MAIZE GENETICS COOPERATION

NEWS LETTER

44

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Department of Botany
Indiana University
Bloomington, Indiana

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I. FOREWORD

Once again it is my privilege to express on behalf of all readers of the Maize Genetics Cooperation News Letters our appreciation of Miss Ellen Dempsey's dedicated and efficient services. She was solely responsible for all editing and supervisory work entailed in publishing the 1970 volume. It is also a pleasure to acknowledge the voluntary assistance provided by Prem Chourey, Paul Nel, Reid Palmer, and Edward Ward in proof reading.

Volumes 1-29 and Volume 33 have been microfilmed. Copies can be obtained from this laboratory for $8.50. Checks should be made out to M. M. Rhoades.

Enclosed in the mailing of this year's News Letter is the Author and Name Index for the News Letter volumes 3 through 43 prepared under the supervision of E. H. Coe, Jr. and provided by him in published form for distribution. You will find it a useful index and Ed merits a warm expression of our gratitude.

The cost of publishing this year's News Letter has been met from a grant by the National Science Foundation to the Maize Genetics Stock Center at the University of Illinois. We are truly grateful for this essential financial help.

Our attention has been called to the following errata in the Maize Genetics News Letter volume 43:

Page 49: Line 20 Should read as follows:

"One of these proved to be indistinguishable from $\underline{Rp_1}^c$; the other appeared to carry a modified $\underline{Rp_1}^k$.

Page 67: Column 1 "prophase" should be "meiotic prophase"
"early" should be "mitotic prophase"
"late" should be "interphase"

M. M. Rhoades

II. REPORTS FROM COOPERATORS

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1. Further studies on the occurrence of twin seedlings in Coix aquatica.

The occurrence of twin seedlings in Coix aquatica is believed to be the result of two ovaries, consequently two seeds, developing within the same spathe (MNL 43:4-6, 1969). Further observations on this aspect are made and reported here.

325 spathes each possessing multiple stigmas instead of a normal bifid stigma were found in 1968 plantings. On closer scrutiny, in 148 of these, multiple branches of the stigma emerged from a single style and a random sample of 25 spathes on breaking open have been found to contain only one well developed ovary. The rest of the 177 spathes had two separate bifid styles and on closer examination, 25 random spathes of this group possessed two well developed ovaries, each of which in turn had a style of its own. Since the spathes with two bifid styles are potentially able to form two seeds at maturity, the remaining 152 were pollinated and bagged. 108 of these turned hard and black (the appearance of normal healthy spathes possessing seed) while the rest were chalky white and soft and usually sterile (the result of failure of fertilization in both the ovules). Of the 108 well developed spathes, 50 were broken open. 18 of these had two seeds while 32 had only one seed in each (possibly due to failure of fertilization in one or the other of the two ovules). Of the remaining 58 spathes, when sown in June, 1969, 46 germinated and among these 10 produced double seedlings (in one case triple seedlings). 5 of the spathes giving rise to multiple seedlings were broken open carefully and in all cases except one each of the seedlings originated from a separate seed. In the exceptional spathe, both seedlings arose from the same seed. The occurrence of this exception and of triple seedlings from a spathe where only two seeds are possible is a clear indication of polyembryony. A cytological check of the 21 plants that arose as double seedlings revealed a diploid chromosome number in all.

In an embryological study of spathes with multiple as well as single styles, some interesting observations were recorded in a low proportion of cases. In the ovule the nucellus is partitioned vertically into two halves by a wall reaching well up to the funicle; in one half there is a well developed embryo sac and in the other there is a suggestion of an embryo sac developing. If the two embryo sacs give rise to two embryos and they in turn to two seedlings, then both the seedlings would come from the same seed. The occurrence of several four nucleate unreduced embryo sacs in each ovule (MNL 40:164, 1966) of the pistillate inflorescences produced towards the end of the season also provides an opportunity for the occurrence of more than one embryo in a seed. Thus it is borne out by the embryological study that cases where twin seedlings arise from the same seed may be due to the occurrence of two embryo sacs in an ovule rather than to one arising from the fertilized egg and the other from a haploid nucleus of the same embryo sac. The diploid nature of the twins as observed affords further proof for this assumption. When two embryo sacs occur in an ovule, whether both are sexual, one sexual and one unreduced, or both unreduced is, however, not known. Further studies are underway to determine the origin and nature of multiple embryo sacs occurring in an ovule. It appears that a search for monoploids by screening of twin seedlings is not of much help in Coix.

The frequency of double seeds in a random lot of spathes is quite low (0.0045%, MNL 43:4-6, 1969). However, the frequency is much higher when spathes with multiple styles were chosen (more than 15%). Therefore, it appears that only such spathes and ovules with twin embryo sacs contribute to double and triple seedlings in the population. Although spathes with multiple styles are less frequent in the general population, particular lines show a greater frequency of such spathes. For example, all the 325 spathes in the present study came from seven plants of the same line although not all spathes on any one plant are multistyled. Of the 21 plants that arose as double seedlings only 8 produced spathes with multiple styles of varying frequencies. Whether the multistyled (double seeded) condition is a mutant character with incomplete penetrance and

variable expression is not known. The genetic nature of multistyly is under study.

J. Venkateswarlu
Panuganti N. Rao
Konika Dey

2. Similar mutants in corn and Coix

Some of the segregants located in experimental populations of *Coix lacryma-jobi* and *C. aquatica* have a close resemblance to some of the well described mutants in corn, although the nature of their inheritance in *Coix* is yet to be studied. They are listed in the table below.

	Mutants in *Coix*	Similar to mutants in corn	
	Coix lacryma-jobi		
1.	'*Virescent*' - seedling yellow, turns green slowly.	Virescent	v_2, v_4 and v_{16}
2.	'*Luteus*' - lethal yellow seedling, seedling dies at 2 or 3 leaf stage.	Luteus	l_2
3.	'*Knotted leaf*' - seedling leaves show a knotted appearance, plant leaves normal.	Knotted	*Kn*
4.	'*Crinkled leaf*' - plant more or less short, leaves wrinkled.	Crinkled leaf	cr_1
5.	'*Adherent*' - first seedling leaves stick together, plant leaves normal.	Adherent	ad_1
6.	'*Gold stripe*' - yellowish longitudinal stripes, often broad, on margins and blades of leaf throughout the life of the plant.	Old gold stripe	*Og*
7.	'*Pygmy*' - leaves short, broad and pointed, plant more or less short.	Pygmy	*py*
8.	'*Styleless*' - styles not produced, ovules abort, young spathes wrinkled.	Silkless	*sk*
	C. aquatica		
9.	'*Luteus*' seedling and plant yellowish green.	Luteus	l_7
10.	'*Yellow stripe*' - leaves with yellow tissue between leaf veins.	Yellow stripe	ys_1

	Mutants in Coix	Similar to mutants in corn	
11.	'Striate' - very narrow white longitudinal striations on margins of leaves in older plants.	Striate	sr_1
12.	'Narrow leaf' - leaf blades narrow.	Narrow leaf	nl
13.	'Brachytic' - shortening of internodes, leaves semi-erect.	Brachytic	br_1
14.	'Male sterile' - anthers fail to exsert.	Male sterile	ms_2 and ms_8
15.	'Tassel seed' - in C. aquatica and C. lacryma-jobi-anthers and styles produced by male spikelets.	Tassel seed	Ts_3

J. Venkateswarlu
Panuganti N. Rao

3. Somatic mutation affecting style colour in Coix.

In an otherwise white styled plant, a single pistillate spikelet in Coix aquatica and an entire tiller in Coix lacryma-jobi showed purple style. This might be the result of the occurrence of somatic mutations in the primordia from which the particular pistillate spikelet and tiller arose in C. aquatica and C. lacryma-jobi, respectively. As earlier studies showed that purple style is dominant over white style, the tiller with purple style in C. lacryma-jobi should be heterozygous and this was selfed to check for segregation of style colour.

Panuganti N. Rao

4. Androgenic haploid from an autotetraploid Coix lacryma-jobi.

Autotetraploid (4n = 40) and diploid (2n = 20) plants of Coix lacryma-jobi were grown in alternate rows in June, 1967. The diploids were characterized by green colour of seedling base, white style and presence of long hairs on the upper surface of leaves and the tetraploids by purple colour of seedling base, purple style and glabrous leaves. Purple style and purple colour of seedling are dominant over white style and green seedling, respectively and the

presence of hairs on leaves is incompletely dominant over glabrous leaves (MNL 43:3-4, 1969). One way of rapidly screening triploids through natural crossing (Coix being naturally cross pollinated) between tetraploids and diploids is to harvest seeds only from the recessive parent (diploid) and to raise the progeny. Individuals of this progeny showing dominant traits would be triploids. Since one of the genetic markers used is a seedling character, a large progeny can be raised and scoring can be done in germinator trays. Several hundred seeds from the diploid parent were harvested in November-December, 1967 and 800 of these seeds were space planted in germinator trays in June, 1968. 504 seeds germinated and 12 of the seedlings showed a purple base. These were identified tentatively as triploids and removed to pots kept in a greenhouse. At maturity 11 of these plants had a purple style and short hairs on the leaves while a single plant showed purple style but glabrous leaves. The former showed a triploid chromosome number (numbers ranged from $3n = 29$ to $3n = 31$) and low seed setting while the latter exhibited a diploid chromosome number and good seed setting. Since this plant showed all the genetic characters of the tetraploid male parent but had a diploid chromosome number, it is believed that this individual was derived as an androgenic haploid (autopolyhaploid) from the autotetraploid parent by the development of the male gamete in the ovule of the diploid female parent. As seeds from the diploid recessive parent were harvested by hand and germinator trays were filled with fresh saw dust, the possibility that this might be a contaminant or self sown seed of a normal diploid with dominant traits is overruled.

Panuganti N. Rao

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1. Fine structure of meiotic chromosomes in haploid and diploid maize.

Since the finding of a synaptonemal complex in the spermatocytes of crayfish, pigeon, cat, man etc. was reported, it is estimated that from five to eight research communications on this organelle were published annually. Nevertheless, when one reviews these articles and tries to draw a conclusion on the structure and function of this organelle, one encounters a great difficulty. For instance, evidence in support of the role of the synaptonemal complex in chromosome synapsis at meiotic prophase comes from observations of this complex in the microsporocytes of F_1 hybrids of Lycopersicon-Solanum, in the spermatocytes of Panorpa, and in the sporocytes of many other higher plants and animals. On the other hand, evidence is available which argues against the idea that the synaptonemal complex plays a role in chromosome synapsis at meiotic prophase. For example, in the spermatocytes of Tipula and Drosophila chromosome pairing is present but no complex was found while in spermatocytes of XO type male insects where the X chromosome appeared as univalent, a synaptonemal complex related with that chromosome was identified. With regard to the postulated role of the complex in crossing over, controversial reports were likewise found. For instance, the absence of this complex in the spermatocytes of Drosophila and in the oocytes of the homozygous mutant C(3)G indicates that the complex plays a role in crossing over. On the contrary, evidence against this idea comes from the lack of the complex in mitoses of Drosophila and in prokaryotes. In view of these conflicting studies, a further investigation of the complex was needed. Therefore, a study of the synaptonemal complex in haploid and diploid maize was commenced a year ago.

The techniques followed throughout the investigation were those of standard light and electron microscopy. The stages of division in the microsporocytes of these plants were determined by the following procedure: One of the three anthers of a single spikelet was fixed in an aceto-alcohol fixative, the other two, in glutaraldehyde. One day later, the

anthers in aceto-alcohol were squashed for light microscopy. The stages of division in the other two anthers were predicted on the basis of findings with the light microscope, because the three anthers of any spikelet are generally synchronized in development.

For diploids, five plants were studied. A synaptonemal complex was found in the microsporocytes of all of them, from zygotene to pachytene. The diameter of the frontal view measured about 1200 A°, the lateral elements measured about 300 A°, the central element, 200 A°, and the areas between the lateral and central elements, 200 A°. For haploid plants, three plants were studied. With the light microscope it was found that at zygotene and pachytene stages all of the chromosomes synapsed non-homologously. Most of the pairing was of the foldback type. With the electron microscope at the same stages of division synaptonemal complexes were consistently observed in all of the plants examined. These complexes appeared the same as those in the diploids.

Both cytological and genetical evidence indicates that the diploids undergo normal recombination. Evidence of crossing over in haploids was sought by crossing more than 50 haploid plants with pollen from diploid inbreds. Microsporocytes of the F_1 hybrids from these crosses were cytologically examined. Theoretically, if there were intrachromosomal crossovers in the haploids, inversions should appear in the F_1 hybrids. If there were interchromosomal crossovers, reciprocal translocations should be observed in the F_1. However, in more than 200 plants studied during the last eight years, neither inversions nor translocations were found. It seems correct to conclude that there is no, or rare, crossing over in haploids.

From this study the author is led to conclude that the synaptonemal complex is the product of chromosome synapsis, both homologous and non-homologous, at the meiotic prophase in maize. This complex is not a permanent component of the chromosomes throughout the meiotic division. Because of the presence of this complex in haploid microsporocytes of maize and because of the absence of recombination in haploids, it appears convincing that the existence of this complex does not necessarily lead to crossing over in general.

Y. C. Ting
Mary Dougall

2. A new teosinte mutant.

Last summer, 22 plants were grown from open-pollinated seeds of Guanajuato teosinte of central Mexico. When these plants were about two-months old, it was found that one of them was extremely different from its sibs. It was weedy. Its leaves were narrow, light-green, and pubescent. It was diminutive in height but tillered profusely. Hence, it was tentatively named a new mutant of Guanajuato teosinte.

Several male inflorescences of this mutant were fixed for cytological examination. However, no gross structural abnormalities of the chromosomes were identified. It was a diploid. The stainability of the chromosomes was generally poor. At both diakinesis and metaphase I, the bivalents appeared diffuse but were otherwise normal.

The pollen was poorly developed. Less than 10 percent of the ovules set seeds. Since the mutant was suspected to represent a primitive type of teosinte, a detailed study is in progress.

Y. C. Ting

3. Determination of the cell cycle (mitotic) of maize.

The cell cycle of maize was determined by autoradiography using tritiated thymidine. Seeds were germinated at room temperature in the dark and the sprouts were transferred to Hoagland's nutrient solution. After a day in Hoagland's solution they were transferred to the same solution with 1 uC/ml of tritiated thymidine. They remained in the the isotope solution thirty minutes and then were rinsed well and transferred back to fresh Hoagland's solution for continued growth.

Root tips were collected at varying time intervals after isotope treatment. They were then rinsed with fresh water, fixed with Carnoy's fixative, and stained with Schiff's reagent. The slides were prepared following the standard method and treated with Kodak NTB emulsion. After exposure for 13 days, the slides were developed and fixed. Under the light microscope, the slides were studied. Labelled and unlabelled prophase and metaphase figures were counted.

A total of 645 cells undergoing mitotic division was examined. The percentages of labelled mitotic cells were determined and plotted against time after labelling.

By using the method described by Wimber (1966), the duration of G_2 + M/2 (second growth period and half of mitosis), S (DNA synthesis), C (complete cycle), and that of G_1 + M/2 (first growth period and half of mitosis) were estimated. The duration of G_2 + M/2 equals 5.5 hours; S, 8.3 hours; C, 13.0 hours; and G_1 + M/2, -0.8 hours. From examination of all mitotic figures the results were: G_2 + M/2, equals 6.3 hours; S, 7.4 hours; C, 12.7 hours; and G_1 + M/2, - 1.0 hours.

The percentage of cells in mitosis was determined by counting the number of dividing and non-dividing cells. It was found that 14.11% of the total cells counted were in mitosis; therefore, mitosis consists of 14.11% of the complete cycle. This was calculated to be 1.83 hours by using the prophase results and 1.79 hours by using the combined results.

With this information the four parts of the cell cycle were estimated. The results in hours are as follows:

	C	S	G_2	M	G_1
Prophase	13.0	8.3	4.58	1.83	-1.72
Combined figures	12.7	7.4	5.40	1.79	-1.90

The large negative value for G_1, especially in the results of the combined figures, is difficult to interpret and no explanation can be given here for this. According to Clowes (1965), the negative value obtained for G_1 indicates that this stage does not exist separately but is probably accommodated in mitosis. But the large negative value for G_1 (-1.90) as found in the combined results could not possibly be so accounted for, since mitosis was calculated to be 1.79.

Mary E. Dougall

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1. Further studies on induction of endosperm mutations in maize with ethyl methanesulfonate.

Most of the mutations used by geneticists and plant breeders have arisen spontaneously, hence at a low frequency. Therefore, the chemical mutagen ethyl methanesulfonate (EMS) was used because its ability to induce a high mutation frequency has been well established. The use of this mutagen with an efficient screening procedure can show the relative genetic response to mutagenic treatments; in addition, mutations potentially useful to geneticists and plant breeders may be obtained.

Procedures to induce endosperm mutations in an inbred line of maize with EMS and the utilization of these mutations have been previously reported (2). In the first experiments the mutagen treated seeds were planted wet; in the studies reported here the treated seeds were dried before planting. Advantages of drying mutagen treated seeds compared to planting them wet were given by Briggs (1).

Mutation research in maize needs to be conducted differently than in self-pollinated plants. Mutants in many self-pollinated plants, e.g., barley, are readily recovered by growing seeds of individual heads of the M_1 plants, since the male and female organs are in the same flower. Even if the mutant involves only a small sector, most segregate in the M_2 generation. In maize, however, small mutant sectors may not involve both the ear (female inflorescence) and tassel (male inflorescence) and the mutant will not segregate in the M_2 generation. A mutation in either the

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

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ear or tassel would result in a heterozygous plant in the second generation which segregates in the third generation. These differences were pointed out by Singleton (5) when he proposed procedures of inducing mutants in maize. Briggs (2) confirmed his procedures and further data were reported by Singleton (6).

Singleton pointed out that mutagenic treatments on seeds could be used more effectively if the treated seeds were planted in an isolated field and allowed to interpollinate for one generation before an attempt was made to recover the mutants. In this manner mutants could be readily recovered if a generation of random mating (M_1) were followed by self-pollination of the M_2 generation. Every mutant would be in the heterozygous condition and involve a whole plant, not a sector. The purpose of carrying mutagen treated material into subsequent generations in this research was to provide plant geneticists and breeders an opportunity to develop plant and endosperm mutations in the entire genome of maize for use in their research as well as to obtain an estimate of the effects of mutagenic treatments.

Seeds of the inbred line M14 were treated with 0.005 or 0.01 M EMS (Eastman Organic Co.) for 10 h at 25° ± 0.02° C in a 0.05 M aqueous phosphate buffer (pH 7.5). The seeds had been stored at 60% relative humidity and had a moisture content of approximately 11.5%. After treatment they were rinsed in distilled water and soaked at 3° ± 0.02° C in distilled-deionized water for 48 hrs. The contents of the treatment flasks, in which the water was changed every 24 hrs., were agitated by a platform shaker operated to make 75 excursions per min. After post-soaking, the seeds were dried for 72 hrs. in a room maintained at 22° C and 60% relative humidity. The material was planted in isolation, and the M_1 plants were self-pollinated. Sixty-eight M_1 ears were obtained from the 0.005 M treatment and 77 M_1 ears from the 0.01 M treatment. In the next generation, 30 seeds were planted from each M_1 ear, and the plants were later thinned to 15 per row. These plants were self-pollinated, and M_2 ears with M_3 seed on them were harvested and visually scanned for mutants segregating on the ears.

The procedure used in handling the treated material through subsequent generations was as follows:

M_1 seed	M_2 seed
↓	↓
M_1 plant (ears)	M_2 plant (ears)
↓ self-pollinate	↓ self-pollinate
M_2 seed on ear	M_3 seed on ear
FIRST POLLINATION	SECOND POLLINATION

An M_1 seed (normal or wild-type seed treated with a mutagen) is planted; this seed produces an M_1 plant, which is self-pollinated and has M_1 ears with M_2 seed on them. These M_2 seeds are planted in a subsequent growing season and in turn produce M_2 plants, which are self-pollinated and have M_2 ears with M_3 seed on them. Mutants produced by treating the M_1 seed with a mutagen will segregate in the M_3 seed generation.

The mutants were detected in the M_3 seed generation, but the material was pedigreed from an M_1 ear. Therefore, the number of independently occurring mutations was divided by the number of M_1 ears to give the M_1 mutation frequency. To obtain the M_3 mutation frequency the number of independently occurring mutations was divided by the number of ears with M_3 seed on them.

When sterility occurred with the mutants (Tables 1 and 2), its percentage was calculated by a method similar to that used for obtaining the mutation frequency. Further details on calculating sterility can be found in last year's Maize News Letter (2). If an ear is ¼ sterile the cause of sterility is assumed to be genetic; if the ear is ½ sterile the cause is assumed to be chromosomal, i.e., a chromosomal rearrangement.

To make this maize mutation research more meaningful a classification system for the mutants was devised. The phenotypes used in this classification system, as well as mutation and sterility percentages from two EMS treatments, are given in Tables 1 and 2. The phenotypes of the mutants are based on the classification system as reported by Kramer et al. (4) and by Creech (3). However, additional phenotypic classifications were needed for this research. The phenotypic classification (Tables 1 and

Table 1

Phenotypes and mutation and sterility percentages from an ethyl methanesulfonate treatment (0.005 M, seeds planted dry).

Phenotype	All mutants			Mutants grown			Mutants that produced plants			Mutants that produced seed		
	M_1	M_3	Nr.	M_1	M_3	Nr.	M_1	M_3	Nr.	M_1	M_3	Nr.
Slightly opaque	2.94	0.25	2	2.94	0.25	2	1.47	0.12	1	1.47	0.12	1
Translucent, tarnished	4.41	0.37	3	2.94	0.25	2	1.47	0.12	1	1.47	0.12	1
Sterile*	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1
Translucent, shrunken	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1
Wrinkled, glassy	—	—	-	—	—	-	—	—	-	—	—	-
Opaque	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1
Floury	29.41	2.46	20	13.24	1.11	9	11.76	0.98	8	5.88	0.49	4
Sterile*	1.47	0.12	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Lemon	8.82	0.74	6	8.82	0.74	6	5.88	0.49	4	4.41	0.37	3
Orange	—	—	-	—	—	-	—	—	-	—	—	-
White	—	—	-	—	—	-	—	—	-	—	—	-
Miscellaneous	5.88	0.49	4	4.41	0.37	3	4.41	0.37	3	1.47	0.12	1
Sterile*	1.47	0.12	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Total	54.40	4.55	37	35.29	2.96	24	27.94	2.34	19	17.65	1.48	12
Sterile*	4.41	0.36	3	1.47	0.12	1	1.47	0.12	1	1.47	0.12	1
68 M_1 ears 813 M_3 ears												

*¼ sterility

2) does not imply genotype or allelism. Therefore, one must be cognizant of the definite distinction between the phenotypic classification in these tables and the genotypic classification of existing genes that have the same names; e.g., as used by Kramer and in this paper the opaque phenotype is the waxy genotype, and there are genotypes that are opaque (as opaque-1 and opaque-2). The miscellaneous class was used for rarely occurring mutants or ones that were combinations of the other phenotypes.

The number of mutations and mutation frequencies by phenotypic classification is given for both the M_1 and M_3 generations (Tables 1 and 2). The mutants are classed as "all mutants", i.e., all of those detected. The classification "mutants grown" included those actually selected for planting in the field. The classifications "mutants that produced plants" and "mutants that produced seeds" are self explanatory. The total mutation frequency for an experiment and the total number of M_1 ears and the number of ears that had M_3 seed on them are given at the bottom of the tables.

The M_1 mutation frequency for the 0.005 M EMS treatment was 54.40% and the sterility was 4.41%. However, the higher dose of 0.01 M produced a mutation rate of 36.37% and the sterility was 13.00%. This may have been because a 0.01 M EMS treatment produced a relatively large amount of plant damage in the first generation; hence many cells were killed that may have had mutations. The fact that the 0.01 M treatment produced more sterility than the 0.005 M treatment was probably a reflection of this damage from the higher dose. This relationship of relatively high sterility of the 0.01 M treatment compared to the 0.005 M treatment exists in the M_4 seed generation.

After the mutants were observed on the ears, the usual mutation frequencies were calculated ("all mutants"). Some mutants ("mutants grown") were selected to be grown to the M_4 generation, since one objective of this experiment was to determine whether viable and useful mutants could be obtained. The main reason not all mutants were grown to the M_4 generation was that some, in addition to being endosperm mutants as listed in the tables, had seeds that were miniature. With the 0.005 M EMS treatment 79% of the mutants planted grew and 50% produced seed. With the 0.01 M

Table 2

Phenotypes and mutation and sterility percentages from an ethyl methanesulfonate treatment (0.01 M, seeds planted dry).

Phenotype	All mutants			Mutants grown			Mutants that produced plants			Mutants that produced seed		
	M_1	M_3	Nr.	M_1	M_3	Nr.	M_1	M_3	Nr.	M_1	M_3	Nr.
Slightly opaque	2.60	0.35	2	2.60	0.35	2	2.60	0.35	2	1.30	0.17	1
Translucent, tarnished	9.09	1.21	7	9.09	1.21	7	5.19	0.69	4	3.90	0.52	3
Sterile*	3.90	0.52	3	3.90	0.52	3	2.60	0.35	2	2.60	0.35	2
Translucent, shrunken	2.60	0.35	2	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Sterile*	1.30	0.17	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Wrinkled, glassy	—	—	-	—	—	-	—	—	-	—	—	-
Opaque	—	—	-	—	—	-	—	—	-	—	—	-
Floury	5.19	0.69	4	3.90	0.52	3	1.30	0.17	1	1.30	0.17	1
Sterile*	1.30	0.17	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Lemon	9.09	1.21	7	7.79	1.04	6	5.19	0.69	4	5.19	0.69	4
Sterile*	3.90	0.52	3	2.60	0.35	2	1.30	0.17	1	1.30	0.17	1
Orange	3.90	0.52	3	3.90	0.52	3	3.90	0.52	3	3.90	0.52	3
Sterile*	1.30	0.17	1	1.30	0.17	1	1.30	0.17	1	1.30	0.17	1
White	—	—	-	—	—	-	—	—	-	—	—	-
Miscellaneous	3.90	0.52	3	2.60	0.35	2	1.30	0.17	1	0.00	0.00	0
Sterile*	1.30	0.17	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Total	36.37	4.85	28	29.88	3.99	23	19.48	2.59	15	15.59	2.07	12
Sterile*	13.00	1.72	10	7.80	1.04	6	5.20	0.69	4	5.20	0.69	4
77 M_1 ears; 578 M_3 ears												

*¼ sterility

treatment 65% of the mutants grew and 52% produced seed.

More discussion on utilization of EMS treatments in maize and its application to plant breeding can be found in last year's Maize News Letter (2).

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Robert W. Briggs

CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO
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1. Dominant ramosa ear character.

A few years ago Ing. Ramón Covarrubias Celis found plants with ramosa ears in the variety Yucatán 85 of the race Nal-Tel while he was a professor of genetics at the Graduate School of Chapingo, Mexico. His preliminary observations showed that this character was a dominant one not previously reported and probably controlled by a single gene.

Ramosa eared plants were crossed with normal plants from Yucatán 7 (Race Nal-Tel) and V520C (Race Tuxpeño). All the F_1 plants had the ramosa ear character showing that the trait is dominant over the normal. By sib pollinations the F_2 was obtained and normal and ramosa plants in the F_2 generation were counted. The results are given in Table 1.

Table 1

Observed and expected number of plants in the F_2 of a cross between ramosa eared and normal plants of Nal-Tel, Yucatán 7 (progeny 1) and Tuxpeño V520C (progeny 2) and the X^2 tests.

F_2 progeny	Observed		1:3 Expected		Total	d.f.	X^2	Prob.
	Normal	Ramosa	Normal	Ramosa				
1	39	121	40.00	120.00	160	1	.0333	.9-.8
2	56	191	61.75	185.25	247	1	.7139	.7-.5
Total	95	312	101.75	305.25	407	1	.5970	.7-.5

These results clearly indicate (1) that the character is dominant over the normal and (2) that this new ramosa ear character is monogenic and follows a Mendelian type of inheritance.

An interesting feature of this mutant is that the plants are fully fertile developing kernels inside of the branched part of the ear.

The tassel of the ramosa plant is normal with the exception that the distal end of the main branch frequently becomes bifurcated.

The above information indicates that the new ramosa ear character is different from the $\underline{ra}_1$ and $\underline{ra}_2$ already reported.

Localization of the gene on the corn chromosomes is underway.

T. Angel Kato Y.

2. Influence of B chromosomes on 4 characters.

In order to find out whether certain variations in morphological or physiological characters are related to the number of B chromosomes in the plants, a preliminary correlation study was carried out.

The variety Nayarit 39 of the race Reventador was planted at Tepalcingo, State of Morelos, during the winter of 1967-68. Microsporocytes were collected from 200 plants and the number of B chromosomes determined. Data were also collected concerning the following 4 characters: days to male and female flowering, plant height, and number of

tillers. With such data several correlation coefficients were calculated which are presented in Table 2.

Table 2

Correlation coefficients and their statistical significance between 5 characters in Nayarit 39 of the race Reventador.

Characters	Days to male flowering	Days to female flowering	Plant height	Number of tillers
Number of B chromosomes (range 0 to 13)	0.2043* n=131	0.0968 n=131	-0.1876* n=124	-0.1103 n=139
Days to male flowering		0.7841** n=131	0.6747** n=124	
Days to female flowering			-0.0293 n=124	

*Significant at 5% level.
**Significant at 1% level.
n = Number of plants used.

The r values may indicate that B chromosomes have some influence on days to male flowering and on plant height. It seems that as B chromosomes increase, the plants are later in flowering and shorter in height. It must be said that the correlations presented here are probably smaller than they are in reality because data were taken from plants with and without complete competition.

Similar information has been found in rye (Jones and Rees, 1968).

An interesting observation is that the days to male flowering, apparently affected by the B's, has a high correlation with plant height and that the days to female flowering, which is indifferent to the presence of the B's, has no correlation with plant height.

Pollen was also collected from 25 plants with different numbers of B's and 100 grains were measured on each plant. The average pollen grain diameter and its variability were computed. The results are presented in Table 3.

Table 3

Data on B chromosome constitution, the average pollen grain size and its variability in 25 plants of Nayarit 39 of the race Reventador. Also the correlation coefficient values computed are presented.

Plant Number	Number B's (X_1)	Average Pollen Diameter u (X_2)	s^2 (X_3)
1	0	90.7	14.62
2	2	86.9	7.12
3	3	92.1	21.35
4	4	88.0	29.03
5	4	88.7	9.96
6	4	92.9	14.58
7	5	92.4	14.75
8	5	86.7	15.12
9	5	92.2	11.09
10	5	95.4	12.35
11	5	90.5	19.29
12	5	92.7	15.51
13	5	91.8	13.15
14	5	91.9	15.48
15	5	93.9	10.64
16	6	88.2	9.75
17	6	83.4	8.90
18	7	94.5	9.65
19	7	89.6	8.43
20	8	88.7	7.02
21	8	96.6	15.96
22	9	91.7	10.61
23	10	91.8	7.80
24	10	93.2	12.57
25	11	92.9	14.27

$r_{X_1X_2} = 0.2505$ $\qquad$ $r_{X_1X_3} = -0.2884$

With these data the correlation coefficients between number of B's and average pollen grain size and its variance were computed. The r values obtained were 0.2505 and -0.2884, respectively, showing no statistical significance. These results mean that there is no apparent influence of the presence of B's on the pollen grain size and there is no change in the variability of the pollen grain size.

The fact that B chromosomes do not have any apparent influence on pollen grain size suggests that plants with B chromosomes have cell sizes similar to those of plants without B's, at least within a certain range of B numbers. If this is true, an explanation is needed for the mechanism by which B's affect male flowering and plant size. One possible explanation is that the presence of B's affects the timing of the cell division cycle, and/or the speed of cell growth is changed by changing the cell metabolic processes. This idea is supported by the findings of Ayonoadu and Rees (1968) who have presented data showing that the duration of the complete mitotic cycle in root tip meristems of rye increases in the presence of B chromosomes.

References.

Jones, R. N. and H. Rees. 1968. The influence of B-chromosomes upon the nuclear phenotype in rye. Chromosoma 24:158-176.

Ayonoadu, U. W. and H. Rees. 1968. The regulation of mitosis by B-chromosomes in rye. Exp. Cell Res. 52:284-290.

T. Angel Kato Y.

3. Frequencies of maize by teosinte crosses in a simulation of a natural association.

A study was carried on to learn about the frequency with which different maize and teosinte races would hybridize in nature.

Several maize races (table 1) and Chalco (T_1) and Guerrero (T_2) teosintes were planted in Tepalcingo Experimental Station in Morelos State in Mexico. At flowering time, 5 pollinations were made on Jala race shoots using a mixture of equal volumes of pollen of Jala race and T_1. Another 5 pollinations were made on Cuba 12 shoots using a mixture of pollen of Cuba 12 and T_1 and so on until 5 pollinations were made on

Table 1

Estimated percentages of maize-teosinte crosses that may happen in nature if different races were associated.

Maize Race	Observed % of Crosses with Chalco Teosinte	Maize Race	Observed % of Crosses with Guerrero Teosinte
Jala	31.8	Camelia Vicuña	42.4
Cuba 12	8.8	Arrocillo Amarillo	40.4
Guatemala 127	6.9	Tuxpeño	22.4
Arrocillo Amarillo	4.9	Guatemala 55 H	12.3
Cuba 54	3.8	Jala	9.1
Vandeño	3.4	Tabloncillo	5.9
Bolita	3.3	Cuba 54	4.2
Nal-Tel Guat.	2.9	Tehua	3.8
Cónico	2.8	Zapalote Grande	3.8
Tabloncillo	2.4	Olotillo	2.4
Honduras 19	2.2	Flint Guarani	1.6
Guatemala 806	1.8	Chapalote	0
Cónico Norteño	1.5	Reventador	0
Cuba 63	1.2	Vandeño	0
Chapalote	0	Harinoso de ocho	0
Reventador	0	Maíz Dulce	0
Harinoso de ocho	0	Cónico Norteño	0
Maíz Dulce	0	Bolita	0
Guerrero 250	0	Cónico	0
Celaya	0	Guerrero 200	0
Jalisco 78	0	Caingang	0
Palomero Toluqueño	0	Comiteco	0
Serrano	0	Pepitilla	0
Guatemala 114	0	Comun Segregaciones	0
Guatemala 145	0	Puya Segregaciones	0
Nal-Tel de 8	0	Entrelocado duro	0
Quicheño precoz	0		
Cuba 31	0		
Costa Rica 30	0		
Canario de 8	0		
Martinica 2	0		

Martinica 2 with a mixture of pollen of Martinica 2 and T_1. Mixing equal pollen volumes from maize and teosinte would simulate a hypothetical situation in which such populations would grow together and would coincide in their flowering periods. The same procedure was used in the case of T_2 to pollinate the maize races; however, due to the lack of knowledge of the

date of flowering of some of the races involved, it was not possible to get all possible maize-teosinte combinations. No attempt was made to use teosinte populations as females.

The pollinations of each particular maize-teosinte successful combination (3 or more pollinations) were harvested together and a 100 seed composite was prepared by mixing equal numbers of seeds from the 3-5 ears harvested. The 100 seed composites of the successful maize-teosinte combinations were then planted in a 4 row plot each. After flowering time counts were made in each plot of the total number of plants and the number of maize-teosinte crosses to get the percentage of crossing.

If no selective fertilization occurred, one would expect to get about 50% maize-teosinte crosses in all cases. However, 58% of the maize races pollinated with a maize plus Guerrero teosinte mixture showed a definite selection in favor of maize pollen (0% crosses with teosinte). Thirty-five of the maize races permitted some crosses with Guerrero-teosinte to occur, but there was a strong selection in favor of maize pollen. Two races of maize, Camelia Vicuña and Arrocillo Amarillo (7%), showed no evidence of any mechanism preventing teosinte pollen from fertilizing maize ovules, even with competition from maize pollen. As can be seen in Table 1, a similar situation was observed in the group of maize races pollinated with maize plus Chalco-teosinte mixtures.

The races of maize Celaya, Maíz Dulce, Bolita, Vandeño, Palomero, Toluqueño, Jala, Cónico Norteño, Zapalote Grande, Zapalote Chico, Nal-Tel, Arrocillo Amarillo, Harinoso de Ocho, Dzit Bacal and the collection Martinica 2 were used as females in crosses with pure pollen of teosinte and in all cases a good seed set was obtained. Thus, in most cases, competition with maize pollen seems to be the reason for the lack or reduced number of maize-teosinte crosses.

A similar study on individual F_2 plants from crosses of Camelia Vicuña and Arrocillo Amarillo with maizes that showed no crosses with teosinte may increase our understanding of the genetic mechanism (if any) involved in the selective fertilization observed in maize-teosinte associations. Likewise, we could more readily understand the way by which teosinte and maize populations can grow together, being compatible

in crosses and still maintaining their identities even when their flowering periods overlap.

Mario Castro Gil

4. Some reasons for depressed yield in dwarf corns.

Productivity in corn has frequently been reduced when dwarfing genes have been introduced into varieties or hybrids.

Leaves of brachytic-2 corn plants and other dwarf types emerge from the nodes in a single vertical plane, internodes are really short, leaf width is frequently increased and as a result the tassel is proportionately very big. It appeared to us that one of the main reasons for depressed yield in most dwarf corn types could be increased intra-plant competition for light. Since dwarfing genes could be of extreme importance in corn breeding programs, a study was set up to determine the effect on yield of varying light penetration by changing the canopy arrangement. A homozygous brachytic-2 open pollinated variety (having 75% of Puebla Group 1, 12.5% of Tuxpeño and 12.5% of Cónico Norteño) was grown in Roque, Guanajuato, Mexico in 1969 and subjected to 4 treatments:

a) Normal planting (control).

b) Leaves above ear positioned upright from flowering time on (UL).*

c) Midribs of leaves oriented East to West (EW).**

d) Midribs of leaves oriented East to West and leaves above ear positioned upright from flowering time on (UL + EW).

The plant density was 60,000 plants/ha. A two replicate randomized complete block design was used. The plot size was 6 rows 6 m long.

Grain yields are presented in Table 1 for the 4 treatments.

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*Leaves were positioned upright with transparent plastic bands holding them from the stalk.

**Seedlings were oriented East to West 10 days after emergence in very wet soil.

Table 1

Yields of brachytic Puebla Group 1 variety under four arrangements of the canopy.

Arrangements of the canopy	Grain yield (Ton/ha.)
Control or normal planting	9.93
UL	10.71
EW	11.10
UL + EW	12.15

5% LSD = 1.28

Our results clearly show that the productivity of Puebla Group 1 brachytic could be raised substantially by selecting genotypes that permit a better penetration of the light into the canopy. It may well be that reduced light penetration is responsible for low yields in other dwarfs. The information presented here is intended to help breeders to understand better the characteristics they should be looking for while selecting in dwarf types. As far as we know the plant characteristics that may help to improve light penetration are: erect narrow leaves, reduced tassel size, and unbranched and also longer internodes. Unless practical and economic systems are developed to orient plants in the field, genotypes with leaves emerging from the nodes in different directions should be preferred because intraplant competition for light would not be as intense as it is in plants with all leaves emerging in the same direction.

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1. Equation of heredity to include cytoplasmic effects.

Results from our experiments on female and male cytoplasmic effects in the F_1 and F_2 generations of double-cross maize hybrids suggest that we alter the common equation of heredity, $P = G + E$, to include cytoplasmic effects.

The final expression of the phenotype (P) is the manifestation of the genotype (nuclear genes), the cumulative effect of the cytoplasms, and the environment. Thus, the new equation which we suggest to include cytoplasmic effects is $P = G + (C_f + C_m) + E$.

A. A. Fleming
H. L. Jaggi

2. Does the male contribute cytoplasm?

"Yes," is our answer to this question. Our affirmative answer is given on the basis of the effects of the male cytoplasm on the zygote.

It was once thought that no cytoplasm is contributed to the offspring by the male parent. We have obtained data from several experiments which reveal differential male cytoplasmic effects and differential female cytoplasmic effects on the expression of various agronomic characters.

In our most recent F_1 experiments, significant effects of the male cytoplasm were obtained for time of silking, ear height, leaves below top ear, leaves above top ear, total leaves, number of shoots, and number of green ears. We also found significant effects of the female cytoplasm for time of silking, stalk diameter, leaves below top ear, leaves above top ear, number of green ears, number of shoots, and ear number at harvest.

Data for plant height, ear number, and yield approached the .05 level of significance in the F_1 experiments on male cytoplasm. Characters approaching the .05 level for the female cytoplasm were total leaves, erect plants, and yield.

F_2 data show that the male cytoplasms produced significant differences in time of silking, erect plants, and yield. The F_2 female cytoplasmic data indicate a significant effect on time of silking and erect plants.

A. A. Fleming
H. L. Jaggi

3. Female vs. male cytoplasm.

The effects of these two kinds of cytoplasm on the offspring may not necessarily be in direct proportion to the amount of cytoplasm that is contributed to the zygote by each parent. Significant effects may be obtained from apparently small amounts or large amounts of contributed cytoplasm in certain genotypic-cytoplasmic combinations. This statement is made on the assumption that only a small amount of cytoplasm is obtained through the male.

In addition, as reported in Maize Genetics Cooperation News Letter 41: p. 39, 1967, by Fleming and Campbell, the expression of the male cytoplasm can be influenced by the female cytoplasm.

A. A. Fleming

4. New character affects hybrid performance.

Six stocks of the long-time white inbred, Tx61M, were crossed to a single-cross tester, T105 x K64. The Texas stock has the greatest amount of brachyism, a character previously reported (Fleming and Kozelnicky, 1964, Maize Genetics Cooperation News Letter 38:47). The short internodes above the top ear cause a bunching effect of the upper leaves.

In the three-way testcrosses, the Texas stock caused significantly more brachyism in the hybrid than the five Tx61M stocks from Alabama, Georgia, Kentucky, North Carolina, and Tennessee.

A. A. Fleming

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1. Variability in fatty acid composition of oil in inbred lines.

Long-term inbred lines of corn are generally considered to be homozygous in their genetic constitution. However, in recent years, several studies have shown that variability in quantitatively inherited characters may persist in certain inbred lines. During the past several years, numerous inbred lines have been received from throughout the corn growing region of the U.S. Oil has been extracted from these inbred lines and analyzed by gas-liquid chromatography to determine fatty acid composition of oil. Although most inbred lines are quite uniform in fatty acid composition of oil, many were variable. An ear-to-row selection procedure might be useful within variable inbred lines to obtain near isogenic sublines with different oil composition, but which are uniform in oil composition within sublines. Examples of variability existing in several inbred lines are shown in Table 1. Seed of A96 was received from the University of Minnesota and from Cornell University. Oil composition was similar for the original seed from both sources. Three ears selfed in Georgia from the Minnesota source were uniform in oil composition and similar to the original seed. Five ears selfed in Georgia from the New York source were variable in oleic and linoleic acids. Data for A96 indicate little influence of environment on oil composition; however, this may not be the case with all inbred lines.

Inbred lines Oh43, W9, and B9A had an intermediate amount of variability in oleic and linoleic acids among selfed ears (Table 1). However, selection within these lines should be effective in shifting the composition of oleic and linoleic acids in either direction to obtain an oil with different iodine values (measure of the degree of unsaturation). Much larger differences in oleic and linoleic acid composition among ears were found in B54, CI-19, CI-45, and P40. Progeny from these ears will be grown (ear-to-row) to compare plant type and uniformity in oil composition in subsequent generations.

