these 16 chromosomes. All appeared to be quite normal. Crossing over occurred with expected frequencies between the marked intervals, and the homozygotes were normal in appearance. It was concluded that each of these 16 chromosomes was produced by a crossover that had occurred between Ds and Sh.

All of the plants derived from the 14 colorless sh kernels were bz in phenotype. One plant was very small and produced no pollen or ear. Testcross ears were obtained from the remaining 13 plants, and from their progeny. All 13 plants had received a chromosome 9 with the null segment and also sh and bz. The presence of Ds in this chromosome was detected in the progeny of 4 of these initial 13 plants. Its exact location was not

Table 4
See Text for Explanation of Contents of Table

Case No.	Year of Cross	Total No. of Kernels	Phenotypes of "crossovers" in region 1		Percent crossing over† Regions			Phenotypes of selected kernels		
			C Sh Bz	c sh	1	2	3	C Sh Bz Wx	c sh Wx	c sh wx
1	1955,1956	14,989	5	8	0.06	2.7	24.4	3		3
2	1956	7,261	6	10	0.16	2.9	27.4			
3	1956	6,066	17	8	0.54	2.4	31.2			
4	1955,1956	12,910	15	8	0.23	2.0	24.2	8		2
5	1956	7,391	14	14	0.35	2.0	31.5			
6	1956	7,100	11	8	0.31	2.3	29.4			
7	1955,1956	15,078	39	32	0.51	3.6	16.6	9	1	8
	Totals	70,795	107*	88+				20	1	13

† Calculated from the C carrying classes of kernels.

* Includes 5 double crossovers, regions 1 and 3

\+ Includes 5 double crossovers, regions 1 and 3

determined although it could be placed distal to the Wx locus. Tests of the presence of Ds in this chromosome in the progeny of the remaining 9 plants were not completed.

The project was discontinued at this juncture even though crosses had been made to obtain plants with proper constitution to determine the location of Ds in the chromosomes carrying the null segment. The main questions -- whether crossing over occurs and where this may occur -- appeared to be answered by the results already obtained. It was occurring, and between Ds and Sh and not between the null segment and Ds. At the time, it was considered that the rewards that could be expected by pursuing this project would be too meager to justify the considerable amount of effort involved in the pursuit. It should be emphasized, however, that this Ds, in the presence of Ac, causes modification in expression of Sh, located proximal to it, and this has occurred to Sh in those chromosomes that have the null segment located just distal to Ds.

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1. An analysis of chromosomal behavior during meiosis in asynaptic maize: Distribution of bivalents.

The expression of the asynaptic gene is highly variable, bivalents per cell ranging between 0 and 10. Swaminathan and Murty (Genetics 44: 1271-1280, 1959) made the interesting observation that although variation in bivalent frequency follows a binomial or Poisson distribution when the mean value per cell is low, marked deviation from a binomial distribution can be noted when this value is high and approaches half of the potential number of bivalents. This was explained on the assumption that certain pairs of homologous chromosomes entered into bivalent association more frequently than others. These authors based their conclusions on an analysis of

Beadle's (<u>Cytologia</u> 4: 269-287, 1933) data on asynaptic maize as well as data on asynapsis in other organisms. The present study was undertaken to examine the situation more critically and determine as far as possible the cause of the deviation. The recent data of Miller (<u>Genetics</u> 48: 1445-1463, 1963) were analyzed for the purpose. The method of analysis is outlined below.

The expectations for the frequency of varying numbers of bivalents can be obtained from the expansion of the binomial $(p+q)^{10}$, where p is the coefficient of synapsis or the probability that a pair of homologues would enter into synapsis (= one-tenth of the mean number of bivalents per cell), and q is the probability that a given pair would show asynapsis and equals (1-p). In case all homologous pairs within a meiocyte and all meiocytes behave alike (or if 'p' varies but slightly), observed frequencies should not differ significantly from these expectations. Deviations from a binomial distribution may result under two different situations and correspondingly two models can be set up as follows, depending on (1) differential behavior of homologous pairs within a meiocyte or (2) differences between cell populations.

<u>Model 1</u> --- Assuming the first situation, suppose there are two groups within a meiocyte with n_1 and n_2 chromosomes (so that $n_1+n_2 = 10$) with two different values of 'p' (and correspondingly two different values of 'q'). Let these values be p_1, p_2 and q_1 and q_2. It can be proven by assigning different numerical values to n_1, n_2, p_1, p_2, q_1 and q_2 that (1) the deviation would follow unimodal distribution; (2) the frequencies at the extremes would be less than those expected from binomial distribution; and (3) the frequencies in the middle would be higher than those expected from binomial distribution. The pattern of deviation can be roughly represented by Figure 1.

<u>Model 2</u> --- According to this model, the population of meiocytes (= N) may comprise groups (say, N_1 and N_2) such that (1) each of N_1 cells has p_1 and q_1 as coefficients of synapsis and asynapsis respectively and (2) each of N_2 cells has p_2 and q_2 as the same coefficients. It can be proven that the deviation according to this model would be characterized by the following. (1) Frequencies at the ends would be more than those expected from binomial distribution. (2) Frequencies in the middle would be correspondingly less. (3) The deviating distribution would be either unimodal or bimodal depending on the ratio N_1:N_2. The patterns of deviation have been indicated in Figure 2.

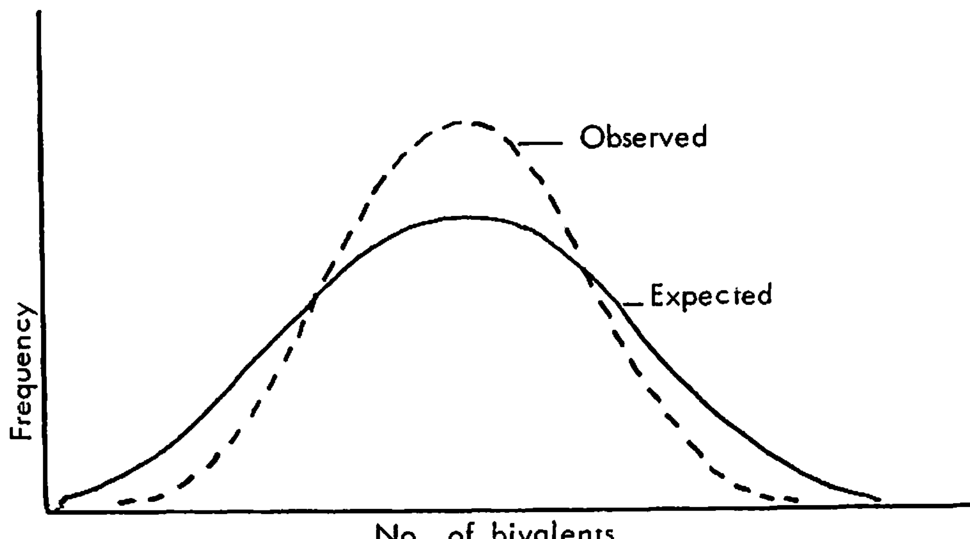

Fig. 1
Deviation from binomial distribution according to Model 1. ($p = 0.5$)

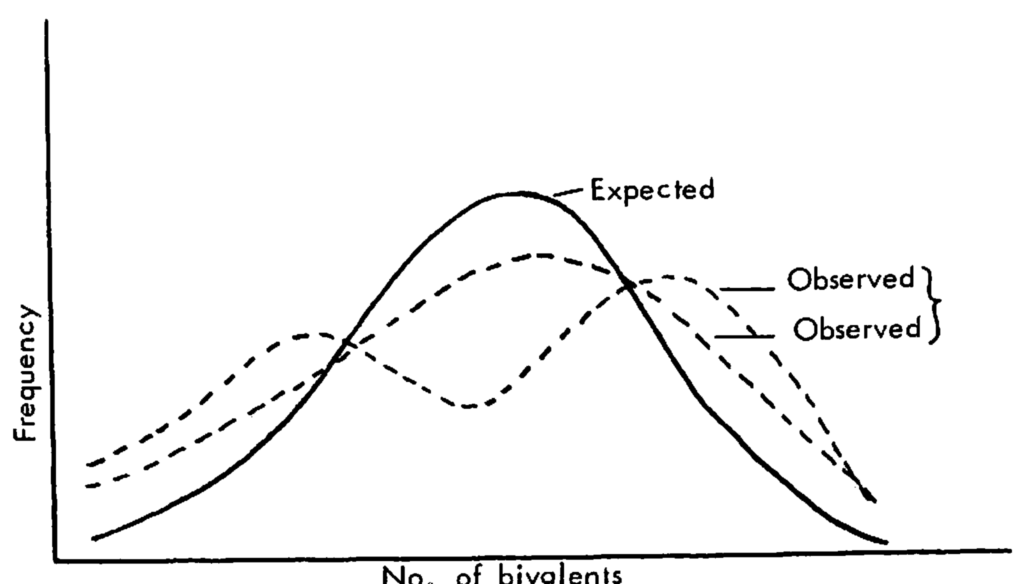

Fig. 2
Deviation from binomial distribution according to Model 2. ($p = 0.5$)

The results of actual analysis of Miller's data have been presented in Table 1. The following observations can be made:

(1) For 'p' values close to 1, the frequencies of bivalents follow a binomial distribution.

(2) For 'p' values much below 1, the observed frequencies differ significantly from those expected on the basis of binomial distribution.

(3) The deviation is of the type expected according to Model 2.

The conclusion that can be drawn from this study is different from that of Swaminathan and Murty, who inferred a differential behavior of chromosomes within meiocytes (equivalent to Model 1). However, no evidence was offered by them from the analysis of data and their inference was based on the extrapolation of certain types of preferential or nonrandom behavior of chromosomes within single cells in other organisms. The correspondence of the deviation in the present study to Model 2 may mean several possibilities such as (1) variation in chromosomal behavior (different 'p' values) in different regions (e.g. upper, middle and basal) of the same anther, (2) variation in different anthers, (3) variation in different spikelets. But there is no indication of particular chromosomes within a meiocyte being highly different in their behavior (i.e. with 'p' values deviating significantly from the average).

It is relevant to mention here that the observations of Rees and Naylor (Heredity 15: 17-27, 1960) and Rees (Heredity 17: 427-38, 1962) regarding variability in chromosomal behavior within individual anthers of rye are consistent with the present finding as to the variable expressivity of the asynaptic gene in different groups of meiocytes. As postulated by Rees (1962), such differences may be causally related to the division sequence, i.e. how early or late meiosis takes place in a meiocyte. Presumably the variable metabolic status of the cells undergoing meiosis at different times affects the expressivity of genes controlling meiotic behavior of chromosomes.

The present study helps to emphasize the fact that interesting variations in chromosomal behavior can be noted by recording and analyzing the data on individual anthers, spikelets and plants and even different regions of the same anther separately before pooling the data. Further, it may be noted that such an analytical method as employed in the present investigation would elicit more

Table 1
Analysis of Distribution of Bivalents and Pattern of Deviation from Binomial Distribution

Plant Number as in Miller (1963)	Mean No. of bivalents per cell (p)	Frequency of bivalents of varying number (Upper figures are actual observations and lower ones are those expected from binomial distribution)											Deviation significant (S) or non-significant (NS)
		0	1	2	3	4	5	6	7	8	9	10	
# 3	0.015	178 171.9	16 26.2	5 1.8	1 0								S
# 4	0.200	17 5.4	10 13.4	4 15.1	7 10.1	5 4.4	3 1.3	2 0.3	2 0				S
# 5	0.408	38 1.1	13 7.3	18 22.7	25 41.6	22 50.1	21 41.4	13 23.7	13 9.3	13 2.4	15 0.4	9 0	S
# 6	0.704	4 0	8 0	6 0.3	9 1.7	8 7.0	13 20.0	18 39.4	27 53.4	31 47.5	42 25.0	34 5.9	S
# 7	0.727	0 0	0 0	2 0.1	7 0.5	5 2.4	4 7.8	13 17.2	16 26.2	20 26.2	18 15.5	15 4.1	S
# 8	0.886					1 0	1 0.3	7 2.2	6 9.9	28 28.9	35 49.9	52 38.8	S
# 9	0.888						0 0	8 3.8	13 14.7	43 43.6	67 76.9	69 61.0	NS
#10	0.900				1 0	0 0	2 0.1	0 0.6	2 9.7	6 9.7	15 19.4	24 17.4	S
#11	0.917						1 0.1	1 1.2	8 7.5	23 31.0	39 76.1	119 84.1	NS
#12	0.976									9 4.6	30 38.6	161 156.9	NS
#13	0.995									2 0.5	18 21.5	430 428.0	NS
#14	0.995										5 4.8	95 95.2	NS

information from the data gathered from cytological studies, and thus would provide a useful supplement to the latter.

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1. Polarized variation in R-locus expression among gametes from single plants.

It is a common assumption in genetics that within the same organism gametic equivalence for a specific phenotype is the rule under conditions where explanations invoking segregating modifiers can be eliminated. In the tassel of a single heterozygous plant (*Rr*) it is expected that all pollen which carries the *R* gene will produce the same endosperm phenotypes when testcrosses are made to inbreds which carry those genes necessary for pigment production. The data presented below show that this equivalence for *R*-locus expression for pollen from within a single tassel cannot be taken for granted.

RR^{st} plants in corn grass background (a background selected for its tillering ability) were pollinated with *rr* to isolate *Rr* heterozygotes. Because of the effect of R^{st} (paramutation) the ability of *R* to produce pigment is reduced and symbolized by *R'*. The *R'r* heterozygotes were grown under field conditions; numbered plants on the first and fifth day of anthesis were testcrossed to Inbred W22 *rr*. Testcross kernels were then scored for amount of endosperm pigment present by matching *R'* phenotypes against a set of standard kernels which ranged from 0 - 22, colorless through completely pigmented respectively.

It can be noted from the data that the earliest pollen samples from a tassel have produced the lightest phenotypes; those pollinations made from florets which shed pollen on the fifth day were measurably darker.

R' Phenotypes From Pollen Collected the First and Fifth Day of Anthesis

Day Pollen Collected	50-kernel Ear Means From Five Different Tassels Tassel No.				
	1	2	3	4	5
1st	3.34	4.74	2.56	4.40	3.86
5th	5.58	5.16	4.76	6.14	4.22

It would be expected from the above data that comparisons of pollen samples from tillers of the same plant might also reveal differences similar to those found from the main tassel above. The tassels from the earliest tillers might be expected to give lighter scores than those tassels going through anthesis several days later.. The results given below show that this is the case. The tassel of the main axis, the first to begin anthesis, produces the lightest phenotypes; subsequent tassels on the same plant can be considerably darker. Thus, within each of the tassels and between each of the tassels of a single plant the R-locus expression appears to be polarized within the plant. The lightest phenotypes are produced by pollen from the upper part of the tassel among florets which pass through anthesis earliest; darker expressions will be found from pollen samples from lower florets and lower tassels which pass through anthesis several days later. Tests will be conducted to see if these differences are carried over into the next generation.

R' Endosperm Pigment Scores From Different Tassels of Same Plant

Tassel	Plant						
	#1	#2	#3	#4	#5	#6	#7
Main Stem	3.34	6.28	2.46	9.04	3.80	6.14	2.46
Tiller #1	7.74	11.06	2.56	11.18	5.00	13.80	8.14
Tiller #2	6.58	8.90	4.40	12.18	9.00	10.66	3.90
Tiller #3	6.94		3.86				

Since the above differences originated from gametes, it was of interest to enquire whether a polarized expression could also be found in somatic tissues. Closely linked to R is a gene responsible for anthocyanin pigment in anthers. The two genes have been symbolized as R^r where the superscript represents the presence of a factor for anther pigment. Plants of Inbred W22 with R^r were grown under greenhouse conditions and twenty anthers were sampled from florets at the tips and bases of tassel branches. Anthocyanin was extracted from anther walls in .1 N HCl.

Results below show that the tips of the tassel branches tend to produce anthers with less extractable pigment, while the basal florets of branches tend to produce anthers with more pigment. The pigment variation in the somatic tissue of the anther wall parallels that of the pigment produced by gametes with R' from the same relative positions.

Comparison of Anthocyanin Pigment Extracted from Anther Walls

	% Light Absorption in Anther Extracts from Different Tassel Branches*									
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10
Florets from upper part of a branch	48	35	32	23	13	79	76	72	37	37
Florets from lower part of a branch	51	37	37	28	44	82	78	83	42	45

*Samples were made from Inbred W22 RR and Rr plants.

It may be objected that the above observations are peculiar to R' expression (paramutated R) and cannot be related to "normal" R genes which have not undergone treatment with R^{st}. Where the standard R gene has been put into a tillering background and the Rr heterozygote has been testcrossed, somewhat the same orientation of phenotypes can be observed as was described above for R' expression. The variation in expression of R from pollen from the earliest tassels and latest tassels is

not as great as that of plants with R'. As seen from the data below the main tassel tends to be slightly but consistently lighter than the tillers. It has long been known that in testcrosses of R the resulting endosperm will give a "mottle" expression. The data below shows that the degree of mottling can be determined by the position of origin of the gamete in the tassel.

R-locus Expressions From Rr Heterozygotes

	Scores from four separate plants and their tillers			
	#1	#2	#3	#4
Main Tassel	15.32	18.68	20.68	18.18
Tiller #1	20.44	19.56	19.76	18.08
Tiller #2	19.90	20.16	21.40	20.14
Tiller #3	20.84	19.76	21.12	19.88

Bernard C. Mikula
Scott Warren
William Meyer
Steven Green

DEKALB AGRICULTURAL ASSOCIATION, INC.
DeKalb, Illinois

1. Screening for monoploids of maize by use of a purple embryo marker.

A new system for differentiating putative monoploids from diploids in the embryonic stage may eliminate need for germination of large numbers of kernels. This system utilizes a male parent which we have called the "Purple Embryo Marker". This marker carries a set of genes, b pl A C $R^{nj:Cudu}$ pr P^{wr} which produce a deep purple pigment in the embryo. This color is visible in the dormant kernel itself. The purple embryo marker stock also produces a purple aleurone color by which contaminant kernels, produced by accidental pollination with

male parents other than the Purple Embryo Marker, can be recognized. The kernels which do not show any purple color in the embryo but do have the purple aleurone pigment are selected as putative monoploids. These include monoploids, diploids with mutated color genes, maternal diploids and possibly other non-colored individuals. By this technique, 90% or more of the marked kernels can be discarded before germination. The few kernels saved are then germinated, the developing embryos rechecked for the marker color and root-tips taken from the putative monoploids to make chromosome counts. Those seedlings that have only one set of chromosomes per cell, the monoploids, are then saved for development of homozygous diploids. The possible value of the PEM marker was suggested to us by Dr. Irwin Greenblatt.

Sherret S. Chase
Devender K. Nanda

2. Photo-induced transformation of inflorescences in maize-teosinte hybrids.

Maize (*Zea mays* L.) - teosinte (*Zea perennis* (Hitchc.) Reeves and Mangelsdorf) crosses were made to study genotype-cytoplasm relations between the two species. The maize plants involved in this study were normal diploids, 2n=20. The perennial teosinte plants were tetraploids, 4n=40. The seeds of the first generation hybrid of the above species were planted directly in the field, near DeKalb, Illinois, during the summer of 1964. These plants grew well in the field but failed to show any signs of floral development under the influence of long day lengths. During October, 1964, a few tillers, with roots, of several of these plants were transferred to the greenhouse and subjected to the shorter day lengths of the fall season. After floral induction had been initiated, the plants were accidentally subjected to an artificially lengthened photo-period. At flowering time, partial transformation of the male inflorescences to a vegetative condition was observed.

The transformed inflorescences resembled the malformed tassels produced by the disease of maize known as "crazy top", caused by the fungus *Sclerospora macrospora* (Sacc.) Thirum. In some cases the vegetatively transformed

florets look like little seedlings growing from the tassel. Some of these "seedlings" were separated and propagated vegetatively.

Sherret S. Chase
Devender K. Nanda

3. Nodal proliferations in maize (Zea mays L.).

Leaf-life proliferations arising from the basal region of the nodal disc have been observed in Illinois and Nebraska in the inbred line DeKalb 9061 derived from an open-pollinated variety, Golden Republic, and in certain hybrids involving this line. These proliferations develop most strikingly on the two to three nodes below and the two to three nodes above the ear as well as the ear-bearing node itself. These leaf-like structures are quite brittle. The number of such proliferations may vary from a few (two to three) per node to as many as fifteen or more, and the number may be different on various nodes of the same plant. The size of these vegetative out-growths is relatively small in the inbred line itself, being about half an inch to one inch in length, while in single, three-way and double crosses, these proliferations may be very prominent and may vary from 2.5 to 3.0 inches in length. The presence or absence, and the degree of development of the proliferations is apparently greatly influenced by environment. Although the proliferations themselves do not appear to be smut induced, smut is often found associated with them. Attempts are presently being made to study the inheritance of this characteristic.

Sherret S. Chase
Warren Holdridge

4. Recovery of a cytoplasmic male-sterile androgenetic monoploid from a 4nTx2n cross in maize.

In androgenesis in maize, the male gamete, essentially a naked nucleus, presumably utilizes the cytoplasm of the female for its development into a sporophyte. Androgenesis has been found to occur at the rate of about 1/80,000 in diploid progenies of maize. If either the frequency of androgenetic individuals can be increased or their detection made more effective, this phenomenon may be profitably employed in the conversion of homozygous lines with normal cytoplasm to forms with "Texas male-sterile" cytoplasm.

Androgenesis is an abnormal event. It is conceivable that it may occur more frequently in tetraploid x diploid matings or in other wide crosses as compared to its frequency in diploid x diploid progenies. In earlier experiments, a diploid male-sterile androgenetic individual was obtained from a cross of a tetraploid cytoplasmic donor by a diploid inbred line, H52 (Chase, S. S., Jour. Hered. 54: 152-158, 1963). This plant was partially fertile and set some seed upon self-pollination. Most individuals of the second generation were completely male sterile, with the barren tassels characteristic of male cytosterility; a few plants were partially fertile; all were phenotypically indistinguishable in other characteristics from the normal diploid line.

In the present investigations, a diploid maize line, DeKalb 7088, with normal cytoplasm, was used as a male parent on the same tetraploid male cytosterile donor stock used in the prior study. This marker itself is completely male-sterile. Normal hybrids of this cross are purple triploid individuals. They are also male-sterile, due both to the cytoplasmic male-sterility inherited from the female parent as well as the reduced fertility resulting from the triploid number of chromosomes. A single monoploid individual was obtained among the progeny of the above cross. The phenotype of this monoploid was that of the male parent, with the exception that it was completely male-sterile and smaller in size. This male-sterility could be attributed to the condition of monoploidy as well as to the presence of male-sterile cytoplasm. For comparison with this androgenetic monoploid individual, a number of parthenogenetic monoploids of line 7088 were also available. The phenotypic appearance of the androgenetic individual and the parthenogenetic monoploids was very similar, as expected, and the identification of the former is considered positive. Line 7088 is itself a monoploid derivative, highly uniform, and has a very distinctive type of plant that can be readily recognized. The androgenetic individual was pollinated by normal (diploid) 7088. Twelve kernels were obtained. Nine of these kernels were planted in Florida during the winter 1964-65 for increase and observation. Seven of the plants survived to maturity. Theoretically, all of these plants should have been male-sterile but instead, only one was male-sterile and the remaining six were pollen fertile. Line 7088 itself is readily converted to cytoplasmic male-sterility by the backcross method.

We do not at present have an adequate explanation of male fertility observed in the two androgenetic progeny. We are fairly certain that it cannot be explained by error of technique or seed mixture. The important facts seem to be that

1) the tetraploid donor stock used was cytosterile,
2) the triploid ('normal') progeny of the $4n^T/2n$ crosses were completely male-sterile (more sterile than would be expected from triploidy alone),
3) the two progeny in question, the original H52 diploid and the more recent DeKalb 7088 monoploid, were undoubtedly of male origin,
4) both H52 and DeKalb 7088 can be readily converted to cytosterility by the standard backcrossing method,
5) both androgenetic individuals gave rise to progenies with some male-sterile and some male-fertile plants.

Could the explanation be a transfer of cytoplasm from the male mixing with cytoplasm from the female, this being sorted out on a particulate basis in the progeny?

Sherret S. Chase
Devender K. Nanda

5. Long term survival of pod-seed.

In 1964 volunteer plants of pod-corn appeared in a section of our breeding nurseries. The land on which the nursery was located had last been used for corn in 1962. At that time pod-corn was grown in the same area. It seems that seed must have survived without germinating or rotting through two winters and one growing season. This is of considerable interest in regard to survival of ancestral corn in the wild.

Sherret S. Chase

GEORGIA EXPERIMENT STATION
Experiment, Georgia
Department of Agronomy

1. The relative importance of genetic and environmental factors in determining oil content and oil composition of corn grain.

The relative magnitude of variance component estimates is useful in determining the importance of sources of variation. The importance of genetic (hybrids) variation relative to environmental (planting dates and locations) variation for oil content and oil composition was studied in 1962 and 1963. Nine commercial hybrids were planted on three dates (1962: April 20, May 9, May 25; 1963: April 10, May 3, May 27) at Experiment, Georgia. Variance component estimates for oil content and for 5 fatty acids of corn oil are given in Table 1. The component of variance due to hybrids was about 6 or more times greater than the variance due to planting date. The variance component due to the hybrid X planting date interaction was very small as compared to the other variance components. The results show that the genetic or hybrid factor is much more important than the environmental or planting date factor in determining oil content and oil composition.

Nine commercial hybrids were grown at 5 locations in 1962 and at 6 locations in 1963 for determination of oil content and oil composition of the grain. Locations in Georgia included the Mountain, Limestone Valley, Piedmont, and Upper Coastal Plain regions. These locations differ in soil type, temperature, and amount of rainfall. Variance component estimates for oil content and for 5 fatty acids are given in Table 2 for both years. The relative magnitude of the variance component due to locations was from 2 to 3 times less than the hybrid variance component in 1962 and even greater differences existed in 1963. Although the hybrid X location interaction was significant for several characters, the magnitude of this variance component was quite small as compared to the other sources of variation. Therefore, hybrids (genetic factors) were more important in determining oil content and oil composition than locations (environmental factors).

Total oil content was determined with Nuclear Magnetic Resonance (NMR) by the Clinton Corn Processing Company, Clinton, Iowa. Fatty acid composition of the oil was

Table 1
Variance Component Estimates from the Combined Analysis of 9 Hybrids Planted on 3 dates in 1962 and 1963

Character	σ^2_d 1962	σ^2_d 1963	σ^2_h 1962	σ^2_h 1963	σ^2_{hd} 1962	σ^2_{hd} 1963	σ^2_e 1962	σ^2_e 1963
Palmitic	0.00	0.00	0.80**	0.60**	0.06	0.10	0.15	0.44
Stearic	0.01*	0.06**	0.07**	0.12**	0.01	0.00	0.04	0.04
Oleic	0.07	0.47**	1.78**	2.74**	0.00	0.28	1.85	1.51
Linoleic	0.22	0.78**	3.31**	4.76**	0.00	0.17	1.80	2.22
Linolenic	0.00**	0.00	0.01**	0.00	0.00	0.01	0.01	0.03
Oil (%)	0.00	0.01**	0.27**	0.21**	0.00	0.01	0.04	0.02

*, ** Mean square significant at the 5% and 1% level, respectively.

σ^2_d = variance due to date of planting; σ^2_h = variance due to hybrids; etc.

Table 2
Variance Component Estimates from the Combined Analysis of 9 Hybrids Planted at 5 Locations in 1962 and 6 Locations in 1963

Character	σ^2_l 1962	σ^2_l 1963	σ^2_h 1962	σ^2_h 1963	σ^2_{hl} 1962	σ^2_{hl} 1963	σ^2_e 1962	σ^2_e 1963
Palmitic	0.18**	0.14**	0.77**	1.04**	0.00	0.09*	0.27	0.22
Stearic	0.06**	0.07**	0.07**	0.08**	0.03**	0.02*	0.02	0.04
Oleic	0.97**	1.42**	1.77**	4.05**	0.85*	0.21	1.34	1.80
Linoleic	2.03**	2.88**	3.73**	8.06**	1.09*	0.33	1.73	1.70
Linolenic	0.01**	0.01**	0.01**	0.00*	0.00	0.00	0.01	0.04
Oil (%)	0.07**	0.07**	0.21**	0.22**	0.04**	0.04**	0.03	0.03

*, ** Mean square significant at the 5% and 1% level, respectively.

σ^2_l = variance due to locations; σ^2_h = variance due to hybrids; etc.

determined with gas chromatography by J. E. Marion of the Food Processing Department at the Georgia Experiment Station.

M. D. Jellum

2. Correlation coefficients involving oil content and five fatty acids of corn oil.

In addition to genetic studies involving fatty acids of corn oil, it is desirable to determine the relationships which exist among the fatty acids or between the fatty acids and total oil content. Nine commercial hybrids were grown at five locations in 1962 and at six locations in 1963. Plantings were made on three dates at one of these locations in both years. Correlation coefficients were calculated for hybrids at individual locations and also for individual hybrids over locations. Results were similar for both 1962 and 1963. Therefore, only a representative sample of correlation coefficients are given in Table 1 for the individual locations in 1963 and for the total over locations in 1962 and 1963.

In general, all correlations involving linolenic acid were very low and nonsignificant. As palmitic acid increased, there was a tendency for stearic acid to increase. Palmitic acid and oil content were positively correlated and palmitic acid and linoleic acid were negatively correlated. Stearic acid had a weak positive correlation with oleic acid and oil content. A quite high negative correlation was obtained between stearic and linoleic acids. The two major fatty acids in corn oil are oleic and linoleic. These two fatty acids have a very high negative correlation coefficient. Work at the University of Illinois has indicated that oleic and linoleic acid content of the oil is controlled by a single gene. The Illinois workers have proposed that oleic acid is the precursor of linoleic acid. If this is true, then a negative correlation approaching the value of 1 would be expected on a single kernel basis. A quite high positive correlation existed between oleic acid and oil content and a high negative correlation was shown between linoleic acid and oil content. However, the relationship of oleic and linoleic acids with oil content is not so high that selection for high oil and high linoleic acid could not be made. Some inbred lines and hybrids have been found to be high in oil content and in linoleic acid proportion of the oil.

