MAIZE GENETICS COOPERATION

NEWS LETTER

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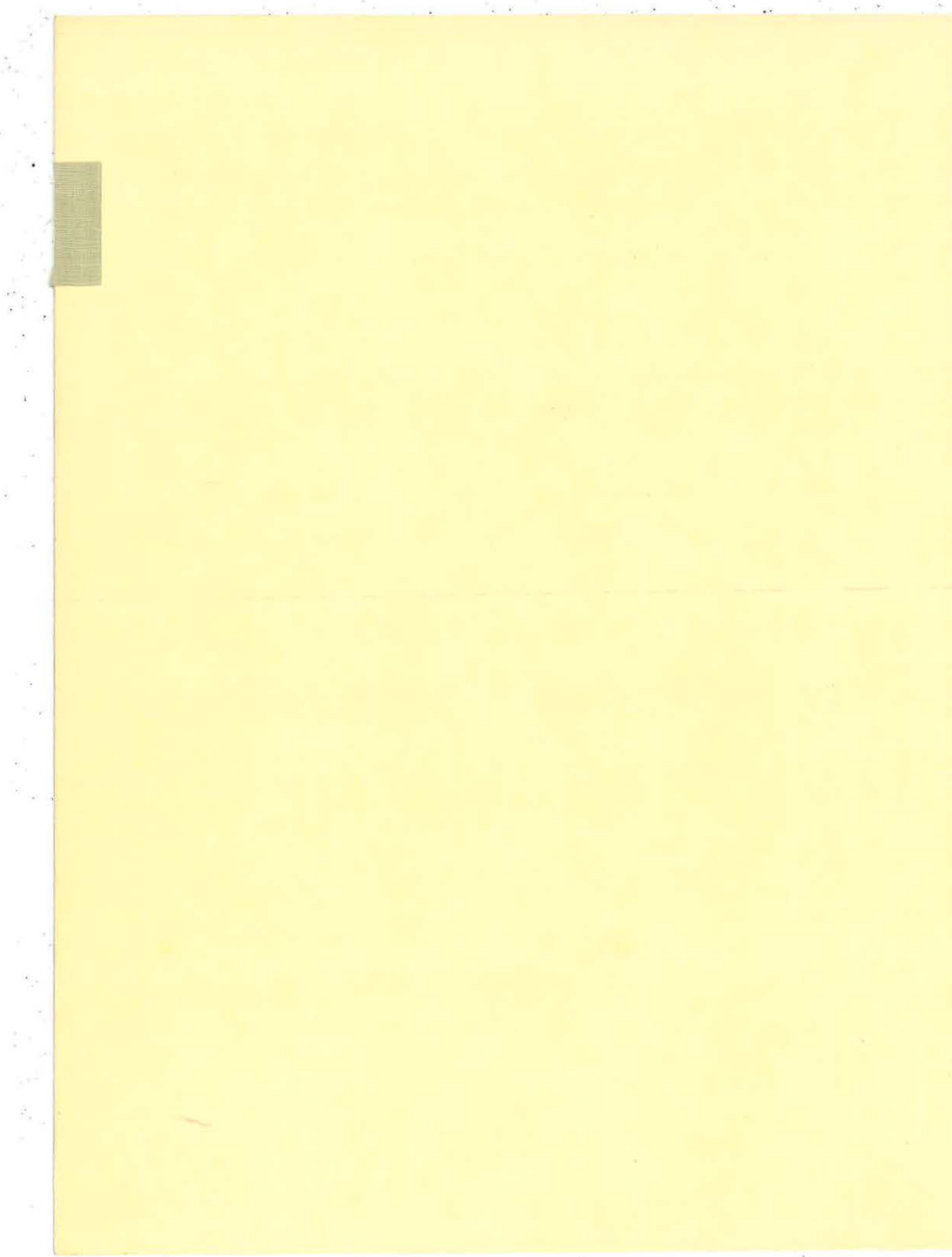

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I. FOREWORD

Once again it is a pleasure to express on behalf of all who profit from reading the Maize Genetics Cooperation News Letter our appreciation of the dedicated labors of Miss Ellen Dempsey in publishing these annual reports. She and she alone has been responsible for carrying out all of the editorial and supervisory details entailed in the assemblage of informal reports from maize geneticists throughout the world. Hers is a demanding task which is done exceedingly well.

The cost of publishing the 1972 News Letter has been met from a grant by the National Science Foundation to the Maize Genetics Stock Center at the University of Illinois. Without this financial assistance, there would be no News Letter and it is with heartfelt thanks that we acknowledge the help of the National Science Foundation.

M. M. Rhoades

II. Announcements

1. Maize Virus Information Service

The Library of the Ohio Agricultural Research and Development Center (Wooster, Ohio) in cooperation with the Center's maize virus research staff is developing a "Maize Virus Information Service" (MAVIS) which will cover information on maize viruses and corn stunt. The purpose of this service is to accumulate all available information on these subjects and to have it readily available to interested persons. Along this line the Library is now accumulating copies of all papers, abstracts and theses on these subjects. Furthermore, the Library is planning to produce a yearly computer listing of all publications in these areas. Retrieval of information from the computer listing will be mainly by author and subject matter (keyword). Photocopies of articles and of the computer listing will be sent to interested persons upon request at regular library rates.

2. Method for producing cytoplasmic male sterility patented.

Our attention has been called to U.S. Patent 3,594,152 issued in July, 1971 to D. F. Petrov, E. S. Fokina and N. B. Zheleznova of Novosibirsk, USSR. The patent describes a method for producing cytoplasmic male sterility in maize by treatment of sprouted seeds with various concentrations of streptomycin. A brief announcement concerning the patent was made to the participants of the annual corn meetings at Allerton Park by Dr. Robert I. Brawn.

3. Microfilm

Volumes 1-29 and Volume 33 of this News Letter have been placed on microfilm. The price of the microfilm has recently been increased to $9.50. Copies may be obtained from this laboratory. Checks should be made out to M. M. Rhoades.

III. REPORTS FROM COOPERATORS

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1. Heterosis of the yield components in sister-line hybrids of lines related to B 14.

We studied the heterosis of the yield components of lines related to B 14 and their sister-line crosses. The rate of heterosis was expressed by "heterosis index," which is the ratio of the yield component in a sister line hybrid to the average yield components of both parents. A sample of 15-20 ears per entry was collected and those were evaluated individually.

The inbred lines related to B 14 studied were American A 632, A 635, A 636, donors: Mt 42 and Nd 203, France F 522, F 542, F 546, donors: Ic 201, F 47 and 11 Hungarian lines including H Mv 1327, H Mv 1329 and others, in which the donor was: 01 early dent Hungarian line. Yield components and yielding ability of these inbred lines as well as the recurrent parent and the donor are summarized in Table 1. Beside the yielding ability of B 14 relatives, it is remarkable that they are 11-20 days earlier than the original B 14.

Table 2 contains the heterosis index values of the diallel sister-line hybrids of A 632, A 635 and A 636 and the same 14-14 sister-line hybrids, produced by two tester lines: A 632 and A 636. From Table 2 it can be seen that the heterosis index values of 28 sister-line hybrids practically are the same or are better than the corresponding mean values of the diallel group, respectively. These data indicate that the parent lines of the 28 sister-lines and the diallel group are genetically close to each other. At the same time it can be stated that the sister line hybrid produced on A 632 and A 636 tester lines gave a 21.2% higher yield and was three days earlier (4.8%) than the hybrids of the diallel group.

Table 1. Yield components, yielding ability and earliness of inbred lines related to B 14

Lines	Ear length cm	Number of rows	Number of kernels per row	Kernel length mm	Thousand grain weight g	Shelling per-centage	Yield per plant g	Days to mid-tas-seling
A 632	14.9	15.4	22.8	7.3	263.9	80.9	73.5	86
A 635	12.1	13.2	17.0	6.0	226.1	80.1	43.4	86
A 636	14.8	13.2	22.0	4.0	256.9	76.4	69.1	87
F 522	18.8	18.2	33.4	5.5	229.6	82.5	127.5	82
F 542	18.4	12.3	22.5	4.5	304.9	77.3	78.7	87
F 546	16.7	13.0	23.3	4.0	298.8	71.8	59.4	83
H Mv 1327	14.7	14.3	29.7	7.8	264.3	87.5	96.9	81
H Mv 1327-2	14.3	15.1	29.8	7.0	221.6	86.3	87.6	81
H Mv 1329	13.8	15.8	26.3	6.5	212.7	87.1	75.9	80
H Mv 1329-4	11.6	12.7	24.8	7.6	218.6	89.3	62.9	78
H Mv 1331	15.0	15.8	25.6	8.0	230.0	81.0	71.7	78
H Mv 1331-1	14.2	14.6	25.0	6.0	189.7	85.5	73.4	78
H Mv 1331-2	12.4	18.0	24.4	7.0	177.8	84.6	73.1	72
H Mv 1331-3	14.0	16.3	30.9	7.5	159.5	83.2	69.5	74
H Mv 1331-4	14.5	15.1	19.3	5.5	210.2	81.4	65.1	74
H Mv 1331-5	14.8	17.6	28.3	6.0	222.6	83.4	94.7	73
H Mv 1331-6	15.7	17.0	31.8	6.0	197.8	82.2	70.5	73
B 14	15.9	14.8	23.4	7.1	234.6	70.8	76.1	92
O1	14.2	14.7	22.4	7.2	217.9	88.3	49.0	75
Mean	14.7	15.1	25.7	6.2	228.5	82.4	76.0	79.5

Table 2. Yield components, yielding ability and earliness of the sister-line hybrids produced from lines related to B 14

Sister-line hybrids	Ear length cm	Number of rows	Number of kernels per row	Kernel length mm	Thousand grain weight g	Shelling per-centage	Yield per plant g	Days to mid-tas-seling
A 632 x A 636	16.8	14.5	30.4	5.8	268.2	81.0	112.4	81.0
Heterosis index value	113.1	101.4	135.7	102.1	103.0	103.0	157.6	93.6
A 632 x A 635	18.4	15.9	33.6	6.5	258.2	84.4	131.5	81.0
Heterosis index value	136.3	111.2	168.8	97.7	105.4	104.8	225.0	94.2
A 635 x A 636	16.8	13.8	28.2	5.5	273.6	81.5	95.4	81.0
Heterosis index value	124.9	104.5	144.6	110.0	113.3	104.2	169.6	93.6
Mean	17.3	14.7	30.7	5.9	266.6	82.3	113.1	81.0
	124.8	105.7	149.7	103.2	107.2	104.0	184.0	93.8
A 632 x B 14 relatives (14)	18.4	16.4	34.6	8.0	275.8	85.4	147.3	79.0
Heterosis index value	123.9	106.1	140.4	118.2	120.4	104.1	194.5	96.3
A 636 x B 14 relatives (14)	17.0	16.0	33.6	6.2	263.3	83.0	127.0	77.0
Heterosis index value	118.5	112.3	138.4	120.6	109.6	103.0	172.9	94.1
Mean	17.7	16.2	34.1	7.1	269.5	84.2	137.1	78.0
	121.2	109.2	139.4	119.4	115.0	103.6	183.7	95.2
Ratio of the yield components in the percentage of the diallel group	102.3	110.2	111.1	120.3	101.1	102.3	121.2	96.2

With the presented A 632' and A 636' sister-line crosses, the following correlations were ascertained between the same yield component of B 14 relative line and its hybrid:

Number of kernels per row: $r = 0.9164^{+++}$

Kernel length: $r = 0.6427^{+++}$

Shelling percentage: $r = 0.6550^{+++}$

Thousand grain weight: $r = 0.6539^{+++}$

Ear length: $r = 0.5461^{++}$

Dry grain yield: NS, but significant at 10 per cent level

Row number: NS

$^{+++}$ = Significant at 0.1 per cent level

$^{++}$ = Significant at 1 per cent level

$^{+}$ = Significant at 5 per cent level

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1. Synaptonemal complex in teosinte.

A study on the chromosome fine structure of maize and teosinte was continued last year. Anthers of diploid Michrona teosinte (Mexico) were fixed in glutaraldehyde and post fixed with osmium tetroxide. Then they were dehydrated by following alcohol series and embedded in Epon. The sections were generally 1000 A° in thickness. Stainings were made with both uranyl acetate (0.5%) and Reynolds lead citrate. The determination of division stages of the anthers for electron microscopy was made by following the standard aceto-carmine squash techniques by which one of the three anthers in each floret was fixed in aceto-alcohol fixative.

Particular attention was paid to the fine structure of pachytene chromosomes. At this stage, the synaptonemal complex was consistently observed. Three elements of this complex, two lateral elements and a central element, were clearly shown. The lateral elements measured about

300 A°, while the central measured 430 A°. The two clear zones flanking the central element were approximately 400 A° crosswise. Therefore, in frontal view, the diameter of the complex was about 1830 A°. In the cross-sections of the complex, these elements were also discernible.

With some of the clear electron micrographs it was possible to identify two fibrils, 100 A° across, within the central element of the complex. These fibrils were parallel with the central element. However, the transverse fibrils reported in several organisms were not revealed in my micrographs.

In addition, cytoplasmic invaginations into the nucleus were frequently observed. With the same procedures, these invaginations were never found in either haploid or diploid maize. Whether this is due to genetical control is unclear.

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1. Identification of the genotype of cultivar Ionia as to the Rf genes.

Dr. J. R. Edwardson, University of Florida, has kindly provided the senior author with a seed sample of the cultivars Moldavian (cytoplasmic male sterile) and Ionia (the maintainer), which he had obtained from the Soviet Union. He has identified the cytoplasm of the former to be S-type, although it is called M-type in the Soviet Union (Edwardson, personal communication). At the same time, he identified the genotype of both lines as $rf_3 rf_3$, but he has not examined them for Rf_1 and Rf_2.

To identify the genotype of these materials, Ionia was crossed as the male to Minn A158T and R273N* female parents. The genotypes of both lines had been identified as follows:

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*These genetic lines have been provided by Dr. D. N. Duvick, Pioneer HiBred Corn Co., for which we are grateful.

Minn A158T (T) $\underline{rf_1 rf_1 Rf_2 Rf_2 rf_3 rf_3}$

R273N (N) $\underline{Rf_1 Rf_1 rf_2 rf_2}$

Fifty F_1 kernels each of the crosses Minn A158T x Ionia and R273N x Ionia were planted on the experimental field of the Faculty of Agriculture, University of Cantho. Of these, 42 and 48 germinated, respectively, and were grown during the dry season of 1971. Anthers were examined for male fertility or sterility in 42 and 46 individuals, respectively.

All of the anthers of the F_1 hybrids involving Minn 158T were small in size, slender in shape, brownish in color, and empty; that is, practically no pollen grains were observed. On the contrary, all of the F_1 hybrids involving R273 had normal anthers with fertile pollen grains.

From the above observation it can be concluded that the genotype of Ionia is $\underline{rf_1 rf_1 rf_3 rf_3}$. It was not possible, however, to identify the genotype for $\underline{Rf_2}$ from the present experiment.

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1. Retention of Euchlaena as a genus separate from Zea.

During the 3 decades since Reeves and Mangelsdorf cited cytogenetic evidence in support of the transfer of the genus *Euchlaena* to the genus *Zea*, as originally proposed by Kuntze in 1904 and subsequently ignored by Hitchcock and other grass taxonomists, much additional botanical and archeological information has become available that does, in my opinion, fully justify the retention of *Euchlaena* as an autonomous genus. Reeves and Mangelsdorf conceded that *Zea* and *Euchlaena* are morphologically distinct, but argued that their cross-fertility, the similarity of their chromosomes and linkage relations, and the observed

prevalence of natural hybrids in certain areas of sympatric association with indigenous races of Mexican and Guatemalan maize, justified a congeneric status. Retention of Tripsacum as a separate genus was recommended by Reeves and Mangelsdorf although admitting that it was very similar to Euchlaena with respect to various morphological characteristics. They had also produced maize-tripsacum hybrids and obtained fertile progeny from backcrosses to maize, as others have done in conducting cytogenetic studies of their homeologous chromosomes.

The occurrence of fertile teosinte-maize hybrids would be a more convincing argument in favor of the congeneric status of Zea and Euchlaena if it were not obvious from field observations of populations where sympatric associations are prevalent that teosinte has retained all of the more important morphological characteristics by which its generic status was first recognized by Hooker, the famous English taxonomist, nearly 100 years ago.

In evaluating the taxonomic status of Euchlaena, Tripsacum and Zea, very thoroughly reviewed by Wilkes in 1967, it is noteworthy that they were first classified as members of the tribe Maydeae by Hackel in 1890, and less closely related genera such as Manisuris and Elionurus were placed by him in the Andropogoneae. Members of this latter tribe have perfect flowers and differ chiefly in this respect from the Maydeae which have staminate and pistillate flowers arranged either in different positions in the plant, or in different parts of the same inflorescence--the former occurring in Zea and Euchlaena and the latter in Tripsacum. Subsequent retention of Hackel's treatment by Bentham and Hooker, Hitchcock, and other grass taxonomists has continued to meet with the approval of horticulturists, agronomists and plant breeders who are, like many other plantsmen, dependent on readily recognizable morphological differences to identify plants they are working with in the field and garden--as well as in the herbarium.

It is well known that teosinte and maize have the same number of chromosomes and the same frequencies of genetic crossing-over that have been tested. However, the significant differences in reported frequencies of occurrence of intercalary and terminal chromosome knobs, especially

in Guatemalan races of teosinte and maize, suggest that the homology of their chromosomes is not as intimate as generally assumed; or, perhaps in areas where teosinte-maize hybrids are most prevalent, as in neglected corn fields near Chalco, Mexico, such differences in chromosome morphology do not exist.

Emphasis on chromosome homologies in evolutionary studies of natural relationships is well deserved, but many obvious limitations to their usefulness that have been experienced by taxonomists concerned primarily with the naming of plants is coming to be more generally recognized. Now it is becoming increasingly apparent that archeology and anthropology also are making important contributions to existing knowledge of the evolutionary history of maize and teosinte.

Very recent archeological discoveries in the Valley of Mexico, which I have been privileged to discuss with Dr. Peter Lorenzo, director of the Department of Prehistory in Mexico City, have revealed the existence at Tlapacaya near Chalco of well preserved teosinte kernels of an age contemporary with that of the oldest Tehuacan cobs, established as approximately 7,000 B.P. Also, in the Oaxaca area of southwestern Mexico kernels of teosinte, much like those of triangular shape characteristic of existing populations in the neighboring state of Guerrero, have been discovered recently by Dr. Kent Flannery, professor of anthropology at University of Michigan who, in personal conversations a few months ago, estimated their age as dating from about 1500 A.D. Thus, it appears from these discoveries and other less relevant archeological evidence that teosinte has retained for at least 7,000 years its unique and highly efficient method of seed production and dispersal, comprising caryopsis and seed case structures wholly different from the caryopsis and cob morphology evolved under domestication by the races of maize with which it was closely associated for prolonged periods of time.