Table 1

Fatty acid composition of oil among ears within inbred lines

Inbred	Ear No.	Fatty Acid Composition of Oil (%)				
		Palmitic	Stearic	Oleic	Linoleic	Linolenic
A96 Minnesota seed		11.0	1.89	24.1	62.3	.75
Ga. grown	1	11.4	1.75	24.3	61.9	.63
	2	11.4	1.66	22.5	63.6	.84
	3	11.6	1.56	23.3	62.9	.71
New York seed		11.0	1.76	24.1	61.4	.70
Ga. grown	1	11.8	1.97	27.4	57.9	.74
	2	11.6	1.78	27.0	58.8	.69
	3	11.5	1.54	21.6	64.3	.74
	4	11.3	1.61	25.3	60.9	.75
	5	11.7	1.67	23.8	61.8	.83
Oh43	1	13.3	1.68	21.6	62.6	.85
	2	14.5	1.85	20.1	62.8	.78
	3	14.1	1.91	22.4	60.8	.70
	4	15.1	1.74	21.5	61.0	.67
	5	13.5	1.52	18.5	65.7	.84
	6	14.4	1.66	21.2	61.9	.81
W9	1	11.3	.74	20.3	66.6	1.06
	2	12.6	.84	18.5	66.9	1.04
	3	10.8	.90	25.7	61.6	.97
	4	10.6	1.02	25.6	62.0	.81
	5	9.6	.88	27.8	60.9	.83
	6	10.9	.99	30.7	56.6	.77
B9A	1	13.4	1.57	23.6	60.5	.88
	2	12.8	1.22	19.4	65.8	.79
	3	11.9	.97	18.1	68.3	.80
B54	1	11.8	1.11	25.1	61.1	.87
	2	12.4	1.87	39.7	45.0	1.05
CI-19	1	14.8	1.83	40.2	42.6	.59
	2	13.4	2.01	47.5	36.8	.34
	3	12.0	1.68	18.6	67.2	.56
CI-45	1	11.9	1.72	37.7	47.1	1.53
	2	11.8	1.77	20.3	64.7	1.29
	3	11.1	2.07	21.5	64.1	1.20
P40	1	12.9	2.00	23.6	60.3	.79
	2	14.4	1.81	20.9	62.2	.73
	3	13.3	1.79	39.7	44.6	.57

Variability in oil composition of inbred lines may be advantageous if selection can be practiced toward a better oil quality (such as higher linoleic acid percent). However, the variability in oil composition which may be present in inbred lines should be examined before inbred lines are used in studies concerning fatty acid composition of oil. Considerable error could be introduced into genetic studies as well as other studies where uniform genetic material is desired, unless preliminary analyses of oil composition are made. At this Station, individually selfed ears are maintained separately within inbred lines and single-kernel analyses are made for oil composition to determine uniformity before use of a particular inbred in further studies.

M. D. Jellum

2. Plant introductions with high stearic acid composition of oil.

The fatty acid composition of commercial corn oil includes about 2.0% stearic acid. Most inbred lines have oil with between 1 and 4% stearic acid. Approximately 1500 inbred lines of U.S. origin have been analyzed for oil composition over the past several years. Very few inbred lines had stearic acid composition between 4 and 6% and only one inbred line had stearic acid slightly above 6% of total oil.

Early in 1968, kernels of 144 plant introductions from 52 different foreign countries were received from the North Central Regional Plant Introduction Station, Ames, Iowa. Kernels were analyzed individually for fatty acid composition of oil from the original sib pollinated sample and from first generation selfed ears produced in Georgia. Results of five plant introductions in which high stearic acid composition was found are shown in Table 2. Sibbed kernels of P. I. 214124 (Bolivia) were received from the Plant Introduction Station in 1969 and no additional analyses have been made. Original seeds were variable in stearic acid composition and were high in stearic acid as compared with other plant introductions. Original seed of P. I. 175334 (Nepal) had a range in stearic acid of 1.70 to 6.22%. However, the average oil composition of two S_1 ears had stearic acid composition which was considerably higher. The range in stearic acid percent of individual kernels from S_1 ear No. 4 and of S_2

Table 2

Percent stearic acid composition of total oil

P.I. No.	Origin	Original sibbed kernels	Avg. of S_1 ears	Single kernels from S_1 ears				
[a]214124	Bolivia	8.27						
		10.36						
		3.75						
		5.90						
		7.39						
175334	Nepal	3.93	4.86					
		6.21	10.71					
		1.70	2.76					
		2.80	11.54	10.82	10.48	14.46	13.06	9.08
		6.22	3.83					
				[b]12.13	11.16	13.10	12.37	8.87
				[b]11.88	15.10	12.13	14.83	13.54
				[b]13.32	13.09	13.19	13.47	13.11
197503	Ethiopia	1.33	3.25					
		2.61	11.18					
		2.57	5.53					
		8.42	2.51					
		7.96	1.72					
185619	Egypt	1.04	1.27	1.55	1.03	1.54	2.06	1.71
		2.47	3.48					
		1.90	2.77					
		2.07	1.41					
		2.63	6.19					
			6.20					
			9.29	7.15	6.79	13.42	9.01	5.74
177651	Syria	2.87	2.21					
		2.69	2.13					
		1.80	8.55					
		1.71	4.12					
		2.61						

[a]Additional analyses of S_1 ears have not been made for this P. I.

[b]Single kernel analyses made on three selected S_2 ears. Seed originated from S_1 ear with 11.54% stearic acid.

ears is shown in Table 2. A wide range in stearic acid composition was observed among original sibbed kernels and S_1 ears of P. I. 197503 (Ethiopia). P. I. 185619 (Egypt) and P. I. 177651 (Syria) had typical stearic acid composition in original kernels, but had high stearic acid in some S_1 ears.

Stearic acid is a saturated fatty acid and a high percentage may not be desired in corn oil for commercial food use. However, the high composition found in certain plant introductions is of considerable interest for future genetic and biochemical studies. Some of these high stearic acid lines have been crossed with low stearic acid inbred lines for genetic studies. Of biochemical interest, lines which are high in stearic acid have also had a much higher than usual amount of arachidic acid. Selfing in this material is being continued to obtain homozygous lines with high stearic acid composition.

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1. Multiple character analysis and chromosome studies in the Tripsacum lanceolatum-pilosum complex.

The genus Tripsacum has nine recognized species all of which are native to the new world. The range of their distribution extends from northern South America through Central America and Mexico into the United States. There are four diploid (2n = 36) species (T. floridanum, T. australe, T. maizar and T. zopilotense). T. dactyloides has both diploid and tetraploid (2n = 72) forms while T. laxum, T. latifolium, T. lanceolatum and T. pilosum exist as tetraploids. While the diploid species of Tripsacum are morphologically very distinct the tetraploid "species" are not so sharply delimited. This is nowhere better illustrated than in the tetraploid populations in Mexico. Even though these tetraploids are referred to as T. lanceolatum or T. pilosum, there are a

Table 1

Mean values and standard deviations for eight morphological characters studied in four populations of *Tripsacum*.

Species		Plant Height (Meters)	Blade Length (Cms.)	Blade Width (Mms.)	Pilosity Score of Leaf Sheath	Condition of the Auricle	Number of Branches in the Terminal Spike	Venation Index	Pedicel Length of the Accessory Male Spikelet (Mms.)
T. maizar	Mean	3.545	182.494	69.939	2.250	1.875	22.535	4.738	3.204
	S.D.	0.328	21.156	6.609	0.463	0.835	5.014	0.598	0.466
T. zopilotense	Mean	1.179	59.490	9.161	0.083	0.583	1.233	10.250	0.208
	S.D.	0.100	7.413	1.163	0	0.515	0.287	1.072	0.108
T. pilosum	Mean	3.121	157.017	41.317	1.652	1.261	9.877	5.257	2.400
	S.D.	0.456	17.430	9.182	0.935	0.752	4.191	0.865	0.750
T. lanceolatum	Mean	2.506	126.838	18.913	1.091	0.818	2.495	8.218	0.601
	S.D.	0.299	23.019	6.644	0.701	0.603	0.738	1.715	0.152

Table 2

Pairwise comparison of "distances" and probable errors for eight morphological characters studied in four populations of *Tripsacum*.

Pairs of Populations		Plant Height	Blade Length	Blade Width	Pilosity Score of Leaf Sheath	Auricle Score	Number of Branches in Main Spike	Venation Index	Pedicel Length of Male Spikelet
T. maizar vs. *T. zopilotense*	Distance	11.048	8.612	15.638	9.722	1.914	8.036	6.602	10.424
	Prob. error	0.00200	0.00675	0.00200	0.00387	0.19199	0.00899	0.01842	0.00272
T. maizar vs. *T. pilosum*	Distance	1.080	1.320	3.624	0.856	0.774	2.750	0.710	1.322
	Prob. error	0.29128	0.25836	0.68163	0.32898	0.33950	0.12639	0.35061	0.25820
T. maizar vs. *T. lanceolatum*	Distance	3.310	2.520	7.700	1.992	1.470	6.968	3.010	5.424
	Prob. error	0.09555	0.14184	0.01064	0.18465	0.23972	0.01534	0.11095	0.00741
T. zopilotense vs. *T. pilosum*	Distance	6.984	7.852	4.216	3.536	1.070	3.860	5.156	5.106
	Prob. error	0.01522	0.00986	0.02233	0.08536	0.29287	0.07256	0.03798	0.03893
T. zopilotense vs. *T. lanceolatum*	Distance	6.644	4.426	2.498	3.114	0.420	2.406	1.458	3.020
	Prob. error	0.01805	0.05468	0.14338	0.10538	0.40536	0.04611	0.24118	0.11046
T. pilosum vs. *T. lanceolatum*	Distance	1.628	1.492	2.832	0.686	0.654	2.992	2.296	3.990
	Prob. error	0.22153	0.23710	0.12137	0.35474	0.36063	0.11182	0.18861	0.06800

wide range of morphological forms connecting the so called "typical" T. pilosum and T. lanceolatum.

It has been proposed by Randolph (Randolph and Hernandez-Xolocotzi, 1950; Randolph, 1955) that the Mexican and Central American tetraploids of Tripsacum originated as amphiploids of T. maizar and T. zopilotense or similar diploid species whose chromosomes are sufficiently similar to permit genetic exchange.

Recently, Tantravahi (1968) proposed that the tetraploid T. lanceolatum-pilosum complex in Mexico might have originated as segmental allopolyploids as a result of hybridization between T. maizar and T. zopilotense.

Even though the existence of polymorphic populations of Tripsacum in Mexico has been recognized by everyone that has seen them, so far a quantitative morphological study and detailed chromosome analysis of these populations has not been undertaken. In the present study, 55 plants belonging to the tetraploid T. lanceolatum-pilosum complex and its supposed diploid parents have been subjected to a detailed morphological study (1) to obtain information on the limits of morphological variations in the diploid species and in the tetraploids, (2) to see if a given specimen can be assigned with reasonable accuracy to a species to which it is closely related and finally (3) to see if the data would support the hypothesis stated above. Initially 15 morphological characters were chosen. Of these eight were finally selected (Table 1). The characters were not randomly selected but were chosen because of their value in distinguishing the parental diploid species. The same eight characters have been used for the tetraploids. The means and standard deviations have been computed for the eight characters. Single character "distances" have been obtained for a given pair of species by dividing the difference in the means of that pair by the average standard deviation (Table 2). The "distance" statistics would give the relative usefulness of a particular character in distinguishing a given pair of species. For example, blade width is of greatest importance in distinguishing T. maizar from T. zopilotense. The condition of the accessory male spikelet (Pedicellate or Sessile) and venation index are useful in distinguishing the so called T. pilosum from T. lanceolatum.

Table 3

Pairwise discriminant analysis of *T. maizar*, *T. zopilotense*, *T. lanceolatum*, and *T. pilosum*.

Morphological Character	Discriminant Coefficients					
	T. maizar vs. *T. zopilotense*	*T. maizar* vs. *T. pilosum*	*T. maizar* vs. *T. lanceolatum*	*T. zopilotense* vs. *T. pilosum*	*T. zopilotense* vs. *T. lanceolatum*	*T. pilosum* vs. *T. lanceolatum*
Plant height	4.009	-0.140	0.264	0.054	-0.869	-0.221
Blade length	0.081	0.006	0.007	-0.015	-0.013	0.005
Blade width	0.117	0.015	0.076	-0.005	0.062	0.006
Pilosity score of leaf sheath	0.182	0.044	0.256	-0.019	-0.328	0.028
Auricle score	0.449	-0.004	0.043	0.033	-0.021	0.014
No. of branches in main spike	0.081	0.024	-0.017	-0.031	-0.578	0.007
Venation index	0.033	0.079	0.099	0.057	0.091	-0.004
Pedicel length of male spikelet	1.292	0.005	1.600	-0.084	-2.200	0.183
Average discriminant function for						
T. maizar	44.434	2.736	13.435			
T. zopilotense	11.573			-0.343	-1.530	
T. pilosum		1.909		-2.637		0.823
T. lanceolatum			5.071		-5.085	0.269
D^2(D)	591.6 (24.4)	23.9 (4.9)	142.1 (11.9)	75.7 (8.7)	74.6 (8.6)	17.7 (4.2)

The technique of linear discrimination as described by Kendall (1951) has been used. The computations were done on an IBM 7094 computer using the BIMD 05 program developed by the medical school of the University of California at Los Angeles. This technique finds the weighted sum of a number of characters that distinguish the populations best. The sum itself is the discriminant function. The weights determined by these computations are called discriminant coefficients (Table 3). The average value of the discriminant function for a given population can be obtained by multiplying the average value of each character by the corresponding coefficient and then summing. The discriminant coefficients have been computed for the eight characters used in a pairwise comparison for all four populations. These data together with D^2 and D values are presented in Table 3. The last value is roughly the difference in the standard deviations between the mean value of the functions of a particular pair of populations. For example T. maizar differs from T. zopilotense by 24 standard deviations while T. lanceolatum and the so called T. pilosum differ from each other by only about four standard deviations.

The method of multiple character analysis as used in the present study has two advantages over simple pairwise comparison of single characters. This method takes all characters together in assigning weights to them. Characters that best distinguish a given pair of populations will have higher weights, strikingly bringing out the differences. This method in fact pulls the populations apart as far as possible making the evaluation of relationships more meaningful and discrete. Secondly, using the coefficients it is possible to assign any doubtful specimen, a posteriori, to one of the populations to which it is closest in its relationship. In the present study three plants (65-1236, 65-1237 and 65-1238) all collected at the same locality and assigned to the so called T. pilosum showed a diploid chromosome number of 36 instead of the expected 72 (Table 4). These plants have to be included under T. pilosum (originating as parthenogenetic diploids) or T. maizar, one of the diploid parents with which T. pilosum shows some morphological resemblance.

Table 4

Frequency distribution of various types of associations observed at diakinesis in plants belonging to the Tripsacum lanceolatum-pilosum complex.

Plant Number	Diploid Chromosome Number	Frequencies of the types of associations			
		Quadrivalents	Trivalents	Bivalents	Univalents
F.T.G 65-1221	70 (?)	20.7	-	77.3	2.0
65-1235	72	16.3	4.3	72.8	6.6
65-1236	36	-	-	90.6	9.4
65-1237	36	-	-	89.5	10.5
65-1238	36	-	-	93.4	6.6
65-1239	72	16.3	-	83.7	-
65-1240	72	19.3	2.8	73.3	4.6
65-1241	72	18.6	1.4	73.5	6.5
65-1242	72	13.4	0.8	74.0	11.8
65-1243	72	15.8	2.9	70.1	11.2
65-1243a	72	20.9	-	79.1	-
65-1246	36	-	-	97.7	2.3
65-1247	72	12.8	1.2	84.5	1.5
65-1248	72	23.1	1.1	67.6	8.2
65-1249	72	19.9	-	80.1	-
65-1250	72	15.4	5.5	71.5	7.6
65-1251	72	17.6	3.2	75.8	3.3
65-1252	72	13.8	2.2	79.7	4.3

The discriminant functions have been computed for these three plants and the values are 2.098, 1.945 and 2.060, respectively. All these values are lower than the average discriminant function of T. maizar vs. T. pilosum which is $\frac{(2.736 + 1.909)}{2} = 2.323$ (Table 3). It is evident that these plants are more closely related to T. pilosum than to T. maizar. Again, specimens 65-1239 and 65-1243 were tentatively assigned to the so called T. pilosum even though these plants have narrower blades and showed a resemblance to T. lanceolatum in their growth habit, because of the presence of pedicellate accessory male spikelets, a character common to T. pilosum. The discriminant functions of these specimens are 0.736 and 0.727 respectively. These values are higher than the average discriminant function (0.546) for T. pilosum vs. T. lanceolatum suggesting that these specimens are "nearer" to the so called T. pilosum. Since the so called T. pilosum and T. lanceolatum differ from each other by only about four standard deviations, morphological types of one "species" should be expected to resemble the other and vice versa.

A clear view of the degree of separation of the populations is achieved by plotting the discriminant functions using T. maizar-pilosum as the abscissa and T. pilosum-lanceolatum as the ordinate (Fig. 1). This graph shows that there is no overlapping between T. maizar and T. zopilotense, the two parental diploid species. This shows that the two species are very distinct. They occupy opposite corners of the graph. Members of the T. lanceolatum-pilosum complex overlap with each other as expected and lie in the center of the graph. The fact that the members of T. lanceolatum-pilosum complex are intermediate in the eight morphological characters that distinguish its supposed diploid parents and that they are distributed in the center of the graph is strong evidence that the T. lanceolatum-pilosum complex could have originated as a result of hybridization between T. maizar and T. zopilotense followed by chromosome doubling.

Detailed chromosome analysis has been made on 21 plants belonging to the T. lanceolatum-pilosum complex and the two diploid parental species. The diploid species showed regular pachytene pairing resulting in 18 bivalents at diakinesis and Metaphase I. The tetraploids showed

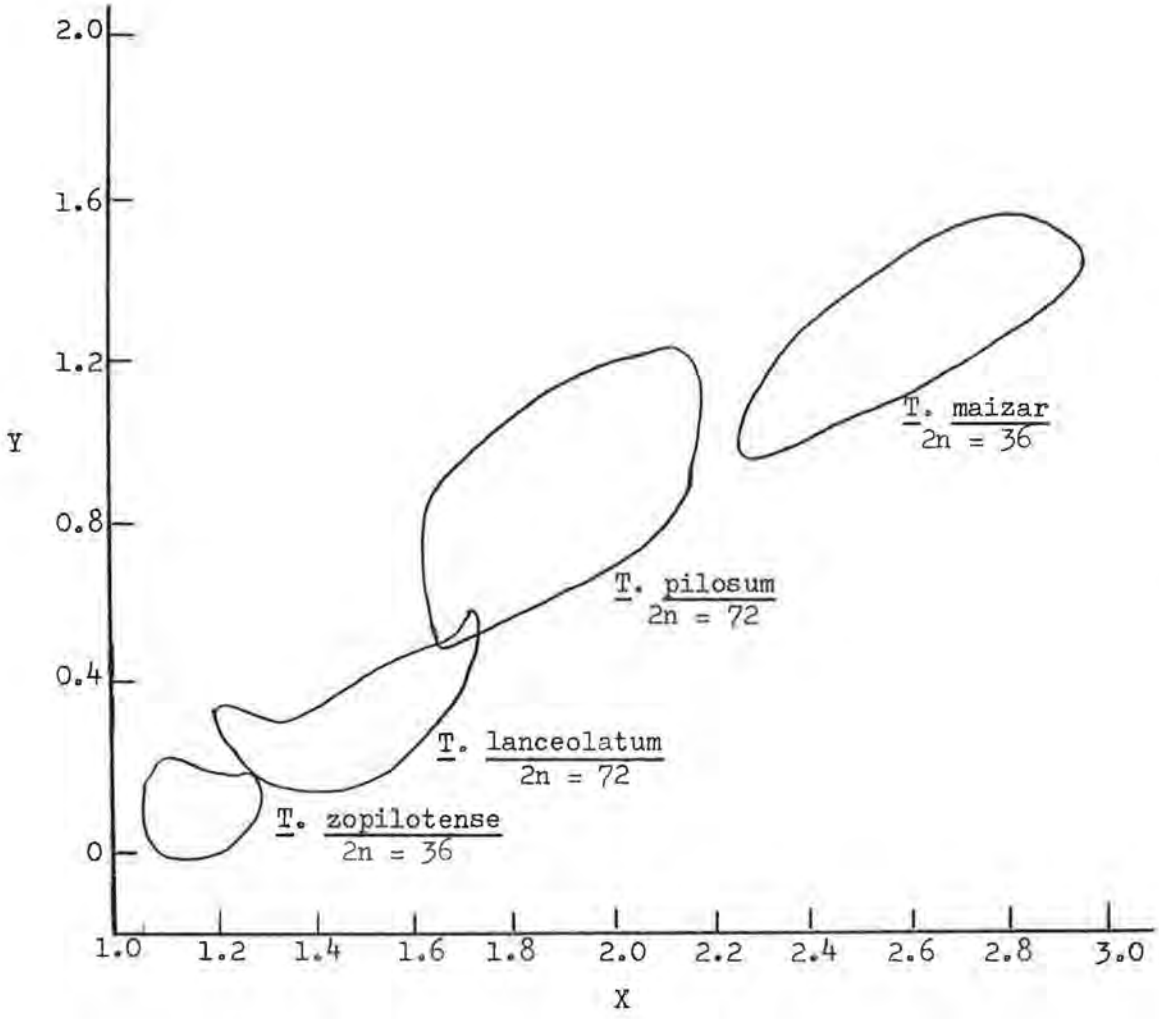

Figure 1. Graph showing the relative disposition of four populations of Tripsacum. The discriminant functions of T. maizar-pilosum are used as the abscissa while those of T. pilosum-lanceolatum are used as the ordinate.

"associations of four" chromosomes followed by exchange of partners at pachytene. At diakinesis varying numbers of multivalents, bivalents and univalents are observed (Table 4).

Of the ten possible types of quadrivalents (Darlington, 1931), those requiring multiple chiasma formation were observed in low frequencies. Types 11 and 17 were found in much higher frequencies (Table 5). Since exchange of partners takes place between "homeologous" chromosomes leading to the heterogenetic association of quadrivalents, there is

Table 5

Frequency distribution of the various types of quadrivalents observed at diakinesis in the T. lanceolatum-pilosum complex.

Plant number	Frequencies of quadrivalent types									
	11	12	13	14	15	16	17	18	19	20
F.T.G 65-1221	21.0	5.0	-	-	-	-	67.0	7.0	-	-
65-1235	38.6	9.5	-	-	6.9	-	37.4	7.6	-	-
65-1239	40.0	-	-	-	-	-	53.3	6.7	-	-
65-1240	16.4	9.1	3.6	-	12.7	-	52.7	5.5	-	-
65-1241	24.1	-	-	-	-	-	69.0	6.9	-	-
65-1242	26.9	19.2	20.5	-	-	-	32.1	1.3	-	-
65-1243	22.4	6.6	1.3	-	-	-	64.5	5.2	-	-
65-1243a	19.4	3.2	-	-	5.3	-	65.6	6.5	-	-
65-1247	24.3	-	3.0	-	-	-	66.7	6.0	-	-
65-1248	23.1	2.9	-	-	1.9	-	62.5	9.6	-	-
65-1249	17.4	-	-	-	-	-	67.4	15.2	-	-
65-1250	30.7	5.3	4.7	-	-	-	55.7	3.6	-	-
65-1251	26.2	10.2	-	-	3.4	-	52.3	7.9	-	-

segregation in these tetraploid "species" for the morphological characters that distinguish the diploid parents. It is the hybrid origin of these populations that makes them so variable.

Even though the names T. pilosum and T. lanceolatum may be used for the purposes of classifying a given specimen, in view of the presence of a wide range of morphological characters and the small D value between the so called T. pilosum and T. lanceolatum it seems better to regard the whole group of tetraploids as a T. lanceolatum complex which includes a wide range of morphological forms.

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1. Electron microscopy of the chlamydospores of corn smut (Ustilago maydis (DC.) Corda).*

This report is based on our preliminary observations with carbon replicas of the chlamydospores of corn smut at the ultrastructural level. The replication method employed here is a methyl-methacrylate heat-pressure technique. The technique has been slightly improved by us in order to use this method in fungal palynology.

The chlamydospores suspended in water are evenly spread on the flat surface of a prepolymerized, methacrylate plastic plate (about 15 by 20 mm in size). The preparations are then allowed to air-dry overnight in a clean chamber. Further the plate, with a thin layer of dried spores, is sandwiched between glass plates, held tightly with clamps and heated to about 105 degrees C for ca. 15 to 20 minutes. After cooling to room

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*This work was partly done at the Biology Department, Yale University, New Haven, Conn.

temperature the spore debris is removed mechanically, and spore impressions are then shadowed with 150 Å thick carbon and chromium. The carbon-chromium replica is then scored into small pieces with a sharp razor blade and suspended in a mixture of benzene and chloroform (1:1 by volume) to remove the plastic. Individual pieces of the replicas are then placed on 250 mesh copper grids for viewing. The electron microscopes Hitachi HS-7S and RCA EMU-3D are used for photography.

Under the electron microscope the spore shape appears spherical, the size varies from 7 - 12 u, and the spores are covered with sparsely situated prominent spines (echinate). Occasionally some spines are slightly curved at the tips. Each spine is covered all over with very fine micro-spinules; in side view the spines appear finely serrated. At the base of each spine, the micro-spinules are found in rings. The spore membrane between the spines is smooth to slightly granular. We consider that the use of such micro-characters may be helpful in identification of various genetic races of corn smut, which so far has not been possible with the conventional light microscope.

U. C. Banerjee
S. Banerjee*

2. Electron microscopy of the pollen grains of maize, teosinte, and Tripsacum.

Precise identification of the pollen grains of maize, teosinte, and Tripsacum has great potential in tracing the past agricultural activities in the New World. Several distinguishing characters such as pollen grain size, pore-axis ratio, exine pattern, and spinule density per unit area were studied previously in this laboratory with conventional light and phase-contrast light microscopy (Barghoorn et al., 1954; Irwin and Barghoorn, 1962, 1965; and Bartlett et al., 1969).

The present report provides further observations on the ektexine (outer sculptured layer of exine) pattern at the ultrastructural level, using the scanning electron microscope (SEM) and the transmission electron microscope (TEM). The pollen grain samples of these genera

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were collected locally, or from herbarium sheets, and prepared for observation by using a standard acetolysis treatment (Erdtman, 1960). A portion of each sample was deposited on copper cylinders and thinly coated with a palladium-gold alloy by evaporating it under a very high vacuum, and finally the pollen grains were photographed at high magnifications with SEM. The remaining samples were used to prepare reference slides for light microscopy by mounting them in glycerine jelly, and to make carbon replicas for TEM by means of the methyl-methacrylate heat-pressure double-stage technique.

In maize (Zea mays) the ektexine shows the presence of evenly distributed spinules (except in a few pop-corn races where there is occasional clumping of 2 - 3 or rarely 4 spinules). The TEM pictures, at high magnification, show that the exine is perforated by minute holes. These holes are distributed between and around the spinules. We consider the patterning of these holes to be a very important, usable criterion for identification of grass pollen grains. In teosinte (Euchlaena mexicana) the ektexine spinules exhibit occasional clumping (2 - 4 spinules) as well as isolated spinules as in maize. The spinules are very similar to the maize spinules in their size and shape. The minute holes are also present and are distributed all over the ektexine, except between the clumped spinules. The diameter of the holes in the exine of maize and teosinte grains is quite similar.

Tripsacum dactyloides and T. floridanum show an entirely different ektexine pattern from maize and teosinte, which we consider negatively-reticuloid (a cluster of spinules present at the elevated lacuna (lumina) and the reticulum incised or depressed). The holes are not present between the spinules, but are restricted to the incised reticulum. The size of the spinules is also much smaller than those of maize and teosinte.

U. C. Banerjee
E. S. Barghoorn

3. Acetolysis: a positive test for the identification of normal and aborted pollen grains in grasses.

The importance of recognition of normal and aborted pollen grains in maize and other cereal crops is well known to plant breeders. Various staining procedures are used, such as cotton blue in lacto-phenol, aceto-carmine, various tetrazolium salts, iodine and potassium iodide in dilute alcohol. But most of these stains are either nuclear or protoplast dyes and often show fading when permanent mounts are made.

We have used the standard acetolysis technique following Erdtman (Sv. Bot. Tidskr., Vol. 54(4): 561 - 564; 1960), except we have increased the timing to 5 - 6 min. to give a differential staining of the pollen grain exine.

Permanent slides are made by mounting the acetolysed pollen grains in standard glycerine jelly, and the exine color is stable.

The normal pollen grains stain a dark-brown color, while the exine of aborted pollen grains is lighter and shows a pale yellow color. In addition, in glycerine jelly mounts the large majority of the aborted pollen grains collapse, and we consider this difference as a distinct character of the aborted pollen grain exine.

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4. Similarity of the ektexine pattern of normal and aborted pollen grains in maize and other grasses.

In an earlier study with the pollen grains of maize, Tsukada and Rowley (1964) postulated that the density of the spinules of the ektexine (outer sculptured layer of the exine) was different in normal and aborted (sterile) pollen grains, when spinules were counted per unit area. The spinule density in aborted pollen grains was always higher in comparison to the spinules of normal pollen grains.

Our observations, using an electron microscope, show that there is no such difference present among grasses when normal and aborted pollen grains are obtained from genetically similar lines. The only obvious difference we have noticed is that the pollen grains exhibit differential stainability when subjected to a prolonged acetolysis treatment. The

normal pollen grains are dark brown, while the exine of the aborted pollen grains becomes pale yellow. The acetolysed, aborted pollen grains also collapse when they are mounted in glycerine jelly. We suspect that this difference is due to a difference in chemistry of the pollen walls of the two types, or due to variation in wall thickness (not distinct with the light microscope). Immature pollen grains are not taken into consideration because they often stain like the aborted pollen grains.

We think that the basic exine pattern is not controlled entirely by the haploid protoplast, but is established by the proto-exine (primexine) during early stages of microsporogenesis, when the microspores are in the quartet stage, enclosed in a thick, callose wall. After the microspores are released into the anther locules, wall building substrates (sporopollenin) begin to deposit on the proto-exine framework, resulting in a similar ektexine pattern, irrespective of the presence of the pollen grain protoplast.

During the sporopollenin deposition the microspores increase in size and secondary spinules are added to the ektexine of the pollen grains by the Ubisch bodies (orbicules), regardless of their normal or aborted nature, and finally a characteristic, mature ektexine pattern of the species is formed.

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5. The structure of the Ubisch bodies (orbicules) and their control on mature ektexine pattern of grass pollen grains.

Zea mays and its related species were chosen for this investigation. The results reported here are based on electron microscopic observations. Among grasses, the Ubisch bodies (orbicules) are small, spinulate, spheroidal structures which are formed on the inner tangential, and partly on the radial surfaces, of the tapetal cells that are exposed to the thecal fluid (periplasmodium) of the anther locules. In fact, these minute structures are formed as a part of the tapetal membranes, as reported earlier by Banerjee (1967) and Banerjee and Barghoorn (1969). In the palynological literature, it has been often reported that either the function of these objects is unknown or they are a functionless,

space-filling material around and between the tetraspores (microspores) (Frey-Wyssling and Muhlethaler, 1965). We have made histochemical tests to check the chemical composition of these structures; it is found to be similar to that of the pollen grain exine, i.e. sporopollenin. Ontogenetically, the formation of these bodies begins either prior to or after the microspores are released from the quartet into the thecal fluid of the anther locules. It is at this phase, when maximum deposition of sporopollenin occurs on the templated protoexine (primexine, chemically, which is cellulosic in nature) of the microspores, and simultaneously on the inner face (tapetal surface) of the locules, that Ubisch bodies are formed. Almost simultaneously the microspores orient themselves within the locule (the germ pore facing outwards), and then enlarge in size and come in close contact with the Ubisch bodies. New spinules are added to the microspore ektexine at this stage by the formation of physical continuities between the microspores and the Ubisch body spinules, forming sporopollenin strands. In Zea mays microspores, Skvarla and Larson (1966) have shown that during early developmental stages the spinules of the ektexine are essentially extensions of the supporting columellae, further indicating that no spinules are added after template formation. But, at exine maturity, they were unable to match the number of spinules of the ektexine with the number of columellae present. Our observations clearly indicate that new spinules (secondary spinules) are added to the ektexine by the Ubisch bodies after the increase in size of the pollen grain and its orientation.

In our earlier report we have also shown that shortly before anther dehiscence the contacts of the sporopollenin strands between the Ubisch body spinules and the pollen grain spinules are lost, which allows the pollen grains to disperse at anther dehiscence.

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1. Leaf-fleck mutant in maize.

A leaf-fleck phenotype, first observed in 1968, has segregated in our stocks as a monogenic recessive mutant. The mutant appeared first in a $\underline{y}$ $\underline{o}_2$ stock of Tuxpeno origin and appears to be distinguishable from other reported leaf-flecking or blotching diseases or mutants by the rusty color and small size of the spots.

Leaf blades of the mutants are characterized by abundant punctate rusty-colored spots, 1-3 mm. in diameter, surrounded by a chlorotic halo usually less than 1 mm. wide. The spots are extremely abundant on mature leaves, overlapping and appearing to coalesce, often cutting the photosynthetic area by as much as 75%. Segregating seedlings could not be classified during 15 days growth in petri dishes. Newly emerging leaves show only minute chlorotic spots, which expand more or less in direct proportion to the expansion of the leaf blade. The rusty coloration appears comparatively late, after full expansion of the leaf blades, and is less apparent on leaf sheaths. Husks and glumes are apparently unaffected.

Mutant plants were fully fertile, although slightly reduced in stature, attaining about 3/4 of the dry weight of normal sibs. Studies by the University of Hawaii Plant Disease Clinic could reveal no pathogen associated with the lesions, nor was it mechanically transmissable. No aphids or leafhoppers were associated with appearance of lesions, as reported for the leaf-fleck disease described by Atanasoff (Phytopath. Zeitschr. 52:98, 56:25). Seedlings were grown for two generations and in 5 separate nurseries this year, following appearance of the initial segregants, and the kind of seed-transmissal of a viral agent suggested by Atanasoff was entirely precluded by the data.

The mutant has been provisionally assigned the gene symbol, $\underline{lf}_1$, and has been entered in crosses to translocation stocks to determine its chromosomal location.

Information and seedstocks of similar mutants are solicited.

James L. Brewbaker

2. Peroxidase isoenzyme loci in maize.

Peroxidase isoenzyme polymorphism in maize tissues as observed using starch gel electrophoretic techniques has previously been described (Hamill and Brewbaker, Physiologia Plantarum 22:945-958, 1969). Of some 21 different peroxidase polymorphisms found, 5 of these systems have been subjected to genetic analysis and found to be under the control of 5 different loci. These loci have been designated $\underline{Px}_1$, $\underline{Px}_2$, $\underline{Px}_3$, $\underline{Px}_4$, and $\underline{Px}_5$.

The $\underline{Px}_1$ system moved cathodally on starch gel in the pH 8.1 buffer used, to a position -36 relative to the front on the anodal side. This isoenzyme was found first in seedling root tissues and subsequently, bands moving to the same position were seen in mature roots and some leafy tissues. Genetic analyses for this system were all carried out on seedling root tissue extracts. This locus was previously reported as having 2 alleles (Hamill, Maize News Letter 42:36-37, 1968), each conditioning the production of an isoenzyme with a slightly different electrophoretic mobility. Two additional patterns were found, another isoenzyme variant moving slightly slower than the others, and a null condition in which none of the bands was present. These 4 peroxidase patterns were crossed in all possible combinations and F_2 and backcross progenies were produced to test for allelism. In all cases, F_1's possessed both parental isoenzymes, and the F_2 and backcross progenies segregated with ratios which fit those expected for a single locus with 4 alleles, $\underline{Px}_1^1$, $\underline{Px}_1^2$, $\underline{Px}_1^3$, and $\underline{Px}_1^{null}$.

An attempt was made to localize $\underline{Px}_1$ on its chromosome using B translocation stocks as described by Roman (PNAS 34:36-42, 1948). To date, the long arm of chromosomes 3, 4, and 10, and the short arms of 7 and 9 have been eliminated as the site of $\underline{Px}_1$, but further location of $\underline{Px}_1$ remains to be determined.

The $\underline{Px}_2$ peroxidases stained very densely and very rapidly and were found exclusively in mature pollen following anthesis. There were 2 variants for $\underline{Px}_2$, one moving to position 67 and one to position 62 relative to the front. F_2 and backcross progenies were produced from a cross between the two and ratios were obtained indicating that the 2 isoenzymes

were due to 2 alleles at a single locus. This was designated $\underline{Px}_2$ with alleles $\underline{Px}_2^1$ and $\underline{Px}_2^2$. No null was observed for this locus.

The $\underline{Px}_3$ peroxidase system was observed in mature leaves, internode, husk, and root tissues, but always was seen most clearly in mature leaves. This system consisted of a series of anodal bands in positions 10, 20, 29, and 38. A second variant of this pattern consisted of a series of bands displaced slightly more toward the anode. These isoenzymes showed faintly in seedling and young tissues and reached maximum clarity in mature tissues which had stopped elongation. Data from segregating progenies from both leaf and root extracts indicated that each of these patterns was conditioned by an allele of a single locus, designated $\underline{Px}_3$ with alleles $\underline{Px}_3^1$ and $\underline{Px}_3^2$. Since the $\underline{Px}_3$ peroxidases were most distinct in leaf, internode, or root when the tissue had completed elongation, it might be suggested that these peroxidase isoenzymes are acting as indoleacetic acid oxidases, bringing about the oxidation of auxin and hence cessation of growth. This remains to be proven.

$\underline{Px}_4$, a peroxidase isoenzyme found in leaf tissues, moved cathodally to a position -18 on the starch gel. No variants were observed for this band, except the null condition. Segregating populations from a cross of presence x absence gave data which indicated that the $\underline{Px}_4$ system consisted of a single locus with presence and absence alleles, with the absence allele being dominant. The same ratios would be obtained however, if presence were dominant and under the control of a dominant independently segregating regulatory locus. This possibility has not yet been examined.

The $\underline{Px}_5$ peroxidase was found in leaf tissues and moved cathodally to a position of -24. Like $\underline{Px}_4$, this peroxidase also consisted of presence and absence conditions. Only one inbred (L289) of 64 studied was found to lack this isoenzyme. F_2 and backcross progenies indicated that these were due to a single locus with 2 alleles, with presence dominant.

$\underline{Px}_3$, $\underline{Px}_4$, and $\underline{Px}_5$ were tested for linkage. No evidence of linkage was found for these 3 loci.

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1. Potassium content of opaque-2, floury-2, double mutant and normal versions of certain inbreds and hybrids.

Potassium was first reported to be higher in opaque-2 kernels by Goodsell (Crop Sci. 8:281-282). He used F_2 kernels from segregating ears to make his comparisons and found that opaque-2 kernels averaged 41% higher in potassium than normal siblings on the same ear. The data in Table 1 are from homozygous ears of inbred lines converted to opaque-2. Here again, o_2/o_2 segregates are higher in potassium than normal segregates in all cases. However, the level of potassium is a function of the inbred line and can vary quite extensively. Since the assay for potassium is simpler, cheaper, and more precise than that for lysine, it was proposed at one time that potassium level be used as a rough screening technique for lysine level. But this data would tend to suggest that in a heterogeneous opaque-2 population, the level of potassium would be independent of lysine level. The limited data for floury-2 and the double mutant are shown, but little should be made of them because they are in the initial stages of conversion to the inbred line.

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1. Chlorophyll-deficient mutants have differential capacities to accumulate assimilation starch.

Five chlorophyll-deficient mutants (l_3, l_4, l_7, l_{4920}, w_{11}) out of 17 stocks tested (former plus w_1, w_2, w_3, yw_{8896}, wh_{8657}, cl_1, l_1w_2, l_6, l_{4923}, lw_1, lw_2, lw_3lw_4) accumulated significantly less assimilation starch from exogenous glucose than their normal sibs. Initial screening

Table 1

Lysine and potassium content of mature corn kernels

	Normal		o_2/o_2		fl_2/fl_2		o_2/o_2 fl_2/fl_2	
	lys	K	lys	K	lys	K	lys	K
R803	.35	.40	.56	.63				
R801	.36	.30	.51	.48				
R109	.35	.36	.60	.46				
WF9	.36	.36	.50	.47				
R75	.39	.45	.61	.58		.50		.50
o_7N	.34	.32	.49	.44				
R802	.37	.34	.60	.46				
oh45	.31	.28	.58	.53	.42	.39	.55	.43
R801 x R75	.41	.40	.54	.52				
R802 x R803	.30	.41	.51	.60				

r = .17 for lysine and K within the opaques.

(See top of previous page for explanation of table.)

was accomplished by floating 1 cm leaf segments from etiolated seedlings on 0.5 M glucose for 24 hr in darkness at 27°C, killing in boiling 95% ethanol, and staining with an aqueous solution of 0.01 M I_2 + 0.03 M KI. Segments containing starch stained brown to blue-black whereas segments without starch and control segments incubated on distilled water stained light brown. The mutants varied in staining intensity from dark as normals to light as water treated controls.

The starch content of glucose incubated segments of the "starchless" mutants, their normal sibs (homozygotes + heterozygotes), and a dent hybrid, WF9 x M14, was determined by the method of Hassid and Neufeld (Methods in Carbohydrate Chemistry, Vol. IV) as modified in our laboratory for small samples of fresh material. The starch content of the mutants varied over a five-fold range and their ranking on the basis of starch content was the inverse of their normal sibs. The normal sibs of $\underline{l}_{4920}$ and $\underline{w}_{11}$ contained significantly less starch than the normal sib of $\underline{l}_4$, indicating the possibility of genetic variability for the capacity of "normal" leaves to accumulate starch from exogenous glucose. The starch data, given as ug/gfw ± std. error, are summarized in the table.

Table 1

Starch content (ug/gfw ± std error) of incubated leaf segments from five chlorophyll mutants, their normal sibs, and a dent hybrid.

Stock	Water Treated		Glucose Treated	
	Normal	Mutant	Normal	Mutant
WF9 x M14	72.1 ± 27.9	-	4,751 ± 384	-
l_4	20.8 ± 2.1	87.4	3,506 ± 175	116 ± 6
l_7	28.8 ± 4.8	-	2,732 ± 37	122 ± 6
l_3	26.7 ± 5.4	35.6 ± 2.4	2,210 ± 60	406 ± 7
w_{11}	32.9 ± 8.6	3.2 ± 0.4	1,713 ± 413	599 ± 82
l_{4920}	34.4 ± 13.8	-	1,591 ± 90	464 ± 51

Cross sections of normal green leaves and treated segments were stained with IKI and examined under the microscope to determine the pattern of distribution of starch in the tissues. No starch was detectable in etiolated and water incubated tissues. Starch was present in normal green leaves in large amounts only in bundle sheath cells. Glucose incubation of etiolated segments resulted in accumulation of massive quantities of starch in both bundle sheath and mesophyll cells. The IKI stainable material which accumulated during glucose treatment was removed by incubating cross sections in α-amylase (11.1 units/ml) for two hr.

The nature and location of the mutations causing the observed effects are unknown. It is possible, but improbable, that the "starchless" phenotype is due to a separate mutation that is closely linked to the chlorophyll-deficiency factor in all five stocks. A more likely explanation invokes a single mutation that affects the synthesis or utilization of some essential amino acid, co-factor, or protein(s). Further studies to determine the activities of the enzymes of the starch biosynthetic pathway (ADP-glucose pyrophosphorylase, ADP-glucose glucosyltransferase, and starch phosphorylase) and of other chloroplast-specific enzymes are being initiated. These studies should provide much-needed information about the general scheme of formation of assimilation starch and some insight into the nature of these specific mutations.

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1. Genetic modifiers affecting the rate of chromosome loss induced by B chromosomes.