M. D. Jellum

Table 1
Correlation Coefficients Among Five Fatty Acids of Corn Oil and Between Fatty Acids and Total Oil Content

Character		Locations (1) Exper-iment	(2) Hamil Farm	(3) Perry	(4) Calhoun	(5) Blairs-ville	(6) Florida Nursery	(7) 1963 Total	(8) 1962 Total
Palmitic	- Stearic	0.29	0.25	0.50*	0.26	0.60**	0.53*	0.38**	0.46**
"	- Oleic	0.04	0.44	0.29	0.03	0.55*	0.24	0.27**	0.12
"	- Linoleic	-0.50*	-0.68**	-0.66**	-0.41	-0.77**	-0.66**	-0.61**	-0.54**
"	- Linolenic	-0.25	-0.57*	0.12	-0.08	-0.34	-0.01	-0.14	-0.11
"	- Oil (%)	0.50*	0.57*	0.64**	0.42	0.72**	0.70**	0.57**	0.59**
Stearic	- Oleic	0.10	0.26	0.63**	0.51*	0.65**	0.51*	0.48**	0.43**
"	- Linoleic	-0.38	-0.39	-0.78**	-0.65**	-0.74**	-0.66**	-0.64**	-0.66**
"	- Linolenic	0.12	0.00	-0.12	0.00	-0.13	-0.36	0.01	0.28**
"	- Oil (%)	0.11	0.38	0.49*	0.29	0.63**	0.34	0.31**	0.43**
Oleic	- Linoleic	-0.86**	-0.95**	-0.90**	-0.91**	-0.95**	-0.89**	-0.91**	-0.88**
"	- Linolenic	-0.53*	-0.69**	-0.41	-0.11	-0.15	-0.22	-0.30**	-0.12
"	- Oil (%)	0.62**	0.77**	0.69**	0.71**	0.80**	0.45	0.56**	0.58**
Linoleic	- Linolenic	0.47*	0.67**	0.20	0.04	0.12	0.14	0.20*	0.06
"	- Oil (%)	-0.75**	-0.79**	-0.80**	-0.81**	-0.86**	-0.67**	-0.68**	-0.73**
Linolenic-	Oil (%)	-0.40	-0.72**	-0.11	0.02	-0.21	-0.02	-0.08	-0.23**

(1) Experiment: Data from the first planting date. Located in the Piedmont region.
(2) Hamil Farm: Located near Experiment. Corn grown at high fertility level.
(3) Perry: Located in the Upper Coastal Plain region.
(4) Calhoun: Located in the Limestone Valley region.
(5) Blairsville: Located in the Mountain region.
(6) Florida Nursery: Grown at Goulds, Florida during the 1963-1964 winter.
(7) Total of six locations including the three planting dates at the Experiment location.
(8) Total of five locations including three planting dates at the Experiment location.

HARVARD UNIVERSITY
Cambridge, Massachusetts

1. The tunicate locus further dissected.

In last year's News Letter I mentioned the possibility that one of the components, tu^d, of the Tu locus is itself compound. This now clearly seems to be the case. The two tu^d mutants associated with the su Gl_3 crossover genotype, which occurred in our previously reported dissection experiment, are quite different, one being quite strong in various phenotypic expressions of tunicate characteristics the other much weaker. These facts suggest that the Tu locus may have three components, tu^l, tu^m, and tu^d. We have made crosses designed to isolate the middle component, tu^m, and may obtain the desired genotype from our winter planting in Florida. In the meantime we can be reasonably certain from other results that the three components differ in their effects. Table 1 shows seven different genotypes arranged in order of the degree of expression of various tunicate characteristics:

Table 1
Tassels of Certain Tunicate Genotypes Ranked in Order of Degree of Expression of Tunicate Characteristics

Rank	Genotype	Components	No. of Components
1	Tu Tu	l md l md	6
2	Tu tu^{md}	l md md	5
3	tu^{md} tu^{md}	md md	4
4	Tu tu^l	l md l	4
5	Tu tu^d	l md d	4
6	tu^l tu^d	l d	2
7	tu^d tu^d	d d	2

Comparison of genotypes 4 with 5 (4 components) and of 6 with 7 (2 components) show that $\underline{tu}^{l}$ has a stronger expression than $\underline{tu}^{d}$. A comparison of genotype 3 with 4 shows that md is stronger than ll and since l is stronger than d, it would seem to follow that m is stronger than either l or d.

P. C. Mangelsdorf
W. C. Galinat

2. The identification of the pollen of maize, teosinte, and Tripsacum by phase-contrast microscopy.

Size characteristics, both of pollen diameter and the pore-axis ratio have been used in the past to distinguish the pollen of maize from that of teosinte and Tripsacum. Use of measurements alone involves difficulties and size characteristics are affected to some extent by environment. Morphological characteristics of the exine studied under phase-contrast light give more conclusive discrimination even when dealing with a few grains. The pollen exine, which with ordinary light microscopy appears smooth, is shown with phase-contrast light to be beset with spinules. In maize these are regularly spaced, in Tripsacum they appear to be in clusters, in varieties of teosinte and in a maize-Tripsacum hybrid the spacing is intermediate. Quite regular spacing occurs in the fossil pollens from the Belles Artes core taken from 74 meters below the present site of Mexico City and in the pollen from the lowest level of Bat Cave. Regular spacing is also characteristic of the pollen of the Ancient Indigenous races of Mexico, Nal-Tel and Chapalote and of the primitive Peruvian races, Pureño and Confite Morocho. Highly tripsacoid maize represented by the race, Huesillo, has a pattern similar to that of the most maize-like teosintes. Lines of A158 and 4R3 modified by substituting chromosomes of teosinte for those of maize are more teosinte-like in their spinule pattern than the original lines. Guatemalan teosintes are more tripsacoid in their patterns than Mexican teosintes. Both maize and teosinte are easily distinguished from Tripsacum. Not all maize can be distinguished from all teosinte, but primitive maize can usually be distinguished from strongly tripsacoid teosinte.

Henry Irwin
E. S. Barghoorn

3. Apomixis in teosinte.

Living hybrid plants of teosinte and *Tripsacum* have not previously been obtained. In the summer of 1964, attempts were made to hybridize five varieties of teosinte with *Tripsacum floridanum*. These were grown in a well-isolated garden and the tassels and staminate tips of lateral spikes of all the plants were removed before any anthers were exserted. Before pollination with *Tripsacum*, the silks were cut back to about the length of the silks of the male parent.

Seventeen days after pollination the fruits were collected and the embryos were dissected and transferred to a nutrient agar medium under sterile conditions. A total of 90 embryos were obtained from 3223 silks pollinated (Table 1). Embryos of Chalco teosinte remained viable for a few days and died; those of Guanajuato teosinte differentiated into coleoptiles and roots but developed no further. Embryos of other teosintes grew into normal plants which appeared to be teosinte plants and all of which had 20 root-tip chromosomes instead of the 28 expected in hybrid plants. Since there is no possibility that these plants are the result of accidental self-pollination, they must be the product of some form of apomixis.

Because teosinte is normally sexually reproducing, apomixis may be an isolating mechanism preventing hybridization with *Tripsacum* similar to the *Ga* gene, characteristic of many popcorns, which produces cross sterility with *Tripsacum*.

Table 1
Results of Pollinating Five Varieties of Teosinte by *Tripsacum floridanum*

Variety of Teosinte	No. of Silks Pollinated	No. of Embryos Obtained	No. of Plants Obtained
Arroyo Seco	865	6	4
Chalco	618	37	0
Guanajuato	437	4	0
Huehuetenango	217	2	1
Jutiapa	1086	41	41

Ramana Tantravahi

4. Teosinte populations in Nobogame Valley, Mexico.

Field studies begun two years ago in Mexico (MNL 37, 1963, MNL 38, 1964) were continued and the final and most northern of the teosinte populations in the Nobogame Valley were studied. This valley is located in the Sierra Madre Occidental of Chihuahua about eight miles northeast of Guadelupe y Calvo. In all areas in both Guatemala and Mexico where teosinte and maize occur together, I have been able to find some evidence (only a single F_1 hybrid in some cases) of hybridization, but never have I found such a large number of hybrids and clear and unmistakable effects of teosinte introgression in maize cobs as exist in Nobogame. The proportion of F_1 hybrids was comparable to Chalco (MNL 37, 1963) but the extent of introgression is much clearer and, unlike Chalco, teosinte was not limited to the cultivated fields but occurred in dense stands along the streams and in protected areas on the surrounding hills (1800-1850 meters).

The most effective isolating mechanism in most areas where teosinte and maize overlap has been the mean mid-flowering date, with maize flowering two to five weeks ahead of teosinte. Nobogame teosinte is unique in that it is the only teosinte population not seasonally isolated from maize. Maize of the Nobogame Valley is a five-month type planted in May and harvested in September before the early killing frost. Both teosinte and maize reach mid-flowering in August. This is three to seven weeks earlier than the mean mid-flowering date for teosinte in the rest of Mexico.

H. Garrison Wilkes

5. Tripsacum population studies.

Field studies and collections of the Tripsacum species native to Mexico and Guatemala were begun this year. Two months were spent collecting seed, herbarium material, and live root stocks for propagation. An effort was made to collect not only all the known species but also to sample the variation typical of several parts of Mexico. Preliminary study of the collections has indicated that rigidly applied species concepts will not work with much of our material and we therefore hesitate to use species names.

The genus Tripsacum occurs throughout Mexico but is most abundant on the Pacific slopes. The greatest concentration of variation occurs in the Balsas Basin

north along the western side of the Central Plateau in Jalisco. This distribution is remarkably parallel to that of teosinte (MNL 38, 1964). Ecologically, Tripsacum shares with teosinte a preference for limestone rock and elevations from 800 to 1850 meters. The mean month of flowering is October but some of the narrower leaved forms flower in September.

Our collections include an amazing range of variation, some of which has never been described in the literature. Besides the usually mentioned variation in plant habit, (leaf length and width, spike characteristics and pilosity) we have a wealth of variation in plant colors (anthers, glumes, sheaths, leaf bases etc.). We hope to make material available for general study from 15 localities in Mexico and 5 in Guatemala as soon as clones are well established.

H. Garrison Wilkes
Raju S. K. Chaganti

6. Classification of Corn Belt inbreds.

Since the maize of the Corn Belt originated from the hybridization of southern dents and northern flints, present day inbreds can be arranged with respect to their flint or dent characteristics (Anderson and Brown, 1952). Further distinctions can be made with each of these groups on the basis of leaf and plant morphology, chromosome knob number, internal cob morphology, and ear attributes. Depending upon the degree of modification, four classes can be recognized altogether.

Table 1
The Classification of Twelve Inbreds

Dents	Modified Dents	Modified Flints	Flints
WF9	Ill A	Oh51A	Oh40B
OS420	W22	38-11	Oh07
HY		L317	
		Oh45	
		C103	

A combining ability analysis (method 2, Model I of Griffing, 1956) of the diallel crosses from the above inbreds was conducted.

Table 2
Estimated General and Specific Combining Ability Effects for Yield Per Plant from Specific Combinations of Inbreds

Parents	Gen. Comb. Ability	Dent	Modified Dent	Modified Flint	Flint
Dent	8.50	-7.21	17.17	2.65	5.69
Modified Dent	4.80		-23.22	-1.76	1.78
Modified Flint	-4.43			6.29	-5.19
Flint	2.21				-9.41

Standard Error GCA 4.37, SCA 15.84

The estimated effects for specific combining ability, with one exception, show that morphological similarity of inbreds produces low yield in hybrids.

G. S. Johnston

7. Tripsacum or teosinte introgression an obstacle to convergent improvement.

Mangelsdorf (MNL 37) has suggested that convergent improvement is not successful in developing more productive single crosses because of the deleterious effects of homozygous blocks of genes from teosinte or Tripsacum. He further surmised that this method is not a sound means of distinguishing between the different types of gene action if these blocks of genes are partially responsible for heterosis.

This situation was tested by comparing the mean performance in hybrid combination with the degree of "tripsacoidness" of the original and recovered lines of WF9 and 38-11 (obtained from J. H. Lonnquist). A tripsacoid index (Sehgal, 1964), based on the angle of rachilla inclination and induration of the rachis, was used to estimate the tripsacoid nature of each line.

Table 1
Mean Performance of the Original and Three Convergent "Improved" Lines of WF9 and 38-11 in Hybrid Combination (yield per plant in grams)

Female Parent	Male Parent				
	38-11	38-11A	38-11B	38-11C	Mean
WF9	246.8	191.6	197.9	188.1	206.1
WF9A	189.9	169.7	146.1	165.8	167.9
WF9B	220.6	186.2	176.2	170.8	188.5
WF9C	188.0	171.4	171.5	155.8	171.7
Mean	211.3	179.7	172.9	170.1	

The fact that all 15 of the crosses involving the "improved" lines are inferior in yield to the single cross of the original lines is highly significant. If differences in yield in this experiment were no more than random fluctuations, the results obtained would be expected only about once in more than 10,000 times.

Table 2
The Tripsacoid Index of the Original and Convergent "Improved" Lines of WF9 and 38-11

Line	Index	Line	Index
WF9	26.00	38-11	23.01
WF9A	26.10	38-11A	28.45
WF9B	26.10	38-11B	32.30
WF9C	27.90	38-11C	35.80

The tripsacoid index of the lines is negatively correlated (r = -0.885**) with the mean hybrid performance of the single crosses.

G. S. Johnston

8. The tripsacoid nature of dwarf versions of WF9 and HY.

Mangelsdorf and Galinat (MNL 37) found that in certain instances a reduction in plant stature was associated with tripsacoid features of the ear. Normal and dwarf versions of WF9 and HY were compared with respect to the tripsacoid index.

	WF9	WF9 Dwarf	HY	HY Dwarf
Index	26.00	35.05	29.75	39.80

WF9 dwarf has been found to be a form of brachytic-2 (Lonnquist) and has its locus on chromosome 1 (Lambert). In isolating chromosomes with strong effects from teosinte or from tripsacoid races of maize of Mexico, Central and South America, Mangelsdorf found chromosome 1 to be frequently represented as the chromosome responsible for the tripsacoid effects.

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1. Tripsacum dactyloides homeolog to corn chromosome 9 covers three short arm recessives.

The recessives sh_1, *bz* and *wx* on the short arm of chromosome 9 have dominant counterparts on one chromosome in *Tripsacum*. The long arm will also be analyzed.

W. C. Galinat
P. C. Mangelsdorf

2. Chromosome arm differences between corn and Tripsacum.

Two cases have appeared where genes on one arm of a corn chromosome correspond to a different Tripsacum chromosome than those from the other arm. These involve the arms of chromosomes 2 and 4. The results from two species of Tripsacum, *T. dactyloides* and *T. floridanum*, were identical.

In the case of chromosome 2 of corn, the v_4 locus on the long arm has a dominant counterpart in Tripsacum on a different chromosome than the short arm genes lg_1 gl_2 as well as a third locus, ws_3, tested by Maguire (1962). In our "addition monosomic" (20+1) stocks on lg_1 gl_2 v_4 corn, the extra chromosome from Tripsacum has dominants which covered only lg_1 gl_2 but never v_4 in some stocks, while in other stocks the v_4 locus is covered but never lg_1 gl_2.

Maguire (1962) noted that while the three loci (ws_3, lg_1, gl_2) are on the short arm of a corn chromosome, they are on the long arm of a Tripsacum chromosome. This agrees with our location of the v_4 locus on a different Tripsacum chromosome than the other three genes mentioned. Apparently an ancient removal of all or part of the v_4 locus arm from the original chromosome 2, changed the relative length relationships of its armsin present day Tripsacum, at least in *T. dactyloides* and *T. floridanum*.

In the case of chromosome 4 of corn, the su_1 locus on the short arm has a dominant counterpart in Tripsacum on a different chromosome than the gl_3 locus on the long arm. Thus, as in the previous example, the extra chromosome originally from Tripsacum can cover sugary but not glossy-3 whereas a different extra chromosome in other stocks covers glossy-3 but not sugary. Furthermore, the Gl_3^T chromosome of Tripsacum has been observed by Chaganti to be smaller and distinct from the Su_1^T chromosome of Tripsacum.

W. C. Galinat
P. C. Mangelsdorf

3. Gross translocations or fragmentation in Tripsacum chromosomes?

In discussing Tripsacum as a possible ancestor of modern corn, Cutler (Lloydia 10:229-234, 1947) mentions that the chromosome number in present day Tripsacum

could have been increased from 10 to 18 by either duplication or fragmentation. We have already ruled out duplication on a basis of the transmission rate of dominantly marked Tripsacum chromosomes onto seven recessively marked corn chromosomes in the "WMT" stock and also on a basis of the number of Tripsacum chromosomes which are unmarkable in terms of the "WMT" marker genes.

If our hypothesis that Tripsacum is an amphidiploid of wild corn and Manisuris is correct, then we may also rule out fragmentation. The fact that some of the Tripsacum chromosomes, which are unmarkable in terms of the "WMT" genes, have Manisuris-like effects supports this hypothesis (MNL 38: 50-51, 1964). However, the data presented in the previous item suggests that some translocations involving entire arms of chromosomes have occurred and have set the stage for introgressive evolution. Following an introgression of this "manisuroid" germplasm into corn, two forms of selection have yielded two distinct products. Teosinte is the product of natural dissemination and modern corn is the product of dissemination by man.

W. C. Galinat

4. Possible unreduced eggs in corn x *T. floridanum* hybrids and hybrid derivatives.

The success in making the first backcross of a corn-Tripsacum hybrid to corn is dependent upon the production of unreduced eggs by this hybrid. In the case of our WMT corn x *T. dactyloides* hybrid, we had to resort to doubling the chromosomes with colchicine in order to get these fertile, "unreduced-type" eggs. But corn x *T. floridanum* hybrids are highly fertile without doubling the chromosomes and this has led Chaganti to suspect that this species may contain a factor similar to the elongate gene which causes unreduced eggs in corn.

This suspicion has been strengthened by the peculiar nature of a segregation involving *T. floridanum* chromosomes. Although the transmission rate for the homeolog to the short arm of chromosome 2 from *T. dactyloides* has remained constant at about 23% for four generations, a much higher transmission frequency as well as some large off-type plants have occurred in the second backcross to corn of a lg_1 gl_2 v_4 x *T. floridanum* hybrid. The increase in transmission over that expected for the random segregation of a Tripsacum chromosome corresponds to the frequency (25%) of these large plants, as shown in the table. They are highly suggestive of their 3n parent

in being excessively tall and profusely tillered. Chaganti suggests they result from unreduced eggs and is studying the cytology of these plants at Andhra University in Waltair, India in order to determine this.

Genetic Data for Transmission Rate to 57 $\underline{lg_1}$ $\underline{gl_2}$ $\underline{v_4}$ Corn Plants of Two Dominantly Marked *T. floridanum* Chromosomes Derived from a Corn-Tripsacum BC_1 Hybrid

	Arm of corn chromosome 2	
	Short	Long
Dominants from Tripsacum	Lg_1Gl_2	V_4
Rate (%) excluding plants from "unreduced eggs"*	54.5	38.6
Rate (%) including plants from "unreduced eggs"	63.2	66.6

*The large plants resembling their 3n parent and which may be Z(ZZT).

W. C. Galinat
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1. Year-round corn in Hawaii.

Sweet and field corn varieties are grown regularly throughout the year at most of the 13 field experiment stations of the University of Hawaii. The stations embrace a wide range of climates, from wet to arid, subtropical to temperate. Corn is grown commerically from sea level to 4000', almost exclusively in summer months. A picture of the range of variation encountered is given below for Golden Cross Bantam sweet corn (7' in height, 85 days to harvest, in corn belt):

Station	Elevation, Conditions	Annual Rainfall	Month Planted	Mature Height	Days to Harvest	Relative Yield
Poamoho	100'; clear	50"	June	7'	64	100%
"	"	50"	Dec.	5½'	68	90%
Waimanalo	Sea level; partial overcast	60"	June	6'	66	90%
"	"	60"	Dec.	5'	70	75%
Haleakala	3000'; partial overcast	100"	June	4½'	85	75%
"	"	100"	Dec.	3½'	102	50%

At the lower elevations in Hawaii, it appears that the short daylengths (11.5 to 12.5 hours) combine with high night temperatures (avg. 72 in July and 69 in January in Honolulu) to telescope down the growing seasons of corn belt varieties and hybrids, reducing ear lengths and yields. At higher elevations in Hawaii, the cool temperatures lengthen growing seasons. Adaptability to the short daylengths, rather simply inherited, is fairly widespread among field and pop corns, but uncommon among sweets (most of which trace to northeastern flints). Present corn breeding in Hawaii is confined largely to sugary and shrunken stocks.

Genetic marker stocks, such as McClintock's Chromosome 9 marker lines, have been planted in most months of the past three years and satisfactory seed yields obtained. Control of earworms and of leafhoppers which transmit a serious sweet corn mosaic is practiced routinely; Helminthosporium has not posed a significant problem. We would entertain interest in genetic nurseries in Hawaii during winter seasons.

J. L. Brewbaker

2. Genetic resistance to a mosaic-stripe virus transmitted by *Peregrinus maidis*.

A devastating disease of corn in Hawaii and Central America is corn mosaic, transmitted by the leafhopper, *Peregrinus maidis*. Epiphytotics maintained at the University of Hawaii stunt all commercial sweet corn hybrids to non-flowering dwarfs under two feet in height. The mosaic, known as corn stripe in Central America, is distinguished also by clearing immediately above the veins.

Resistance to corn mosaic was found to characterize most plants of three tropical sweet corns -- Hawaiian Sugar (bred by Al Mangelsdorf from USDA34), Pajimaca (Cuba), and Maiz Chiripo Dulce (Mexico), as well as some plants among a dozen other tropical and field pop corn varieties. Over 200 other accessions were wholly susceptible.

Resistance of Hawaiian Sugar was shown to be under monogenic control with dominance lacking (full data to be published). Hybrids of resistant x susceptible inbred lines varied widely in mosaic severity, ranging from symptom-free plants to severely-stunted plants. Mosaic scores of 14,207 plants on a 1 (resistant) to 6 (severely stunted) scale averaged as follows:

Resistant Parent	1.25	F_2	3.44
Susceptible Parent	2.46	Backcross to Res.	1.92
F_1	2.46	Backcross to Susc.	4.07

Monogenic control was determined from a semi-quantitative approach to these data. The data represented ten different combinations of 6 susceptible and 6 resistant inbreds; no genetic differences were observed within the two groups of inbreds.

The mosaic resistant locus has been designated *rM/rm* (*r*esistant to *m*osaic). Since the field reaction of heterozygotes appeared more like that of the resistant parent, the *rM* allele has been used to designate resistance, without inferring dominance of this allele.

Crosses were made of a resistant inbred to the *wx* translocation stocks (mosaic susceptible) from the Maize Genetics Coop. Unfortunately, the waxy tester (McClintock's) used for backcrosses later proved to have some resistance, obscuring segregations; nonetheless, crosses with both Chromosome 1 and Chromosome 6 testers were aberrant enough to warrant further study.

Resistance does not involve reduction of leafhopper oviposition. Rather, it appears to involve the suppression of viral development in relation to dosage of the rM allele.

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1. Female fertility of maize x Tripsacum dactyloides (4N) hybrids.

In last year's newsletter (38) results were reported on hybrids between certain maize translocation stocks and certain Tripsacum dactyloides plants collected in Illinois. All F_1 hybrids obtained were grown in the nursery and backcrossed to maize. Female fertility of some of the F_1 hybrid plants was greater than expected. The hybrid plants with exceptional female fertility all involved 4N Tripsacums as the male parents. Hybrids of this type have 10 corn and 36 Tripsacum chromosomes, and as a result of this high degree of chromosome imbalance a large percentage of female sterility should result.

The number of seeds set on these exceptional F_1 hybrid plants is presented in the following table:

	No. Plants	No. Seeds Set	Total No. Ovules	Mean % Set	Range in Percent High Low
1. T_1-6c x T.d. Horseshoe Lake E-11 (4N)	22	250	1466	17.05	48.31-0
2. T_1-6c x T.d. Horseshoe Lake E-10 (4N)	3	78	157	49.68	71.43-0
3. T_1-6c x T.d. Horseshoe Lake N-15 (4N)	8	118	706	16.71	83.33-0

For two of three hybrids the female fertility (as measured by number of seeds set) is not greatly different from the ten percent female fertility usually obtained from hybrids between 2N Tripsacums and maize. However, the third hybrid averaged 49.68% female fertility for three plants. In addition, the range in female fertility was large for each of the crosses. In number three one plant had 83.33 percent female fertility, but only ten seeds were obtained from twelve possible, which is a very small sample. However, one plant in hybrid number two had 71.23 percent female fertility. This plant produced 52 seeds out of a total possible of 73.

Individual rachises varied considerably in amount of female fertility. Three rachises out of 16 had 100 percent female fertility and 6 had more than 50 percent female fertility.

Farquharson (Am. J. Bot. 42-737) has reported the occurrence of facultative apomicts in *Tripsacum dactyloides*. Her results indicated that this type of apomixis was limited to 4N plants studied. The high degree of female fertility observed in these hybrid plants could have been the result of apomixis. This type of reproduction may have been transmitted from the Tripsacum parent to the hybrid. However, further analysis of the offspring is necessary before verification is possible.

R. J. Lambert

2. *Aberrant segregation of a brittle-1 allele from teosinte.*

In a program to evaluate strains of teosinte by backcrossing to maize, a brittle-1 allele was isolated from backcross-3 progeny selfed which contained Guerrero 258 as the teosinte parent. The test for allelism to brittle-1 produced progeny that were all brittle-1. Tests with other endosperm mutants were negative. Testcross data were 150 $Bt_1/-$:132 bt_1/bt_1 (P = .5-.3). However, a selfed ear, produced in 1963, from homozygous brittle seed gave a ratio of 105 $Bt_1/-$:103 bt_1/bt_1. The possibility of contamination or misclassification of $Bt_1/-$ seed from this ear could not be ruled out. When brittle-1 seed from this ear was planted in 1964 and selfed, one ear again gave a definite 1:1 segregation ratio (44 $Bt_1/-$:40 bt_1/bt_1). A tentative explanation for this aberrant segregation is that the endosperm classes have the following phenotypes:

$\underline{Bt_1}$ $\underline{Bt_1}$ $\underline{Bt_1}$	Normal
$\underline{Bt_1}$ $\underline{Bt_1}$ $\underline{bt_1}$	Normal
$\underline{Bt_1}$ $\underline{bt_1}$ $\underline{bt_1}$	Brittle *(unusual class)
$\underline{bt_1}$ $\underline{bt_1}$ $\underline{bt_1}$	Brittle

Work is planned to determine the frequency of this aberrant ratio in the population in an attempt to clarify further this unusual segregation ratio.

R. J. Lambert

3. Location of glossy-4 in relation to cytological breakpoints of paracentric inversions in chromosome 4L.

A series of paracentric inversions obtained from Dr. Gregory Doyle was crossed to su gl_4 stocks in order to determine the location of glossy-4 in relation to the proximal breakpoints of six different paracentric inversions of 4L. The recombination value between sugary-1 and glossy-4 was used as a measure of the location of glossy-4 in relation to the cytological breakpoints. The following table gives the results for the testcross data:

Testcross	Parent Types		Cross-overs		% Recombination
	Su_1 Gl_4	su_1 gl_4	Su_1 gl_4	su_1 Gl_4	
Inv. 4e (.16L-.81L) x su gl4 / su gl4	463	400	5	5	1.16
Inv. 4f (.17L-.63L) x su gl4 / su gl4	604	622	7	9	1.30
Inv. 4i (.19L-.66L) x su gl4 / su gl4	576	555	6	2	0.07
Inv. 4j (.24L-.66L) x su gl4 / su gl4	682	688	87	75	11.82
Inv. 4a (.30L-.90L) x su gl4 / su gl4	634	649	45	36	6.31
Inv. 4d (.40L-.96L) x su gl4 / su gl4	618	619	71	60	10.59

Cytological breakpoints determined by D. Morgan, R. Morris and A. E. Longley.

Based on normal recombination values (15%) between su_1 and gl_4, the data indicate that glossy-4 is proximal to the breakpoint in inversions 4j, 4d and probably 4a. Glossy-4 is probably distal to the proximal breakpoint in inversion 4e, 4f and 4i. The recombination value between su-gl_4 (6.31%) for inversion 4a is lower than expected. This may be the result of the proximal breakpoint reducing crossing-over in the su-gl_4 region. Additional material will be analyzed to determine the frequency of the inversion in the crossover classes to obtain a more precise location of glossy-4 in relation to the inversions.

R. J. Lambert

4. Inheritance of linoleic acid in corn.

Gas-liquid chromatographic analyses were made on individual kernels of R84, Illinois High Oil, and the F_1, F_2 and backcross progenies. Oil was extracted with petroleum ether, esterified and then dissolved in approximately 1 ml petroleum ether. Three µl of the solution was injected into the chromatograph. All analyses were made on an Aerograph Hi-Fi 600 using the standard diethyleneglycol succinate-chromosorb W Column. A flame ionization detector was used.

The frequency distributions in the backcross populations strongly suggest monohybrid inheritance for oleic and linoleic acids, i.e., low linoleic is dominant to high, and low oleic is recessive to high. The F_2 data were less convincing, although individual F_2 ear analyses revealed that the ratio in only one ear out of six was quite deviate, presumably because Illinois High Oil was heterogeneous with respect to the alleles in the system. Segregation in only one of the six F_2 ears is shown in Figure 1.