The possibility, suggested by Reeves and Mangelsdorf, that several of the characteristics of survival value possessed by teosinte and not by maize probably would be the first to be selected against if the domestication of teosinte were undertaken, appears at the present time to be of relatively little significance in relation to questions

concerning the taxonomic status of Euchlaena as congeneric with Zea; now it seems more relevant as having been a portent of the current interest among maizologists in exploring more thoroughly than in the past the possibility that teosinte was the progenitor of domesticated maize.

In the accompanying table are listed contrasting morphological and ecological characteristics of major significance in differentiating modern maize and teosinte, and in this same table there is also a separate listing of similarly contrasting traits of archeological maize and teosinte that have been identified in the well preserved oldest Tehuacan maize cobs, possibly in early stages of domestication and dating from about 7,000 B.P., and in the equally well preserved seed cases and enclosed kernels of teosinte of contemporary age from Tlapacaya in the Valley of Mexico. Of the 14 traits distinguishing modern maize and teosinte, seven (nos. 1 to 4, 6, 7 and 10) similarly distinguish existing races of Mexican maize and all known species of tripsacum. In addition several species of tripsacum have culms as slender or more slender than those of teosinte, equally strong responses to photoperiod, climatic and edaphic tolerances, and even more restricted distributions in Mesoamerica. But these many similarities of teosinte and tripsacum were not considered by Reeves and Mangelsdorf to be ample justification for treating both Euchlaena and Tripsacum as congeneric with Zea, perhaps because the Tripsacum karyotype is more dissimilar to that of Zea than is the Euchlaena karyotype and Tripsacum-maize hybrids are less fertile than those of teosinte and maize.

From comparisons of the above mentioned differences separating Zea, Euchlaena and Tripsacum with those appearing in descriptions of related genera of the Andropogoneae, there is ample justification for the retention of Euchlaena as a separate genus. The partial similarity of maize and teosinte chromosomes, exclusive of their knob morphology, their similar linkage relations and the fertility of their hybrids should not be considered of primary significance in evaluating the taxonomic status of Zea and Euchlaena. It is now clearly apparent from field studies of teosinte populations, including those in which intimate sympatric associations with maize have produced apparently significant

Table 1. Characteristics of Taxonomic Significance Differentiating *Zea* and *Euchlaena*

Maize	Teosinte
Comparisons of modern maize and teosinte applicable to their representative existing races and cultivars	
1. Paired pistillate spikelets	1. Unpaired pistillate spikelets
2. Pedicellate pistillate spikelets	2. Sessile pistillate spikelets
3. Outer glume of pistillate spikelet membranous	3. Outer glume of pistillate spikelet corneous
4. Rachis (cob) intact at maturity and non-corneous	4. Rachis disarticulating at maturity
5. Cobs borne singly at one or few nodes	5. Bundles of cobs ordinarily produced at many nodes
6. Cobs of large size bearing many kernels	6. Cobs of miniature size bearing few kernels
7. Large kernels adhering to surface of mature cob at maturity	7. Small kernels within seed case shattering at maturity
8. Mature ears enclosed by numerous husks	8. Mature ears rarely fully enclosed by single husk at maturity
9. Culm diameter and leaf width exceeding those of teosinte	9. Culms more slender and leaves narrower than in maize
10. Culms unbranched at upper nodes	10. Culms often branched at upper nodes
11. Terminal staminate inflorescence has central spike	11. Terminal staminate inflorescence typically has no central spike
12. Weak response to photoperiod	12. Strong response to photoperiod
13. Broad climatic and edaphic tolerances	13. Narrow climatic and edaphic tolerances
14. Worldwide distribution in temperate and tropical climates	14. Limited distribution in Mesoamerica

Table 1 (Continued)

Maize	Teosinte
Comparisons of archeological maize and teosinte including oldest Tehuacan maize cobs and contemporary Tlapacaya teosinte kernels of the Valley of Mexico dated from about 7,000 B.P.	
1. Paired pistillate spikelets	1. Unpaired pistillate spikelets
2. Pedicellate pistillate spikelets	2. Sessile pistillate spikelets
3. Outer glume of pistillate spikelet membranous	3. Outer glume of pistillate spikelet corneous
4. Kernels not completely enclosed by glumes of pistillate spikelet at maturity	4. Kernels completely enclosed by outer glume of pistillate spikelet at maturity
5. Cobs not disarticulating at maturity	5. Cob disarticulating at maturity
6. Cobs at maturity of chiefly noncorneous tissue	6. Cobs at maturity corneous
7. Glumes of pistillate spikelet chaffy and nonfunctional at maturity	7. Kernels at maturity enclosed within seed case by outer glume
8. Effective method of seed dispersal lacking	8. Shattering of seed cases at maturity provides effective method of seed dispersal

numbers of fertile hybrids and backcrosses to one or both parents, that teosinte has retained its status as a good species having most, if not all, of the identifying characteristics listed in the table as differentiating modern races of maize and teosinte. This retention of its identity in recent years is now known from reliable archeological evidence to have extended into the remote past when the domestication of maize was being initiated. It is equally apparent from comparisons of the oldest Tehuacan cobs with those of modern maize that there is an equivalent similarity between archeological and modern maize with respect to the 8 characteristics listed in Part II of the table. The possible significance of such apparent genetic stability over prolonged periods of time in related species, of which one is cultivated and the other not, is of current interest in relation to unsolved problems concerning the origin of maize that are amenable to experimental verification and will be discussed in more detail later.

Participation in a teosinte mutation hunt in November, 1971 at the invitation of Dr. George Beadle, president of the Chicago Horticultural Society, provided a favorable opportunity to examine closely large populations of teosinte growing in intimate sympatric association with indigenous races of maize in southwestern Mexico. Near Mazatlan in the state of Guerrero, between 20 and 30 km south of Chilpancingo, there are large populations of teosinte adjoining corn fields and in neighboring areas not being actively utilized for farming purposes. The group of participants with which I was associated examined large numbers of plants at four separately located sites in this area where teosinte was most abundant. Large populations at three additional sites on canyon slopes where altitudes ranged from 1100 to 1350 meters approximately 37, 45 and 69 km southwest of Valle de Bravo in the state of Mexico also were inspected for maize-like mutants and naturally occurring hybrids of maize and teosinte. At two of the Mazatlan sites _Tripsacum dactyloides_ was growing together with teosinte at the edge of a cornfield, where earlier in the season it had been noted that all three were silking and shedding pollen at the same time. But a diligent search in the surrounding area within range of their windblown pollen for hybrids

either of tripsacum and maize, tripsacum and teosinte, or teosinte and maize resulted in the detection only of 6 teosinte-maize hybrids.

The following procedure was found to be effective in examining individual plants for mutants (including sectors as well as whole-plant mutants) and hybrids not readily identifiable except from cob and kernel characteristics--especially those resulting from first and second back-crosses to teosinte. When first entering a site of maximum plant density within a teosinte population usually near one or more corn fields, where densities of 20 to 30 teosinte plants per cm_2 were not unusual, an over-all inspection of nearby plants was made to detect exceptional phenotypes--especially F_1 teosinte-maize hybrids which often could be spotted in this manner. A more careful inspection was then made of individual teo-sinte and off-type corn plants. This included the examination among teosinte plants of the clusters of distichous spikes (ears), preferably from at least two successive midculm nodes to minimize the possibility of overlooking sectorial mutants involving not more than one or a few ears, such mutant sectors having been identified previously in tripsacum. The number of plants examined individually in this manner was recorded by placing a seed from each plant in a "Beadle bottle" supplied by the ingenious organizer of the expedition. The kinds of mutants of special interest, which would make teosinte a more acceptable food plant in-cluded: intact nonshattering cobs, cobs of softer noncorneous tissue, paired pistillate spikelets, spikelets with noncorneous outer glumes, pedicellate rather than sessile spikelets, and increased caryopsis size and/or number per individual ear. Since the oldest Tehuacan maize had most of these characteristics it must have been a more attractive food plant than teosinte even at that early stage of its domestication, and its spontaneous hybrids with teosinte would have had appreciably more food value than either parent if they were at all like the F_1 hybrids seen during the mutation hunt.

During 5½ days in the field at Mazatlan and in the Valle de Bravo area, approximately 4500 plants were examined individually for mutant and hybrid characteristics. During 1½ days at Mazatlan Site IV, my tally count was 1568 but somewhat lower numbers were examined daily at

less accessible sites elsewhere in these areas. A total of 8 teosinte-maize hybrids were identified at 3 of the 4 sites in the Mazatlan area, but none was discovered in an equally thorough inspection of 3 sites at Valle de Bravo. Two of these 8 hybrids were classed as F_1's, one as resulting from a first or second backcross to maize, and 5 as being from first or second backcrosses to teosinte. These classifications were made with the assistance of Dr. Walton Galinat, who has been especially interested in the comparative morphology of teosinte, maize and tripsacum. The 8 plants classed as hybrids, with one exception, exhibited 2 or more of the parental characteristics of cobs, kernels and spikelets differentiating maize and teosinte; in addition there were intermediate expressions of cob and outer glume induration, husk development, culm diameter and leaf width. The exceptional plant appeared to differ from normal teosinte plants only with respect to such an extreme modification of the seed case in which the caryopis ordinarily is enclosed that more than a single gene difference was suspected of being involved; for this reason it was tentatively classed as a hybrid rather than as a mutant.

It was not possible definitely to identify, in the teosinte populations, progenies from successive backcrosses to teosinte beyond the first and second generations, although it was obvious from the fertility of the backcrossed plants previously identified in these populations that such backcrossing might be taking place. However, none of the various maize characteristics readily identifiable in the F_1 maize-teosinte hybrids and backcrosses to teosinte was detected among the many otherwise typical teosinte plants of these same populations. Perhaps the negative survival value of such apparently nonrecoverable characteristics explained their absence in these wild populations actively competing with other rank-growing tropical plants, farm animals and a climate in which the morphologically less well protected seeds of these hybrids may fail to survive from one growing season to the next. There was, however, in all of the populations inspected during the mutation hunt ample evidence of residual heterozygosity for traits such as extreme amounts of tassel branching and tillering, secondary branching

at upper nodes, many conspicuous variations in seed case color and differences in seed case size and shape ranging from triangular to trapezoidal. Very few, if any, of these variants plausibly could be attributed to introgression from the nontillering maize with sparsely branched tassels being grown in nearby fields, or to environmental effects.

Although the search for variants definitely identifiable as whole-plant mutants was unsuccessful, interesting sectorial mutants were found with no more than one or a few ears of individual axillary bundles being involved. Among these were ears with intact rachis and delayed shattering of seed cases, extremes of seed case condensation and multiplication, and one noteworthy occurrence of reduced seed case development, partly exposed kernels and more pronounced glume development like that of the ancient indigenous race of Chapalote popcorn described by Wellhausen et al. as being of very limited distribution in northwestern Mexico. As possible examples of weak penetrance at least some of these variants may prove to be heritable and, as more prominently developed phenotypes, serve as encouraging indicators of the mutability of these and other loci that might have made teosinte a more attractive food plant in prehistoric times.

Unfortunately, there are conflicting reports concerning the mode of inheritance of the various characteristics differentiating modern and archeological maize and teosinte. From currently available data including his own, Dr. Galinat told me recently that at least two genes probably are involved in the expression of the first 4 and possibly other characteristics listed in the accompanying table as applicable to modern maize. Only for alleles at the tunicate locus, described by Mangelsdorf et al. as having pleiotropic effects on rachis, seed case and cupule development, is there convincing evidence of monogenic inheritance. With respect to dominance, our inspection of several F_1 teosinte-maize hybrids during the mutation hunt showed that the 1st and 4th characteristics listed in the table as applicable to modern maize are inherited as dominants, the 2nd, 5th, 6th and 10th as recessives and the other 4 of the first 10 as intermediate expressions of differences

between maize and teosinte. Thus, it appears that mutations in both directions--from recessive to dominant as well as from dominant to recessive states--and at more than 4 loci, would be required to transform teosinte into a primitive maize-like plant with respect only to the first 4 of these items. Also, the mutation frequencies observed by L. J. Stadler for dominant to recessive endosperm characters, ranging from about 1:150,000 to 1:2,000,000 or more, might be much less frequent for the loci under consideration since at some of these loci reverse mutations from recessive to dominant would be required and all would involve reproductive structures which have been shown by the archeological record of the past 7,000 years not to have changed significantly during that time. However, after having accumulated the required mutations it could be assumed that teosinte would have a bright future as an important food plant.

L. F. Randolph

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1. Non-liguleless liguleless-1.

A narrow-based Cuzco flour corn synthetic was found to be segregating for upright leaves as a discrete phenotypic class. Plants having the extreme upright leaves were sib pollinated and outcrossed to 26 standard inbred lines. The sibbed progeny was uniformly extreme upright-leaved, and have bred true for this phenotype in two further successive generations. The 26 F_1's involving standard inbred lines were each backcrossed to the respective inbred parent, and then selfed once. The combined BC_1I_1 populations segregated cleanly in the 7:1 ratio expected if the trait were monogenically inherited. In all 26 backgrounds, the gene was clearly expressed and always produced the extremely upright leaf condition. Development of the ligule was normal or nearly normal in all inbred backgrounds.

BC_1I_1 segregates were outcrossed to lg_1 and lg_2 synthetics as a test for allelism. Progeny of the lg_2 outcross was all normal. Progeny of the lg_1 outcross all had extremely upright leaves and normal ligules. We propose the nomenclature for this new allele of lg_1 to be "lg_1^u", the "u" superscript designating "upright leaves." It is interesting to note that if lg_1^u had been the first allele to be described at this locus, it might have been named "ul" instead of "lg_1".

D. L. Shaver
Dennis Chamberlain

2. Tp fails to replace pe in the expression of perennialism in 2n maize.

Shaver (J. Hered. 58:271-273, 1967) showed that perennial 2n maize could be produced on the basis of a simple genetic change involving only the three genes id, gt, and pe. However, the evidence for the existence of pe as a single gene was only circumstantial. Upon attempting to transfer this locus to diploid maize singly, he succeeded only once in identifying a clear phenotype that could be ascribed to the presumed gene, when there was a clear segregation in the inbred line backgrounds, K55W and K64W, for the pe phenotype: Ear branches were replaced by a semi-vegetative branch, plants had a slightly slower growth rate, but later achieved a somewhat greater height. In following years, further evidence for pe was obtained in experiments wherein perennial plants were obtained only from crosses involving stocks having the presumed pe gene, with stocks having gt and id.

Dr. L. M. Josephson furnished a stock of "Potch Teopod" which, besides having the extreme tillering phenotype, has the ear on the main culm replaced by a semi-vegetative branch, similar to the once-observed effect of pe in K55 and K64. However, upon attempting to produce perennial diploids of the genetic constitution, gt/gt id/id tp/tp, none was found to be perennial.

D. L. Shaver

3. Perennialism attributes from Cuzco flour corn.

In our very long growing season at Greenfield, Calif. we have never seen black spot formation in Cuzco maize as long as growing cultural conditions are maintained. Vegetative senescence is likewise delayed indefinitely, until the intervention of an outside condition. Upon using Cuzco as a parent in crosses to an id/id gt/gt stock and sibbing to recover multiply recessive plants, vigorously perennial, vegetatively totipotent segregates were obtained. A field work thinning error prevented determination of a meaningful segregating ratio, but it is certain that Cuzco carries pe or a factor(s) that can produce the same effect in combination with homozygous gt and id. Anyone wishing to repeat this work should remember that Cuzco Flour Corn is a very heterogeneous population. Good insurance would indicate the use of a population of Cuzco, rather than single plants, in initiating an experiment.

D. L. Shaver

4. Failure to obtain ear-fertile perennial 2n maize.

Even though perennial maize can produce tassel seed (and under certain conditions regularly does so) without undergoing senescence and death of the seed-producing plant, it is regularly ear-barren. Dr. D. E. Johnson (Hamill) only once succeeded in obtaining a normal, many kernel rowed ear from the classical clone, 65-32-1, in a Brookhaven Lab. greenhouse from a very tall, old, potbound propagation of 65-32-1.

It seemed that the major reason for barrenness might simply be related to the fact that all perennial maize is id/id. Homozygous id maize is almost invariably barren, even in a very early background which permits flowering at a time of the summer very favorable for ear formation. Accordingly, a project was undertaken to incorporate id into an early Gaspe-based synthetic in which selection for ear fertility could be practiced. By sibbing with mass selection among the initially infrequent ear-fertile id/id plants a highly (more than 90%) ear-fertile

id/id synthetic was finally derived. However, upon introducing the other two perennialism genes, pe and gt, into this ear-fertile synthetic background, it was found that only ear-barren plants were perennial, while those producing ears never were. The latter were often able to produce more than one successive vegetative generation, but each was successively less totipotent, and inexorably "ran out" in a manner described for the gt-pe phenotype (Shaver, Genetics 50:393-406, 1964). This work indicates that the differentiation of the ear as a floral, rather than as a vegetative, branch imposes difficulties or even precludes vegetative totipotency in maize. It may be that the addition of tassel seed genes to the perennial genotype would be the best way to regularly produce perennials from seed.

D. L. Shaver

5. id/id as a "macromutation" in maize.

Students of speciation have often turned up presumptive evidence for sudden origination of species or biotypes. "Cataclysm" was once a respectable word among taxonomists and paleobotanists. It has often occurred to me that the id gene in maize ought to qualify as a concrete example of how a sudden origination could occur. This one genetic step exerts a profound spectrum of changes in the maize plant: Vegetative development is drastically slowed, though many more plastochrons are eventually completed. An id/id plant is much like sorghum in its ability to tolerate long unfavorable periods and then respond vigorously to the restoration of good cultural factors. New leaf types appear in the form of beautifully regular decussate (opposite and rotated 90°) phyllotaxy. Other plants have regular and equal triphyllous nodes. At the ear-bearing node, either two or three equal ears are formed as axillary branches, depending upon the number of leaves at the node. id/id plants are aphid-susceptible before flowering, but become very aphid-resistant afterwards. The flowering period is made drastically later than in an equivalent non id/id population, and the plant would thus be immediately isolated reproductively from its ancestral form. It would not be difficult to conceive of conditions in nature which might favor a so-different

phenotype. Addition of complementary genes via the Baldwin Effect to reinforce the changes conveying selective advantages would stabilize the admittedly variable id/id phenotype in whatever form most "fitted" in the new niche.