In discussing the results of experiments on the loss of knobbed A chromosomes or knobbed arms induced by B chromosomes (MNL 1969), we stated that the bulk of our data came from the original line in which loss was first observed and that a number of problems remained to be resolved. Among these are: (1) what is the effect of the genetic background on the rate of loss, (2) are B chromosomes from unrelated strains as effective in inducing loss as the B's of the high loss strain, and (3) is the rate of loss knob specific? In the 1969 News Letter preliminary data were presented on the frequency of loss of the A_1 allele in the male gametes of F_1 plants derived from a cross of a Black Mexican plant with nine B's onto the silks of an individual with one B from the high loss line. The low loss rate in F_1 plants with 5-7 B's could be attributed either to modifying genes for low loss rate contributed by the Black Mexican parent or to the ineffectiveness of the Black Mexican B chromosomes in inducing loss of the knobbed chromosome 3. Experiments conducted in the summer of 1969 permit some clarification of the above problems. Data comparable to those given in the 1969 News Letter were obtained from F_1 plants from the cross of a Black Mexican strain with B's by a high loss plant with no B's; in contrast to the earlier test, these F_1 individuals received B chromosomes only from the Black Mexican parent. The data produced when the F_1's were used as pollen parents on an a_1 tester are as follows:

Plant	No. of B's	% A loss	Population
30119-5	5	3.1	767
" -1	4-5	2.7	336
" -4	5	1.3	479
" -8	5-7	2.4	1595
" -11	6	1.3	1079

These results are similar to those reported in 1969 and unequivocally demonstrate that B's from Black Mexican can induce loss. However, they permit no discrimination between the hypotheses of inefficient

B's and modifiers for a low loss rate. Convincing evidence for genetic modifiers came from tests of individuals derived from the backcross of 0 B high loss ♀ X $\frac{\text{0 B high loss}}{\text{Black Mex. with B's}}$ ♂ . The progeny would on the average have 3/4 of their genes from the high loss line and all B's would be from Black Mexican. When two individuals from this cross, each homozygous for the large knob in 3L and with 6 B chromosomes, were used as the pollen parent in crosses with $\underline{a}_1$ testers the following results were obtained:

Plant	Constitution	A kernels	a kernels	Σ	% a
30123B-10	6 B's K3L/K3L	2201	224	2425	9.2
" -12	6 B's K3L/K3L	2067	76	2143	3.5

The 9.2% rate of A loss approaches that previously found for 6 B plants in the high loss line. It can be concluded that the ensemble of B's from the Black Mexican strain induces chromatin loss as readily as do the B's of the high loss line although differences may exist between members of the two pools. The difference in loss rate between plants 10 and 12 cannot be attributed to sampling errors and must reflect differences in genetic modifiers present in the two sister plants.

We believe that we have at least a tentative answer to the first two questions raised in the opening paragraph of this report. The remaining question is that of knob specificity. We know that in knobbed/knobless heterozygotes, it is the knobbed chromosome that is preferentially eliminated but we have no information as yet on the loss rate of different sized knobs or if knobs of the same size from different strains will have an identical response to B chromosomes. However, we have demonstrated that the loss of the terminal knob on 9S can be induced by B chromosomes. When plant 30115-5, with three B chromosomes and two chromosomes 9 each with the C allele and a large knob on the tip of 9S, was used as the pollen parent in crosses with a c tester there were 68 kernels with the recessive c phenotype in a total of 1080 (6.3%). This is a loss rate slightly higher than the 4.9% reported in the 1969 News Letter for the loss of the A allele from a knobbed chromosome 3 in a plant with three B chromosomes. Clearly, the large knob on 3L is not unique in its response to elimination by B chromosomes.

M. M. Rhoades
Ellen Dempsey

2. Crossing over and preferential segregation in chromosome 10 induced by abnormal chromosome 10.

Inasmuch as abnormal chromosome 10 has been shown to enhance recombination in the proximal segments of chromosomes 3 and 5, it appeared desirable to see if an increase would be found when similarly placed regions in chromosome 10 were tested. Earlier crossover data for the G-R region in K10 k10 plants (Rhoades 1952) indicated an essentially normal recombination frequency for this centrally placed region, but nothing was known about possible enhancement in a more proximal segment in chromosome 10.

In the summer of 1967, backcross progenies were grown from sib plants all heterozygous for the Du, G, and R alleles and differing in that some had one abnormal 10 and the others only normal chromosomes 10. The waxy gene was homozygous so accurate classification of the du phenotype was possible. The following data were obtained from test-crossing Du G R k10/ du g r k10 plants as the female parent:

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	
Du	du	Du	du	Du	du	Du	du	
G	g	g	G	G	g	g	G	
R	r	r	R	r	R	R	r	
658	527	260	188	131	108	13	13	Σ = 1898

Region (1) Du-G = 25.0%

Region (2) G-R = 14.0%

% Du = 55.9 % G = 52.2 % R = 50.9

(The lower field germination of du kernels accounts for the excess over 50% of Du).

Calculated tetrad ranks:

nons = 27.6%
(1) = 44.5%
(2) = 22.4%
(1-2) = 5.5%

Data from sister plants of Du G R K10/ du g r k10 constitution gave the following:

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	
Du	du	Du	du	Du	du	Du	du	
G	g	g	G	G	g	g	G	
R	r	r	R	r	R	R	r	
600	253	240	485	42	110	31	27	Σ = 1788

Region (1) Du-G = 43.8%

Region (2) G-R = 11.9%

% Du = 51.1 % G = 64.5 % R = 68.6

Calculated tetrad ranks:

nons = 1.9%
(1) = 74.6%
(2) = 10.5%
(1-2) = 13.0%

The calculations of tetrad ranks reveal that in K10 k10 female parents, compared to k10 k10, there were markedly fewer noncrossover tetrads, more with single exchanges in (1), only half as many singles in (2), and 2½ times as many double exchange tetrads. The G-R recombination value in K10 k10 plants is somewhat less than in k10 k10 individuals. Indeed, Gavazzi and Avila (MNL, 1969) reported an even greater reduction for the G-R region in K10 k10 compared to k10 k10 bivalents (10.7% vs 19.5%). The observations indicate that K10 causes a decrease rather than an increase in the G-R region. The increase in the more proximal Du-G region could be attributed to the influence of K10 on proximal segments.

However, it could be argued that the higher value for the Du-G interval was a compensatory increase due to the virtual elimination of crossing over in the distal R-sr_2 region in K 10/ N 10 heterozygotes (Kikudome 1959). If the distal region of structural dissimilarity does not include the adjacent G-R segment, a compensating increase in G-R recombination might be expected. Since no increase was observed, one could conclude that a portion of the G-R region shows no (or reduced) recombination while the remainder shows an increase, the net result in our data approaching a normal frequency for G-R recombination. According to this argument, the recombination differences in K10 k10 and k10 k10 plants stem from the fact that K10 plants have a reduction in distal exchanges and a compensatory increase in proximal crossing over. However, the data can also be interpreted to indicate that K10 increases crossing over in the proximal segment of chromosome 10 as it does for the other tested chromosomes. The situation in chromosome 10 is more complicated because the proximal increase can be ascribed to two causes. The present data afford no unequivocal decision between these two alternatives, but a definitive answer should be obtained from recombination values in homozygous K10 bivalents.

M. M. Rhoades
Ellen Dempsey

3. The effect of abnormal 10 on the anaphase movement of knobbed and knobless acentric fragments.

Plants homozygous for abnormal chromosome 10 produce neocentromeres at knobbed regions of AI and AII chromosomes. Our earlier studies indicated that acentric fragments, derived from crossing over in bivalents heterozygous for a paracentric inversion, also exhibited neocentric activity if the fragment possessed a knob. Knobless fragments appeared to be passive at AI, but nothing was known of the fate of either fragment at the end of meiosis. A comparative study of the behavior of knobbed and knobless fragments in related plants of K10 K10 and k10 k10 constitution was made in order to determine the extent to which acentric fragments were preserved in the nucleus.

Counts were made of the frequency of AI cells with fragments (including cells having a single bridge and single fragment, a double bridge and two fragments, an acentric fragment only, and those with a single bridge and attached fragment). Interphase and quartet stages were examined and the frequency of a fragment in the cytoplasm was determined. The cytoplasmic fragments were expressed as percentage of total fragments excluded from the nucleus and the reciprocal of this value was adopted as an estimate of the rate of inclusion of the fragment within a TI or TII nucleus. The observed AI fragment frequencies and calculated frequencies of inclusion at the end of the first and second meiotic divisions are given in Table 1. Knobless fragments were derived from crossing over in In 3a/N3 heterozygotes in which both chromosomes 3 were knobless. Knobbed fragments were produced in In 7a/N7 plants homozygous for a knob in the inverted region. Cells were counted from two plants in each category; the frequency given is an average of the values in the two plants and the total number of cells is shown in parentheses.

		AI Obs. Freq. of Frag.	Frequency of Fragment in Nucleus (1 - Frag. in Cytoplasm / Total Frag.) First Division	Second Division
In 3a/ N 3 k3/k3	K10 K10	64.2 (407)	55.3 (442)	61.6 (383)
	N10 N10	28.7 (430)	23.9 (317)	35.5 (626)
In 7a/ N 7 K7/K7	K10 K10	83.1 (356)	98.9 (510)	91.4 (744)
	N10 N10	83.5 (539)	25.9 (699)	30.5 (403)

With In 3a/N3 heterozygotes the generation of fragments occurred at a higher rate in K10 K10 individuals than in the N10 N10. This is due to increased crossing over in the loop induced by K10. No increase in fragment frequency was noted in In 7a/N7 heterozygotes of K10 K10 constitution. The rate of fragment production in N10 N10 plants is already very high since the inverted segment is longer than in In 3a. It is believed that in k10 k10 plants, a maximum rate of fragment formation has been reached and that conversion of singles to doubles in the loop by K10 would not increase the fragment frequency since 25% of the double chiasmata (2 strand doubles) give cells without fragments. Variations in overall production of fragments, however, should not affect the data presented in the remainder of the Table since they are based only on that proportion of the AI cells that contain fragments.

It is clear that the knobbed acentric fragment in K10 K10 microsporocytes is nearly always included in the TI and TII nuclei. If the four categories of plants are ranked with regard to capacity to preserve the fragment as a nuclear chromosome throughout meiosis, the following order is obtained: K10 K10 In 7a/N 7 > K10 K10, In 3a/N 3 > N10 N10, In 7a/N 7 = N10 N10 In 3a/N 3. In K10 K10 plants the inclusion of the knobbed 7a fragment in the nucleus is not surprising since at AI it is often found near one pole. The attenuation of its

poleward tip is suggestive of spindle fiber attachment. The knobless 3a fragment in K10 K10 plants does not pass rapidly to the pole but shows a delayed poleward movement and is drawn into the nucleus in about one half of the cells with fragments. Even in N10 N10 plants, acentric fragments of both types were included in some of the interphase and quartet nuclei. This behavior was not anticipated and cannot be attributed to attachment of the fragments to centric chromosomes in AI, since the frequency of attached fragments was low.

During second division the knobbed 7a fragment in K10 K10 plants is found at the pole of the spindle as early as MII. About half of the knobless fragments in K10 K10 plants are also found at the pole at MII and these may represent fragments which had been included in the interphase nucleus. In neither case did the fragment show any indication of spindle fiber attachment. We believe that the movement of the fragment at second division is passive, resembling the poleward movement of acentric fragments and other particles in mitotic cells of the endosperm described by Ostergren, Molè-Bajer, and Bajer (1960). Thus, any acentric fragment incorporated into the nucleus at the end of the first division rapidly moves to the pole in the second division, with the exception of attached fragments which may be released into a dead zone at the equatorial plane of the spindle.

The question remains whether or not the fragment persists through additional mitotic divisions. Genetic tests of the transmission of deficient bridge chromatids by pollen grains in which the vegetative nucleus contains an acentric fragment are in progress and mitotic divisions following fertilization will also be examined for presence of the fragment.

Ellen Dempsey
M. M. Rhoades

4. Evidence for an effect of the elongate gene on crossing over in chromosome 5.

The elongate gene has a number of effects when homozygous. These include, among others, the production of unreduced eggs in varying proportions with haploid eggs, pollen and ovule abortion, uncoiling of the

Table 1

Comparison of recombination in El el and el el sibs: family 713

	El el plants				el el plants			
Used as:	No. of progeny	% Recombination			No. of progeny	% Recombination		
		A-Bt	Bt-Pr	Total		A-Bt	Bt-Pr	Total
♀	458	3.5	15.7	19.2	336	10.1	30.1	40.2
	459	4.8	14.7	19.5	137	13.1	27.1	40.2
	522	1.3	18.5	19.8	114	10.5	30.6	41.1
	488	2.7	19.8	22.5	279	13.3	32.2	45.5
	339	7.7	20.5	28.2	202	8.4	37.9	46.3
	439	6.4	22.5	28.9	207	7.7	40.3	48.0*
	464	5.0	25.4	30.4	100	11.0	37.8	48.8
	422	6.2	24.8	31.0				
	546	3.3	30.6	33.9				
	481	6.7	32.8	39.5				
	427	5.4	35.5	40.9				
Wt. mean		4.6	23.8	28.4		10.5	33.6	44.1
♂	288	4.2	22.3	26.5	290	10.7	28.2	38.9
	396	7.1	23.4	30.5	387	14.7	31.9	46.6
	418	5.5	27.4	32.9	328	13.7	33.8	47.5
	344	3.8	30.7	34.5	364	20.6	29.7	50.3
	240	2.5	32.4	34.9	328	16.8	34.2	51.0
	341	5.0	31.4	36.4	326	15.3	37.1	52.4
	250	6.8	33.6	40.4	418	17.9	36.1	54.0
Wt. mean		5.1	28.4	33.5		15.9	33.1	49.0

*Combined data of 3 ears.

chromonemata at both meiotic anaphases and telophases, sporadic neocentromere formation at M II and occasional misdivision of the centromere at M II (Rhoades & Dempsey, Genetics 54:505-522, 1966). That this mutant may also influence crossing over is indicated by the following experiments.

Plants of two families which were of the genotype $\underline{A}_2$ $\underline{Bt}_1$ $\underline{pr}$/ $\underline{a}_2$ $\underline{bt}_1$ $\underline{Pr}$ and segregating for $\underline{El}$ $\underline{el}$ and $\underline{el}$ $\underline{el}$ were backcrossed as males and as females to $\underline{a}_2$ $\underline{bt}_1$ $\underline{pr}$ testers. The elongate plants were identified on the basis of pollen abortion and the presence of both plump and shriveled kernels on the ears. Where these plants were used as females, the recombination values were derived from the plump kernels, i.e. those which had developed from haploid eggs. All recombination percentages for the $\underline{Bt}_1$-$\underline{Pr}$ region were calculated from the $\underline{A}_2$ classes only, since $\underline{a}_2$ kernels lack aleurone color and cannot be directly classified for $\underline{Pr}$ and $\underline{pr}$. The results are given in Tables 1 and 2.

It is clear that the recombination percentages for the elongate plants are higher than for their $\underline{El}$ $\underline{el}$ sibs and that the effect is particularly striking in the case of the $\underline{A}_2$-$\underline{Bt}_1$ region, where the increase is approximately two- to threefold.

Possible explanations of these differences in recombination are:

1. A factor linked to the elongate locus affects crossing over. If this is the case, the linkage is close because an examination of the $\underline{A}_2$-$\underline{Bt}_1$ recombination values for male flowers, which show the greatest differences, reveals that there is no overlap between the figures for $\underline{El}$ $\underline{el}$ and $\underline{el}$ $\underline{el}$ plants. With loose linkage, some overlap would be expected among the 30 plants tested, due to crossing over between the elongate locus and the site of the "crossover factor" in the $\underline{El}$ $\underline{el}$ parent of each of the two families which were backcrossed.

2. The elongate gene itself affects crossing over. Since elongate is known to affect the behavior and appearance of meiotic chromosomes, this would seem to be the more likely possibility.

In an experiment similar to those described above, $\underline{Sh}_1$, $\underline{Bz}_1$, and $\underline{Wx}$, which are located distally on the short arm of chromosome 9, were used as markers. Progeny sizes were as follows:

Table 2

Comparison of recombination in El el and el el sibs: family 717

Used as:	El el plants				el el plants			
	No. of progeny	% Recombination			No. of progeny	% Recombination		
		A-Bt	Bt-Pr	Total		A-Bt	Bt-Pr	Total
♀	542	4.2	20.9	25.1	157	7.0	18.7	25.7
	472	3.6	22.0	25.6	129	5.4	29.7	35.1
	334	4.2	21.4	25.6	147	4.8	36.0	40.8
	428	3.3	22.3	25.6	165	8.5	33.8	42.3*
	353	2.8	25.4	28.2	134	10.4	32.8	43.2
	483	4.8	24.3	29.1	143	10.5	37.9	48.4
	456	4.2	27.6	31.8				
	464	4.3	27.6	31.9				
	323	4.6	30.4	35.0				
Wt. mean		4.0	24.6	28.6		7.8	31.4	39.2
♂	299	7.4	15.8	23.2	319	11.3	27.7	39.0
	274	4.0	20.8	24.8	208	12.5	27.9	40.4
	437	3.2	24.6	27.8	337	13.6	33.8	47.4
	248	7.3	22.8	30.1	396	14.4	38.6	53.0
	457	4.2	26.0	30.2	318	13.2	40.8	54.0
	326	7.4	24.7	32.1	429	15.4	40.3	55.7
	270	6.3	26.5	32.8	362	17.1	39.8	56.9
	435	8.3	26.4	34.7	234	20.9	39.8	60.7
Wt. mean		5.9	23.8	29.7		14.8	36.6	51.4

*Combined data of 4 ears.

El el ♀ ♀ = 4968	El el ♂ ♂ = 3914
el el ♀ ♀ = 2165	el el ♂ ♂ = 3472

Little or no differences in recombination between elongate plants and their normal sibs were detected. This is in agreement with the finding of Rhoades & Dempsey that crossing over between Sh_1 and Wx and also between the distal Lg_2 and A_1 markers of chromosome 3 in elongate plants corresponds well with the standard values.

While the lack of an effect on recombination in these two regions could be due to differences in genetic background or to the absence of a "crossover factor" linked to el, it is suggested that the effect of elongate, or the linked factor as the case may be, on crossing over differs in different portions of the genome. The A_2-Pr region spans the centromere of chromosome 5 with Bt_1 marking the centromere, and is known to be very sensitive to certain other genetic factors which influence crossing over. The fact that the differences in recombination are greater in the shorter, and therefore more proximal, A_2-Bt_1 region than in the longer Bt_1-Pr region could be an indication that the effect is more pronounced closer to the centromere.

A further point of interest which may be noted here is the variable way in which recombination in chromosome 5 is influenced by sex. Rhoades (J. Am. Soc. Agron. 33:603-615, 1941) reported that crossing over in the A_2-Pr region is higher in male than in female sporocytes. Most structurally normal stocks tested have shown this sex difference, which may vary from large to small, while in a few cases (Phillips, Genetics 61:117-127, 1969) it has not been found. Examples of extremes in the range of variation are illustrated in Table 2, where the male and female values for El el plants are very similar, and in Table 1 on page 67 of this Newsletter, where recombination is very much higher in male than in female flowers of both the normal and As as classes.

Paul M. Nel

5. A genetic factor which affects crossing over in chromosome 5.

In an effort to determine whether the mutant asynaptic affects crossing over when in heterozygous condition, F_1 plants of the cross $\underline{A_2}\ \underline{Bt_1}\ \underline{Pr}/\underline{A_2}\ \underline{Bt_1}\ \underline{Pr}$; $\underline{As}/\underline{as}$ ♀ x $\underline{a_2}\ \underline{bt_1}\ \underline{pr}/\underline{a_2}\ \underline{bt_1}\ \underline{pr}$; $\underline{As}/\underline{As}$ ♂ were backcrossed as males and as females to $\underline{a_2}\ \underline{bt_1}\ \underline{pr}$ testers. Recombination values for the $\underline{A_2}$-$\underline{Bt_1}$ and $\underline{Bt_1}$-$\underline{Pr}$ regions were calculated, those for the latter region being obtained by the method described in the above note on the action of elongate.

To ascertain their genotypes with respect to As, the F_1 plants were also crossed as males to asynaptic testers which were either As as or as as. Progenies of these crosses were planted in the field and scored for the presence of as as plants by examining the tassels and the open-pollinated ears. If a progeny contained several asynaptic plants, its male parent was classified as being As as; where all the plants had a normal, As phenotype, the male parent was considered to be As As, provided the progeny was of a sufficient size. Most of the progenies were large enough so that the probability of error in classifying an F_1 plant as As As is less than 0.1% and in none of the cases reported in Table 1 is the level of probability greater than 0.5%.

The two sets of data on each line of the table refer to the same plant, used as a female on the left and as a male on the right hand side. The mean recombination values for As as plants are lower than those for their As As sibs and the decrease percentage-wise is more striking in the females than in the males. The distribution pattern of the female total recombination percentages (column no. 5) also appears to be unimodal for the As As group and bimodal for the As as group. However, these distributions could be distorted and may not accurately reflect the corresponding characteristics of the populations due to the small sample sizes of 11 and 18 plants, respectively. Additional data, obtained by planting more F_1 seed from the original ear and repeating the backcrosses on a larger scale, should give a clearer picture of the two distributions.

The lower recombination in the As as plants could be due to:

1. A factor segregating independently of as.

Table 1

Comparison of recombination in *As As* and *As as* sibs.

Genotype	F_1 plants used as ♀♀				F_1 plants used as ♂♂			
	No. of progeny	% Recombination			No. of progeny	% Recombination		
		A-Bt	Bt-Pr	Total		A-Bt	Bt-Pr	Total
As As	423	3.5	13.9	17.4	561	8.9	28.4	37.3
	435	3.9	14.6	18.5	310	26.5	30.5	57.0
	383	4.7	16.2	20.9	263	18.3	44.1	62.4
	374	5.9	18.6	24.5	522	19.3	27.6	46.9
	430	6.0	19.2	25.2	376	13.6	40.6	54.2
	432	8.1	18.6	26.7	598	20.9	36.4	57.3
	462	5.8	21.2	27.0	541	11.1	33.4	44.5
	402	9.2	19.4	28.6	605	25.5	40.2	65.7
	444	4.7	24.4	29.1	758	14.2	26.7	40.9
	476	5.5	24.0	29.5	668	19.8	35.3	55.1
	391	6.4	27.6	34.0	334	18.3	32.3	50.6
Wt. mean		5.8	19.9	25.7		17.6	33.6	51.2
As as	198	1.5	4.7	6.2	568	11.4	27.9	39.3
	350	1.4	8.0	9.4	212	8.5	26.5	35.0
	237	0.8	9.7	10.5	430	5.8	18.3	24.1
	252	0.4	10.5	10.9	622	11.6	28.8	40.4
	460	1.1	10.0	11.1	529	6.4	17.1	23.5
	415	2.4	8.9	11.3	732	15.4	28.9	44.3
	343	1.2	10.3	11.5	449	9.8	33.0	42.8
	463	1.7	10.4	12.1	356	12.9	29.9	42.8
	330	2.1	10.2	12.3	464	11.9	19.5	31.4
	354	2.8	12.0	14.8	543	15.7	31.1	46.8
	507	2.0	13.2	15.2	635	8.7	26.6	35.3
	336	1.2	14.3	15.5	550	20.7	31.6	52.3
	389	3.6	16.7	20.3	289	9.7	25.3	35.0
	484	2.7	18.6	21.3	246	15.0	36.9	51.9
	230	4.8	16.8	21.6	192	10.4	17.1	27.5
	459	3.3	19.6	22.9	640	14.8	29.7	44.5
	446	2.7	20.7	23.4	507	19.3	31.4	50.7
	311	4.8	20.6	25.4	470	16.0	28.2	44.2
					550	20.7	31.6	52.3
Wt. mean		2.3	13.4	15.7		12.9	27.6	40.5

2. A factor linked to *as*.

3. The asynaptic gene itself.

Recombination between *as* and a linked or independently segregating factor in the original *As as* parent would be expected to cause some of the A_2-Bt_1-*Pr* values in the *As As* class to be low and some of those in the *As as* class to be high. On the female side, where the differences in recombination are most pronounced, the six to eight *As as* plants with the highest total values might be interpreted as being recombinants. In the *As As* group, however, there is no clear indication of any of the reciprocal recombinants being present. The lowest two values are well above the mean of the would-be nonrecombinant class in the *As as* group. There is even less evidence of a reciprocal recombinant class when considering the following values for six plants which have a high probability of being *As As* but were not included in the table because the chances of error in classifying them as *As As* were slightly higher than the 0.5% limit used: 19.3, 23.0, 24.7, 24.8, 27.5 and 29.9.

Taken together, the available data thus give a strong indication that the factor causing reduced recombination in the A_2-Bt_1-*Pr* region of chromosome 5 is either linked to *as* on chromosome 1 or that it is *as* itself.

There are two additional observations in respect of the *As as* plants used as females that are at present still unexplained. In the first place, the range in progeny sizes is greater than that of their *As As* sibs and the mean number of kernels is lower, viz. 365 and 423 respectively. Secondly, there is an excess of the A_2 Bt_1 progeny class over the a_2 bt_1 class and this can be traced to about half of the first 12 *As as* plants listed in the table.

A similar experiment in which chromosome 3 was marked by Gl_6, Lg_2, and A_1 revealed little or no difference in recombination between *As As* and *As as* classes.

Paul M. Nel

6. Further studies of the effect on crossing over of the gene ameiotic.

In a preliminary test of crossing over in chromosome 2 and in chromosome 9, no difference was found between microsporocytes from Am Am and Am am plants (MNL 43:61-63, 1969). However, in view of the variable effect of heterozygous asynaptic on crossing over in different chromosomes (see page 66, this Newsletter), a more exhaustive study of the ameiotic material was carried out. Comparisons of Am Am chromosome 3 heterozygotes with Am am heterozygotes, Table 1, show no differences in crossing over. This was true for the two genetic regions studied in both the MMC's and the PMC's. The chromosome 5 data (Table 2) are more difficult to interpret. When chromosome 5 heterozygotes of Am Am constitution were compared with Am am heterozygotes, crossing over for the A_2-Bt_1 and Bt_1-Pr regions was found to be higher in MMC's of the Am am plants than in those of the Am Am. Within environments, the male gametes showed no difference between Am Am and Am am. However, crossover values from PMC's tested in both Indiana and Florida plantings were significantly higher than values from MMC's. A difference in crossing over in male versus female gametes has been well established for chromosome 5.

In the Florida backcrosses the frequencies of both the a_2 and bt_1 classes were significantly higher than the expected 50%. The male parents in the Florida tests differed slightly in genetic background from the Indiana male parents, and the chromosome 5 tester used as female parent in the Florida backcrosses was not the same as the stock used in Indiana backcrosses. Consequently, the off ratio could be attributed to a gametophyte factor affecting interaction with styles of different constitutions. Crossing over for the A_2-Bt_1 and Bt_1-Pr regions in PMC's was statistically different in plants backcrossed in Indiana and Florida. Higher crossover values from Florida grown plants may be due to environmental differences.

Chromosome 9 heterozygotes of Am Am and Am am constitution showed no differences in crossing over for the Sh-Bz region in either the male or female gametes (Table 3). Recombination in the Bz-Wx region was slightly higher in Am am female parents than in the Am Am sibs. The

Table 1

Recombination in chromosome 3 heterozygotes.

	Genotype of Male Parent $\frac{Gl\ Lg\ A_1}{gl\ lg\ a_1}$		Genotype of Female Parent $\frac{Gl\ Lg\ A_1}{gl\ lg\ a_1}$	
	Am/Am	Am/am	Am/Am	Am/am
Total number of kernels	2617	3227	3100	3720
Gl Lg A	580	678	623	756
gl lg a	545	653	638	789
gl Lg A	356	472	449	563
Gl lg a	378	441	461	519
gl lg A	316	379	358	411
Gl Lg a	300	393	383	433
Gl lg A	68	101	90	118
gl Lg a	74	110	98	131
% Recombination				
Lg - A	29.0	30.5	30.0	29.4
Gl - Lg	33.5	34.8	35.4	35.8

Table 2

Recombination in chromosome 5 heterozygotes.

	Genotype of Male Parent $\frac{A_2\ Bt_1\ pr}{a_2\ bt_1\ Pr}$				Genotype of Female Parent $\frac{A_2\ Bt_1\ pr}{a_2\ bt_1\ Pr}$	
	Am/Am*	Am/am*	Am/Am**	Am/am**	Am/Am**	Am/am**
Total number of kernels	5308	4845	1924	1788	3836	6136
A Bt Pr	749	684	261	250	442	743
A Bt pr	1180	1019	586	543	1402	2033
A bt Pr	199	194	88	75	110	225
A bt pr	160	172	28	26	28	47
a Bt	389	355	101	97	128	281
a bt	2631	2403	860	797	1726	2807
% Recombination						
A - Bt	14.1	14.9	11.3	11.1	6.9	9.0+
Bt - Pr	34.3	35.3	30.0	30.9	24.4	25.8+

*Florida 1969

**Indiana 1968

+Significant at the 5% level

Table 3

Recombination in chromosome 9 heterozygotes.

	Genotype of Male Parent $\frac{\text{Yg Sh Bz Wx}}{\text{yg sh bz wx}}$		Genotype of Female Parent $\frac{\text{Yg Sh Bz Wx}}{\text{yg sh bz wx}}$	
	Am/Am	Am/am	Am/Am	Am/am
Total number of kernels	3745	4233	5305	4992
Yg Sh Bz Wx	1088	1211	1566	1453
yg sh bz wx	1052	1158	1559	1392
Yg Sh Bz wx	315	356	409	454
yg sh bz Wx	347	372	405	462
Yg Sh bz wx	45	40	32	34
yg sh Bz Wx	40	38	46	52
Yg sh bz wx	372	475	579	525
yg Sh Bz Wx	397	485	621	514
Yg sh Bz Wx	4	1	19	15
yg Sh bz wx	10	14	11	9
Yg sh bz Wx	29	45	22	43
yg Sh Bz wx	35	29	31	33
Yg Sh bz Wx	6	5	2	2
yg sh Bz wx	1	3	2	2
Yg sh Bz wx	0	0	0	2
yg Sh bz Wx	1	1	1	0
% Recombination				
Yg - Sh	22.7	24.8	24.2	22.9
Sh - Bz	2.9	2.4	2.1	2.3
Bz - Wx	19.6	19.2	16.4	20.0

four values for the Yg-Sh region fell into two statistically distinct classes, 22.7% and 22.9% versus 24.2% and 24.8%. While significant differences between Am Am and Am am plants occurred in both types of backcross, the Am am genotype gave the higher Yg-Sh recombination when male gametes were tested, and the Am Am was higher in tests of female gametes.

A difference in the effect of Am Am and Am am on crossing over in chromosomes 3, 5, and 9 was not critically established. With the chromosome 3 markers, Gl, Lg, and A_1, no difference in crossing over attributable to heterozygosity for am was apparent in male or female gametes. With the chromosome 5 markers, recombination in Am am megasporocytes was higher for both regions studied than in corresponding Am Am cells. Comparisons of Am Am and Am am microsporocytes, however, showed no difference in the A_2-Bt_1 or Bt_1-Pr recombination. The absence of an effect of the Am am genotype on crossing over in chromosome 5 was observed in two different environments and with different genetic backgrounds. The Yg-Sh region of chromosome 9 showed a decrease in crossing over in the megasporocytes in the presence of Am am, while a slight increase occurred in the microsporocytes.

Reid G. Palmer

7. Location of ameiotic on chromosome 5.

Preliminary linkage data suggested that the Am locus was in chromosome 5, but its placement in the linear map was unknown. In order to determine the precise location of am on chromosome 5, crosses were made between stocks segregating am and stocks containing the recessive markers a_2, bt_1, and pr. Since it was impossible to backcross to am am plants due to their almost complete sterility, linkage data were obtained from analyses of F_2 progenies. The amount of recombination between am-A_2, am-Bt_1 and am-Pr was then calculated by means of the tables of Immer (Genetics 15:81-98, 1930). The first linkage tests involved heterozygotes where am was in repulsion phase with chromosome 5 markers (Table 1). Since F_2 data in repulsion can yield a relatively imprecise estimate of linkage intensity, the 1969 tests were based on heterozygotes in coupling.

Table 1

Linkage of Am with chromosome 5 markers A_2, Bt_1, and Pr based on F_2 data.

Constitution of Self pollinated plant	Linkage Phase	Phenotypic Classes				Number of Plants Classified	% Recombination
		Am Pr	am Pr	Am pr	am pr		
$\frac{\text{Am pr}}{\text{am Pr}}$	repulsion	463	171	136	55	825	51
		Am Bt	am Bt	Am bt	am bt		
$\frac{\text{Am bt}_1}{\text{am Bt}_1}$	repulsion	437	146	102	21	706	43
		Am A	am A	Am a	am a		
$\frac{\text{Am a}_2}{\text{am A}_2}$	repulsion	1290	561	518	81	2450	35.5
		Am A	am A	Am a	am a		
$\frac{\text{Am A}_2}{\text{am a}_2}$	coupling	3438	753	731	619	5541	32.5

The ameiotic gene on chromosome 5 was shown to be more closely linked with $\underline{A}_2$ than with $\underline{Bt}_1$. Ameiotic segregated independently from Pr, which is in the long arm of chromosome 5. Good agreement between F_2 coupling and F_2 repulsion data indicated that 32-36% recombination occurred between Am and $\underline{A}_2$.

Reid G. Palmer

8. Cytological studies with ameiotic and normal sibs.

Cells undergoing mitotic divisions were observed by Sinha (1960, Ph.D. thesis, Indiana Univ.) in ameiotic anthers. He concluded that a mitotic division replaced meiosis in ameiotic plants. Recently, we have made a cytological comparison of ameiotic and normal sibs, in which anther length was chosen as the most reliable criterion in identification of stages. The nuclear divisions in ameiotic, which previously were considered to be a substitute for meiosis, are now believed to be the last premeiotic mitosis. Thus, ameiotic plants do not undergo a normal or a modified meiosis. Anthers from 1.2 - 2.1 mm. in length, collected from either ameiotic or normal plants, contain sporogenous cells in the last premeiotic mitosis (Table 1). The chromosomes in mitotic prophase are characterized by a marked elongation of the chromonemata, as compared to the chromosomes of somatic cells in prophase. It is not certain whether there is a particular orientation of the chromosomes at this stage as has been suggested. In the anaphase cells from both ameiotic and normal plants which we have examined there was no indication of premeiotic pairing. After telophase in normal plants there is a long interphase before the first meiotic stage, leptonema, is evident. However, in ameiotic plants after telophase, the interphase condition persists and the diameter of the nucleus and cell remains the same even though anther elongation continues. The frequency of sporogenous cells found in prophase-telophase was low in normal plants, while a higher (2-3 fold) frequency was found in ameiotic plants. However, larger populations of premeiotic nuclei are needed to confirm this observation. Further studies are in progress.

Table 1

Anther length and the cytological stage in normal and ameiotic sib plants.

Anther length (mm.)	Normal	Ameiotic
0.8 - 0.9	interphase	interphase
1.0 - 1.1	interphase	interphase
1.2 - 1.3	interphase, mitosis	interphase mitosis
1.4 - 1.5	interphase, mitosis	interphase, mitosis
1.6 - 1.7	interphase, mitosis	interphase, mitosis
1.8 - 1.9	interphase, mitosis	interphase, mitosis
2.0 - 2.1	interphase, mitosis, leptonema	interphase mitosis
2.2 - 2.3	interphase, leptonema	interphase
2.4 - 2.5	interphase, leptonema, zygonema	
2.6 - 2.7	leptonema, zygonema	
2.8 - 2.9	leptonema, zygonema, pachynema	
3.0 - 3.1	zygonema, pachynema, metaphase I	
3.2 - 3.3	zygonema, pachynema, metaphase I	
3.4 - 3.5	pachynema, M I, diplonema, diakinesis, A I	
3.6 - 3.7	M II, A II, quartets	
3.8 - 3.9	A II, quartets	
4.0 - 4.1	quartets	interphase

9. Interallelic complementation at the Sh_1 locus.

EMS induced mutations at the Sh_1 locus were reported last year (MNL 42:53). Six of the 16 mutants are CRM^+ by immunological tests and the presence of a Sh_1 protein band can be demonstrated electrophoretically. Two of these mutants, designated sh_1^F (fast) and sh_1^S (slow), show an altered rate of migration of the protein in starch gel electrophoresis. The migration rate of the Sh_1 protein in the other four CRM^+ mutants, designated sh_1^A, sh_1^B, sh_1^C and sh_1^D, is not altered.

F_1 hybrids were made between all the mutants to test for interallelic complementation at this locus. Positive results, as indicated by the occurrence of plump nonshrunken seeds in the F_1 hybrid, have been obtained. Complementation is observed in heterozygotes where the sh_1^S allele is combined with sh_1^F, sh_1^A, sh_1^B, sh_1^C, or sh_1^D. No other combination shows complementation. These alleles give rise to the typical sh_1 phenotype when homozygous or heterozygous with the standard sh_1 allele. The complementation at the phenotypic level is complete since the complemented phenotype of the hybrid is indistinguishable from the Sh_1 phenotype. The starch gel electrophoretic analysis of the complementing hybrid always reveals the two parental protein bands and no hybrid band is seen.

The complemented hybrid on selfing segregates in a 1:1 ratio for plump and shrunken seeds as expected and when crossed to the standard sh_1 yields seeds of only mutant phenotype. The individual endosperms of a selfed ear of a sh_1^S/sh_1^F hybrid, when subjected to starch gel electrophoresis, gave a segregation ratio of 1F:2FS:1S and those produced in the testcross to sh_1 exhibited 1F:1S (Table 1).

Protein subunit interaction has been shown to be the molecular basis of interallelic complementation in fungi and bacteria. A similar mechanism probably occurs in this system. No hybrid band is present in the complementing heterozygote although such a band could easily be detected if present. However, a hybrid protein may actually exist *in vivo* and its absence after electrophoresis may be an artifact of the electrophoretic technique, as is the case with the hybrid hemoglobins.

Prem S. Chourey

Table 1

Type of Cross	Segregation in F_2 and Testcross Generation						
	Seed Phenotype			Electrophoretic Pattern of 20 Day Old Endosperm			
	Plump	Shrunken	X^2	F	S	FS	Total
sh_1^S/sh_1^F ⊗	1275	1520	1.65	19	24	39	82
sh_1^S/sh_1^F x sh_1/sh_1	0	1200	-	34	38	0	72

(See article 9 by Prem S. Chourey on preceding page.)

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1. Intra-genic recombination at various positions in the maize genome.

Utilizing Nelson's results and methodology (Genetics 47:737; Genetics 60:507) on the mapping of the wx locus, an investigation was initiated with this locus to examine the effect of changes in the position of this locus on intragenic recombination by moving this locus to various locations in the maize genome. The general plan includes the crossing of four of the wx alleles (C,90,H21 and B and hereafter referred to by numbers without the wx) to translocation stocks, the isolation of the desired crossover, followed by the intercrossing of the desired wx-translocation strains with each other in order to secure heteroallelic combinations in homozygous translocation lines with which to test for the frequency of wx recombinants. Fourteen translocations are utilized in this study; seven involve breaks proximal to wx so as to move the locus to various positions away from the centromere and seven, involving the lengthening of the chromosome, are distal to wx. Four of the forty-two possible combinations in the proximal series are reported here. In the following table the results from the analysis of two different years of two of the combinations as well as controls (heteroalleles on standard chromosomes) are given:

	Approx. distance of wx to centromere (u)	Crosses	Wx frequency x10^{-5}	Year Collected
Standard chromosomes:	7.7	C x B	63.19	1969
		C x 90	69.60	"
		C x H21	57.21	"
		B x 90	1.33	"
		B x H21	94.20	"
		90 x H21	37.22	"
Translocation chromosomes:	26.7	T 5-9a; B/H21	19.75	1967
		" " ; " "	22.71	1968
	24.1	T 5-9 4871; B/H21	35.87	1967
		" " ; " "	45.73	1968
		" " ; C/B	30.06	"
		" " ; C/H21	30.03	"

Considering first the Wx recombinants observed among the standard chromosomes, it is evident that the map derived from these data is roughly equivalent with Nelson's map, i.e., H21 is distal to C, 90 is proximal to C, while B and 90 do not recombine. There is an inconsistency in these data in that the 90/H21 heteroallele yields a value of 37.22×10^{-5} Wx recombinants, which is lower than expected in view of the relation between B and 90. B and 90 appear very close together and give equivalent values with C.

In the "relocated" wx series, the recombination values are reduced. The wx intragenic recombination value with T 5-9 4871 is less than one-half of that of the standard chromosomes, and in T 5-9a, one-quarter. Apparently, there is also an effect of season as is obvious in a comparison of the results from two different years (1967 and 1968). The data show that the shift of recombination values over seasons is unidirectional for both of the translocations in the consecutive years.

Ming-Hung Yu
Peter A. Peterson

2. The synchrony of the mutation event.

One of the most obvious features of unstable loci in maize is the prevalence of states that are distinguishable in the time and frequency of the mutation event, i.e., phenotypically observable as size and distribution of colored spots on a colorless background. In a screening test for the origin of unstable a_2 alleles (a_2^m) from A_2, one unstable allele was found in which the mutation event occurred very late in the ontogeny of the corn kernel. It has been identified as $a_2^{m(4\ 1629)}$ and in this report will be referred to as a_2^m.

In order to measure the size and distribution of the mutation event (colored spots on a colorless background), counts were made of the various sized spots in designated quadrants at the crown of the kernel. Under a dissecting microscope, colored aleurone cells can be clearly and individually distinguished and the mutation events that cover one, two, three, four, etc. cells can be separated into classes. The kernels

examined were derived from testcross progeny with the $\underline{a}_2^m$ allele in the female parent.

The lines were divided (for other reasons) into two groups and the distribution (in %) of sizes is given:

	A	B
1 cell	92.00	93.50
2 cells	5.40	3.85
3 "	1.25	.12
4 "	1.05	.10
5 and more	.30	2.43

It appears from the examination of the above abbreviated table that the mutation event takes place most of the time following the last cell division, since most are of the one cell type. This supports the allegation of the synchrony of the mutation event both within the kernel and between kernels on the same ear. The similarity in values even between different crosses (i.e., in a comparison of sib lines) shows a striking uniformity here also. At this time, it is hypothesized that the particular physiology associated with the terminal division of the aleurone triggers the event.

This particular $\underline{a}_2^m$ cannot at this time be ascribed to the En system since it is unable to give positive results in the standard test for En. This may be a consequence of the lateness of the event for which the standard test for En is not sensitive enough.

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1. Phenotypic and genetic analysis of a new endosperm mutant y_9.

In 1961 Dr. Kermicle gave me a new pale yellow endosperm mutant. The temporary symbol $w_{\text{Kermicle \#3}}$ was given to it and this symbol has

been used in past News Letters. It is now proposed that the permanent symbol y_9 be substituted for the temporary one.

This mutant was first noticed in a culture of W23 grown at the University of Wisconsin. It is characterized by a pale yellow endosperm which can vary from an off-white to lemon yellow depending upon the genetic background. I have never observed the pure white seeds such as y_1 gives in certain backgrounds. The mutant has a tendency to be viviparous. However, unlike most other white endosperm viviparous mutants, the seedlings of y_9 are not albino. Seedlings are usually green. Occasional ones are found that will have pale green leaf tips and infrequently completely pale green seedlings are observed. Seedlings grown at higher temperatures (35°C) tend to have more pale green tissue but the temperature effect is not consistent. Mutant seedlings will grow into mature plants which in the original inbred background were later and weaker than normal siblings and tended to have a zebra phenotype. As the gene has been transferred into more vigorous stocks, mutant plants closely approximating normals have been observed. Last summer the mutant plants were very vigorous and could not readily be distinguished from normals. No zebra phenotype was observed. The performance of mutant plants is probably dependent upon genetic background and environmental factors.

Analysis of chlorophyll and carotene in seedlings of this mutant reveals that they occur in near normal concentrations. However, unlike normals, y_9 seedlings accumulate carotene precursors, phytoene, phytofluene and zeta-carotene. In this regard y_9 is similar to all known white endosperm, viviparous-albino mutants which accumulate one or more precursors of carotene.