Table 1
Mean Linoleic and Oleic Acid Content of Individual Kernels of Parents, F_1, F_2 and Backcross Generations

Population	Percent of Total Oil		
	Linoleic[1]	Oleic[2]	Sum
R84 ⊗	61.3	24.5	85.8
IHO ⊗	48.8	35.3	84.1
F_1(R84 ♀)	52.2	31.3	83.5
F_1(IHO ♀)	47.6	36.1	83.7
BC R84	54.3	29.1	83.4
BC IHO	51.2	32.5	83.7
F_2	51.5	32.3	83.8

[1]Standard deviation = ±1.32%
[2]Standard deviation = ±0.78%

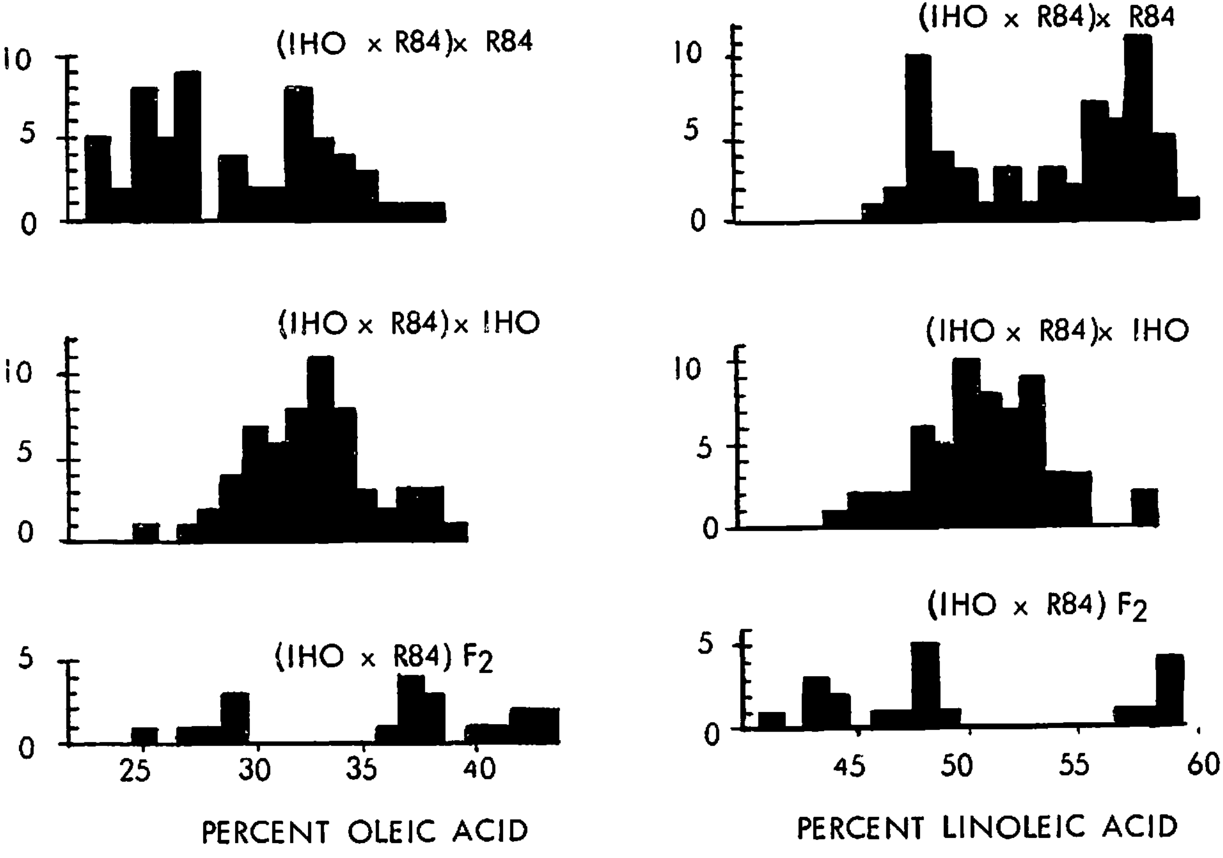

Figure 1
Frequency distributions of linoleic and oleic acid content of individual kernels

In corn, Jellum and others, found a high negative correlation between oleic and linoleic acids. In our studies involving analysis of individual kernels, (1) low linoleic acid content was always associated with high oleic acid content and vice-versa, and (2) the genetic models for the control of amount of each acid are "mirror images". The data suggest that the two are closely related in the unsaturated fat bio-synthetic pathway.

It has already been suggested by others that oleic acid is the precursor of linoleic acid in higher plants. Our evidence supports this proposal, that is:

$$\underset{18C^{\Delta 9}}{\text{Oleic}} \xrightarrow[\text{Lnl, lnl}]{} \underset{18C^{\Delta 9,12}}{\text{Linoleic}}$$

If _Lnl_ is present, desaturation at the 12-13 position proceeds so that the oleic-linoleic pool maintains an approximate 35:49 ratio, whereas if the genotype is _lnl/lnl_, a ratio of approximately 25:61 is maintained. That is, if _Lnl_ is present, net desaturation is lower, bringing about an accumulation of oleic acid, whereas in _lnl/lnl_ individuals, net desaturation is higher, thus increasing the linoleic pool and decreasing oleic.

Further genetic studies are underway, involving newly-discovered strains possessing 42 percent linoleic acid.

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1. Location of _Ht_ in the long arm of Chromosome 2.

In the 1963 Maize News Letter, the symbol _Ht_ was proposed to designate the dominant gene in Inbred GE440 for chlorotic-lesion resistance to _Helminthosporium turcicum_. Data were reported showing that in plants heterozygous for Inversion 2a (2S.7; 2L.8), recombination between _gl_$_2$ and _Ht_ was about 17 percent.

Testcross data involving v4 and Ch show that Ht is in the central region of the long arm of Chromosome 2:

$$\frac{v4 \quad + \quad Ch}{+ \quad Ht \quad +} ♀ \quad X \quad v4 \quad + \quad + ♂$$

Classes	Families 4019-20	4021-22	4023-24	4025-26	Total
(0) v + Ch	17	18	20	20	75
(0) + Ht +	21	25	22	19	87
(1) v Ht +	5	7	8	9	29
(1) + + Ch	11	6	8	8	33
(2) v + +	16	13	9	15	53
(2) + Ht Ch	14	17	7	12	50
(1,2)v Ht Ch	3	2	1	3	9
(1,2)+ + +	2	1	5	4	12
	89	89	80	90	348

Recombination:

v4 - Ht   83/348 = 23.9%

Ht - Ch   124/348 = 35.6%

v4 - Ch   165/348 = 47.4%

Order: v4 - Ht - Ch

The linkage values above suggest that Ht may be fairly near the locus of w3. Crosses to determine the linkage relations and order of Ht, w3, and Ch will be grown next summer.

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1. A mutant dehydrogenase.

Mammalian tissue shows high lactate dehydrogenase activity and little if any malate dehydrogenase. The opposite is the case in corn. There is little if any lactate but much malate dehydrogenase activity in endosperm and seedling material. In starch gel electrophoresis this activity is found distributed in two major and one minor bands. This note deals with studies on an alcohol dehydrogenase which is found in endosperm and seedling material. The enzyme migrates to the anode at pH 8.5. A mutant form of this dehydrogenase has been found in an su_2 strain of corn but the mutant enzyme and mutant phenotype are independently controlled. The mutant enzyme also migrates to the anode but at a slower rate than the common form. A hybrid dehydrogenase with an intermediate migration rate is formed in heterozygotes. Homozygotes for the common or mutant alleles show only a single band while three dehydrogenase bands are found in the heterozygotes.

The mutant dehydrogenase shows reduced activity in comparison with the common form. In heterozygous endosperm having two doses of the common allele and a single dose of the mutant, the fastest migrating band is the most intense, the intermediate hybrid band is much lighter, and the slow migrating band can hardly be detected. In endosperm from the reciprocal cross, with two doses of the mutant allele, the isozyme pattern is quite different. The fast and slow migrating bands are about equal in intensity and the hybrid band is heavier, giving about a 1:2:1 ratio for the three bands. If the common and mutant alleles were equally active and the enzymes specified by these alleles were also equally active, the three bands formed from random dimerization of the monomers in heterozygous endosperm with two doses of the mutant allele should occur in a ratio of 1:4:4 for the fast, hybrid, and slow migrating bands, respectively. Since the slow band has about the same intensity as the fast band we conclude that either the mutant allele is one-fourth as active as the common allele, or the slow migrating dehydrogenase is only one-fourth as active enzymatically as the fastest migrating dehydrogenase. The former is the favored hypothesis. This dehydrogenase is also found in the very young seedling. In heterozygous seedlings the three bands occur in a 1:2:1 ratio as would be expected from equal activity of both alleles and both enzyme

forms in diploid tissue. It is unlikely that the enzymes formed by the same allele in different tissues have different specific activities, but not impossible. We propose that in the seedling both alleles are equally active but in the endosperm the mutant allele is partially repressed. A similar situation was found for the pH 7.5 esterase when the relative activity of two alleles in different tissues was compared.

Drew Schwartz
Toru Endo

2. Further studies on preferential segregation.

In the 1958 Maize News Letter data were presented showing that the preferential segregation produced in non-homologous chromosomes by abnormal 10 occurred only when there was crossing over between the knob and the centromere to produce heteromorphic dyads consisting of one knobbed and one knobless chromatid. The test referred to above came from plants with a normal chromosome 9 and one in which a piece of 3L had been inserted into 9S between the Sh and Wx loci. The latter chromosome was designated Dp9. Crossing over in the entire length of 9S was found to be greatly reduced when the Dp9 chromosome was heterozygous. When plants heterozygous for Dp9 and abnormal 10 and also heterozygous for the terminal knob in 9S were testcrossed as the female parent, there was a striking reduction in the degree of preferential segregation for the distal Yg2 marker in 9S compared to that found in sib plants homozygous for normal chromosomes 9. The conclusion was drawn that the formation of heteromorphic dyads via crossing over is an essential antecedent to preferential segregation. That this conclusion is indeed valid is shown by the following experiments involving chromosomes 3 and 9.

The rearranged chromosome 9, (R)9, studied by McClintock (1944) is known to drastically reduce the amount of crossing over in the short arm of 9. The (R)9 chromosome possesses a terminal knob of medium size on its short arm. Plants heterozygous for the (R)9 chromosome and for the wd and wx markers were test-crossed as the female parent. Sib plants with and without abnormal 10 were available. As expected there was an extremely low amount of crossing over between wd-wx in the homozygous k10 plants and the contrasting alleles for the two segregating loci were each recovered in 50% of the progeny. Although plants heterozygous for a knobbed 9 and a knobless 9 (wd) undergo preferential

segregation if K10 is present, no marked deviations from a 1:1 ratio for Wd:wd would be expected in K10 plants if crossing over was a requisite for preferential segregation. On the other hand, the usual percentage of preferential segregation found in K9 k9 heterozygotes should occur if preferential segregation of K9 chromatids to the basal megaspore is unrelated to recombination and is due to some intrinsic property of the knobs. The data obtained from both K10 k10 and k10 k10 backcrossed individuals show a very close fit to a 1:1 ratio for both the wd and wx loci. This experiment, like the Dp9 tests, indicates that preferential segregation is dependent on crossing over.

Substantiating data were also obtained from studies of plants heterozygous for three paracentric inversions involving the long arm of chromosome 3. The breakpoints of In 3a are 3L .4 and .95, the breakpoints of In 3b are 3L .25 and .75, while In 3c involves nearly the whole long arm with the proximal break near the centromere and the distal one near the tip. The knob at .6 is included in the inverted segment of all three inversions. Gl_6 is in the proximal uninverted segment of In 3a while Lg_2 and A_1 are included in the inversion. Lg is in the inverted region of In 3b, Gl is in the proximal segment, and A is in the distal non-inverted segment. All three loci are in the inverted portion of In 3c with one breakpoint close to Gl and the A locus approximately 5 crossover units from the distal break.

The testcrosses of K10 k10 plants singly heterozygous for the three inversions, for the large knob in 3L, and for the Gl Lg A loci gave the following percentages of recovery of the alleles carried by the knobbed chromosome 3.

	% Gl	% Lg	% A
In 3a/N	52.7	60.4	60.1
In 3b/N	50.3	51.6	49.7
In 3c/N	50.0	56.1	49.9

The complete backcross data from the In 3b heterozygotes were presented in the 1964 News Letter. The In 3a/N and the In 3c/N data are presented in Table 1. No data are presently available for comparison of sib k10 k10 and K10 k10 plants heteroyzgous for In 3c.

Table 1
Testcross Data from Plants Heterozygous for In 3a or In 3c Showing Preferential Segregation of the Knobbed Chromosome 3

Female Parent	(1) Gl Lg A	(2-3) Gl lg A	(0) gl Lg A	(3-4) gl lg A	(3-4) Gl Lg a	(0) Gl lg a	(2-3) gl Lg a	(1) gl lg a	Σ	% gl	% Lg	% A	Recombination % Gl-Lg	Lg-A
25971														
Gl a k lg In3a k10 / gl A K Lg N k10	138	2	1020	0	5	1035	10	140	2350	49.8	49.9	49.4	12.0	0.7
Gl a k lg In3a K10 / gl A K Lg N k10	279	13	736	17	24	507	11	152	1739	52.7	60.4	60.1	27.1	3.7

Female Parent	(0)	(2-3)	(1-3) (3-4)	(1-2) (2-4)	(1-2) (2-4)	(1-3) (3-4)	(2-3)	(0)	Σ	% Gl	% Lg	% A	Recombination % Gl-Lg	Lg-A
Fla. 64-212														
a k lg gl In3c K10 / A K Lg Gl N k10	603	126	45	28	46	29	208	523	1608	50.0	56.1	49.9	25.4	25.4

The varying percentages of recovered alleles in the three inversions are intelligible on the assumption that heteromorphic dyads are required for preferential segregation to occur. With In 3a, crossing over is frequent in the proximal segment between Gl and the first breakpoint. This leads to preferential segregation for alleles distal to the crossover. Lg and A are recovered with the same frequency since they are separated only by rare double crossovers in the loop. In In 3b heterozygotes, heteromorphic dyads are produced following the single crossovers in the proximal region and with certain of the double crossovers. The genetic data show that these crossovers were infrequent although when they did occur the reciprocal classes were not equal (see MNL 38: 75). In 3c is a long inversion and double crossovers within the loop are frequent. When one crossover occurs to the right and one to the left of Lg, heteromorphic dyads result and preferential segregation for Lg is found. Since one of the two crossovers usually separates Lg and A, the A locus shows random segregation.

The question next considered was whether or not preferential segregation invariably occurred in all heteromorphic dyads and to the same degree. The answer to this was obtained from the testcrosses of K10 k10 N3 N3 Gl Lg K A/ gl lg k a plants which gave the following data (previously reported data from similar crosses were not used because of the disturbing effect of the segregating et allele):

26549 and 25938	(0) Gl Lg A	(0) gl lg a	(1) Gl lg a	(1) gl Lg A	(2) Gl Lg a	(2) gl lg A	(1-2) Gl lg A	(1-2) gl Lg a
	777	359	272	661	343	197	108	250
	26.2%	12.1%	9.2%	22.3%	11.6%	6.6%	3.6%	8.4%

$\Sigma = 2967$

The double crossover chromatids arise from heteromorphic dyads. Therefore, the percentage of double crossover strands with a knobbed chromatid gives a direct measure of the frequency of preferential segregation in bivalents having double chiasmata. Since Lg is close to the knob, this locus can be used in following transmission of the knob. Three hundred and fifty-eight double crossover strands were found, of which 250 or 70% had the Lg

allele. Double crossover bivalents contribute single crossover strands to the region (1) and region (2) classes and noncrossover strands to the (0) class and it was assumed the complementary strands would occur in the same proportion of 70% Lg and 30% lg. Bivalents with single chiasmata in region (1) also give rise to heteromorphic dyads and again the assumption of 70% preferential segregation was made. Noncrossover bivalents and bivalents having a single chiasma in region 2, according to the crossover hypothesis, result in homomorphic dyads and random segregation. If there is no chromatid interference, the percentage of megasporocytes with double chiasmata, with a single chiasma in region 2 (Lg-A), with a single chiasma in region 1 (Gl-Lg), and with no chiasma in the long arm of chromosome 3 can be calculated. The chiasma values can then be converted back to strand frequencies. The calculated frequencies of the different kinds of chromatids are given below with the actual numbers obtained.

	(0) Gl Lg A	(0) gl lg a	(1) gl Lg A	(1) Gl lg a	(2) Gl Lg a	(2) gl lg A	(1-2) gl Lg a	(1-2) Gl lg A
obs.%	26.2	12.1	22.3	9.2	11.6	6.6	8.4	3.6
calc.%	25.5	12.8	22.1	9.4	11.5	6.7	8.4*	3.6*

*Observed values used as basis for calculation.

The close agreement between the calculated and observed values suggests that the same amount of preferential segregation takes place in all heteromorphic dyads and is further indication of the validity of the crossover hypothesis.

M. M. Rhoades

3. A test of preferential segregation in microsporogenesis.

Preferential segregation through the female of heterozygous abnormal chromosome 10 and other chromosomes heterozygous for knobs in the presence of

abnormal 10 has been studied thoroughly. Based on these studies, the theory has been proposed that preferential segregation is dependent upon crossing over and preferential orientation of knobbed chromosomes toward the functional basal megaspore in the linear tetrad. Preferential orientation is attributed to the abnormal 10 associated neocentric activity in the regions of chromosomal knobs. No reports of attempts to obtain preferential segregation through the male have yet appeared. Since the tetrad of microspores is non-linear, preferential orientation might, therefore, not be expected though neocentric activity is present. Thus, tests for preferential segregation throug the male could begin to test the above theory through negative results could be attributed to other possible differences in microsporogenesis and megasporogenesis.

In order to study the effects of abnormal 10 through the male, one cannot merely score for segregation of a gene closely linked to a knob which is heterozygous since all pollen grains function. The type of preferential segregation which might be observed must necessarily involve at least two different heterozygously knobbed chromosomes and their heterozygous markers closely linked to the knobs. Segregation in such a female with abnormal 10 results in more megaspores carrying both knobs and their linked markers than is expected by chance alone. Crosses were therefore set up to determine whether segregation of knobbed chromosomes through the male also might result in more microspores carrying both knobbed chromosomes, and/or the reciprocal class of neither knobbed chromosome, than would be expected by chance alone.

In the first experiment segregation of abnormal 10 itself was not scored. Followed instead were markers closely linked to two other knobs known to be affected by abnormal chromosome 10 in the female.

$$\frac{k9\ wd}{k9\ wd}\ \frac{k3\ lg}{k3\ lg}\ \frac{k10}{k10}\ ♀ \quad x \quad \frac{K^{M}9\ Wd}{k9\ \ wd}\ \frac{K^{M}_{3}\ Lg}{k3\ lg}\ \frac{K^{L}10}{k10}\ ♂$$

Wd Lg	Wd lg	wd Lg	wd lg
2782	2720	2641	2700

The second experiment involved abnormal 10 marked by r and knobbed chromosome 3 marked by Lg.

$\frac{k3\ lg}{k3\ lg}$	$\frac{k10\ r}{k10\ r}$ ♀	x	$\frac{K^{L}3\ Lg}{k3\ lg}$	$\frac{K^{L}10\ r}{k10\ R}$ ♂

r Lg	r lg	R Lg	R lg
1755	1683	1812	1811

These results indicate preferential segregation does not take place in the male under the conditions of these experiments. Since the above data only apply to segregation at MII, further crosses are being made to determine MI segregation as well as MII segregation in plants with knob consitutions differing from those in the crosses reported here.

Annette Waters

4. Studies with tetraploids and haploids containing abnormal 10.

The perennial question as to the relative influence of chromosomal and genetic effects on autotetraploid sterility is being re-examined in maize. Tetraploid seeds, with and without abnormal 10 (K10), have been obtained by selecting full grains from the cross, K10/k10 as X 4N, and will be grown this summer, sporocyted, and selfed to determine fertility levels. Data on chromosome association and anaphase behavior will be collected from the sporocyte material and correlated with the fertility data to determine the effects of K10-induced meiotic alterations on fertility.

Haploid plants, with and without K10, will be selected this summer from among the gl seedlings resulting from the cross, K10/k10 gl X Coe's haploid inducer stock-6. These plants will be sporocyted and outcrossed as females to provide material amenable to an analysis of the effect of K10 on the nature of crossing-over in maize haploids (see Alexander, 1964, Nature 201:737).

A. J. Snope

5. Recombination in homozygous T6-9b and normal chromosome 9.

Crossover studies with $\frac{Yg\ c\ wx}{wd\ C\ Wx}$ $\frac{T6\text{-}9b}{T6\text{-}9b}$ individuals showed an altered distribution of exchanges when compared with standard values for the same regions in plants having normal chromosome structure. Crossing

over was increased in the *C*-*Wx* region and decreased in the *Yg*-*C* region (MNL 35: 64). The results were open to question, however, first because no adequate control was available and secondly because the difference in chiasma distribution might have been due to the *wd* deficiency instead of to the T6-9b translocation.

The effect of the deficiency on crossing over in normal chromosomes 9 was tested in K^S *Yg Sh Wx*/ *wd sh wx* compounds with sibs of K^S *Yg Sh Wx*/ K^S *yg sh wx* constitution as controls. The following data were obtained:

Table 1
Recombination Between Homologues of Chromosome 9 with Different Knob Constitutions

	Sh-Wx		Yg-Sh	Σ	Total Recomb.
26726 K^S/K^S ♀	20.8	1008	21.4	588	42.2
♂	25.2	1716	22.3	1502	47.5
26726 K^S/wd ♀*	18.3	350	4.3	325	22.6
♂	30.8	1205	7.7	1111	38.5

* Based on one ear.

It is evident that heterozygosity for *wd* causes a drastic reduction in crossing over in the region distal to *Sh* which, in the microsporocytes, is accompanied by an increase in the *Sh*-*Wx* region. The small population from female gametes does not show the compensation effect in the *Sh*-*Wx* region. In both K^S/K^S and K^S/*wd* compounds, the total recombination is higher in the male gametes than in the female.

The *wd* deficiency includes the terminal knob and half of the first chromomere (McClintock, Genetics 29: 478). However, gametophytes carrying the deficiency function as well as *Wd* gametophytes. The K^S/*wd* compounds of Table 1 used as pollen parents gave 7.7% crossing over between *Wd* and *Sh*. McClintock (Carnegie Inst. Wash. Year Book No. 42, 1943) reported values of 17.0 and 21.1 for the *Df*-*C* region in pollen parents heterozygous for a deficiency including the knob and the entire first chromomere. If the reduction in crossing over in *Wd*/*wd*

heterozygotes is due entirely to the loss of terminal chromatin in which chiasma formation is very frequent (McClintock, Carnegie Inst. Wash. Year Book No. 42, 1943), one would expect to find more crossing over in the Wd-Sh segment than in the Df-C region which is shorter. However, another factor known to influence crossing over is knob heterozygosity and part of the reduction in the Wd-Sh segment is probably attributable to the K^S/wd (as opposed to K^S/K^S) constitution. Kikudome found lower Wd-Wx values in K^L/wd plants than in K^M/wd compounds and the highest values occurred in K^S/wd plants. Even higher values would be expected in k/wd individuals. The highest Wd-C value (14.1%) obtained in my material was found in k/wd T/T female parents and crossing over in the male gametes should be increased above this amount. Thus, if we discount the influence of modifier genes on crossing over in my $\frac{K^S\ Wd\ Sh}{wd\ sh}$ and McClintock's $\frac{Df\ C}{N\ c}$ plants, the higher crossover frequency in the latter could be accounted for if the N c chromosome were knobless.

T/T individuals without the wd deficiency were used as female parents in testcrosses. These included both K^S/K^S and K^S/k constitutions for the terminal knob in the 6^9 chromosome and all were heterozygous for C and Wx. On the basis of crossover frequency in the C-Wx region, the plants were divided into two groups. Group I with a population of 1042 averaged 23.9% and group II with a population of 1305 averaged 34.4%. Sibs of N/N constitution gave 22.4% C-Wx. Unfortunately, there was no correlation of crossover values and knob constitution and at present no explanation for the different frequencies in T/T plants can be advanced. Plants heterozygous for $\frac{Yg\ C\ Wx}{yg\ c\ wx}$ and homozygous T/T gave 18.1% Yg-C and 21.3% C-Wx in a progegy of 537. These values are very similar to the 21.4% Yg-C and 20.8% C-Wx found in the unrelated K^S/K^S compounds with normal chromosomes cited in Table 1. It appears that entirely normal values for the 2 regions are possible in T/T chromosomes and fluctuations in these values cannot be attributed to the translocation per se.

Ellen Dempsey

6. The effects of x-rays on the bronze locus.

Stadler and Roman (1948) found no intragenic changes at the A_1 locus as a result of x-irradiation. Although their tests on induced mutation were extensive, they were confined to a single locus. The conclusion that x-rays do not induce intragenic changes in maize requires further support from studies on other loci. The bronze locus on the short arm of chromosome 9 has been chosen as a favorable gene for mutation experiments. Chromosome 9 carries the markers sh, 2 map units to the left of bz, and wx, 21 map units to the right.

Two crosses involving Bz stocks were made. In cross #1, pollen from plants homozygous for A_1 A_2 C R^r Pr B Pl Sh Bz Wx was x-rayed with a dose of 1000r and used to pollinate plants homozygous for A_1 A_2 C R^g Pr b pl sh bz wx. R^r was the contamination marker. In cross #2, the male parent was irradiated with the same dosage approximately 13-19 days prior to anthesis. This was suggested by Caspar as an attempt to induce mutations in the generative nucleus before the second microspore division. The resulting F_1 seeds would carry the same mutation in the embryo and endosperm, thus eliminating the laborious task of screening large numbers of seedlings. The male parent in this cross was homozygous for A_1 A_2 C R^r Pr B Pl Sh Bz Wx Og and was crossed to plants homozygous for A_1 A_2 C R^r Pr B Pl sh bz wx og. Og was the contamination marker in this case.

Mutants from Bz→bz due to gross chromosomal aberrations will appear as sh bz in phenotype and may be either Wx or wx, depending on the extent of the aberration. Any putative point mutations will be Sh bz Wx in phenotype.

Bronze seedlings carrying A_1 A_2 B Pl R^r show no red pigmentation in the stem, coleoptile, roots or leaf tips. In cross #1, F_1 seedlings of this phenotype were selected and transplanted. All bronze mutants were classified for pollen abortion and backcrossed to a sh bz wx stock. The presence of pollen abortion indicates that a chromosomal aberration exists; however, it is not necessarily in chromosome 9. Therefore, kernels from this backcross were screened for Sh bz Wx phenotypes as an indication of a possible point mutation at the bronze locus.

In cross #2, the attempt to cause mutations before the second microspore division was only partially successful. Some bronze mutations in the endosperm corresponded with bronze mutations in the embryo, and some did not. Therefore, all seeds are being planted and screened as in cross #1. The following table contains results from

these two crosses.

Table 1

Cross #	Total F_1 pop.	sh bz mutants		Sh bz Wx mutants		Fractionals and/or mosaics in endosperm
		endo.	emb.	endo.	emb.	
1	66,337	608	345**	2	1	272
2*	26,151	375	incomplete counts	4	incomplete counts	80

* Tabulations on this cross have not been completed. Partial results are indicated.

** These mutants could not be classified for sh since none were transmitted.

The one bronze mutant from cross #1 (Table 1) carrying the Sh and Wx markers is designated bz-X_1. The F_1 plant was normal in appearance and exhibited no aborted or sub-normal pollen. The plant was backcrossed to a sh bz wx tester. When used as the female parent, it yielded a small ear with 15 Sh bz Wx seeds, 20 sh bz Wx seeds and only 1 sh bz wx seed. Seed set was poor. Further tests will be made to determine the cause of this unexpected ratio.

The following data were obtained using the above F_1 plant as the male parent in crosses to a sh Bz wx stock.

Table 2

Total pop.	Recomb. classes		Non-recomb. classes		Recombination
	Sh wx	sh Wx	sh wx	Sh Wx	Sh-Wx
373	2	38	333	0	10.7%

The recombinants must be backcrossed to determine if they are carrying the mutant region. If such is the case, transmission of the markers linked with the bz-X_1 allele will be sub-normal.

Average recombination between sh and wx is 21% (Emerson, Beadle and Fraser, 1935); however, control values have not been determined for the stocks involved in this experiment. In the second backcross using 5 of the 15 Sh bz Wx kernels, the following results were obtained.

Table 3

	Sh bz-X_1 Wx / sh bz wx ♀ x sh bz wx ♂				
	Recomb. classes		Non-recomb. classes		% recomb.
Family	Sh wx	sh Wx	Sh Wx	sh wx	Sh-Wx
851-1	1	26	14	111	17.8
851-2	7	28	5	71	31.5
851-3	5	26	3	112	21.2
851-4	2	33	2	169	17.0
851-5	6	19	5	128	15.8
Total	21	132	29	591	19.8
	sh bz wx ♀ x Sh bz-X_1 Wx / sh bz wx ♂				
851-1	9	80	0	449	16.5
851-2	5	104	0	722	13.1
851-3	-	--	-	--	---
851-4	1	25	0	84	23.6
851-5	7	61	0	554	10.9
Total	22	270	0	1809	13.9

An additional group of bz-X_1 plants which were used only as male parents in crosses to sh bz wx testers yielded an average recombination value of 12.8%. One bz-X_1

plant which was not included in this group exhibited greater than 23% recombination between Sh and Wx. Only two Sh bz Wx seeds were recovered, probably resulting from double crossovers. Therefore the aberrant chromosome was present. The total number of seeds obtained using this plant as a male parent was 1121. A value greater than 23% was obtained also from the cross of sh bz wx ♀ x 851-4 ♂ (Table 3); however this was based on a progeny of only 110, indicating that the resulting percentage of recombination may not be significant.

In the female gametes, a wide range of recombination between Sh and Wx was observed (Table 3). The average value was 19.8% as compared to 13.9% in the male gametes from the same plants. A reduction in crossing over due to non-homologous pairing is expected if a deletion is present; however, if one can extrapolate from data of other aberrations, (Dempsey, MNL 35: 63, and Burnham, MNL 35: 86) the greater recombination value would be expected in the male gametes.

Further genetic and cytological observations will be made to determine the nature of this mutation.

The work done so far on a population of 92,488 corroborates the evidence of Stadler and Roman that intragenic changes do not occur in maize as a result of x-rays, when the plants are irradiated post-meiotically.

John P. Mottinger

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1. En at the mutable locus, a_1^m.

The identification of the regulatory element En at a mutable locus can be facilitated by the diversity of the forms of mutability that exist. Among the diverse mutable alleles, one that mutates to a readily identifiable mixture of pale and deep purple dots a_1^m (p and p) is available. Colorless forms, noted as $a^m(r)$, also exist and these respond to the presence of En in a predictably recognizable manner (Peterson, Genetics 1961). When a heterozygote is made between a_1^m (p and p) and $a_1^m(r)$ the resulting expression is a very heavily mutable form showing the effect of En on $a_1^m(r)$. Proof that it is the En of the a_1^m(p and p) allele that is causing the mutability is obtained by testcrossing the heterozygote (by a_1sh/a_1sh). The resulting progeny shows the separation of kernels -- 1/2 of which are pale and purple dotting and 1/2 are colorless, $a_1^m(r)$, since the En is coupled with the a_1^m(p and p) allele. A small percentage of exceptions appear and these will be discussed in the next section.