D. L. Shaver

6. Non-Mendelian inheritance at the P locus.

In attempting to produce maize hybrids specifically tailored to the needs of human-consumption as milled products of corn, cob color is a criterion of desirability. In all of our standard lines, if the line has a red cob, we convert the line to white cob. On the other hand, if the line is originally white-cobbed, we convert it to red. Neither conversion is easy to make, and in neither case does the inheritance of cob color behave as a simply inherited trait. However, the latter conversion of a white condition to a red state is the more instructive. Several such lines, instead of giving a simple 1:1 segregation in the advanced backcross generations, have something like a 2:1:1 wherein about ½ of the progeny are white cobbed, as expected, but the other half segregate for deeper and lighter colors of red in about equal numbers. This seems to vary widely from line to line, though we have never used sufficient progeny sizes within a line to adduce comprehensive data. However, if one backcrosses the progeny from a lightly colored cob, all may be found to have white cobs. In such a case, one would have to assume that the red cob was present as a maternal effect, rather than from an autogenous gene, since the trait was thus not passed on in heredity. In other cases, even though one selects a progeny from a deeper red cob to further backcross, all the progeny may have white, or only very pale, cobs.

D. L. Shaver

7. Apparent parahereditary transmission of infectious viruses in maize.

In conducting the first winter breeding nurseries in Hawaii, outbreaks of Hawaiian Corn Mosaic (described by Brewbaker, Crop Sci. 5:412-415, 1965) were sometimes suffered because of infestations of

plantings by the leafhopper vector. As with the California virus disease of corn, "Sugar Cane Mosaic Virus," if infections occur later in a plant's ontogeny, damage to the plant may be minimal or subliminal, and the plant will produce seed normally. Several times we have grown seed from Hawaii in which specific lots of seed germinate poorly and produce plants which have abnormal chlorophyll development, so that the leaves appear finely mottled or textured. Upon reproducing these plants sexually, normalcy is restored.

A much clearer case of apparently temporary inheritance of virus effects has occurred in plants infected with the Calif. SCMV virus. We placed the long-time inbred B37 in a disease nursery in California's San Joaquin Valley. By delaying the time of mechanical innoculation with the virus, we have been able to increase the SCMV resistance of this line by taking advantage of within-line variability and/or mutation. The progeny of such innoculated B37 was grown in the 1971 Hawaii winter nursery, where it segregated for frequent (11 of 308) plants having many degrees of chlorophyll striping, similar to the Iojap pattern. These plants were perfectly typical of B37, came from a continuous lineage of ear-to-row selfing, and had no known striped ancestors. Chlorophyll-deficient areas included whole plants or only portions thereof. Sectors sometimes included all or part of an ear or tassel or leaf. Sectors were white, yellow, pale green, and sometimes tinged with anthocyanin.

Sexual structures within normal and abnormal sectors were selfed, sibbed, and outcrossed to an unrelated line. Defective x defective sibs and/or crosses were never fertile, but normal x defective and defective x normal sibs and crosses did succeed, especially the former. However, upon selfing such plants having one defective parent, chlorophyll-deficient progeny were never obtained, again a case of heredity effective for only one generation.

These two non-Mendelian occurrences are tentatively explained as cases of transmission of viruses through the gamete(s) in an integrated form so that they influence the phenotype of derived cell lines in ontogeny, but are not effective in further transmission either in heredity or infection. In such a state, the virus must not be perfectly attuned

to equality of distribution of cellular components at mitosis, thus accounting for sectoring. Moreover, it would seem to have lost a primary quality of infectiveness in its failure to reproduce independently of cellular reproduction. Hence, its state might be described as imperfectly integrated.

D. L. Shaver

8. Another case of simple inheritance of highly variable partial pollen restoration.

The inbred line, K64 restores partial and seemingly complete fertility to T cytoplasm which is variable according to environment, dosage effects, and genetic background, similar to the behavior of the classical inbred line, M14. Shaver (MGCNL 30:159) showed that the seemingly complex restoring characteristics of that inbred were actually controlled by a single locus which could be converted to nonrestoring state by simple backcrossing techniques. This finding was later confirmed in extenso by Duvick. Likewise, in K64, all of the seemingly endless degrees of restoration are controlled by a factor that segregates as a single gene in backcross recovery progeny.

D. L. Shaver

9. The use of id/id in production of super early corn.

In maize, the physiological limit to earliness would seem to be the need for a sufficiently long vegetative period to develop a plant "factory" large enough to support ear and grain production. Galinat has hypothesized that very early New England sweetcorns are always highly tillered because selection pressures have produced main culms which flower so early that they have insufficient photosynthetic capability, without tillers, to produce a realistically sized ear of table corn. Brawn, and later Shaver, have shown that Gaspe is so early that the main culm is florally induced as a maternal effect embryonically, while the meristematic apex is still within the seed. If one wishes to inbreed and thus further reduce an already minimal size of plant, special difficulties are experienced in barrenness or very marginal yield performance in the seedfield.

If, however, one works such super early types within the id/id state or phenotype, the very adverse effects of super earliness are avoided, since the plants are only cryptically early, and in reality grow to normal sized (id/id) plants before flowering and ear production. Such plants produce large ears and shed copious, fertile pollen over a long period and would thus be very desirable seedfield parents. If the other parent of the hybrid were normal (Id/Id), the derived seed would all be of normal phenotype, and thus the super-earliness of the id/id parent would be unmasked and made economically available in the form of an early hybrid.

Following this line of reasoning, one can immediately seize upon the idea that, in working for further earliness cryptically in id/id, one might be able to supercede the former limits of earliness described above, and proceed to a whole new plateau of earliness in maize. However, the maternal induction effect might set a limit to earliness in id/id, but this should be tested in other backgrounds than Gaspe Flint. At any rate, it is certain that one can by using id/id, develop super early lines of maize without paying the penalty of small plant size and utter dependence upon a long summer day environment for their successful production.

D. L. Shaver

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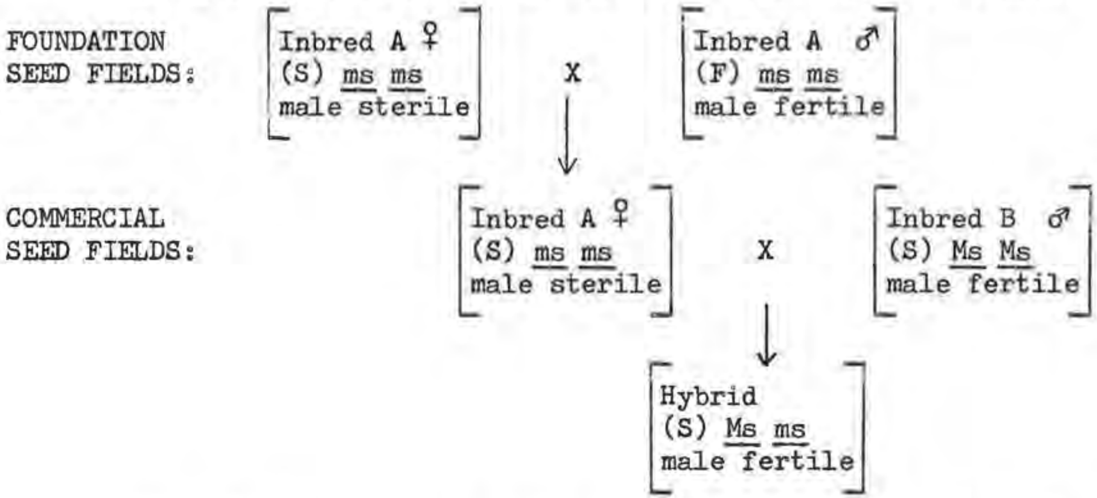
Bloomington, Illinois

1. Cytoplasmic restoration of ms - sterility.

Cytoplasms may occur which restore fertility in single recessive genetic male sterile lines. That is, the various ms genes may be analogous to the rf genes and produce male sterility in the presence of a specific cytoplasm or conversely a specific ms gene may not produce male sterility in the presence of a certain cytoplasm. If such a cytoplasm should be found, a male sterile (S) ms ms line could be increased using the male fertile counterpart (F) ms ms as a male. The female rows

in hybrid seed production fields would consist only of genetic male sterile plants (Hermsen, 1968).

The hybrid production system could be represented as follows:



This hybrid production system is not handicapped by a single cytoplasmic background as is true with the maize seed production with T, C, S or other sterile type cytoplasms. The genetic male sterile characteristic could be incorporated into the cytoplasmic background of any seed parent. The cytoplasm restoring fertility would only be used as the male parent for foundation seed increase.

All presently used maize lines are (S) Ms Ms and would restore fertility in commercial grain fields. Any inbred could be converted to (S) ms ms by backcrossing. We have not identified the (F) cytoplasm.

(F) cytoplasms may not have had many opportunities to be identified in maize genetic studies because the genetic male sterile is usually used as the seed parent. In addition, only a small number of cytoplasms may have been sampled. The (F) cytoplasm, if it occurs, could be identified through two different approaches.

1. Crossing the unknown, hopefully (F), cytoplasms using (S) Ms ms as a male parent and determining if non-segregating fertile F_2 populations are present. If all F_2 populations are male fertile, the unknown female parent contains the (F) cytoplasm.

2. A second approach involves using the male sterile (S) ms ms as the female and the unknown, hopefully (F), cytoplasm as the male parent. If the F_1 is (S) ms ms, all plants will be sterile and the fertile

cytoplasm has been identified. The male parent would not be able to shed visible pollen unless it had an (F) cytoplasm. If the F_1's are all fertile, then the cytoplasmic source must have dominant male sterile genes and may or may not have the fertile cytoplasm.

The first approach is more expensive per cytoplasmic source tested; however, it will identify an (F) cytoplasm in an Ms Ms genetic background. The second approach will not provide such identity.

The author is not aware of attempts to locate this type of cytoplasm in maize. This is a preliminary report on an attempt to identify an (F) cytoplasm. Genetic male steriles ms 1, 2, 5, 6, 7, 8, 9, 10, 12, 13, 14 and 17 are being crossed on each of 25 distantly related genetic sources. About half of the genetic sources involve diverse sources which conform to the general plant type common in commercial maize hybrids. The remainder involve exotic type plant introductions.

At this date, 82 different genetic male sterile and cytoplasm crosses have been observed in the F_2. Six F_2 populations did not demonstrate sterile plants. These six conformations are being re-evaluated. One of the six may be a result of small population size, while the other five are unexplained at this date.

References

Hermsen, Th. G. J. (1968). A discussion on cytoplasmic restoration of ms-sterility. Euphytica Supp. No. 1:63-67.

Richard F. Washnok

2. Complementation among EMS-induced lemon endosperm mutants.

There was a relatively large number of lemon endosperm mutants among those previously reported in MGNL 43:23-31, 1969 and MGNL 44:11-17. Eleven of these mutants were crossed together in a diallel and the F_1 ears were examined for complementation. All possible crosses among these mutants were not obtained; however, results of the partial diallel show complementation for three of the mutants. This does not mean that three separate genes are involved, for these three mutants could be at the same locus. One of the mutants that showed complementation was phenotypically classed as slightly lemon; hence, it might have been expected

to show complementation. All of these lemon endosperm mutants produce plants with green color.

There is good indication from the data available that EMS could be used to induce lemon endosperm mutants in material and the probability is high that the mutants would be at the same locus. These data are also of practical value since corn with lemon colored endosperm is valued in the human food industry.

Robert W. Briggs

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1. Inheritance of a new brachyism.

Four experiments with Tx61M (Texas stock) and T61 (Tenn. stock) on the inheritance of brachyism (above the ear) reveal that two pairs of genes differentiate the parents for this new character. Partial phenotypic dominance toward the T61 non-brachytic parent occurred in three out of four families.

A negative association with an r value of -.43 exists between the brachytic trait and plant height. The r value of .18 between brachyism and stalk diameter is much lower.

The lack of a significant correlation between ear height and brachyism may give the new brachytic an advantage over other brachytic genes in that a reduction in plant height is not accompanied by a reduction in ear height and yield.

J. G. Legg
A. A. Fleming

2. South American flints.

Flint corns from South America in 1971 averaged 74 bu./a in yield compared to 139 bu./a for U.S. dents and 98 bu./a for a flint-dent South American hybrid.

A. A. Fleming

3. Differential reaction of cytoplasms and genotypes to H. maydis, Race T.

H. maydis (Race T) on green maize plants was first found in 1971 in our nurseries and tests at Athens on July 9 on corn that was planted May 20. Inbreds were rated for reaction on the standard 0; - 5.0 H. maydis scale at 10-day intervals from July 14 to August 24.

The following results indicate a differential reaction not only for cytoplasms but also for genotypes (genes on the chromosomes).

Inbred	Reaction to H. maydis, Race T				
	Athens, Georgia				
	7/14	7/24	8/4	8/14	8/24
GA 152 (N)	1.0	1.0	1.0	1.5	2.5
GA 152 (T cms)	2.0	3.0	4.0	4.5	5.0
Pa 33 (N)	1.0	1.0	1.5	3.0	4.5
Pa 33 (T cms)	2.5	3.5	5.0	5.0	5.0
NY 821 (N)	2.0	2.0	2.5	3.0	4.5
NY 821 (T cms)	3.0	4.0	5.0	5.0	5.0
WF 9 (N)	1.0	1.0	2.5	3.5	4.0
WF 9 (C cms)	2.0	2.0	2.5	3.5	4.0
M 14 (N)	.8	1.0	1.5	2.0	2.5
M 14 (S)	1.0	1.0	1.5	2.5	3.0

A. A. Fleming

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1. The maize peroxidases; designation of seven loci governing peroxidase polymorphisms in maize.

Maize peroxidases have been the subject of our continuing genetic studies, although descriptions have been published for only one of the 7

genetic loci we have encountered (Hamill, MNL 42:36-7, 1968). These loci have been referred to briefly in a summary of 30 maize isozyme genes (Macdonald and Brewbaker, J. Heredity, in press, 1972), and are described in detail below.

There are ten principal peroxidases of maize, as defined by the presence of 10 principal regions of activity on starch and acrylamide gels. These 10 regions are shown in Figure 1, as they occur on acrylamide gels at pH 8.1 (Brewbaker et al., Physiol. Plant 21:930-940, 1968). Approximate Rf values are 74 for $\underline{Px_8}$, 51 for $\underline{Px_6}$ and 24 for $\underline{Px_3}$, allele 1. On starch gels, the peroxidases 7, 9, and 10 are tightly clustered near the origin, while at lower pH levels, cathodal regions migrate very rapidly. Below pH7, little movement occurs of the anodal bands. Eight of the 10 peroxidases have been characterized in our materials by multiple isozymes, largely under allelic control. Each of the peroxidases has tissue specificities or substrate responses that distinguish it and its respective isozymes. Further study will unquestionably reveal new isozymes within these regions.

Peroxidase Px 1 was described briefly by Hamill (MNL 42:36-37) and is an enzyme present in most tissues (exceptions: pollen, seed). Genetic polymorphisms are controlled by the $\underline{Px_1}$ locus, with three common isozymes governed by co-dominant alleles and a null form conditioned by an allele designated $\underline{Px_1^{null}}$. Allele $\underline{Px_1^2}$ is the most frequent (70% of US inbreds).

Peroxidase Px 2 is an enzyme found in glumes and pollen; two co-dominant alleles of the locus $\underline{Px_2}$ govern the two bands observed, with the slow allele $\underline{Px_2^2}$ rare.

Peroxidase Px 3 is our standard reference region and is the most polymorphic, genetically, of the peroxidases. It is most active in leaf, coleoptile and mesocotyl and repressed in pollen, silks and roots. It is derepressed late in the development of all tissues, and becomes very intense in senescing tissues, where multiple bands, diminishing in intensity and equally spaced, are observed (similar peroxidases are found in many grasses). Genetic polymorphisms are under control of the $\underline{Px_3}$ locus with at least 6 alleles, of which one is an apparent duplication. Alleles $\underline{Px_3^1}$ (in 60% of US inbreds) and $\underline{Px_3^2}$ predominate, while $\underline{Px_3^3}$ (a very slow

	REGION	ISOZYMES	LOCI
+	Px 8	1, 2	
	Px 2	1, 2	*Px*$_2$
	Px 6	1, 2	*Px*$_6$
	Px 3	5, 4, 1, 2, 3	*Px*$_3$
	Px 9	1	
	Px 10	1, 2	
	Px 7	1, 2	*Px*$_7$
O			
	Px 4	2, 1	*Px*$_4$
	Px 5	1	*Px*$_5$
–	Px 1	3, 2, 1	*Px*$_1$

Figure 1. Ten principal peroxidases of maize as they occur on acrylamide gels at pH 8.1.

isozyme) and $\underline{Px}_3^4$ (a fast band) were obtained from the race Clavo. $\underline{Px}_3^5$ (extremely fast band) was obtained from the race Puya segregaciones, where it occurred together with a unique twin-band phenotype. The latter has provisionally been designated by the allele $\underline{Px}_3^6$, acting as an allele that governs synthesis of both isozymes 1 and 2. Alleles for the 1 and 2 bands are present in race Puya, as indeed they have been in almost all of the 80 races studied. The possibility exists that $\underline{Px}_3^6$ is a duplication of the $\underline{Px}_3^1$ and $\underline{Px}_3^2$ alleles. Null variants have never been encountered.

Peroxidase Px 4 is an enzyme that stains intensely in most mature tissues, but is repressed in juvenile leaf, endosperm, coleoptile and ear. A single locus governs the common fast isozyme, $\underline{Px}_4^1$, and a slow variant, $\underline{Px}_4^3$, in Corn Belt materials; an intermediate band, $\underline{Px}_4^2$, has been obtained from the race Clavo, and preliminary data suggest its allelism to this locus. Null variants have not been observed.

Peroxidase Px 5 is repressed in most tissues, and is perhaps observed best in the endosperm, pericarp, and etiolated mesocotyl. A null phenotype (inbred L289) was studied in mature leaves and proved to be under control of a recessive allele at a locus designated $\underline{Px}_5$.

Peroxidase Px 6 is active in most tissues, but repressed in silks and mature leaves. A null phenotype, studied in seedling leaf and coleoptile, characterizes inbred C103, sweet corn inbred P39, and related lines, and is under control of a recessive allele, designated $\underline{Px}_6^{null}$. The Px 6 peroxidase clearly resolves into two closely paired bands on some gels. A slow variant has been observed, but not studied genetically, in teosinte.

Peroxidase Px 7 is a major enzyme of the silk, mature leaf, and pericarp, but is repressed in many other tissues. The common slow band (allele $\underline{Px}_7^2$), with an isoelectric point near pH 7.5, migrates a limited distance from the origin at pH 8.1. A fast variant has been observed in several inbreds (e.g., sweet corn lines T24, T36, and T55) under apparent control of an allele, $\underline{Px}_7^1$. A null or "extremely repressed" phenotype is observed in inbreds B37, CI66, W64A, and others, and preliminary evidence suggests control by a null allele.