Linkage tests with a series of chromosome nine translocations placed this gene on chromosome ten. With translocation T9-10b (9S.13, 10S.40), no crossovers were observed in 568 plants tested. The results of linkage tests with $\underline{r}$, $\underline{g_1}$ and $\underline{bf_2}$ are given in Table 1.

Table 1

Linkage test of y_9 with r, g_1 and bf_2.

Region tested	Testcross progeny				Total	#C.O.	%C.O.
y_9 - r	+ R	y_9 r	y_9 R	+ r			
	137	143	37	37	354	74	20.9
y_9 - g_1	+ g_1	y_9 +	y_9 g_1	+ +			
	120	107	22	23	272	45	16.5
y_9 - bf_2	+ bf_2	y_9 +	y_9 bf_2	+ +			
	133	130	4	2	269	6	2.2

The latest linkage map of chromosome 10 indicates 14 crossover units between g_1 and r. Thus, on the basis of the linkage data in Table 1, y_9 is 16.5 units to the left of g_1. This would place it in the short arm of chromosome 10, which is in agreement with very close linkage between T9-10b (breakpoint 10S.40) and y_9. Because bf_2 has not been mapped on chromosome 10, it cannot be placed with respect to y_9. Since there are only 2.2 crossover units between y_9 and bf_2, the latter gene is also probably in the short arm of chromosome 10. Three point tests involving y_9, bf_2 and g_1 have been initiated. Tests with TB-10a (10L.35) are in agreement with the above placement of y_9. This translocation does not uncover y_9. However, when deficient plants carrying y_9 were crossed to homozygous y_9 plants, 20.5% crossing over was observed between the TB breakpoint and y_9 (see following report for details). The breakpoint of TB-10a is known to be proximal to r. How far proximal is not known, but if it is close to r the value of 20.5% crossing over is in close agreement with the 20.9% crossing over observed between r and y_9.

Donald S. Robertson

2. Crossing over in deficient TB-10a plants: Effect of male and female origin on the recovery of crossover chromatids.

As mentioned in the previous report, TB-10a was crossed to plants heterozygous for $\underline{y}_9$. Since the F_1's did not segregate for pale yellow seeds, it was assumed that $\underline{y}_9$ was proximal to the TB breakpoint in chromosome 10 (10L.35). To find the distance of $\underline{y}_9$ from the breakpoint, deficient plants were crossed to those homozygous for $\underline{y}_9$. The TB-10a plants were homozygous for the $\underline{R}_2^{scm}$ allele of $\underline{r}$, which gives a self colored endosperm in a single dose and also produces color in the scutellum. Therefore, purple seeds with colorless scutella were selected from the cross with TB-10a. These seeds had deficient embryos and since the plants pollinated were heterozygous, half of them carried $\underline{y}_9$ on the normal chromosome 10. Because only the normal chromosome 10 will be transmitted from deficient plants, most of the progeny seeds should be $\underline{y}_9$ when crossed with this stock, if $\underline{y}_9$ is close to the breakpoint. Crossing over between the breakpoint and the $\underline{y}_9$ locus will result in gametes carrying the normal allele. Thus, the percentage of yellow seeds in the cross between deficient and $\underline{y}_9$ plants will indicate the crossing over that has taken place between the TB-10a breakpoint and $\underline{y}_9$.

Table 1 gives the crossing over when the deficient plants were used as females. The grand total crossing over was 15.2 $\pm$ 1.05%. For individual crosses the crossing over ranged from 5.7% to 18.3%. The value of 5.7% for plant 8005-6 seems unusually low. It is at least half the value for the next lowest figure (11.9%). The difference between the percentages for these two crosses is just barely not significant at the 5% level. However, the difference between the percentage of 8005-6 and those of the other two crosses involving 8005 plants is significant at the 5% level. It is possible that there is something special about plant 8005-6 that is responsible for its unusually low level of crossing over. Because of 8005-6's low value, calculations have been made with and without the data from this plant.

Table 1

Crossovers recovered when plants heterozygous for y_9 and deficient for B^{10} are crossed as females with homozygous y_9 plants.

Parent Plants	C.O. Seeds (yellow)	Non-C.O. Seeds (pale yellow)	Total	%C.O.
8005-6/9005-7	6	99	105	5.7
8005-7/9006-6	17	89	106	16.0
8005-9/9006-5	18	133	151	11.9
8005-10/9005-7	16	76	92	17.4
Total	57	397	454	12.6 ± 1.6
Total minus 8005-6	51	298	349	14.6 ± 1.9
8006-4/9007-5	42	236	278	15.1
8006-6/9006-6	38	178	216	17.6
8006-9/9006-6	22	98	120	18.3
8006-10/9006-6	18	82	100	18.0
Total	120	594	714	16.8 ± 1.4
Grand Total	177	991	1168	15.2 ± 1.05
Grand Total minus 8005-6	171	892	1063	16.1 ± 1.1
Total pollinated by 9005	22	175	197	11.2 ± 2.2
Total pollinated by 9005 minus 8005-6	16	76	92	17.4 ± 3.9
Total pollinated by 9006	113	580	693	16.3 ± 1.4
Total pollinated by 9007	42	236	278	15.1 ± 2.1

Table 2

Crossover recovered when plants heterozygous for y_9 and deficient for B^{10} are crossed as males with homozygous y_9 plants.

Parent Plants	C.O. Seeds (yellow)	Non-C.O. Seeds (pale yellow)	Total	%C.O.
9005-2/8005-10	103	294	397	25.9
9005-3/8005-10	73	285	358	25.6
9005-5/8005-9	86	225	311	27.7
Total	262	804	1066	24.6 ± 1.3
9006-1/8005-9	57	165	222	25.7
9006-3/8005-7	60	165	225	26.7
9006-7/8005-6	12	93	105	11.4
Total	129	423	552	23.4 ± 1.8
Total minus 8005-6	117	330	447	26.2 ± 2.1
9007-2/8005-8	65	250	315	20.6
9007-4/8006-6	56	227	283	19.8
9007-5/8006-10	63	283	346	18.2
9007-6/8006-9	58	159	217	26.7
Total	242	919	1161	20.8 ± 1.2
Grand Total	633	2146	2779	22.8 ± 0.8
Grand Total minus 8005-6	621	2053	2674	23.2 ± 0.8
Total pollinated by 8005	456	1477	1933	23.6 ± 1.0
Total pollinated by 8005 minus 8005-6	444	1384	1828	24.3 ± 1.0
Total pollinated by 8006	177	669	846	20.9 ± 1.4

Table 2 shows the crossover values for deficient plants used as males. The grand total crossing over is 22.8 ± 0.8%. For individuals the crossing over ranged from 11.4% to 27.7%. Again, the cross involving plant 8005-6 has the lowest value (11.4%). This is considerably lower than the next lowest value (18.2%). However, the difference between the percentages of these two crosses fall just short of being significant at the 5% level. The same is true of the difference between 8005-6 and the next highest crossover percentage (19.8%). However, the difference in percentage between 8005-6 and the next highest percentage (20.6%) is significant at the 5% level and the percentage of 8005-6 differs significantly from those of all other crosses at the 1% level. Thus, again there is evidence that plant 8005-6 has an unusually low level of crossing over and this is observed when it is crossed as a male or female.

Table 3 shows the total crossing over for both male and female transmission. The value is 20.5 ± .06% with the incorporation of data from plant 8005-6 and 21.2 ± 0.7 without.

Table 3

Total crossing over obtained by combining male and female transmission.

Parent Plants	C.O. Seeds (yellow)	Non-C.O. Seeds (pale yellow)	Total	%C.O.
Total crossed as ♀ (Table 1) and crossed as ♂ (Table 2)	810	3137	3947	20.5 ± 0.6
Total crossed as ♀ (Table 1) and crossed as ♂ (Table 2) minus 8005-6	792	2945	3737	21.2 ± 0.7

Table 4 lists comparisons between male and female transmission of crossovers. The grand percentages for male and female transmission differ significantly with and without the inclusion of 8005-6. Thus, there appears to be significantly more crossing over when F_1 plants are used as

Table 4

Comparisons of differences between male and female transmission of crossovers.

Classes Compared	% C.O. ♂	% C.O. ♀	% Difference
Grand Totals	22.8 ± .8	15.2 ± 1.05	7.6**
Grand Totals minus 8005-6	23.2 ± .8	16.1 ± 1.1	7.1**
Total: F_1's pollinated by 9005 *vs.* 9005 pollinated by F_1	24.6 ± 1.3	11.2 ± 2.2	13.4**
Total: F_1's pollinated by 9005 (minus 8005-6) *vs.* 9005 pollinated by F_1	24.6 ± 1.3	17.4 ± 3.9	7.2
Total: 8005 F_1's pollinated by homozygous $\bar{y}_9$ *vs.* homozygous y_9 pollinated by 8005 F_1's	23.6 ± 1.0	12.6 ± 1.6	11.0**
Total: 8005 F_1's (minus 8005-6) pollinated by homozygous $\bar{y}_9$ *vs.* homozygous y_9 pollinated by 8005 (minus 8005-6) F_1's	24.3 ± 1.0	14.6 ± 1.9	9.7**
Total: F_1's pollinated by 9006 *vs.* 9006 pollinated by F_1	23.4 ± 1.8	16.3 ± 1.4	7.1**
Total: F_1's pollinated by 9006 *vs.* 9006 (minus 8005-6) pollinated by F_1	26.2 ± 2.1	16.3 ± 1.4	9.9**
Total: 8006 F_1's pollinated by homozygous $\bar{y}_9$ *vs* homozygous y_9 pollinated by 8006	20.9 ± 1.4	16.8 ± 1.4	4.1*
Total: F_1 pollinated by 9007 *vs.* 9007 pollinated by F_1	20.8 ± 1.2	15.1 ± 2.1	5.7*

*Significant at 5% level of probability.

**Significant at 1% level of probability.

males than when crossed as females. Such differences in crossing over have been found for other regions of the genome with and without the presence of abberrations (see Phillips, R. L., Genetics 61:117-127, 1969, for such data and review of earlier observations). Like most, but not all, previous studies there is more crossing over when heterozygous plants are crossed as males. Also in Table 4 reciprocal crosses are compared for individual F_1 and homozygous y_9 families. In all cases except one, significant differences are found with the male transmission being the highest. The one exception was the reciprocal cross involving the homozygous y_9 family 9005 after data from 8005-6 had been eliminated. When this was done, only one F_1 plant remained with a rather low number of seeds (92) and a high standard error (3.9%) which probably contributed to the lack of a significant difference.

In Table 5 comparisons are made between the percentages for the F_1 families and between the homozygous y_9 families. For the F_1 families a significant difference at the 5% level was observed between 8005 and 8006 but this was probably due to the incorporation of the unusually low value of 8005-6. When the data for this plant are removed, there is no longer a significant difference. For the homozygous y_9 families two significant differences are observed at the 5% level. Both involve family 9007, which had a lower crossover percentage than 9005 and 9006. This might have been just a chance fluctuation since one of the four crosses involving this family had a crossover percentage that was as high as those from families 9005 and 9006.

Table 5

Comparison between families of F_1's and families of homozygous y_9

Families 1	2	%C.O. Family 1	%C.O. Family 2	% Difference
F_1's:				
8005	8006	12.6 ± 1.6	16.8 ± 1.4	4.2*
8005 minus 8005-6	8006	14.6 ± 1.9	16.8 ± 1.4	2.2
Homozygous y_9:				
9005	9006	24.6 ± 1.3	23.4 ± 1.8	1.1
9005	9006 minus 8005-6	24.6 ± 1.3	26.2 + 2.1	1.6
9006	9007	23.4 ± 1.8	20.8 ± 1.2	2.6
9006 minus 8005-6	9007	26.2 ± 2.1	20.8 ± 1.2	5.4*
9005	9007	24.6 ± 1.3	20.8 ± 1.2	3.8*

*Significant at 5% level of probability.

In summary, it has been demonstrated that more crossovers are recovered from deficient TB-10a plants heterozygous for y_9 when they are crossed as males than when they are crossed as females. Also, there is evidence that some factor might be responsible for lowering the rate of both male and female transmission of crossovers in certain plants.

Further tests of these deficient plants will be made next year using exact reciprocal crosses to obtain more precise data. Also tests will be initiated to establish if there is a differential transmission of crossovers through the microspores and megaspores of plants heterozygous for normal chromosome 10. Previous tests by other workers have shown similar recombination frequencies in both sexes for chromosome 10.

Plants deficient for other A-B translocations will also be tested to determine if this phenomenon is common to all of them.

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1. A test for involvement of the polar nuclei in preferential fertilization.

Roman demonstrated (1948) that sperm carrying B^A chromosomes fertilize the egg more often than the polar nuclei when in competition with other sperm. Two general explanations for this phenomenon can be proposed:

1. Sperm with B-type chromosomes are more capable of fertilizing the egg than other sperm. Either a positional advantage in the embryo sac, or a specific chemical attribute of the sperm could be responsible.
2. Sperm containing B-type chromosomes are less able to fertilize the polar nuclei. This could result from the sperm position in the embryo sac, or from a specific chemical property.

The two ideas were tested by a method which eliminates any role of the polar nuclei in fertilization and allows competition between the sperm for the egg alone. Kernels were selected in which heterofertilization had occurred, and the polar nuclei were fertilized by sperm from a different pollen grain than the egg. Both sperm from one pollen grain are therefore able to compete for the egg. If preferential fertilization persists in this situation, the first hypothesis is supported. The second explanation predicts the absence of preferential fertilization.

Crosses were made between a chromosome 9 tester and the A-B translocation, TB-9b: sh bz wx B Pl X 9^{c} sh Bz wx $_{9}B^{Wx}$ $_{B}9^{wd}$ C sh bz. The Bz wx kernels (9,560) were selected and planted on the sand bench. Seedlings that appeared bz were transplanted to the field and grown to maturity. Presumably the endosperm was fertilized by sperm carrying

9^{c} sh Bz wx, and the embryo by sperm carrying the 9^{B}Wx plus zero, one, or two B^{9}wd C sh bz's. Confirmation of the heterofertilization was made by crossing the plants and looking for the presence of Wx and by examination of pollen fertility. (The Wx locus marks the 9^{B} chromosome, and crossing over between it and the translocation breakpoint occurs less than 0.5% of the time--Robertson). Each of the plants resulting from heterofertilization was crossed to c sh wx and sh bz wx testers to determine the number of B^{9}'s present. Distinctly different testcross results are obtained from plants with 0, 1, and 2 B^{9}'s (Robertson). A total of 45 plants was classified with the following results:

	Hyperploid TB-9b ($9\ 9^{B}\ B^{9}\ B^{9}$)	Hypoploid TB-9b ($9\ 9^{B}$)	Heterozygous TB-9b ($9\ 9^{B}\ B^{9}$)
Number of Plants	25	12	8

Plants with one B^{9} may be disregarded, since both sperm of the parental pollen grain contained one B^{9} and competition between sperm was not possible. The other classes, however, result from nondisjunction of the B^{9} at the second pollen mitosis and fertilization of the egg either by the sperm with two B^{9}'s (hyperploid progeny) or by the sperm lacking B^{9}'s (hypoploid progeny). Fertilization of the egg by the sperm containing two B^{9}'s occurred in 67% of the cases (25/37), a rate significantly higher than 50% (at the 5% level of significance). Since the normal rate of preferential fertilization with TB-9b is 65-70%, the results suggest that the polar nuclei are not involved in preferential fertilization.

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1. Further data on the cp_2 (collapsed-2) location.

According to Dr. Nuffer's suggestion the collapsed endosperm trait previously indicated as "cl" (M.G.N.L. 40: 77-78, 1966) will be hereafter designated as "cp_2". Additional data on the recombination between o_2, gl_1 and cp_2 are now available:

Gene pair	Phase	AB	Ab	aB	ab	Recombination ± standard error
o_2-cp_2	R*	3567	2369	1760	22	9.6 ± 0.7
gl_1-cp_2	R*	1181	614	546	5	9.2 ± 1.3
	C*	3277	164	178	768	8.6 ± 0.1
	R**	101	978	956	77	8.4 ± 0.4
o_2-gl_1	R*	2316	931	1125	15	13.2 ± 1.0
	C*	634	54	72	104	16.6 ± 0.9

*Self-fertilization data.

**Backcross data.

The cp_2 location appears now to be intermediate between o_2 and gl_1 and not distal to gl_1 as previously reported (M.G.C.N.L. 40: 77-78). The order of these markers on the chromosome 7 map should be as follows:

o_2 (9.6%) cp_2 (8.7%) gl_1

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F. Salamini

2. A rt (rootless) mutant detectable at an early seedling stage.

In 1968 a progeny segregating for a defective root seedling was detected among breeding material. At the four leaf stage the root development of the mutant is poor (about 1/5 of normal). The mutant seedlings are also smaller than the normal and do not reach the reproductive stage. In 1969, heterozygous material was selfed and 22 progenies

obtained: 13 were segregating for the rt phenotype while 9 did not segregate. Among the segregating progenies 802 seedlings were normal while 255 (24.1% possessed the mutant phenotype. On the basis of these results the rt phenotype seems to be inherited as a monomendelian character.

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3. Induced E.M.S. mutations for kernel characters: absence of specificity for selected loci.

From ethyl methane sulphonate (E.M.S.) treatment (1.5%, 14 h, 22°C) of maize kernels, one hundred self fertilized ears were collected. A subsequent self-fertilization permitted isolation of 95 kernel mutants classified as:

1. defective endosperm (normal plant)
2. defective endosperm (lethal plant)
3. germless

Within each class of mutation, allelism tests were performed. The results are as follows:

Mutant class	Number of isolated mutants	Number of mutants considered	Number of crosses performed	Cases of allelism	Number of independent loci
1	17	12	22	3	large
2	59	35	507	3 (+ 1?)	large
3	18	8	85	6	3

The 8 germless mutations can be recognized as allelic to three independent loci. As to the endosperm defective mutations, it has not been possible to recognize them as alleles of a reduced number of loci. The conclusion follows that E.M.S. mutagenic action is not specific for selected loci.

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1. Pachytene pairing in translocation heterozygotes having a huge knob close to the breakpoint.

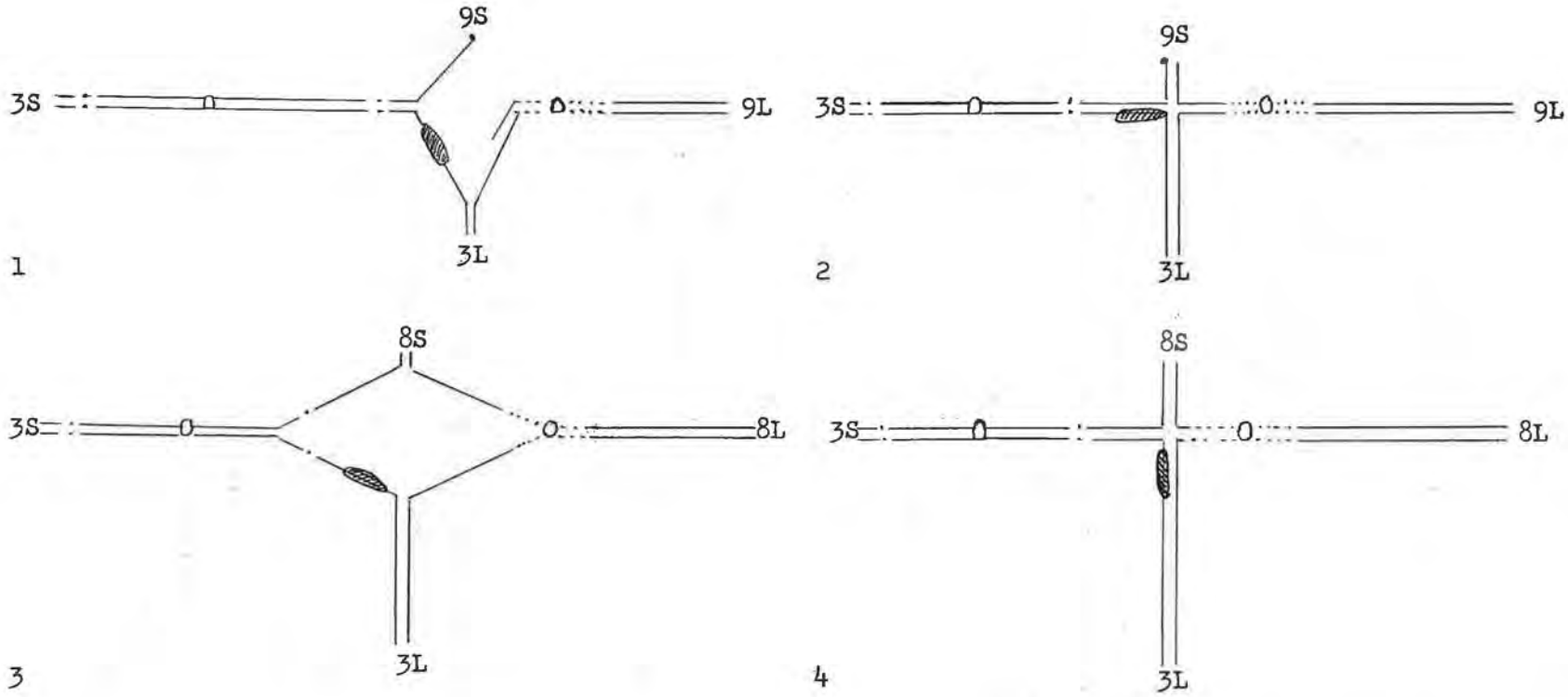
An exceptionally huge knob ($3L^{111}$) was found by the present author on the long arm of chromosome 3 (position .58) in an inbred line, N. C. Inb. No. 12, derived from the variety Jarvis Golden Prolific (Ohta 1965, Maize News Letter 39:142).

To examine the effect of this huge mass of heterochromatin on synapsis during meiotic prophase, two translocation heterozygotes having the breakpoint close enough, one proximal and the other distal, to the knob position were selected for hybridization to the inbred line. Strains T3-8h, the breakpoint at .53, and T3-9F, at .63, were obtained from Dr. E. B. Patterson, for which the author is grateful to him. They were crossed to the inbred line, $3L^{111}$, and the F_1 hybrids were examined cytologically.

Pachytene pairing in a translocation heterozygote, $3L^{111}$/T3-9f, was analyzed. Three major types were found:

1. Complete asynapsis or asynapsis in each of the four arms of the cross-shaped configuration in segments adjacent to the breakpoint was observed in about 50 per cent of the cells analyzed. The lengths of asynaptic arms varied; Fig. 1 shows an extreme case.
2. Asynapsis in two or three arms of the cross-shaped configuration was observed in about 35 per cent of the cells.
3. Complete homologous pairing throughout the cross-shaped configuration was found in the rest of the cells (Fig. 2), in which two cases existed: either the huge knob paired with the knobless homologue or it folded back on itself in a U-shape (partly non-homologous pairing in a strict sense).

In the most extreme case of (1) the asynaptic segment was as long as about two-fifths of the length of the long arm of chromosome 3, but no case of asynapsis beyond the centromere was observed.



Figs. 1-4. Schematic drawing of pachytene pairing of the translocation heterozygotes.

1. $3L^{111}$/T3-9f, complete asynapsis in the segments adjacent to the breakpoint.
2. $3L^{111}$/T3-9f, complete homologous pairing.
3. $3L^{111}$/T3-8h, complete asynapsis in the segments adjacent to the breakpoint.
4. $3L^{111}$/T3-8h, complete homologous pairing.

Pachytene pairing in another translocation heterozygote, $3L^{111}$/ T3-8h, was also analyzed. Three major types were found: (1) complete asynapsis or asynapsis in each arm of the cross-shaped configuration in the segments adjacent to the breakpoint (Fig. 3), (2) complete homologous pairing throughout the cross-shaped configuration (Fig. 4) and, (3) partly homologous pairing and partly asynapsis. The observed frequently of each of the three types was about 1 : 1 : 1.

From the above observation the following conclusion is drawn: Heterochromatin, when present in a huge amount heterozygously, prevents pairing of homologous chromomeres or ordinary chromosome segments in the region adjacent to it, but it does not affect homologous centromeres, indicating that different mechanisms are involved in the synapsis of chromomeres and that of centromeres during meiotic prophase.

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1. Evidence for the influence of B-chromosomes on the recovery of Dp-Df chromosomes.

The recovery of duplicate-deficient (Dp-Df) chromosomes in the megaspores of plants heterozygous for Inversion 3a (breakpoints 3L.40-.95) was reported by Rhoades and Dempsey (Amer. J. Bot. 40:405-424). They demonstrated that Dp-Df chromosomes arise following crossing-over between two genes within the inverted region and subsequent bridge breakage. Recovery of Dp-Df strands was measured by inequality of reciprocal crossover classes since these chromosomes contribute to only one of the classes. Once isolated, they were followed by decreased transmission of the deficient chromosome. In their study, Rhoades and Dempsey found no difference in crossing over in megasporocytes and microsporocytes when a correction was made for the Dp-Df chromosomes in the functional megaspores.

Further studies of In 3a heterozygotes have shown that inequality of reciprocal crossover classes is not always observed, suggesting that

Table 1

Reciprocal testcross data from plants heterozygous for In 3a and carrying one or more B chromosomes. The normal 3 derived from inbreds KYS or L-289.

Female Parent		(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	Σ	Recombination % Gl-Lg	Recombination % Lg-A
gl a k lg In 3a / Gl Lg k A (L-289)		853	771	95	85	26	7	8	17	1862	11.0	3.1
	**	853	771	95	85	7	7	8	8	1834	10.7	1.6
gl a k lg In 3a / Gl Lg k A (KYS)		454	500	72	85	13	4	4	5	1137	14.6	2.3
	**	454	500	72	85	4	4	4	4	1127	14.6	1.4
Male Parent												
gl a k lg In 3a / Gl Lg k A (L-289)		566	488	74	82	4	6	4	6	1230	13.5	1.6
gl a k lg In 3a / Gl Lg k A (KYS)		496	496	99	86	5	5	8	2	1197	16.3	1.7

**Corrected strand frequencies with presumed Dp-Df chromosomes removed.

Table 2

Reciprocal testcross data from plants heterozygous for In 3a and lacking B chromosomes.

Female Parent	(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	Σ	Recombination % Gl-Lg	Recombination % Lg-A
k10 Gl a k lg In 3a / k10 gl Lg K A N	1016	1024	92	107	3	1	4	5	2252	9.2	0.6
K10 Gl a k lg In 3a / k10 gl Lg k A N	188	193	62	62	2	3	2	4	516	25.2	2.1
Male Parent											
k10 Gl a k lg In 3a / k10 gl Lg K A N	291	254	31	43	2	2	4	5	632	13.1	2.1
k10 Gl a k lg In 3a / k10 gl Lg k A N	177	133	21	37	5	0	1	4	378	16.7	2.6

Reciprocal testcross data from plants heterozygous for In 3a segregating a and lg (including above data).

	Female Parent (0) lg a	(0) Lg A	(1) lg A	(1) Lg a	Σ	Recombination % Lg-A	Male Parent (0) lg a	(0) Lg A	(1) lg A	(1) Lg a	Σ	Recombination % Lg-A
k10 a k lg In 3a / k10 Lg K A N	4206	4195	30	31	8462	0.7	728	780	21	32	1564	3.4
k10 a k lg In 3a / k10 Lg k A N	882	938	5	7	1832	0.7	214	154	9	1	378	2.6
K10 a k lg In 3a / k10 Lg k A N	929	869	22	31	1851	2.9						

Dp-Df chromosomes are not invariably recovered in the megaspores. Moreover, in plants showing equivalence of crossover classes, the recombination frequency in microsporocytes is higher than in megasporocytes.

Plants homozygous for the genes gl lg a and heterozygous for In 3a were crossed to inbreds KYS and L-289. Data from reciprocal testcrosses of the F_1 plants are shown in Table 1. Equivalence of the Lg a and lg A crossover classes is found in crosses using the inversion heterozygote as pollen parent. On the other hand, when the F_1 is used as egg parent, the crossover classes are not equal; the excess of Lg a over lg A crossovers is due to the functioning of Dp-Df chromosomes. Recovery of Dp-Df types in the megaspores artificially increases the recombination values in megasporocytes. If it is assumed that reciprocal crossover strands are produced in equal numbers in microspores and megaspores, and if the presumed Dp-Df chromosomes contributing to one of the classes are removed, the recombination frequencies are essentially the same in male and female inflorescences.

The testcross data in Table 2 are from inversion heterozygotes produced in the following cross:

$$\frac{\text{K10}}{\text{k10}}\ \frac{\text{gl Lg K A}}{\text{Gl Lg k A}} \times \frac{\text{k10}}{\text{k10}}\ \frac{\text{Gl a k lg In 3a}}{\text{Gl a k lg In 3a}}$$

The equality of Lg a and lg A classes in the megasporocytes indicates that, in plants heterozygous for In 3a, Dp-Df chromosomes are not always recovered. In addition, crossover values are consistently lower in the megasporocytes than in the microsporocytes. Comparisons can be made only between plants with the same constitution with regard to K10 and K3, since these knobs are known to affect crossing over.

Preliminary evidence suggests the difference between these tests can be accounted for by the presence of supernumerary B chromosomes. Plants showing similar crossover values in male and female flowers and recovery of Dp-Df chromosomes in megaspores carry at least one B-chromosome, while plants producing different recombination values in microsporocytes and megasporocytes and equality of reciprocal crossover strands have no B-chromosomes.

Further experiments to test the effect of B-chromosomes on the recovery of Dp-Df chromosomes and recombination in inversion heterozygotes are underway.

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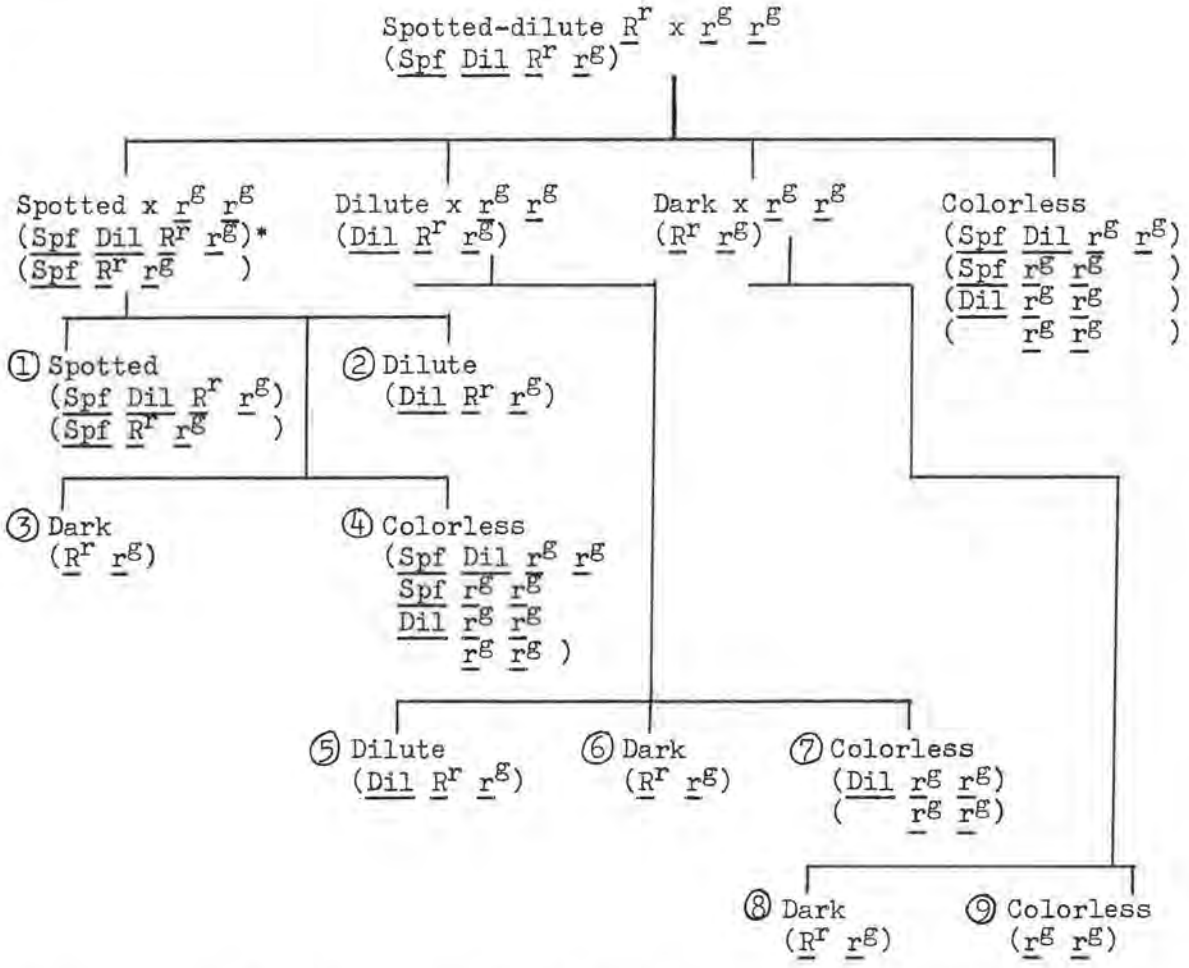
1. Spotted-dilute and the instability of $\underline{R}^r$.

Some years ago Dr. M. Emmerling sent Dr. Brink several unstable R alleles described as Spotted-dilutes. These alleles gave dark spots on a colorless or lightly pigmented background in the aleurone. After several backcrosses to W22 (A C r^g or A C r^r), only two alleles (#2 and #4) were found to retain the original unstable pattern. The following information concerns the spotted-dilute R^r (#2).

The spotting pattern appears only in the aleurone tissue, and the anther color of the spotted-dilute stock is not distinguishable from normal A C R^r. On crossing to r^g r^g, the spotted-dilute R^r r^g segregates into spotted, uniformly dilute, dark, and colorless phenotypes. The dark phenotype is indistinguishable from that of standard R^r R^r. Plants grown from the dark kernels (R^r r^g) segregate only into dark and colorless kernels. Plants from the dilute kernels, on the other hand, show both dark and dilute kernels within the colored class. Spotted kernels never reappear in the stocks developed from dilute and dark kernels.

It is postulated that the patterns described above are affected by two dominant modifiers, one reacting with R^r to cause spotting and the other diluting the normal phenotype of R^r. These two factors will be referred to as Spf (spotting factor) and Dil (diluting factor). It is also assumed that the backcross parent W22 r^g r^g is free from the modifiers. Based on this terminology, the breeding behavior of the spotted-dilute R^r can be described in the following way:



*According to this scheme we should have two types of spotted kernels: (a) those which segregate into spotted and dilute and (b) those which give rise only to spotteds. We have both of these. Spf Dil R^r r^g and Spf R^r r^g cannot be phenotypically distinguished.

If the above hypothesis is true, then some colorless segregants (r^g r^g) from the spotted-dilute stock should carry the modifiers. Some plants from class 4, for example, should carry Spf or Dil or both or none. Similarly plants from class 7 should carry the Dil factor, while class 9 should carry no modifiers. To test these possibilities, plants were grown from all the colorless classes and each plant was selfed and crossed on the plants grown from (a) dilute kernels (Dil R^r r^g), (b) dark kernels (R^r r^g) and (c) R^{ch} R^{ch} plants. (The last mentioned cross was included in the program since the aleurone pigmenting capacity of R^{ch} was known to

be sensitive to the effect of other diluting modifiers). Results from these crosses came out according to the predictions. Some matings of the class 4 $\underline{r}^g\ \underline{r}^g$ x Dil $\underline{R}^r\ \underline{r}^g$ showed spotted kernels. Some crosses involving class 4 $\underline{r}^g\ \underline{r}^g$ x $\underline{R}^{ch}\ \underline{R}^{ch}$ showed both spotted kernels and dilute kernels, some showed dilute kernels and some showed spotteds. Half of the ears from the matings involving class 7 plants showed dilute kernels and there were no ears with the spotting pattern. Thus the data confirm the modifier hypothesis.

The fact that the spotting and dilute phenotypes are determined by modifiers of the R locus is also supported by another line of evidence. During selfing of the spotted-dilute stock we observed many ears which were homozygous for R but segregated for spotted and dilute patterns.

Further investigations showed that the standard $\underline{R}^r$ and Ecuador 1172 $\underline{R}^r$ are not sensitive to the action of Spf and Dil. Spf and Dil are independent of the R locus and independent of each other.

There was one puzzle from the beginning of the present investigations. When plants from classes 4 and 7 were crossed with the plants grown from dark kernels, the resultant ears showed only dark and colorless kernels. (Half of them should have showed spotted and dilute kernels on the modifier hypothesis.) These crosses were repeated with the $\underline{r}^g\ \underline{r}^g$ lines known to contain the modifiers. (These lines were developed from the selfed ears mentioned above and their constitution regarding the modifiers was determined from the crosses made on the dilute and $\underline{R}^{ch}\ \underline{R}^{ch}$ plants). Even these tests gave negative results, showing the plants obtained from the dark kernels do not respond to Spf and Dil. Although these experiments were carried out on a large scale, we were not successful in reconstituting dilute and spotted phenotypes from the dark kernels. It appears $\underline{R}^r$ in the spotted-dilute stock can maintain its sensitivity only if it is kept under control either by Spf or Dil. Once the nucleus is freed from the modifiers $\underline{R}^r$ loses the sensitivity and cannot regain it. At present we are not aware if there are any special conditions in which $\underline{R}^r$ can maintain or regain the sensitivity. $\underline{R}^{ch}$, however, is different in this respect and can maintain sensitivity even if Spf and Dil are absent.

Some tests were conducted to study the relationship between the spotted-dilute system and other well known controlling systems. The crosses $\frac{C^1\ Ds}{C^1\ Ds}\ \frac{R^r}{R^r}$ No *Ac* x $\frac{C}{C}\ \frac{R^r}{r^g}$ *Spf Dil* gave all colorless kernels indicating that *Ds* was not activated by any factors in the spotted-dilute stock.

Tests with McClintock's *Spm* system, however, gave some positive results. The functional homology between *Spm* and *Spf* has been partially established in the following way. $R^r/R^r\ a_2^{m-1}/a_2^{m-1}$ without *Spm* was crossed with $R^r/R^r\ A_2/A_2$ *Spf Dil*. The F_1 kernels ($a_2^{m-1}/A_2\ R^r/R^r$ with all combinations of *Spf* and *Dil*) showed uniform pigmentation. This demonstrates that the R^r in the a_2^{m-1} stock is not sensitive to the action of *Spf* and *Dil*. When the F_1 was backcrossed to a_2^{m-1}/a_2^{m-1} R^r/R^r (without *Spm*) a quarter of the total kernels in about half of the plants exhibited variegated kernels, showing that a_2^{m-1} was activated. Tests with a_1^{m-1} also gave similar results. Neither standard R^r nor $r^g\ r^g$ (all in W22 background like the spotted-dilute) carry *Spm*. Other preliminary tests on inheritance showed that *Spm* and *Spf* are functionally similar. The question whether R^{ch} will be sensitive to the action of McClintock's *Spm* (to produce spotted aleurone) is under investigation at Leeds.

If *Spf* and *Spm* are similar, what is the nature of *Dil*? It appears to act as a second *Spm* element with an ineffective component-2; also *Dil* functions as a weak *Spm* when tested against a_2^{m-1} and a_1^{m-1}. We observed frequent changes of *Spf* to *Dil* in the spotted-dilute stock.

Originally these studies were initiated to investigate paramutation of spotted-dilute R^r. In this context the following points are of interest:

1. The R^r in the spotted-dilute stock is paramutable.
2. The aleurone pigmenting capacity of R^{ch} is also paramutable and is sensitive to *Spf* and *Dil*.
3. Although the standard R^r is paramutable, it is not sensitive to the action of *Spf* and *Dil*.
4. Ecuador 1172 R^r is neither paramutable nor sensitive to the action of *Spf* and *Dil*. Thus, paramutability and sensitivity to *Spf* and *Dil* are independent features of the *R* locus.

With regard to the relationship between the Spm controlling system and the spotted-dilute $\underline{R}^r$ system, the following features should be emphasized.

1. The loss of sensitivity of the structural gene ($\underline{R}^r$) in the absence of controlling elements is not known in McClintock's Spm system. In this respect, $\underline{R}^{ch}$ resembles more closely $\underline{a}_2^{m-1}$ and $\underline{a}_1^{m-1}$.
2. The numerous different states of the structural genes reported by McClintock have not been observed at the R locus.

The spotted-dilute $\underline{R}^r$ (#4) resembles #2 in some respects but it does not appear to carry the Dil factor. This stock is under detailed investigation at Leeds. This work was initiated by one of us (G.R.K.S.) at the University of Wisconsin.

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1. Nucleolar number at premeiotic interkinesis.

Although the majority of interkinetic cells in the meristem of the root tip have a single nucleolus due to nucleolar fusion, cells with dual nucleoli are also apparent. Meiotic material of KYS was collected during early developmental phases to determine if dual nucleoli occur at premeiotic interkinesis. Successive early stages were not obtained in side branches of the tassels. Accordingly, to maintain orientation and sequence, leptonema was located in the main tassels and progressively younger anthers examined until the mitotic divisions preceding meiosis were encountered.

At leptonema, unpaired strands were clearly evident; the nuclei of cells intermediate in development between leptonema and premeiotic mitosis appeared more granular or chromomeric with strands less obvious. The string of premeiotic cells, squeezed out of young anthers in aceto-carmine, was more difficult to disrupt into individual cells than at later stages. In comparison with the rounded appearance of micro-sporocytes during division I in smear preparations, cells at premeiotic interkinesis were irregular in shape. Nucleolar number was scored at premeiotic interkinesis. A single nucleolus occurred in each of 519 cells; one cell had dual nucleoli. Nuclear and nucleolar sizes were also determined for comparison with a similar study of mitotic inter-kinesis. Although analysis is incomplete, dual nucleoli occur much more frequently at interkinesis in cells from the terminal part of the meristem of the root tip. A comparison may provide information con-cerning the spatial distribution of chromosome pair 6 in the nuclei at mitotic and premeiotic interkinesis.

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1. Day-neutral teosinte renamed "northern teosinte".

Because the day-neutral teosinte, as reported in last year's MNL, is not truly insensitive to day length, a better name for it would be northern teosinte. It was developed because of the inconvenience in giving artificial short-day treatment to the Mexican teosintes in order to get them to flower in my cultures. In Massachusetts, the main culm of northern teosinte flowers at about a height of one foot, while the tillers continue to grow for another month until the days are shorter and then flower when they have attained a height of 5 to 6 feet.

A genetic factor causing the preinduction of flowering in the main culm in day-neutral and short-day maize was observed previously by Brawn (MNL 39). This characteristic derived from Gaspé Flint was merely transferred to teosinte in my cultures. Northern teosinte was selected among the progeny from a backcross to teosinte of the hybrid Guerrero teosinte x Gaspé Flint. A similar project using Chalco teosinte rather than Guerrero teosinte did not yield the desired results, probably because of the heavier load of modern maize germplasm borne by Chalco teosinte.

W. C. Galinat

2. A warning on the possible hazards of northern teosinte.

Distribution of my recently created stock of northern teosinte has been made to a number of agronomists interested in developing a new forage-silage plant and to botanists interested in the maize-teosinte relationship in the United States, in South America and in Africa. Because this teosinte is as resistant to Atrazine as is maize, its escape in areas where this herbicide is the common means of weed control in maize fields may create a problem as it already has in my own corn field. I have not as yet observed it to be spread by birds although if this comes about, we may have a "Frankenstein monster" to contend with. Birds are known to feed on teosinte in Guatemala.