Peter A. Peterson

2. Changes at the a_1^m(p and p) allele: The status of En.

Among the progeny arising from testcrosses (by a_1sh/a_1sh) of the a_1^m(p and p) allele, stable non-dotting pale types ($a^p(nr)$) and colorless types ($a^m(nr)$)* are observed. It has previously been reported (Peterson, 1961 Genetics) that the colorless types do not respond to the presence of En and are designated $a_1^m(nr)$. Similarly, the pales do not respond to the presence of En and are therefore nr (non-responding) types. If these derivatives are canvassed for the presence of En, it is found that they invariably do possess En. In crosses of $a^p(nr)$ and $a^m(nr)$ by $a^m(r)$ (Cross #1), mutability is observed in the heterozygote. In testcrossing these heterozygotes -- $a^p(nr)$*/$a^m(r)$* x a_1sh/a_1sh (Cross #2) -- a variable percentage of mutable kernels results. These mutable kernels represent the effect of En on the $a_1^m(r)$ allele. This would indicate that the nr kernels possess En in coupling $a_1^p(nr)$ En and the distance between $a_1^p(nr)$ and En is proportional to the frequency of mutable kernels that arose from Cross #2**.

This position of En can be verified by resubmitting these mutable kernels to a further testcross -- Cross #3 (dotted kernels Sh/a_1sh x a_1sh/a_1sh). In the progeny of Cross #3 the frequency of colorless Sh kernels should equal the frequency of mutable kernels in Cross #2 described above.

Examples of Cross #2: $a_1^p\ Sh/a_1^{m(r)}Sh$ x a_1sh/a_1sh

	(A) colorless Sh	(B) pale-stable Sh	(C) purple dots on colorless bkgd Sh	$\frac{C}{A + C}$ %
3 92-3	45	69	9	16.6
3 92-4	58	68	6	9.4

Examples of Cross #3: dotted from column (C) above

	colorless Sh	%	dotted Sh	
4 107-3	10	5.05	168	from '3 923**
4 108-1	16	10.9	131	from '3 924

There is some agreement between the expected results from Cross #3 when related to those of Cross #2. This would indicate that En is relocated on the chromosome associated with the mutable locus following the change from a^p and p to pale-stable. This would agree with the results of previous workers on the probable site of the relocation of controlling elements following a mutation event (Van Schaik and Brink, 1959 Genetics) and (Greenblatt and Brink, 1962 Genetics).

* Unless indicated (by sh) the kernel types are non-shrunken (Sh).

** The colorless sh kernels represent ½ of the segregating ear and are not included in the data. The a_1^{dt} does not respond to En. The reciprocal cross-over event yielding an a_1 sh En linkage cannot be detected in this cross.

Peter A. Peterson

3. The effect of B chromosomes (continued).

In a previous report (MGCNL 37), it was noted that the effect of B chromosomes could be evaluated by studying the variances of pollen grain size. In comparisons of B and non-B containing lines, differences could be detected at the 10% level of significance with the increased variance in the B-chromosome containing lines. Subsequent analyses have confirmed this result and at the 5% level of significance. This would confirm the previous result that B-chromosomes can affect the physiology of pollen grain growth.

Peter A. Peterson

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1. A dormant allele of vp_1.

Viviparous-1 is a premature germinating mutant which is located in the distal nine-tenths of the long arm of chromosome 3 (the region translocated in TB-3a). It is probably located just distal to the break point of TB-3a since it shows close linkage with T3-9a (3L.19) and T3-9c (3L.15) and very little or no linkage with a_1.

The viviparous seedlings of this mutant are green and they grow into normal plants. Seeds that are of the genotype vp_1 vp_1 are not only viviparous but they also produce little or no aleurone color in stocks that are otherwise homozygous for the genes responsible for colored aleurone. Frequently, the color inhibition is not complete, resulting in seeds with a slight tinge of color similar to that seen in seeds of the constitution C^ICC.

In 1961 crosses were made between heterozygous Vp_1 plants which were homozygous for purple aleurone and a stock obtained from K. S. McWhirter, then at the Univ. of Wisconsin. The McWhirter stock was supposed to be homozygous purple aleurone but was segregating for a non-purple mutant which showed a tendency to be viviparous. The segregating F_1 ears of this cross produced 3 purple : 1 non-purple seeds. No viviparous seeds were observed on these ears. In 1962 fifteen

non-purple seeds from these F_1 ears were planted and the resulting plants were self pollinated. All of these ears were non-purple and with approximately 1/4 of the seeds viviparous. In every case the ears had some seeds with the slight tinge of purple associated with homozygous $\underline{vp_1}$ seeds in an otherwise purple genotype. In 1963 twelve more non-purple F_1 seeds were grown with the same results as in 1962.

The F_1 plants from non-purple seeds grown in 1963 were at the same time crossed to heterozygous $\underline{vp_1}$ plants (homozygous purple aleurone) and plants heterozygous for the McWhirter allele. The backcrosses to $\underline{vp_1}$ stocks gave ears with half the seeds purple and half non-purple. Approximately 1/2 of the non-purple seeds were viviparous. The backcrosses to plants heterozygous for the McWhirter allele gave ears that had approximately 1/2 purple and 1/2 non-purple seeds. Only an occasional viviparous seed was observed on these ears.

Also in 1963 self pollination of 11 plants from purple seeds of the original F_1 ears gave 7 plants that were segregating 3 purple : 1 non-purple viviparous seeds and 4 plants that were segregating 3 purple : 1 non-purple dormant seeds.

These F_1 plants were at the same time crossed to heterozygous $\underline{vp_1}$ plants (homozygous purple aleurone) and plants heterozygous for the McWhirter allele. In the backcrosses to the $\underline{vp_1}$ stock, viviparous seeds were observed on the backcross ears if the F_1 plants segregated for vivipary but no viviparous seeds were observed on backcross ears if the F_1 plants were segregating for non-purple dormant seeds. In the backcrosses to plants with the McWhirter allele all segregating backcross ears had non-purple dormant seeds whether or not the F_1 parents were segregating for vivipary.

These results are consistent with the hypothesis that the McWhirter mutant was allelic to $\underline{vp_1}$ and that the McWhirter allele is much less likely to be viviparous. In the crosses outlined in this report only occasional seeds which were carrying the McWhirter allele would be observed to germinate prematurely. The marked propensity for dormancy of the McWhirter allele is dominant to the strong viviparous tendency of the $\underline{vp_1}$ allele.

Crosses of non-purple segregants to $\underline{a_1}$, $\underline{a_2}$, $\underline{c_1}$, $\underline{c_2}$, and $\underline{r}$ testers confirmed that these stocks were homozygous for the dominant alleles at these loci and thus the lack of color was due to the $\underline{vp_1}$ and McWhirter alleles.

Donald S. Robertson

2. Linkage studies of 51 chromosome-nine translocations.

The use of *wx* marked chromosome-nine translocations in linkage studies has proven to be a very useful genetic technique. So far only a limited number of such translocations are being utilized, although many more chromosome-nine translocations are available for use. However, very little if anything is known about the amount of crossing over between *wx* and the breakpoint in these translocations, nor has the recessive *wx* allele been introduced into the translocated chromosomes.

For the past several years a cooperative project has been underway to determine the *wx* breakpoint distances for a series of chromosome-nine translocations. In the process, crossovers which incorporate the *wx* allele in the translocated chromosome have been obtained for most of the translocations. The F_1 crosses for these tests were made by E. G. Anderson (Univ. of Missouri). The testcrosses were made by E. H. Coe, Jr. (Univ. of Missouri) and the testcross progeny were grown at Iowa State Univ. and classified and analyzed by D. S. Robertson, Darrel S. English and Allen L. Millard. The latter two workers participated in this program as National Science Foundation Research Participants in the summers of 1963 and 1964, respectively.

Table 1 summarizes the linkage data for the 51 translocations so far analyzed.

E. G. Anderson
E. H. Coe
Univ. of Missouri

D. S. Robertson
Iowa State University

Darrel S. English
Allen L. Millard
NSF College Teacher
Research Participants,
Iowa State Univ.

Table 1

Translocation	Chrom. 9 Break point	Non-chrom. 9 Break point	Parental Classes		Recombination Classes		Total	% C. O.
1-9024-7	L.13	S.71	69	76	2	1	148	2.03
1-94398	S.19	L.51	113	135	7	4	259	4.25
1-94995	S.20	L.19	264	264	12	2	542	2.58
1-98129	L.27	S.53	151	166	10	3	330	3.94
1-98302	L.29	S.55	50	56	5	5	116	8.62
1-98389	L.13	L.74	182	144	4	7	337	3.26
1-98460	L.24	S.13	102	96	4	7	209	5.26
1-98918	L.20	S.21	118	124	4	4	250	3.20
2-95257	L.20	L.28	174	172	1	2	349	0.86
2-95711	L.23	S.24	168	183	5	4	360	2.50
3-9e	L.26	L.06	165	168	23	12	368	9.51
3-9g	L.14	L.40	186	180	8	13	387	5.43
3-9020-59	ctr	ctr	142	143	3	3	291	2.06
3-95775	S.24	L.09	249	256	19	6	530	4.72
3-98447	L.14	S.44	100	106	5	4	215	4.19
3-98562	L.22	L.65	63	67	3	2	135	3.70
4-9c	L.29	L.82	127	112	7	12	258	7.36
4-9d	L.17	L.12	88	66	1	28	183	15.85
4-9e	L.26	S.53	118	117	4	6	245	4.08
4-9f	L.18	L.55	35	36	2	1	74	4.05
4-9g	L.27	S.27	77	83	5	2	167	4.19
4-9004-7	L.26	L.28	148	136	4	7	295	3.73
4-94373	L.39	L.29	88	53	5	3	149	5.37

Translocation	Chrom. 9 Break point	Non-chrom. 9 Break point	Parental Classes		Recombination Classes		Total	% C. O.
4-95657	S.25	L.33	135	104	1	3	243	1.65
5-9008-18	L.26	L.29	166	137	7	12	322	5.90
5-9020-7	ctr	ctr	102	75	8	18	203	12.81
5-94817	S.07	L.06	80	70	49	49	248	39.52
5-94871	S.38	L.71	152	128	0	1	281	0.36
5-96057	S.52	S.15	30	27	4	15	76	25.00
5-98386	S.13	L.87	407	391	8	21	827	3.51
5-98591	L.25	S.09	55	39	8	5	107	12.15
6-95454	S.75	ctr	106	158	77	13	354	25.42
6-95831	L.30	L.27	111	112	9	4	236	5.51
6-96019	L.26	L.27	36	37	4	4	81	9.88
6-96270	L.28	L.19	119	113	4	8	244	4.92
6-98536	S.81	L.18	31	42	16	12	101	27.72
7-9a	S.07	L.63	262	276	2	6	546	1.47
7-9c	L.22	L.14	177	167	8	14	366	6.01
7-9071-1	L.07	S.70	130	131	10	5	276	5.44
7-94363	ctr	ctr	182	169	1	5	357	1.68
7-96225	ctr	ctr	186	173	0	9	368	2.45
7-97074	S.80	L.03	69	90	10	42	211	24.64
7-98383	ctr	ctr	234	180	5	5	424	2.36
8-9043-6	S.34	L.17	70	62	0	1	133	0.75
8-94453	S.68	L.86	155	131	7	19	312	8.33
8-94643	L.11	S.37	157	140	4	4	305	2.62

Translocation	Chrom. 9 Break point	Non-chrom. 9 Break point	Parental Classes		Recombination Classes		Total	% C. O.
8-9$_{5300}$	S.43	L.85	214	201	0	0	415	0.0
8-9$_{5391}$	S.33	L.07	188	188	3	4	383	1.83
8-9$_{6921}$	L.15	L.85	277	195	7	5	484	2.48
9-10$_{4303}$	L.26	S.44	151	149	5	5	310	3.23
9-10$_{8630}$	S.28	L.37	121	136	0	3	260	1.15

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1. A possible study of crossing-over on the basis of pollen traits.

The strict linkage between the waxy gene and Ga$_8$ (gametophyte factor detected by Schwartz - MNL, 25 : 30, and by myself, MNL, 31 : 40) offers a case, perhaps unique, for studying crossing-over on the basis of pollen grain characters. We have done some attempts, collecting and fixing, after different times since hand pollination was performed on plants of given genotypes.

Plants of constitution Ga Wx/ga wx, when selfed, are known to produce ears with no or very few wx kernels. The genotype Ga wx/ ga Wx, on the contrary, following self-pollination, gives wx kernels with a percentage even over 45%.

When self-pollinated silk of the former type are scored for germinating pollen grains, results of the following type are obtained:

Plant and Ear	No.	Kernel Type		Pollen Type		Fixing Time in Hours, after Hand Pollination
		Wx	wx	Wx	wx	
1096 - 17		112	14	452	7	1
				500	54	2
				276	63	3
1096 - 54		291	9	478	22	1
				411	96	2
				312	167	3
1097 - 30		77	8	447	15	1
				193	67	2
				275	172	3

The repulsion condition, in a different genetical background, has produced data of the following type:

Plant and Ear	No.	Kernel Type		Pollen Type		Fixing Time in Hours after Hand Pollination
		Wx	wx	Wx	wx	
1101 - 2		171	183	100	395	2
				31	469	6
				13	487	8
1101 - 83		107	89	65	364	2
				27	389	6
				5	154	8
1102 - 8		114	86	21	93	2
				21	143	6
				23	314	8

It seems, from these data, that the waxy and gametophyte-8 factors can constitute a new type of genetic material for studies of various kind. However, the proper time for the scoring should be carefully identified. The genetic background, e.g., of the coupling phase stock, which is associated with earlier flowering, seems to be adequate for screening the pollen grains 1-2 hours after

pollination. In the other stock, which is a late one, the differential germination of the two pollen types appears to show better several hours later.

A. Bianchi
M. R. Parlavecchio

2. Reversion frequency of alleles of the gl_1 locus and of some of their compounds.

As reported in the previous MNL a quite large proportion of the glossy types detected in the Italian open pollinated varieties turned out to be mutants of the locus gl_1. This has provided the opportunity for analysing their nature by studying the reversion frequency of some of these mutants in comparison with some of their compounds. The data so far collected, for the self-pollinated mutants, are presented in the following table:

Identification No. of the gl_1 Mutant	Total No. of Seedlings	No. of Gl Seedlings	Frequency of Gl Seedlings $\times 10^{-4}$	Fiducial Limits (P=.05) $\times 10^{-4}$
'63- 302	7538	1	1.33	0.03 - 7.39
'63- 305	1522	0	0.00	0.00 -24.24
'63- 307	20931	1	0.48	0.01 - 2.66
'63- 324	14332	29	20.23	19.35 -21.11
'63- 329	1692	0	0.00	0.00 -21.81
'63- 334	4782	0	0.00	0.00 - 7.72
'63- 359	6223	0	0.00	0.00 - 5.93
'63- 350	5209	0	0.00	0.00 - 7.08
'63- 347	1295	0	0.00	0.00 -28.5
'63- 796	41601	0	0.00	0.00 - 0.89
'62- 824	17927	0	0.00	0.00 - 2.06
'63- 51 } '63- 495 }	12375	2	1.62	0.02 - 4.5

The compound types which have been studied have yielded the following data:

Compound Type		Total No. of Seedlings	No. of Gl Seed-lings	Frequency of Gl Seedlings x 10^{-4}	Fiducial Limits (P=.05) x 10^{-4}
'63-	302/307	120,850	28.5*	2.36	1.49 - 3.22
'63-	302/350	58,316	36	6.7	5.49 - 7.2
'63- '63-	302/51 } 302/59 }	47,686	15	3.55	2.93 - 4.19
'63-	324/325	32,714	24	7.34	4.77 - 10.27
'63-	329/334	30,411	5	1.64	0.53 - 3.84
'63-	331/335	14,191	22	15.5	13.17 - 18.82
'63-	331/334	6,757	4	5.92	1.61 - 15.15
'63-	345/347	8,431	6	7.11	2.61 - 15.49
'63-	348/350	45,131	1	0.22	0.0056 - 1.23
'63-	351/359	12,144	6	4.94	1.81 - 10.75
'63- '63-	359/51 } 359/59 }	50,056	58	11.58	10.31 - 13.1
'63-	5002/495	25,617	18	7.026	5.56 - 8.68
'63- '63-	797/495 } 796/495 }	92,326	96	10.4	9.51 - 11.46
'62-	824/601	54,945	6	1.9	0.4 - 2.38
'62-	815/601	35,515	2	0.56	0.068 - 2.033
'61-	173/122	68,632	20	2.91	2.34 - 3.56
'61-	175/122	50,360	11	2.18	1.65 - 2.84

* In this compound 5 seedlings, each one partially normal and partially glossy, have been found. Each of these seedlings has been rated .5.

A higher frequency of reversion is obvious in most of the compounds, although, at this stage of the study, it is impossible to decide whether this is due to intracistron recombination (as appears likely) among different mutational sites, or to higher mutation rate s.s. promoted by mutator systems, as controlling elements, brought together in the hybrids.

B. Borghi
C. Lorenzoni
M. Pozzi
F. Salamini

3. Cases of close linkages between endosperm and seedling traits.

Among the mutants detected in Italian varieties three independently detected cases of "collapsed endosperm" (cl) have turned out to be identical or allelic to the same locus on chromosome 7.

The "collapsed endosperm" is fairly vital even in field conditions. Such a mutant is "uncovered" by the TB-7 stock.

Linkage between this trait and gl_1 was clearly indicated by F_2 progenies as well as by backcross data, as follows (repulsion phase):

Row Identification	Progeny Type	Segregation				Recombination % ± St. Error
		Gl Cl	Gl cl	gl Cl	gl cl	
62 - 539	F_2	739	370	359	3	9 ± 1.7
64 - 386/389	B	101	978	956	77	8.4 ± .4

Crossing of gl_1 gl_1 by TB-7 provided data on the non-disjunction of the chromosome B7, as follows:

Cl		cl	
Gl	gl	Gl	gl
38	93	88	8

A case of close linkage between the waxy gene on chromosome 9 and a white seedling (w) trait appears from the following data (repulsion phase):

Row Identification	Segregation				Recombination % ± St. Error
	Wx W	Wx w	wx W	wx w	
63 - 878	227	126	117	1	8.8 ± 3.2
64 - 1278/'80, 848	1794	851	770	3	6.4 ± 1.1

A third case of linkage between the y factor on chromosome 6 and a japonica trait expressed in seedling stage is indicated by the following F_2 data:

Y kernels		y kernels	
J	j	J	j
201	85	76	0
243	114	83	0

C. Lorenzoni
F. Salamini

4. Another case of balanced lethal factors.

A series of self-pollinations carried out on plants derived from crossing individuals segregating for de^t 13 and de^t 25 (two extreme types of defective endosperm factors from maize-teosinte derivatives) has given the following results:

Number of ears segregating		
both defectives (in repulsion)	one defective (or two in coupling)	no defective
202	62	2

In the first group the defective seeds form about 50% of the total number of kernels, whereas in the second group the percentage varies from 20-25 to 30-35.

The data suggest that this is another balanced lethal system.

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M. Pozzi

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1. Crossing-over in the Lg - Gl - V region.

Recombination data for markers of chromosome 2 in different genetic backgrounds are reported in the following table (backcross of the multiple recessive stock to heterozygous plants possessing T cytoplasm): (Table 1)

Table 1

Inbred Line	Lg_1 V_4 Gl_2	lg_1 V_4 Gl_2	Lg_1 v_4 gl_2	Lg_1 v_4 Gl_2	lg_1 V_4 gl_2	Lg_1 V_4 gl_2	lg_1 v_4 Gl_2	lg_1 v_4 gl_2
A 158	463	136	103	358	458	93	79	456
W 22	451	121	119	246	320	38	43	419
WF 9	722	204	178	581	534	108	74	749

Table 2

Genetic Region	A 158	W 22	WF 9	Average
Lg_1 - Gl_2	19.15 ± 0.84	18.26 ± 0.92	17.90 ± 0.69	18.38
Gl_2 - V_4	46.03 ± 1.06	36.82 ± 1.18	41.17 ± 0.88	41.57
Lg_1 - V_4	49.16 ± 1.08	45.87 ± 1.19	47.52 ± 0.89	47.61
Double crossing over	8.01 ± 0.52	4.61 ± 0.57	5.77 ± 0.43	6.16
Coefficient of coincidence	0.91	0.69	0.78	

From these data the following recombination frequencies may be calculated, together with their standard errors obtained using as $\bar{p}$ the average value, from the pooled data: (Table 2).

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M. Monotti

2. Reversion frequency of waxy pollen type in normal and hypoploid maize plants.

In some organisms, and especially in *Saccharomyces cerevisiae*, it has recently been found that reversion rate of some biochemical mutants is much higher (tenfold or more) in diploid condition than in the haploid one, and that this is largely associated with chromosomal exchanges in the region involved (restoration of a normal genetic sequence as a consequence of unequal crossing-over).

To test the validity of such a phenomenon in maize the frequency of *Wx* pollen grains in normally diploid plants and in hypoploid individuals (obtained following appropriate screening of genetically marked X-rayed material) has been estimated, and is presented in the table on page 117.

It is evident that these data show no clear difference between the reversion rate at the *wx* locus of the haploid condition and that of the diploid one. These results, and the heterogeneity of the values exhibited by the different plants as well as within different sectors of the same tassel, may find their explanation in the nature of the mutant studied, as will be discussed in the paper which is being prepared for publication.

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Reversion Rate at the *wx* Locus

Year and Chromosome Type	Tassel No.	Estimated Number of Pollen Grains	No. of *Wx* Pollen Grains	Frequency of *Wx* Pollen Grains x 10^{-5}
1963	1092-3	572,669	28	4.89
	1064-1	112,616	1	0.89
Hypoploid	1064-2	733,192	68	9.27
	1069-	386,501	70	18.11
	1064-4	103,400	0	0.00
Total and average		1,908,378	167	8.75
1963	56-1	618,021	13	2.10
	56-7	695,767	21	3.02
Normal	56-11	1,540,347	229	14.87
	56-16	2,256,349	374	16.57
	56-2	2,030,517	168	8.27
	56-3	3,288,372	128	3.89
	56-4	3,086,460	48	1.55
Total and average		13,515,833	981	7.25
1964	1309	448,860	29	6.46
	1291	73,010	0	0.00
Hypoploid	1298	406,630	12	2.95
	1282	74,080	15	20.24
	1290	914,850	6	0.65
	1283	989,550	7	0.70
	1291	1,117,350	19	1.70
Total and average		4,024,330	88	2.18
1964	1267-1	1,967,200	14	0.71
	" -2	343,880	4	1.16
Normal	" -3	3,000,680	57	1.89
	" -4	669,210	7	1.04
Total and average		5,980,970	82	1.37

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1. Golden-2.

The location of golden-2 is still in doubt (MGCNL 36:49). Further evidence that it is not near Bn on chromosome 7 where it is placed in some publications comes from the following data:

G2 Tp CB 32 35 29 36 total = 132 48% recombination

In this cross golden-2 segregated independently of Teopod which is located at 46 on the seventh chromosome, while Bn is located 25 units away at 71.

R. I. Brawn

2. Aleurone color in the presence of a_1.

A stock in my culture with the genotype a_1 A_2 C_1 C_2 R pr in y has a pronounced "blush" of color in the aleurone with occasional patches of deep red pigment, particularly in the region of silk attachment. Germless kernels in this background are nearly full red.

When c_1 segregates in this background, both blushed and pure white kernels appear.

It has not been determined whether the a-allele in this stock is unique, but the aleurone is completely colorless in the cross a_1 A_2 C_1 C_2 R pr in y x au_3 A_2 C_1 C_2 R pr in y, suggesting that intensifier 'In' may be responsible for the pigment and not the particular a-allele.

R. I. Brawn

3. Further tests for paramutation at the P locus.

The standard Wisconsin variegated pericarp allele (P^{vv}) has been shown to be non-paramutagenic with P^{rr} (MGCNL 35:86, 1961). Three additional unstable alleles are known at the P locus (PNAS 40:1118-1126, 1954) which condition pericarp striping of individually identifiable

pattern. It has now been determined that these alleles, $\underline{P}^{mo}$ (mosaic pericarp), $\underline{P}^{Boyaca}$, and $\underline{P}^{Q36}$, are also non-paramutagenic with a $\underline{P}^{rr}$ allele derived from an old Cornell stock.

Heterozygotes between each of the unstable alleles and $\underline{P}^{rr}$ in the same inbred W9 background were established and then crossed reciprocally with a $\underline{P}^{ww}$ stock. The red and striped ears within each set of reciprocal crosses were compared with each other and with similar heterozygotes with $\underline{P}^{ww}$ which had arisen from a previous heterozygote with $\underline{P}^{ww}$. No differences in either the striped pattern or the solid red pericarp color were noted which could be attributed to the peculiar ancestry of the allele in question.

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1. Diffuse action in Chocolate pericarp.

Pericarp and aleurone pigment genetics share in common the $\underline{A}_1$ locus as a major conditioner and/or modifier (with one known exception). It was not surprising then to discover that the Diffuse gene (Idf) initially recognized as an inhibitor of pericarp pigment also inhibits aleurone pigments (MNL 33). Subsequent tests also disclosed that the plant pigments of B Pl (either $\underline{a}_1$ or $\underline{A}_1$) are also susceptible to Idf action (unpublished data). The exception, the subject of this report, is the Chocolate pigment of the pericarp conditioned by the dominant Ch locus on the long arm of chromosome 2. This locus conditions a brownish pigment only in the pericarp. It was of interest therefore to test the inhibitory action of Idf in a Ch background. While there must be some major modifiers of Ch action (an extremely variable phenotype), Idf does not seem to be one of them.

Three levels of Idf action were tested in Ch backgrounds, (1) a high mutable state, (2) a low mutable state, and (3) an active stable state. All three test types provided no detectable reduction in pigment (the mutable forms would have been expected to produce a striping pattern in the pericarp) when compared to non-diffuse (idf) sib segregants serving as controls.

In the pericarp the red pigment conditioned by $\underline{A_1}$, $\underline{P}^{rr}$ and the brown pigment conditioned by Ch apparently both come to expression in individuals carrying all three dominant alleles. Idf-mutable will suppress the red pigment in the typical mutable pericarp pattern of such individuals while not affecting the co-present brown pigments. Inasmuch as the brown pigment conditioned by $\underline{A_1}$ b $\underline{P}^{rr}$ does not develop in the presence of Idf it may be concluded that these two brown pigments are not the same.

Another brown pericarp pigment, recessive bp bp on chromosome 9 is known to interact with $\underline{P}^{rr}$ and thus would be expected to respond to Idf. A direct test of this assumption is now in progress.

Irwin M. Greenblatt

2. Tests for Ac and Spm in Diffuse stocks.

In recent years loci in corn exhibiting high rates of somatic instability have generally been found to involve one or another of the recognized transposable elements. Since the Diffuse gene (Idf) is characterized by a high degree of somatic mutability it is of major interest to determine if one of the now recognized transposable elements is involved in this case.

By utilizing tester stocks (developed by Dr. B. McClintock) Idf was evaluated for Ac and Spm factors. This was accomplished by the following matings:

1. Test for the presence of Ac by using a C-Ds tester.

   C Ds, A_1, R, idf x c -, A_1, r, Idf

   If Idf could substitute for Ac a pattern of C ⟶ c breaks would be expected on the resultant kernels. No such C ⟶ c events occurred.

2. Test for the presence of Spm by using a c_2^{mt} tester.

   c_2^{mt}/c_2, A_1, C_1, R, idf x C_2, A_1, C_1, R, Idf

   In this case if Idf could substitute for Spm one-half of the kernels would exhibit a spotting of dark purple in a dilute purple background. No such spots were observed on seven test ears.

In the above matings all recognized states of the Idf allele were utilized, i.e. mutable (high), mutable (very low), stable (but highly active phenotypically).

Thus Idf does not seem to substitute for two known transposable elements, Ac and Spm. A test to determine if Idf can substitute for Dt induced a_1-mutability will be made. However, another negative result is expected in this test for the following reasons: Two main features of transposable elements are lacking from the Idf spectrum of mutations: (1) No regular stable class (either phenotypically active or inactive) occurs among the Idf mutant types. (2) Non-diffuse segregants from Diffuse heterozygotes do not carry any modifiers of the diffuse phenotype as might be expected were transposable elements involved.

It is currently believed that the cause of Idf mutability is most likely not a transposable element but some other gene action control type mechanism.

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3. Karyotype stability of haploid and diploid maize root tissue cultures.

In our first attempts to determine karyotype stability in maize root tissue cultures, chromosomes were counted nine months after callus initiation and again after twelve months. Counts made at nine months showed all cultures to be diploid except one (8 cultures out of 9) which was a chimera of 2n/4n. The second round of counts made at 12 months showed all to be diploid (the culture with a chimera was not recounted due to poor growth) (MNL 1963).

On the basis of these results it was considered important to inquire into the relative stability of haploids. Haploids were obtained from the mating 22 A C r^g x 22 A C R^{sc} by selecting the resultant kernels having purple aleurone and colorless scutellum.

Such presumed haploids (with diploid controls) were germinated sterilely on agar media. When seedlings were transferred to modified White's media, root tips were removed and fixed in acetic alcohol for later confirmation of presumed chromosome numbers. The assessment of chromosome numbers in a cell was made of late prophase, metaphase, and early anaphase periods of cell division. Only rapidly growing tissue could provide the various periods for examination.

Three different growth factors were used in the media: 2,4-dichlorophenoxyacetic acid, 2,4,5-trichlorophenoxyacetic acid, and 2,4,5-trichlorophenoxypropionic acid. Samples of callus tissue taken for chromosome counts were fixed in 3:1 acetic alcohol, stained and squashed in aceto carmine. Counts were made from temporary slides. Sampling of cultures for counts began three months after germination.

These initial assessments revealed that both haploid and diploid cultures had unstable chromosome complements, diploid cultures giving 2n, 4n and 8n counts and haploid cultures giving n, 2n, 4n and 8n counts. In addition, both sets of cultures gave occasional counts of 15 or 16 and 25 to 31. The odd counts obtained (15, 25, etc.) were not the result of chromatids falling apart -- in those cells in which odd numbers of chromosomes were counted, all chromosomes consisted of two chromatids. There was also a variance in "normal" chromosome counts -- haploid roots and callus tissue gave counts of 9, 10 and 11 (the mean value was 10); diploid cells gave 19, 20 and 21 chromosomes (the mean value was 20) per nucleus. In these cases also, two chromatids were seen for each chromosome. In none of the cells examined were chromosome bridges or fragments found.