Peroxidase Px 8 is observed convincingly only in root tissues, although very low concentrations may occur in leafy tissues, and is often seen as two closely-paired isozymes. It shows high activity on eugenol and appears unrelated to other maize peroxidases. No genetic polymorphisms have been discerned in the limited materials studied.

Peroxidase Px 9, like Px 8, stains intensely in root extracts, although it is observed variably in the cob. It stains intensely on guaiacol, unlike most other peroxidases of maize. Genetic polymorphisms have not been observed.

Peroxidase Px 10 stains intensely in the coleoptile, mesocotyl, and ear, but is absent from leaf, silk, pollen, and other tissues. Two bands and a probable third have been observed in this region but have not yet succumbed to genetic analysis.

James L. Brewbaker
Elizabeth Hamill Johnson

2. Genetic marker stocks in tropical flint background.

Through the years, we have been introducing various genetic markers, especially those affecting the endosperm, into a vigorous tropically-adapted stock to facilitate our breeding and academic studies (Brewbaker, M.N.L. 42:37-8). Despite the vigor and generally wide adaptability of stocks maintained by the Maize Cooperative, they lack resistance to several major tropical pests, and often require rather careful handling in the tropics.

The line chosen for these conversions was CM104, an inbred recognized to have high combining ability from the Coordinated Maize Improvement Scheme of India. CM104 was derived largely by sibbing from the Colombian yellow flint variety, Amarillo Theobromina, pedigree A THEO 21 (B)-6#-15-7#. It has been converted in Hawaii to Mv (resistance to maize mosaic virus I or "corn stripe"), and most marker stocks now carry this resistance. Conversions to Rp_1 (P. sorghi resistance) and Ht_1 (H. turcicum resistance) are nearing completion, and will be used for future backcrosses.

A brief description of CM104 follows:

Seeds: Hard yellow flint, C^I r pr and P^{wr} (red cob, colorless pericarp); high weevil resistance.

Plant: 60 + 70 days (winter) to silk, i.e., mid-late in tropics; 15 leaves, 5.5 feet tall with high ear at 3 feet (leaf 10); internodes above ear dwarfed to 5 cm.; highly resistant to stalk diseases, borers, and many leaf diseases; large tassel; green plant with purple anthers, glumes and brace roots, evidently A b Pl. Tillers rare.

Ear: 5" long, 14 rows, with tight husks and high earworm resitance; high ear and seed rot resistance.

The following is a list of available marker stocks. As noted, many stocks are kept as segregating lines. Few conversions have been carried past BC_4, as vigor has been favored over a high degree of inbreeding or homogeneity in the material. All lines are grown at least twice a year in our breeding nurseries; therefore, alternative stocks, multiple marker crosses, etc., are also available.

Mutant Gene(s)	Description	Map Position	Best Current Seedstock
ACR	Red aleurone	--	71-1019 x CMMR (segr C^I)
ACRPr	Purple aleurone	--	71-951S (segr C^I)
ABPl CRPr	Purple plant, aleurone	--	71-949x-1014 (segr)
a_1; Dt_1	anthocyaninless	3:111	70-674#
ad_1	adherent tassel	1:(108)	71-126# (3:1)
ae wx	amylose extender-waxy	--	71-960#
B; APl	Booster	2:49	71-1014 x CM (1:1)
ba_1	barrenstalk-1	3:72	71-990# (3:1)
ba_2	barrenstalk-2	2:--	71-991# (3:1)
Bf_1	blue-fluorescent	9:134	71-1026 x CM (1:1)
bk_2	brittlestalk-2	9:79	71-979# (3:1)
bm_2	brown midrib-2	1:161	71-968bm#
br_1; f_1 su_1	brachytic-1	1:81	71-133#
br_2	brachytic-2	--	71-964#
bt_1	brittle endosperm-1	5:22	71-963#
bt_2	brittle endosperm-2	4:71+	71-969#bt

Mutant Gene(s)	Description	Map Position	Best Current Seedstock
Ccms Rf/rf	C cytosterility	--	71-1046 x CM
Ch	Chocolate pericarp	2:155	71-1045Ch x CM
Cg	Corngrass	3:31	71-8670P (segr)
Cg; Rp_1^d	"	3:31	71-837x-881 (1:1)
cr_1	crinkly leaf	3:0	71-141# (3:1)
d_1	dwarf-1	3:18	71-972# (3:1)
d_1^{tn}	dwarf-tiny	3:18	70-676x-678 (3:1)
D_8	Dwarf-8	1:--	71-208 x CM
du	dull endosperm	10:33	71-967#du
f_1	fine stripe	1:86	71-959f_1#
fl_1	floury-1 endosperm	2:68	71-1041 x CM (+/fl)
fl_1; y	"	2:68	71-978#
fl_2	floury-2 endosperm	4:63	71-1027 x CM (1:1)
el	elongate	--	71-987S el/el
et	etched endosperm	3:122	70-656#et
gl_1	glossy-1	7:36	71-998# (3:1)
gt	grassy tiller	--	71-965# (3:1)
h	soft starch	--	71-968#h
Ht_1	Resis. to <u>H. turcicum</u>	2:121	71-837xCM
j_1	japonica	8:21	71-140# (3:1)
Kn	Knotted	1:127	69-746# (segr)
lg_1	liguleless-1	2:11	70-642lg#
lg_2	liguleless-2	3:83	71-139# (3:1)
Lg_3	Liguleless-3	3:(46)	71-1039 x CM (1:1)
lw_1	lemon white	1:(128)	71-1023S
mn	miniature seed	2:--	71-950S
ms_8	male-sterile-8	8:14	71-977# (3:1)
ms-si	male sterile-silky	6:(19)	71-127# (3:1)
Mv	resis. to Maize Mosaic Virus I	--	CM-MR2 (1:1)
na_1	nana-1	3:(86)	71-992# (3:1)
na_2	nana-2	--	71-982# (3:1)

Mutant Gene(s)	Description	Map Position	Best Current Seedstock
o_1	opaque-1	4:--	71-954#o
o_2	opaque-2	7:16	71-958#o, 70-621#o
$o_2;y$	"	7:16	71-660#
$o_2;\ r_2\ v_5$	"	7:16	71-961#o
P^{mo}	mosaic pericarp	1:26	71-994P^{mo}#
P^{rr}	red pericarp	"	71-1040P^{rr}xCM (1:1)
P^{vv}	variegated pericarp	"	70-723P^{vv}x CM (1:1)
pl;A, b	plant color	6:48	71-973#Abpl
Px_3^4	Peroxidase-3	--	71-1331-12 x CM
Px_3^5	"	--	71-1293 X 71-847-5
py	pigmy	6:68	71-989# (3:1)
r^g; su	colorless	10:57	71-953S
R^{nj}	Navajo aleurone	10:57	71-952S (segr)
$ra_1;\ v_5\ o_2$	ramosa-1	7:32	71-961#
ra_2	ramosa-2	3:26	71-997# (3:1)
ra_3	ramosa-3	4:--	71-998# (3:1)
Rp_1^d	Resis. to <u>Puccinia sorghi</u>	10:0	71-1780 x CM
sh_1;ACR	shrunken endosperm	9:29	71-983#sh
sh_2	shrunken-2	3:111.2	71-967#
Tcms Rf	T cytoplasmic male sterility	--	71-1036TmsRf x CM
$ts_2;\ bm_2$	tassel seed-2	1:24	71-119# (3:1)
ts_4	tassel seed-4	3:55	71-974# (3:1)
Ts_5	Tassel seed-5	4:56	71-1020 x CM (1:1)
vp_5	viviparous	5:18	71-145# (segr)
wi	wilted	6:--	71-984# (3:1)
wx;y	waxy endosperm	9:59	71-975# y wx
y_1	yellow/white endosperm	6:17	71-1052 x CM (= +/y)
$y_1;\ fl_1$	"	6:17	71-978#yfl
zn	zebra necrotic	10:35	71-995# (3:1)

Genotype Unknown (Origin in parenthesis):

Hairy sheath (Mexican composites)	71-1035 x CM (segreg)
Hoya arrugada, rugose leaf (Chalqueno)	71-971# (segreg)
Low ear position (Oh 43)	71-966# (segreg)
Normal internode elongation above ear	71-873 P x CM (segreg)
Square stalk (Roque 47 Y#, R/F Mexico)	71-1000S (segreg)
Zebra leaf	71-955# (segreg)

James L. Brewbaker

ILLINOIS FOUNDATION SEEDS, INC.
Champaign, Illinois

1. ACR genotype of Illini Xtra-Sweet and Early Xtra-Sweet hybrids.

Most corn varieties are of the genotype of A_1A_2cr, with some varieties A_1A_2Cr.

In 1970 an F_1 cross of $a_1A_2CRy_1$ x $A_1A_2CRy_1$ was planted to produce ears which would express the phenotypic ratio of 3 purple to 1 white. This cross was planted adjacent to the Illini Xtra-Sweet variety expecting the timing and the wind would favor a minimum of contamination. Both the silking and the wind were such that pollination of some $A_1a_1y_1y_1$ silks with Illini Xtra-Sweet pollen occurred.

It was anticipated there would be an excess of purple kernels in the cases of cross pollination. The sibbed ears were expected to express a 3 purple to 1 white seed color ratio. At harvest it was promptly noted many ears appeared to have both white and yellow seeds, as well as, the purple kernels. Some ears on the A_1a_1 rows immediately adjacent to the Illini Xtra-Sweet had only yellow and purple kernels, which appeared to be segregating on a 1:1 basis.

Dr. Earl Patterson, University of Illinois, called it to our attention that a_1 and sh_2 are closely linked on chromosome 3. In the conversion of stocks from su_1 to sh_2, a_1sh_2 stocks must have been used in the conversion program with the a_1sh_2 linkage not being broken.

Subsequently in 1971, $A_1a_1y_1y_1$ stocks were crossed, by hand pollination, by both Illini Xtra-Sweet and Early Xtra-Sweet. At harvest it

was noted that in both cases the ears were segregating in a 1 purple to 1 yellow seed ratio. This identified the fact that Xtra-Sweet varieties are both of the $a_1 a_1 sh_2\ sh_2$ genotype.

In 1971 ears which would give a seed ratio of 1 purple dent: 1 yellow dent: 1 purple shrunken: 1 yellow shrunken were being produced by planting a stock of $A_1 A_2 CcRSh_2 sh_2 y_1 y_1$ in an isolation plot, detasseling this hybrid, and allowing it to pollinate with pollen from the Xtra-Sweet parents. The resulting crossed ears expressed no segregation for color, all the kernels being purple. This would indicate that both Illini Xtra-Sweet and Early Xtra-Sweet are of a dominant CC genotype.

Clarion B. Henderson

2. Seedlings segregating on a 9:3:3:1 phenotypic ratio.

It is relatively easy to have maize ears which express phenotypic ratios of 3:1 and 9:3:3:1. It is also easy to have seedlings which express a 3:1 ratio. To our knowledge there is little or no seed available which, when planted, will produce seedlings expressing a 9:3:3:1 ratio.

In working with both lw_1 (lemon-white albino-chromosome 1) and d_1 ($dwarf_1$-chromosome 3) the idea occurred to us to combine these two mutants in such a way to produce seedlings which would exhibit 9:3:3:1 ratio, when planted.

The first attempt to produce this material was made by crossing heterozygous dwarf-1 by $Lw_1 Lw_1$ (or $Lw_1 lw_1$) stocks. At the same time these $Lw_1 Lw_1$ (or $Lw_1 lw_1$) plants were selfed by progeny number. The $D_1 d_1$ plants crossed by $Lw_1 Lw_1$ were discarded. Only the $D_1 d_1$ plants crossed by $Lw_1 lw_1$ were harvested. The cross of $D_1 d_1$ x $Lw_1 lw_1$ was then planted and each plant selfed. At the harvest of these selfs all ears not expressing a segregation for lemon-white were discarded (approximately 50% of the selfed plants). The remaining ears were individually germinated to ascertain those segregating for both d_1 and lw_1, not for just lw_1 alone.

The second procedure selected was the crossing of $Lw_1 Lw_1$ (or $Lw_1 lw_1$) stocks by homozygous dwarf-1 plants. To more aptly make this cross the dwarf-1 plants were carefully treated with gibberellic acid.

Untreated dwarf-1 plants grow to a height of about 8 to 12 inches. With our gibberellic acid treatment, the dwarf-1 plants grow to a height of approximately 3 feet.

At harvest all the crossed ears are saved and separately shelled. Some seed from each ear was then planted and selfed to determine whether the $Lw_1 Lw_1$ or $Lw_1 lw_1$ genotype was crossed by d_1 plants. Progenies producing ears segregating for lemon-white were saved and the remnant seed used to produce additional seed segregating for both lw_1 and d_1.

In developing this second procedure it was apparent that approximately half the crossed ears segregated for both lw_1 and d_1. Of the selected progenies producing the lw_1 phenotype, these rows contained plants of which ½ were found to be segregating for both lw_1 and d_1. All the progenies and all the selfs produced seed segregating for dwarf-1 expression.

The phenotypes produced by this second procedure would be for a 9 tall green:3 tall albino:3 dwarf green:1 dwarf albino ratio, or for a 3 tall green:1 dwarf green ratio.

Clarion B. Henderson

3. Studies and classification of cytoplasm variations.

Because of the seriousness of both *Helminthosporium maydis* race T Southern Leaf Blight and Yellow Leaf Blight and their attack on corn varieties in the T cytoplasm background, a study was initiated with cytoplasms that did not show susceptibility to these two diseases.

When this relationship of disease susceptibility and cytoplasm background became apparent, Dr. M. S. Zuber, University of Wisconsin, recalled some previous work of Dr. Jack Beckett, while Dr. Beckett was with the University of Illinois. Dr. Beckett had accumulated and studied various sources of corn which gave some expression of sterility in the different backgrounds. With the transfer of Dr. Beckett from the University of Illinois, to the University of Missouri, studies of this project were discontinued. Dr. Zuber, in recognizing the potential availability and use of this material, accumulated these stocks and made them available to research workers. Dr. A. L. Hooker, University of Illinois, and

Dr. M. S. Zuber studied the correlation of the available cytoplasms with their reaction to the T maydis Southern Leaf Blight, and released only cytoplasms not showing susceptibility.

Dr. Zuber and Dr. Hooker selected 26 cytoplasms from the pool of material. Dr. Beckett, in his work, had incorporated these cytoplasms into 10 isogenic inbred backgrounds. It was felt previously there was a high degree of similarity in these cytoplasms collected. However, it was never conclusively ascertained whether the cytoplasms were similar or dissimilar in their sterility, restoration, or disease reactions. Those 10 original inbreds are not widely used in present day hybrids. Because of the outdated nature of the germplasm and the fact that many newer inbreds are more extensively used in hybrid combinations, it was decided to initiate an incorporation program and further study the cytoplasms.

Previous and more extensive work had been initiated in regard to both the C and the S cytoplasms so these were not included in this program. The remaining 24 cytoplasms, all in the 38-11 inbred background, except for ML cyto in the Tr background, were secured from Dr. Hooker. Also included, as a check, in this program was 38-11 in its normal cytoplasm. For crossing with these 25 cytoplasms, we selected 20 of the most common and representative inbreds. At the time the F_1 crosses were being made in Hawaii, it was apparent there was little or no indication of good sterility with these cytoplasms, in the 38-11 background, with all of these varying from fully fertile, or restored, to light partial shedding. It became evident from this that the BC_1 or more advanced generations would be required before the desired information could begin to be obtained.

$Backcross_1$ generation was then made in a second generation Hawaii planting. The seed from this was returned to Champaign for observation and continued backcrossing. At Champaign, additional backcrosses were made to each of the 500 combinations, selecting the most sterile plants appearing in the BC_1 progenies. At the same time, all rows were evaluated as to whether sterile segregates were present.

Table 1. Classification of BC_1 progenies from crosses incorporating various sources of cytoplasm into twenty inbred lines.

Inbred	38-11 normal	EK	M	MY	G	IA	SD	PS	ML	TC	VG	J	H	CA	W	L	K	I	RB	R	TA	F	B	D	ME	T	C
FR2ATRf													X	X	X			X									
FR2BTRf													X	X	?	X	X										
FR3																			X							*	*
FR4																				X						*	*
FR5																			X							*	*
FR14A																		X								*	*
Mo17		X	X	X	X	X	X	X	X	X	X	X	*	X	X	X	X	X	X	X	X	X				*	*
FR21E																										*	
FRN28		X	X	X	X	X	X	?					X	X	X	X	X	X	X	X						*	*
FR37		X	X	X	X	X	X	X	X	X	X	X	X	*	X	X	X	X	X	X	X	X	X			*	*
FR43																										*	
B57		X	X	*	X	X	X	X					X	X	X			X			X	X					
FR64A		X	X		*	X	X	X	X	X	X	X	X	X	X	X				X	X	X	X			*	
FR103D							X												X								
FR619																X						X				*	
FR632																										*	*
33-16																										*	
CI64																										*	*
CI66													X	?	?					X	*	?	X				
Ky226		X	X	X	X	X	X		?	X	X	X				X			X	X						*	*

X = Sterile segregates * = Row completely sterile ? = Need further observation

Table 1 summarizes the crosses observed and those in which there appeared to be sterile segregates. In a few cases, especially with CI66, the stands and backcross generation were not such that results are indicated or reported. In five cases, the BC_1 rows observed were completely sterile. In the other identified cases, the rows were segregating for sterile plants. In some instances, we have question marks. These rows were F_1 crosses and the pattern of behavior would indicate these combinations especially should be checked further.

The investigations are being continued by making additional backcrosses and studying these further. The five cases where the BC_1 rows were completely sterile are in an annual program of three generations to speed along the incorporation. The rows segregating for steriles, as well as those progenies in question, are presently on a two generation program. The balance of the progenies will be continued on a one generation per year basis. In this way, we shall be recovering isogenic versions of all cytoplasms. The program is also being expanded to include three additional cytoplasms, namely El Salvador (Es), Brazilian Flint (Bb), and Argentina Parana (PA).

Since in the BC_1 generation all backcrosses were made to the most sterile plants, it is anticipated it will be possible in the succeeding generations to evaluate each of the progenies as to the fertility, or the degree of fertility. This should give further evidence as to the relative similarity of the cytoplasms.

It may be necessary to initiate a progeny selfing-backcrossing program since some variation in the results may be due to the genotypic difference within a given inbred. This program may be especially helpful in securing "non-restoring" maintainer versions of the various inbreds. This progeny selfing-backcrossing program is being conducted on many inbreds in the C cytoplasm, sterile incorporation program. Here the attempt is to secure maintainer progenies, which, used with their sterile counterpart, will bring about complete sterility rather than a segregation for sterility and partial fertility.