W. C. Galinat

3. A comparison between the chromosome 4 syndrome of Zea and the Q segment of Triticum (wheat).

A considerable length of chromosome 4 in Zea, estimated to include the whole short arm as marked by the Su locus, is known to control a group of floral characteristics which separate maize from teosinte (Mangelsdorf and Reeves, 1958). Although in some respects its action is similar to that of the "Q segment" which separates normal Triticum vulgare from its speltoid mutants, apparently it is much longer in terms of gene linkages or map units. The Q segment is described as a short block of closely linked genes, sometimes called a supergene, which controls the development of several separate floral characters. In both cases there

is control of disarticulation of the rachis, internode length, number of fertile grain-bearing florets (in Triticum) or spikelets (in Zea) and structure of the glume. In Zea other floral characters such as inclination of the spikelet and degree of cupule development are also involved (Galinat, 1963; Sehgal, 1963). The Q segment appears to control the action of genes located elsewhere in the genome, while the functions of genes on teosinte chromosome 4 are partially duplicated on at least four other chromosomes (1, 3, 9 and 10) according to Mangelsdorf (1947).

The speltoid mutants result from a deficiency for the Q segment. The linked genes which are known to be located in chromosome 4 of Zea do not occur as a single linkage group in tripsacum, the second closest relative of maize, although its genes or their functions are dispersed to several different chromosomes.

Because of the hexaploid nature of Triticum vulgare, it is to be expected that loci elsewhere in the other two genomes would have complementary, if not duplicating, effects to those of the Q segment. The partially duplicating effects of the several different teosinte segments to that on Zea chromosome 4 are not so easily explained.

If similarity in length is important to an analogy, perhaps the tunicate locus, which is compound and also on Zea chromosome 4, might be a better comparison to the Q segment and/or a supergene, as suggested by Mangelsdorf (unpub.).

W. C. Galinat

4. The genetic differences between primitive maize and teosinte.

A knowledge of the number of allelic differences which separate maize from teosinte would be helpful in estimating the rate at which teosinte might have become transformed into maize, but not necessarily a criterion of whether teosinte could be the ancestor of maize. Unfortunately studies of segregation among maize x teosinte hybrids must be based partly on an arbitrary and difficult separation into classes of characters such as induration score, disarticulation score, day-length response and even the ranking (distichous vs polystichous). The expression of distichous is often variable within the plant and it may be genetically unstable in maize.

Despite its variability, there has been some agreement between various investigators that when the F_2 segregation for distichous vs polystichous from corn-teosinte hybrids is based upon scoring of the uppermost central ear, the ratio approaches a 3:1. In our tests, a population of 100 F_2 plants from a cross between northern teosinte and string pop yielded 22 distichous ears and 80 polystichous ears. Although this might be interpreted as a 4:1 ratio, it is more probably a deviation from a 3:1 ratio. Langham (1940) found Mendelian inheritance for certain other characters separating these relatives, but Mangelsdorf (1947) and Rogers (1950) failed to get such evidence. Some results reported by Mangelsdorf and Reeves (1939) suggested that the genes which distinguish teosinte from maize are concentrated in only four chromosome segments while other data indicated that these genes are distributed among most of the ten chromosomes of maize (Mangelsdorf, 1947; Rogers, 1950).

These varying results could stem primarily from differences in the maize backgrounds as well as from the maize germplasm which might have previously introgressed into the teosinte parent. According to both Rogers and Mangelsdorf (op cit) the inheritance and/or linkage of these characters varies with the variety of teosinte involved in the cross. Mangelsdorf also found that the variety of maize had an effect, for, in his cross of Durango teosinte with Guarany maize, the spikelets were predominantly single in the F_1, whereas in crosses of the same teosinte with North American maize, they are predominantly paired.

In an attempt to minimize the importance of such complicating factors, it would seem desirable to make use of the most primitive races of maize that are now available. How could one expect to get simple segregation ratios between teosinte and modern maize when the genetic difference between modern maize and primitive maize which could have evolved from teosinte is already complex?

With this approach in mind, Confite Morocho, probably the most primitive living race of maize now available, was adapted to growing conditions in Massachusetts by incorporating some germplasm from Tom Thumb popcorn. It is hoped that the resulting string popcorn line will provide a sufficiently low level of modifier genes to make possible a

more meaningful test of the old hypothesis that domesticated maize originated from teosinte by an accumulation of mutations.

W. C. Galinat

5. The possible evolution of a high sink (energy utilization or deposition) capacity in the ear of modern maize and teosinte.

In an F_2 of 100 ears from a cross between northern teosinte and a primitive string cob popcorn, there was little or no induration (hardness) in the glumes and rachis in contrast to the high induration which ordinarily characterizes maize-teosinte segregants. A comparable F_2 progeny from the same teosinte outcrossed to modern maize (A158) did give the usual preponderance of highly indurated types.

The teosinte used in these crosses was the special northern stock created in my cultures as previously described in the first item. The string cob popcorn was derived from a cross between Tom Thumb popcorn and the primitive short-day Peruvian race, Confite Morocho.

The relatively small F_2 population involving string pop yielded four good maize ears but no teosinte-like ones. The four exceptional maize ears were more indurated, had deeper cupules and were longer than the string popcorn which went into the original cross. Apparently the modern teosinte germplasm which segregated to the four plants involved had increased their capacity to produce a more productive ear. Most of the F_2 plants did not have this capability to deposit abounding energy in the glumes, rachis and kernels. While it is possible that a weak tunicate allele similar to that of Chapalote in the string pop parent was partly responsible for the lowered sink level, the indurated segregants were too few (4%) to represent the effects of only one recessive gene.

The capacity of the maize ear to function as a high energy sink could have developed during selection under domestication for more productive ears. The modern high yielding ear would combine genes for a large many-rowed cob with genes for a large ear-sink capacity. The high induration in the cupulate fruit cases of modern teosinte would represent an expression of this high-sink capacity in the presence of a tiny storage

organ. Thus the pronounced induration of modern teosinte may be a character derived from modern maize, a view opposite to that generally held. A given level of sink capacity which would allow induration in a tiny spike of teosinte with its 6 to 10 kernels might not be sufficiently high to provide for induration in even a primitive ear of maize bearing about 50 kernels.

While the morphological evidence of teosinte introgression in both archaeological and modern maize is generally accepted, it is possible that in some cases, the high induration on which the evidence is partly based may be independent of the introgression and due rather to a combination of genes for a small ear together with a high sink capacity.

One of the methods which we are using to investigate the maize-teosinte relationship is to compare the effects of teosinte germplasm, especially that of chromosome 4, upon the spikes in the F_2 progeny from parallel crosses of teosinte by primitive maize versus teosinte by modern maize.

W. C. Galinat

6. Ontogeny and phylogeny of the cupule.

In the early stages of floral ontogeny in maize, the orientation of the primordia of the pistillate spikelets is vertical or parallel to the rachis as it is in the other American Maydeae and most closely related Andropogoneae. In the American Maydeae, the primordia are embedded within cupules in the rachis. In teosinte and tripsacum, the young pistillate spikelets remain within the confines of their individual cupules while these structures expand and differentiate simultaneously. Eventually the developing outer glume of the embedded spikelet completes the enclosure of a unique protective device, the cupulate fruit case. As the fruit case matures, it becomes indurated (hardened) and an abscission layer develops at each node (underface of the trace).

Although the lining of the cupule is derived from tissue homologous to that of the hairy pulvinus, it is glabrous within the tight confines of the fruit case, except where it surrounds the pulvinus notch on either side of the spikelet. A dense tuft of hair fills the pore so that it is

nearly impenetrable except by the primary root during germination and by water to initiate this germination.

In teosinte, mechanical support and protection to the spike as a whole during its final stages of maturation comes from a single enveloping husk leaf. After maturation, the disarticulated fruit cases usually sift out through the open top of the husk after the dead plant bends toward the ground or, if shredded by storms and/or birds, they may escape through tattered husks.

In modern maize, however, the young pistillate spikelets elongate outward and bend away from their individual cupules in coordination with an arrest in further cupule development. The timing of this spikelet inclination and its associated control over cupule development varies with the degree of teosinte introgression as shown experimentally with the A158 derivatives of teosinte. Also, fortuitous changes to either single spikelets or to multiplications above two result in cupule widths which match precisely those of the associated spikelets.

The oldest archaeological maize from Mexico, especially the Chapalote related material, has deep, triangular cupules which approach those of teosinte except for a general pubescence over the surface. Apparently the hairy nature of the pulvinar tissue has been reasserted after the protective function of the cupule was lost. The specialized hairy pulvinus notch remains in maize, also without function.

That the maize cupule is not merely an artifact of ontogeny is shown by its ready response to genetic selection and by the presence of the specialized pore, the pulvinus notch. In a relatively small breeding project for reduced cupule development, a non-cupulate cob was selected in my cultures through recombining certain genes derived from Confite Morocho of Peru and a sweet corn inbred (Ia. 5125) which appears to be related to Chullpi (Chuspillu) also from Peru. This non-cupulate rachis, which is also known archaeologically from Peru, is probably a derived condition following drift away from teosinte rather than a primitive one because the cupulate state and the associated tendency for vertically-oriented spikelets provides a better sequential connection to all of the known relatives of maize.

My interpretation of the cupule in maize as a vestige of the cupulate fruit case of teosinte and tripsacum does not invalidate my earlier views on the homologies of the cupule within the framework of the phytomer, as previously described (Galinat, 1963).

W. C. Galinat

7. The role of the cupule in the modern maize cob.

While the cupule has a functional role in the relatives of maize, at first glance it does not appear to have a function in the maize cob. Yet, cupules are always present in the cobs of modern maize. Despite this, selection for smaller cupules is possible and the ultimate non-cupulate rachis may be controlled by as few as two recessive genes.

If the cupule is now vestigial in maize and yet genetically controlled, why does it persist in the cobs of all the modern races? Some observations presented here suggest an answer.

In studying the cupules of the various races of maize, I have observed that the flour corns tend to have the widest cupules while the flints, the popcorns, the dents and some of the dent-related sweet corn varieties have progressively smaller cupules in the order listed. Derivatives from crosses between these variants, in which kernels of different sizes and endosperm types are combined with a cupule smaller than that of the original parental stock, tend to have two types of difficulties. (1) The kernels may develop mold in the field which usually results from a splitting of the pericarp and an accompanying release of sugar from endosperm tissue. Sudden changes in the moisture level of both cob and kernels may cause this pericarp splitting through unequal stresses. (2) The second difficulty is shattering which occurs later during drying of the mature ears. The kernels shrink to a fixed minimal size before the cob shrinks. If the cob subsequently contracts more than that attained by the kernels, some of the kernels are mechanically pushed out and off from the cob. In the case of the flour corns, which have excessively large kernels that do not shrink appreciably on drying, selection is strong for a wide and indurated cupule which provides the necessary dimensional stability (hardness) to the drying cob.

While the original protective function of the cupule has been lost, it has acquired a new secondary function in giving structural stability and strength to the modern maize cob. The checkered arrangement of wide lignified cupules is a mechanically strong design which in effect increases the thickness of the rind.

W. C. Galinat

8. Cytological map of Tripsacum dactyloides (2n = 36).

Since the "Bussey clone" of T. dactyloides (2n = 36) of Manhattan, Kansas is the source of most of the extracted chromosomes from tripsacum which we are comparing cytogenetically to their homeologs in the maize genome, the preparation of an idiogram for its chromosome complement is basic to our approach in analyzing the evolution of the American Maydeae. Furthermore, the genome of this collection of tripsacum is part of a permanent bridge over which we will continue to extract the desired chromosomes of tripsacum for many years in the future. Its complement is maintained in a perennial amphidiploid hybrid with Mangelsdorf's multiple tester, the origin and use of which have been previously described (Galinat: MNL 34, 1960).

The spread of chromosomes at pachytene is extremely poor; there is considerable fusion of many of the terminal knobs and extensive non-homologous association of the centromeres. Occasionally, however, some of the chromosomes lie free of the rest, either individually or in groups of about 4 or 5 chromosomes, in each of the nuclei. Correlatable data obtained from 238 observations selected from over 500, on individual chromosomes 1 to 18, are presented in the following table.

Morphology of the Pachytene Chromosomes of Tripsacum dactyloides (2n=36)

Chromosome No.	No. of Observations	Length in microns			Arm ratio	Remarks
		Short arm	Long arm	Total		
1	3	17.3	29.5	48.6	1.7	TKL, TKS
2	6	6.1	36.4	45.0	6.0	TKL
3	7	9.4	29.5	40.3	3.1	TKL
4	8	10.8	22.3	35.3	2.1	TKL
5	14	5.4	25.2	32.4	4.6	TKL
6	12	3.6	21.6	27.0	6.0	TKL
7	8	6.1	19.8	27.0	3.2	-
8	20	9.0	16.2	27.0	1.8	-
9	10	9.0	15.1	25.9	1.7	TKL
10	15	5.4	18.7	25.2	3.7	TKL
11	20	5.8	15.8	23.4	2.7	TKL
12	15	3.6	16.9	22.3	4.7	TKL
13	13	4.3	15.1	21.6	3.5	TKL
14	15	3.6	15.5	20.9	4.3	TKL
15	20	6.1	13.0	20.9	2.1	TKL
16	7	6.1	12.2	19.8	2.0	N.O Internal in LA - TKS
17	30	5.8	10.8	18.0	1.9	-
18	15	3.6	10.8	16.2	3.0	-

TKL - Terminal knob in long arm.

TKS - Terminal knob in short arm.

N.O. - Nucleolus organizing body.

Arm ratio - Length of long arm/short arm.

Total length includes centromere region.

The presence of the numerous knobs on the chromosomes of this collection of T. dactyloides, which made the spreading of its chromosomes so poor and the preparation of its idiogram so extremely difficult, now

renders a highly advantageous function in helping to cytologically identify the tripsacum chromosomes after they have been transferred to the genome of maize.

As a result of the preparation of this cytological map of T. dactyloides, a few of the cytogenetically analyzed chromosomes extracted from tripsacum have now been assigned to their respective positions within the complement of tripsacum, as described in another item of this MNL (item 16).

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9. Morphology of the homeolog for corn chromosome II derived from Tripsacum dactyloides (2n = 36).*

One of the Tripsacum chromosomes, as previously reported by us as well as Maguire (1956, 1961), is homeologous to the short arm of corn chromosome II and so far as is known covers the recessives ws, lg_1, gl_2 sk and fl_1. Its pachytene morphology, ascertained from addition disomic stocks in which the extra pair shows uniform and regular homologous pairing, is described in this report. Its probable identity within the complement of T. dactyloides is also suggested.

The total length of the chromosome is about 23 microns; the two arms measure about 8 and 13 microns to give an arm ratio of 1.7 and the long arm is terminated by a knob, by means of all of which this chromosome can be easily distinguished from those of corn in the pachytene nuclei.

These figures are at variance with the data of Maguire who reported a total length of about 35 microns and an arm ratio of over 3.0 for the homeolog identified in her material. While Maguire's data are based upon a univalent that had undergone an interchange (reciprocal) in an earlier generation, and therefore was possibly altered, the chromosome described now in its disomic condition is believed to be the unaltered form. Tantravahi (1968) reports normal pairing in the hybrid T. dactyloides x

*In this and following articles, the maize chromosomes are identified by Roman numerals and Tripsacum chromosomes by arabic numerals.

T. floridanum, and both he and Chaganti (1965) have described the occurrence of chromosomes similar to the one reported now in the complements of T. floridanum. Furthermore, our own data on the cytological map of the Kansas form (Bussey clone) of T. dactyloides, from which this particular chromosome was extracted, indicate that chromosome 9 of its complement is nearly identical to that reported now (vide items 8 & 16).

Preferential pairing of the corn II homologues to the exclusion of the extra tripsacum chromosome(s) is observed at meiosis in both the 20+1 and 20+2 stocks; crossover products involving the two loci tested (Lg Gl) are recovered only at a low frequency among thousands of plants. It would thus appear that the tripsacum chromosome, when transmitted to the progeny, has remained virtually unaltered in most of our materials.

Other differences with Maguire's observations are:

While she reports total pollen sterility in her 21 chromosome plants of the constitution 2, $2+T^2$ and 2, 2^T+T^2, most of our stocks have been nearly normal and fertile. Crossing over between lg and gl was rare in her material, while we have recovered both the reciprocal products at a low but regular frequency in each of the generations.

B. G. S. Rao
W. C. Galinat

10. Cytology of lg_1 Gl_2 and Lg_1 gl_2 crossover progenies of a corn-Tripsacum hybrid.

Both of the reciprocal crossovers lg Gl and Lg gl are recovered at a frequency of about 3-5% when the 20+1 Lg Gl plants are selfed. The regularity in the appearance of these phenotypes in each of the generations indicates that crossing over does take place between the short arm of corn chromosome II and the long arm of its tripsacum homeolog (T9), although at a relatively low rate. In the lg Gl plants, over a hundred PMCs at diakinesis show a trivalent frequency of nearly 90%. Analysable pachytene nuclei, however, give a frequency of only a little over 50%. In the remainder the univalent chromosome shows nonhomologous centric associations with the centromeres of corn bivalents. It appears that these associations persist up to and possibly beyond diakinesis and give the appearance of trivalents, which they are not.

When the lg Gl interchanged tripsacum chromosome (T^c) formed a trivalent with corn II, the configuration could be resolved into three regions at pachytene: AB: corn segment distally located on T^c; BC: the univalent portion in the long arm of T^c, apparently not involved in the interchange with corn II and therefore possibly unaltered to that extent, and CD: the centromere and the short arm of T^c, also unrelated to the interchange. While region AB paired uniformly with the corresponding portion in one of the corn II homologues, BC and CD remained asynapsed most frequently; occasional inside pairing (torsion pairing) was noticed to variable degrees in these regions. Illegitimate pairing of the BC and CD segments with the other corn chromosome II was observed in about 20% of these configurations. The average lengths of each of these regions is compared below with the unaltered TT chromosome:

	TT chromosome from 20+2 LgGl plants (microns)	T^c chromosome from 20+1 lgGl plants (microns)	
Length of long arm:	13.2	AB:	18.3
		BC:	12.9
Length of short arm:	7.7	CD:	7.2
Total length:	22.3		39.6
Terminal knob:	present		absent

If the length of the paired region involving the distal portion of normal corn II and its homologue on the T^c chromosome (region AB) is any indication of the extent of the interchanged segment, it would seem that about 25% of the total length of the normal corn II has been transposed on to the TT chromosome. These data also indicate that the breakpoint for the TT chromosome in this interchange is very near the terminal knob, which would locate the allele Lg in its close proximity; in fact, it is so close that the phenotype Lg or lg can be correlated with the presence or absence of the terminal knob. The T^c chromosome can therefore be interpreted as a product of unequal crossing over involving segments of different lengths of the two homeologs. Whether this unequal crossing over is the result of pairing between homeologs without exact juxtaposition of the alleles or is due to the alleles being located differently on the two chromosomes needs to be examined. Considering that the total length

of the tripsacum chromosome is about 70% of the short arm of corn II, linkage values other than those obtaining in corn might be expected, although the order of sequence of the common loci could be the same.

Studies on the Lg gl plants have not yielded any meaningful results. The interchanged Tripsacum chromosome in this case had the terminal knob, as expected, and showed inside pairing, illegitimate pairing as well as nonhomologous associations to variable degrees in each cell where it could be identified. The inconsistency in its behaviour at pachytene is attributable to the presence of a sufficiently large segment of corn in an intercalary position. It appears that a small portion proximal to the terminal knob, the region adjacent to the centromere, and the short arm represent the original segments of the tripsacum chromosome, while a greater part of the long arm represents the corresponding intercalary segment of the normal corn II. Intercrosses of the lg Gl and Lg gl plants, which are under study, might yield some information on this aspect.

B. G. S. Rao
W. C. Galinat

11. The discovery of the booster locus (b) on Chromosome 9 of Tripsacum dactyloides.

In the F_2 segregants from a heterozygous substitution for the corn-tripsacum interchange, homeologous to corn Chromosome IIS, the phenotype of recessive b appeared in the derived homozygotes for the interchange. As the corn marker stock contained only dominant B (lg_1 gl_2 B v_4), it is apparent that the recessive b allele is contributed by the tripsacum segment along with linked dominants (Lg_1 Gl_2). The data are as follows:

F_2 for a C-T heterozygous substitution for the homeolog to corn Chromosome II S.

Color	Green	Purple	Purple
Phenotype	Lg Gl b	Lg Gl B	lg gl B
Constitution of Chromosome II	C^T C^T	C^T C	C C
No. of plants observed	9	30	11

After observing that only the homozygous substitution plants for the C-T interchange were green (b) in the above F_2 (69-294 to 300), it was realized that all previously isolated homozygous substitutions for this interchange C-T chromosome were also b.

The discovery of the b locus on chromosome 9 of T. dactyloides increases the number of loci held in common with the short arm of corn II to six.

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12. Multiple homeologies of chromosome 9 of Tripsacum dactyloides.

In some of the microsporocytes from 20+2 Lg Gl plants, chromosome 9 of T. dactyloides is seen to be occasionally associated at pachytene with corn chromosome X in addition to its association with corn II S. Sometimes, the otherwise homomorphic pair of this extra chromosome is found to be deficient for a greater part of its long arm including the terminal knob and the corresponding segment is found attached, as a univalent, to the short arm of corn X. Less frequently, the distal knobbed univalent portions of both these pairs also show homologous pairing in these regions, and in related stocks the terminal knob of tripsacum 9 is found in the short arm of corn X. The breakpoints for these interchanges, which seem to be confined to a few nuclei, are estimated to be in the proximal half of the long arm of the tripsacum chromosome and in the distal portion of the short arm of corn X. Spontaneous breakage (fragmentation) and reunion is ruled out because of the somewhat regular, but low, frequency with which such configurations appear among the pachytene nuclei. Further, identical pachytene associations and altered chromosome types have been observed in the Lg Gl homeolog extracted independently from T. floridanum (vide item 17). From these observations it seems reasonable to assume that there exist some unidentified homeologies between tripsacum chromosome 9 and corn X, in addition to its already known affinities to the short arm of corn II, and that the alterations in the form of these chromosomes is not due merely to breakage and reunion of the concerned segments.

It is already verified cytologically that the two loci $\underline{Su}_1$ and $\underline{Gl}_3$ of corn chromosome IV occur on two different tripsacum chromosomes. In the present case, it seems that a single tripsacum chromosome has loci belonging to different linkage groups in corn. Considering the quite different chromosome numbers and the cytological maps, perhaps a reasonable amount of redistribution of their common loci might be expected in these two genera.

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13. Recombination potential between chromosome VII of corn and its homeolog from T. dactyloides.

As previously reported, one of the tripsacum chromosomes is partly homeologous to chromosome VII of corn and is capable of covering the recessives $\underline{v}_5$, $\underline{ra}_1$, $\underline{gl}_1$ and $\underline{ij}$. Plants carrying one or a pair of these extra chromosomes were backcrossed to the male corn parent and the combined segregation data for three loci tested are given in table 1.

By virtue of the irregular transmission of the tripsacum chromosome, certain basic assumptions have to be made in an interpretation of the segregation data for the parental as well as the recombinant characters. First, the dominant phenotypes are expressed only when the original tripsacum chromosome (TT) or its interchanged products (C^T or T^C) are included in the genome. With regular meiotic events observed for the corn (CC) or the corn-tripsacum interchange (C^T) chromosomes, recombinants of the higher order in each class of crossovers are regarded as due to the transmission of the C^T chromosomes; the number of reciprocal crossovers revealed in each of the three classes, being dependent upon the irregular transmission frequency of the corresponding T^C chromosome, would appear in less than the equal numbers normally expected. With the noninclusion of the T^C for any of these classes, there would be a corresponding enhancement of the recessive phenotypes; likewise when both the interchanged chromosomes C^T and T^C are included in the same gamete there would be an increase in the expression of all the dominants which would cover up the phenotypic expression of the crossover recessives. It is therefore considered that both of the observed parental combinations,

Ij, Ra, Gl and ij, ra, gl, are somewhat enhanced to the extent that the two reciprocally interchanged chromosomes are included in the same gamete on the one hand, and on the other to the extent to which the interchanged T^C chromosomes, in each of the crossover classes, are eliminated from the functional gamete. In a population of 663 plants classified for these three loci, the transmission frequency of the chromosome with the tripsacum centromere (T or T^C) is found to be 25.6%. The theoretical probability calculated on this basis is taken into account in giving the expected values for the parental combinations, while the reciprocal crossovers in each class, involving the T^C chromosome are taken as being about equal to the maximum observed values for the corresponding reciprocal on the C^T chromosome.

Table 1

Backcross data for Tripsacum homeolog to corn chromosome VII (66-376 to 434A)

(The theoretically expected data are not based on the known linkage values for corn chromosome VII but represent figures assumed to be the minimum probability for the unknown genetic content of the Tripsacum chromosome.)

	Chromosome type	Phenotype	No. observed	No. expected (theoretical)	Percent
Parental:	CC	ij ra gl	395	347	70.44
	TT	Ij Ra Gl	163	120	
Crossover I	C^T	Ij ra gl	24	24	7.24
	T^C	ij Ra Gl	7	24	
Crossover II	C^T	Ij Ra gl	66	66	19.77
	T^C	ij ra Gl	0	66	
Double crossover, I & II	C^T	Ij ra Gl	8	8	2.41
	T^C	ij Ra gl	0	8	
		Total	663	663	

Reduction or absence of phenotypes governed by T^C is due to its elimination and to that extent ij ra gl are enhanced; masking of the recessive crossover phenotypes by the inclusion of both C^T and T^C in the same gamete results in an increased value for the triple dominant Ij Ra Gl phenotypes. In addition, we have also to contend with some degree of suppression of crossing over due to nonhomologous pairing between the tripsacum and corn homeologs. Therefore, while these recombination data do not reflect the actual crossover frequencies, they do reflect the recombination potential and the probable difference in gene sequence. It seems that the Gl and Ij loci are in an inverted order between these two chromosomes. What is more important to recognize now is that despite their generic differentiation, morphologically as well as cytologically, these two forms are capable of genetic exchange. With refinement of the techniques in experimentation and selection of the proper material, it should be possible eventually to construct a comparative genetic map of tripsacum.

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14. The gene sequence of the Tripsacum homeolog to corn chromosome IX.

A comparison of the gene sequence of chromosomes which are homeologous between corn and tripsacum is possible when the heterozygous substitution is backcrossed to the marker stock of corn. The initial substitution chromosome derived from tripsacum is frequently an interchange chromosome which may not reflect its original structure. However, in the case of the tripsacum homeolog to corn IX, an early evaluation of its genetic content on an 8 recessive marker stock (yg_2, C_1, sh_1, bz_1, wx, gl_{15}, bk_2, and bm_4) made possible the selection and development in the heterozygous substitution of a noncrossover tripsacum chromosome for backcrossing to the tester stock. The data given below are based on the bronze and glossy-15 loci, which are separated by 38 crossover units spanning the centromere in maize.

Phenotype:	Bz_1 Gl_{15}	Bz_1 gl_{15}	bz_1 Gl_{15}	bz_1 gl_{15}	Total
No. recovered	219	17	14	233	483

Contrary to our expectations there were no other crossovers for the rest of the tested loci, with exception of two crossover individuals showing the waxy (wx) phenotype. Suppression of crossing over as well as differences in gene sequence and/or their map distances on the tripsacum chromosome seem to be the plausible explanations for the lowered value of 6.6% recombination observed in our testcross. Further tests are in progress.

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15. The possible occurrence of a gene for asynapsis (as)in chromosome 5 of T. dactyloides.

Both the 20+1 and 20+2 chromosome plants, carrying one or two extra tripsacum chromosomes homeologous to corn IX marked with 8 recessives, show near normal fertility and seed set. In contrast, their 20 chromosome derivatives, representing homozygous substitutions for all dominants from tripsacum, were either partly or totally sterile. The results of 276 self-pollinations of homozygous substitutions are summarized below:

a) No. of pollinations (69-651 to 69-700):	276	
b) No. of ears without any kernels:	177*	(64.1%)
c) No. of ears with kernel set:		
(i) greater than 50%:	16	(5.8%)
(ii) less than 50%:	83	(30.1%)

*Of these, 40 ears were from 11 rows in which all the plants selfed, without exception, gave no kernels.

Cytological studies made from samples collected at random from either the same plants or related ones revealed partial or total asynapsis of one or more bivalents at pachytene, variable frequencies of univalents at diakinesis and metaphase I, their uneven segregation at anaphase I, and associated irregularities at meiosis II, resulting in abortive spores. The univalent frequencies ranged from 0 to 20 per cell in different plants or in different sister nuclei of the same plant. The average univalent frequencies and the degree of kernel set in the

Table 1

Comparison of univalent frequency at Meiosis I and percentage kernel set on selfed ears of homozygous substitution stocks (2n=20).

Plant No.	Cytological Observations			Fertility Studies			
	No. of PMC's Observed	Total No. of Univalents	Average Univalent Frequency/ Cell	No. of ears Selfed	Ears with Kernel Set		
					None	More than 50%	Less than 50%
69 - 656	21	82	3.9	5	2	-	3
666	31	12	0.39	5	4	-	1
667	26	154	6.4	7	5	-	2
668	31	16	0.52	3	2	-	1
669	20	128	6.4	4	2	-	2
671	35	16	0.46	6	5	-	1
672	33	58	1.8	6	3	-	3
673	30	92	3.7	6	2	-	4
674	26	508	19.5	2	2	-	-
675	33	34	1.03	1	1	-	-
676	28	500	17.9	3	3	-	-
681	26	58	2.3	7	5	-	2
683	24	84	3.5	7	6	-	1
684	33	90	2.7	3	2	-	1
697	26	60	2.4	4	3	-	1
698	28	44	1.6	7	6	-	1

concerned plants are compared in Table 1. It is apparent that a very high univalent frequency is related to total failure in kernel set but that the contrary is not always true. In one family in particular (68-818) and its F_2 derivatives (69-674 & 676) this asynaptic characteristic acquired both a stronger or complete effect on the majority of individuals. Some degree of independence from the presence of the tripsacum chromosome in the genomes of these substitution stocks was also evident in some of the individuals which were completely fertile, while 25% of their segregants showing the recessive phenotypes for all tested loci became asynaptic and therefore sterile. There are three possible explanations for this variation: (i) some form of mutagenic effect of tripsacum introgression; (ii) spontaneous deletion of a segment with As on chromosome I of corn (As As being regulatory in function, As as also would induce asynapsis and univalency--Baker & Morgan, Genetics, 61, 1969) and (iii) the As in chromosome I being substituted by as of tripsacum subsequent to an interchange involving this locus. The unexpected occurrence of higher associations (quadrivalents or trivalents + univalents) in some of the related stocks, suggestive of additional homeologies to chromosomes other than chromosome IX, as previously reported (MNL, 1969), would seem to favor an interchange between this tripsacum chromosome and corn chromosome I, while at the same time maintaining its greater homeologies to chromosome IX. Absence of a direct correlation between univalent frequency and the degree of fertility observed could be due to the inherent variability in the expression of as as or ds ds recognized for maize and other genera (Riley & Law, Adv. Genet., 13, 1965).

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16. Progress on the cytogenetic comparison of maize and Tripsacum chromosomes.

The morphological features at pachytene of the tripsacum chromosomes homeologous to the different corn chromosomes ascertained from both the genomes of maize and Tripsacum dactyloides are compared on p. 127. The rela-

Chromosome No. in maize genome	Identified loci common to maize and Tripsacum	Length and arm ratio of the Tripsacum homeolog observed in the genome of				
		Maize		T. dactyloides		
		Total length (microns)	Arm ratio	Total length (microns)	Arm ratio	Assigned no.
IIS	Ws Lg_1 Gl_2 b Sk Fl_1	22.3(TKL)	1.7	25.9(TKL)	1.7	9
IVS	Su_1 (but not La)	29.3	2.8	27.0	3.2	7
IVL	Gl_3 (but not Bm_3 Ra_3 J_2)	22.4(TKL)	3.5	21.6(TKL)	3.5	13
VII	V_5: Ra_1 Gl_1 Ij	*				
IX	Yg_2 C Sh_1 Bz_1 Wx: Gl_{15} Bk_2 Bm_4	34.0(TKL)	4.0	32.4(TKL)	4.6	5

TKL: Terminal knob present in long arm.

*The Tripsacum homeolog described previously (MNL 1969) has since been found to be an altered form.

tive positions each of these extracted chromosomes occupy in the normal complement of T. dactyloides are also included to facilitate their identification.

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17. Internuclear variability in the form and pairing behaviour of the homeolog for corn chromosome II derived from T. floridanum.

Analysis of 35 pachytene nuclei from microsporocytes of six 20+2 Lg Gl plants, in which the added chromosome pair is derived from T. floridanum, revealed the presence of two distinct chromosome types of tripsacum in different sister nuclei. Their morphological features and that of chromosome 9 of T. dactyloides, all of which are homeologous to corn II, are compared in Table 1.

Table 1

Source of extraction	Length in microns			Arm ratio
	short arm	long arm	Total	
T. dactyloides:	7.7	13.2 (TK)	22.3	1.7
T. floridanum:				
*Type 1	6.6	11.4 (TK)	19.2	1.7
*Type 2	5.7	15.4 (TK)	22.3	2.7

*Represent averages of 21 and 14 observations, respectively, for types 1 and 2; TK - terminal knob present.

In addition to the types 1 and 2, the following variations with respect to the extra chromosome pair were also observed in some of the pachytene nuclei:

(a) partial or total asynapsis of the long arms with one of them loosely paired with a corn bivalent;

(b) heteromorphy for only the terminal knob accompanied by asynapsis in that region;

(c) deficiency for the terminal knob and part of the long arm, leaving the normal homologue as a univalent; the deficient segment of this pair occurs terminally in the short arm of a corn bivalent (probably chromosome X), which therefore assumes heteromorphy; occasionally the two heteromorphic bivalents pair in the univalent regions bearing the terminal knob; the expected quadrivalents, however, are not found in later stages;

(d) Homomorphic but devoid of the two terminal knobs; these are located terminally on two univalent chromosomes of the corn genome within the same nucleus.

Because of the close similarity of type 1 of T. floridanum with the chromosome extracted from T. dactyloides, it is probably the unaltered form of the homeolog. Such an interpretation would also be consistent with the regular and normal pairing reported in the F_1 of T. dactyloides x T. floridanum (Tantravahi, 1968) at least in so far as this chromosome is concerned. Consequently type 2, which has a higher arm ratio resulting from an increased length of its long arm, has to be regarded as the derived condition, which in all probability is related to the variations described under (a) to (d).

Occurrence of types 1 and 2 as well as the phenomena (a) to (d) among sister nuclei of the same anther seems to indicate that these chromosomal alterations took place in the pre-pachytene nuclei. Natural fragmentation and reunion of the bits resulting repeatedly in the same types of altered forms seems improbable, unless we assume some sort of break-susceptibility of particular regions on the concerned chromosomes.

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18. Spontaneous duplication of the nucleolus organizing body of chromosome VI in the genome of maize.

Supernumerary nucleoli were observed in the pollen mother cells of Lg gl plants which were derived from an interchange between the short arm of chromosome II of the recessive maize parent and its homeolog from T. dactyloides (chromosome 9) carrying the dominant alleles Lg_1 and Gl_2.

Detailed studies at pachytene and diakinesis of 482 cells have shown that, in addition to chromosome VI primarily concerned with the organization of the nucleolus, there is one other satellited chromosome pair in the complement. Both the primary and the secondary nucleolar chromosome pairs may undergo fusion of their nucleolar organizers and form a common nucleolus or they may form two separate nucleoli; in the latter case, the two nucleoli either remain distinct or may subsequently undergo fusion. The frequency of cells with one or more nucleoli in each of them and the mode of occurrence of the two bivalents concerned in their organization are given below:

	No. of cells observed		
	Pachytene	Diakinesis	Total
1. PMCs with a single nucleolus:			
(a) with two bivalents attached separately to nucleolus:	65	166	231
(b) with two bivalents showing fusion of nucleolar organizers	73	125	198
2. PMCs with two nucleoli:			
(a) with two bivalents separate--one pair for each of the two nucleoli:	15	5	20
(b) with two bivalents showing fusion of nucleolar organizers and associated with one nucleolus, while the other had no chromosome associated	17	10	27
3. PMCs with more than two nucleoli:			
(a) 3 nucleoli	2	2	4
(b) 4 nucleoli	-	2	2
Total	172	310	482

In the 73 pachytene nuclei showing fusion of the nucleolar organizers of the two bivalents, the short arm between the centromere and the nucleolar organizer of chromosome VI was not paired to any degree

with the region proximal to the satellited portion of the secondary nucleolar chromosome. The duplication therefore is confined only to the nucleolus organizing body and its satellited part. Such a view is confirmed from the absence of quadrivalents at metaphase I, which would normally be expected in at least a small proportion of the 100 cells examined had there been any duplication of the short arm of chromosome VI.

As to its origin, it is obviously due to a break at the region of the nucleolus organizing body followed by its transposition to the terminal region of a non-homologous chromosome within the genome. Since fusion can take place only between two broken ends, apparently the recipient chromosome also suffered a simultaneous fracture. Such chromosome breakages could be of a spontaneous type or due to some form of mutagenic effect resulting from the introduction of an alien chromosome into the genome, under particular conditions. Pedigrees of the stocks used in this study show that the breakage-transposition-duplication reported now could not have occurred more than three generations ago:

Pedigree of the material used in the study: (Each generation was selfed)

Plant or Stock No.	Phenotype	
1967-230-4	Lg gl	20+2 corn and tripsacum chromosomes; no evidence of supernumerary nucleoli or other abnormalities at meiosis.
1968-177	Lg gl	Only one plant survived; cytology not studied.
1969-332-3	Lg gl	20+2 chromosomes; supernumerary nucleoli and duplication of nucleolar organizer and satellite noticed.
-4	"	
-5	"	

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19. Comparative studies of American Maydeae and the Andropogoneae: I. Morphology of pachytene chromosomes of Elyonurus tripsacoides.

A knowledge of the morphology of their pachytene chromosomes could indicate the most probable hybrid bridge between the American Maydeae and the more closely related Andropogoneae. If such a hybrid were then produced experimentally, the data on chromosome morphology would serve

further as a basis for an evaluation of their cytogenetic relationships.

Elyonurus and Manisuris share certain floral features leading to the formation of the cupulate fruitcase in the American Maydeae. Except for the knowledge that these two genera have a 2n chromosome number of 20 and 18, they are little understood cytologically. The results from our initial exploratory studies on chromosome morphology in a form of Elyonurus tripsacoides from Veracruz, Mexico, are reported now.

At pachytene the 20 chromosomes form 10 bivalents regularly, of which one is the nucleolus organizing pair. This chromosome differs from maize chromosome 6 in all its essential features. The nucleolus organizing body, though terminally located with the satellited portion distal to it, is present in the long arm; it has an arm ratio of 1.2, a total length of about 26 microns and occupies the 9th position in the order of its length relative to others within the complement. The rest of the chromosomes fall into 9 other length categories and have their centromeres in the median to submedian positions. There are no other markers such as knobs or distinctive chromomere patterns for any of the chromosomes; however, the regions adjacent to the centromere are more darkly stained than the rest of the arms. Besides the nucleolus organizing chromosome, chromosome 6 can be readily distinguished by virtue of its distinctive arm ratio of over 6.0. The other chromosomes can be identified only when both the total length and arm ratio are considered together as diagnostic criteria.

Although 317 observations have been made on individual chromosomes, the entire chromosome complement could be traced in nine pollen mother cells. Averages from the latter are given in the following table.

Length and arm ratios of the pachytene chromosomes of Elyonurus tripsacoides (2n=20).

Chromosome No.	Short arm (microns)	Long arm (microns)	Total length (microns)	Arm ratio
1	24.3	27.5	53.5	1.1
2	18.0	25.2	44.6	1.4
3	14.0	24.9	40.0	1.8
4	14.0	20.6	35.8	1.5
5	12.6	17.2	30.9	1.4
6	4.0	24.6	29.5	6.2
7	12.6	13.7	27.5	1.1
8	9.7	15.4	26.3	1.6
9	11.2	13.7*	26.3	1.3
10	8.9	10.6	20.6	1.2

*Nucleolus organizing body terminal on this arm.

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20. Rate of pollen tube growth.

Because the apparent transmission rate of a tripsacum chromosome marked by the Su locus varied with the quantity of pollen applied to the styles, an attempt was made to determine if a differential rate in Su vs su tube growth was involved. Equality in transmission between the sugary pollen with 10 chromosomes and the pollen with 10+1 chromosomes, in which the extra chromosome was marked by the starchy gene, should yield a 1 su to 1 Su ratio on homozygous sugary styles. Although cutting the styles back by one inch at 4, 5 and 6 hours after pollination did not change the set of Su to su kernels, the data on rate of tube growth are of interest in regard to the safe time for cutting back exposed styles (Table 1).

Table 1

Seed set after cutting styles by one inch at various times after pollination.

Hours after pollination for cut:	4 hrs.	5 hrs.	6 hrs.	Control
Total ears pollinated	22	11	12	12
Ears with seed	0	4	10	12
Ears with 25 or more seed	0	2	4	12
Ears with seed lower half	0	2	3	12

No attempt was made to experiment with the physiological conditions.

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21. Supernumerary chromosomes in the Bussey clone of T. dactyloides.

According to Tantravahi (1968) presence of B chromosomes has not been previously established for any of the tripsacums, other than those reported by him for T. floridanum, T. maizar and T. zopilotense. In each of these species, a single B chromosome was recognized by him at pachytene and later stages of meiosis I.

In the course of studies to prepare the cytological map of T. dactyloides, it was found that one of our cultures contained variable numbers of chromosomes in excess of the expected 18 pairs for the species. These supernumerary chromosomes were either organized as bivalents or occurred as univalents. At pachytene, it was difficult to distinguish them from the A chromosomes because of heavy clumping. But, where discernible, some of them were darkly stained while others were nearly normal. Distinction between a paired bivalent or a univalent with a fold back, and the position of the centromeres were also uncertain. Often they were attached to the terminal knobs of the A chromosomes. The range of variation in their number and behaviour scored from PMC's at diakinesis is summarized below:

No. of chromosomes 2n	Type of association	No. of cells observed
36	18_{II}	18
	$16_{II} + 1_{IV}$	2*
	$17_{II} + 2_{I}$	2
38	19_{II}	7
	$18_{II} + 2_{I}$	8
	$16_{II} + 6_{I}$	1
39	$18_{II} + 3_{I}$	1
40	20_{II}	8
	$19_{II} + 2_{I}$	4
	$17_{II} + 1_{IV} + 2_{I}$	1*
	$16_{II} + 2_{IV}$	1*

*Quadrivalents need to be confirmed at pachytene and metaphase I.

From their behaviour at anaphase I, it seems some of the extra chromosomes are centric (B chromosomes) while the rest are probably acentric fragments. Since this is the first report of their occurrence in T. dactyloides and since such high numbers have not been found in any of the tripsacums, their origin needs to be examined.

The different cultures, vegetatively maintained by us over many years, represent some of the seedlings derived from an initial cross of T. dactyloides x maize. Among thousands of hand pollinations made, only a few seeds were obtained. These seeds germinated to give rise to 36 chromosome tripsacums, obviously due to apomixis. In many of their morphological characters, each of these was quite different from the maternal parent, possibly due to the homozygosity attained for some of the recessive characters. That one of these plants should contain B chromosomes in such numbers is somewhat surprising. Gradual accumulation

of the same chromosome is ruled out because of their distinct features at pachytene. From the known history of their pedigree, these B chromosomes seem to have originated from the A's. But their continued presence, without loss, if they are acentric fragments or the origin of separate centromeres for those that are centric and form bivalents regularly is difficult to explain.

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1. Peroxidase isozymes of maize: Genetic, ontogenetic and specificity studies.

Genetic variants of peroxidase have been found in pollen and endosperm extracts of several inbred maize strains. The two variants most easily discernible in the pollen extracts appear to follow simple Mendelian rules and are apparently regulated by codominant alleles at one locus. The genetic evidence supports a monomeric structure for the peroxidase products of this locus. In addition to these variants, five other zones of peroxidase activity are present in zymograms of pollen extracts which segregate in a manner suggesting other gene loci. Examination of the liquid endosperm of these strains shows a total of 7-8 peroxidases.