This variability in chromosome number led to the suggestion that, since the previous counts had been made nine months after initiation, perhaps these cultures would also be stable after that length of time. Further counts of haploid and diploid cultures were then postponed until nine months after initiation.

To determine whether karyotype instability was dependent on time, counts were pooled according to the time the sample was taken after callus initiation (Table 1). The later samples of diploid cultures showed chromosome numbers to be stabilized primarily at the 2n level (two cultures were 2n/4n chimeras). Haploid cultures, even after nine months, showed an unstable chromosome number; however, the proportion of haploid to diploid cells increased with time. Since all sampled cultures did not grow at the same rate, relative time (first sample, second sample, etc.) was compared with absolute time (three months, four months, etc.). When this was done, diploids seemed to be stable at the diploid level generally by the second sample; haploids were unstable throughout.

Table 1
Chromosome counts (in percent) compiled by age of culture

	3 Months					4 Months					5 Months				
	n	2n	4n	8n	odd	n	2n	4n	8n	odd	n	2n	4n	8n	odd
Diploid Cultures*		67.38	19.56		13.05		52.23	27.3	5.65	14.81		75.01	24.99		
Number of Samples**	-	3	1	-	1	-	14	8	3	4	-	4	1	-	-

	6 Months					9 Months				
	n	2n	4n	8n	odd	n	2n	4n	8n	odd
Diploid Cultures*		50	50			6.84	63.28	29.87		
Number of Samples**	-	1	1	-	-	1[1]	13	2	-	-

	3 Months					4 Months					5 Months				
	n	2n	4n	8n	odd	n	2n	4n	8n	odd	n	2n	4n	8n	odd
Haploid Cultures*	16.37	55.56	13.45		14.62	28.58	46.02	21.74	3.65		35.6	35.42	28.97		
Number of Samples**	1	4	2	-	2	6	8	4	1	-	4	5	2	-	-

	6 Months					9 Months				
	n	2n	4n	8n	odd	n	2n	4n	8n	odd
Haploid Cultures*	47.37	38.14	12.46	2.02		66.47	30.09	1.65		1.79
Number of Samples**	1	6	2	1	-	6	6	1	-	1

*, ** See Table 2. [1] One cell in one sample

Table 2
Chromosome counts (in percent) compiled on the basis of media used

	2, 4-D					2, 4, 5-T					2, 4, 5-TP				
	n	2n	4n	8n	odd	n	2n	4n	8n	odd	n	2n	4n	8n	odd
Diploid Cultures*		53.64	25.28	7.44	13.63		51.16	48.84			5.52	52.56	25.12	4.23	12.57
Number of Samples**	-	14	6	1	2	-	7	1	-	-	1	14	6	2	3
Haploid Cultures*	34.06	38.83	16.42	3.05	7.65	46.01	32.41	21.58			54.06	45.94			
Number of Samples**	11	19	9	2	3	5	4	2	-	-	2	6	-	-	-

* Percentage of values adjusted to a sample size of 100

** Number of samples used in each category

To determine whether a component of the instability was due to the different growth factors in the media (2,4-D; 2,4,5-T; or 2,4,5-TP), all counts were pooled for this assessment according to media type (Table 2). Both diploid and haploid cultures did not appear to have been affected by the different growth factors in the media.

Whether complete chromosome stability would be realized upon continued growth of these cultures cannot be as yet determined. However, finding such a high proportion of cells with the stable karyotype after nine months of culturing suggests that they serve as the primary progenitors in future callus growth. Otherwise their relative frequency should decline with time.

The data reported here show that studies of somatic mutability would be profitably undertaken under such a technical regime of tissue culture. In the case of haploid callus it would seem at this time to be workable material for a study of induced mutation rates. Since a completely defined media is available, mutations affecting basic metabolic pathways could be selected for. It does not now seem out of place to suggest that this technology of tissue culturing could yield genetic information of the order found in microbial genetics of today with the exception of not having a high resolution recombination system.

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1. Linkage relationship between *Y*-*y* and *Rf2*-*rf2* on chromosome 6.

From tests involving *Rf2* and a series of chromosomal translocations, it appears that *Rf2* is located on the short arm of chromosome 6 (Beckett, Maize Genetics Coop. News Letter 36:31, 1962).

The data which follow were obtained from crosses involving *Y*-*y* and *Rf2*-*rf2*. Since *Y*-*y* is reported to be located approximately 13 crossover units from the distal end of the short arm of chromosome 6, it was expected that *Y*-*y* would be closely linked with *Rf2*-*rf2*.

From the following linkage data it appears that these two genes are not linked and therefore Rf_2-rf_2 is not on the short arm of chromosome 6.

Cross #1 — Parent A $Rf_1Rf_1rf_2rf_2YY^T$ x Parent B $Rf_1Rf_1Rf_2Rf_2yy$

		Expected F_2 Ratio	Actual F_2 Ratio	
X^2 for Y-y Segregation	3.43	(9)	69	Yellow Fertile
X^2 for Rf-rf Segregation	3.43	(3)	35	Yellow Sterile
X^2 for Linkage	1.37	(3)	35	White Fertile
X^2 for Total	8.24	(1)	14	White Sterile
			153	

P = .50 - .20 for Linkage X^2

Cross #2 — Parent C $rf_1rf_1Rf_2Rf_2YY$ x Parent D $Rf_1Rf_1rf_2rf_2yy$

		Expected F_2 Ratio	Actual F_2 Ratio	
X^2 for Y-y Segregation	0.04	(27)	164	Yellow Fertile
X^2 for Rf-rf Segregation	2.97	(21)	97	Yellow Sterile
X^2 for Linkage	1.63	(9)	49	White Fertile
X^2 for Total	4.64	(7)	40	White Sterile
			350	

P = 0.20 for Linkage X^2

Backcross #1

Parent C $rf_1rf_1Rf_2Rf_2YY$ x Parent D $Rf_1Rf_1rf_2rf_2yy$ Parent D

		Expected BC Ratio	Actual Backcross Ratio
X^2 for Y-y Segregation	4.32	(1)	160 Yellow Fertile
X^2 for Rf-rf Segregation	4.32	(1)	150 Yellow Sterile
X^2 for Linkage	3.11	(1)	151 White Fertile
X^2 for Total	11.75	(1)	213 White Sterile
			674

P = .10 - .05 for Linkage X^2

Cross #3

Parent C $rf_1rf_1Rf_2Rf_2YY$ x Parent D $Rf_1Rf_1rf_2rf_2yy$

(F_1) $Rf_1rf_1Rf_2rf_2Yy$ x $Rf_1Rf_1Rf_2rf_2yy$ Parent E

		Expected Ratio	Actual Ratio
X^2 for Y-y Segregation	0.14	(3)	141 Yellow Fertile
X^2 for Rf-rf Segregation	0.74	(1)	38 Yellow Sterile
X^2 for Linkage	0.74	(3)	127 White Fertile
X^2 for Total	1.62	(1)	42 White Sterile
			448

P = .50 - .20 for Linkage X^2

Cross #4 Parent A $Rf_1Rf_1rf_2rf_2YY$ x Parent F $rf_1rf_1Rf_2Rf_2yy$

	Expected F_2 Ratio		Actual F_2 Ratio	
X^2 for Y-y Segregation	1.04	(27)	125	Yellow Fertile
X^2 for Rf-rf Segregation	1.24	(21)	114	Yellow Sterile
X^2 for Linkage	0.50	(9)	50	White Fertile
X^2 for Total	1.78	(7)	40	White Sterile
			329	

P = .50 for Linkage X^2

Cross #5 Parent A $Rf_1Rf_1rf_2rf_2YY$ x Parent G $rf_1rf_1Rf_2Rf_2yy$

	Expected F_2 Ratio		Actual F_2 Ratio	
X^2 for Y-y Segregation	.06	(27)	68	Yellow Fertile
X^2 for Rf-rf Segregation	.00	(21)	46	Yellow Sterile
X^2 for Linkage	.92	(9)	18	White Fertile
X^2 for Total	0.98	(7)	22	White Sterile
			154	

P = .50 - .20 for Linkage X^2

The parents involved in each cross were test crossed to lines of know Rf genotypes in order to verify parental Rf genotypes.

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1. Progress on big rings (corn and barley).

A multiple interchange homozygote that combines 2-3d, 2-4b, 2-9, 9-10b has been established. Crosses of it with 1-5-6-7-8 are expected to give plants having 2⊙10.

Two additional stocks, one completed, the other in progress are expected to produce hybrids with 2⊙10.

It may be of some interest that a multiple interchange line has been produced in barley which in crosses with normal produces plants with a ⊙14. (See 1965 barley news letter).

2. Early line, good pachytene spreading.

A 76 to 80-day yellow dent hybrid, Minn. A.E.S. 101 has given excellent pachytene chromosome spreads.

3. Notes on a group of 2-6 interchanges.

As stated by Dr. Longley (personal conversation at last year's meetings), the interchanges listed as having breaks at 6 S.7 or higher are very likely in the nucleolus organizer or in the satellite. Interchanges T2-6 (8786), 2-6(5419), and 2-6(8441) have the break in 6 in the nucleolar organizer. Interchange T2-6 (001-15) has the break in 6 in the satellite.

4. Chromosome pairing studies.

Intercrosses between a series of 2-6 interchange stocks and between a series of 1-5 interchange stocks are being used for a study of chromosome pairing. All crosses with standard normal had a ⊙4. A few of those in the 2-6 series involve some chromosome other than 2. A few of those in the 1-5 series involve chromosome 1 or 5, not both, since the crosses with other 1-5 lines produce plants showing a ⊙6. It is possible that a second interchange may have been in the original plant, or some change occurred in subsequent increases.

Cytological checking of the homozygous and heterozygous parental stocks is necessary before a critical analysis of the pairing configurations observed at pachytene and later stages of meiosis in the intercrosses can be made.

Note:
Based on our results, the procedure of crossing the interchanges belonging to a particular group, e.g. all the 1-5's, with one interchange stock in the group is useful as a check on identification. In this type of test, it is highly desirable to cross only homozygous lines.

C. R. Burnham,
assisted by Ronald
Phillips, Gary
Stringam, Joseph
Neubauer, and John
Stout

5. Power tool for pericarp and aleurone removal.

A battery powered commercial manicure unit has been recently employed in rapidly removing small areas of the pericarp and aleurone. Endosperm characters may then be easily classified. The emery unit, held in the hand, is 2 1/2" long and 1" wide and is equipped with an emery drum attachment. A 2' long cord runs from the unit to a 5" x 3 1/2" case which encloses two flashlight batteries and provides space for storage of the unit. This unit, called "Lady Manicure by Patricia Thompson", is manufactured by Thompson Designs, Inc., 125 Factory Road, Addison, Illinois. Retail Price: $5.95.

Ronald Phillips

6. Interchange stocks segregating wx.

It may be of interest to persons working with interchanges that the following stocks are segregating for waxy. 1. Source: University of Illinois: 5-6 (8590), 5-6 (8665), 5-6 (8696), 6-7 (027-6), 6-7 (4545), 6-7 (8143). 2. Source: Iowa State University: 5-6 (5906), 5-6 (6522), 5-6 (6559), 6-7 (4337). 3. Source: Purdue University: 5-6 b.

Ronald Phillips

7. Double reduction at the waxy locus.

Counts of waxy pollen grains from 27 autotetraploid maize plants were used to study double reduction at the waxy locus. All pollen samples were stained with the same KI concentration and above-stage lighting was used. Counts for simplex, duplex, and triplex were made randomly in time, and on a hemocytometer slide. Although root tip counts to screen for aneuploidy were not made, microsporocytes from some tillers appeared to be euploid at diakinesis. Alpha values were computed using a maximum likelihood formula.

Information about the numbers of pollen grains counted for each class, observed and expected percentages of waxy, and alpha values are presented below. With no double reduction (D.R.), alpha equals 0, and with maximum D.R., alpha equals 1/6 or 0.167.

Class	No. of grains		Percent waxy			Computed alpha values
			obs.	expected		
	total	per plt.		no D.R.	max. D.R.	
simplex	2270	324	50.2	50.0	54.0	0.007
duplex	4812	437	20.8	16.7	22.2	0.13
triplex	3214	357	1.5	0.0	4.2	0.06
simplex + duplex + triplex						0.079

Percentages of waxy and alpha values from the three genotypes are clearly inconsistent. The observed duplex percentage is close to that expected for random chromatid assortment, whereas simplex and triplex classes indicated low and intermediate amounts of double reduction, respectively. Correspondingly, alpha values indicated waxy is almost 50 map units from the centromere in simplex, very near the centromere in duplex, and intermediate in triplex. The alpha value based on all three classes is also intermediate, but meaningless due to the variation among classes.

As non-waxy autotetraploid pollen often exhibited different degrees of staining, dosage effects resulting in mis-classification of heterozygous grains offer one possible explanation for the discrepancies. Other factors such as numerical non-disjunction, and variable quadrivalent formation and separation could also have affected segregation.

Previously, Dempsey (1956 Maize News Letter) reported 50.1 and 48.8 percent waxy for simplex and 18.7 percent for duplex segregations. Levings (1963 Thesis, Illinois) reported about 17 percent waxy segregation for duplex and computed an alpha value of 0.0097 for duplex.

As the differences between the percentages expected for no double reduction and for maximum double reduction are not great, alpha values, and consequently map units from centromere, vary considerably for even small percentage changes. Hence, double reduction and alpha values determined in this way may be of little value in mapping the centromere.

E. T. Bingham

8. Bivalent pairing in autotetraploids.

In autotetraploid maize and alfalfa, it is not known whether the bivalent pairing that occurs is preferential or at random. Consequently, a linkage method has been devised to determine which type of pairing actually occurs. Although single locus segregations are affected by the type of pairing, differences will be much greater where linkage is involved, and the linkage test is more discriminating.

Autotetraploid alfalfa produces mostly bivalents at meiosis, and the test was conceived for use on alfalfa. However, the principles also apply to putative allotetraploids such as 4n maize X 4n teosinte hybrids, and to lines of 4n maize which consistenly produce some bivalents. Many 4n maize lines observed at Minnesota produced two or more bivalents per cell, probably chromosome 10, and presumably the number will increase in time through 'diploidization'.

The technique in its simplest form requires:

1) two linked genes in a biduplex X binulliplex testcross,
2) phenotypic classification of progeny, and
3) chi-square tests of observed to expected segregations for random or preferential pairing.

The three possible modes of bivalent pairing for four 'homologous' chromosomes are given below. A biduplex repulsion genotype is illustrated.

1	2	3	4
A	A	a	a
b	b	B	B

Mode

I Homogenic preferential (Autosyndetic in alloploids) — 1 pairs with 2; 3 with 4

II Heterogenic preferential (allosyndetic in alloploids) — 1 " " 3; 2 " 4
1 " " 4; 2 " 3

III Random pairing - 1/3 homogenic + 2/3 heterogenic

With homogenic pairing, no phenotypic segregation is expected in the first testcross and it may be easily distinguished. With partial or complete heterogenic pairing, however, chi-square tests will be required to accurately distinguish it from random pairing.

Percentages of each phenotype expected from the bi-duplex X binulliplex testcross and the chi-square differences between random and heterogenic preferential pairing are listed below. Chi-square values are based on a population of 200.

COUPLING	50% recomb.			10% recomb.		
	Homo-genic	Random	Hetero-genic	Homo-genic	Random	Hetero-genic
A-B-	100	70.83	56.25	100	80.16	70.25
A-bb		12.50	18.75		3.17	4.75
aaB-		12.50	18.75		3.17	4.75
aabb		4.17	6.25		13.50	20.25
		$\chi^2 = 17.28$**			$\chi^2 = 9.41$*	

REPULSION			
A-B-	(same as above for coupling) 100	66.83	50.25
A-bb		16.50	24.75
aaB-		16.50	24.75
aabb		.17[1]	.25[1]
		$\chi^2 = 22.0$**	

[1]This class is very small and may be eliminated from the test.
**Probability exceeds the 1 percent level.
* " " " 5 " " .

Comparisons of the chi-square values for coupling and repulsion indicate that the difference in repulsion increases as the strength of linkage increases. Therefore, the test in repulsion should be the most useful, especially when it is necessary to distinguish frequencies of preferential pairing that are close to those expected for random pairing.

In a self-pollinating species, the same test could be carried out using F_2 genotypic classifications based on F_3 segregations.

E. T. Bingham

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1. Viruses as agents for mutation and chromosome breakage.

The resemblance of the variegated phenotype produced by certain mutable systems in corn and the variegated symptoms produced by certain viruses in other plants suggests a possible relationship. Perhaps viruses are involved in the production of controlling elements or perhaps systems of mutability represent latent forms of infectious viruses. To test these possibilities a number of experiments have been conducted including one designed to determine whether particular viruses that infect corn can cause gene mutation or chromosome breakage. Evidence has already been presented by Sprague, McKinney and Greeley (1963) that corn plants infected with barley-stripe-mosaic have a higher frequency of loss of the dominant endosperm markers A Su and Pr than do healthy plants.

This experiment consisted of inoculating seedlings of an A^b (αβ) Sh, Dt stock with a virus and then using the pollen from infected and healthy plants, when they matured, to pollinate ears of the genotype a^m-sh, dt. In addition, some of the healthy and the infected pollen parents were treated with X-rays, either premeiotically or postmeiotically applied. The doses were 750r and 2000r respectively, and were given to provide broken chromosome ends for possible interaction with the virus and for comparison with virus results.

Table 1

Frequencies per 10,000 seeds of whole and fractional endosperm losses of the dominant markers of the α β Sh segment from the cross of healthy and infected A^b-Sh, Dt pollen parents on a^m-sh dt ear stock. Treatments of healthy and infected plants with X-rays are also included.

Treatment	Population	Whole endosperm				Fractional endosperm			
		α β Sh	Sh	α β	β	α β Sh	Sh	α β	β
Healthy	45,769	2.2	0	0	0	27.0	0	0	.2
SMV-infected	56,376	1.2	0	0	0	36.0	.2	0	.3
Healthy post-meiotic x-ray, 2000r	17,208	850.0	2.3	.6	0	137.0	1.2	0	0
SMV-infected post-meiotic x-ray, 2000r	27,565	863.0	2.2	.7	0	131.0	0	0	0
Healthy pre-meiotic x-ray, 750r	6,594	120.0	0	0	0	36.0	0	0	0
SMV-infected pre-meiotic x-ray, 750r	3,882	34.0	0	0	0	7.0	.3	0	0

The F_1 kernels were examined for changes of a single component of the $\alpha\beta$ Sh segment, more particularly of β alone which may be considered as gene mutation, and of losses of more than one adjacent component which would indicate chromosome breakage.

The viruses used were bromegrass-mosaic (BMV), wheat-streak-mosaic (WSMV), and sugar-cane-mosaic (SMV). Inoculations were made by the leaf-rubbing method. Plants inoculated with BMV showed early local-lesions followed several days by systemic symptoms which were so severe that all the infected plants died. Plants inoculated with WSMV failed to develop any symptoms and were not used further. About 85% of the plants inoculated with SMV developed clear systemic symptoms. These were used to produce the data recorded in Table 1.

The results which constitute an adequate test clearly show that infection with SMV does not increase the frequency either of mutation of the components of the A locus or of breakage of chromosome #3. The contrast between these results and those reported with barley-stripe-mosaic virus (Sprague et.al.) are striking, indicating that viruses may differ in their relationships with the host genetic material. Similar negative results have been obtained with SMV by Sprague and McKinney (personal communication).

M. G. Neuffer
O. P. Sehgal

2. Infection and movement of sugar-cane mosaic virus (SMV) in certain chlorophyll-deficient mutants of corn.

Virus infections in higher plants, in a majority of cases, induce a yellow-green mosaic pattern of symptoms indicating possible interaction of viruses with chloroplasts and/or chlorophyll content of plants. Several investigators have suggested that chloroplasts are the sites of virus-biosynthesis or virus-maturation processes. It is of considerable interest, therefore, to study infection and multiplication of viruses in chlorophyll-deficient plants as such a study would be helpful in establishing relationships if any, between chloroplasts and virus multiplication. In preliminary trials, we tested albino mutants lw_1, lw_2, cl_1, W8629 and lw_a with several plant viruses. In this report, results of experiments using albino lw_a and SMV, a virus easily transmissible to corn, are presented.

Seeds were sown in white sand and seedlings regularly irrigated with Hoagland's solution fortified with micronutrients. Of the several methods tried to supply sucrose solutions to albino plants, feeding 10% solution through cut-ends of leaves was found most satisfactory. Inoculations were made by the leaf-rubbing method with plant sap extracted from SMV-infected green plants on the first leaf of 8-10 days old seedlings.

Symptoms appeared on green seedlings 4-5 days after inoculation. No visible signs of infection, however, were evident on albino seedlings supplied with or without sucrose. However, SMV was recovered from albino seedlings when the inoculated and non-inoculated leaves of these plants were tested for the presence of virus by back-inoculations to susceptible plants, indicating thereby, transmission and movement of the virus in albino plants. The virus was not recovered from the roots of green and albino plants indicating possibly the presence of a virus-inactivating system in the roots. The virus recovered from albinos appeared similar to the one originally used to infect these plants and apparently SMV was not changed on passage through albino hosts.

Studies are in progress to determine to what extent SMV multiplies in albinos and with which particulate cell component (chloroplasts, nuclei, ribosomes, etc.) the virus is most closely associated.

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1. Chromosome 9 mapping.

New 2-point data, combined with earlier data for the same intervals, are presented in Table 1. New 3-point data are presented in Table 2.

The order Wx-V-Gl_{15} is firmly established; new orders Wx-V-Ms_2 and Wx-Ar-Ms_2 are strongly indicated by recovery of one wx v ms crossover strand from

+ + ms/wx v + selfed, and similar strands for Ar. Unquestioned orders are Wx-D_3-Pg12-Ms2-Gl15-Bk_2-Wc-Bf-Bm4 and Wx-D_3-Ar-V-Gl15. If Ms_2 is to the right of V and Ar, then Ar, V, and Pg12 are consecutive "non-alleles" and will require special tests for placement. Accepting all presumed orders, the Wx-Bk_2 interval would be as follows:

Wx - 3 - D_3 - 2? - (Ar,Pg_{12}) - 1 - V - 1? - Ms_2 - 2 -

Gl_{15} - 10? - Bk_2

Data for v8587 indicate it to be to the right of wx. It is a yellow virescent, from E. G. Anderson, non-allelic to ar and v1 and phenotypically unlike pg12. Data for Wh8-9b, a dominant white endosperm character with dosage effects, also from Anderson, indicate placement in the distal part of 9L. This is a clear-cut character in strong yellow stocks when segregating in the female, it is unlike Wc, causing uniform dilution rather than white cap.

The correct position for bk_2 is distal to TB-9a (9L.5); previous tests (Newsletter 38:110 note) were inadequate. Four hypoploids from bk_2 bm_4 x +/TB-9a were bk bm.

E. H. Coe, Jr.

Table 1
Recombination data for 2-point intervals in Chromosome 9

XY	Phase	XY	Xy	xY	xy	Total	Recombination Number	Recombination Percent
Bf V8587	RS	88	55	46	10	199	-	35.4±6.1
Bf Wh8-9b	CB	236	31	24	204	495	55	11.1±1.4
Bk_2 V	RB	16	139	95	15	265	31	11.7±2.0
D_3 Gl_{15}	CB	348	14	15	306	683	29	4
	RB	0	99	65	1	165	1	1
						848	30	3.5±0.6
D_3 V	RB	7	142	143	2	294	9	3
	CB	118	3	6	111	238	9	4
						532	18	3.4±0.8
Gl_{15} Ms2	RB	5	339	335	5	684	10	1.5±0.5
Gl_{15} Pg12	RB	1	79	70	2	152	3	2
	CB	509	21	22	566	1118	43	4
						1270	46	3.6±0.5
Gl_{15} V	RB	0	20	16	1	37	1	3
	CB	120	4	2	157	283	6	2
						320	7	2.2±0.8
Sh V8587	RS	121	37	31	2	191	-	29±7
V_{8587} Wx	RS	107	39	45	0	191	-	<17

Table 2
3-point Testcrosses in Chromosome 9

F_1	Parental	Reg. 1	Reg. 2	1-2	Total
$\frac{+\ \ +\ \ +}{wx\ \ d_3\ \ gl_{15}}$	277 245 522	4 13 17 3.0±0.7	13 11 24 4.3±0.9	0 0 0 c=0	563
$\frac{+\ \ +\ \ v}{wx\ \ d_3\ \ +}$	43 46 89	1 0 1 1.1±1.1	0 1 1 1.1±1.1	0 0 0 c=0	91
$\frac{+\ \ +\ \ +}{wx\ \ d_3\ \ v}$	114 106 220	5 4 9 3.8±1.2	3 6 9 3.8±1.2	0 0 0 c=0	238
$\frac{+\ \ ms_2\ \ +}{wx\ \ +\ \ gl_{15}}$	67 60 127	21 7 28 18.1±3.1	0 0 0	0 0 0	155*
$\frac{+\ \ +\ \ +}{wx\ \ pg_{12}\ \ gl_{15}}$	448 528 976	38 61 99 9.4±0.9	20 17 37 3.8±0.6	4 2 6 c=1.5	1118
$\frac{+\ \ +\ \ bk_2}{wx\ \ v\ \ +}$	50 88 138	4 8 12 8.7±2.1	11 9 20 13.3±2.6	0 3 3 c=1.5	173
$\frac{+\ \ +\ \ +}{wx\ \ v\ \ gl_{15}}$	116 151 267	6 4 10 3.9±1.2	2 3 5 2.1±0.9	1 0 1 c=4	283

*F_1 used as male; heterofertilizations resolved

2. Recombination and cytological analysis of B'.

Dr. A. E. Longley has obligingly examined sporocytes from plants involving different combinations of B, B', and b. No aberrations in chromosome 2 were found in 3 plants of B B, 7 of B' B, 1 of B' B', 9 of B b, and 11 of B' b, including several sib or parallel-origin comparisons.

Most of these plants were + + +/lg gl_2 v_4, and were backcrossed to lg gl v (Tables 1 - 3).

Table 1
Lg - Gl_2 - V_4 Recombination

Genotype*	Parental	Region 1	Region 2	Doubles	Total
B'/mB	173	84	97	14	368
b/mB	314	130	207	39	690
B'/mb	572	162	297	45	1076
B/mb	219	53	145	17	434
Total	1278	429	746	115	2568

*mB and mb represent B and b with recessive markers

Table 2
Recombination Percentages and Coincidence

Genotype	Lg-Gl	Gl-V	Coincidence
B'/mB	26.6*	30.2	0.47± 0.107
b/mB	24.5*	35.7	0.65± 0.082
B'/mb	19.3	31.8	0.68± 0.083
B/mb	16.1**	37.3	0.65± 0.128
All Samples	21.2	33.5	0.63± 0.048

*,** Significant at 5% and 1% levels, respectively, relative to total (X^2 test)

Table 3
Combined data for B'-bearing and B'-free

Genotype	Lg-Gl	Gl-V	Coincidence
B'-bearing	21.12±1.07	31.37±1.22**	0.62±0.067
B'-free	21.26±1.22	36.30±1.43	0.65±0.070
All samples	21.2	33.5	0.63

**Highly significant difference from B'-free value

Apparently B' decreases crossing-over slightly in the Gl - V region but does not influence interference, although an increase in interference may occur in "converting" heterozygotes. These observations are consistent with conception of B' as involving an appended element or material, or altered parachromatin.

E. H. Coe, Jr.

3. A negative transformation experiment.

Simple modifications of the Marmur technique (J. Mol. Biol. 3: 208-218, 1961) yield very promising DNA preparations from young seedlings.

Germination: 500g of kernels are soaked in aerated water for 8 hours, then placed in a pipette basket wrapped in black plastic and sprayed with a mist for 4 days, loosening frequently by shaking, then harvested and weighed (1-2 kg).

Extraction: Seedlings, including kernels, are chilled in iced distilled water, then blended for 2 minutes, in portions, with minimal volumes of cold saline-EDTA (0.15 M NaCl plus 0.1 M EDTA, total 250-300 ml) and portions of saturated sodium lauryl sulfate (20 ml). The mash is strained crudely through two layers of cheesecloth, divided into two cold one-liter stoppered graduates, brought to 1M sodium perchlorate by addition of 1 part cold 5M sodium perchlorate to 4 parts mash, then mixed and emulsified with a half-volume of iced chloroform-isoamyl alcohol (24 parts chloroform to 1 part isoamyl), and shaken for 20 minutes, with chilling. The emulsion is centrifuged in the cold (10 min., 5,000 rpm) and the upper (aqueous) layer is collected in a large beaker. Two volumes of iced ethanol are added to precipitate the nucleic acids in bulk, and precipitation and settling are allowed to proceed in an ice bath for 30-60 minutes. Most of the liquid is decanted off, and the precipitate is collected by centrifugation (5 min., 3,000 rpm) and promptly dissolved in cold saline-citrate (0.15 M NaCl plus 0.015M sodium citrate, 40 ml or more in portions, preferably dissolving rapidly and completely in small volumes of 1/10 strength followed by addition of 10x strength to bring to proper concentration). Sodium perchlorate is then added (5M, 1 part to 4), and the solution is shaken with an equal volume of chloroform-isoamyl for 15 minutes, centrifuged, and the aqueous layer removed and overlaid carefully with two volumes of ethanol. The threads at the interface are then collected by winding on a wooden swab stick. The collected threads, largely DNA, are redissolved in saline-citrate and can be deproteinized repeatedly by proceeding through the perchlorate-chloroform step several times. Saline-citrate seems to be a satisfactory solvent for injection into corn seedlings.