Summary--Based on the preliminary studies of the sterile segregates of approximately 500 BC_1 crosses, it appears there is a difference

in the cytoplasms being evaluated. The cytoplasms of EK, M, MY, G, IA, SD, and PS appear to fall into an almost identical pattern. This pattern is different from that of the other 17 cytoplasms. The ML, TC, VG, and J cytoplasms appear to fall into a second group. The H, CA, and W cytoplasms fall into yet a third group. There is additional variation among the remaining cytos. Further evidence secured by additional back-crossing should substantiate, or possibly disprove, the comprehensive data obtained thus far.

Clarion B. Henderson

4. Precautions for use of "normal" 33-16 inbred.

In the reversion from ear parent inbreds which are T sterile back to so called normal versions, a review of what is normal must be considered. This is especially true in the case of 33-16.

Prior to the extensive knowledge and use of sterile and restorer inbreds in production, a case of scattergrain fill was reported with a hybrid which used 33-16 as its female parent. It was later learned that 33-16 had a special cytoplasm, which in some instances could be sterile.

With this knowledge, the inbred 33-16 was delegated for use as a male parent, either in making seed of the single crosses for hybrid production, or as the male parent in the production of the final hybrid.

During the time T cytoplasm material was being used, the 33-16 inbred was converted from its "normal" cytoplasm to the T cytoplasm version. Here the use of blending, or restorers for T cytoplasm, was relied on. Hence there was little or no concern of ample pollination in the farmers' field.

With the outdating of the T cytoplasm, 33-16 with its regular cytoplasm was brought back into production. Recently the 33-16 inbred has been classified as having the J type cytoplasm. The indiscriminant use of 33-16 could again cause problems.

In the use of regular 33-16 as the ear parent inbred either in a three way cross or in a 4 way hybrid, the following condition might exist, assuming that H21, K55, and Ky27 or similar inbreds might not restore fertility to a J sterile:

33-16 x W21 = Rf rf (all fertile)

(33-16 x H21) x K55 " x Ky27 " x (K55xKy27)	1 Rf rf (fertile) 1 rf rf (sterile)

Under ordinary conditions, and assuming that the 33-16 inbred fertility is brought about by full restoration of the J cytoplasm, one would expect 50% of the plants would be fertile and the remaining would be sterile. However, assume that the 33-16 inbred is more of a heavy partial type fertility, and in our judgment, this may be the case. Further, assume that environmental conditions, especially in the white corn growing area, are not ideal at pollination time. It would then be easily possible to have far less than 50% of the viable abundant pollen which would be expected. This might well have been the case in the scattergrain fill, as previously reported.

Realizing the seriousness of the situation in regards to 33-16, Illinois Foundation Seeds has taken the following three precautionary steps in preventing pollination problems from arising:

(1) The bulk of the foundation single cross production was made reciprocally. Both versions will be available for seed production. As an example, both 33-16 x Ky201 and Ky201 x 33-16 are available, thereby assuring that not all seed sold farmer customers needs to have the J cytoplasm.

(2) J cytoplasm crosses are being studied so that combinations can be recommended in which other inbreds can contribute a higher degree of restoration, or fertility, in case it is necessary to use only 33-16 J as the female parent.

(3) A 33-16 which has the cytoplasm of B37 has been increased and will be used in future production. This will thereby eliminate the concern of the J type cytoplasm. This 33-16 strain came about, and was possible, through the program in which 33-16 was being converted to a floury endosperm type. (The normal kernels rather than floury were selected and increased.)

Caution also might be advisable in the use of new cytoplasms where fertility might be the result of heavy partial restoration rather than full restoration. A case in question could be the restoration of the S type cytoplasm. Even though some testcrosses appear to have a great amount of fertility, much of this fertility does have more of a semblance of heavy partial rather than actual full and positive restoration.

Clarion B. Henderson

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1. Translocations generated by monosome X diploid crosses in Zea mays.*

It is well documented that certain regions of the genome are present in duplicate in maize as well as in other organisms. If a given monosomic chromosome bears a region which is also present on another chromosome, these two regions might occasionally pair in the monosome and recombination might take place between the duplicate regions. If this happens, reciprocal translocations would be found in the progeny of monosome X diploid crosses.

Plants confirmed to be monsomic for chromosomes 2, 4, 6, 7, 8, or 10 have been used successfully as males and monosomes 4, 6, 7, 8, and 10 as females in our cultures. Large numbers of progeny from crosses between specific monosomes and diploid inbreds are being analyzed for plants with about 50% ovule and pollen abortion. Three translocations have been cytologically confirmed from such crosses and 20 additional lines carrying transmissible semisterility have been isolated. Thus, translocations are obtained in the progeny of monosome X diploid crosses.

Through the use of a given monosome, a specific chromosome is tested against the entire genome for redundant segments; thus such segments can be determined chromosome by chromosome. If a specific translocation were repeatedly found this would indicate homology between two chromosome segments. However, if a random array of translocations is

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found between a monosomic chromosome and the rest of the genome, this might indicate that illegitimate recombination is taking place between nonhomologously synapsed segments.

David F. Weber

2. The relative concentrations of different fatty acids in monosomic *Zea mays* embryos as determined by gas liquid chromatography analysis.*

Monosomes generated by the $r\text{-}x_1$ deficiency are being used to detect genes that have a dosage effect on the relative concentrations of the different fatty acids of *Z. mays* embryos. By comparing a monosome with its diploid sibling it is possible to evaluate one versus two doses of every gene on a given chromosome at the same time. Using this experimental approach, we previously demonstrated that genes or gene complexes that alter the total lipid content of maize embryos are located on chromosomes 2, 6, and 10. No such genes were detected on chromosome 8 (Plewa, 1971; Plewa and Weber, 1971); thus monosomy *per se* does not alter lipid content. The present study will determine the effect of monosomy on the proportions of different fatty acids composing the extractable lipid fraction of maize embryos. This paper discusses the procedure of the study.

Experimental kernels were obtained from a cross between a W22 inbred line carrying the $r\text{-}x_1$ deficiency and inbred Mangelsdorf's Multiple Chromosome Tester (bm_2; lg_1; a_1; su_1; pr; y_1; gl_1; j_1; wx; g_1). A scutellum sample of approximately 1.5 mg adjacent to the embryonic axis was removed from each F_1 kernel ($r/r\text{-}x_1$). Each scutellum sample was placed in a separate vial, coded, and stored at -22°C. The corresponding kernels were planted. The monosomic plants were detected at the seedling stage by expression of appropriate genetic markers and confirmed by cytological analysis. The scutellum samples from the monosomes and their control diploid siblings were subsequently prepared for gas liquid chromatography (GLC) analysis of the lipid fraction. The fatty acid extraction and methylation followed a modification of procedure 1 as described by Jellum (1970). The samples were analyzed using a Hewlett-Packard model

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5750 GLC with a 1/4 inch stainless steel column (10% EGSS-X 100/120 gas chromatography-Q: Applied Science Laboratories). The carrier gas was nitrogen and the column temperature was 190°C. The samples were kept under N_2 during lipid extraction and fatty acid methylation. The methylated fatty acid samples were stored under N_2 at -22°C.

Preliminary data from this approach are summarized in Table 1. The fatty acids detected were: palmitic (16:0), stearic (18:0), oleic (18:1), and linoleic (18:2). The fatty acid distribution of each embryo is expressed as the relative proportion of a specific fatty acid to the total fatty acid content of the sample. Since there were repeated diploid, monosome 8, and monosome 10 plants produced, an Analysis of Variance was conducted for each fatty acid fraction. Where rejection of the null hypothesis was indicated, the Fisher Least Significant Difference technique was employed to test specific differences.

Table 1. Average relative concentrations of fatty acids from *Zea mays* embryos

	Sample Number	Fatty Acids			
		Palmitic	Stearic	Oleic	Linoleic
2N Control	MP34-24	0.1661	0.0254	0.3378	0.4707
2N Control	MP34-33	0.1423	0.0223	0.3521	0.4833
2N Control	MP34-34	0.1571	0.0216	0.3357	0.4857
2N Control	MP34-35	0.1468	0.0207	0.3527	0.4798
2N Control	MP34-38	0.1544	0.0239	0.3397	0.4838
2N Control	MP34-45	0.1310	0.0379	0.3875	0.4436
2N Control	MP34-47	0.1596	0.0238	0.3464	0.4703
2N Control	MP34-54	0.1757	0.0199	0.3356	0.4689
2N Control	MP34-55	0.1281	0.0272	0.3647	0.4800
Aneuploids					
Monosome 2*	MP34-37	0.1467	0.0301	0.3945	0.4207
Monosome 7	MP34-16	0.1375	0.0120	0.3045	0.5460
Monosome 8	MP34-57	0.1999	0.0285	0.3303	0.4412
Monosome 8	MP34-62	0.2009	0.0203	0.3181	0.4608
Monosome 10	MP34-19	0.1108	0.0304	0.3578	0.5010
Monosome 10	MP34-8	0.1193	0.0255	0.3735	0.4814
Double Monosome 8-?	MP34-43	0.3968	0.0743	0.4404	0.0896

*0.0079 of this proportion is involved with an unidentified fatty acid; probably 12:0.

The statistics indicate that there is a significant difference ($\alpha = 0.05$) in the proportion of palmitic acid in both monosome 8 and monosome 10 samples as compared with the control. The data for the other fatty acids indicate no significant difference from the diploid control.

A double monosome plant, involving chromosome 8 and a presently unidentified chromosome, was produced and its fatty acid distribution differs remarkably from its diploid siblings (see MP34-43 in Table 1).

The data indicate that this approach merits further investigation and specific genes involved in fatty acid biosynthesis may be uncovered.

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1. Knob constitution and the rate of chromatin loss.

Previous experiments with _K3 A Sh/ k3 a Sh_ plants, in which the knobbed chromosome was marked by _A_ and the knobless by _a_, indicated that the knobbed chromosome was lost at the second microspore division more often than the knobless chromosome. Loss of the dominant _Sh_ in a spore containing the _a_ chromosome was attributed to a prior crossover between the _A_ locus and the knob and it was concluded that the only chromosomes undergoing loss were _K A_ noncrossovers or _K a_ crossovers.

In order to test the correctness of this interpretation, a second experiment was set up involving a cross of lg k a sh female parents with lg k a Sh/ Lg K A Sh high loss male parents. F_1 kernels of sh phenotype are produced when a sperm deficient for the Sh allele in 3L fertilizes the polar nuclei. In the absence of heterofertilization, the embryos in these kernels arise from the second sperm in the same pollen grain which contains a normal chromosome 3 predicted to carry the knob and the closely linked Lg marker (ca. 5% recombination, Dempsey, unpublished). A total of 524 sh kernels was obtained in a population of 11,200 (families 30131 & 30776). Although germination of sh kernels was poor, 147 Lg and 64 lg plants were obtained. The majority of the plants carried the knob marker as predicted, but the sizeable group of lg plants (presumed to have a knobless chromosome 3) was unexpected. The question arises as to whether the 64 lg plants came from spores with a knobless chromosome 3 which nevertheless underwent chromosome loss or whether they can be accounted for by some other mechanism.

The data may be interpreted in three ways: (1) The knobless homologue undergoes loss approximately half as frequently as does the knobbed chromosome 3. Such a conclusion is at variance with the data from other crosses which indicated that B-chromosome-induced loss of knobless chromosomes rarely occurred. (2) Heterofertilization could account for lg seedlings arising from a sh kernels. On this explanation, the embryo of the exceptional a sh kernel would have a knobless 3. It would be necessary to assume that loss of a knobbed chromosome 3 in one microspore, producing a sperm deficient for the A Sh alleles which fertilized the polar nuclei to form the endosperm, was frequently associated with fertilization of the egg nucleus by a lg k sperm from a second pollen grain. Nothing is known about the frequency of hetero-fertilization in this experiment although in related tests it was low. (3) It is possible that linkage of the Lg locus with the K3 knob is not as close as previously indicated and that the exceptional a sh kernels giving rise to lg seedlings are the result of loss involving a lg K chromosome coming from crossing over. A limited sample of five lg plants has been examined cytologically; all had a knobbed chromosome 3,

indicating that a crossover lg K chromosome rather than a noncrossover lg k chromosome 3 had fertilized the egg. These cytological data, fragmentary though they be, lend no support to explanation (2) and are in accord with the constitution of the embryo expected on explanation (3).

If loss is restricted to the knobbed 3 and there is no heterofertilization, all of the 147 Lg seedlings from a sh kernels carried a Lg K chromosome 3 and all of the 64 lg plants should possess a crossover lg K chromosome. If all lg plants from the exceptional a sh kernels are the consequence of crossing over between lg and K and if the same proportion of lg K recombinants occurs among the plants from the Sh kernels, the lg and K loci would be independently inherited and recombination would greatly exceed the 5% found by Dempsey. There is no reason to question the validity of her estimate of recombination for this interval and our studies on preferential segregation would also place the lg locus close to the knob. Unlikely though it may seem, we have tentatively concluded that in the high loss strain a crossover between lg and K, occurring in meiotic prophase, predisposes in some unknown manner the crossover chromosome to undergo chromatin loss at the second microspore division.

Although our studies are incomplete we have yet to find an unequivocal instance of B chromosome-induced loss of a knobless chromosome 3 at the second microspore mitosis. If knobless chromosomes are subject to loss at this mitosis it is an infrequent event compared to the rate of loss of knobbed chromosomes.

Data on knob size and the rate of loss came from studies of high loss plants having the following chromosome 9 constitution: K^L Yg C/ K^S yg C. Both knobs terminate the end of the short arm but the K^L knob is much larger than K^S, which is approximately the size of the knob in Kys. The chromosome 9 with the large knob carries the closely linked Yg allele while the homologous chromosome 9 has the small knob and the recessive yg allele. When silks of yg c individuals were pollinated by K^L Yg C/ K^S yg C high loss plants, all of the F_1 kernels would have colored aleurone except in those cases where there was loss of the C allele in the sperm uniting with the polar nuclei. If the colorless kernels arose from loss induced in the K^L Yg microspores the embryos of

the exceptional kernels would have the Yg allele contributed by the sister sperm cell and give rise to green seedlings. Loss of the C allele from the chromosome 9 with the small knob would also result in a colorless kernel when the deficient sperm fertilized the polar nuclei but the embryo would produce a yellow green seedling. In short, a green seedling from a colorless kernel denotes loss of the K^L chromosome while a yellow green plant from a colorless kernel is the consequence of loss of the K^S chromosome. In a preliminary experiment we obtained 37 green and four yellow green seedlings from colorless kernels. Not unexpectedly, the chromosome with the larger knob is most frequently lost.

M. M. Rhoades
Ellen Dempsey

2. Possible causes of variations in the frequency of chromatin loss induced by B chromosomes.

In the 1970 growing season, unusually high rates of endosperm loss of A_1 (around 20%) occurred when a number of high loss plants with 6 or more B's were used as male parents in crosses with several a tester stocks. The high loss plants were derived by self and sib pollinations within a stock which in preceding generations had given uniformly lower rates (about 12%) in crosses with six different female parents. The higher frequencies were attributed to an undefined environmental effect since the segregation of modifying genes or the differential performance on different females appeared unlikely. Moreover, in 1970 two high loss individuals gave both high and low rates of loss when used as the male parent on two a stocks. In both instances, the cross with the late maturing $d_1 lg_2 a_1$ stock gave a lower rate than did the cross with the earlier a_1 B Pl stock. Population totals are given in parentheses.

♂ parent	# B's	Endosperm loss of A with ♀ parent: d_1 lg_2 a_1	a_1 B Pl
30785-24	7	12.7 (529)	21.7 (1634)
30785-23	8	8.9 (615)	19.5 (2110)

The different rates of endosperm loss observed in the two crosses could be ascribed to the ability of the female parent to affect the

pattern of fertilization. Thus, the lower endosperm loss of both pollen parents in the d lg a crosses might be due to the preferential fertilization of the egg by deficient sperm while in the a B Pl crosses the reverse would occur. If this indeed is the correct explanation, the low endosperm loss observed in the d lg a crosses should be combined with a high rate of loss in the embryo and the high endosperm loss of the a B Pl crosses should be associated with low embryo loss. That this is not true was shown for plant 24. In field grown plants from the a B Pl crosses, 19.3% of the progeny came from colorless kernels (loss of A in the endosperm) while the frequency of embryo loss was 9.4% (detected as anthocyaninless plants with 50% pollen or ovule abortion). Comparable values for the d lg a crosses were 8.3% endosperm and 3.6% embryo loss (detected by colorless plant phenotype, by pollen and ovule abortion, and by progeny testing). There was no compensating increase in embryo loss if endosperm loss was low and vice versa. The total loss rate in endosperm and embryo differed when the same individual plant was crossed onto two tester stocks.

It is possible that the 20% rate of endosperm loss reflects an environmental difference; the lower rate of loss found in crosses onto the d lg a stock might also be assigned to an environmental effect were it not for the fact that, in both plants 23 and 24, the pollen tested for loss in the a B Pl crosses came from the main stalk and that used in the d lg a crosses was produced by a tiller. It is true that the second microspore division in the tiller occurred at a later time and presumably under different growing conditions than it did in the main tassel. This would argue for an environmental effect such as variation in temperature. However, a difference in genetic constitution of main stalk and tiller might be responsible. Elimination of several B chromosomes from the tiller at the time it originated from the main stalk would give a tassel with a lower loss potential. Whether or not the main stalk differs from its tillers in numbers of B's has not been studied in maize, but this somewhat fanciful hypothesis is made more credible by the variation in the number of B's during tiller differentiation in Dactylis (Puteyevsky and Zohary, 1970). Mitotic instability in number of B's has also been

found in several species (see Battaglia, 1964 for references). The influence of environmental factors on chromatin elimination induced by B's remains to be demonstrated, as does the likelihood of somatic variation in numbers of B's between main stalk and tiller. Experiments have been set up to resolve these questions.

M. M. Rhoades
Ellen Dempsey

3. Effects of various segments of the B chromosome on recombination and nondisjunction.

A) Analysis of the B chromosome segments responsible for enhanced crossing over.

Hanson studied recombination in chromosomes 9 and 3 and reported slightly higher values in plants with B chromosomes. These effects were not discernible until about four B's were present in the plant, at which time most of the enhancement was in double crossover classes. Since then Nel has found that B's appreciably augment exchanges in the centromere regions of chromosomes 5 and 9. The most spectacular promotion of recombination by B chromosomes, however, was discovered by Rhoades. A segment of 3L was transposed to the short arm of chromosome 9 and intercalated between C and Wx. Crossing over between the chromosome 9 markers was little affected when the transposition was homozygous, even though the physical distance was extended. This situation was drastically altered when a single B was present. Recombination was increased as much as 110% by the addition of a B chromosome, and a dosage effect was evident. The transposition line was utilized in crosses with selected A-B translocations in an attempt to determine which portion(s) of the B chromosome was involved in the enhancement of recombination.