Differential distribution of these peroxidases in specific tissues or organs of the maize sporophyte was reported previously (Scandalios, 1964). Experiments done to determine the subcellular distribution of these peroxidases inidcate that most, if not all, are probably associated with cell wall components. Chloroplasts, isolated intact and purified, show no peroxidase activity when such activity is measured both qualitatively and quantitatively. Chloroplasts have been isolated from five

different inbred maize strains and from several pea mutants, and all gave negative peroxidase activity.

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2. The genetics of amylases in maize.

Amylases of maize were separated into two zones by acrylamide gel electrophoresis, at pH 8.2. The fast (Zone-1) and slow (Zone-2) anodal zones are tentatively identified as alpha- and beta-amylase, respectively. Genetic variants were found in both Zone-1 and Zone-2. Genetic analysis of the Zone-2 amylase showed that the variants at this zone are under the control of two alleles acting without dominance. The resolution of Zone-1 amylase was found to be best by assaying endosperm extracts from 10-day old seedlings. Preliminary genetic analysis of 220 F_2 seedlings indicates that Zone-1 amylase is controlled by two alleles independently from the Zone-2 amylase.

The possibility of genetic linkage between Zone-2 amylase and several other genetically well-defined isozyme systems in maize was examined in our efforts to assign the amylase genes on specific chromosomes. Genetic linkage was assessed through backcross and F_2 progeny by electrophoretically assaying individual kernels, 16-20 days after pollination. The data from such experiments are summarized in the table below. It appears that Amy-2 and Ct (catalase) are linked on a chromosome within 5 map units of each other. No linkage was detected between AcP (acid phosphatase) and Amy-2 or Ct.

The crossover frequencies among the three loci, Amy-2, Ct, and AcP.

Crosses	Amy-2:Ct		Amy-2:AcP		Ct:AcP	
	Total	Crossover	Total	Crossover	Total	Crossover
W64A x (W64A x 6)	180	0.09± 0.02	100	0.53± 0.05	101	0.53± 0.05
6 x (W64A x 6)	118	0.05± 0.02	120	0.54± 0.05	119	0.50± 0.05
(W64A x 6) x (W64A x 6)	278	0.05± 0.01	312	0.49± 0.03	298	0.49± 0.03

The genotypes of the two inbreds are:

$$W64A = \frac{Amy\text{-}2^{B}\ Ct^{S}\ AcP^{A}}{Amy\text{-}2^{B}\ Ct^{S}\ AcP^{A}} \; ; \; 6 = \frac{Amy\text{-}2^{A}\ Ct^{F}\ AcP^{B}}{Amy\text{-}2^{A}\ Ct^{F}\ AcP^{B}}$$

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1. Transfer of instability of the P S^{st} complex to the P component.

The compoundness of the R locus allows an analysis of the manner in which the P component of R is affected by its association in coupling with an unstable S component (S^{st}). The first step of this analysis is the recovery of P S^{st} intralocus recombinants. Two of these recombinants have been previously isolated (Gavazzi and Avila, M.N.L. 1968) and reproduced.

Contrary to our earlier observations, descendants of these intralocus recombinants show pigment variegation in their sporophytic tissues. The variegation, when roots or coleoptile tissues are observed at low magnification (20x), consists of a series of contiguous red stripes.

We have observed a third case of root variegation in the descendants of a single colorless kernel. Originally this kernel was isolated as a putative seed mutant (s) on an ear produced from the cross of a p S^{st}/P S individual with a p s/p s line. Since no R outside markers were present in the heterozygous parent, the association of the "colorless" mutant with a recombinational event could not be established.

This exceptional individual and its descendants, whose structural organization at the R locus (in terms of p and s) is not clear, will be referred to as "mutant." Descendants of the "mutant" were colorless in their aleurone and devoid of pigment in their sporophytic tissues. However, in a few individuals clear stripes of anthocyanin were produced either on the roots or on the coleoptile or in the anthers.

Kernels obtained by testcrossing individuals genotypically p s/ "mutant" (i.e. with one chromosome 10 marked with p and s and its homolog carrying the R "mutant") with a ps/ps line were germinated and scored for variegation in their sporophytic tissues. Out of 2044 kernels germinated, 270 were variegated in either their roots or coleoptile, 8 were completely red and the remaining 1766 were without pigment at all. If we assume that seedling variegation is controlled by the "mutant" only (as shown below), it then appears that variegation is expressed in only 26.4% (270/1022) of the seedlings that have the "mutant" in their genotype.

Evidence that the root variegation is associated with the R region of the "mutant" was obtained by crossing heterozygous p s/"mutant" individuals with a p S/p S homozygous line. Individuals so obtained are genotypically separable into two classes: (i) "mutant"/p S and (ii) p s/p S.

They were both testcrossed with a p s/p s line.

Ears obtained from plants of genotype (i) could be easily distinguished from those of genotype (ii) since the "mutant" had maintained the paramutagenic capacity of the S^{st} ancestor. Germination of colored and colorless seeds from the two groups of ears proved that root variegation is associated with the R "mutant" since only colorless kernels from testcross (i) were exhibiting, upon germination, pigment variegation in their sporophytic tissues.

If we assume that S^{st} is a compound structure consisting of S plus an adjacent regulatory component (Rg), the most likely interpretation of these observations is that the R "mutant" originated from an intralocus recombination of the oblique type (Emmerling 1958) that gave rise to a crossover strand deficient for the S component and with the regulatory component (Rg) in coupling with P.

The event leading to the appearance of a similar strand is depicted below:

These observations, even though limited, seem to suggest that the mechanism leading to S instability can extend its action to the P component of R when both P and S are brought in coupling on the same chromosome.

G. Gavazzi

2. Mutability of the S component of the R locus.

As previously outlined, the S component of R^{st} is unstable. The instability consists of frequent changes of S from an inactive to an active state, leading to a variegated aleurone phenotype. If this change occurs in the germ line cells, it gives rise to a stable form of S. This form is symbolized S^{sc} (self colored) to distinguish it from the S components present in the R^{r} and R^{ch} gene complexes. S^{sc} in fact determines pigmentation in both the scutellum and aleurone and it conditions a full pigmentation of the aleurone even when present in a single dose ($s\ s\ S^{sc}$). The other two S components do not extend the pigmentation to the scutellum tissues and condition a mottled aleurone phenotype (S of R^{r}) or a pale phenotype (S of R^{ch}) when present in a single dose.

It is likely that these phenotypic differences reflect a difference in the structural organization of the genetic material at the R locus in the three different forms of R.

This possibility has been tested by comparing the frequency and spectrum of mutation of the S component of the three forms of R. The results obtained are reported in Table 1. The S^{sc} gametes analyzed were obtained from individuals heterozygous for two S^{sc} isolates of

independent origin. In this way the mutational behaviour of 7 different $\underline{S}^{sc}$ isolates was studied.

The data presented in the Table indicate that while the $\underline{S}$ component of $\underline{R}^{r}$ and $\underline{R}^{ch}$ mutates to $\underline{s}$ (null level allele) with a frequency of about 1%, $\underline{S}^{sc}$ gives rise only to mutants conditioning an intermediate level of pigmentation with a very low frequency. No $\underline{S}^{sc} \longrightarrow \underline{s}$ mutation has been observed.

The mutational behavior of $\underline{S}^{sc}$ could be explained by assuming that $\underline{S}^{sc}$ consists of a series of reiterated $\underline{S}$ genes that originated through a process of gene duplication not associated with gene divergence. According to this hypothesis the mutation of $\underline{S}^{sc}$ to the null level $\underline{s}$ allele could arise through two or more succeeding steps. This would represent a rare event not easily observable in the sample of gametes we analyzed. On the other hand, the "mutation" to intermediate level alleles could be the result of unequal crossing over between either sister or nonsister strands with the production of a crossover strand lacking one or more $\underline{S}$ duplicates.

We are presently trying to obtain experimental evidence in favor of this hypothesis.

Table 1

Frequency and spectrum of mutation of $\underline{S}$ components of different origin.

Origin	n (no. gametes tested)	Colorless		Nearly colorless		Pale		Slightly pale	
		Isol.	Tested	Isol.	Tested	Isol.	Tested	Isol.	Tested
R^{sc} R^{sc*}	36,137	0	0	1	0	1	1	3	2
R^{r} R^{r}	24,207	24	18	0	0	0	0	0	0
R^{ch} R^{ch}	42,390	47	0	0	0	6	0	0	0

*$\underline{R}^{sc}$ indicates a form of $\underline{R}$ carrying a stable $\underline{S}^{sc}$, isolated from an unstable $\underline{S}$.

G. Gavazzi
G. Avila

3. Inheritable instability of the B^4 chromosome.

When individuals of the genotype $4\underline{su}$, $4\underline{su}$, + $B^4\underline{Su}$ were crossed as the male parent to a $\underline{su}_1$ tester, about 16% of the progeny showed the Su phenotype as the result of the transmission of the supernumerary B^4 chromosome marked with Su (see M.N.L. 42, p. 70, 1968).

While most of these kernels appeared uniform (starchy and round), a number of them showed single su sectors of various sizes resulting from the loss, in the endosperm tissue, of the dominant marker which is present in the supernumerary chromosome. The nature of the loss observed in the form of sharp sectors is not known, although the indications are that this phenomenon is the result of chromosomal behavior rather than of genic instability. Chromosome lagging, non-disjunction, or breakage (proximal to Su) would be equally able to produce the same effect. Sectors were obtained on progeny kernels of plants grown from any Su kernels, whether or not their endosperm showed su sectors, and the variation observed in the frequency of the appearance of sectors is possibly due to the influence of several factors (background and/or environment).

A different phenotype, however, was found in some of the kernels which appeared as Su/su mosaics. In these cases the Su phenotype was frequently lost during endosperm development. Some of these kernels were planted in the summer of 1966 and later to be crossed to a $\underline{su}_1$ tester. An examination of their progeny revealed the following facts which are summarized below:

cross: $\underline{su}_1$ ♀ x $4\underline{su}, 4\underline{su}$, + $B^4\underline{Su}$ ♂ Phenotype of the male parent: mosaic Su/su	No. of ears
Transmission of stable Su with a typical frequency	4
Transmission of stable Su at a very low rate	8
Transmission of Su/su mosaics (at a very low rate)	5
No transmission of Su (su only recovered)	10
Total No. of ears	27

The appearance of mosaics in the progeny of mosaic kernels of the type described above (which was reported at the Maize Genetics Conference, Allerton, 1969) showed the inheritability of this phenomenon. The results obtained with the B^4 chromosome compare well with unstable B^9 derivatives obtained by W. Carlson (personal communication, and M.N.L. 43, p. 79, 1969).

progeny of unstable B^4Su		progeny of unstable B^9C	
Stable Su	12	Solid color C	12
Mosaics Su/su	5	Mosaics C/c	7
su only	10	c only	12
Total	27		31

A common feature is that mosaics are recovered from one out of every 4 or 5 plants grown from a mosaic kernel. When mosaics are not recovered, the chromosome apparently either regained its stability or was lost with nearly equal frequencies. It seems that events of breakage are detected and selected for. In the case of B^4 the frequency of transmission of stable Su types was rated either "typical" or "low." In the first case, the event that led to the mosaicism was probably limited to the endosperm. In the second case, a breakage distal to Su which occurred during or after meiosis possibly started a breakage-fusion-bridge cycle which continued in the endosperm tissue, while the embryo had a modified B^4 chromosome whose broken end healed. This chromosome could be either deficient or have deficient + duplicate regions resulting from the b-f-b cycle, and this change in its structure would be responsible for the low recovery which has been observed through both male and female gametes.

The transmission of mosaics is certainly due to an unstable chromosome structure whose behavior is similar in many regards to that of ring chromosomes. In root tip cells it is difficult to study the structure of the supernumerary chromosome involved, which is much smaller than the original B^4; this observation supports the idea that breakage was

responsible for the mosaic phenotype. Pachytene also is of little help since this chromosome is a single one and appears backfolded on itself. However, in premeiotic prophases where the cells are large and the chromosomes are in a favorable stage for observation, a ring structure was clearly seen in the only plant so far investigated.

The recovery of su only, from mosaic kernels, was found in a high number of cases. Noncorrespondence between embryo and endosperm is often due to nondisjunction in the 2nd microspore division when B or B^A chromosomes are involved. But this is apparently not the case, since no 4^B is present (Roman found 4^B necessary for the nondisjunction of B^4) and, moreover, the endosperm showed a mosaic phenotype indicating a chromosomal instability which led to the loss of the dominant Su in one of the sperms. Heterofertilization in ten out of 27 mosaics is unlikely. Finally, transmission of su only occurs in a few cases from mosaics of the inheritable type, and, in reciprocal crosses, the unstable structure is recovered much more frequently through the pollen than through the egg. This was seen in 20 of the 22 plants so far tested. The two exceptional cases unfortunately were lost.

The formation of a ring chromosome requires two breakages, one in each arm if the centromere is to be included. Since the B^4 chromosome is subtelocentric, only a high frequency of breakage in the very short arm could account for the high frequency of ring formation. The finding of these spontaneously formed unstable structures (which are inheritable) with such a high frequency is unprecedented and remains unexplained. However, the chromosome involved is a supernumerary one and therefore not necessary to the viability. The cells where this chromosome undergoes breakage, disintegration, or rearrangement are then easily detected if the phenomenon occurs in the germ line.

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1. Linkage tests in homozygous interchange stocks.

2-6(001-15)2S.78-6 (sat.): Break between gl_2 and v_4; lg gl_2 segment attached to 6 replacing at least part of the satellite. Based on 115 plants, recombination values are: lg-gl 22.6; gl-v_4 53.0; Y-lg 35.2; Y-gl 17.7; Y-v_4 52.1.

2-6b S.69-L.49; Breakpoint in 2 between gl_2 and v_4.

2-6(5472)S.25-L.15; Breakpoint in 2 between gl_2 and v_4.

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2. Albino seedling W7748. (see M.N.L. 43:113-114, 1969).

Crosses with the aleurone color testers show that r is the one with which this character is linked. Crosses have been made with other markers in this chromosome.

C. R. Burnham

3. White tip seedling.

This character was described last year (M.N.L. 43:114). It appeared among the self progeny of plants from crosses of A188 inbred with pollen from white-striped sib plants, and also in crosses on A188 interchange stocks. The latter F_1's were backcrossed to white-tipped.

Segregation for the white-tipped character was close to 1:1, but most cultures had a few white-striped plants similar to the original ones, ranging from plants with a few white stripes to ones mostly white. Only in one culture was the segregation close to 3:1 (49 striped, 157 green).

There was no evidence of close linkage with T1-3 (5883), T5-7 (5179), T5-7e, or T3-7c. There was linkage with T2-10 (6061) (designated in Longley's ARS 34-16 list as T5-10 (6061)). The data are:

Culture	Interchange breaks		+ S.S.	+ F	wh.tip S.S.	wh.tip F
19247	2-10 (6061)	S.60( )-L.57	67	1	8	44
19248	"	"	43	0	2	9
			38	23	22	13
19224,5	2-4L	L.59-S.40	43	47	32	34
19226,7	2-6b	S.69-L.49	29	23	24	18
19233	5-10(5290)	L.78-S.49	21	13	19	14
19245	1-3(5883)		31	10	18	14
19246	"					

Only part of the plants were classified for sterility by pollen examination. Contrary to the statement in last year's report, the white-tipped plants were less vigorous than the normal sibs (on poor soil). Many of them had ears too small to be classifiable for sterility. This is reflected in the data for T2-10 (6061). The observed numbers give a recombination value of 6.3%, but the actual value is probably much lower than this. It is assumed that the breakpoints originally reported on chromosome 5 can be applied to chromosome 2. Since data for 2-6b with the break also in 2S and for T5-10 (5290) with the break in 10 in the short arm show independence, it is probable that this gene is in 10L.

The data for T1-3 (5883) are included as an illustration of the fact that occasionally (for no apparent reason) results based on only the dominant class for the character may be misleading. All but a few plants in these two cultures were classified on the basis of pollen sterility.

C. R. Burnham

4. Effects of colchicine on multiple interchange heterozygotes.

In M.N.L. 42:120 1968, it was reported that plants heterozygous for two rings of 10 produced sectors that extruded anthers and shed pollen when treated with colchicine as seedlings. The filled grains were much larger than normal. A few seeds were obtained by self pollination.

This seed was planted in the greenhouse and two plants transplanted to the field. The one plant that survived also had large pollen and was self-pollinated. The ear was well-filled but the kernels varied in size. Plants from both the large and small kernels

were all diploid. A few have been crossed with standard normal diploids. These will be grown this summer. The colchicine treatments will be repeated.

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1. Frequency of sector size for R alleles.

The expression of R alleles, reflecting their regulation, is complex; study of somatic pigment expression in the intensity and pattern of cell sectors in aleurone tissue may provide a basis for understanding the processes involved in regulation and in the paramutation phenomenon.

Studies were carried out on kernels carrying a single dose of R^{st}, R^{r}, $R^{r'}$ (R^{r} exposed once to stippled) and $R^{r''''}$ (R^{r} exposed multiple times to stippled) to analyze the size of sectors, their frequency, and the intensity of pigment in the cells.

Stippled (R^{st}) produces mostly uniform sectors and uniform pigmentation surrounded by extremely light colored cells presumably due to diffusion. Fig. 1 shows the relationship between size of sector and frequency. The most distinct feature observed was that peaks were prevalent for sectors having an even number of cells: 2, 4, 6, 8, 10 etc. The highest frequency was observed for 4-cell sectors.

In contrast to stippled, R^{r} (mottling), $R^{r'}$ and $R^{r''''}$ show a quite different pattern of sectors containing non-uniform and unevenly distributed cells of three color levels that are distinguishable under the microscope. There were significant differences in the frequencies of color levels among these R alleles. Following is the distribution of the three types of cells in percentage:

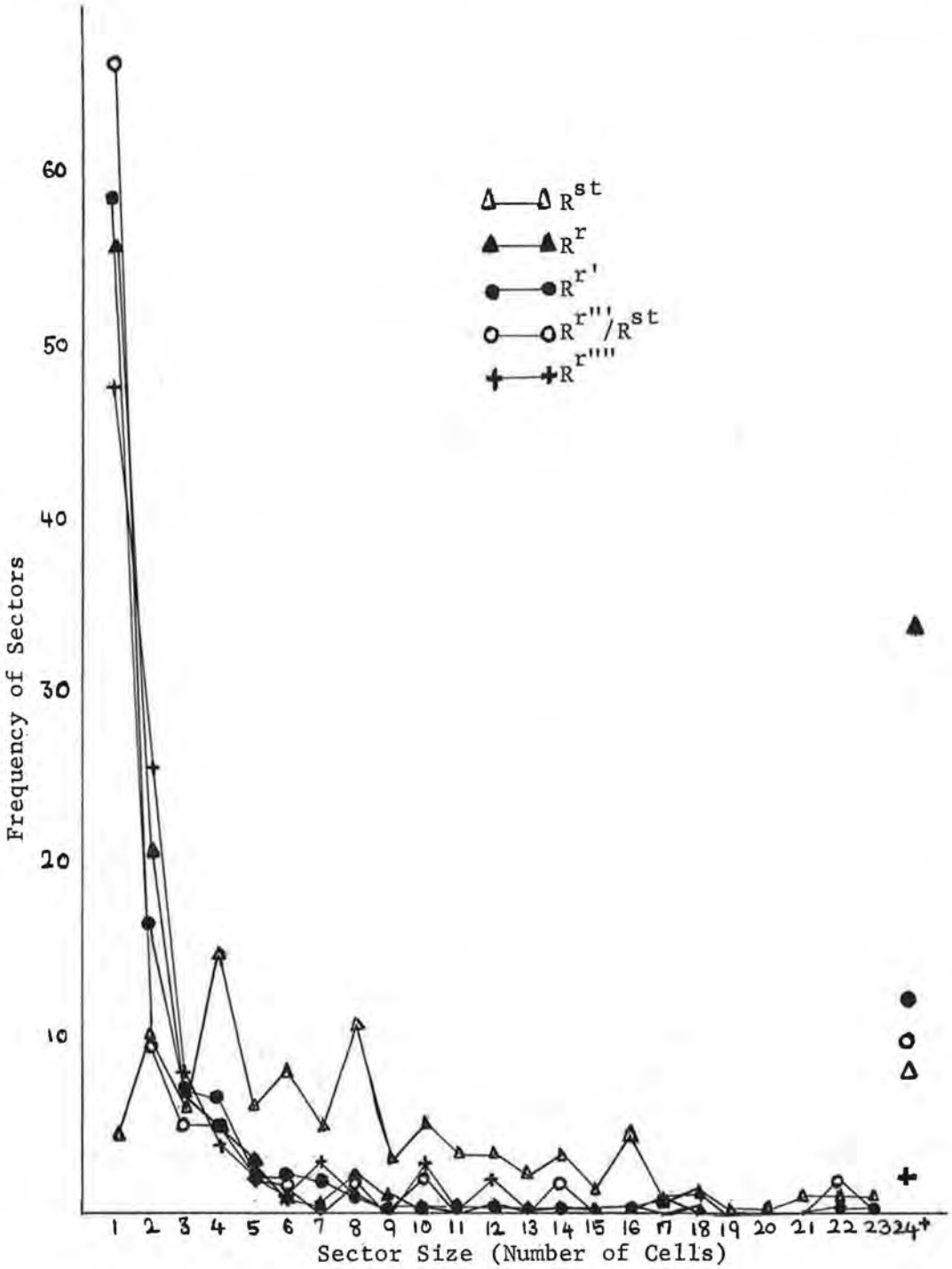

Fig. 1. Distribution of sector size for R alleles. Connected points show percentages of individual sector sizes in a total of all sectors up to 23 cells. Points for 24^{+} cells are based on the percentage in the total of all sectors.

$\underline{R}^r$ Source	Percent Colored Cells			Colored Cells
	Dark	Medium	Light	Frequency in Percent
$\underline{R}^r\ \underline{R}^r$	69.93	9.47	20.43	52.90
$\underline{R}^r\ \underline{R}^{st}$	51.13	17.27	31.59	13.24
$\underline{R}^{r'''}\ \underline{R}^{r''''}$	44.52	12.43	43.04	0.037
$\underline{R}^{r'''}\ \underline{R}^{st}$	49.79	13.59	36.61	0.037

There was a significant rise in the proportion of medium and light colored cells in $\underline{R}^{r'}$ and $\underline{R}^{''''}$ compared to $\underline{R}^r$, while the frequency of colored cells dropped significantly from $\underline{R}^r$ to $\underline{R}^{r'}$ to $\underline{R}^{r''''}$.

The $\underline{R}^r$ allele showed a distribution very different from that for $\underline{R}^{st}$ (Fig. 1), but all of the $\underline{R}$ alleles were similar in distribution of sector size. Their most frequent sector type was single cell; the distribution drops rapidly and tapers. Small peaks were notable at 4, 8, and 16-cell size.

Chandra Mouli
E. H. Coe, Jr.

2. Effects of extractables from whole pollen on pollen function.

Toward analysis of the "population effect" found earlier for pollen suspended in aqueous media (see 1969 Newsletter), a test for effects of rapidly extractable substances was conducted in 1969. The control series used one ml of pollen suspended in 25 ml of aqueous medium, held for 40 seconds and then applied to ears with a brush at 10 second intervals. The treated series used the same proportions and timings, but the aqueous medium was derived by first mixing 25 ml with 10 ml of pollen; this mixture was held for 5 minutes and filtered. The clear filtrate was then brought to 25 ml with aqueous medium and used for the experimental pollen. Figure 2 shows the changes in seed set with time, as a running average of 5 ears. The effects of extractables are in agreement with those reported last year for the "population effect"--namely, that long-term survival is influenced, though not

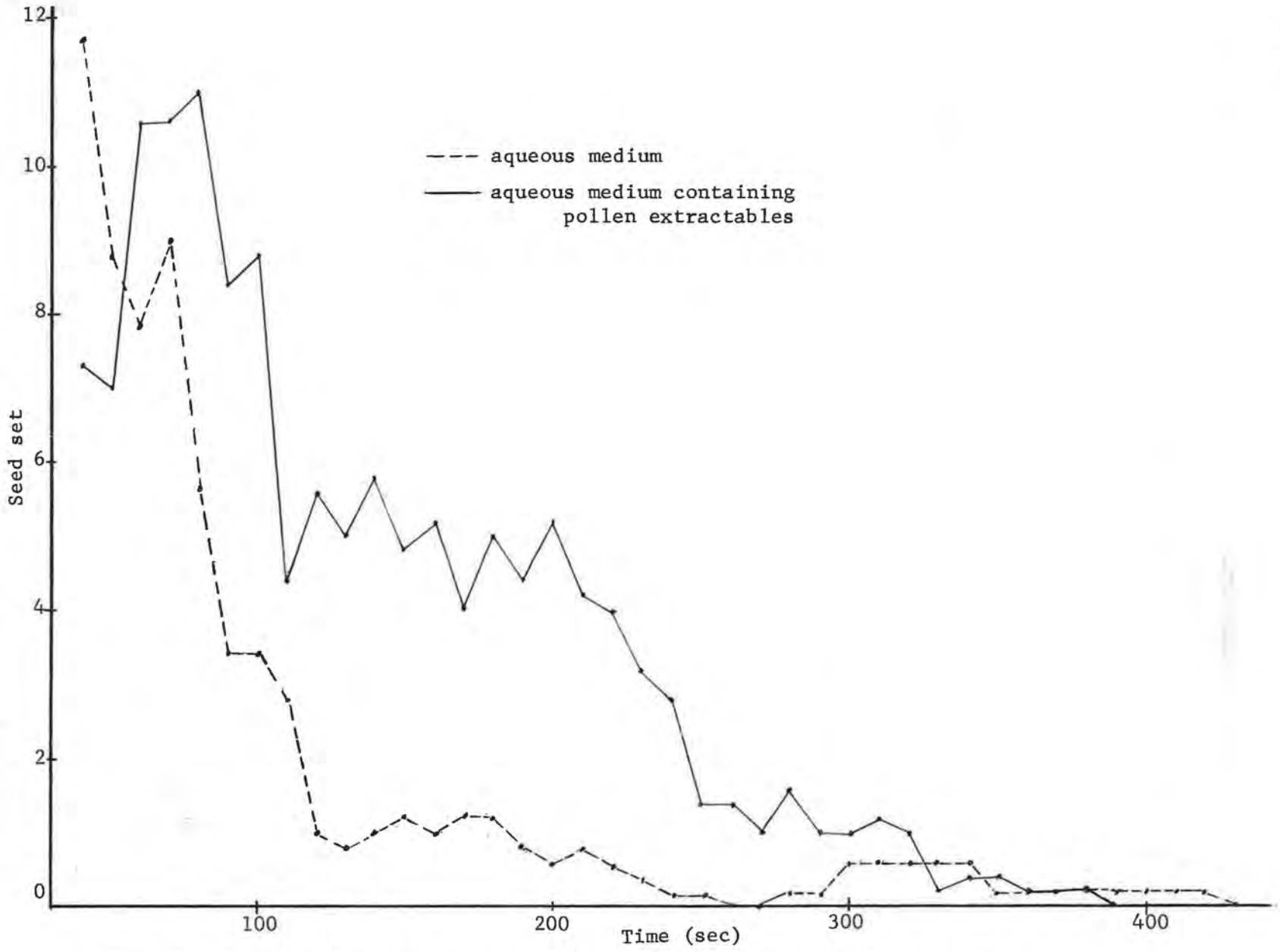

Fig. 2. Seed set (running average of 5 ears) in relation to time in medium.

permanently augmented, by the presence either of more pollen or of pollen extractables.

In the control series 67 kernels were obtained from one ml of pollen, while 208 were obtained in the experimental series. The overload requirement (thousands more pollen grains were applied than kernels obtained) was still not greatly altered, and remains puzzling.

E. H. Coe, Jr.

3. Tests of selection for pollen resistance to exposure to aqueous media.

Repeated trials have failed to support the idea that heritable variation might exist among pollen grains in respect to their ability to withstand exposure, brief or prolonged, to aqueous media. The current data are presented here as examples. Three lines (W23; N, a purple-seeded standard; K55) have been tested by simply planting the kernels that resulted from pollinations with exposed pollen, and selfing the plants with again-exposed pollen. In the following table are data for the third or fourth exposure for each of four media (Y is the aqueous medium; YD contains 5% dimethyl sulfoxide, YSC saline citrate, and YT 2% Tween 80).

Medium	Line	Selection Cycles	No. retested plants with seed set of				
			0	1	2	3	5
Y	W23	2	19	1			
	N	3	2				
	K55	2	4				
YD	W23	2	1				
	N	3	21	6		1	1
	K55	2	4				
YSC	W23	3	1				
	K55	2	2				
YT	W23	2	21				
	N	2	24	3	1		
	K55	2	11	1			

E. H. Coe, Jr.

4. Pollination with small counted samples of pollen.

In a test conducted by Y. H. Chang in 1967, counted samples of fresh pollen from A C R were carefully applied to silks of c tester ears in a large block of this genotype (i.e., contaminations would be unlikely to be C). The results were as follows (A stands for applied counted pollen grains, P for purple kernels obtained, Y for yellow contaminants, and E for 100P/A as a measure of efficiency):

A	20	20	50	50	50	50	100	100	100	100	150	150	150	150
P	2	5	5	10	13	17	7	28	14	25	6	27	21	33
Y	1	2	4	7	10	6	3	1	2	3	0	0	3	5
E	10	25	10	20	26	34	7	28	14	25	4	18	14	22

I carried out a similar test last summer, with W23/M14 (c c r r) as ear parent, with the following results:

A	7	9	12	12	16	18	20	20	37	38	41	43	78
P	1	2	0	1	0	2	3	0	5	5	4	6	9
Y	2	2	9	0	0	3	0	2	5	5	5	0	9
E	14	22	0	8	0	11	15	0	14	13	10	14	12

At these levels of pollination no "population effect" is operating, since the efficiency seems neither to decrease with higher counts nor to change with higher contamination. The most efficient one of these trials (17 kernels from 50 pollen grains) is evidence, though not proof, that more than one of each four microspores is functional. If only one microspore were functional, only 10% of random samples of 50 grains would include as many as 17 functional grains.

E. H. Coe, Jr.

5. Allelism and expression of Wh and Wc.

Linkage data have established that Wh and Wc are in the same region of chromosome 9. A test for allelism establishes that they are essentially allelic; discrimination tests indicate that Wh is slightly more expressive than Wc. Among 10 ears from the cross of +Wc/bk Wh x bk +, no clearly yellow (wild type) kernels were found in a population of 3,708 kernels. Progeny tests of 14 kernels that were the yellowest from each ear showed segregation of dominant "white" in each instance. The

expression of Wc (white cap) in contrast to Wh (lemon endosperm) was not clearly distinguishable in the testcross ears, but some variation in the endosperm color was suspected, so separations were made of 10 darker yellow and 10 lighter yellow from each ear. The plants were classified for bk_2, which shows about 25% recombination with Wc. The darker yellow class showed a +:bk ratio of 55:36, the lighter class 46:41. In addition, among the class chosen as possible yellow exceptions (for progeny test as above) the ratio was 16:7. The separation of Wc from Wh is by no means perfect, but Wc kernels seem to be slightly more yellow. This agrees with earlier impressions of Wh versus Wc classification.

E. H. Coe, Jr.

6. Dominant dilute aleurone color factor on chromosome 7.

A factor with dilute expression has been located near in on chromosome 7; it is tentatively designated In^D. Progeny from $\frac{o_2 + gl}{+ In^D +} \times \frac{o_2 + gl}{}$ were as follows:

$\frac{+ In^D +}{}$	$\frac{o + gl}{}$	$\frac{+ + gl}{}$	$\frac{o In^D +}{}$	$\frac{+ In^D gl}{}$	$\frac{o + +}{}$	$\frac{+ + +}{}$	$\frac{o In^D gl}{}$
109	111	4	5	5	4	0	0

$o_2 - In^D = 0.04$ $\qquad$ $In^D - Gl = 0.04$

The expression of In^D is quite clear, even in the presence of o_2. Homozygotes have very faintly pigmented aleurone tissue. In homozygous pr, the aleurone color is a unique lavender. No plant color effect can be detected.

E. H. Coe, Jr.

7. The development of pigments in germinating colorless seeds.

Germinating seeds of c_1 tester synthesize anthocyanin pigments in the aleurone tissue. The pigments look similar to those of A_1A_2CR genotype, yet less concentrated. There are some variations among c_1 kernels from different sources, in the sense of quantity and quality. Certain lines can develop very strong and uniform pigmentation while certain others develop little or none. Plant color genes, B and Pl, may control

germinating pigmentation in aleurone tissue in some cases. Since positive lines (which can develop pigment during germination) and negative lines (which cannot) give rise to positive F_1's, there may be a dominant factor present in these positive lines. The pigmentation is inhibited by $\underline{C}^I$ (with some exceptions), and colored spots are found on the kernels of $\underline{c}\ \underline{c}\ \underline{C}^I$ after germination. This is presumed to be caused by chromosome breakage in the short arm of chromosome 9, followed by loss of $\underline{C}^I$. Neither $\underline{a}_1$ tester nor $\underline{r}$ tester has the capacity.

Light is essential to the development of germinating pigment in most of the $\underline{c}_1$ lines, although there are a few strains which can develop pigment in the dark. A short-time (5 minutes), low energy illumination is sufficient to induce detectable amounts of pigment. The effect of light is limited to the stages before the young root stretches out of the pericarp. Red light of around 650 nm is the most effective wave length, and infrared has an inhibiting effect. The mechanism of light induction of germinating pigmentation in aleurone tissue and the genetic factors involved are under study.

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1. Location of TB-3b with respect to marker loci.

TB-3b, induced originally by X-rays, has now been satisfactorily located; it is situated on the short arm of chromosome 3 proximal to $\underline{cr}_1$, $\underline{d}_1$, $\underline{ra}_2$, and $\underline{cl}_1$. The breakpoint is distal to $\underline{rt}$.

Although dominant genes are not easily located by means of B-type translocations, plants with a poorly expressed corn-grass phenotype were observed to segregate in a progeny of $\underline{cg}/\underline{Cg}$ x TB-3b; these were probably hyperploids of the constitution $3^{Cg}\ 3^{B}\ B^{3}\ cg\ B^{3}\ cg$ showing modification

of the corn-grass phenotype by dosage effect. Therefore, Cg is apparently distal to the translocation, as would be expected from its map position.

J. B. Beckett

2. Location of TB-5a with respect to marker loci.

A B-type translocation involving the long arm of chromosome 5 has apparently been separated from the X-ray induced translocation complex, involving chromosomes 5, 6, and a supernumerary, reported in MNL 42:132. Pollen sterility has dropped from the original 60-75% to about 30%. It now seems appropriate to name this translocation, so it is designated TB-5a.

The breakpoint of TB-5a lies between v_3 and bv_1, the former being proximal and the latter distal.

Incidental information regarding td (thick-tassel dwarf) and na_2 may be of interest here. Both are proximal to TB-5a and both appear to be closely linked to the translocation. Since bv_1, td, and na_2 plants are all somewhat dwarfed, the stocks were intercrossed to test for allelism; Na_2/na_2 x bv_1 and Td/td x na_2 gave wholly normal progenies. The additional observation that na_2 and td are proximal to TB-5a and that bv_1 is distal makes it evident that the three represent distinct loci.

J. B. Beckett

3. Patterns of nucleolar distribution at the quartet stage of meiosis in tetraploids.

There are two nucleolar organizers located on the short arm of chromosome 6 in each microspore of a quartet formed from meiosis in a tetraploid. They each may form a small nucleolus or they may combine to form one large nucleolus. The greater the proximity of the nucleolar organizers, the greater is the probability that they will function together to form only one nucleolus. Consequently, the presence of only one nucleolus indicates that the short arms of chromosome 6 are close together.

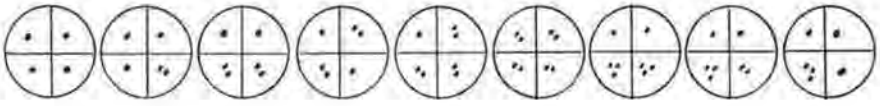
There are six major types of patterns possible in a quartet. They are shown in Table 1. The plane of first division is very difficult

to see in tetraploid quartets. If it could be seen clearly, then type 4 could be sub-divided into two classes, one with the two mononucleolate spores on the same side of the plane of first division and one with one mononucleolate spore on each side. In addition, three other types were observed--patterns 7, 8, and 9. These are the result of 3 to 1 disjunctions of the chromosomes 6. Types 7, 8 and 9 were found in 21 out of 2,482 quartets or 0.8% of the cases. It is probable that some 3 to 1 disjunction events gave patterns like those of 1, 2, or 3. However, the error from this source is probably small and will be neglected. Excluding the known 3 to 1 disjunctional types, a total of 2,461 quartets was examined from eight plants. The observed and expected frequencies of the six different patterns are given in Table 1. The formula for determining the expected frequencies is an expansion of the binomial $(m + d)^4$ where m is the frequency of mononucleolate spores and d is the frequency of dinucleolate spores. The values of m and d are .7252 and .2748, respectively.

It is apparent from the data that the relative proximity of the short arms of chromosome 6 tends to be similar in the nuclei derived from a single second metaphase configuration. This is understandable since there probably is very little lateral movement during anaphase or much shifting around of the chromosomes at telophase. Note the low frequencies of types 2 and 4.

Table 1

Patterns of nucleolar distribution at the quartet stage of tetraploid meiosis

Quartet type	1	2	3	4	5	6	7	8	9
									
Frequency									
observed no.	1,093	524	432	62	207	143	11	6	4
%	44.4	21.3	17.6	2.5	8.4	5.8			
expected no.	681	1,032	391	195	148	14			
%	27.7	41.9	15.9	7.9	6.0	0.6			
formula	m^4	$4m^3d$	$4m^2d^2$	$2m^2d^2$	$4md^3$	d^4			

The relatively high frequency of type 6 may be the result of there being two bivalents of chromosome 6 at the first metaphase in these cases. If these bivalents are far apart on the first metaphase plate, the two chromosomes 6 will probably be far apart in the first telophase nuclei and all through second division. However, from the high frequency of type 3, we could perhaps say that in mose cases the mirror image spatial relationships of the chromosomes in the two first telophase nuclei are generally lost in the "swing flanking movement" of the chromosomes to form the second metaphase plates which are, of course, 90 degrees off from the plane of the first metaphase plate.

The results are very preliminary. The system is simple but needs definition. Studies will be made to see if the frequency of mononucleolate spores is related to the rate of quadrivalent formation for chromosome 6. Tetraploids heterozygous for an inversion on chromosome 6 should have a higher frequency of dinucleolate spores. Also by correlating the size of the spore after it leaves the quartet with the number of nucleoli, it should be possible to determine the time sequence of nucleolar fusion.

G. G. Doyle

4. Tetraploid gene segregation as studied with a repulsion phase marking system.

This system has been described in previous reports. It allows for the identification of all of the euploid and aneuploid types of tetraploids and the determination of many of the parameters of tetraploid gene segregation such as double reduction, numerical nondisjunction, the relative transmission frequencies of euploid and aneuploid gametes, and the viabilities of aneuploid zygotes and plants.

The gene segregation patterns of three euploid and four aneuploid types are given in Table 2.

Table 2

Gene Segregation of Euploid and Aneuploid Tetraploid Maize

Genotype	No. of plants tested	No. of gametes tested	Observed		Expected	
			% A sh	% a Sh	% A sh	% a Sh
2(A sh)2(a Sh)	320	62,431	20.11	21.01	21.43	21.43
3(A sh)1(a Sh)	54	9,344	49.78	2.95	53.57	3.57
1(A sh)3(a Sh)	49	8,175	2.41	52.27	3.57	53.57
3(A sh)2(a Sh)	11	1,730	28.67	7.05	25.00	8.33
2(A sh)3(a Sh)	11	1,561	6.66	27.48	8.33	25.00
2(A sh)1(a Sh)	25	3,840	47.27	21.22	53.33	20.00
1(A sh)2(a Sh)	13	1,625	20.86	49.54	20.00	53.33

The observed values are in general agreement with the expected values, which are computed on the basis of random chromatid assortment. There is a small deficiency in most of the A sh classes. This probably is the result of the ears getting wet, since shrunken kernels disintegrate rapidly. The last two harvest seasons have been very rainy. The data should be corrected for this.

In the case of the (4n-1) or trisomic tetraploids the expected frequency of A sh gametes from the 2(A sh)1(a Sh) plants is 53.33% while the observed value is only 47.27%. There is a corresponding decrease in the number of a Sh gametes from the 1(A sh)2(a Sh) plants. This may be explained on the basis of the lowered transmission frequencies of (2n-1) or monosomic gametes. The gametic output of 1(A sh)2(a Sh) plants on the basis of random chromatid segregation is A sh/A sh 1/30, A sh/a Sh 8/30, a Sh/a Sh 6/30, A sh 5/30 and a Sh 10/30. An equation may be set up to solve for the frequency of monosomic gamete transmission, designated as m.

$$6/15\ (1 - m) + 10/15\ m = .495$$ (decimal fraction of a Sh gametes)

Solving this equation, the percentage of gametes which function are 35.6% monosomic and 64.4% disomic.

A related problem is the relative viability of (4n-2) or disomic tetraploids. Disomic tetraploids should be produced by self-fertilization of trisomic tetraploids in the proportion of 1/4 if there is no competition between euploid and aneuploid gametes. Table 3 gives the results of progeny tests from 63 A Sh kernels produced by selfing two 2(A sh)1(a Sh) plants.

There is a clear indication that disomic plants are probably very rare due to decreased viability or zygotic lethality. The population of 63 plants came from a total of 110 seeds. There were 9 additional plants which did not have enough seeds to be categorized into genotypes. Plants with less than 50 seeds were not tabulated. These nine plants all had some A Sh seed so they were not disomic. Out of 72 plants not one was a disomic; if disomics were fully viable and there was no gametic competition, we would expect 18 of them. There is also a reduction in the number of trisomics. If disomic plants are inviable, then 52.6% or 33 plants should be trisomic. There were 27% or 17 trisomic plants.

Aneuploidy is, therefore, an important factor in tetraploid semisterility.

Table 3

Genotypes resulting from the self fertilization of two 2(A sh)1(a Sh) plants

Parent	3(Ash) 1(aSh)	2(Ash) 2(aSh)	1(Ash) 3(aSh)	2(Ash) 1(aSh)	1(Ash) 2(aSh)	1(Ash) 1(aSh)
1	23	17	2	8	5	0
2	0	3	1	1	3	0
Total	23	20	3	9	8	0
Ob. Percent	36.5	31.8	4.8	14.3	12.7	0
Expected Percent	15.8	12.5	2.6	36.2	16.4	16.4

Aneuploidy is caused by numerical non-disjunction originally. Aneuploids in the population contribute additional aneuploids to the next generation, but at reduced frequencies. They would probably be eliminated

from the population in a few generations, but the supply is being constantly replenished by errors in the meiosis of eutetraploids. Additional data on numerical non-disjunction are presented in Table 4.

Table 4

Numerical non-disjunction in tetraploid maize

Cross	Number of plants with the genotypes of:				
	2(Ash) 2(aSh)	3(Ash) 2(aSh)	2(Ash) 3(aSh)	2(Ash) 1(aSh)	1(Ash) 2(aSh)
4(aSh) X 4(Ash)	219	3	6	6	1
4(Ash) X 4(aSh)	62	2	3	1	0
Total	281	5	9	7	1

Progeny tests were made on 303 plants from a cross of 4(aSh) X 4(Ash) or the reciprocal. It may be seen from Table 2 that each of the five expected genotypes gives very characteristic ratios and may be readily distinguished. All ears with fewer than 100 kernels were discarded.