Transformation trial: Source seedlings were B A Y Pl Yg C Sh Wx Rg, C Sh Wx R^r. Recipients were b A y Pl yg c sh wx Rg, permitting observation in the immediate plants for B, Yg, and R^r, and in seed and seedling progenies for Y, Yg, C, Sh, and Wx. Crude preparations with and

without spermine (0.05%), a stabilizing agent, were injected by puncturing repeatedly into the area of the growing point, and half of the treated seedlings and controls were x-rayed promptly (1000 r) in hopes of opening membranes, inhibiting nucleases, and providing sites for incorporation. Seedlings, were injected at 1 to 2 weeks, 3 weeks, and 4 weeks after planting, including some repeated at all three stages. Although variable leaf-streaking simulating Yg was seen in a few plants, no B sectors or purple anthers were observed in over 250 treated survivors. In over 26,000 seeds obtained from intercrosses among the plants, five exceptional seeds were found (4 C Sh Wx, 1 C sh? Wx), in both treated and control material; these are presumably contaminations but are to be tested. Half of the 26,000 seeds were planted in the sand bench and scanned for Yg; no exceptions were found.

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1. Chromosome knobs of North Carolina inbred lines.

Cytological examination was made of the inbred lines of two varieties which have been and are being studied for quantitative analysis. The objectives are: 1) To find inbreds from both varieties with identical knob constitutions to provide material for further studies involving K10 effects on genetic variances and recombination and, 2) to provide a characterization of the differences between the two varieties with respect to frequency of various knobs which, in turn, may provide a useful background in planning experiments to study the nature of quantitative genetic differences between varieties.

Two sets of inbred lines have originated in 1953 from 300 random selfed ears of varieties Jarvis Golden Prolific and Indian Chief, and each ear was used to establish an inbred line. In order to minimize selection during the following inbreeding period, every line in every generation was raised from a single selfed ear of the first plant in the row in the preceding generation. Currently available are 64 lines of Jarvis and 125 lines of Indian Chief.

Table 1
Knob constitution of the inbred lines from Jarvis

Line No.	Total Knob No.	Position and size of each knob*											
		1S	1L	2L	3L	4L	5L	$6L_2$	$6L_3$	7L	$8L_1$	9S	9L
18	3							t	t	m			
21	4						t	t	t	l			
30	5						t	t	t	m	m[a]		
15	5						l	t	m	l	m		
4	5						t	t	l	l	l		
34	4						l		t	m	m		
68	5							t	t	m	m	t	
22	4						t		t	l		t	
20	5						t	t		l	m	t	
9	5					l	t	t		l		t	
13	5					l	m	t		l		t	
10	5					ll		t	t	l	l		
3	6			l		l	t	t		l	m		
5	6			l		l	t	t	s	m			
19	7			s		l	l	t		l	l	t	
7	7			l		ll	m	t		l	l	t	
14	8			l		l	t	t	s	l	m	t	
8	3			l			l			l			
78	4			l			l		t	l			
11	4			l				t		l		t	
32	4			l					t	m		t	
65	5			ll				t	t	m	l		
16	5			l			t	t		l	l		
17	6			ll			t	t	t	l	m		
6	6			ll			m	t		l	l	t	
2	5			l			l		t	l		t	

Table 1 Continued

Line No.	Total Knob No.	1S	1L	2L	3L	4S	5L	$6L_2$	$6L_3$	7L	$8L_1$	9S	9L
73	5			l			s	t		m		t	
42	7			l			t	t	t	m	m	t	
76	5			ll			t		t	m			t
12	6			ll	ll[b]		l	t	t	m			
46	6					l	t	t	t	m		t	

*t=tiny, s=small, m=medium, l=large, ll=very large.
Knobs are all homozygous expect (a), which was homozygous in 2 plants, heterozygous in 3 plants, and none in 2 plants.
b-extra large knob.

Table 2
Knob constitution of the inbred lines from Indian Chief

Line No.	Total Knob No.	Position and size of each knob*											
		1S	1L	2L	3L	4S	4L	5L	$6L_2$	$6L_3$	7L	$8L_1$	9S
166	3				s			t			l		
165	4				s			t		t[a]	l		
119 & 172	4				s			l		t	l		
140	5				s			t	t	t	l		
135	5				s			l	t	t	m		
139	4			l	s			t			l		
163	5			ll	s			l		t	l		
190	5			l				t		t	l	l	
216 & 227	4							l		t	m	s	
179	4				s			t			m	s	
116	5	m			s			t			l	m	
168	4	s						t		t	m		
169	4	s						t		t	l		
125	6	s		l	s			t			l		t

*t=tiny, s=small, m=medium, l=large, ll=very large. All the knobs are homozygous.

[a]Homozygous in 4 plants but none in 5 plants.

Out of them, 31 lines of Jarvis and 16 of Indian Chief were chosen at random. Knob composition of each line was determined by examination of the first five plants whenever it was identical for all of them, but more plants were examined in a few cases in which it was different among individual plants. In addition to the pachytene stage, late pachytene or early diplotene stages were examined to determine whether knobs are homozygous or not, although these lines are inbred. All knobs were classified into five arbitrary categories: tiny, small, medium, large, and very large, for a truly objective method of determining knob size and shape is not possible. The results are shown in Tables 1 and 2.

There were no two lines with identical knob composition for lines of Jarvis; every line of 31 examined differs from every other in knob composition. Contrasting to the above, two sets of lines with identical knob composition were found out of 16 lines examined for Indian Chief. This situation, diversity in Jarvis and close relationship in Indian Chief, agreed well with the facts which have been indicated by analyses of certain quantitative traits.

A series of data is available of inbreeding depression between those lines providing sets of lines indicating a large value (.2700-.3650) or a small value (.0400-.1100) (unpublished data by Dr. R. H. Moll). Attempts were made to find any association between inbreeding depression and knob composition, e.g., knob number, number of knob positions different as to presence vs. absence of knobs, or presence or absence of particular knobs. No consistent association was found.

Three sets of lines, so far, were determined to have almost identical knob compositions, that is, identical knob positions with a slight difference in size at one particular knob (Table 3). Lines of these sets will be used for the experiments to evaluate the effects of abnormal chromosome 10 on the recombination frequency among linked genes which affect quantitative traits. Incorporation of abnormal chromosome 10 into these lines is already under way.

Table 3
Comparison of knob constitution of selected inbred lines

Line	Position and size of each knob					
	2L	3L	5L	$6L_3$	7L	$8L_1$
CI 21			l	t	l	m
# 34 of Jarvis			l	t	m	m
# 216 & # 227 of Indian Chief			l	t	m	s
NC 45	l		t	t	l	
# 78 of Jarvis	l		l	t	l	
# 165 of Indian Chief		s	t	t	l	
# 119 & # 172 of Indian Chief		s	l	t	l	

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1. <u>Inheritance and nitrogen metabolism of a lutescent maize mutant.</u>

Characterization of a recently reported (MNL 38:116) lutescent mutant from the viewpoint of classification and expression, inheritance information and nitrogen metabolism is being investigated. Classification is generally good, but expression has been shown to be light and/or temperature sensitive, being much better under field conditions than in the greenhouse. Viability is rather good, but seed set and vigor are only fair.

The mutant was crossed with several standard inbred lines; selfs of these crosses produced 269 normal green and 81 mutant plants. Crosses were made with Dr. E. G. Anderson's waxy-marked translocation series involving all chromosomes. All F_2 populations showed normal 3:1 segregation except those involving wx 5-9c and wx 8-9d from which the following data were collected. Waxy seeds of the 5-9c translocation material gave 38 normal: 0 mutants; non-waxy seeds gave 3 normal: 1 mutant. Waxy seeds of the 8-9d translocation gave 29 normal: 2 mutant; non-waxy seeds gave 12 normal: 0 mutant. These data suggest that the gene is located on chromosome 5.

Embryo-cultured mutant seedlings grown under sterile conditions on an agar medium with mineral salts (including nitrate) and sucrose show good mutant expression under artificial lighting. Chlorophyll content was determined spectrophotometrically. Mutants contained roughly one-half as much chlorophyll, per fresh weight, as normal plants under the same conditions. The addition of ammonium ion, urea, or one of the common naturally occurring amino acids to the medium resulted in an increase in chlorophyll content of the mutants to various degrees - up to 44% above that of mutant controls. The greatest amount of greening resulted with the addition of L-alanine.

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1. Evaluation of root systems as measured by resistance to uprooting.

In the maize breeding program carried out at the University of Pretoria, South Africa, it has become increasingly apparent that root systems are of great importance in maize to be grown in a relatively dry climate. Casual observation had led us to believe that a good root system was strongly correlated to yield, but in order to test this hypothesis, it was necessary to devise some method of evaluating the root system of a plant.

An apparatus to measure the pull necessary to uproot individual plants was designed and found to be practical in field trials. The apparatus consists of a lever, mounted on two legs, which exerts a vertical pull (measured by an attached scale) on a clamping head. The head is clamped around the stalk of the plant to be pulled as close to the ground as possible and then a steady pressure exerted on the lever until the plant is uprooted. The maximum pull needed to uproot the plant is then read from the scale.

Since resistance to uprooting would be expected to vary for different soil types, moisture conditions, and plant growth stages, all preliminary trials were conducted

with plants of the same age (about 4 weeks before harvesting) and all pulling was done on the same day, thus under the same moisture conditions. Experiments to determine pulling differences due to soils, moisture and plant age are now in progress.

Resistance to uprooting was tested in a double lattice experiment with 64 entries and 4 replications. Yield data were taken from 40-plant plots and uprooting resistance data from the first 4 plants in each plot. The Coefficient of Variability for yield in this experiment was 6% while that of uprooting resistance was 5%. The Coefficient of Correlation of yield to uprooting resistance was +0.67. These results seem to bear out the following points:

1. A good root system as measured by resistance to uprooting is strongly correlated to yield under South African field conditions.
2. Four plants of each type give the necessary information on resistance to uprooting. Since this number of plants is so low, the uprooting can be carried out easily in field trials.

A preliminary unreplicated trial in which 10 plants of each type were uprooted gave the results shown in Table 1. The maximum pull needed to uproot a single plant in our experiments was of the order of 900 lbs.

Table 1

Maize type	Pull needed to uproot in pounds
South African Varieties	
Potchefstroom Pêrel	224
Pretoria Potchefstroom Pêrel	329
Natal Potchefstroom Pêrel	241
Peruvian	271
Sahara	278
Gobi	259
South African Hybrids	
SA 4	378
SA 100	332
SA 200	296
SA 60	355
SA 9N	376
SA 11	316
SA 33	301

Table 1 Continued

Maize type	Pull needed to uproot in pounds
Inbred Lines	
T15R	439
A17	96
K64	282
K64R	277
CI 64	236
Mexico 155	374
Mo 21 A	408
CI 90A	188
Miscellaneous	
Texan	438
American IV-1	317
Hooker B	245

Preliminary experiments on the mode of inheritance of uprooting resistance indicate a relatively simple form of inheritance. Since most of the South African types tested were low or intermediate in resistance to pulling it is hoped that good improvement in root systems can be made by selection for this characteristic.

Drawings of the apparatus used to measure resistance to uprooting will be furnished to interested parties on request.

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1. An apparent interaction of chemical mutagens when applied in combination.

The alkylating agents, Diethylsulphate (DES), Ethylenimine (EI), Ethylmethanesulfonate (EMS), and Diepoxybutane (DEB), were applied in an aqueous solution to soaked and dry maize kernels singly and in all possible combinations. The homozygous genotype $\underline{A_1}$ $\underline{A_2}$ $\underline{Pr}$ $\underline{C}$ $\underline{Sh_1}$ $\underline{Wx}$ $\underline{Yg_2}$ was used in the endosperm marker technique. Pilot greenhouse and laboratory studies were conducted to establish a 70% survival rate for each chemical concentration and exposure.

The combination treatments were made by applying two single chemical treatments in succession, e.g. kernels were placed in the DES solution for 1 hour, rinsed in water and placed in the EI solution for 1 hour to produce the DES:EI treatment combination. The soaking pretreatment altered the response of the plant to individual chemicals, but not the overall maximum rate of mutation.

Tables 1 and 2 compare the effect of the pretreatments. Nearly all the treatments exceed the upper fiducial limit of the control for endosperm mutation rate. The combination treatments of EMS:DEB, DES:EMS, (Table 1), EMS:DES, and DEB:EI, (Table 2), produced a fourfold increase in mutation rate over that seen in the control and almost doubled the rate of the most effective single treatment. The agronomic data indicate no lethal response to successive treatments by two different chemicals, whereas a single treatment in one chemical concentration of similar duration will produce lethality. This synergistic response, which utilizes an apparent interaction of the chemical mutagens to produce a high rate of endosperm mutation without the usual loss of plant material, is a possible means of broadening the mutant spectrum and increasing the efficiency of chemical mutagens.

Table 1
Soaked Seed Pretreatment

Treatments Chemical	Conc. M.	Time Hrs.	Plant Height Ins.	Pollen shed *	Survival N = 45 %	Mutation rate %	Fiducial limits .05 level
EMS:DEB			57	11	67	1.17	.9 — 1.5
DES:EMS			61	8	87	1.03	.8 — 1.4
EI:DEB			80	4	69	.95	.7 — 1.3
EI:DES			57	7	69	.80	.6 — 1.0
DEB:DES			61	3	78	.77	.6 — 1.0
EI	.050	1	70	9	53	.60	.4 — .9
DEB:EI			74	4	69	.55	.4 — .8
DEB:EMS			59	7	67	.52	.3 — .8
DES:DEB			70	8	56	.51	.4 — .7
DES	.045	1	67	3	93	.45	.3 — .6
EMS:EI			48	10	51	.43	.2 — .8
DEB	.003	1	89	1	67	.41	.3 — .6
DES:EI			62	10	53	.36	.2 — .6
EMS:DES			32	11	82	.33	.1 — 1.2
EMS	.010	12	61	6	84	.30	.2 — .4
EI:EMS			44	16	20	0	-- — --
Control			93	0	90	.36	.3 — .4

*Days after control.

Table 2
Non-soaked Seed Pretreatment.

Treatments Chemical	Conc. M.	Time Hrs.	Plant Height Ins.	Pollen shed *	Survival N = 45 %	Mutation rate %	Fiducial limits .05 level
EMS:DES			48	9	80	1.16	.9 — 1.5
DEB:EI			80	6	7	1.00	.5 — 1.5
DES:EI			67	4	29	.79	.5 — 1.2
DES:EMS			58	8	95	.72	.3 — .9
EMS	.010	12	61	5	78	.65	.5 — .9
EI:EMS			61	10	33	.64	.4 — .9
EI:DEB			84	4	22	.59	.4 — .9
EMS:DEB			65	9	62	.55	.4 — .8
DEB:DES			81	1	98	.53	.4 — .7
DEB	.006	1	95	1	93	.52	.4 — .7
EI:DES			78	3	49	.47	.3 — .7
EMS:EI			61	7	56	.45	.3 — .9
DES:DEB			81	5	13	.38	.1 — .9

Table 2 Continued

Treatments			Plant	Pollen	Survival	Mutation	Fiducial
Chemical	Conc. M.	Time Hrs.	Height Ins.	shed *	N = 45 %	rate %	limits .05 level
DES	.045	3	71	9	87	.31	.2 — .5
DEB:EMS			61	8	78	.29	.1 — .4
EI	.050	1	0	0	0	0	-- — --
Control			93	0	89	.27	.2 — .3

* Days after control.

H. R. Lund
D. V. Glover

2. Location of small plant (spl) on chromosome 6.

Small plant (spl) mutant stocks were crossed to a series of stocks homozygous for waxy marked chromosome-nine translocations. The F_1 plants were selfed and F_2 starchy and waxy seeds from each translocation cross were planted separately and examined for small plant (spl) segregations.

Expected ratios (25%) of small plant were obtained with all translocations except T6-9[4]505-4. Within the F_2 waxy seed class planted involving this cross a significant association was demonstrated between the small plant (spl) gene and the translocation tester T6-9[4]505-4. Two hundred and seventy starchy and 230 waxy seeds from 7 selfed F_1 plants were planted. Not all of the starchy seeds were planted out for observation thus accounting for the discrepancy in the Wx:wx ratio. The data from the progenies involving T6-9[4]505-4(6L.13 and 9 ctr.) were as follows: starchy seeds gave 158 normal:42 spl and 70 failed to grow; waxy seeds gave 148 normal:4 spl and 78 failed to grow. Progenies of waxy seed gave 2.6% small plants, from which it is apparent that small plant is located on chromosome 6 near the Y locus. However, there is a discrepancy in the progenies of the starchy seed since fewer small plants were observed than expected. Testcrosses have been made and will be analyzed to confirm the location and linkage on chromosome 6.

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1. Correlation of enzymatic activity with Wx dosage.

Recent studies on the waxy locus in our laboratory indicate that this locus probably is structural rather than regulatory in nature. One of the most important findings is that starch granule preparations from both diploid and tetraploid stocks show increased enzymatic activity with increasing numbers of Wx alleles.

Self pollinations and reciprocal crosses between wx^c and Wx were made in both diploid and tetraploid stocks. The starch granules were prepared from developing seed frozen 16 days after pollination in the diploid series while those of the tetraploid series were prepared from endosperm collected 22 days after pollination.

The enzymatic activity is based on the measurement of the release of the ADP from ADP-glucose. It is clear from Table 1 that the enzymatic activity is related in a nearly linear manner with the number of Wx alleles. The enzyme preparations from the diploid series included the embryo which contains the same level of active ADP-G transferase in both wx^c and Wx and its activity contributes about 1.5 mμM ADP per Mg. of preparation. A correction has been made in the diploid series in order to get a hypothetical value for the enzymatic activity of endosperms.

The protein content of the tetraploid series was measured by the Lowry method. As shown in Table 2, the protein content increased about 0.2 μg per mg. of starch granules for each Wx allele added. It is obvious that the increase in enzymatic activity is almost proportional to the number of Wx alleles, and protein content above the base level, which might suggest that the Wx allele is responsible for the coding of the active enzyme protein while no protein is produced by the wx^c allele.

Table 3 shows the percentage of amylose in starch of the diploid and tetraploid series; the percentage is measured on the basis of the Blue Value method (M. Ulmann and S. Augustat). In the case of Wx/Wx/Wx endosperms, the percentage of amylose increases with age and reaches a maximum of about 25% at maturity. As we know that the ADP-glucose transferase is responsible for amylose synthesis, it is not surprising that in both diploid and

tetraploid with two doses of Wx alleles the same percentage of amylose is found. The percentage of amylose increases with the increase in Wx alleles. However, the increase is not linearly proportional.

We have reported that wx endosperm gives a measurable level of enzymatic activity and that this activity might be entirely due to the contamination from the closely adherent maternal tissue. Now we have been able to prepare the starch granules from wx pollen grains where no question of contamination from maternal tissue exists. We still find low but measurable activity as shown in Table 4. Enzymatic activities are enhanced by the addition of a primer, maltodextim. Three mutants, wx^{c}, wx^{B}, and wx^{90}, were studied in this experiment. They show the same Km value, 5×10^{-4}M, and the same increase in activity with temperature within a certain range and are also similar in thermostability etc.

Starch granules also have been prepared from Wx pollen grains. This preparation is quite similar to the Wx/Wx/Wx endosperm preparation by all criteria employed.

Table 1
Enzymatic activities of ADP-glucose transferase in diploid and tetraploid Wx dosage series

Preparations	activities(mμM ADP/mg.)
Diploid	
0 Wx	2.5
1 Wx	6.9
2 Wx	19.3
3 Wx	27.3
Tetraploid	
0 Wx	2.4
2 Wx	15.2
4 Wx	34.8
6 Wx	46.6

Table 2
Protein content* of starch granules in tetraploid
_Wx_ dosage series

Preparations	Protein content(μg/mg.)
0 _Wx_	1.1
2 _Wx_	1.6
4 _Wx_	2.0
6 _Wx_	2.4

*Protein content was measured by Lowry method with bovine serum albumin as standard.

Table 3
The percentage of amylose of starch granules in both diploid and tetraploid series with regard to the number of _Wx_ alleles

Preparations	Percentage of amylose*
Diploid	
0 _Wx_	2
1 _Wx_	6.5
2 _Wx_	14.0
3 _Wx_	17.5
Tetraploid	
0 _Wx_	0.5
2 _Wx_	15.0
4 _Wx_	20.0
6 _Wx_	21.5

*The percentage of amylose was measured by the Blue Value method.

Table 4
The release of ADP mμM/mg from ADP-glucose in preparations of starch granules from pollen grains of wx^c, wx^B, wx^{90} and Wx

Preparations	- maltodextim	+ maltodextim
wx^c	1.3	5.6
wx^B	1.4	4.6
wx^{90}	3.2	7.8
Wx	24.0	50.0

Chia-Yin Tsai

2. The use of wx, ae stocks in genetic investigations of the wx locus.

For several years we have been using wx, ae stocks in our investigations of the wx locus. The interaction between wx and ae is such that the double mutant seeds have defective endosperms reminiscent of the sugary mutant. Seeds that are Wx/wx/wx; ae/ae/ae seem to be distinguishable from wx/wx/wx; ae/ae/ae or Wx/wx/wx; Ae/ae/ae seeds. Thus if all stocks are made double mutant wx^x; ae, in conventional analyses of crosses between 2 different wx alleles, the distinctive phenotypes can be used to detect the Wx; ae recombinants as well as Wx, ae contaminants.

Such a system has been used to repeat the conventional analysis of the cross between wx^{90} and wx^{Coe}. The F_1 Bz wx^{90} V / bz wx^{Coe} v; ae/ae was used to pollinate the tester stock bz wx^{Coe} v; ae. The reciprocal pollinations were also made. Of 36 plants from suspected Wx/wx/wx; ae/ae/ae kernels on which test crosses by bz wx^{Coe} v; ae were obtained, 31 were Wx/wx; ae/ae as originally identified; 2 were Wx/wx; Ae/ae contaminants; 3 were wx/wx; ae/ae and were either misclassified or due to heterofertilization. Of 5 plants from kernels originally identified as Wx/wx/wx; Ae/ae/ae (contaminants), all were Wx/wx; Ae/ae.

Of the 29 Wx recombinants coming from the pollinations in which the wx^{90}/wx^{Coe} heterozygote was the male parent, 18 were Bz v, 9 bz v, 1 Bz V, and 1 bz V. Table 1 compares these data to those gathered in 1960. The ratio of Bz V to bz v gametes in both tests is quite similar. However, in the 1963 test where

contaminants (which would be Bz V) could be detected, the percentage of Bz V gametes was much lower. This suggests that some of the Bz V recombinants detected in 1960 were due to contamination.

Table 1
The assortment of outside markers in Wx recombinants from the cross Bz wx^{90} V/ bz wx^{Coe} v for 1960 and 1963

	1963		1960	
	No.	%	No.	%
Bz v	18	62	63	58
bz v	9	31	27	25
Bz V	1	3.4	15	14
bz V	1	3.4	3	2.7
	29		108	

Oliver Nelson

3. The location of the waxy mutant H21.

One of the waxy alleles with which we originally worked was wx^{H21}. On the basis of recombinational frequencies (Wx) in intercrosses with C, 90, B, and a, it was felt that the most probable order was C, 90, H21. It has since been shown by conventional genetic analyses that C(Coe) is located distally to 90 as (Bz) C 90 (V).

A similar analysis has now been made for H21. Pollen from plants of the F_1 $\frac{\text{Bz } wx^{H21} \text{ V}}{\text{bz } wx^{coe} \text{ v}}$; $\frac{\text{ae}}{\text{ae}}$ was used to pollinate the tester stock bz wx^{Coe} v ae. Tassel collections were also made for estimates of Wx frequency by our standard pollen scoring techniques.

In a total population of 1,571,000 pollen grains from 9 plants, 776 Wx were detected or 49×10^{-5}. This compares with 46×10^{-5} estimated for the cross between C and H21 in our original experiments.

Due to poor germination and dry weather, the conventional analysis yielded a total population of only 21,698. Of these 9 (41×10^{-5}) were apparently Wx, ae seeds. Of the nine apparent recombinants, 8 were carrying the bz marker and 1 Bz indicating a location for H21 distal to C contrary to earlier hypothesis.

Oliver Nelson

4. Location of miniature seed (mn) on chromosome 2.

Crosses were made between a series of translocation stocks in which waxy (wx) was used as a marker for the chromosomal interchanges and a miniature seed (mn) Wx stock. These F_1 plants were then selfed, and the miniature seeds checked with iodine solution for waxy endosperm.

Slightly lower than expected ratios (25%) of waxy were obtained with all translocations except T 2-9 b. Progenies involving T 2-9 b, which has break points on the short arm of chromosome 2 at .18 and on the long arm of chromosome 9 at .22, gave 1.2% waxy seeds. It is therefore apparent that miniature seed is located on Chromosome 2.

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1. Further studies on trivalent frequency in an array of maize chromosome 2-Tripsacum interchange chromosome constitutions.

An attempt was made to synthesize additional 21 chromosome constitutions combining the available primary and secondary maize chromosome 2-Tripsacum interchange chromosomes in various ways. A number of the plants derived repeated constitutions which have been reported earlier (Genetics 51: 23-40. 1965), and showed metaphase I trivalent frequencies very similar to those described before. Four previously unknown 21 chromosome constitutions were also derived. Metaphase I trivalent frequencies from microsporocyte samples of three of these four constitutions were approximately consistent with expectation from previous findings in that: 1. a constitution fitting into the general category

described as having maximum extent of homology in the short chromosome and no parts present in triplicate gave an average metaphase I trivalent frequency of 92 percent (as compared to 90, 93, and 95 percent in former findings); 2. two constitutions with approximately half maximum extent in the short chromosome and no parts present in triplicate gave average metaphase trivalent frequencies of 43 percent and 54 percent respectively (as compared to 48 percent for the previously known type of this category). However, a plant of a new constitution, in which the maximum extent of homology was present in the short chromosome with approximately half this region present in triplicate and half in duplicate, gave a metaphase I trivalent frequency of 83 percent in contrast to 67, 71, and 72 percent found earlier in comparable constitutions. More plants of this type will be sought to study whether this departure from expectation is consistent and meaningful. The constitution differs from the others of its category in that the chromosome region present only in duplicate is terminal and maize instead of Tripsacum in origin.

M. P. Maguire

2. Anaphase I distribution of an extra, interchange chromosome.

In certain 21 chromosome constitutions tests are possible for the frequency with which an extra chromosome disjoins from its partial homologue at anaphase I, both following its involvement in crossing over and following failure of such involvement. One such test depends upon estimation of chiasma frequency in the pertinent chromosome region in microsporocytes and determination of disjunctive versus non-disjunctive frequency of these elements from genetic tests in the progeny (Genetics 49: 69-80. 1964). Two such progenies are now available (with total plant numbers of 153 and 127 respectively). The total frequencies of non-disjunction of homologous elements in these were 29 and 46 percent suggesting a greater than expected tendency for the extra chromosome to accompany its partial homologue both following and not following chiasma formation. (Previous average non-disjunction frequency following chiasma formation in a different test designed to test this quantity genetically was 19 percent; trivalent frequency of parents was 90 percent). Thus preliminary results are in contrast to the reports of R. F. Grell on Drosophila where univalent single extra chromosomes were found to be distributed randomly. Additional progenies will be scored, and B chromosomes (which are

approximately the same length as the extra chromosome) will be added to test for the possible presence of "distributive pairing".

M. P. Maguire

3. The duration of synizesis.

A Black Mexican sweet corn plant was grown outdoors in a pot and brought into the laboratory at sporocyte stage. The stem was opened and the intact tassel (still attached to the plant) was spread out on a plate supported by a ringstand clamped to the pot. Anthers were removed from every second or third spikelet and scored for stage. The entire tassel and its supporting plate were then enclosed in a plastic bag to prevent drying. (Intact spikelets retained a fresh appearance throughout the entire experiment). Remaining anthers were removed periodically and scored for stage. Assuming that the 13 spikelets bracketed at the beginning of the experiment by spikelets at synizesis were themselves at that stage, the approximate duration of synizesis in this plant (at 25° C) is estimated to have been 50-52 hours. The time to typical early pachytene stage varied from 17 hours to 54 hours, and the mode was in the 46-50 hour class. It is thought that those spikelets requiring near maximum time most nearly represented a full synizetic duration, the others probably having progressed beyond earliest synizesis at the beginning of the experiment. From fewer observations it is guessed that the duration of pachytene under these conditions was approximately 5 hours, and the remainder of meiosis about 1 hour.

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1. Genetics of tillering.

The studies on attempted identification of tillering genes by means of a series of 17 translocations are continuing. Two sets were planted out last year. One group, involving grassy-tillered stock, showed no tillers in either the wx/wx crosses or the Wx/-

crosses, even though these 1800 plants were observed up until frost in October. The other group, involving Pawnee stock, had tillers in equal numbers among 1800 plants in both wx/wx and Wx/- groups. Each of the groups lacked 4 crosses with the proper translocations, however, and these were made in 1964. The cool growing season may also have affected expression of grassy-tiller. Studies on these two and on five other tillering stocks will be continued through 1965.

2. Studies involving the gene rootless.

As reported in the 1962 MGCNL, the gene rt/rt may be modified in its expression by addition of IAA, IBA or NAA in several concentrations when applied at regular intervals throughout the growing season. During 1964, two observations on rt/rt were made to which I have not found previous reference. The stocks employed (Coop stocks) yielded two types of plants from which selfs were obtained. One of these formed only 6-8 roots while still a seedling; no more roots were ever initiated or formed. Such plants had to be supported if they were not to be lost. Eleven such plants were found in 350 plants. All of the other plants in this number were genetically rt/rt and they also did not form true brace roots. They did, however, form fibrous roots at nodes, or just above them, as in normal plants, provided that the nodes were underground. It is most probable that the darkness influenced root formation. Selfs have also been obtained in these stocks. Relationships between light, the gene rootless, auxin production, transportation, destruction and correlations with root formation are under current study.

3. Studies involving the gene Knotted.

Homozygous Kn/Kn stocks have been obtained in which the knots which develop are up to 5 cm in length. Ontogenetic formation of these knots can be either retarded or arrested completely by NAA applied daily to the plants in the proper concentration. Anatomical correlations of untreated and treated plants in various stages of development and in normal, heterozygous and homozygous individuals are being studied.

4. Masking of v4 by growth substances.

This mutant is best expressed under cool growing temperatures; this past season provided ideal conditions for a study of overcoming the effects (i.e., causing the plant to become greener sooner). Each of the substances IAA, IBA and NAA was effective, provided they were applied daily during the growing season. At a time when control plants were only pale green in the older leaves and clear yellow in the younger leaves, IBA caused the older leaves to be more intensely green, but had little effect on the very youngest leaves, which were often yellower than in control plants. NAA caused all leaves to be greener and shorter than controls. IAA had least effect, but still plants were greener than controls. Three rows of 60 plants each in four randomized groups per row formed the basis of these results.