Translocation stocks TB-4a, TB-3a, TB-6a, and TB-8a were made homozygous for the transposition and heterozygous for the markers C and Wx. Chromosomal constitutions of the resulting families were determined by pachytene analysis, root tip chromosome counts, and/or pollen abortion. The results of testcrosses are given in Table 1, and B chromosome breakpoints are shown in the accompanying drawing.

Table 1. Testcross data from C Tp Wx/ c Tp wx female parents varying in TB-A constitution, and a drawing of the B chromosome with breakpoints indicated by horizontal lines.

Total population	% C-Wx Recomb.	Constitution
2030	26.5	88^{B}
1861	27.3	88
4597	32.4	$88B^{8*}$
3499	38.6	$88^{B}B^{8}B^{8**}$
1486	21.5	33
3059	30.2	$33B^{3**}$
3115	36.0	$33^{B}B^{3**}$
792	16.8	66
4048	27.7	$66B^{6*}$
6550	31.3	$66^{B}B^{6**}$
5704	37.6	$66^{B}B^{6}B^{6**}$
3154	22.4	44
3169	28.7	$44B^{4**}$
2395	33.9	$44^{B}B^{4*}$
4414	38.2	$44^{B}B^{4}B^{4*}$

5 TB-8a
4
TB-3a
3
TB-6a
2
TB-4a
1

*,** values are significantly greater than those in the compound immediately above at the 1% (*) and 0.1% (**) levels.

The lack of any increase in C-Wx recombination in the 88^{B} plants in relation to the control 88 class indicates that the distal-most region of the B chromosome, containing only two chromomeres, has no activity in the promotion of crossing over. As might be expected, the

B^8 chromosome is an effective inducer when only one is present, and two B^8's enhance exchange even further. The higher recombination in the $33^B B^3$ class than in the $33B^3$ category indicates that the region of the B between the breakpoints of TB-3a and TB-8a is able to influence crossing over. The participation of the region of the B proximal to the TB-3a breakpoint is demonstrated by the promotion of crossing over by B^4, B^3, and B^6. The increase noted with the B^4 chromosome indicates that the euchromatic segment of the B (region 1) probably has activity in this phenomenon (the short arm or the centric heterochromatin of the long arm could be the center of activity). The heterochromatin between the TB-4a and TB-3a breakpoints (regions 2 + 3) may contribute to the enhancement of recombination or the B^3 and B^6 chromosomes could derive their activity from the presence of region 1 alone.

In an attempt to determine if segments 2 + 3 increase crossing over, the relative contributions of each portion of the B were estimated. Since the translocation lines were from different backgrounds, direct comparisons of recombination could not be made. However, if the exchange increment of the balanced translocation heterozygote above the control (with no translocation and no intact B's) represents 100% of the effect of an intact B chromosome, the percent contribution of each B^A chromosome can be estimated by: $AAB^A - AA \times 100/ AA^B B^A - AA$, where AA, AAB^A, and $AA^B B^A$ are the percent recombination in plants of that constitution. The results of these calculations are as follows:

B^4 - 55%; B^6 - 75%; B^3 - 60%; B^8 - 100%.

The B^4 chromosome, containing only the proximal euchromatin of the B, has about 55% of the activity of an intact B chromosome. The 75% contribution of B^6 therefore suggests that 55% of the enhancement effect is due to region 1, while about 20% of the activity resides in region 2. The remaining contribution to the enhancement of crossing over by a B^8 or intact B must come from segments 3 + 4.

The 60% contribution to the enhancement of crossing over by B^3 is difficult to understand. With the breakpoint more distal than B^6, one might expect that B^3 would cause a greater increase in recombination than B^6. The region between the TB-6a and TB-3a breakpoints (region 3) may be inhibitory to crossing over and may counteract the stimulatory

effect of the more proximal regions. Whether or not an antagonistic condition exists, it is difficult to assign a percentage contribution to the segments studied. The most that can be stated at this time is that all segments of the B, with the exception of the distal chromomeres, appear to affect recombination in Tp9Tp9.

Since as yet no reliable data have been obtained on the effects of trisomics on recombination in the tested segment of chromosome 9, the possibility remains that some of the enhancement attributed to the B^A chromosomes may be due to partial trisomy for the A chromosome involved in the translocation. Recombination in one trisomic 4 plant was not higher than that found in a closely related disomic. It is therefore likely that the B^4 enhancement of crossing over in Tp9Tp9 is a result of the presence of the B chromosome segment and not trisomy for chromosome 4 chromatin.

B) Control site for B chromosome nondisjunction.

With the establishment of the B chromosome breakpoint for TB-8a it became obvious that the opportunity existed to test the activity of the few distal chromomeres in the control of B chromosome nondisjunction. If the controlling segment lies in the region distal to the breakpoint, nondisjunction of the B^8 would occur only in $8^B B^8$ spores. However, if activity is confined to a portion proximal to the TB-8a breakpoint, the B^8 chromosome would undergo nondisjunction in both $8B^8$ and $8^B B^8$ spores.

Plants of constitution $88B^8$ were crossed as pollen parent by normal (88) individuals and chromosome counts were made on root tips of the progeny. The results are given in Table 2. In a total of 507 seedlings, 431 had 20 chromosomes, 73 had 21 chromosomes, and 3 were mosaic for chromosome number. Of the latter three, cells with 20, 21, and 22 chromosomes were found in two of the plants while the remaining seedling had cells with either 21 or 22 chromosomes. No plants with 22 chromosomes were found. The transmission of the B^8 through the pollen varied considerably, but averaged about 30%.

A further test for nondisjunction allowed for selection of seedlings which contained the B^8 chromosome, and made root tip analysis of large populations unnecessary. The procedure was as follows:

$8^v8^v \times 8^v8^v{}_B{}^{8V}$
↓
8^v8^v
$8^v8^v{}_B{}^{8V}$ - from normal disjunction
$(8^v8^v{}_B{}^{8V}{}_B{}^{8V})$ - could arise from nondisjunction

Only green seedlings were analyzed for chromosome number, and they were expected to have 21 chromosomes if nondisjunction did not occur. Seedlings having two B^8 chromosomes would result from nondisjunction at the second microspore division followed by fertilization of the egg by the hyperploid sperm. Fourteen green seedlings were found in a total population of 119; all had 21 chromosomes.

When the data are pooled from both experiments, there were 87 plants having a single B^8 plus three seedlings in which somatic nondisjunction was occurring. Nondisjunction at the second microspore division was not observed in $88B^8$ plants. However, nondisjunction did occur with a high frequency in $8^B B^8$ spores of $88^B B^8$ and $88^B B^8 B^8$ plants.

The most tenable conclusion from these experiments is that the control of B chromosome nondisjunction resides in the short distal euchromatic portion, containing only two chromomeres. It is interesting to note that this segment had no effect on recombination and thus these two phenomena are controlled independently.

Table 2. Root tip chromosome numbers from progeny of $88B^8$ males.

Male plant	Progeny chromosome number			Total
	20	21	*	
461-4	76	20	0	96
728-49	35	2	0	37
728-33	102	17	1	120
728-43	29	9	0	38
728-25	52	2	0	54
728-8	85	23	2	110
728-65	30	0	0	30
728-61	22	0	0	22
Total	431	73	3	507

*root tips were found to be mosaic for 20-21-22 chromosomes in two plants and 21-22 in the other.

C) A new observation of the effects of B chromosomes on recombination.

The recombination in the balanced heterozygotes of each of the TB-A translocations in section A can be considered to be equivalent to the crossing over occurring in Tp9Tp9 when a single intact B is present in the cell. The percentage increases from the AA class to the $AA^{B}{}_{B}{}^{A}$ group for each translocation were calculated and entered in Table 3. No balanced heterozygotes were successfully testcrossed in TB-8a, but absence of an effect on recombination by the distal chromomeres indicates that the B^8 has 100% of the activity of an intact B, and plants of $88B^8$ constitution were utilized in place of the balanced heterozygote. The data in Table 3 demonstrate that the lower the control value the greater the effect of the B chromosome. Regardless of the amount of crossing over in the controls, C-Wx recombination is usually increased to about 33-34%. Rhoades' results with OB vs. 1B classes are not inconsistent with these observations. Recombination in his OB plants was 17.7%, increasing to 37% with the addition of a B. This represents a 109% increase.

Table 3. Comparison of the increase in recombination in Tp9Tp9 caused by the B chromosome as represented by the balanced heterozygotes of TB-3a, TB-4a, and TB-6a and by the B^8 of TB-8a.

Constitution	% C-Wx Recomb.	% increase
88	27.3	18.7
$88B^8$	32.4	
44	22.4	51.5
$44^{B}{}_{B}{}^{4}$	33.9	
33	21.5	67.5
$33^{B}{}_{B}{}^{3}$	36.0	
66	16.8	86.5
$66^{B}{}_{B}{}^{6}$	31.3	

Kikudome found a comparable situation when he studied the effect of K10 on crossing over in a chromosome 9 bivalent heteromorphic for a knobless chromosome and a small, medium, or large knob. Crossing over increased from 26.9% to 31.5%, from 17.7% to 26.8%, and from 12.7% to 30.3%, respectively. These results represent increases of 17.1%, 51.5%, and 140%. It was suggested that there was an upper limit of about 30% recombination in the region investigated. In tests of Tp9Tp9 recombination there is a dosage effect of B chromosomes; therefore, the 33-34% commonly found with one B cannot be an upper limit.

Edward Ward

4. Detection of somatic redundancy for the Adh_1 gene of maize: a genetic strategy and preliminary data.

With few exceptions, the genetic information specifying the unique amino-acid sequence of an enzyme-subunit polypeptide is transmitted through meiosis as a single cistron. A diploid cell contains "one" paternal and "one" maternal allele for each gene, where the number "one" connotes one unit of genetically transmissible information (allele), as opposed to one unit of biosynthesis (here called "cistron"). Certain somatic cells might contain many redundant copies (cistrons) of one gene, copies which are transmitted through mitosis, without violating Mendelian laws. Even gametes may be redundant for any genetically single allele if one invokes the speculative "master-slave" relationship (Callan, 1960; 1967) among the redundant cistrons. Cytological and biochemical techniques presently available lack the resolution needed to detect small amounts of redundancy. This short note outlines a genetic strategy theoretically able to discover redundancies between zero and about twenty copies of a specific enzyme-specifying allele, and gives preliminary data for one of the alcohol dehydrogenase genes (Adh_1; ADH enzyme, EC 1.1.1.1.) in maize root primordial cells. This strategy may have general applications.

Experimental strategy:

There are two alleles for each gene in a diploid somatic cell. If each allele were represented by but one cistron, then the maximum number of different polypeptides specified by a particular gene is two

per diploid cell. If, on the other hand, a number of cistrons represent each allele in a single cell, then a somatic mutation affecting one of the redundant cistrons could yield a single cell with three different polypeptides specified by only two genetically defined alleles. The following strategy may provide: (1) a way to detect relatively small amounts of a mutant polypeptide; (2) a control to ascertain whether that cistron specifying the mutant polypeptide was really in the same cell with both non-mutant parental alleles; and (3) a simple method by which a single somatic root primordial cell can be cloned within the living plant.

Mutant cistrons which specify enzyme subunits with an altered net surface charge can be detected by electrophoretic procedures. The $\underline{Adh_1}$ gene of maize specifies product which is assembled into ADH enzyme dimers (Schwartz, 1966). A number of mutant and variant alleles exist for the $\underline{Adh_1}$ gene (Schwartz, 1966). For example, Fig. 1 represents electrophoretograms--gels specifically stained for ADH activity--characterizing the three genotypes segregating on an $\underline{Adh_1}^S / \underline{Adh_1}^F$ self-pollinated ear, where superscripts "S" and "F" denote alleles which specify subunits conferring a relatively "slower" or "faster" anodal electrophoretic migration rate to the ADH dimers containing these subunits (Schwartz, 1966). Most ADH dimers are stable in extracts and gels, and none has displayed the slightest tendency to dissociate and reassociate under standard _in vitro_ conditions. The presence of a hybrid enzyme, marked by an arrow in Fig. 1, implies that there are _at least two_ cistrons for the $\underline{Adh_1}$ gene per cell, since there are at least two qualitatively different subunits synthesized. This conclusion is trivial. However, in the following test involving somatic mutation and clonal analysis, the presence of an "unexpected" hybrid enzyme may identify a somatically redundant allele.

Given a single somatic cell heterozygous for a normal $\underline{Adh_1}$ allele (_+_) and an $\underline{Adh_1}$ deletion or mutant allele specifying inactive, non-dimerizing polypeptides (_o_), it is possible to treat this _+/o_ cell with a mutagen, wash out or discontinue treatment, allow clones to develop, and then electrophoretically analyze the clone. The reason for using an _o_ mutant allele is to permit the analysis of but one $\underline{Adh_1}$ allele of

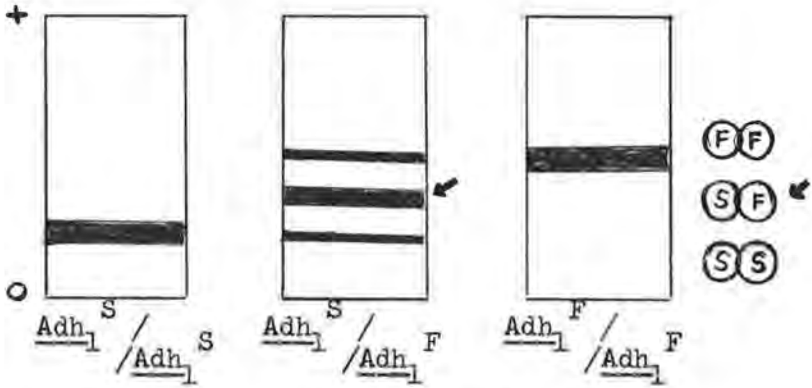
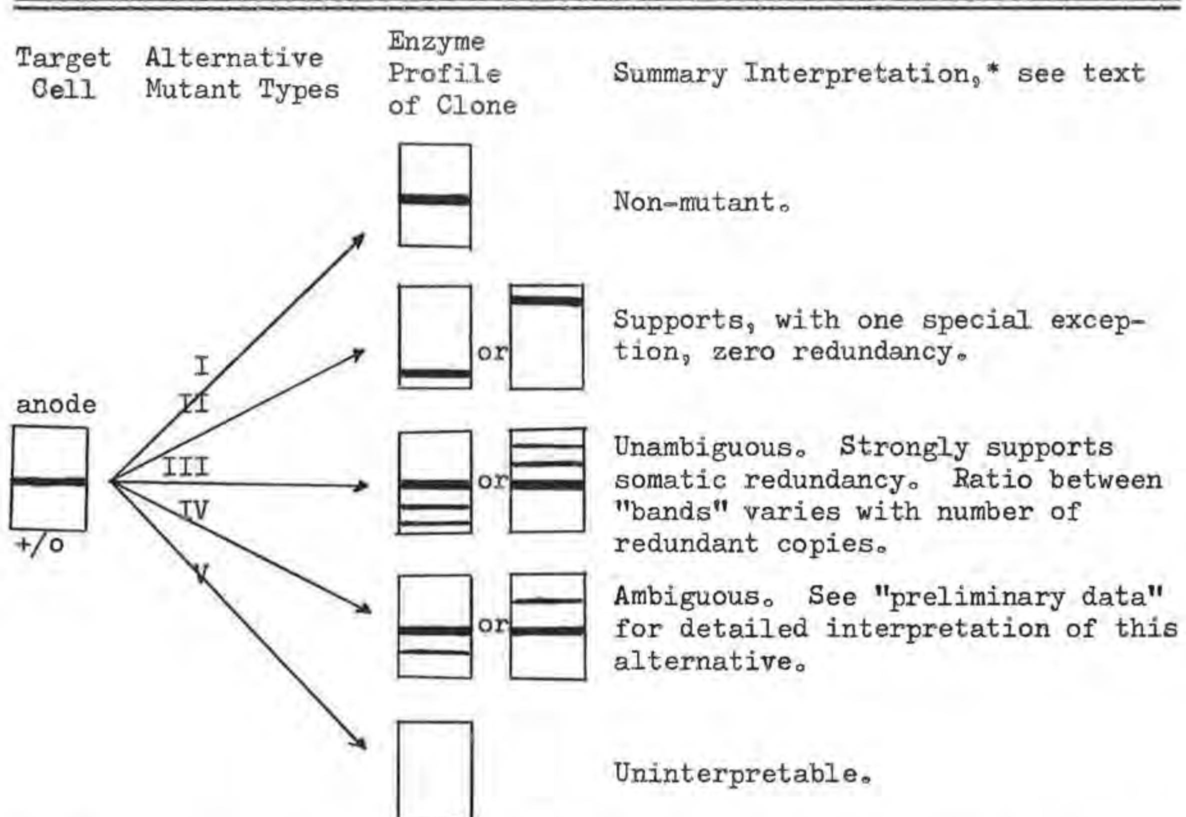


Fig. 1. Three example electrophoretograms representing the three genotypes segregating on an $\underline{Adh_1}^S$/ $\underline{Adh_1}^F$ self-pollinated ear. The arrow marks the "hybrid enzyme."



*All interpretations are based on the assumption that the "o" allele does not participate in the specification of any enzyme profile.

Fig. 2. Alternative types of $\pm$ allele mutations in a target cell as expressed in the enzyme profile of the mutant clone, with summary interpretations. See text for detailed interpretations and their bases.

the somatic cell. It is assumed that the rate of back-mutation or somatic crossover mediated o reactivation yielding a dimerizing subunit (o $\rightarrow$ + or m) is negligible compared to the rate of forward mutation (+ $\rightarrow$ m) of the normal + allele.

Fig. 2 diagrams some of the alternative types of + allele mutations in a somatic target cell, as expressed in the enzyme profiles of the mutant clones. Interpretations assume that the o allele does not participate in the specification of these electrophoretograms. Alternatives II and III are most valuable, and ought to be mutually exclusive. Alternative II argues strongly against somatic redundancy since a single mutation (+ $\rightarrow$ m) changed all of the active ADH enzyme of the clone to a form with a new net surface charge, (but this can also be explained if a master Adh_1^{mutant} allele corrects all slaves at each mitosis). In alternative III, one of a group of + cistrons must have mutated to a new cistron(m) specifying an active, dimerizing subunit with an altered surface charge. This alternative strongly supports somatic redundancy. The more + cistron copies extant in the mutated cell, the more difficult it becomes to detect a mutant cistron (m), since the mutant ADH's would be a diminishing proportion of the total ADH specified. Whether the "clone" is actually a clone, or a mixture of mutant (m/o) and non-mutant (+/o) cells certainly affects the feasibility of the test, but does not lead to erroneous interpretations. Alternative II requires a clone to be expressed; alternative III supports redundancy in a clone or in a cell mixture.