There were 14 plants (4.53%) which resulted from trisomic gametes and 8 (2.59%) which were from monosomic gametes. If this difference is valid, it probably is due to the fact that hypoploid zygotes are less viable than hyperploid ones. It would appear also that aneuploid gametes function more frequently on the female side than they do on the male. There were 14 cases of aneuploidy attributible to the female and only 8 in the case of the male. Additional data are required to settle some of these points.

G. G. Doyle

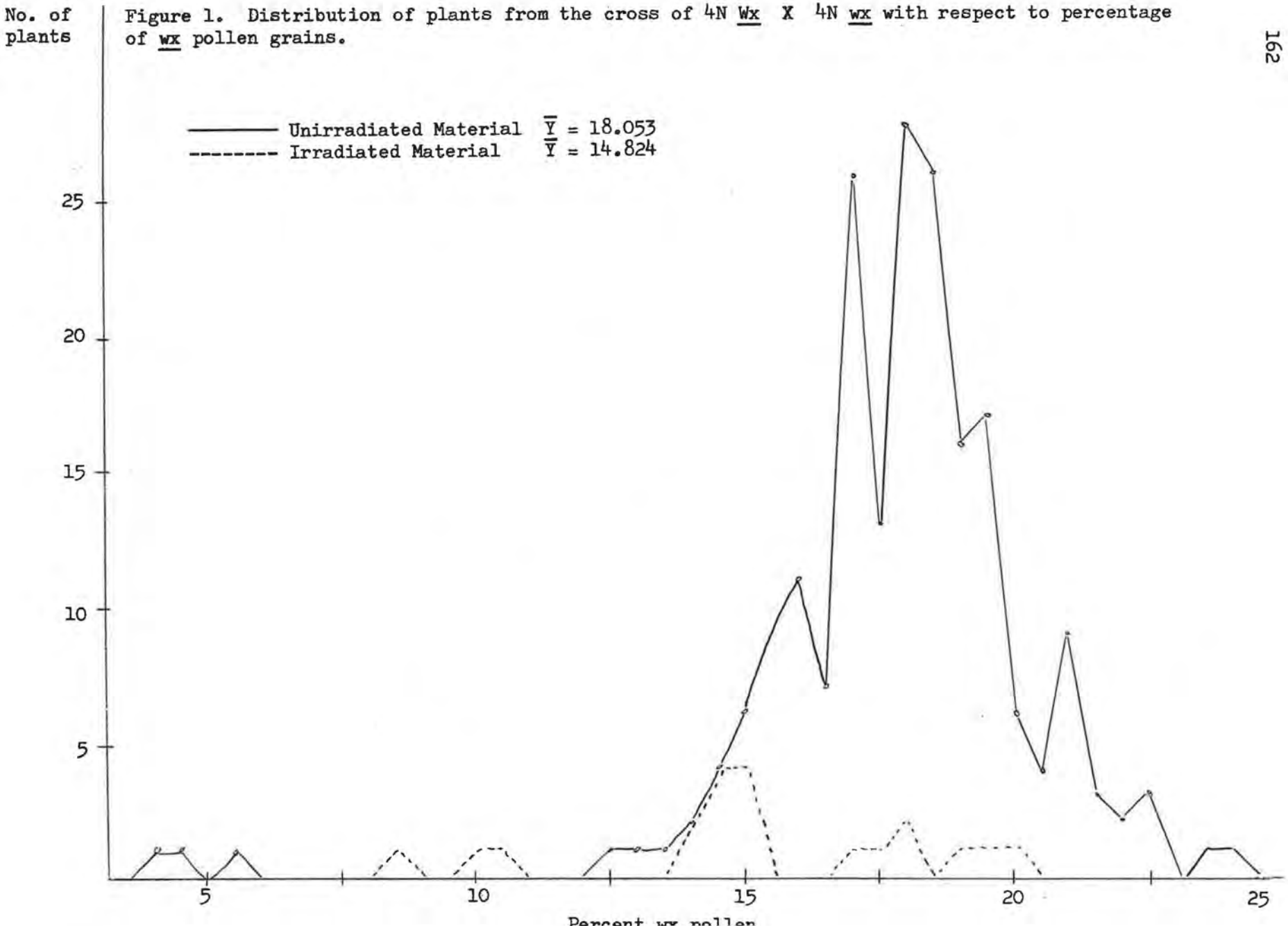
5. The synthesis of artificial allotetraploid maize.

An artificial allotetraploid maize would be true breeding for chromosome number and the partial sterility resulting from aneuploidy could be eliminated. In addition, it would be a true breeding hybrid.

Since maize is not closely related to any other species (with the exception of teosinte), it is necessary to create a "new species" of maize in order to produce an allotetraploid. This is theoretically possible to do in two ways. A maize genome must be produced which has very little pairing affinity with the standard genome. Structural rearrangements of the chromosomes have been shown to produce a decrease in pairing affinity. Therefore, 21 inbred lines of maize have been irradiated for seven generations with an accumulated dose of 35,000 r. Also, a tetraploid line (a selection from Alexander's Synthetic B) has been likewise irradiated for five generations with an accumulated dose of 25,000 r.

Alternatively, we can take advantage of the fact that maize is a widely spread species which has a great number of races. These races have been shown by preferential pairing studies in trisomic 3 racial hybrids to be quite variable in their chromosome structure. It is possible, by a system of recurrent selection to be described later, to concentrate these small structural differences in a few lines and then to cross them with the standard genome. There is a question as to whether these small structural differences, which modify pairing affinity on the trisomic level, will also do so on the tetraploid level. Consequently, a 4n wx stock was crossed with seventy-eight different 4n Wx plants. These plants were a heterogeneous mixture of various marker stocks derived from various sources and newly synthesized tetraploids. They were not homozygous and cannot be characterized as to origin. They probably represent only a small fraction of the variability in chromosome structure to be found among the races of maize. Tassel samples from three plants in each of the progenies of the seventy-eight crosses were taken and preserved in 70% alcohol with a dash of formalin. Pollen from anthers of 6 florets was stained with I-KI solution and between 600 and 700 pollen grains were counted. The results are given in Figure 1. A total of 198 tassel samples was examined and found to be of the desired constitution (Wx/Wx/wx/wx); a number of others were found to be simplex-- either Wx/wx/wx (from numerical non-disjunction) or Wx/wx/wx/wx (from unsuspected Wx/Wx/Wx/wx triplexes in the "4n Wx" parents). These tassel samples were discarded. Also three tassel samples gave very low

Figure 1. Distribution of plants from the cross of 4N Wx X 4N wx with respect to percentage of wx pollen grains.



percentages of wx; these plants were probably pentasomics (Wx/Wx/Wx/wx/wx) which arose from numerical non-disjunction. They are shown at the left side of the graph, but the data from them are not included in computing the mean.

The distribution appears to be trimodal. A total of 136,694 pollen grains was counted, of which 18.053% were wx. There were seventeen plants which had significantly higher percentages of wx pollen and fifteen plants where the percentage was significantly lower. This is believed to be indicative of the presence of structural dissimilarity in regard to chromosome 9. The deviations above the mean frequency have been observed in analogous experiments with trisomes. It is believed that structural differences affect the patterns of multivalent disjunction in a yet unexplained manner.

Likewise, 20 tassel samples were taken from the progenies of nine crosses between tetraploid wx and the tetraploid Wx strain which had been subjected to irradiation for several generations. A total of 14,706 pollen grains was counted and 14.82% were wx. Thirteen out of 22 plants showed a significantly lower percentage of wx pollen.

These results indicate that there is a wealth of naturally occurring structural differences which affect pairing affinity at the tetraploid level and also that they can be readily produced by irradiation. Consequently, a breeding program designed to concentrate these differences in a single genome would have something to work with and would have a good chance of success.

Any breeding system in tetraploids must take into account that there are no good inbred lines available and that only a small fraction of the available germ plasm has been introduced into the tetraploid level. Consequently, we must work with material which is equivalent to open-pollinated varieties and allow for the introduction of new material into the breeding system as it becomes available.

The proposed method is to create a pool composed of samples from all the tetraploid strains available to which will be added new strains as they are produced. The gene ameiotic (am) is being introduced into a wide variety of exotic races and into irradiated and unirradiated

Corn Belt inbred lines. When a diploid plant homozygous for am is crossed by a tetraploid pollen parent, a few tetraploid kernels are formed. All possible crosses and selfs will be made in this pool and kept separate. Every year plants from this pool will be self-fertilized and used as the male parents in crosses with tetraploids which are homozygous for one or more of the markers: bz_2, lg_1, a_1, su_1, pr, y_1, gl_1, v_{16}, wx, and g_1. There is one marker for each of the 10 chromosomes. Ideally, all these markers would be in the same strain. Since some of the traits interfere with expression of other traits (a_1 with bz_2 for example), two or three strains will be used. These strains will be made as closely related as possible and will arbitrarily be called the standard. In the following year the hybrids will be testcrossed onto the standard multiple recessives and a value called the allosyndetic index will be computed. The allosyndetic index is the sum of the percentages of all 10 recessive segregants. It has a theoretical maximum of 214 and a minimum of 0. The maximum occurs when all genes are segregating as in random chromatid assortment. The minimum would be found in a true breeding allotetraploid. Strains which have a high allosyndetic index will be discarded from the pool, and those with low indices will be retained and crossed with each other in an effort to concentrate the structural differences responsible. Several strains which have high allosyndetic indices will be maintained outside the pool to provide the eventual breeding partners with the modified strains.

G. G. Doyle

6. X-ray induced duplications from translocations between homologous chromosomes.

This experiment has been described in great detail in previous reports. Translocations between the same arms of homologous chromosomes form a chromosome with an interstitial deletion and a chromosome with a tandem duplication. The probability of this occurrence is rather low in relation to the frequency of translocations between nonhomologous chromosomes. For a particular gene to be included in the tandem duplication the probability is $1/4(n-1)(1/2n)(1/2)T$, where n is the haploid number of chromosomes and T is the frequency of translocations between

nonhomologous chromsomes. The observed value of T was 15.4%. In the experiment reported earlier, 1,169 ears were tested for tandem duplications involving any one of six genes. The expected number of cases would then be 0.72.

However, if there is a tendency for homologous chromosomes to be in a semi-paired condition in the interphase nucleus, then we would expect the frequency of tandem duplication production to be considerably higher since the probability of two broken ends of chromosomes uniting to form a new combination is a function of the distance between them.

In last year's report, 36 cases which suggested the presence of tandem duplications were cited. In order to verify the presence of a tandem duplication, the presumptive duplication chromosome must be made heterozygous with a chromosome carrying the dominant gene and backcrossed to the recessive to see if there are any recessive revertants. In other words, the original state must be restored.

All of these tests were made and the results were completely negative in all cases. Some odd patterns of inheritance were observed but they do not conform to theoretical expectations. In some cases sublethal genes were induced which were linked to the recessive gene and modified what should have been a 1 : 1 ratio. In the case of the "Lg-lg duplications" the so called lg revertants reported last year proved to have normal ligules on the second and higher leaves. Sandbench classifications were made on the first leaf and this is not reliable. Apparently some modifiers of the expression of lg were present or induced in the material. Also, some errors in classification probably occurred, particularly in the case of golden which, in some backgrounds, is a poor sandbench character. It was thought that there were some spurious cases. It appears they all are.

The second method of detecting tandem duplications is faring a little better. The procedure is to irradiate kernels which have two very closely linked markers in the repulsion phase (in this case A sh/a Sh) and to cross the plants grown from these kernels to the double recessive. Kernels in the progeny with a tandem duplication involving the loci will have the constitution (A sh-a Sh/a sh) which may be distinguished from normal crossover events (A Sh/a sh) by

crossing the plants grown from these kernels to homozygous a Sh plants and detecting the presence of A sh gametes in the next generation. However, there is a third source of A Sh kernels which was recognized but not noted in the last report because it was thought of negligible importance. It is the result of the non-disjunction of either the A sh or the a Sh chromosome which produces trisomic sectors on the ears of the X_1 generation. These sectors yield trisomic kernels of the genotype A sh/a Sh/a sh which are phenotypically A Sh.

Much of the excess in the number of A Sh in the irradiated material over the controls is due to this. In the control there were three trisomic 3 plants out of 14 A Sh kernels tested. In the irradiated material 20 out of 44 A Sh plants were trisomics. Irradiation probably increases the frequency of non-disjunction. A great volume of material was obtained last summer in a repetition of the original experiment and the results of this experiment will be reported later in greater detail.

In 19 out of the 33 cases of trisomy there was non-correspondence between the phenotypes of the endosperm and the genotype of the embryo, which probably indicates some sort of tetrasporic development of the megagametophyte, as suggested by Neuffer.

It appears that tandem duplications are extremely hard to obtain. Oddly enough, this difficulty may be used in support of the hypothesis that homologous chromosomes tend to be in a semi-paired state in the interphase nucleus. If the hypothesis is true then most of the tandem duplications produced would tend to be very short and the probability that a duplication would include the loci followed would be very low.

G. G. Doyle

THE MOEWS COMPANIES
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1. An observed alteration of the opaque-2 phenotype.

The opaque-2 recoveries of 2 inbred lines of corn (hereafter referred to as Line A and Line B) were crossed reciprocally to obtain F_1

seed. Seed of the cross A x B was all of the opaque phenotype. Seed of the reciprocal cross B x A, however, was of two distinct phenotypes, opaque and normal. Lysine analysis of the different phenotypes from this cross indicate that both types are similar in lysine content and within the range expected for the opaque-2 homozygote. The bioassay method was used for lysine analysis of whole kernel samples. Kjeldahl analysis indicates that both types are also similar in total nitrogen content.

The inbred lines involved were derived from yellow dent lines. They were included in our breeding program and converted to white endosperm before incorporation of the opaque-2 gene. It is suspected that the germ plasm used as the source of white endosperm contributed the factor or factors that apparently alter the opaque phenotype.

Since plant to plant crosses were not made and no phenotypic ratios obtained, no attempt can be made at this time to explain the observed results genetically. Further studies are being carried out and any new information will be included in subsequent reports.

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1. Mutants induced by thermal neutrons in B14 inbred.

The 1969 News Letter contained an item regarding the induction of seedling mutants by thermal neutrons. The mutants were observed in the M3 generation following open pollination of the M2 in an isolated field. Seeds of stocks segregating are now available. These are as follows:

Segregating albinos	32 progenies
Segregating dwarf	1 progeny
Segregating luteus	6 progenies
Segregating virescent	2 progenies
Segregating viviparous	1 progeny
Segregating defective seed	110 progenies
Segregating germless seed	5 progenies
Segregating small seed	1 progeny
Segregating defective and germless	1 progeny
Segregating semisterile ears	28 progenies
Segregating defective and semisterile	55 progenies

In addition, one M3 progeny was segregating for an endosperm mutant phenotypically similar to $\underline{sh}_2$. Crosses with $\underline{sh}_2$ and $\underline{su}_1$ produced plus kernels. Hence it is not $\underline{sh}_2$ or $\underline{su}_1$. Allelic tests with $\underline{bt}_1$ and $\underline{bt}_2$ should be made, also with $\underline{su}_2$.

Limited quantities of all of these stocks are available. The aleurone constitution is A c r Pr homozygous. I do not plan to make allelic tests since I will retire on 1 July, 1970.

W. Ralph Singleton

2. Old varieties of corn.

In response to my request for antique varieties of corn last year, Dr. Paul Harvey in North Carolina sent one variety, Indian Chief, that has been grown in North Carolina for many years. It is rather unusual in that it is a yellow dent variety with a white cob. Another interesting feature was its rapid growth at the National Colonial Farm in Maryland.

There are now four old varieties of field corn in the antique corn collection at the Colonial Farm as follows:

1. Virginia Gourdseed, large white dent kernel.
2. Hasting's Prolific, white dent, with tendency for multiple ear.
3. Canada Flint Yellow Flint, obtained originally from Connecticut.
4. Indian Chief, rich yellow kernel, white cob, vigorous grower.

In addition there are two sweet corn varieties Black Mexican (ACR Pr) and Catawba Blue (ACR pr, contrary to name). Seed is available of all these varieties.

W. Ralph Singleton

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1. Role of cyclic hydroxamic acid on monogenic resistance to Helminthosporium turcicum in maize.

Cyclic hydroxamic acids in maize were first reported in 1959, but their biological significance has yet to be clearly established. The production of the fungitoxic aglycone 2,4-dihydroxy-7-methoxy-1,4-benzoxazine-3-one from its glucoside upon cellular disruption has been implicated in resistance to several pathogens.

To observe their effects on monogenic resistance, we crossed a genotype deficient in these compounds (hthtbxbx) with the normal resistant genotype (HtHtBxBx). The deficient genotype is an S_1 line, designated no. 59C32-1, obtained from R. H. Hamilton at Penn State. Deficient seeds were detected by crushing a root tip on filter paper impregnated with M/10 $FeCl_3$. A blue colored chelate at the oxidized peptide bond of the hydroxamic acids is formed in normal seeds.

Seedlings are inoculated at the three leaf stage and incubated for 18 hours at 68°F and 100% humidity. The degree of infection is determined by measuring the total area of the fourth leaf and the area of the leaf covered with lesions. Areas are measured with the use of a transparent grid containing 100 squares to the square inch.

Significant effects on the susceptibility of the HtHt and Htht genotypes are presently being observed in the F_3. Lesions on resistant deficient (Ht-bxbx) seedlings enlarge rapidly and have a general chlorosis. Resistant normal lesions (HtHtBxBx) generally do not enlarge

and remain as chlorotic spots. It appears that the fungitoxic compounds modified by the Bx gene act in containing the spread of the fungus.

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D. G. Routley
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Genetics Department

1. A polyphenol oxidase oxidizable flavonoid difference in corn silks.

Silks from certain stocks turn a brown color when ground up and allowed to stand a few minutes, while with other stocks the ground silks remain yellow-green (i.e. no change in color occurs). Furthermore, differences in ground up silk color can be detected on the plant by cutting back the silks and observing the cut ends an hour later. If the cut ends turn brown, then the silks turn brown upon grinding. Likewise if the cut ends don't change color, then the ground silks don't change color. For convenience, the phenotype shown when cut silks ends and ground up silks turn brown is designated "brown," while that where no change in color of cut silks ends or ground up silks is observed is called "colorless." The inbred line NC232 has the brown phenotype while NC236 has the colorless. The F_1 between NC232 and NC236 has the brown phenotype. A testcross gave 37 brown and 44 colorless types. This fits a 1:1 ratio with a probability of .4-.5. These results indicate a monohybrid segregation with the brown phenotype being dominant to the colorless.

Analysis of the brown phenotype has indicated that the brown color in ground silks is due to the oxidation of a polyphenolic compound and the subsequent polymerization of the resulting quinones. Polyphenol oxidase is the enzyme responsible for the oxidation of the polyphenol. The browning reaction can be inhibited by DIECA (sodium diethyldithiocarbonate), a selective inhibitor of polyphenol oxidase. The brown

reaction might be catalyzed by peroxidase, but appropriate peroxides are apparently missing in the silks and this reaction requires the addition of hydrogen peroxide. Enzyme preparations from the brown and colorless phenotype both have polyphenol oxidase activity. However, polyphenol preparations from silks of the brown and colorless phenotypes differ. The polyphenol preparation from the brown phenotype turns brown when added to enzyme preparations from either the brown or colorless phenotype. But, the polyphenol preparation from the colorless phenotype remains colorless when added to enzyme preparations from the brown or colorless types. These results indicate the presence of a polyphenolic compound in the brown phenotype which is oxidized by polyphenol oxidase that is not present in the colorless phenotype. This compound has been isolated but not rigorously identified. It is tentatively identified as a flavonol based upon the following results. The compound has a yellow color; it turns yellow with a base and is unstable in air, becoming brown; it is orange in concentrated H_2SO_4; and it is magenta in alcoholic Mg plus HCl.

C. S. Levings III
C. W. Stuber

2. Segregation for colored nodes.

A plant was found in the variety, Jarvis Golden Prolific, which had a red stripe approximately 1/8" wide encircling the culm at each node. The color appears beneath the leaf sheath and varies in intensity up and down the plant. The stripe is usually most vivid on 2 or 3 of the nodes immediately below the ear. The trait segregates as a single dominant gene; out of 597 progeny, 458 showed the red stripe and 139 had normal colored nodes. In testcrosses to normal plants, 200 plants had the stripe and 190 were normal. Tests for possible allelism with known loci which affect plant color are planned.

R. H. Moll

3. Non-random fertilization of pollen in mixtures.

Two experiments have been conducted to study the relative effectiveness of pollen of different strains in pollen mixtures.

The first experiment involved two yellow varieties, Jarvis and Krug, and two white varieties, Weekley and Zapalote Chico. Four pollen mixtures were made by mixing pollen of 5 plants of a yellow variety with that of 5 plants of a white variety. Each mixture was applied to the silks of at least 6 plants of each of the four varieties. At harvest, two 100 kernel samples of each ear were classified as having been fertilized by white or yellow pollen. Ears which were difficult to classify were discarded.

The results (Table 1) show that a greater proportion of white pollen functioned on the parental variety with white endosperm than on the parental yellow variety. This difference is statistically significant and indicates that pollen in mixtures tends to be more effective on the strain from which it came. The magnitude of the selective fertilization effect varies among varieties as indicated by a significant interaction between mixtures and varieties. There is no significant difference for percent white (or cream) kernels between the non-parental strains which indicates that the effect is not associated with white or yellow endosperm per se.

The second experiment involves divergent selection for selective fertilization in the varieties Jarvis and Weekley. Two hundred plants of each variety were planted in adjacent rows. Pollen mixtures were made by selecting two plants, one from Jarvis and the other from Weekley, which flowered at exactly the same time. Pollen collected from these two plants was mixed, and the mixture was applied to their silks. At harvest, 120 pairs of ears were obtained in which each had been pollinated by its own pollen mixed with that of the other member of the pair. One hundred kernels of each ear were classified as having been fertilized by a white or a yellow pollen grain. Pure white kernels on the ear of the white variety and deep yellow kernels on the ear of the yellow variety represent self-fertilized seeds. Selfed seed of pairs of plants was selected on the basis of the proportion of selfed to outcrossed kernels.

Table 1

The relative effectiveness of pollen of white and yellow endosperm varieties in pollen mixtures.

Pollen** Mixture	Percentage of White or Cream* Kernels			
	Parental Variety		Non-Parental Variety	
	Yellow	White	Yellow	White
J + Z	33	56	42	42
K + Z	35	66	35	44
J + W	49	51	54	50
K + W	48	67	44	69

*White kernels on a white tester; cream kernels on a yellow tester.

**J = Jarvis Golden Prolific (Yellow Endosperm)
Z = Zapalote Chico (White Endosperm)
K = Krug Yellow Dent (Yellow Endosperm)
W = Weekley (White Endosperm)

Table 2

The result of divergent selection for percentage of self seed on pairs of plants pollinated with a mixture of their pollen.

Sub-population*	Percent Self Seed		Percent of pairs of ears with more than 50% self seed
	Mean	Range	
Inbreeders	57.05	44 - 71	78.9
Neutrals	50.82	34 - 64	57.9
Outbreeders	47.45	31 - 62	33.3

*Inbreeders: Selected for high proportion of self seed.
Neutrals: Selected for approximately 50% self seed.
Outbreeders: Selected for low proportion of self seed.

Three selection criteria were employed: high proportion of selfed seed (inbreeders), low proportion of selfed seed (outbreeders), and 50% selfed seed (neutrals).

Selfed progeny of selected pairs were self-pollinated in a winter nursery and any segregating ears were discarded. S_2 progeny of each pair were planted in adjacent rows, and individually paired plants within the S_2 progenies were pollinated by mixtures of their pollen, and the classification and selection processes described above were repeated. Selfed progeny of selected pairs were self-pollinated in a winter nursery to eliminate segregating ears. S_4 progeny of the surviving lines of each variety which had been selected by each criteria were intermated to produce pairs of subpopulations designated as inbreeders, outbreeders and neutrals.

The second cycle of selection was initiated within pairs of subpopulations of the two varieties in the manner described above. The data obtained for the initiation of the second cycle provide an evaluation of the effectiveness of the first selection cycle (Table 2). Selection response occurred in both directions, although the mean difference from the neutral population suggests that selection for a high proportion of selfing (inbreeders) was more effective than selection for a low proportion of selfing (outbreeders). The greatest difference among the three subpopulations is shown by the percentage of pairs with more than 50% self seed.

The response to divergent selection demonstrates that individual genotypes exist in these populations which cause selective fertilization, and that both negative and positive assortative mating occurs. The fact that both kinds of deviations from random fertilization occur is further evidence that endosperm color is not in itself associated with selective fertilization.

The existence of gametic selection in pollen mixtures has a bearing upon techniques employed in the intermating and maintenance of populations, particularly in the early generations of composite or synthetic populations. A commonly used technique is to collect and mix pollen of a large number of plants and then pollinate at random a number of ears.

This may result in significant departures from random mating, as demonstrated by the differential effectiveness of pollen in mixtures. The alternative techniques of making controlled plant to plant crosses will avoid gametic selection between pollens of different plants and may result in fewer deviations from random mating.

R. H. Moll

4. Comparison of selection methods for increased yield.

Four selection experiments which involve the two open-pollinated varieties, Jarvis and Indian Chief, provide a comparison among three alternative methods for systematic improvement of grain yield. Two of the three methods lead to improvement of the varietal hybrid, whereas the third method involves improvement of the varietal composite. One method being studied is direct selection for performance of the varietal hybrid by reciprocal recurrent selection procedures. Another of the methods is full-sib family selection within each variety separately. The improved varieties are crossed, and their improvements are utilized indirectly in their hybrid. The third method is to intermate the original variety hybrid for several generations to form the varietal composite, and subsequently to improve the varietal composite by full-sib selection.

Comparisons have been made among these procedures after 3 selection cycles and again after 6 selection cycles. After 3 selection cycles there was no detectable difference between the two methods which lead to an improved variety hybrid. The improved variety hybrid was distinctly superior to the improved varietal composite. However, after 6 selection cycles, the highest yield was obtained in the varietal hybrid resulting from reciprocal recurrent selection. This crossbred population was 20.4% greater in yield than the original varietal hybrid, and 10.7% greater than the average yield of two commercial double cross hybrids. The yield of the crossbred when the varieties were improved separately was 15.1% greater than the yield of the original varietal hybrid, and approximately 5.3% above the average of the two commercial hybrids. The yield of the varietal composite after 6 selection cycles is

approximately equal to the yield of the original variety hybrid.

Heterosis in the varietal hybrid appears to have decreased slightly following independent selection within each variety. Heterosis following reciprocal recurrent selection appears to have increased markedly from 19.2% in the original to 30.2% following 6 selection cycles even though the midparent has also increased.

R. H. Moll

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1. Chlorophyll mutation in DES treated opaque-2 maize.

It was reported earlier that out of 559 surviving plants from homozygous opaque-2 seeds treated with nine different concentrations of DES, 176 plants showed three types of chlorophyll sectors, i.e. yellow, albino, and yellow green (MNL 43:136, 1969).

One particular plant in the 0.005 M treatment had a yellow green sector on the 13th leaf. When selfed, it segregated 21 normal and 28 yellow green plants in the M_2. The M_3 segregation from six yellow green and three normal plants is shown in the following table.

Table 1

M_3 Segregation of mutant seedlings from selfed yellow green and normal plants.

S. No.	Line	Total No. of plants	Yellow green	Yellow	Albino
1	Yellow green	6	-	6	-
2	"	12	7	4	1
3	"	11	4	7	-
4	"	16	6	3	7
5	"	7	5	-	2
6	"	9	4	4	1
7	Normal	14	10	4	-
8	"	7	-	5	2
9	"	9	-	4	5
		91	36	37	18

The yellow green seedlings continued to be yellow green even at maturity, similar to the parent yellow green plant in the M_2.

It is surprising how the selfed yellow green and also normal segregated to give 37 yellow and 18 albino in the M_3 out of a total of 91 seedlings. It is possible that these mutants might be segregating in the M_3. Further tests are in progress.

V. S. Bharathi
G. M. Reddy

2. Thin layer chromatographic studies of DES induced chlorophyll mutants.

The chlorophyll of about one-two week old seedling leaves of normals and DES induced yellow and yellow green mutants was extracted with petroleum ether and acetone (8:3). The chlorophyll extracts were spotted on glass plates spread with silica gel G (E. Merck), and developed with petroleum ether-acetone solvent (5:2). Table 1 illustrates the qualitative and quantitative differences between normals, yellow green, and yellow mutants.

Table 1

Phenotype	No. of spots	R_f Values				
		Green	Yellow	Bluish green	Dark green	Yellow
Normal	5	0.361	0.399	0.476	0.861	0.987
Yellow green	5	0.361	0.399	0.476	0.861	0.987
Yellow	2	0.361	0.399	-	-	-

In general, the normal has all the five spots which were intense. In yellow greens, the yellow pigment (R_f 0.399) was more intense and dark green (R_f = 0.861) was quite weak compared to normal. In the yellow mutant, only two spots, R_f values 0.361 and 0.399, were present. The identification and the spectrophotometric studies of these substances are in progress.

S. Annapurna
V. S. Bharathi
G. M. Reddy

3. Opaque-2 shrunken endosperm mutant.

In the M_2 generation of homozygous opaque-2, seed treated with a 0.0025M concentration of DES, upon selfing, showed segregation for shrunken endosperm. Out of 254 kernels, 197 were normal and 57 were shrunken suggesting a single gene mutation of normal Sh to sh (shrunken).

V. S. Bharathi
G. M. Reddy

4. Induction of mutations in a multiple stock with DES.

When about 100 seeds of a homozygous dominant multiple stock, Bm_2 Lg_1 A_1 Su_1 Pr Y_1 Gl_1 J_1 Wx G_1, were treated with 0.006 M DES, two liguleless plants were observed in the M_2, which may be due to a mutation at the Lg_1 locus. One of the two liguleless plants had a brown midrib, which suggests that simultaneous mutations occurred at two loci, Bm_2 and Lg_1.

V. S. Bharathi
G. M. Reddy

5. Induction of specific locus mutations by DES and hydrazine.

Seed of a multiple stock homozygous for gl_6 lg_2 a_1 et, A_2, Dt C, and R was pre-soaked for 24 hours prior to treatment with ten different concentrations of DES ranging from 0.003M to 0.01M for 8 hours. Out of total 739 treated seed, 541 germinated. Among the resulting population were plants with three types of chlorophyll sectors (yellow green, yellow, and albino) as well as 9 bifurcated and 14 trifurcated leaves. Pollen sterility was about 13% in the 0.003M treatment whereas in the 0.005M, it was about 24%. There seems to be an increase in percentage of pollen sterility with increase in concentration of DES treatment.

Out of 269 seedlings, five reversions from liguleless to normal were observed, two in the 0.003M, two in the 0.0035M, and one in the 0.004M treatment.

Seed of the homozygous multiple dominant stock, Bm_2 Lg_1 A_1 Su_1 Pr Y_1 Gl_1 J_1 Wx and G_1, was treated with 0.009M hydrazine hydrate (80%) for 23 hours after one hour of pre-soaking. Two golden and two yellow

seedlings were observed in the M_1. In the selfed progeny, a colorless sugary seed, which could be due to simultaneous mutations at three different loci $\underline{A}_1$ $\underline{Y}_1$ $\underline{Su}_1$, and four normal colorless seeds, which could be due to simultaneous mutations at two loci $\underline{A}_1$ and $\underline{Y}_1$, were observed. These observations suggest that hydrazine may induce recessive mutations at specific loci even in the M_1.

V. S. G. Chandra Sekhar
G. M. Reddy

6. Position of the purple gene (Pr/pr) in gene action sequences of anthocyanin biosynthesis.

The U.V. absorption spectra of the alcoholic extracts of aleurone tissue of $\underline{a}_1$, $\underline{a}_2$, $\underline{c}_1$, $\underline{c}_2$, $\underline{r}$ testers and homozygous double recessive mutants of $\underline{a}_1$ $\underline{pr}$, $\underline{a}_2$ $\underline{pr}$, $\underline{c}_1$ $\underline{pr}$, $\underline{c}_2$ $\underline{pr}$, and $\underline{in}$ $\underline{pr}$ were compared.

All the single and double mutant extracts gave the same absorption maxima, i.e. 320mu, 286mu, and 275mu, with the exception of $\underline{a}_1$ $\underline{pr}$ and $\underline{a}_2$ $\underline{pr}$, which gave 308mu and 310mu respectively in addition to 286mu and 275mu. The spectral pattern of tissue extracts of $\underline{pr}$ differs from $\underline{Pr}$ extracts only in the $\underline{a}_1$ $\underline{pr}$ and $\underline{a}_2$ $\underline{pr}$ combinations whereas in combination with $\underline{c}_1$, $\underline{c}_2$, $\underline{in}$, and $\underline{r}$ the pattern is the same. This might suggest that the $\underline{Pr}/\underline{pr}$ locus actively controls the nature of the accumulated substance(s) only in $\underline{a}_1$ and $\underline{a}_2$, if the spectral pattern and absorption maxima are controlled by the $\underline{Pr}/\underline{pr}$ locus in the aleurone tissue. Thus, $\underline{Pr}/\underline{pr}$ may act prior to $\underline{A}_1$ and after $\underline{R}$ in the gene action sequence (MNL 36:62, 1962).

It is possible that the $\underline{Pr}/\underline{pr}$ locus, which controls the hydroxylation of the B-ring, may not necessarily shift the observed absorption maxima and/or spectral pattern.

G. Hari Kishen
K. Vaidyanath
G. M. Reddy

7. Opaque-2 synthetic variety of maize.

Several Indian inbred lines were selected to incorporate the opaque-2 gene to develop hybrids (MNL 42:148, 1968). The yellow opaque-2

seed was recovered by selfing after each backcross. After two backcrosses, the yellow opaque seed were selected from CM 104, CM 105, CM 109, CM 110, CM 111, CM 201, CM 202, Eto-25-F, Eto-182, and Eto-297 to develop a synthetic variety. About 100 seed from each inbred were mixed thoroughly to randomize. These seeds were planted in isolation and free inter-pollination among the inbreds was allowed. The F_1 seed was harvested and yield trials in the F_2 are in progress. Studies on the incorporation of opaque-2 by the backcross method into Indian inbreds and the development of new varieties are in progress. The assessment of protein quality and quantity in these varieties is in progress.

G. M. Reddy
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K. Vaidyanath

UNIVERSITY OF PRETORIA
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1. Adaptation of maize cultivars under South African conditions.

The research project was motivated by the need for greater reliability in determining maize cultivar adaptability in the different maize areas of South Africa. Data from South African cultivar trials, which were carried out during the four seasons 1965/66 to 1968/69, were used for further analysis. Various methods were used and computor programs which facilitated analysis have been developed.

The regression lines of specific cultivar yield over mean yield of standards were represented graphically and, on testing, found to be linear. Basically six types of lines can be differentiated, namely:

1. lines with a negative regression coefficient and an intercept of nought,
2. lines with a positive regression coefficient and an intercept of nought
3. lines with a positive intercept and a negative regression coefficient,

4. lines with a negative intercept and a positive regression coefficient and,
5. and 6. lines with regression coefficients of nought but with positive and negative intercepts, respectively.

Lines with positive regression coefficients represented cultivars with a higher production in the high yield areas than in the low yield areas. Conversely, lines with negative regression coefficients are representative of cultivars with better performance in low yield areas than in high yield areas. A performance index can be read from the graphs. The portion of the line above the X-axis (the standards' line) indicates performance higher than the mean of standards and the portion of the line below the X-axis represents a consistently lower performance than that of the mean of standards. The magnitude of difference can be read from the Y-axis.

The closer to the horizontal or X-axis, the more uniformly such lines would perform in relation to the standards and such lines are representative of cultivars showing maximum adaptability.

Multiple correlations with specific cultivar yield as the dependent variable were also calculated. In every case a linear correlation was found between specific cultivar yield and mean trial yield.

A multiple correlation with mean trial yield as the dependent variable showed that this variable was determined by certain causal climatic factors such as mean yearly rainfall and height above sea level. A cultivar that shows the best trend in the same region of the X-axis as the mean potential of a particular area would thus be the best adapted for that area.

The initiation of this project has thus been justified to a large degree by the positive and practically applicable results which resulted.

Pieter J. Robbertse

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1. Mutable alleles from x-rayed stocks.

From previous experiments (Mottinger, MNL 39:98 and 43:148) no evidence was obtained for the induction of intragenic mutations at the bronze locus when x-rays were applied at post-meiotic stages. From the experiments of Russell and Russell on mice (Rad. Res. (Suppl. 1): 296-305, 1959 and Jour. Cell. and Comp. Physiol. 56 (Suppl. 1) 169-188, 1960) mutations which appeared to be intragenic were obtained when x-rays were applied to gonial cells at pre-meiotic stages. It therefore was deemed advisable to conduct similar experiments in maize.

To ensure that sporocytes to be treated were at a pre-meiotic stage, stalks were opened and visual observations were made.

Among the F_1 progeny of crosses between sh bz wx ear parents and Sh Bz Wx stocks x-rayed at a pre-meiotic stage, two kernels of Sh bz Wx phenotype (designated bz-x3 and bz-x4) were obtained in a population of ca. 130,000. A third kernel of Sh bz Wx phenotype with a cluster of Bz spots (bz-x5) was also observed.

Among testcross progeny from each of the mutations, kernels mosaic for the Bz and bz phenotypes were observed. The revertant sectors, however, were generally quite small, in most instances involving only a few aleurone cells each. Thus, in all probability, the original bz-x3 and bz-x4 kernels possessed revertant tissue but it went undetected.

In progeny from testcrosses of the original bz-x3 kernel, most reversions occurred late in development of the endosperm; however, a few kernels exhibited early reversions. In subsequent testcrosses of kernels with revertant tissue, progeny exhibited many more instances of early reversions, some including entire kernels.

In the case of bz-x4, the reversion frequency in the original testcross was much lower than that of bz-x3. In the second testcrosses, this frequency remained about the same.

Kernels of bz-x5/bz constitution showed the lowest number of reversions in all testcrosses and the frequency did not increase in

subsequent generations. Both early and late events were observed but the former were quite rare.

These data would seem to indicate that gene control systems affecting the bronze locus have either been induced by x-rays or existed previously in the stocks. Control experiments with the same original stocks will be conducted to determine which of the two alternatives is correct.

A second question to be answered is whether these systems involve one or two elements. In all three cases, the reversion events show tight linkage with the Sh allele; therefore, if the systems involve two elements, the second resides on chromosome nine. The exact location of this element cannot be ascertained until progeny tests are made of all individuals. If a kernel does not exhibit any reversions, it may contain the mutable allele and the reversion-inducing element, but the time of activation may be so late that no reversions have occurred before the endosperm has matured. Reversions may or may not be observed in subsequent testcrosses.

At the present time, tests are being conducted to determine (1) whether these mutable alleles respond to Ac or Spm, (2) whether these stocks can affect mutable alleles which do respond to Ac or Spm, (3) whether reversion patterns remain stable or unstable and (4) if an increased dosage of the mutable alleles has any observable effect.

Although no apparent intragenic changes at the bronze locus arose in these experiments, a number of mutations at the Sh_1 locus have yet to be tested.

John P. Mottinger

2. Reversion of sh-bz-x2.

In a greenhouse planting of sh-bz-x2 A/sh-bz-x2 a individuals (for background data on sh-bz-x2 see MNL 39:98 and 43:148) an open-pollinated ear was observed which segregated for ShBz and sh bz kernels. The phenotypic counts were 180 A Sh Bz, 63 A sh bz, 70 a Sh and 21 a sh. Since only sh-bz-x2 homozygotes were present, contamination could be ruled out as a source of the dominant phenotypes. And, since the plant bearing this unusual ear was bz in phenotype, heterofertilization in the kernel from

which the plant arose could not be the cause of the A Sh Bz or a Sh progeny.

The above ratio can be explained by an hypothesis which states that the sh-bz-x2 allele is invariably reverting as a unit in only one homolog. The gametic ratio would then be 1 A Sh Bz : 1 A sh bz : 1 a Sh Bz : 1 a sh bz in both male and female flowers. Since no major air disturbances occurred in the greenhouse, the phenotypic ratio apparently resulted from self-pollination of most of the silks. Some foreign pollen may have alighted on silks of this plant, but not enough to cause much deviation from a 9:3:3:1 ratio.

In a much larger field planting of sh-bz-x2 A/sh-bz-x2 a individuals, two bronze plants bore ears which segregated for dominant and recessive phenotypes. On the first ear which had been sibbed (1538-1 x 1538-2) the phenotypic counts were 48 A Sh Bz, 50 A sh bz, 51 a Sh, 49 a sh and 13 a Sh kernels which had a slight amount of diffuse purple pigment at the crown. Progeny tests of the a Sh and a sh individuals indicated that they were Bz and bz respectively.

Judging from the appearance of plants exhibiting the dominant phenotypes, the time of the reversion event appears to be after formation of the meiocytes. If reversions occurred earlier, Bz sectors on the plant would occur.

When just the Sh and Bz loci are considered, the 1:1 ratio of Sh Bz : sh bz in the 1538-1 x 1538-2 progeny fits the expectation if both alleles on one homolog, in one parent, invariably revert and if there is a failure of crossing over between Sh and Bz. The gametic ratio of this plant would then be 1 Sh Bz : 1 sh bz. However, the ratio of A : a in the progeny should be 3 : 1 since both parents were heterozygous. No hypotheses have been formed at present to explain this aberrancy.

The second ear with reversions (1538-2) arose on a bz plant and was either a sib or a self; the notation on the bag had been obscured by weather and was unreadable. The phenotypic classes were 121 A Sh Bz, 53 A sh bz, 119 a Sh and 60 a sh. Again, the a Sh and a sh kernels proved to be Bz and bz, respectively, from progeny tests. On this ear, the ratio of Sh Bz : sh bz classes was 2 : 1 but that of A : a was 1 : 1. The results fit neither the expected ratio of a sib or self cross, an enigma still under consideration.

On the remaining ears of this planting, single Sh Bz kernels were observed on a few individuals, but contamination cannot be eliminated as the source of these phenotypes.

The sh-bz-x2 mutant is not affected by the presence of Ac but has not as yet been tested with Spm.

Although the cause of the ratios observed to date is open to speculation, it cannot be denied that sh-bz-x2 is reverting, apparently as a unit.

Experimentation with this double mutant is made difficult by the fact that (1) reversions show no regular pattern except that independent reversions of neither sh nor bz have been observed and (2) reversions which do occur are relatively rare.

Hopefully, data collected in future experiments will shed more light on this puzzling but fascinating situation.

John P. Mottinger

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1. Relative frequencies of meiotic stages.

Relative frequencies of meiotic stages were estimated in microsporocytes of a KYS/Inversion 5083 stock grown under controlled environmental conditions (light cycle: 14 hours light, 10 hours dark; relative humidity 85 percent to 95 percent; temperature 24°C to 25°C at sporocyte level). Samples were collected at 8½ hours into the light cycle, fixed in alcohol-acetic 3:1 mixture, and stored in a freezer until examination. Tassel branches were selected for study which contained a seriation of four stages: either synizesis, pachytene, diplotene-through-telophase II (counted as a single stage in this instance), and quartets, or pachytene, diplotene-through-telophase II, quartets, and spores. In the first type of branch comparisons were made of the relative frequencies of pachytene vs diplotene-through telophase II, in the second of diplotene-through-

telophase II vs quartets. It was considered that such comparisons of stage frequencies might constitute a valid estimate of stage duration only where the stages compared were bracketed within the branch by a preceding and a succeeding stage. All three anthers of each first flower were examined; where differences existed among or within anthers, the flower was classified as at the predominant stage. Twelve suitable branches yielded a mean frequency of pachytene 0.46 vs diplotene-through-telophase II 0.54. (s.d. = .0118), while 17 suitable branches gave a frequency of diplotene-through-telophase II 0.47 vs quartets 0.53 (s.d. = .0130). (Branches were not heterogeneous at the 10 percent level in either case.)