5. Dry-weight increases in 2 genetic strains of milo.

10-day interval treatments of both 38-day and 44-day milo with TIBA, an auxin antagonist, results in dry-weight increases in roots and shoots. Such data indicate that the plants may owe their dwarfness to an excess rather than a deficiency of substances concerned with cell elongation. Studies are continuing.

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1. Mutagenic effects of barley stripe mosaic on corn.

The most common effect, and the one most extensively studied, is a type of segregation distortion. One set of typical data is presented in Table 1. Progenies 752 and 753 were A a and a a in genotype and were derived from a 1963 culture exhibiting segregation distortion. Male and female transmission deviate significantly from the expected 50:50.

All treatments were applied to a susceptible,multiple marked dominant stock. The multiple marked recessive female appears to be immune to the virus. Previous tests have demonstrated that the virus is not transmitted through either the seed or pollen. All effects are therefore presumed to trace back to effects induced in the original virus infected male. The following tentative conclusions appear justified on the basis of studies thus far completed.

a. The types of segregation distortion illustrated in Table 1 occur with a frequency slightly greater than 1:500 and have been observed for each of the marker genes studied: A, Pr and Su. The effect is local rather than general in character, segregation at one locus being aberrant and at other loci normal.

b. Segregation distortion, in some cultures, has persisted through 3 backcross (A a x a a) generations.

c. Distortion may exhibit 3 states: (1) high frequency of the recessive; (2) low frequency of the recessive and (3) normal segregation. Stocks carrying A (virus exposed), when used as either males or females can transmit the abnormal condition to unrelated stocks.

d. Each of the abnormal states may shift to the other abnormal state or to normal. The four progenies in Table 1 exhibiting percentages of a in the 20's represent cases of shift. There is also evidence that the derived "normals" can revert to a high or low state but the incidence of reversion in this direction appears to be low.

Table 1
Data on the transmission of A and a alleles in reciprocal backcrosses

Culture and Plant Number	Female Transmission A	a	%a	Male Transmission A	a	%a
64:752-1 x 753-8	279	92	24.8	299	107	26.4
752-2 x 753-3	370	121	24.6	269	81	23.1
752-4 x 753-11	97	195	66.8	119	207	63.5
752-6 x 753-13	164	259	61.2	129	192	59.8
752-7 x 753-14	214	346	61.8	137	195	58.7
752-8 x 753-15	107	164	60.5	74	149	66.8
752-12 x 753-1	186	53	22.2	215	71	24.8
752-13 x 753-12	184	49	21.0	278	98	26.1
752-14 x 753-4	125	182	59.3	120	210	63.6
752-17 x 753-5	176	285	61.8	124	236	65.6
752-18 x 753-7	71	163	69.7	146	244	62.6

e. The source of the a a genotype in the A a x a a backcrosses has no appreciable effect on male or female transmission values.

f. Cytological studies have not been made of the "distortion" stocks but neither the appearance of the ears nor of pollen suggests chromosomal deficiencies or translocations.

g. Comparable studies with sugarcane mosaic indicate that this virus has no significant mutagenic effect.

G. F. Sprague
H. H. McKinney
Lester Greeley

2. Linkage of white tip (wt).

This chlorophyll deficient seedling type is characterized by a white tip on the first seedling leaf. In extreme cases this first leaf may be entirely white. Viability is excellent and the mature plant is normal. Backcross linkage data from the cross Lg_1 Gl_2 wt/lg_1 gl_2 Wt are as follows:

Lg_1 Gl_2 Wt	204	lg_1 Gl_2 Wt	17
Lg_1 Gl_2 wt	500	lg_1 Gl_2 wt	124
Lg_1 gl_2 Wt	94	lg_1 gl_2 Wt	475
Lg_1 gl_2 wt	15	lg_1 gl_2 wt	266

lg_1 —— 14.7 —— gl_2 —— 29.6 —— wt

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Corn rootworm studies have been in progress for two full seasons. Several inbred and single-cross lines have shown promise under moderate infestations of the western corn rootworm. Lines have been evaluated in field plots under natural infestations. A rating system of 1.0 to 5.0 was used for rating individual lines and for evaluating washed root systems for size, symmetry, feeding damage by larvae and root regeneration after damage. A rating of 1.0 was considered excellent and 5.0 was unacceptable for further study.

The following inbreds have maintained an average rating of 1.33 to 1.85 in all trials over a two-year period and are ranked in descending order: N38A, HD2187, SD10, C.I.38B, B55, Oh05, A251, Mo22, H51, Mo12, A297, and B57. Other lines that performed creditably with average ratings of 1.85 to 2.5 included H55, SD14, R168, A401, A265, Oh56A, and N25.

A limited number of single-crosses between the better inbreds, particularly with SD10, were tested one season (1964). Generally, the single-crosses involving select inbreds performed very well under rootworm infestation, and in addition, many of them were attractive agronomically. Some of the single-crosses with SD10 have been among the most promising in the trials.

Among the top three inbreds, only SD10 has been released. This action was taken in December, 1964. It was developed from a cross made in 1953 between B8 and Oh56A. During the process of development of SD10, selection was made for standability, plant type, and seed quality.

Several inbred lines developed by the Plant Pathology Department at South Dakota State University for resistance to root rots have performed very well under rootworm infestations. Many of the lines have contributed favorable root and stalk quality to a limited number of single crosses.

Other material of considerable interest include synthetic lines developed by Pioneer Hi-Bred Seed Company. The synthetics were made from corn belt inbreds and lines containing West Indian, Broad Base

Mexican, and Zapalote germ plasm. A fourth group of snythetics involved germ plasm from Stiff-Stalk Synthetic. Several lines from these synthetics have shown a high degree of tolerance to rootworm damage. The Zapalote synthetic lines appeared to be the most promising among these groups.

About 70 topcross lines from the Rockefeller-Mexican Program were evaluated for reaction to rootworm. These lines came from an area where many species of Diabrotica are indigenous. No clear-cut evidence of antibiosis was observed, but the lines did show tremendous vigor and some lines appeared to possess a rather high degree of tolerance to larval feeding.

A wide range of other material, including southern inbreds and synthetics, lines containing teosinte germ plasm, and many experimental hybrids, has been tested.

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1. Pollen tube growth *in situ*.

With cytological techniques, V. H. Rhoades has shown that the pollen germination-tube growth-fertilization sequence in maize is completed in less than 24 hours at 25°C. In our continuing studies on corn pollen biology, we have examined the initial stages of this sequence employing a different approach: limited pollination followed by sequential silk cutting, obtaining the number of kernels on a cob as the datum. The following treatment series have been performed.

The single cross, Oh51A^T x IoB8, and the assay techniques were described earlier (Walden and Everett, Crop Science 1, 1961). Limited pollen was applied to a number of previously prepared 7-day old silk-brushes, a different set every two hours between 9 AM and 9 PM. Starting one hour after pollination and continuing at two hour intervals for 30 hours (excluding 1-6 AM) silks of different treatments were cut to the ear tip. The length of cut silks averaged 2 cm for all treatments. Presumably sperm nuclei which had passed the region of cut-off completed fertilization; thus kernel counts reflected the events measurable after silk cutting.

Such an assumption seems justified as there were silk-cut treatments which scored a kernel value equal to the control, the uncut treatment. Pollinations made prior to and including 2 PM showed the same effect:

About 85% of the sperm nuclei passed the point of cut-off in the interval between 5 and 7 hours post-pollination. About 10% were "precocious germinators", passing through prior to 5 hours and the residual were delayed.

Pollinations made after 2 PM demonstrated an increasing lag phase and a reduced slope to the growth curve, such that pollinations made at 8 PM failed to pass the cut-off point for 12 hours or more. Yet we repeatedly obtain maximum kernel counts in other experiments from pollinations made in late afternoon and early evening, indicating that fertilization is finally accomplished.

This study suggests:

1. On a typical summer day, during which pollination in the field is accomplished by noon, it is followed by rapid pollen germination and pollen tube growth; fertilization is completed within 24 hours, probably during the cool, damp hours of early morning.
2. Pollination delayed until late afternoon or evening results in good fertilization, but only after germination and/or initial pollen tube growth are delayed until the following late morning-afternoon growth period.

D. B. Walden

2. Pollen longevity.

Storage between -5° and +5°C at a high humidity in aseptic cultures will retain a satisfactory number of pollen grains in a viable condition as measured by syngamy for 14 days. Such cultures will show a reduced

viability but more than adequate numbers of pollen grains survive for genetic or plant breeding studies. Pre-treatment of pollen will augment the longevity. Pollen collections before 10AM should be cleaned and spread to dry for 1 - 2 hours before introduction into the storage environment.

Our studies of pollen storage in liquid nitrogen and via centrifugal freeze drying are being continued.

D. B. Walden

3. Soluble-sugars and free amino acids of corn pollen.

Soluble sugars and free amino acids from the pollen of many genotypes have been studied by means of one and two dimensional paper chromatography. Pollen that has been shed, or whole anthers, have been squashed onto Whatman 3MM filter paper and developed by an ascending technique.

For the separation of amino acids the papers were run in the first direction in 3 parts methyl ethyl ketone, 5 parts butanol, 1 part ammonia and 1 part water and in the second direction in 12 parts n-butanol, 3 parts glacial acetic acid and 5 parts water. After drying they were dipped in 0.2% ninhydrin in acetone and heated. Soluble sugars were separated in one dimension using the butanol-acetic acid solvent described above, dipped in an aniline-diphenylamine-phosphoric acid reagent and heated.

Glucose, fructose and sucrose are present in corn pollen in large amounts and in addition trace amounts of other soluble sugars are recovered. The relative amounts of the above named sugars are dependent upon the immediate post-harvest treatment. For example, the amounts of sucrose increase if the pollen remains unrefrigerated for more than 30 minutes between dehiscence and analysis.

We have tentatively identified 9 amino acids in most corn pollen samples examined, including, proline, α-alanine, glutamic acid, aspartic acid, γ-amino butyric acid, serine, glycine, valine, threonine and 2 acid amides, glutamine and asparagine. Some additional unidentified spots have also appeared. Proline shows up in very large amounts relative to the other spots. Quantitative determinations on a dry weight basis are not yet completed.

Khoo and Stinson (1957) and Britikov *et al* (1964) have reported marked reduction in proline content of anthers from male sterile plants (T-cytoplasm) or sterile pollen. Proline in only trace amounts is characteristic of our T and S cytoplasm stocks as well. In addition we have chromatographically identified γ-amino butyric acid in our T-cytoplasm stocks, but recover only trace amounts in the S-cytoplasm stocks. Restorer genes (NY16 and Ky21) convert both S and T to the normal amino acid spectrum. The significance of these amino acid differences is being further studied.

F. S. Cook
D. B. Walden

4. An agar medium for the *in vitro* germination of corn pollen.

In a series of experiments designed to investigate various nutritional and environmental factors which influence the *in vitro* germination of corn pollen, a simple agar medium has been established which will consistently support germination of corn pollen in excess of 70%.

Plants used in these studies were a single-cross (su_1/su_1) hybrid, "Seneca 60" (Robson Seed Co., Hall, New York) grown in the field, in the greenhouse or in a controlled environmental growth room during 1963 and 1964. Day old anthers were removed from the plants the evening prior to pollen collection.

Germination required a carbohydrate and calcium ion. Sucrose and raffinose supported good germination. Lactose, D-glucose, D-galactose, melibiose, L-arabinose, maltose and D-xylose were inferior, and no germination was obtained with D-fructose, D-ribose, D-mannose or D-mannitol.

Although the magnesium ion could partly substitute for calcium, it and other ions that were tested had little or no effect in the presence of calcium. From amongst our data analyzed thus far, no evidence for enhancement (at the 5% level of significance) by boric acid in the presence of calcium can be obtained. However, differences approaching 5% germination have been consistently recorded and since a number of other workers have found boron to be effective in increasing the germination of several kinds of pollen, we have included it in our basal medium. Boric acid in the absence of calcium was ineffective. Phosphate salts at concentrations of 0.7 M and above suppressed germination completely.

The agar substratum influenced the effects of other components of the medium. The medium of Brewbaker and Kwack (Am. J. Botany, 50: 859-865, 1963) supported better germination on leached Special Agar-Noble (Difco Co.) than on unleached plain agar (Difco Bacto-agar). Presumably the addition of some ion(s) altered the concentration to an inhibiting level. The plain agar contained 1.6 times as much total calcium as the Noble agar.

Apart from the need for a high humidity (in excess of 90%), critical control of the environmental factors for germination was not required, although germination was characterized by optima for temperature, pH, tonicity and agar concentration.

All the pollen grains that were to germinate had done so in less than 30 minutes and a rapid assay could be undertaken without concern for contamination of the medium by microorganisms. Since no population effect, such as that described by Brewbaker and Kwack (1963), was demonstrated on the Noble agar medium the density of pollen on the plates was not a variable factor. The mechanics of counting was facilitated by the use of photomicrographs.

The pre-inoculation history of the pollen was important and remained a variable in our experiments. Pre-inoculation treatments did not standardize samples. Corn pollen from a single tassel tended to give successively lower % germination as the number of days from initial dehiscence increased, even though fresh pollen was collected each day.

Consistent estimates of variability (sampling error 2%, replication 3%, and experimental error 3%) suggest that 8-10 subsamples from 3-5 replicates of each treatment provide sufficient experimental units for employment of this bioassay.

A basal medium chosen for subsequent research with corn pollen consists of:

0.35 M Sucrose (12%)
100 ppm H_3BO_3
300 ppm $CaCl_2 \cdot 2H_2O$
with or without 0.7% Difco Special Agar-Noble

The pH of this medium was 6.8 - 7.1. The agar surface in pyrex Petri plates (60 mm x 15 mm) was inoculated by shaking pollen from a camel's hair brush. The open plates were placed over water in sealed incubators,

held at room temperature for 30 minutes and removed for counting. Germinated grains were defined as those with intact tubes at least one grain diameter in length.

The authors gratefully acknowledge the assistance with this work of Miss D. E. Hamill.

F. S. Cook
D. B. Walden

5. Germination of sh_2 pollen grains.

Using the medium described above, we have surveyed several genotypes among our stocks. We first noticed in 1963 a coded entry that consistently demonstrated higher % germination than the control (su_1) or its allelic stock. Repeated analysis in 1964 of material grown in the field, the greenhouse or the growth room showed that our sh_2 source stock surpassed significantly the germination of all other entries. Reciprocal crosses with several stocks have been prepared but not yet tested. The significance in this report resides not in the fact that our sh_2 stock performs better (we have not demonstrated yet that the performance is a precise function of the sh_2 locus) but that the possibility for differential pollen germination may be exploited.

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1. The metastable nature of paramutable *R* alleles.

Paramutable *R* alleles of different geographic origins may be characterized by their differing *Rrr* phenotypes in a common genetic background. These phenotypes form a continuous series with respect to degree of mottling, and range from forms lighter than characteristic for the standard allele commonly used in paramutation studies, to forms which are self-colored. However, this phenotype is not a suitable property for permanent

characterization of individuals within this class of alleles, because all the paramutable R alleles thus far tested are subject to small but heritable and progressive changes in degree of mottling even when maintained in heterozygotes with alleles hitherto considered non-paramutagenic. These changes may be in either direction, up or down the color scale, and by the correct choice of the opposing allele any paramutable allele may be manipulated so as to express different degrees of mottling. Alleles initially mottled may be enhanced to self-colored expression in single dose by continued maintenance opposite the recessive r. Alleles initially self-colored, or nearly so, can be induced to demonstrate a distinctly mottled phenotype if maintained in a heterozygote with a mottled allele, and a darkly mottled allele will become progressively lighter when maintained with another R allele more lightly mottled than itself.

Derek Styles

2. An aleurone color factor seemingly at the B locus.

In the 1964 News Letter it was reported that a duplicate R factor, conditioning colored aleurone and green seedling, had been located on chromosome 2, probably close to the B locus. This duplicate factor will be referred to here provisionally as 'R-2'. Data presented below suggest that R-2 is allelic to B. All crosses were made in W22 stocks homozygous r^g for the chromosome 10 locus but otherwise with all the necessary complementary aleurone color factors. The testcross progeny were scored at the three leaf stage in the greenhouse, at which stage the B phenotype was clearly expressed.

Testcross mating: r-2 B/R-2 b ♀♀ X r-2 b/r-2 b ♂♂

Progeny phenotypes from 34 testcross ears:

Colored kernels		Colorless kernels	
Red seedlings	Green seedlings	Red seedlings	Green seedlings
28	2642	2631	1

The 28 colored kernels giving rise to the red seedlings were distributed among six of the 34 ears as follows: Four ears with one, one ear with five, and one ear with 19. Contamination is a probable source of the majority

of these kernels. The one green seedling from the colorless kernel class started to develop pigment at the six leaf stage, and so may represent a mutation of the B gene.

Derek Styles

3. Interaction of modulator with stippled.

Following introduction of Mp into an R^{st} stock, several ears were observed carrying sectors of kernels with abnormal spotting patterns among the otherwise standard stippled kernels.

Three classes of abnormal stippled kernels, all with reduced amounts of pigmentation and designated R^{st} (l.st.), R^{st} (ll.st.), R^{st} (coless), respectively, have been selected and further analyzed in order to determine:

1. If their phenotype reflects a change at the R locus or at M^{st}, a modifier of stippled 5.7 crossover units distal to the R locus, and

2. Whether alteration in paramutagenic capacity accompanied the change in stippled phenotype.

In regard to point 1, Table 1 indicates that the "abnormal stippled" kernels can be grouped into two classes:

(A) R^{st} (l.st.) and R^{st} (ll.st.) are due to a change of the modifier M^{st} or to its transposition (see next report) and

(B) R^{st} (coless) reflects a change at the R locus.

The test of paramutagenicity indicated that R^{st} (l.st.) does not differ significantly from R^{st} (standard) in capacity to reduce R pigmenting potential.

R^{st} (ll.st.) and R^{st} (coless) seemingly are more paramutagenic than R^{st} (standard). Additional data on this point, however, are needed.

The last finding suggests that paramutation and repression at the R locus exhibited by the R^{st} alleles and derivatives are not independent phenomena.

Table 1
Test to Determine Whether the "Abnormal" Stippled Phenotype reflects a change at the *R* Locus or in the Modifier ($\underline{M}^{st}$)

Test matings	Endosperm Genotypes and Phenotypes Predicted if Alteration is at: (1) R^{st}	or (2) M^{st}
1. r^rM^{st} x abnormal stippled	r^r M^{st}	r^r M^{st}
	r^r M^{st}	r^r M^{st}
	*(-) M^{st}	R^{st} (-)*
	light stippled	standard stippled
2. abnormal stippled x $R^{st}m^{st}$	*(-) M^{st}	R^{st} (-)*
	*(-) M^{st}	R^{st} (-)*
	R^{st} m^{st}	R^{st} m^{st}
	standard stippled.	light stippled

* assumed site of alteration

<u>Results of test matings</u>

Cross made	R^{st} phenotype tested	# ears scored	Showing M^{st} change	Showing R^{st} change	Showing no change
g^{36} x g^9	R^{st} standard	11			11
g^{37} x g^9	R^{st} light st.	20	20		
g^{38} x g^9	R^{st} very light st.	12	12		
g^{39} x g^9	R^{st} standard	7	1		6
g^{40} x g^9	R^{st} light st.	9	9		
g^{41} x g^9	R^{st} very light st.	4	4		
g^{42} x g^9	R^{st} standard	1			1
g^{43} x g^9	R^{st} colorless	8		8	

Results of test matings continued

Cross made	R^{st} phenotype tested	# ears scored	Showing M^{st} change	Showing Rst change	Showing no change
g^{10} x g^{36}	R^{st} standard	6			6
g^{10} x g^{37}	R^{st} light st.	5	5		
g^{10} x g^{38}	R^{st} very light st.	6	6		
g^{10} x g^{39}	R^{st} standard	3			3
g^{10} x g^{40}	R^{st} light st.	9	9		
g^{10} x g^{41}	R^{st} very light st.	3	3		
g^{10} x g^{42}	R^{st} standard	1			1
g^{10} x g^{43}	R^{st} colorless	11		11	

$g^9 = R^{st}\ m^{st}/R^{st}\ m^{st}$

$g^{10} = r^r\ M^{st}/r^r\ M^{st}$

Giuseppe A. Gavazzi

4. Further evidence for transposition of M^{st}, a modifier of the R^{st} phenotype.

M^{st}, a genetic element whose existence and phenotypic expression have been studied by Ashman (1962), lies 5.7 units distal to R^{st}. It increases the frequency of dark spots on the colorless aleurone background.

As indicated in the preceding report, Mp was introduced into a homozygous R^{st}/R^{st} inbred line in order to study the possible interaction of R^{st} with Mp.

When R^{st}/r^r, or derivative "abnormal stippled" heterozygotes with r^r, obtained after the aforementioned cross, were crossed with r^g/r^g, some of the resulting ears gave unexpected results. Besides 1/2 colorless kernels, which are genotypically r^r/r^g, they carried two kinds of stippled kernels, dark and light, often in equal numbers. Similar results were previously observed by Ashman in two exceptional ears. They led him to the conclusion that M^{st} had transposed to a position in which it assorts independently of R^{st}.

Evidence of transposition of $\underline{M}^{st}$ to another chromosome was obtained in the present case by selecting the colorless kernels from exceptional ears and then making crosses with appropriate tester stocks that reveal the presence of the transposed modifier.

If $\underline{M}^{st}$ transposes to a chromosome other than 10 (where $\underline{R}^{st}$ resides), then 1/2 of the colorless kernels would have received one transposed modifier. The occurrence of ears that show 1:1 distributions for dark and light stippled is here considered proof of the transposition of $\underline{M}^{st}$ from the standard position to a point in a different chromosome. The strain used to test for the presence of a transposed modifier in such colorless kernels is a homozygous $\underline{R}^{st}\underline{M}^{st-}/\underline{R}^{st}\underline{M}^{st-}$ stock.

The validity of such a test rests on the assumption, experimentally proved, that kernels of the genotypic constitution $\underline{rM}^{st+}/\underline{rM}^{st+}/\underline{R}^{st}\underline{M}^{st-}$ have a darker phenotype than $\underline{rM}^{st-}/\underline{rM}^{st-}/\underline{R}^{st}\underline{M}^{st-}$ kernels.

In fact, if the colorless kernels derived from the exceptional ears carry a transposed modifier, presence of the latter should be revealed by crossing them with the $\underline{R}^{st}\underline{M}^{st-}/\underline{R}^{st}\underline{M}^{st-}$ tester stocks, since the progeny kernels would exhibit a dark stippled phenotype in 50% of the cases, and a light stippled phenotype in the other 50%. However, if there is no transposed modifier in the genome of the colorless kernels under test, then only progeny kernels with a light stippled phenotype are expected.

Following such crosses, in eight cases out of thirteen examined, evidence of a transposed modifier was found. The frequency of dark and light stippled in the ears carrying transposed $\underline{M}^{st}$ was 1274 dark, 1315 light stippled, values that nicely fit the 50% and 50% ratio predicted.

Giuseppe A. Gavazzi

5. Test for depletion of $\underline{R}^{st}$ paramutagenic action in $\underline{R}^{r}$ $\underline{R}^{st}$ plants.

$\underline{R}^{r}$ $\underline{R}^{st}$ plants were mated recurrently for three generations to a paramutable $\underline{R}^{r}$ $\underline{R}^{r}$ stock. The latter, F_1 $\underline{R}^{r}$ $\underline{R}^{st}$, and $\underline{R}^{r}$ $\underline{R}^{st}$ individuals representing backcrosses 1, 2, and 3 of $\underline{R}^{r}$ $\underline{R}^{st}$ to $\underline{R}^{r}$ $\underline{R}^{r}$ were then testcrossed on $\underline{r}^{g}$ $\underline{r}^{g}$ ♀♀. The resulting sets of $\underline{R}^{r}$ $\underline{r}^{g}$ $\underline{r}^{g}$ kernels were scored for grade of aleurone color to determine whether maintenance of $\underline{R}^{st}$ in freshly constituted $\underline{R}^{r}$ $\underline{R}^{st}$ heterozygotes for a few

generations depleted the paramutagenic action of $\underline{R}^{st}$. The seed used in grading aleurone pigmentation ranged from 1 (coloress) to 7 (self-colored). There is no evidence from the results obtained, summarized in the accompanying table, that continued heterozygosity for a paramutable $\underline{R}^{r}$ reduces the paramutagenicity of $\underline{R}^{st}$.

Male parent in testcross	No. plants tested	Mean aleurone color score
$\underline{R}^{r}$ $\underline{R}^{r}$ - stock	7	6.43
$\underline{R}^{r}$ $\underline{R}^{st}$ - F1	3	4.47
$\underline{R}^{r}$ $\underline{R}^{st}$ - Bx 1 to $\underline{R}^{r}$ $\underline{R}^{r}$	7	4.08
$\underline{R}^{r}$ $\underline{R}^{st}$ - Bx 2 to $\underline{R}^{r}$ $\underline{R}^{r}$	8	3.40
$\underline{R}^{r}$ $\underline{R}^{st}$ - Bx 3 to $\underline{R}^{r}$ $\underline{R}^{r}$	16	3.59

R. A. Brink
D. F. Brown

6. An unstable R allele from Bolivia.

A highly unstable R allele has been isolated from a colored aleurone strain of maize originally collected in Bolivia (Bolivia 724). The allele simulates $\underline{R}^{mb}$ in that coarse patches of pigment are normally observed in the aleurone following backcross to W22 A C r b pl stocks. Unlike $\underline{R}^{mb}$, however, aleurone pigmentation varies in intensity within patches. Likewise ears vary in frequency of kernels with the spotted pattern. The allele mutates with a relatively high frequency (approximately one per 100 kernels) to a form which produces dilute aleurone pigment uniformly distributed over the kernel. Apparently concomitant with the mutation of spotted to dilute aleurone is alteration of a plant color component at the R·locus, since all 12 dilute kernels grown so far have produced mature plants with intensely pigmented leaves and stalks. Plants grown from sib spotted aleurone kernels were uniformly green.

J. Axtell
G. R. K. Sastry

7. A new method of identifying cherry pericarp alleles.

The standard procedure for testing an R allele for cherry pericarp is to cross the stock with Pl and then to examine the pericarp of F_1 plants. In a series of studies on R^{ch}, Pl has been found to be unstable in its capacity to condition cherry pericarp. This unpredictability associated with Pl caused confusion in the beginning, but an accidental finding that even pl R^{ch} or pl r^{ch} plants develop cherry pericarp color if the ears are exposed to light resulted in a new method of identifying cherry alleles. Ears exposed to sunlight about two to three weeks after pollination by removing husks develop intense pigment within forty-eight hours if the plants carry a cherry allele. This pericarp will develop color even under artificial light in the laboratory. If the ears are exposed at a more advanced stage practically no pigment develops. The pigment developed under both artificial and sunlight resembles closely the pigment produced by Pl R^{ch} or Pl r^{ch} plants. All cherry stocks collected from different areas and maintained at Wisconsin responded positively to this test. One important precaution is that the stocks under question should not carry B in their genomes since B pl stocks, even without cherry alleles, develop some pericarp pigment when exposed to the sun.

G. R. K. Sastry

8. Is Pl a compound locus?

With appropriate genotypic constitutions Pl gives purple color to stems, glumes, anthers, and pericarp (Emerson, 1921). Plant color appears when plants are half grown, and classification on W22 background is clear just before anthesis. As a by-product of the experiments to study the nature of R^{ch}, a series of Pl cultures has been isolated with: (1) pl expression in the stems but reacting with R^{ch} to produce cherry pericarp (2) Pl expression in stems but not with R^{ch} to produce cherry pericarp (3) Pl expression in stems and pericarp but giving only red anthers like pl plants and (4) Pl expression in stems and anthers but not with R^{ch}. The fact that it was possible to isolate these different classes from normal Pl stocks raises the question whether Pl is a compound locus.

G. R. K. Sastry

9. The use of pectinase for root tip squash preparations.

Considerable difficulty has been encountered in attempting squash preparations of maize root tips by means conventional for many other plants. Tips squashed directly in carmine or orcein stain following fixation in acetic alcohol and hydrolysis in N HCl yield solid clumps of tissue from which individual cells are not easily freed. Furthermore, the cell walls are fragile and commonly rupture when flattened. Pectinase (Nutritional Biochemicals Corp., Cleveland, Ohio) used according to the procedure described by Östergren and Heneen (Hereditas 1962) for other grasses alleviates the principal difficulties. Partial dissolution of the middle lamella permits ready dispersion of the meristematic region into small groups or individual cells and cell walls are softened such that whole cells may be flattened intact. The following simplification of Östergren and Heneen's technique has been found satisfactory for chromosome counts and tentative identification of several chromosomes. Other of their suggestions may be desirable for detailed study of chromosome morphology.

1. Pretreat tips for four hours at room temperature in 0.002 M aqueous 8-hydroxyquinoline.

2. Fix overnight in 3:1 acetoalcohol (Fixed roots may be stored for at least several weeks at -15°C).

3. Hydrolyze 8 minutes at 60°C in Normal HCl.

4. Either stain with Feulgen reagent for 2 hours then treat with 5% pectinase in distilled water for 2 - 2 1/2 hours at room temperature and squash in 45% acetic acid or treat directly in pectinase and squash in propiono-carmine.

K. V. Satyanarayana
J. L. Kermicle

Addendum:

UNIVERSITY OF AGRICULTURAL SCIENCES
Gödöllő, Hungary
Department of Plant Breeding

1. The change of some quantitative characters of maize by induced mutation.

Introductory remarks: In our induced mutation experiments we tried at first to change the protein content of maize (Bálint et al., 1962). On the basis of the results obtained, we began our investigations on the change of quantitative characters, which are interesting from an economic point of view.

During the course of our experiments we turned our attention to some published data, according to which smaller doses resulted in a greater mutational frequency for qualitative mutants. Therefore, we began to apply smaller doses to produce mutants in quantitative characters.

We employed on corn lines in 1961 the usual 15 and 7 kr x-ray, and in 1962, 15 and 5 kr gamma irradiation, hoping that the smaller doses would produce more variability in the offspring in relation to plus-variants than the usual treatment (15 kr). The M_2 and M_3 progenies which are at our disposal met our requirements for the most part of the characters.