In order to realize the alternatives catalogued in Fig. 2, one demands a system where somatic "target cells" can be mutated and subsequently cloned until enough cells are present for electrophoretic assay. Some cells in culture are amenable to such analysis. The root system in higher plants may present a less obvious method for clonal analyses. Fig. 3 diagrams a possibility: some lateral roots, induced from the primary root by meristem excision, are clones, each of which develops from one and only one primordial cell in the embryo. If this hypothetical cell lineage were true for a reasonable proportion of laterals, mutually exclusive alternatives II and III would be detectable. In this case,

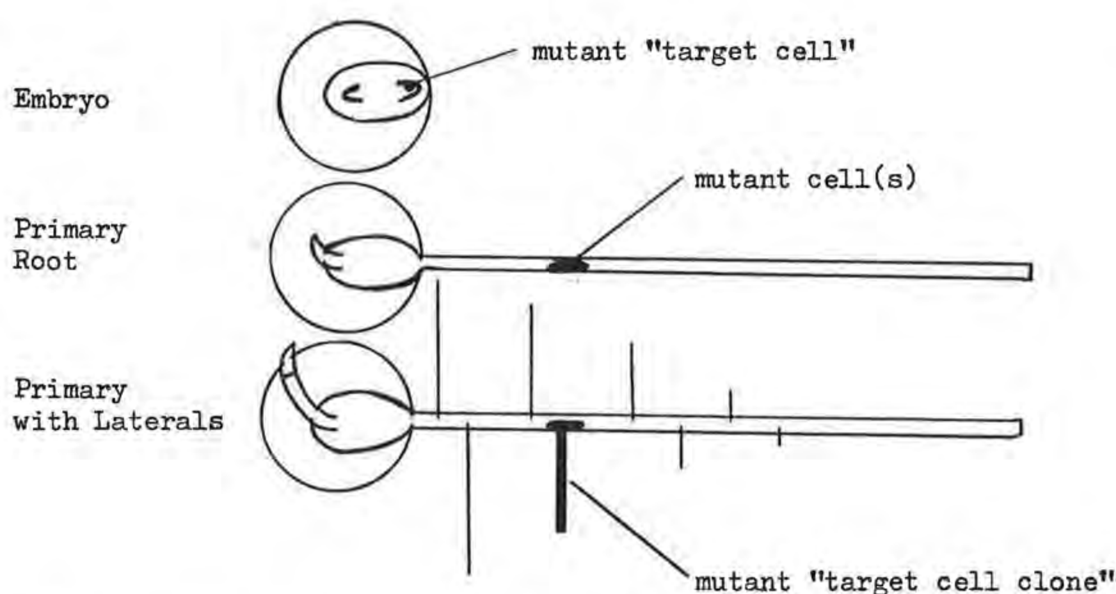


Fig. 3. Possible lineage of the cells of one lateral root from one "target cell" in the embryo of the seed.

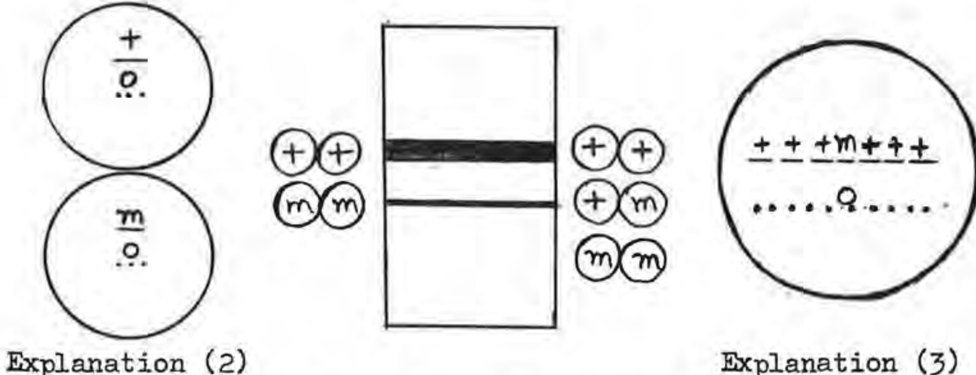


Fig. 4. A representation of the electrophoretograms characterizing the two mutant-type lateral roots, with explanations (2) and (3) diagramed. Explanation (2): mixture of mutant and non-mutant cells. Explanation (3): somatic redundancy, here drawn as unineme for convenience only. See text for details.

seeds are treated with a mutagen and lateral roots are electrophoretically assayed. As mentioned previously, if lateral roots do not develop as suggested the experiment will fail, but will not lead to erroneous conclusions.

It is hoped that this experimental strategy might be generally applied in somatic mutation studies, and might serve as a test for gene redundancy.

Preliminary data:

Seeds of the +/o genotype were treated with ethyl-methanesulfonate, washed, dried and subsequently germinated. 543 lateral roots from 89 seedlings were electrophoretically analyzed following a brief anaerobic treatment to induce ADH activity. A known marker enzyme was present in every gel to exclude electrophoretic artifacts. Two independent, indistinguishable aberrant lateral roots were found, both corresponding to the ambiguous alternative IV of Fig. 2. The other 15 laterals from these two seedlings were normal. Fig. 4 diagrams what was seen in the aberrant electrophoretograms. Each of the following three explanations can account for these data. (1) The assumption on which this strategy is based is false: the new enzyme "band" is totally or in part the product of a reverted o allele. This unlikely explanation is being tested by analyzing somatic mutations of electrophoretically distinguishable + alleles in heterozygotes with the same o allele. (2) The aberrant lateral roots each contain two types of cells: +/o, yielding the normal enzyme, and m/o, specifying the new homodimer "band." In this case, both of the aberrant laterals must have had a very similar mixture of cells. (3) The lateral root primordial cell contains at least one o cistron, at least one + cistron, and at least one m cistron, the latter specifying either enzymatically active or inactive product which does dimerize. In this case, the new enzyme "band" is a hybrid enzyme, and somatic redundancy is supported; the m·m homodimer is not seen in the electrophoretograms either because it is inactive, or because many copies of the + cistron existed in the target primordial cell, or both. Fig. 4 gives a pictorial representation of explanations (2) and (3).

More mutants are needed to distinguish between these three explanations. Schwartz (published and unpublished data) has selected many ethyl-methane-sulfonate-induced $\underline{Adh}_1$ alleles which are genetically transmissible and which specify subunits with altered net surface charges. These mutants specify certain charge transitions (e.g. the net loss of two negative charge units per subunit), but not others. The type of mutant required for explanation (2) to be correct has never been found, while that necessitated by explanation (3) is frequent.

Michael Freeling

In response to the interest expressed by a number of corn geneticsts in kernel photography, the following article was contributed by the director of the Photographic Laboratory at Indiana University.

5. Kernel photography.

Close-up color photographs of corn kernels with clear reproduction of patterns of color variegation may be obtained in the following way. A camera of the single lens reflex type is used with Ektochrome high speed film. The lens used for close-up work is a 48 mm Micro-Tessar lens. A five inch extension tube may be used to increase magnification slightly. Lighting from above and below gives a white background; without the light from below, the background is black. Polarizing filters are of utmost importance for avoiding glare from the surface of the kernel. Filters are placed in front of the lens, as well as on each of the light sources. The highlight reflections on the kernel may be used for focusing; they are then removed by turning the polarizing filters before exposing the film. Dust particles on the kernels should be removed with a staticmaster brush.

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1. Effect of pollination condition on the expression of the gametophyte locus of chromosome 4.

For the past 50 years the gametophyte locus of the fourth chromosome has been the subject of a large number of reports, in particular those of American workers. This communication presents the results of studies carried out throughout 1969-1971 in the zone of northern subtropics along the coast of the Black Sea (Sochi, USSR). The sowing dates were from the end of March to the middle of July. Hybridisation was initiated from the second decade of June and was over by the third decade of September. One and the same F_1 hybrid between popcorn and sweet corn was sown in different years at different times. This made it possible to reveal the response of a definite genotype for the gametophyte locus to conditions prevailing during pollination. The analysis was carried out as described by Jimenez & Nelson (J. Heredity 56:259, 1965). F_1 hybrids of the $Ga^sSu/ga\ su$ genotype were used as testers. As a rule, three phenotypically different classes were distinguished in the course of the experiments. The classes correspond to three different genotypes of F_1 hybrids as follows:

Genotype of F_1 hybrids	Percentage of su in three types of crosses*			Phenotypical class
	⊗	♀	♂	
Ga Su/ga su	14	14	14	I
Ga^mSu/ga su	25	25	14	II
ga Su/ga su	25	25	25	III

*⊗ = self-pollination F_1 hybrids, ♀ = F_1 hybrid pollinated by tester pollen, ♂ = tester pollinated by F_1 hybrid pollen.

The method of analysis used does not differentiate Ga^s and Ga alleles and they produce a constant pattern of segregation corresponding to the first phenotypical class.

Table 1. Influence of pollination conditions on the results of the analysis of the F_1 hybrids

Hybrid	Pollination dates	Number of plants	♀		♂		Phenotypical class
			Total seed number	% su	Total seed number	% su	
Golden Bantam X Rice corn	September 1969	33	9687	26.64	7025	24.70	III
	June 1970	3	733	25.92	589	22.68	III
		6	1473	24.58	954	14.76	II
		10	2511	12.44	2508	13.51	I
	June 1971	15	4619	24.65	3088	23.30	III
	July 1971	8	2605	25.40	1347	10.25	II
		5	1469	23.78	1089	22.34	III
Golden Bantam x Globe White Shelled	September 1969	9	2019	25.92	2469	13.14	II
	June 1970	6	1499	14.14	1502	10.33	I
		3	1102	22.95	780	11.28	II
	June 1971	14	3177	25.13	3494	13.36	II
	July 1971	7	1861	23.15	1121	12.45	II
		5	1193	16.18	874	11.71	I
	September 1971	14	3182	26.15	3089	15.22	II
		2	371	23.62	408	21.87	III

Ga^m refers to the allele which combines the characters of the allele ga (when the F_1 hybrid containing this allele is used as the maternal plant) and the characters of the allele Ga (when the same plant is used as the source of pollen) (Genetika 6:14, 1970). Ga^m is widely distributed in popcorn maize populations (Genetika 8:2, 1972). The initial popcorn maize may be either homozygous or heterozygous for the gametophyte locus; if it is heterozygous, the F_1 hybrids are distributed into two phenotypical classes and if it is homozygous, the F_1 hybrids all belong to a single phenotypical class.

The results obtained in two F_1 hybrids after 4 and 5 repeated sowings of seed from one corn-cob are given in Table 1. Similar or very similar results have been additionally obtained in 23 F_1 hybrids. It should be noted that a part of the repeatedly sown hybrids were always assigned to the same phenotypical class.

Thus, the capacity of pollen tubes having Ga and Ga^m alleles to compete for the allele ga varies considerably depending on the pollination conditions. The environmental factors influencing the manifestation of the gametophyte locus were not analyzed.

S. I. Maletzky
B. N. Siritza

2. Analysis of the gametophyte allele Ga^m in F_2 hybrids.

The gametophyte allele Ga^m, as compared with the allele Ga, has the interesting feature of being active only in the male gametophyte. However, all the alleles of the gametophyte locus are highly variable, which makes difficult their identification and even makes their existence very questionable. An allelic test between the alleles Ga and Ga^m has been carried out earlier (Genetica 6:14, 1970). This is a report of the analysis of F_2 plants from the hybrid Golden Bantam x Globe White Shelled (see communication 1) and the analysis of the F_2 plants from hybrids of Ga Su/ga su genotype. This hybrid was used as tester in the preceding work. In addition to the analysis of genotypes obtained as a result of self-pollination of these F_2 hybrids, a similar analysis of hybrids produced by reciprocal crosses between two of the F_1 hybrids was carried out. The genotypes were identified by the method described in the preceding paper.

On theoretical grounds, nine different genotypes heterozygous for $\underline{su_1}$ are possible in the offspring of the four hybrids. As shown in the diagram, the genotypical classes correspond to 6 phenotypical classes.

	⊗	♀	♂	class
Ga Su/ga su	14	14	14	I
Ga^mSu/ga su	25	25	14	II
Ga^mSu/Ga^msu	25	25	25	III
ga Su/ga su	25	25	25	III
Ga Su/Ga su	25	14	25	IV
Ga Su/Ga^msu	25	14	25	IV
Ga^mSu/Ga su	25	14	25	IV
ga Su/Ga su	36	14	36	V
ga Su/Ga^msu	25	25	36	VI

Table 1 presents the relative occurrence percentage of phenotypical classes predicted in the offspring of four hybrids.

Table 2 gives the actual figures obtained in the experiment. The sample is not large, but the actual figures are in good agreement with those expected on theoretical grounds, in spite of the influence of environmental conditions on the results (in particular, the expression of the phenotypical class 1 in the $\underline{Ga}$ $\underline{Su/ga}$ $\underline{su}$ x $\underline{Ga^m}$$\underline{Su/ga}$ $\underline{su}$ hybrid). In this experiment the inheritance of the allele $\underline{Ga^m}$ is just as clear-cut as that of the allele $\underline{Ga}$.

Table 1. Theoretical phenotypical ratio expected in the F_2 of four hybrids (%)

Genotype of F_1	Phenotypical class					
	1	2	3	4	5	6
1. Ga Su/ga su ⊗	52	-	-	40	8	-
2. Ga^mSu/ga su ⊗	-	52	40	-	-	8
3. Ga Su/ga su x Ga^mSu/ga su	-	52	-	40	-	8
4. Ga^mSu/ga su x Ga Su/ga su	26	26	20	20	4	4

Table 2. Phenotypical ratios obtained in the F_2 of four hybrids

Genotypes of F_1	Number of analyzed plants	Distribution according to classes					
		1	2	3	4	5	6
1. Ga Su/ga su	26	19	-	-	7	-	-
2. Ga^mSu/ga su	50	-	21	25	-	-	4
3. Ga Su/ga su x Ga^mSu/ga su	28	3	15	-	10	-	-
4. Ga^mSu/ga su x Ga Su/ga su	36	10	9	7	4	3	4

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3. Identification of multiple molecular catalase forms in different maize tissues.

Scandalios (Ann. N.Y. Acad. Sci. 151:274, 1968) has described the locus Ct in maize endosperm. The locus has 5 alleles corresponding to 5 electrophoretic catalase variants. The line homozygous for 1 of the 5 alleles shows one zone of enzyme activity. An isozyme pattern in the hybrid consisting of two parental and three hybrid variants of catalase has been established. In studies of a collection of self-fertilized maize lines we have detected 6 electrophoretic variants of catalase (Bull. Isoz. 4:40, 1971).

In 1971 lines were sorted out containing two electrophoretic variants of catalase in their endosperm. Occasionally the two variants are represented by two zones of similar enzyme activity, but usually one catalase zone stains more intensely in comparison with the other weaker staining zone. This additional zone is displayed best at fixation during the early stages of endosperm development, on day 13 after pollination. The main zone of catalase activity appears by day 16 and becomes more intense in the process of endosperm maturation, while the first fraction either remains weakly stained or disappears altogether.

We have also found lines in which seeds of one corn-cob contain one or the other electrophoretic variant of the enzyme. No seeds had

a hybrid enzyme pattern. That each seed possesses its own enzyme variant suggests that different loci, controlling catalase synthesis, function in each seed.

The comparison of endosperm catalase with that of the leaves and seedlings within a single line has shown that the enzyme is tissue specific. The catalase of these tissues differs in the electrophoretic mobility of the enzyme and in the number of zones of enzyme activity.

From the studies on the catalase of maize endosperm, leaves and seedlings it may be inferred that an oligogenic system functions to control the synthesis of multiple molecular forms of the enzyme. The presence of the catalase variant is determined by the type of tissue and its stage of development.

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1. Attempted maize x sorghum hybridization.*

Materials used in our 1971 maize x sorghum crossing nursery are listed in Tables 1 and 2. Three dates of planting (delayed approximately 10 days) were used. To reduce contamination from stray pollen, maize stocks used as females were planted in isolation from their male counterparts and were detasseled. Also, male-sterile sorghums were isolated from male-fertile sorghums. A total of 1,293 reciprocal, controlled pollinations (727 using maize ♀ and 566 using male-sterile sorghum ♀) were made by conventional methods and by a "vial method." The latter technique involved attaching plastic vials (filled with water) to the maize or male-sterile sorghum plants at the bases of the ears or heads. Tassels or male-fertile sorghum heads were inserted into the vials and all components were placed under pollinating bags. Bags were tapped periodically to release pollen onto the stigmatic surfaces. Observations indicated that the "vial method" supplied viable pollen for 3-7 days.

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Table 1. Maize cultivars grown in 1971 maize x sorghum nursery.

Cultivar	Ploidy
A619[a]	2N
B14A[a]	2N
MS214[a]	2N
(A619xA632)[a]	2N
(B37xB70)[a]	2N
(Mo17xN28)[a]	2N
Argentine Popcorn[b]	2N
Japanese Hulless Popcorn	2N
Maiz Chapalote[b]	2N
Zapalote Chico[b]	2N
Syn B 4N (Late)[c]	4N
Syn B 4N (Early)[c]	4N
Syn B 4N (Isol. Bulk)[c]	4N
4N wx[d]	4N
4N su[d]	4N
4N gl_1[d]	4N
Gourdseed[d]	2N
Papago Flour Corn[d]	2N
Tama Flint[d]	2N
Northern Flint[b]	2N

[a]From W. A. Russell, Iowa State University.

[b]From Wm. L. Brown, Pioneer Hi-Bred Corn Company.

[c]From J. W. Dudley, University of Illinois.

[d]From Maize Genetics Cooperative, University of Illinois.

Table 2. Sorghum cultivars grown in 1971 maize x sorghum nursery.

Cultivar	Ploidy
Male-sterile	
Martin A[a]	2N
Kafir 60A[a]	2N
Wheatland A[a]	2N
979 Sorghum x Sudangrass[b]	2N
990 Sorghum x Sudangrass[b]	2N
PS2A Sudangrass[b]	2N
Male-fertile	
Plainsman[a]	2N
Tx7078[a]	2N
Redbine 60[a]	2N
Caprock[a]	2N
Kafir 60B[a]	2N
Sooner Milo[a]	2N
Durra[b]	2N
Kaoliang[a]	2N
Feterita[a]	2N
Hegari[a]	2N
Shallu[b]	2N
Sorghum virgatum[b]	2N
PS2B Sudangrass[b]	2N
PS1R Sudangrass[b]	2N
4N Bulk II[c]	4N
Martin x 4N Bulk II[c]	4N
5AD x 198/12/1[d]	4N
5AD x 270/4/4[d]	4N
3D x 2[d]	4N
Tet. Pop. 72[d]	4N

[a]From R. E. Atkins, Iowa State University.