Further comparisons were drawn within the diplotene-through-telophase II category of frequencies of diplotene, diakinesis, metaphase I, anaphase I, telophase I-through-interkinesis, prophase II, metaphase II, anaphase II and telophase II. In this case records were kept of the predominant stage of individual anthers of all first flowers except those which contained sporocytes at anaphase I; in this latter instance actual counts of stages of all sporocytes were recorded in systematically scanned slides. Results of this study gave the following stage frequencies:

stage	frequency	cumulative frequency
diplotene	.082	.082
diakinesis	.391	.473
metaphase I	.139	.612
anaphase I	.069	.681
telophase I-interkinesis	.153	.834
prophase II	.016	.850
metaphase II	.083	.933
anaphase II	.051	.984
telophase II	.097	1.081

All observations were made by the same person. Discrimination between some successive stages was necessarily arbitrary but reasonably consistent (i.e. synizesis, pachytene; diplotene, diakinesis). It is recognized that synizesis may in large part contain completely synapsed chromosomes and to this extent is technically synonymous with pachytene,

but for the purpose of this study cells were counted as pachytene only if they were past synizesis.

Synizesis was apparently of considerably greater duration than any of the stages compared above. It was rarely included within a single branch (bracketed by a preceding and a succeeding stage), but its duration was shorter than the interval which separates first and second flowers. The duration of synizesis is currently under study by other methods.

The long-stemmed spikelet was more advanced than the short on the average by 0.53 of the duration of diplotene-through-telophase II.

It is not known how other environmental conditions would affect the relationships suggested above or how other stocks might differ.

Marjorie P. Maguire

2. Azure A as a staining technique for maize microsporocytes, microspores, and pollen.

The azure A staining procedure (as described by De Lamater, Stain Tech. 26: 199-204) is a relatively simple technique which gives excellent DNA specific stain of maize chromosomes at certain stages. It is especially superior to acetocarmine for pollen grains (where two densely staining sperm nuclei and a diffuse vegetative nucleus are found consistently). It also seems superior to acetocarmine for microspore chromosomes. While it is inferior to or no better than temporary acetocarmine mounts for most meiotic stages, it survives autoradiographic stripping and developing procedures unscathed where carmine stains may be demolished.

Marjorie P. Maguire

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1. Field studies on hybridization and parallel variation in the wild relatives of maize in Central Mexico II.

Field studies of the wild relatives of maize in Central Mexico begun last year [MGNL 43:182] were continued in the fall of 1969. Selected maize fields were studied along the transect from Cuitzeo to Moro Leon (50 kms) and from Cuitzeo to Churintzio (150 kms). The maize planted throughout the region is basically a rather uniform low elevation Conico-Chalqueno-Celaya complex though there is sometimes considerable variation from field to field and within fields. Teosinte is wild throughout the region and occurs along the margin of fields or as a weed in the fields. The variation in maize from a single field appears to be more extreme in fields where teosinte is present as a weed.

Mapping of fields planted to maize where teosinte was present indicates specific patterns from which a model for the effectiveness of maize x teosinte hybridization and resultant introgression into maize can be constructed. When F_1 hybrids do occur they are often bunched, suggesting a common parent; this is true even in fields where the distribution of teosinte is reasonably uniform throughout the field and indicates the effectiveness of the partial seasonal isolation between teosinte and maize. When teosinte is abundant, the frequency of F_1 hybrids increases proportionally but the frequency of backcrosses to maize does not appear to increase significantly. [Field identification of the first maize backcross is reasonably accurate, the second and third become increasingly more difficult. The first and second backcross to teosinte are detectable, but subsequent backcrosses are difficult to identify in the field. At present, suspected field-collected second and third generation backcrosses in both directions are undergoing genetic experimentation.] When teosinte is present, but not abundant, and distributed throughout the field, the absolute number of F_1 hybrids decreases but the number of subsequent backcrosses increases. Apparently the most effective structure for the introduction of teosinte germplasm into maize is to

have a low percentage of teosinte plants well distributed throughout the field which are partially seasonal isolated from maize. The F_1 hybrids are earlier than teosinte and therefore hybridize with maize, resulting in a greater abundance of backcross progeny than F_1 hybrids.

	Sample Area	Number of Plants Total (Maize & Teosinte)	Teosinte	% Teosinte / Maize	F_1	Mbc
Teosinte not abundant - F_1 hybrids less frequent than backcrosses						
Cuitzeo, Michoacan	5/8 acre	10,622	129	1.2%	2	8
Teosinte abundant - F_1 hybrids more frequent than backcrosses						
Uriangato, Guanajuato	1/2 acre	2,493	473	19%	9	1

The Tripsacum present in and around these fields belong to the T. lanceolatum group. Field-collected clones from the study areas are being maintained for crossing studies in the Maize Relatives - Genetic Garden of Tulane University.

H. Garrison Wilkes

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1. Malate dehydrogenase in maize endosperm.

A. Intracellular Localization

Multiple molecular forms of malate dehydrogenase have been demonstrated in numerous animal and plant tissues and the existence of isozymes appears to be the rule. The endosperm of Zea mays L. has been examined with regard to the presence of this enzyme and several isozymes have been detected using acrylamide gel electrophoresis. Studies have been concentrated on the two isozymes which migrate most rapidly toward

the anode and make up the bulk of the total activity of the enzyme. By using isopycnic or equilibrium density centrifugation, these two major isozymes have been separated and their particulate associations determined. The isozyme which migrates most rapidly toward the anode during electrophoresis is mitochondrial in origin while the second major isozyme is associated with a microbody which resembles the glyoxysomes (peroxisomes) reported in other plant tissues. The microbodies have been observed under the electron microscope in both sections of endosperm and in homogenates. They are membrane bound, 0.5 to 1.0μ in diameter, and contain most of the catalase present in the tissue. Homogeneous preparations of these major isozymes have been obtained using anion-exchange chromatography and their physical and kinetic properties are now under investigation. The remaining isozymes detected in this tissue appear to be soluble or cytoplasmic in origin and together make up a small fraction of the total activity.

B. Changes in Isozyme Pattern During Endosperm Development

Changes in the isozyme pattern of malate dehydrogenase have been studied in developing maize endosperm. The plants used were a single cross ($\underline{su}_1/\underline{su}_1$) hybrid, "Seneca 60". Endosperm was obtained from selfed plants and was harvested from 2 to 20 days after pollination at two day intervals. The endosperm from individual kernels was excised and homogenized in buffer. The resulting homogenate was filtered and used directly for acrylamide gel electrophoresis. Two isozymes were detected in the unfertilized ovule and in the endosperm up to eight days after pollination. These corresponded to the particulate isozymes mentioned in part A, which are associated with the mitochondria and glyoxysomes. From the tenth to the fourteenth day following pollination at least three other isozymes appeared. They migrated more slowly toward the anode and, as evidenced by their staining intensity on the gels, were not present in as high a concentration as the two major particulate isozymes. It appears that all the slower travelling forms are soluble or cytoplasmic in origin. No further changes in isozyme pattern were detected following the fourteenth day after pollination.

D. B. Hayden
F. S. Cook

2. The relationship among leaf number, leaf width, and cell number in ABPHYL.

We reported earlier (MGCNL 41: 197 and MGCNL 42: 169-172) some features of an "opposite leaf" phenotype. Since considerable variability in its expression has been observed, we have renamed the phenomenon "ABPHYL", for ABerrant PHYLlotaxy. Besides confirming our previous observations, our recent observations have concentrated on the number and width of leaves produced by variants. Segregations through the F_5 have continued to confirm previous observations.

We now know that ABPHYL can be expressed at any time from embryo to tassel initiation. In addition, plants have been observed with up to four times more leaves than would be normally expected. Most frequently, however, and especially so in those plants where leaf arrangement is decussate, leaf number is twice the normal number. Leaves from ABPHYL plants most frequently are one-half the width of normal leaves but since length is not significantly different, total leaf area would be expected to be similar. Preliminary measurements support this expectation. Leaves are narrower in ABPHYL due to fewer and not narrower cells.

Thus we now interpret the ABPHYL genotype as expressing itself, at least in part, at the shoot apex through modification of the rate of production, siting and size of leaf primordia. Since some crosses tend to accumulate different features of this genotype, we feel that certain desirable features of this system can eventually be stabilized into a single non-variable expression.

R. I. Greyson
D. B. Walden

3. Effects of 8-hydroxyquinoline on mitosis in maize root tips.

Our protocol for collecting metaphase spreads for eventual use in studies requiring chromosome identification includes incubation of roots in 0.002M 8-hydroxyquinoline (8-OHQ) for 3 hours. Excellent chromosomes and a relatively large number of metaphase spreads is collected by the action of this chemical. However, we were concerned about possible additional effects of 8-OHQ on the cells. From the experiment described below, we have been able to ascertain the effect of 8-OHQ on mitosis.

Roots of 'Seneca 60' (Chen, 1969) were incubated in 0.002M 8-OHQ for 3 hours, washed thoroughly, and returned to the germination chamber (25°C) for further growth. Tritiated thymidine (1 uc/ml final concentration) was applied for 30 minutes to the previously 8-OHQ treated roots in a series of treatments at 2-hour intervals for 22 hours; that is, a total of 12 different treatments over the 22 hour period was collected, such that each treatment was a specific hourly increment from 0 hour, the time at which the roots were removed from the 8-OHQ incubation and the wash initiated.

The root tips were processed for smearing as reported earlier (Chen 1969) and autoradiographs were prepared according to the schedule of Douglas (MGCN 42: 175-178, 1969). For each treatment and control, the mitotic index and labeling index were determined.

Preliminary results indicate that both mitosis and ^{3}H uptake are affected by 8-OHQ. The mitotic index was affected immediately, during the incubation period. Within the two to eight hour period after 8-OHQ incubation, almost no division figures were observed. Mitosis resumed after eight hours and reached the control level at 12 hours. 8-hydroxyquinoline inhibited but did not completely stop ^{3}H uptake. The labeling index decreased slowly in the first six hours after 8-OHQ incubation then sharply thereafter reached a minimum (15%) in 8-10 hours. After 10 hours, the labeling index began to increase and control ^{3}H uptake was recovered in 14-16 hours.

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4. Nuclear cycle in Zea mays L. root tips.

In MGCN 43: 186-190 (1969) we reported the duration of the nuclear cycle in root tips of 'Seneca 60' at 20°, 30°, and 35°C. These earlier investigations have been extended to 25°C. The increments in S, G_2, and M indicated that the cycle components retain a relationship at 25°C proportional to the same components at the other temperatures. However, the

Table 1

Frequency of nuclei scored from root tips following pulse labeling (^{3}H-thymidine, 30 minutes), 25°C

Class	'Seneca 60'		'Chromosome 9 Tester'	
	Long Root	Short Root	Long Root	Short Root
Interphase				
Labeled	30281	30828	23032	19529
Prophase				
Labeled	909	1589	1171	1086
Unlabeled	1342	1868	1014	1340
Metaphase				
Labeled	299	547	417	355
Unlabeled	629	865	488	681
Anaphase				
Labeled	70	151	85	87
Unlabeled	151	218	121	144
Telophase				
Labeled	382	572	402	381
Unlabeled	871	896	438	682
Total	34934	37534	27168	24285

Table 2

Duration of the nuclear cycle in the root tips of Zea mays L. (25°C).

Phase	'Seneca 60'				'Chromosome 9 tester'			
	Long Root		Short Root		Long Root		Short Root	
	hrs.	%	hrs.	%	hrs.	%	hrs.	%
Interphase								
G_1	1.08	11.1	2.00	19.9	1.50	15.0	2.56	24.1
S	5.10	52.0	5.00	50.5	4.70	48.0	4.50	42.5
G_2	2.81	28.7	1.80	18.5	2.70	28.0	2.43	23.0
sub-total	8.99	91.8	8.80	88.9	8.90	91.0	9.49	89.6
Mitosis								
Prophase	0.39	4.0	0.57	5.7	0.50	4.7	0.57	5.3
Metaphase	0.16	1.6	0.23	2.3	0.20	1.9	0.24	2.3
Anaphase	0.04	0.4	0.06	0.6	0.04	0.5	0.05	0.5
Telophase	0.22	2.2	0.24	2.5	0.17	1.9	0.25	2.3
sub-total	0.81	8.2	1.10	11.1	0.91	9.0	1.11	10.4
Total	9.80		9.90		9.81		10.60	

calculated values for G_1, yielding negative numbers, required further investigation. We considered three factors:

i) the labeling time (duration of pulse);

ii) misclassification of prophase and background label;

iii) the length of meristematic region of the root tip included in the study.

In an attempt to broaden the scope of this study, a second stock (a chromosome 9 tester) was added. Employing Chen's (1969) methods, two root tip lengths ("long" = 2.40 $\pm$ 0.08mm and "short" = 1.52 $\pm$ 0.02 mm) were studied at 25°C. All slides from each treatment were coded and scored blindly. The classification data are presented in Table 1 and the new interphase and mitosis estimates at 25°C are presented in Table 2.

The data revealed no differences in the nuclear cycle of the two stocks. Likewise, the data did not reveal major differences between root preparation techniques. The duration of mitosis and its components, and the S period, are unaltered from our earlier estimates (MGCN 43: 186-190, 1969). However, the calculations of G_1 and G_2 yielded new estimates. G_1 and G_2 were partitioned from the residual of the interphase minus S interval; it follows logically that a change in G_1 in one direction will alter G_2 in the opposite direction in so far as we employ the proportion method. Since G_1 and G_2 are derived values from the slopes of the curves, it is clear that the alterations we made in our protocol are responsible for the changes recorded (Table 2) for G_1 and G_2.

We have reduced our acceptable labeled cell from 4 x background to 2 x background. Coupled with a more critical classification of prophase, we feel that this modified protocol more accurately represents the nuclear cycle in maize root tips.

R. S. Verma

5. Chromosome replication profiles from maize root tips.

In MGCN 43: 190-192 (1969) we reported preliminary data from a study of the replication behavior of individual maize somatic chromosomes at 28°C in a chromosome 3 tester stock in which each cell contained one

B-chromosome. This experiment (98 cells) is complete with grain count data for each chromosome arm in each hour during the 7-12 hour period after the ^{3}H-thymidine pulse.

These data were processed as follows.

The mean grain counts per hour of the S period were determined for each chromosome arm. These data or their derivatives, namely the measure of activity in a chromosome segment during S, if plotted against the time intervals of S, are referred to below as a "replication profile." Thus far, we have recognized two kinds of profiles, the "uptake profile" which is a frequency histogram and the "increment profile" which is a plot of the change per unit time of label accumulation. Profiles have been constructed for each arm of all A-type chromosomes in the maize complement.

The profiles obtained from the above study (28°C) revealed little detail in most chromosome arms. The B-chromosome profile did indicate that extensive ^{3}H-thymidine uptake (DNA synthesis) occurs in the last half of the S period, although synthesis does occur during the entire S period. Thus, the uptake of tritium in the B-chromosome is clearly not confined to the S period as has been reported elsewhere.

The lack of detail in profiles at 28°C led us to reason that increased resolution might be obtained by lengthening the S period (by lowering the incubation temperature). Two experiments employing a temperature of 18°C have been completed: one using a chromosome 3 tester stock (164 cells), the other using a stock heteromorphic for abnormal chromosome 10 (300 cells). Experimental procedures were those outlined in MGCN 42: 175-178 (1968) and MGCN 43: 190-192 (1969). In addition, the length of the S period treated in the two experiments was 12 hours.

The profiles of all chromosome arms of the complement in both experiments showed a rapid increase in ^{3}H-thymidine uptake in early S, followed by a gradual decline in uptake toward the end of S. In all cases, there was a marked dip in the profiles at the end of the first one third of the S period. There was a remarkable similarity between profiles of the same chromosome arms in the two experiments.

We have recognized three types of uptake profiles:

1. Profiles in which, at each hour of the S period, the arm ratio

(L/s) is representative of the ratio of ^{3}H uptake (L/s). Chromosome 5 (arm ratio 1.1) is an exemplar chromosome.

2. Profiles in which the arm ratio does not predict the ratio of ^{3}H uptake (L/s) at each hour of the S period. Thus, during a specific interval, the short arm may be accumulating more ^{3}H than the long arm, observed as an intersection of the arm profiles. Chromosome 6 (arm ratio 2.25 less satellite) is an example of this type.
3. Profiles intermediate between types 1 and 2 above, in which there are no arm profile intersections although the areas under the curve (profile) are not representative of the arm lengths. Chromosome 9 (arm ratio 1.6) is an exemplar chromosome.

All A-type chromosomes of maize can be assigned to one of these three types of profile. In so far as ^{3}H uptake represents DNA synthesis, our data support the arguments that the synthesis is time and chromosome segment dependent.

We have examined K10 in addition to A and B chromosomes. Abnormal 10 has a large distal segment, which at mitotic metaphase is approximately equal in length to the long arm of normal chromosome 10; the long arm of K10 is approximately double the length of the long arm of N10. This segment of K10 has no demonstrable effect on the replication profile of the long arm segment proximal to it, since the profile of this region is identical to that of the normal chromosome 10. The profile of the K10 distal segment is different from the profiles of all the chromosome arms of the complement in that:

i) uptake occurs at a constant rate throughout S such that there is no peak in the profile;
ii) ^{3}H uptake at most hours of the S period was greater than that attained by a comparable length of A-type chromosome;
iii) uptake in the K10 segment continued at least one hour after all other arms had completed uptake.

Our data show that for the A-type chromosomes without exception the 18°C profile amplifies the 28°C profile, indicating but not proving that similar processes are involved in uptake at the two temperatures. While

we do not have profiles for the B chromosome (28°C) and the K10 segment (18°C) at the same temperature, it is interesting to note that they present quite dissimilar profiles. If the dissimilarity persists in tests at both temperatures, the ^{3}H uptake profiles may provide strong evidence on which to differentiate between a B chromosome and the distal segment in the long arm of K10.

G. R. Douglas

6. Somatic association as a general phenomenon in maize.

Miles (M.G.C.N.L. 42:77-79) studied the effect of the presence of 0, 1, or 2 abnormal chromosomes K10 on the somatic association of chromosomes 6. From that portion of her study in which K10 was absent, Miles concluded that "during mitotic metaphase in root tip cells the homologous chromosomes are not associated." By studying all possible 190 homologous and non-homologous associations of chromosomes in somatic cells of maize, we have attempted to test whether in fact somatic association is a real event in maize. To the best of our knowledge, this is the first study with plant or animal cells in which all possible chromosome combinations have been examined in a normal stock.

Root tips of the single cross hybrid 'Seneca-60' were treated with 8-hydroxyquinoline for 3 hrs. in one experiment and with cold (5°C) for 24 hrs. in a second experiment. Both treatments have been shown previously to arrest spindle fiber development and permit the accumulation of metaphases. Squash preparations were made following Chen's (1969) protocol. Cells were chosen and photographed which were flat, reasonably circular, and with all 20 chromosomes and their centromeres clearly visible. The chromosomes were projected to a final magnification of 30,000x and measured using a highly accurate ($\pm$ .04mm.) measuring device of our own design and construction. The chromosomes were objectively identified by a computer program that we have written specifically for maize. The program uses a hieristic reasoning sequence to identify the chromosomes from arm ratio and arm length measurements. No pairing of chromosomes for purposes of identification is involved. The distances between chromosomes were calculated from the x, y co-ordinates of the

centromeres and standardized by dividing the distance between any two chromosomes by the greatest distance between two chromosomes in the cell. The output is expressed by the computer as a frequency histogram for the distances between each, any and every chromosome pair. The distributions of distances between each possible chromosome pair were compared to a theoretical distribution. For a description of the statistical considerations, see Feldman (1966) (Feldman, et al., P.N.A.S. 56: 1192-1199, 1966). The theoretical distribution curve has a mean value of 0.453 where x can vary between 0 and 1. The Kolmogorov-Smirnov One-Sample or Two-Sample test of goodness of fit was used to compare the observed distributions with the theoretical distributions. We required at least 20% of the frequency class intervals in the histogram to show a deviation beyond the 95% level before the observed curve was considered significantly different from the theoretical curve.

In Table 1 are summarized the data from the distribution of distances among all 10 homologous pairs of chromosomes.

Table 1

Mean distance between homologues. (N=50).

Treatment	Chromosome									
	1	2	3	4	5	6	7	8	9	10
8-hydroxy-quinoline 3 Hrs.	.420	.331*	.406	.479	.421	.448	.481	.473	.418	.417
Cold (5°C) for 24 Hrs.	.501	.373*	.375*	.346*	.449	.436	.346*	.357*	.343*	.412

*Significant association beyond 95% limit.

Non-homologous associations between all four chromosomes of 3, 7 (.376) and 9, 4 (.351) have been noted in the cold treatment but not in the 8-hydroxyquinoline treatment. Where distribution means of distances between chromosomes, whether homologous or non-homologous, approached the theoretical

mean of .453, the shape of the distribution closely approximated that of the theoretical distribution.

In tests of the association of homologous chromosomes 6 in cells from both treatments, we found, as did Miles, that the mean distance between homologues did not differ significantly from the expected .453. The distribution distance mean (.417, .412) for chromosome 10 also did not deviate significantly from the theoretical curve. However, it appears that other homologous chromosome pairs are associated at metaphase in Seneca-60 and that the degree of this association is affected by the treatment used to arrest spindle development for the accumulation of metaphase spreads.

J. D. Horn

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1. Organization of the pigmenting and paramutagenic determinants of the R-stippled gene in maize.

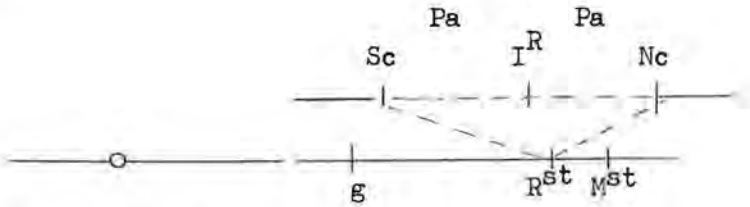
The R-stippled (R^{st}) gene in maize is unstable in aleurone pigmentation and mutates in the germ line to a fully colored form, self-colored (R^{sc}). In mutation to R^{sc} the potential of R^{st} to reduce heritably the pigmenting action of sensitive alleles in heterozygotes (paramutation) may be fully retained, quantitatively reduced, or lost. The basis for the coincident alteration in paramutagenicity with R^{st} to R^{sc} mutation and the topographical arrangement of the components of R-stippled were the main objects of investigation.

Major reductions in paramutagenicity among R^{sc} mutants from $R^{st}R^{st}$, $R^{st}R^{nj}$, and $R^{st}R^{nj:st}$ combinations were found in the class of mutants that arose in conjunction with recombination. Reductions among the noncrossover mutants were small. When exchange in the R region was suppressed by a closely linked heterochromatic knob, or precluded in the case of R^{st} hemizygotes, the reductions were minor and infrequent. The association between recombinant origin of the R^{sc} mutants and major

reduction in paramutagenicity is accounted for by intralocus crossovers which simultaneously separate the seed pigmenting component (Sc) from an instability factor (I^R) and fractionate the paramutagenic component.

Three types of crossover derivatives were obtained from $R^{st}R^r$ plants: (1) unstable plant color (green to red mutations), near-colorless aleurone, (2) r^r, near-colorless aleurone and (3) r^r, colorless aleurone. The medium to strongly paramutagenic $R^{sc}R^r$ combinations yielded the second and third types of derivatives at combined rates equivalent to the total of the three types of derivatives from $R^{st}R^r$. The strongly paramutagenic $R^{sc}R^r$ heterozygotes gave more r^r near-colorless than colorless derivatives. As the paramutagenicity of the R^{sc} allele heterozygous with R^r decreased, however, the frequency of the near-colorless derivatives decreased and that of the colorless increased. Only r^r, colorless crossover derivatives were obtained from the very weakly paramutagenic and nonparamutagenic $R^{sc}R^r$ combinations, and at rates of approximately one-half the total rate of crossover derivatives from $R^{st}R^r$. All crossover r^r, colorless aleurone derivatives from $R^{st}R^r$ and $R^{sc}R^r$ heterozygotes were nonparamutagenic. Most of the near-colorless derivatives were paramutagenic at various levels, all weaker than the respective parent R^{st} or R^{sc} allele. One r^r near-colorless derivative from $R^{st}R^r$ and one to three similar derivatives from each of five $R^{sc}R^r$ heterozygotes were nonparamutagenic. The average level of paramutagenic action of the near-colorless derivatives was stronger when derived from strongly paramutagenic $R^{sc}R^r$ than from weakly paramutagenic $R^{sc}R^r$ combinations.

The present paramutation and recombination data support the conclusions that R-stippled carries two aleurone pigment determiners (Sc) and a near-colorless component (Nc), with the paramutagenic potential distributed along the length of the chromosome segment between (Sc) and (Nc). The instability factor maps approximately in the middle of the paramutagenic component and was shown to be transposable. The paramutagenic segments in the (Sc)--(I^R) and (I^R)--(Nc) intervals seem to consist of many repeats of a basic unit or a small segment.



Pa = paramutagenic determiners

Kante V. Satyanarayana

2. Correction of a published statement concerning a supposed new class of paramutable R alleles of Andean origin.

It was reported in an article entitled "Geographic distribution of paramutable and paramutagenic R alleles in maize" recently published (Genetics 61:677-695) by W. J. Van Der Walt and the writer that certain R alleles of Andean origin undergo a reduction in pigmenting potential on passage through heterozygotes with standard R^r. It was concluded at the time that these Andean alleles represented a previously unrecognized class of paramutable R factors.

Later tests have not confirmed this claim. The mistake is probably attributable to two circumstances: (1) the Andean R alleles in question appear to be subject to significant variation in expression from season to season, in contrast to standard R^r and (2) the testcrosses of the controls (homozygous Andean R R and Andean R/r ♂♂) and of the heterozygotes of Andean R with standard R^r on which the published report was based were made in different years.

Adequately controlled testcrosses with three of the Andean R alleles in question were made in 1969. The results clearly showed no effect of heterozygosity for standard R^r for either one or two generations on level of Andean R action.

R. A. Brink

ADDENDUM:

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1. Doubly and triply monosomic Zea mays.

When plants heterozygous for the $\frac{r}{x-1}$ deficiency are used as females, a high frequency of monosomic individuals are produced in the $\frac{r}{x-1}$ carrying progeny (Satyanarayana, unpublished). These are produced by a nondisjunctional event which takes place after meiosis during the megaspore divisions of the embryo sac.

Over 250 monosomic plants have been obtained in my work this past summer with this system. The monosomic plants are surprisingly vigorous and good microsporocyte samples have been taken from several of the individuals. In addition, a few pollinations have been possible using these plants. In addition to singly monosomic plants, doubly and triply monosomic plants are obtained. The doubly monosomic plants are currently under analysis to determine if distributive pairing is taking place in these plants. The triply monosomic plant had necrotic sectors on its leaf surfaces and it was stunted. At diakinesis in this plant, three univalents and 7 bivalents were regularly found. At metaphase I, the 3 univalents were usually positioned somewhat off of the metaphase plate at random in the cell. It is very surprising that a plant is able to tolerate this very large amount of chromosomal imbalance!

David F. Weber

2. The effect of B chromosomes on intragenic recombination.

Low numbers of B chromosomes apparently have little of no effect on the phenotype of maize while higher numbers cause several abnormalities. Cytological evidence that B chromosomes increase the mean chiasma frequency in maize has been shown by Ayonaadu and Rees (Genetica 39: 74, 1968). B chromosomes have also been shown to increase recombination between loci on chromosome 5 (Nel, M.G.N.L. 42: 63, 1968; 43: 54, 1969) and chromosomes 3 and 9 (Hanson, M.G.N.L. 35: 61, 1961) in maize. The present study was

TABLE 1

(1st genetic background)

Plant Number	Number of B-chromosomes	Recombinants	Population	Crossover Frequency X 10^{-4}
5	0	332	369,585	9.88
6	0	250	210,780	11.86
8	0	278	297,225	10.28
9	0	388	344,745	11.25
12 WIM	0	280	238,815	11.72
Totals		1528	1,461,150	10.457 s=0.87
10	1	416	334,170	12.45
11	2	648	412,785	14.93
15	1 or 2	470	314,640	15.69
Totals		1534	1,061,595	14.449 s=1.68

TABLE 2

(2nd genetic background)

Plant Number	Number of B-chromosomes	Recombinants	Population	Crossover Frequency X 10^{-4}
G 2	1	206	253,080	8.1
G 3	1	112	140,220	7.9
Totals		318	393,300	8.06 s=0.14
G 4	0	178	284,175	6.2
G 6	0	160	247,860	6.4
Totals		338	532,035	6.35 s=0.02

initiated to determine if B chromosomes also increase intragenic recombination in the waxy locus of maize.

Recombination between the $\underline{wx}^{c}$ and $\underline{wx}^{90}$ pseudoalleles of the waxy gene was determined with pollen grains using techniques developed by Nelson (Genetics 60: 507, 1968). These plants contained 0, 1, or 2 B chromosomes.

Two slightly different genetic backgrounds were used to determine the effects of B chromosomes on intragenic crossing over (Tables 1 and 2). All plants in each of the tables were sibs and grown at the same time under the same conditions. The results show that B chromosomes increase intragenic recombination at the waxy locus. Since increased recombination values are found both for intragenic recombination and intergenic recombination in the presence of B chromosomes, this lends support to the idea that one mechanism is involved both in intragenic and intergenic recombination.

Walter I. Melnyczenko

III. REPORT ON MAIZE COOPERATIVE

Seed requests to the Maize Cooperative in 1969 numbered 152. This is a reduction of 16 requests compared to 1968. A total of 95 requests (77 percent) were from 28 states in the United States and 36 (23 percent) requests were from 36 foreign countries. In addition, 62.5 percent of the requests were from Geneticists, 14.6 percent from Plant Breeders, 15.2 percent from physiologists, and 7.7 percent for educational purposes.

The following traits have been received from maize geneticists over the past several years and have been added to the collection:

Gene Symbol	Trait	Chromosome Location	Stock Source
o_4	opaque-4	--	P. L. Crane
eg	expanded glume	5	C. R. Burnham
rgd	ragged	6	E. Dempsey
TB-6a	break 6S .5	6	E. Dempsey
TB-8a	break 8L .7	8	A. Ghidoni
wd	white deficiency	9	G. Kikudome
$K^{10}g_1R^r$	abnormal 10	10	G. Kikudome
Wc	dominant white endosperm	9	E. H. Coe, Jr.
In^D	dominant dilute aleurone	7	E. H. Coe, Jr.
ps	allele of vp_7	5	E. H. Coe, Jr.
ar	argentia	9	E. H. Coe, Jr.
ub	unbranched tassel	--	M. G. Neuffer
Dt_2	dotted-2	6	M. G. Neuffer
Dt_3	dotted-3	7	M. G. Neuffer
lu_1	lutescent	5	D. K. Shortess
pb_1	allele y_1	6	D. S. Robertson

Gene Symbol	Trait	Chromosome Location	Stock Source
w^m	allele y_1	6	D. S. Robertson
pb_4	piebald	6	D. S. Robertson
o_5	opaque-5	7	D. S. Robertson
l_{4120}	luteus	6	D. S. Robertson
WF9 (T)	T cytoplasm	--	J. B. Beckett
N6 (S)	S cytoplasm	--	J. B. Beckett
rf_1rf_2	non restorers	--	J. B. Beckett
Rf_1rf_2	non restorers	--	J. B. Beckett
rf_1Rf_2	non restorers	--	J. B. Beckett
Rf_1Rf_2	restorers	--	J. B. Beckett
td	thick tassel dwarf	5	J. B. Beckett
yg_1	yellow green -1	5	J. B. Beckett
j_2	japonica-2	4	R. I. Brawn
Lc	red leaf color	10	J. Kermicle
E^j	japonica extender	10	J. Kermicle
ct	compact tassel	--	L. F. Bauman
Tp_2	teopod-2	10	J. R. Laughnan
$A_1{}^b$	A_1 allele with α & β	3	J. R. Laughnan
zn_2	zebra necrotic	--	J. Giesbrecht
te	terminal ear	3	C. O. Grogan
lo	lethal ovule	9	O. E. Nelson
Knobless Wilbur's Flint			W. C. Galinat

Through the efforts of Dr. M. D. Thorne, Head, and Dr. C. M. Brown, Associate Head, of the Department of Agronomy, the Maize Cooperative has received nonrecurring funds from the University of Illinois for a cold storage unit. A total $25,000 has been alloted for the cold storage unit and 1,000 self contained steel storage drawers. This cold storage facility should be adequate to house the collection for many years.

During the summer of 1969 certain chromosome tester stocks were increased. Also, a considerable number of stocks were grown out to confirm the pedigree of certain mature plant traits. In addition, 832 rows were grown out and pollen readings taken to determine if certain reciprocal translocation stocks in the collection were homozygous for the translocation. Certain chromosome tester stocks were grown out in 10 row blocks in order to isolate new chromosome tester combinations.

The attached catalogue of stocks represents a listing of currently available genetic stocks. Certain traits and new chromosome combinations have been added to the list. This list of traits should replace the one published in 1967, when requesting seed. A complete listing of all translocation stocks in the collection has been published in Volume 43 of the Maize Newsletter.

Requests for seed and correspondence relative to the stock program should be addressed to:

Dr. R. J. Lambert
S-116 Turner Hall
Department of Agronomy
University of Illinois, Urbana - Champaign
Urbana, Illinois 61801

R. J. Lambert
D. E. Yates

Catalogue of Stocks

Chromosome 1

ad_1 an_1 bm_2

ad_1 bm_2

an_1 bm_2

as

br_1 Vg

br_2

bz_2^m; M

bz_2^m; m

Kn

Kn Ts_6

lw_1

P^{CR}

P^{CW}

P^{MO}

P^{RR}

P^{RW}

P^{VV}

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^{WR} bm_2

P^{WR} an_1 bm_2

P^{WR} an_1 Kn bm_2

Chromosome 1 (Continued)

P^{WR} gs_1 bm_2

P^{WW} br_1 f_1 bm_2

P^{WW} br_1 f_1 ad_1 bm_2

P^{WW} br_1 f_1 an_1 gs_1 bm_2

P^{WW} hm br_1 f_1

rs_2

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

ts_2 P^{WW} br_1 bm_2

Ts_6

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 P^{WW} br_1 f_1 bm_2

zb_4 ts_2 P^{WW}

zb_4 ts_2 P^{WW} bm_2

Chromosome 1 (Continued)

an_{6923}-bz_2 (apparent deficiency including $\underline{an}_1$ and $\underline{bz}_2$)

bm_2

bm_2 br_2

necrotic 8147-31

tb

id

ms_9

ms_{14}

rd

Chromosome 2

al lg_1

al lg_1 gl_2 B sk

al lg_1 gl_2 b sk v_4

ba_2

d_5

fl_1

ts_1

gl_{11}

Ht

lg_1

lg_1 gl_2 wt

lg_1 gl_2 B

lg_1 gl_2 b

lg_1 gl_2 b Ch

lg_1 gl_2 b fl_1 v_4

Chromosome 2 (Continued)

lg_1 gl_2 b fl_1 v_4 Ch

lg_1 gl_2 B gs_2

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

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

lg_1 gl_2 w_3 Ch

ws_3 lg_1 gl_2 B

ws_3 lg_1 gl_2 b

ws_3 lg_1 gl_2 b v_4

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

wt

mn

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^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^m 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 B Pl

a_1 sh_2; A_2 C R dt_1

a_1^{st} Sh_2; A_2 C R Dt_1

a_1^{st} sh_2; A_2 C R Dt_1

a_1^{st} sh_2 et; A_2 C R Dt_1

a_1^{st} et; A_2 C R Dt_1

ba_1

Cg

cl_1

cr_1

cr_1 d_1 Lg_3

d_1

d_1 pm_1

d_1 Lg_3

Chromosome 3 (Continued)

d_1 Rg lg_2

d_1 ts_4 lg_2

d_1 Rg ts_4 lg_2

d_1 Rf_1 ts_4 lg_2

d_1 ts_4 lg_2 a_1; A_2 C R Dt_1

gl_6 lg_2 A^b et; A_2 C R Dt_1

gl_6 lg_2 a_1 et; A_2 C R Dt_1

gl_7

lg_2 A^b Sh et; A_2 C R Dt_1

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

na_1 lg_2

pm

ra_2

ra_2 lg_2

ra_2 lg_2 pm

ra_2 Rg

ra_2 Rg lg_2

Chromosome 3 (Continued)

Rg

ra_2 Rg ts_4 pm_1 lg_2

rt

ts_4

ts_4 na_1

ys_3

pg_2

vp_1

Primary trisomic 3

Chromosome 4

bm_3

bt_2

bt_2 gl_4

c_2; A_1 A_2 C_1 R

fl_2

Ga_1 Su_1

Ga_1^s Su_1

gl_3

gl_3 dp

la su_1 gl_3

la su_1 Tu gl_3

lw_4; lw_3

o_1

st

su_1

Chromosome 4 (Continued)

su_1^{am}

su_1 bm_3

su_1 gl_3

su_1 gl_3 ra_3

su_1 gl_4

su_1 ra_3

su_1 Tu

su_1 Tu gl_3

su_1 zb_6

su_1 zb_6 Tu gl_3

su_1 zb_6 Tu

su_1 o_1

Ts_5

Ts_5 su_1

Ts_5 su_1 zb_6

Ts_5 st

Ts_5 st su_1

Tu gl_3

zb_6

v_8

dp

j_2

Primary trisomic 4

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 b_3 Pr; 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 v_3 pr; A_1 C R

a_2 pr; A_1 C R

ae

ae td

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

bt_1 pr ys_1; in A_1 A_2 C R

gl_5

gl_8

gl_{17}

gl_{17} bt_1

gl_{17} v_2

lw_2

lw_3; lw_4

Chromosome 5 (Continued)

na_2

na_2 pr

pr; A_1 A_2 C R

pr ys_1; A_1 A_2 C R

ys_1

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

ps = allele of vp_7

vp_7 pr; A_1 A_2 C R

eg

lu_1

sh_4 lu_1

sh_4

yg_1

Primary trisomic 5

Chromosome 6

Y_1 rgd

at = allele of si_1

Bh

po Y_1 pl

po y_1 pl

Pt

si_1

Chromosome 6 (Continued)

wi

y_1

w^m = allele of y_1

pb_1 = allele of y_1

y_1 l_{10}

y_1 l_{4120}

y_1 l_{4920}

y_1 pb_4 pl

y_1 pb_4 Pl

Y_1 pg_{11}; Wx pg_{12}

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

Y_1 Pl sm py; A_1 A_2 b P^{RR}

Y_1 pl su_2

y_1 pl su_2

y_1 Pl

y_1 Pl w_1

Dt_2; a_1 A_2 C R

w_1

ms-si = allele of si

orobanche

w_{8657}

Primary trisomic 6

Chromosome 7

Bn

bd

g_2

gl_1

gl_1^m

gl_1 o_5

gl_1 g_2

gl_1 ij bd

gl_1 sl

gl_1 Tp_1

gl_1 g_2 Tp_1

Hs

ij

ij bd

in; pr A_1 A_2 C R

in gl_1; 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 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

Chromosome 7 (Continued)

Tp_1

vp_9 gl_1

Dt_3; a_1 A_2 C R

Primary trisomic 7

Chromosome 8

gl_g

v_{16} j_1

v_{16} ms_8 j_1

necrotic 6697

sienna 7748

Primary trisomic 8

Chromosome 9

Bf_1

Bf_1 bm_4

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 sh_1 ms_2; A_1 A_2 R

C wx; A_1 A_2 R

C Wx bz_1; A_1 A_2 R

C wx ar; A_1 A_2 R

c sh_1 wx gl_{15}

Chromosome 9 (Continued)

c sh_1 wx gl_{15} Bf_1

c sh_1 wx bk_2

c Wx; A_1 A_2 R

c wx; A_1 A_2 R

c wx v_1

c wx Bf_1; A_1 A_2 R

Dt_1; a_1^m A_2 C R

gl_{15}

gl_{15} Bf_1

gl_{15} bm_4

C_1^I Ds Wx

C_1^I wx; A_1 A_2 R B

K_9^L C sh_1 wx; A_1 A_2 R

l_6

l_7

ms_2 sh_1; A_1 A_2 C R

sh_1 bp wx; P^{RR}

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 bk_2 bm_4

Chromosome 9 (Continued)

wx d_3

wx l_6

Wc

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_1 wx; A_1 A_2 R

yg_2 c sh_1 wx gl_{15}; A_1 A_2 R

yg_2 C sh_1 bz_1 wx; A_1 A_2 R

wd

lo

Primary trisomic 9

Chromosome 10

bf_2

du_1

g_1

g_1 Tp_2

g_1 r^g; A_1 A_2 C

g_1 r^{ch}

g_1 r; A_1 A_2 C wx

g_1 $R^r sr_2$; A_1 A_2 C

g_1 R^g sr_2; A_1 A_2 C

g_1 r sr_2; A_1 A_2 C

Chromosome 10 (Continued)

l_1

l_1; 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

oy

r^g; A_1 A_2 C

r^r; A_1 A_2 C

r^r E^j; A_1 A_2 C

r K^{10}; A_1 A_2 C

R^r K^{10} g_1; 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

R^{mb}; A_1 A_2 C

R^{nj}; A_1 A_2 C

R^{st}; A_1 A_2 C

R^r Lc; A_1 A_2 C

v_{18}

w_2

w_2 l_1

zn

Primary trisomic 10

Unplaced Genes

dv

dy

el

gl_{12}

gl_{14}

gl_{16}

h

l_3

l_4

ms_6

ms_{12}

ms_{13}

Rs_1

v_{13}

w_{11}

ws_1 ws_2

ub

zb_1

zb_2

zb_3

zn_2

l_{4923}

"necrotic 8376" (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 Pr

A_1 A_2 C R Pr wx

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 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 y_1 wx

A_1 A_2 C r Pr y_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

hm_1 hm_2

Popcorns

Amber Pearl

Argentine

Black Beauty

Hulless

Ladyfinger

Ohio Yellow

Popcorns (Continued)

Red

South American

Strawberry

Supergold

Tom Thumb

White Rice

Exotics and Varieties

Black Mexican Sweet Corn (with B-chromosomes)

Black Mexican Sweet Corn (without B-chromosomes)

Knobless Tama Flint

Knobless Wilbur's Flint

Gourdseed

Maiz chapolote

Papago Flour Corn

Parker's Flint

Tama Flint

Zapaluta chica

Tetraploid Stocks

P^{RR}

P^{VV}

Ch

B

a_1 A_2 C R Dt_1

su_1

Tetraploid Stocks (Continued)

pr; A_1 A_2 C R

y_1

gl_1

ij

Y_1 sh_1 wx

sh_1 bz_1 wx

wx

A_1 A_2 C R

A_1 A_2 C R B Pl

Cytoplasmic Steriles and Restorers

WF9 - (T)	rf_1 rf_2
N6 (S)	
WF9	rf_1 rf_2
N6	rf_1 Rf_2
R213	Rf_1 rf_2
Ky21	Rf_1 Rf_2

These combinations are also available in other inbred backgrounds.

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

*gl_2 Inv 2a (also available with Ch)	2S.7; 2L.8
*wx Inv 9a	9S.7; 9L.9

Reciprocal translocations

*wx 1-9c	1S.48; 9L.22
*wx 1-9 4995	1L.19; 9S.20
*wx 1-9 8389	1L.74; 9L.13
*wx 2-9b	2S.18; 9L.22
*wx 3-9c	3L.09; 9L.12
wx 3-9 5775	3L.09; 9S.24
*wx 4-9b	4L.90; 9L.29
*wx 4-9 5657	4L.33; 9S.25
*wx 4-9g	4S.27; 9L.27
*wx 5-9a	5L.69; 9S.17
*wx 5-9c	5S.07; 9L.10
*wx 5-9d	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

*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-6a	6S.5	
B-7b	7L.3	Proximal to ra_1
B-8a	8L.7	Proximal to v_{16}
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

IV. RECENT MAIZE PUBLICATIONS

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