Our newer experimental results: In 1963 we treated our C5 and T18 inbred lines with a 0.10% and 0.25% solution of EMS for 24 hours. The line C5 contained 10%, and T18 17%, protein. The germination rate of the latter was double that of the C5 line. The sensibility to EMS, therefore, is smaller than that of line C5.

Observations on 8 quantitative characters in the M_2 generation were made the week following fertilization of the maize ears; for each treatment 150-200 plants were used. We constructed a variational chart for each character; then we set the most important value-number in the table (Table 1). The table shows that the values of the coefficient of variability are higher for the C5 line generally and tend to be higher in the T18 line with the mutagen treatment as compared to the distilled water control. With the C5 line we can also see that the lower concentration (0.10%) was more efficient than the higher one (0.25%) in broadening the variability.

Table 1

Variability of Quantitative Characters in the M_2 Generation of Maize Treated with EMS

Hatvan, 1964

Characters	Mean and variability values	C 5 EMS (0.10%)	C 5 EMS (0.25%)	C 5 Dist. water	T 18 EMS (0.10%)	T 18 EMS (0.25%)	T 18 Dist. water
Plant height	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	198.85±1.19 10.12±0.42	184.50±1.43 8.67±0.55	200.73±1.69 8.28±0.59	161.09±0.99 11.85±0.44	164.39±1.27 10.42±0.55	169.61±1.20 9.69±0.50
Height of ears	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	105.07±0.76 12.12±0.15	100.69±1.03 11.42±0.73	105.56±0.92 8.54±0.62	97.49±0.68 13.26±0.49	99.32±1.11 15.01±0.78	96.02±1.17 16.61±0.86
Length of internodes	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	12.59±0.08 11.28±0.47	11.42±0.10 10.25±0.65	12.36±0.11 9.14±0.66	10.50±0.07 12.29±0.45	9.81±0.09 12.33±0.65	10.15±0.10 13.00±0.67
Leaf number	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	11.56±0.05 7.61±0.31	11.53±0.08 7.55±0.47	11.67±0.03 7.37±0.53	11.10±0.06 11.35±0.41	12.24±0.09 10.62±0.55	12.26±0.10 11.10±0.57
Length of tassels	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	33.14±0.18 9.08±0.38	32.37±0.18 7.48±0.47	34.29±0.25 7.26±0.52	30.18±0.17 10.90±0.40	30.96±0.27 11.76±0.62	32.35±0.21 8.75±0.45
Number of branches in the tassel	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	14.93±0.31 35.96±1.50	14.84±0.47 35.34±2.23	18.82±0.55 28.91±2.07	22.43±0.37 31.70±1.17	21.84±0.41 25.23±1.32	24.14±0.46 25.76±1.33
Length of ears	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	16.40±0.14 13.05±0.59	16.32±0.15 8.27±0.64	16.69±0.22 9.89±0.94	18.00±0.14 14.17±0.55	18.02±0.20 14.87±0.79	19.43±0.18 11.84±0.64
Row Number on the ear	$\bar{x} \pm m$ $S\% \pm m_{S\%}$	16.24±0.13 11.82±0.56	16.62±0.21 10.41±0.89	17.19±0.23 9.94±0.93	15.21±0.10 11.11±0.44	15.56±0.16 13.56±0.72	14.89±0.11 9.94±0.54

With the T18 line, this does not seem to be true. Some characters (leaf number) are slightly, others (for instance, height of the plant) are strongly mutable. Considering the average values, the 0.25% EMS treatment generally gives lower values in relation to the control than does the 0.10% EMS treatment.

Summary: 1. EMS treatment increased the variability of 8 investigated quantitative characters in the M_2 progeny of C5 and T18 inbred lines of maize.

2. In the C5 lines, the 0.10% concentration of EMS was more effective than the 0.25% concentration in changing the variational latitude.

3. The different quantitative characters do not react uniformly upon mutagen treatment.

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J. Sutka

ANDHRA UNVIERSITY
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1. B-chromosomes in the Oriental Maydeae.

Supernumerary or B-chromosomes have been reported and studied extensively in the New World Maydeae, maize, teosinte and *Tripsacum* (c.f. Randolph in Corn and Corn Improvement, pp. 18-19, 1955). In studies of several populations of Oriental Maydeae, we have encountered B-chromosomes in *Coix aquatica* (n=5) and *Chionachne koengii* (n=10). In the *Coix* material two populations, one from Madhya Pradesh and the other from Orissa, exhibited two B-chromosomes in a proportion of plants. The two chromosomes always paired within themselves and organized a single bivalent at meiosis which was more heteropycnotic than the regular A-chromosomes. The B-chromosomes did not show any synaptic relationships with the A-chromosomes.

In two populations of *Chionachne koengii* from Maharashtra and Andhra Pradesh, B-chromosomes varying from one to two per plant were observed. In crosses

designed to study the genetics of B-chromosomes evidence for non-disjunction on the male side was observed. It was not possible to accumulate more than three B-chromosomes in a given plant. Furthermore, in this species, at pachytene the B-chromosomes were seen to be of two morphological types, one with sub-median and the other with sub-terminal centromeres. Our preliminary studies on the effects of B-chromosomes on the chiasma frequency in the A-chromosomes show that the B-chromosome with sub-median centromere has a depressing effect while the sub-terminal one has an enhancing effect on the chiasma frequency of A-chromosomes. When the two morphologically different B-chromosomes are brought together in one plant they pair with each other and in such a situation only the effect of the B-chromosome with the sub-terminal centromere is manifested with reference to the chiasma frequency of the A-chromosomes.

J. Venkateswarlu
Panuganti N. Rao
R. S. K. Chaganti

2. Apomixis in *Coix*.

Apomixis is a common phenomenon in grasses and one way of locating it is by attempting crosses between distantly related genera. In a program aimed at understanding relationships between maize and *Coix* we have made several crosses between the two genera. In none of the crosses true hybrids resulted. But when the cross was made using *Coix* as the female parent a low frequency of diploid *Coix* plants was recovered. In about 900 pollinations involving two species of *Coix* (*C. aquatica* and *C. lachryma-jobi*) as the female parents and maize as the male parent, 13 parthenogenetic-diploid *Coix* plants were obtained.

J. Venkateswarlu
R. S. K. Chaganti

3. Spontaneous chromosomal variation in *Coix aquatica*.

Coix aquatica is characterised by a basic chromosome number of *n*=5 which at meiosis normally organize into five bivalents. In studies on the population dynamics of this species two populations, one from Madhya Pradesh and the other from Orissa, were located which showed high proportions of chromosomal aberrations. The

following categories of cytological variations were found:

1. occasional tetraploid sectors in the sporophytic tissues,
2. triploids,
3. trisomics,
4. translocation heterozygotes,
5. accessory chromosomes and
6. occasional inversion bridges.

The frequencies of the more common variants are given below:

Table 1
Frequencies of the different classes of chromosomal variants in two populations of *Coix aquatica*

Population	Per cent aberrant plants Triploid	Trisomic	Interchange	Accessory Chromosomes
Madhya Pradesh	5	5	20	15
Orissa	5	-	25	10

The triploids were probably the resultants of mating between diploid gametes produced in the tetraploid sectors and of gametes from the normal plants. The trisomics would originate in the progeny of the triploids. Translocations were variable and involved sometimes up to six or eight of the ten chromosomes. The most usual situation, however, was a translocation complex of four chromosomes. The role of these variations in the evolution of *Coix* is under further study.

J. Venkateswarlu
R. S. K. Chaganti

4. *Spontaneous interchange in Coix lachryma-jobi*.

During a cytological study in different populations of *Coix lachryma-jobi* (*n*=10), occurrence of a spontaneous translocation involving four chromosomes was recorded in a single plant of a population raised from seed collected from plants growing wild in the University campus. This is the first record of the occurrence of an interchange in this species. Naturally occurring

translocation heterozygotes have been reported earlier in C. aquatica (Venkateswarlu, J., 1958, Cytological observations on spontaneously occurring ring and chain formation in Coix aquatica, J. Indian Bot. Soc. 37: 329-333; also see in this News Letter-"Spontaneous chromosomal variation in Coix aquatica", J. Venkateswarlu and R. S. K. Chaganti). The segment of interchange seemed to be long enough that a chain or ring of four chromosomes was present in almost all cells examined at diakinesis and metaphse I leading to a high pollen sterility.

J. Venkateswarlu
Panuganti N. Rao

5. Chromosome knobs and B-chromosomes in maize types from North Eastern Frontier Area (NEFA) of India.

During the course of a cytogenetic survey of maize types cultivated in the Himalayan tracts of India, some maize types from the area formed by a part of Assam and Nagaland have been analyzed. One type M 36, from Nagaland has been observed to possess six knobs, one each in the long arms of chromosomes 4, 5, 7 and 8, and one each in the short arms of chromosomes 2 and 9. Following the knob in chromosome 8 there is a prominent chromomere. In another maize type from Assam (M 103) only three knobs have been found, one each in the long arms of chromosomes 7 and 8 and one in the short arm of chromosome 9. Except the knob in chromosome 9 which is terminal, all other knobs are interstitial in both M 36 and M 103. In another Naga type (M 37) one pair of B-chromosomes has been encountered in one plant. B-chromosomes during meiosis did not pair with A-chromosomes and showed the phenomena of precocious division, lagging and non-disjunction.

J. Venkateswarlu

CENTRAL MAIZE RESEARCH STATION
Yousafwala (Montgomery), West Pakistan

1. Quick drying maize hybrids for West Pakistan.

Maize is recognised as the highest yielding cereal crop and as such holds out the promise to solve food problems of countries like Pakistan where fast increasing population has already outstripped available food supplies. Being a short duration crop, it fits in very well in more intensive cropping patterns required for increased agricultural production. But, the farmers cannot put large areas under this crop because of the post-harvest difficulties in drying and shelling of the cobs. Maize cobs are harvested at 28-30% moisture and must be dried to bring the moisture level down to 15% before shelling. Since the maize crop matures for harvesting in the month of November and December, when the season is fairly cold and days are short, it takes quite a long time to dry the cobs out in the sun. During this period, more often than not, rains are received and the cobs are liable to be damaged. Moreover, farmers are extremely busy during this time of the year in sowing the wheat crop, picking cotton and crushing sugarcane, which are the major farm operations and have to be attended. Some of the farmers do not harvest the cobs from the standing maize crop but cut the plants down. After a few days when the plants have dried out a little they tie them into bundles and collect them into small stacks. After they finish the sowing of wheat, they come back and husk out the cobs from the stacks but in doing so the farmers have not only to put in extra labour but they lose a good deal of fodder, as they can utilise the stalks for feeding their cattle if they remove the cobs from the standing crop. Thus what farmers in West Pakistan need is a type of maize that loses moisture very rapidly during maturity and can be shelled directly on harvesting.

Combined picking and shelling is becoming popular in some areas of the United States but they allow their crop to stand in the field long enough that the cobs are dried down to the desired moisture level. On the contrary, the interest of farmers in West Pakistan is to remove the cobs when the plants are still green so that they can utilise the stalks to feed their cattle.

With a view to evolving maize hybrids that lose moisture in the cobs rapidly on maturity and can be shelled directly on harvesting, a large number of double cross hybrids involving lines of both local and foreign origin

were studied at the Central Maize Research Station at Yousafwala (Montgomery). The inbred lines involved in 243 double crosses tested for shelling quality immediately on harvesting are given below:

North American Lines.

1. A375
2. A495
3. A556
4. A204
5. A619
6. A575
7. A554
8. A239
9. A96
10. A486
11. A251
12. A508
13. B37
14. B8
15. B14
16. B21
17. BC3
18. B46
19. C103
20. CMD5
21. G7B
22. Hy
23. H49
24. H19
25. I 153
26. L317
27. M14
28. MS206
29. MS1134
30. M13
31. N104
32. N24
33. N613
34. N624
35. ND203
36. ND230
37. ND255
38. OH41
39. OH07
40. OH51
41. OH45
42. Pa 32
43. P8
44. Pa 86
45. R181
46. R853
47. R71
48. R53
49. R101
50. R172
51. V3
52. W64A
53. WF9
54. W22.
55. W85
56. W32
57. WM13R
58. W182B
59. W9
60. WA374B
61. W33
62. WD
63. W28
64. W10
65. W59M
66. W187
67. 7K
68. 38-11

Indigenous Lines.

1. Pb.7
2. 124Pl
3. 52B
4. 20P
5. Pb.2
6. 54APl
7. 9p3
8. 70No .2
9. 115p3

The double cross hybrids were classified into early, medium and late groups on the basis of days taken from germination to mid-silking stage. It has been observed that several hybrids in each group shelled without damage to the grains on harvesting, while the others needed drying before the grains could be separated from the cobs. Further analysis of the hybrids indicated that six inbred lines viz, M14, Pa32, R181, WM13R, W64A and V3 out of the North American material and 4 lines, i.e., 9p3, 124pl, 20p2 and 54APl out of the indigenous group yielded quick drying hybrids that could be shelled immediately on harvesting. Further studies on the capacity of different hybrids to lose moisture on maturity under West Pakistan conditions are being taken up.

A. G. Bhatti

III. STOCKS AVAILABLE AND WANTED

A. Wanted:

D. S. Robertson, Genetics Department, Iowa State University, Ames, Iowa:

Cytoplasmic male sterile lines of the inbreds M14 and W22.

B. Available:

H. Garrison Wilkes, Botanical Museum, Harvard University:

Teosinte seed from the Sierra Madre Occidental of northern Mexico is now available. This collection now completes all the known sites for teosinte in Mexico and Guatemala (MNL 38, 1964). Nobogame, Chihuahua, altitude 1850 meters.

A. Cornu, Institut National de la Recherche Agronomique, Rabat, Morocco:

The following stocks are available in small quantities:

<u>Genic stocks</u>

Chr. 1	sr P^{WW} bm_2	Chr. 6	py
Chr. 2	lg_1 gl_2 B $\frac{sk}{+}$ v_4		po
Chr. 4	$\frac{la}{+}$ $\frac{Tu}{+}$ gl_3	Chr. 7	o_2
	fl_2	Chr. 8	v_{16} $\frac{ms_8}{+}$ j1
Chr. 5	v_3	Chr. 9	sh_1 wx
	gl_8		gl_{15}
			l_7

<u>Endosperm mutants</u>

h_2

fl_2 h_2

h_1 h_2

<u>Local varieties</u>

Maturity: 200-800
Altitude: 0-1000m.
Endosperm: White-Yellow
Flint-Dent

IV. REPORT ON MAIZE COOPERATIVE

Stocks of several hundred reciprocal translocations have been maintained during recent years by Dr. D. S. Robertson at Iowa State University. Last summer the periodic task of increasing a portion of these was shared. About 65 translocations from this series were increased at Urbana, and an approximately equal number was grown at Ames. It is hoped that during the next few years fresh seed of this entire group can be obtained for permanent transfer to our collection.

Increases were made last season of Chromosome 6, 7, and 8 stocks, primary trisomics, and unplaced genes. Miscellaneous other stocks needing increase or upgrading were also grown.

During 1964, 1614 seed samples were supplied in response to 95 requests. Of the total, 1390 samples were distributed within the U.S. (86 requests) and 224 samples were sent to foreign countries (9 requests).

The following catalogue of stocks represents a complete listing of available stocks, with the exception of reciprocal translocations listed in the 1962 and 1964 Maize Newsletters. Requests for seed or for copies of stock lists should be sent to E. B. Patterson, S-116 Turner Hall, Agronomy Department, University of Illinois, Urbana, Illinois.

<u>Chromosome 1</u>

ad_1 an_1 bm_2

ad_1 bm_2

an_1 bm_2

as

br_1 Vg

br_2

Kn

Kn Ts_6

lw_1

P^{CR}

<u>Chromosome 1 (Continued)</u>

P^{CW}

P^{MO}

P^{RR} ad_1 an_1

P^{RR} ad_1 bm_2

P^{RR} an_1 gs_1 bm_2

P^{RR} br_1 f_1 an_1 gs_1 bm_2

P^{VV}

P^{WR} bm_2

P^{WR} gs_1 bm_2

P^{WW} br_1 f_1 bm_2

Chromosome 1 (Continued)

P^{WW} br_1 f_1 an_1 gs_1 bm_2

P^{WW} hm br_1 f_1

sr_1

sr_1 P^{WR} an_1 bm_2

sr_1 P^{WR} bm_2

sr_1 P^{WR} an_1 gs_1 bm_2

sr_1 zb_4 P^{WW}

ts_2 P^{WW} br_1 bm_2

Ts_6

v19 bm_2

Vg

Vg an_1 bm_2

vp_5

vp_8

zb_4 ms_{17} P^{WW}

zb_4 P^{WW} bm_2

zb_4 P^{WW} br_1

zb_4 ts_2 P^{WW}

an_{6923}-bz2 (includes locus of an_1)

necrotic 8147-31

Chromosome 2

al lg_1 gl_2 B sk

al lg_1 gl_2 b sk

ba_2

fl_1

Chromosome 2 (Continued)

gl_{11}

Ht

lg_1 gl_2 B

lg_1 gl_2 b

lg_1 gl_2 b fl_1 v_4

lg_1 gl_2 b fl_1 v_4 Ch

lg_1 gl_2 B gs_2

lg_1 gl_2 b gs_2 sk

lg_1 gl_2 b gs_2 v_4

lg_1 gl_2 b gs_2 v_4 Ch

lg_1 gl_2 B sk v_4

lg_1 gl_2 b sk v_4

lg_1 gl_2 b sk fl_1 v_4

lg_1 gl_2 B v_4

lg_1 gl_2 b v_4

lg_1 gl_2 b v_4 Ch

lg_1 gs_2 b v_4

w_3

w_3 Ch

ws_3 lg_1 gl_2 B

ws_3 lg_1 gl_2 b

ws_3 lg_1 gl_2 b fl_1 v_4

ws_3 lg_1 gl_2 B sk

ws_3 lg_1 gl_2 b sk

Chromosome 3

A_1 ga_7; A_2 C R

A_1 sh_2; A_2 C R

A^d-31; A_2 C R

A^d-31; A_2 C R Dt_1

A^d-31 sh_2; A_2 C R

a^P et; A_2 C R Dt_1

a_1; A_2 C R B Pl dt_1

a_1 et; A_2 C R Dt_1

a_1 sh_2; A_2 C R Dt_1

a_1 sh_2; A_2 C R dt_1

a_1^{st} sh_2; A_2 C R Dt_1

a_1^{st} et; A_2 C R Dt_1

ba_1

Cg

cr_1

d_1

d_1 gl_6

d_1 Lg_3

d_1 ts_4 lg_2

d_1 ts_4 lg_2 a_1; A_2 C R Dt_1

d_2

gl_6

gl_6 lg_2 a_1 et; A_2 C R Dt_1

gl_6 Lg_3

gl_6 v_{17}

gl_7

Chromosome 3 (Continued)

lg_2 a_1 et; A_2 C R Dt_1

lg_2 a_1 et; A_2 C R dt_1

lg_2 a_1 sh_2 et; A_2 C R Dt_1

lg_2 a_1^{st} et; A_2 C R Dt_1

lg_2 a_1^{st} sh_2; A_2 C R Dt_1

lg_2 pm

Lg_3

Lg_3 Rg

na_1

pg_2

pm

ra_2

ra_2 gl_6 lg_2

ra_2 lg_2 pm

ra_2 Rg

Rg

rt

ts_4 na_1

vp_1

Primary trisomic 3

Chromosome 4

bm_3

bt_2

bt_2 gl_4

de(1 or 16?)

Chromosome 4 (Continued)

Ga_1 Su_1

Ga_1^s Su_1

gl_3

j_2

j_2 gl_3

la su_1 gl_3

lo

lw_4; lw_3

o_1

st

su_1 bm_3

su_1 gl_3

su_1 gl_4

su_1 j_2 gl_3

su_1 o_1

su_1 ra_3

su_1 Tu

su_1 Tu gl_3

su_1 zb_6

su_1 zb_6 Tu

su_1^{am}

Ts_5

Ts_5 su_1

Tu gl_3

v_8

Chromosome 5

a_2; A_1 C R

a_2 bm_1 bt_1 bv_1 pr;A_1 C R

a_2 bm_1 bt_1 pr; A_1 C R

a_2 bm_1 pr v_2; A_1 C R

a_2 bm_1 pr ys_1; A_1 C R

a_2 bt_1 pr; A_1 C R

a_2 bt_1 pr ys_1; A_1 C R

a_2 pr; A_1 C R

ae

bm_1 pr; A_1 A_2 C R

bm_1 pr v_2; A_1 A_2 C R

bm_1 pr ys_1; A_1 A_2 C R

bm_1 pr ys_1 v_2; A_1 A_2 C R

bt_1 pr; A_1 A_2 C R

gl_5

gl_8

gl_{17} bt_1

gl_{17} v_2

lw_2

lw_3; lw_4

na_2

na_2 pr

pr; A_1 A_2 C R

pr ys_1; A_1 A_2 C R

sh^{fl} = "sh_4"

"sh_3" = allele of <u>bt_1</u>

Chromosome 5 (Continued)

v_3 pr; A_1 A_2 C R

v_{12}

vp_2 gl_8

vp_2 pr; A_1 A_2 C R

vp_7

vp_7 pr; A_1 A_2 C R

Primary trisomic 5

Chromosome 6

at = allele of si_1

Bh

po Y_1 pl

po y_1 pl

Pt

si_1

wi

y_1 l_{10}

y_1 $ms_{(1?)}$

Y_1 pb_4 pl

Y_1 pg_{11}; wx pg_{12}

y_1 pg_{11}; wx pg_{12}

y_1 Pl Bh

y_1 pl Bh

Y_1 Pl sm Pt

Y_1 Pl sm py; A_1 A_2 b p^{RR}

Y_1 pl su_2

y_1 pl su_2

Chromosoma 6 (continued)

Y_1 Pl; seg w_1

Y_1 pl; seg w_1

y_1 Pl; seg w_1

y_1 pl; seg w_1

l_{4920}

"male sterile-silky" = allele of si_1

"orobanche" (seedling)

"ragged" (seedling)

"white 8896" (seedling)

Chromosome 7

bd

g_2

gl_1 ij bd

gl_1 sl

gl_1 Tp_1

Hs

ij

in; pr A_1 A_2 C R

o_2

o_2 bd

o_2 gl_1 sl

o_2 ra_1 gl_1

o_2 ra_1 gl_1 ij

o_2 ra_1 gl_1 Tp

o_2 v_5 gl_1; seg ra_1

Chromosome 7 (Continued)

o_2 v_5 ra_1 gl_1

o_2 v_5 ra_1 gl_1 Hs

o_2 v_5 ra_1 gl_1 Tp_1

ra_1 gl_1 ij bd

Tp_1

va_1

vp_9 gl_1; wx

Chromosome 8

gl_g

v_{16} j_1

v_{16} j_1; l_1

v_{16} ms_8 j_1

"necrotic 6697" (seedling)

"sienna 7748" (seedling)

Chromosome 9

Bf_1

bm_4

bp Wx; P^{RR}

C Ds wx

C sh_1 Wx; A_1 A_2 R

C sh_1 wx; A_1 A_2 R

c sh_1 wx; A_1 A_2 R

C wx; A_1 A_2 R

c Wx; A_1 A_2 R

c wx; A_1 A_2 R

Chromosome 9 (Continued)

Dt_1 (See chromosome 3 stocks)

gl_{15} Bf_1

gl_{15} bm_4

I Ds Wx

I wx; A_1 A_2 R B pl

K_9^L C sh_1 wx; A_1 A_2 R

l_6

l_7

ms_2

ms_2 sh_1; A_1 A_2 C R

sh_1 wx gl_{15}

sh_1 wx l_7

sh_1 wx v_1

wx Bf_1

wx Bf_1 bm_4

wx bk_2

wx bk_2 bm_4

wx d_3

wx l_6

Wx pg_{12}; y_1 pg_{11}

wx pg_{12}; Y_1 pg_{11} pl

wx pg_{12}; y_1 pg_{11}

wx^a

yg_2 c sh_1 wx; A_1 A_2 R

yg_2 c sh_1 bz wx; A_1 A_2 R

Chromosome 9 (Continued)

yg_2 C sh_1 bz wx; A_1 A_2 R

Primary trisomic 9

Chromosome 10

a_3

bf_2

du_1

g_1

g_1 r^g; A_1 A_2 C

g_1 r^{ch}

g_1 r; A_1 A_2 C wx

g_1 R sr_2

g_1 r sr_2

gl_9

l_1

l_1; seg w_1

li g_1 R; A_1 A_2 C

li g_1 r; A_1 A_2 C

nl_1 g_1 R; A_1 A_2 C

Og R; A_1 A_2 C B Pl

r^r; A_1 A_2 C

r abnormal 10; A_1 A_2 C

R^g sr_2; A_1 A_2 C

r^r sr_2; A_1 A_2 C

r^g wx; A_1 A_2 C

R^r: Boone; A_1 A_2 C

Chromosome 10 (Continued)

R^{mb}; A_1 A_2 C

R^{nj}; A_1 A_2 C

R^{st}; A_1 A_2 C

v_{18}

w_2

w_2 l_1

zn

"oil yellow" (seedling and plant)

Primary trisomic 10

Unplaced genes

ct

el

fl_2

gl_{12}

gl_{14}

gl_{16}

h

l_3

l_4

mn

ms_5

ms_6

ms_7

ms_9

ms_{10}

Unplaced genes (Continued)

ms_{11}

ms_{12}

ms_{13}

ms_{14}

Mt

rd

Rs_1

rs_2

"sh_5"

v_{13}

va_2

w_{11}

ws_1 ws_2

zb_1

zb_2

zb_3

"luteus 4923" (seedling)

"necrotic 8376"(seedling)

"white 8657" (seedling)

Multiple gene stocks

A_1 A_2 C R^r Pr B Pl

A_1 A_2 C R^g Pr B Pl

A_1 A_2 C R^g Pr B pl lg_1 y_1

A_1 A_2 C R Pr

A_1 A_2 C R Pr wx

Multiple gene stocks (Continued)

A_1 A_2 C R Pr wx gl_1

A_1 A_2 C R Pr wx y_1

A_1 A_2 C R pr

A_1 A_2 C R pr su_1

A_1 A_2 C R pr su_1 y wx

A_1 A_2 C R pr y_1 gl_1

A_1 A_2 C R pr y_1 wx

A_1 A_2 C R pr y_1 wx gl_1

A_1 A_2 c R Pr su_1

A_1 A_2 c R Pr y_1 wx

A_1 A_2 c R Pr y_1 sh_1 wx

A_1 A_2 C r Pr su_1

A_1 A_2 C r Pr su_1 y_1 g_1

A_1 A_2 C r Pr y_1 wx

A_1 A_2 C r Pr y_1 sh_1 wx

bm_2 lg_1 a_1 su_1 pr y_1 gl_1 j_1 wx g_1

colored scutellum

lg_1 su_1 bm_2 y_1 gl_1 j_1

su_1 y_1 wx a_1 A_2 C R^g pr

y_1 wx gl_1

<u>Popcorns</u>

Amber Pearl

Argentine

Black Beauty

Hulless

Ladyfinger

Ohio Yellow

Red

South American

Strawberry

Supergold

Tom Thumb

White Rice

<u>Exotics and Varieties</u>

Black Mexican Sweet Corn
(with B-chromosomes)

Black Mexican Sweet Corn
(without B-chromosomes)

Gourdseed

Maiz chapolote

Papago Flour Corn

Parker's Flint

Tama Flint

Zapaluta chica

Chromosome rearrangements

The following rearrangements are being maintained primarily for use in determining the chromosome locations of new traits. All are marked with closely-linked endosperm or seedling traits.

The cytological positions of Inv 2a were determined by Dr. Morgan; those of Inv 9a were determined by Dr. Li. The indicated interchange points of the reciprocal translocations are taken from published work of Dr. Longley.

Inversions

Stock	Positions
* gl_2 Inv 2a (also available with Ch)	2S.7; 2L.8
* wx Inv 9a	9S.7; 9L.9

Reciprocal translocations

Stock	Interchange points
* wx 1-9c	1S.48; 9L.22
* wx 1-9 4995	1L.19; 9S.20
* wx 1-9 8389	1L.74; 9L.13
* wx 2-9b	2S.18; 9L.22
* wx 3-9c	3L.09; 9L.12
wx 3-9 5775	3L.09; 9S.24
* wx 4-9b	4L.90; 9L.29
* wx 4-9 5657	4L.33; 9S.25
* wx 4-9g	4S.27; 9L.27
* wx 5-9a	5L.69; 9S.17
* wx 5-9c	5S.07; 9L.10
* wx 5-9d	5L.14; 9L.10
wx 5-9 4817	5L.06; 9S.07
* wx 6-9a	6S.79; 9L.40
* wx, y 6-9b	6L.10; 9S.37
wx 6-9 4505	6L.13; 9 cent
wx 6-9 4778	6S.80; 9L.30
* wx 7-9a	7L.63; 9S.07
* wx or gl_1 7-9 4363	7 cent; 9 cent
* wx 8-9d	8L.09; 9S.16
* wx 8-9 6673	8L.35; 9S.31
* wx 9-10b	9S.13; 10S.40
su_1 1-4a	1L.51; 4S.69
su_1 1-4d	1L.27; 4L.30
su_1 4-5j	4L.21; 5L.36
su_1 y 4-6a	4L.37; 6L.43
su_1 4-8a	4S.59; 8L.19
su_1 R 4-10b	4L.15; 10L.60
y 1-6c	1S.25; 6L.27

Reciprocal translocations (Continued)

gl_2 2-3c	2S.46; 3S.52
gl_2 2-3 5304	2S.62; 3L.29
gl_2 2-6b	2S.69; 6L.49
gl_2, R 2-10b	2S.50; 10L.75
gl_1 6-7 4545	6L.25; 7S.73

* These constitute a basic series of twenty rearrangements for use in locating unplaced genes.

Stocks of A-B chromosome translocations

B-1a	1L.2	Proximal to Hm
B-1b	1S.05	
B-3a	3L.1	
B-4a	4S.25	Proximal to su_1
B-7b	7L.3	Proximal to ra_1
B-9a	9L.5	Proximal to Bf_1
B-9b	9S.4	Between C and wx; close to wx
B-10a	10L.35	Proximal to g_1

Earl B. Patterson

V. RECENT MAIZE PUBLICATIONS

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