[b]From Wm. L. Brown, Pioneer Hi-Bred Corn Company.

[c]From Wm. Ross, University of Nebraska.

[d]From L. V. Peters, Serere Research Station, Uganda, East Africa.

The method was more valuable for pollinating sorghum heads, which flower over a period of 7-10 days, than it was for pollinating maize ears.

Also, we cut, to ½-inch length, the silks of approximately one-half the maize ears pollinated. To reduce contamination, a new isolation bag was used for each day's cutting and the knife blade was sterilized with 95% ethanol before each ear was cut.

Ears were removed from maize plants 15 days post-pollination, examined in a portable, sterile chamber in the field, and any with seeds were taken into the laboratory where seeds were examined and embryos were excised and transferred to the culture medium described in Table 3. Approximately 30 maize ears and all pollinated male-sterile sorghum heads were sampled at maturity.

Table 3. Synthetic nutrient medium used to culture seeds and embryos.

Component	Concentration (mg/ml)
Sucrose	20,000.0
Agar	7,500.0
$Ca(NO_3)_2 \cdot 4H_2O$	237.0
KNO_3	85.0
KCl	65.0
$NaH_2PO_4 \cdot H_2O$	16.5
$MgSO_4 \cdot 7H_2O$	36.0
Fe Citrate (Ferric)	30.0
$MnSO_4 \cdot 4H_2O$	0.4
Adenine	0.2
Nicotinic Acid	0.1
Pantothenic Acid	0.05
Pyridoxine Hydrochloride (Vitamin B_6)	0.2
Ascorbic Acid (Vitamin C)	17.8
Thiamine Hydrochloride	0.1
Flavin Mononucleotide	0.2
Myo - Inositol	10.0
Succinic Acid	25.0
Glycine	3.0

Conclusions drawn from analyses of numbers of maize ears setting seed should be viewed with caution since we had no estimate of normal amounts of foreign-pollen contamination for these materials. A few trends, however, should be mentioned. Highest frequency of pollinated ears setting seed was from tetraploid materials ($\bar{x}$ = 36%), whereas lowest frequency ($\bar{x}$ = 24%) was from "unadapted" maize cultivars (Argentine Pop., Japanese Hulless, Zapalote Chico, Gourdseed, Papago Flour Corn, Tama and Northern Flints). Twenty-nine percent of the pollinated ears from adapted materials produced seed. Adapted single-crosses set seed on 37% of their pollinated ears, whereas adapted inbreds set seed on 19%.

The apparent influence of vigor on seed set may be a consequence of more vigorous materials (tetraploids and single-crosses) extruding silks from ear shoot bags or pollinating bags and, therefore, being more prone to contamination. Alternatively, vigorous materials may be capable of overcoming physical and (or) physiological barriers to pollination and fertilization. There was no influence of male-fertile sorghum genotype (used as pollen parents) on frequency of maize ears setting seed.

All seeds recovered from male-sterile sorghum plants came from cultivated sorghums. Maize pollen parent genotype was not correlated with frequency of pollinated heads producing seed.

When compared with the 11,000 seeds obtained in 1970, the 780 seeds recovered in 1971, represent a significant reduction in contamination by foreign pollen. Precautionary measures taken at planting (isolated plantings) and during crossing (detasseling, vial pollinations, and sterile cutting procedures) were effective.

Data concerning presence or absence of embryos in seeds from maize and sorghum females are presented in Table 4. Only 34 seeds were recovered from sorghum females. These seeds were dissected and the embryos were cultured. Five sorghum female seeds (from three pollinations involving Wheatland A x Maize Chapalote) were small and wrinkled; embryos from these seeds were small and failed to develop in culture. From the 29 "normal" seeds, 17 embryos germinated, developed normally, and are growing in the greenhouse. Four embryos from "normal" seeds germinated,

developed abnormally, and are being maintained in culture in hopes of stimulating further development.

Table 4. Data on seeds and embryos recovered from maize and sorghum females.

Maize ears with seeds	208
Seeds recovered from maize ears	746
Seeds dissected 15 days after pollination	627
Seeds with embryos	354
Seeds with embryos $\leq$ 1.0 mm	114
Seeds with neither embryo nor endosperm	273
Seeds recovered from maize ears-mature	119
Mature maize seeds cultured	42
Male-sterile sorghum heads with seeds	20
Seeds recovered from male-sterile sorghum heads-mature	34
Sorghum embryos cultured from mature seeds	33
Mature sorghum seeds cultured	1

Of the maize seeds dissected 15 days post-pollination, 43% were devoid of embryos (Table 4). Many embryoless seeds displayed various degrees of endosperm development. If these seeds were hybrid seeds, the 3N ploidy level (2N maize and 1N sorghum) of the endosperm may have buffered genetic imbalances and permitted this tissue to develop, whereas the 2N (1N maize and 1N sorghum) nature of the embryo could not overcome genetic imbalance and resulted in embryo abortion at an early stage of development. Alternatively, pollination may have stimulated seed and endosperm-like development without fertilization. Distinguishing between these alternatives would be difficult, requiring either that chromosome counts be made in the developing endosperm tissue or that quantitative measurements of DNA content of endosperm nuclei be made.

Seeds containing embryos were in various stages of development. Fifty-two percent of the embryos we dissected were $\leq$ 1.0 mm in length and 15% were only slightly developed (usually < 0.1 mm long).

Success in culturing embryos was dependent upon their size. Generally, embryos < 0.2 mm long would not develop in vitro (several nutrient media and environmental conditions were used). Although these very small embryos failed to germinate, nearly all remained alive for

several months. Most larger embryos (0.2 - 1.0 mm in length) grew but many of them developed abnormally, either forming an undifferentiated callus or only very small roots or shoots. The majority of embryos $>$1.0 mm developed normally and were eventually transferred to soil. These results suggest that the younger the embryos at the time of excision, the more heterotrophic they were, and therefore they were more dependent upon a complex nutrient medium. Either the media we used lacked constituents required for normal development or they contained incorrect concentrations of essential growth factors.

Our data showed no association of embryo size with pollination method, eliminating the possibility that many of the smaller embryos resulted from use of the "vial method" which could have caused pollination to occur several days after crosses were made. Therefore, small embryos may have developed slowly in vivo because of either genetic weaknesses or failure of the endosperm to provide them with optimum nutrients; i.e. they may have been hybrids. Therefore, further work to develop nutrient media which will stimulate and sustain development of extremely small embryos is needed. Only when such embryos can be grown to seedling stages which will permit chromosome counts and observations of seedling morphology will we be capable of presenting conclusive evidence on the feasibility of maize x sorghum hybrids.

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2. Pollen growth in in vitro maize x sorghum pollinations.*

Many seeds recovered from maize x sorghum pollinations were devoid of embryos but contained endosperm tissue (see report in this Newsletter and MGCNL 45:78-80). These seeds may be the result of either parthenogenic seed and endosperm development (possibly stimulated by pollination), embryo abortion after fertilization, or restricted embryo development. The first of these possibilities suggests that pollen germination and gamete union may be the limiting step in maize x sorghum hybridization.

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To determine whether maize or sorghum pollen could germinate on stigmas of the other genus (i.e. sorghum ♀ maize ♂ and maize ♀ x sorghum ♂), we conducted *in vitro* pollen growth studies. The first experiment was conducted during summer, 1971. We used silks from MS214 and Argentine Popcorn and maize pollen from MS214, Argentine Pop., and Japanese Hulless Popcorn. We collected sorghum pollen from Tx7078, Redbine 60, Kafir 60B, Sooner Milo, Durra, Kaoliang, Hegari, (Martin x 4N Bulk II), and 4N Bulk II. Ears, tassels, and heads were removed from field-grown plants during early morning and transported to the laboratory in vials of water. Microscope slides were prepared by affixing fresh pieces of silk to the slides, dusting the silks with appropriate pollen, covering the preparations with cover glasses, and placing them in moist chambers for 3-4 hours. We prepared two replications of 10 slides per maize ♀ x sorghum ♂ pollination, and on each day a new set (two reps of 10) of control slides (maize ♀ x maize ♂) was prepared. Slides were examined under 400X magnification, and pollen grains counted as definitely germinated were those with pollen tubes which had grown into the silk and which displayed protoplasmic streaming. Grains considered questionable showed stunted pollen tube growth and no protoplasmic streaming. Data in Table 1 are percentages of microscope slides containing at least one germinated or questionable pollen grain.

With two exceptions, sorghum pollen displayed only questionable germination when placed on maize silks. No maize ♀ x maize ♂ pollination showed questionable germination. MS214 x Kaoliang showed definite pollen germination. Positive results with Argentine Pop. x Sooner Milo may have been an artifact since the frequency of slides showing germination was low (both slides were from the same rep.) and MS214 x Sooner Milo pollinations showed only questionable responses. Germination was not influenced by amount of pollen on a silk.

During winter, 1971 we conducted a second pollen growth study using greenhouse-grown plants. Maize cultivars used were MS214, SynB 4N, and Japanese Hulless Popcorn. Sorghums studied were Kafir 60B, Kaoliang, Feterita, and 4N Bulk II (pollen sources) and Kafir 60A (male-sterile stigma source).

Table 1. Pollen grain germination in maize ♀ x maize ♂ and maize ♀ x sorghum ♂ *in vitro* pollinations (Field).

Pollination	% Microscope slides		Average No. grains/silk
	Definite germination	Questionable germination	
MS214 ⊗ [a]	52.5	0.0	31.6
Argentine Pop. ⊗	90.0	0.0	85.1
MS214 x Japanese Hulless	85.0	0.0	155.7
MS214 x Redbine 60	0.0	15.0	18.8
MS214 x (Martin x 4N Bulk II)	0.0	30.0	24.0
MS214 x Kafir 60B	0.0	5.0	14.0
MS214 x Sooner Milo	0.0	15.0	40.7
MS214 x Durra	0.0	15.0	52.2
MS214 x 4N Bulk II	0.0	30.0	37.0
MS214 x Kaoliang	65.0	0.0	96.0
MS214 x Tx7078	0.0	20.0	114.3
Argentine Pop. x Sooner Milo	10.0	0.0	89.4
Argentine Pop. x Hegari	0.0	55.0	108.8

[a]Four reps - 10 slides per rep.

Slides were prepared by affixing two fresh maize silks and two fresh male-sterile stigmas to a slide and dusting each with appropriate pollen (e.g. MS214 silks and Kafir 60A stigmas were dusted with MS214 pollen or pollen from one of the male-fertile sorghums), covering with cover glasses, and placing in a moist chamber (room temperature) for 3-4 hours. This procedure permitted examination of maize ♀ x maize ♂, maize ♀ x sorghum ♂, sorghum ♀ x maize ♂, and sorghum ♀ x sorghum ♂ pollinations each day. The number of replications varied.

Another technique, used on a limited basis, involved making *in vivo* pollinations and preparing microscope slides (silks and stigmas) four hours after pollination. Results of this technique are listed as *in vivo* in Table 2.

Table 2. Pollen grain germination in various combinations of maize and sorghum pollinations.
(Greenhouse)

Pollination	Total obs.	% Microscope slides		% Pollen grains		Total pollen grains
		Definite germination	Questionable germination	Definite germination	Questionable germination	
				IN VITRO		
MS214 ⊗	26	100.0	100.0	4.5	10.1	3860
Kafir 60A x MS214	24	12.5	83.3	0.4	3.3	1632
Syn B4N ⊗	4	75.0	100.0	0.2	7.9	470
Kafir 60A x Syn B4N	4	0.0	100.0	0.0	3.8	105
Jap. Hull. ⊗	8	62.5	100.0	0.4	9.6	1617
Kafir 60A x Jap. Hull.	8	0.0	62.5	0.0	1.9	372
MS214 x Kaoliang	8	0.0	100.0	0.0	8.8	1016
Kafir 60A x Kaoliang	8	0.0	100.0	0.0	2.7	843
MS214 x Feterita	8	0.0	100.0	0.0	6.3	1483
Kafir 60A x Feterita	8	0.0	100.0	0.0	2.0	1223
MS214 x Kafir 60B	18	0.0	100.0	0.0	7.1	7279
Kafir 60A x Kafir 60B	16	5.0	94.4	0.1	2.4	2951
MS214 x 4N Bulk II	16	0.0	87.5	0.0	4.6	2660
Kafir 60A x 4N Bulk II	14	0.0	85.7	0.0	2.9	1630
				IN VIVO		
MS214 ⊗	6	0.0	50.0	0.0	2.2	182
Kafir 60A x MS214	6	0.0	33.3	0.0	0.8	241
Syn B4N ⊗	12	0.0	83.3	0.0	6.2	732
Kafir 60A x Syn B4N	12	0.0	16.7	0.0	1.1	179
Kafir 60A x Jap. Hull.	10	0.0	10.0	0.0	1.1	95

In the first study we recorded only the number of slides having at least one pollen grain showing definite or questionable germination. In the second experiment, we not only recorded the number of slides, but also the number of pollen grains showing each type of germination.

Results from this experiment were similar to those obtained in the first experiment; i.e., maize ♀ x maize ♂ pollinations displayed definite germination and pollen tube growth, and maize ♀ x sorghum ♂ pollinations showed only questionable germination (Table 2). Unlike the previous results, maize ♀ x maize ♂ also showed questionable germination; and Kaoliang pollen did not germinate on MS214 silks. MS214 pollen germinated on Kafir 60A stigmas but pollen from SynB 4N and Japanese Hulless did not. Only Kafir 60B pollen germinated on Kafir 60A stigmas (Table 2). Percentages of pollen grains showing either type of germination were low for all pollinations (Table 2). This may be a consequence of _in vitro_ conditions.

Several times during the second experiment slides were kept in the moist chamber for 24 hours before being examined for pollen germination. Neither germination percentages nor type of germination (i.e. definite or questionable) had changed after 24 hours. If pollen germination in maize x sorghum pollinations requires more than 24 hours, it is doubtful that the pollen would be viable enough to effect fertilization. Longer time intervals were not studied.

Pollen (both maize and sorghum) placed on maize silks gave better germination responses than when placed on male-sterile sorghum stigmas (Table 2). Apparently, maize silks provided a better _in vitro_ environment for pollen germination than did sorghum stigmas. However, maize silks may lack germination "stimulators" normally present in sorghum stigmas and, therefore, sorghum pollen could not definitely germinate. The absence of germination in sorghum ♀ x sorghum ♂ pollinations may have been a consequence of the _in vitro_ conditions we used. However, since pollen from Kafir 60B, which is the isogenic fertile counterpart of Kafir 60A, germinated on Kafir 60A stigmas, the phenomenon may be a manifestation of incompatibility between less adapted sorghums (Kaoliang, Feterita, and 4N Bulk II) and adapted Kafir 60A.

Generally _in vivo_ pollinations resulted in poor germination. These results may be misleading, however, since the _in vivo_ technique was used at the close of the greenhouse study and pollen viability during this period was low. Alternatively, poor germination may be a result of techniques not being perfected. The method deserves further study.

In vitro studies of pollen germination on liquid nutrient media also were conducted. All possible combinations of four concentrations (0.00, 0.03, 0.06, and 0.10%) of calcium nitrate, two concentrations (0.00 and 0.02%) of boric acid and four concentrations (10.0, 20.0, 30.0, and 40.0%) of sucrose were tested. Sorghum pollen did not germinate on media which were optimal for pollen from two maize lines, but it germinated on a medium containing a lower sucrose concentration and no boric acid (Table 3). These studies were repeated using 0.10% yeast extract as a medium supplement but no significant effects were observed.

Table 3. Optimal conditions for _in vitro_ germination and growth of maize and sorghum pollen.

	Sucrose	Calcium	Boron
Maize			
MS214[a]	20%	0.06%	0.02%
Syn 4N[b]	30%	0.10%	0.02%
Sorghum			
Kafir 60B[c]	10%	0.06%	0.00%

[a] 6 replications
[b] 5 replications
[c] 4 replications

Although these data are preliminary, they parallel results from the microscope pollen growth studies (i.e., abnormal sorghum pollen germination on maize silks, and vice versa). Perhaps stigmatic surfaces of maize and sorghum are chemically different and pollen from the other genus cannot germinate and grow when placed on them.

Although we did not correlate in vitro with in vivo pollen growth, our results suggest that maize or sorghum pollen, when placed upon stigmas of the other genus, was incapable of sufficient pollen tube growth to effect fertilization. Therefore, embryoless seeds from maize x sorghum pollinations may have resulted from parthenogenesis. Further research on this possibility and on physiology of pollen germination and growth is being conducted.

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Wayne H. Loescher

3. The distribution of meiotic stages in the developing tassel.

Although the progression of microspore mother cell development in the developing tassel is well known to the maize cytogeneticist, there have been few attempts to quantify this process with respect to the interrelationships of each region.

If one divides the developing tassel into four regions (I, II, III and IV) as shown in this diagramatic mature tassel and then standardizes each of the stages numerically one can quantify the relation between the areas and stages of maturation. The stages and their numerical assignment beginning with Leptotene and ending with the immediate post-quartet microspore are:

Leptotene	1	Anaphase I	5
Zygotene	2	Meiosis II	6
Pachytene	3	Quartet	7
Metaphase I	4	Microspore	8

Six inbred lines and seven hybrids were examined and four different tassels were used for each line and each of the hybrids except 101,03/70, 101/40, and 01/70. The numerical values are shown in Table 1. What is obvious to the practicing cytogeneticist is confirmed by these observations--i.e., the four areas of the maturing tassel, from the most advanced (mature) to the least advanced meiotic stages, occur in the following order: II-I-III-IV. The numerical values assignable to each of the areas are significantly different.

Table 1. The numerical average of meiotic stages in four regions of an immature tassel of seven inbreds and their hybrids.

Line	Area			
	I	II	III	IV
01	7.25	7.50	6.00	5.50
03	5.12	5.25	4.75	4.50
30	3.25	4.00	2.62	1.50
60	5.25	5.25	4.25	3.00
70	4.25	5.50	3.50	2.75
80	2.12	3.75	1.75	1.50
101	7.00	8.00	2.00	2.00
Average	4.89	5.61	3.55	2.96
60/80	3.25	3.75	2.37	1.75
60/30	2.00	3.00	2.00	1.00
30/60	4.00	4.62	3.25	2.37
01/70	8.00	8.00	7.50	7.00
03/70	7.50	8.00	7.50	4.00
70/102	6.50	6.87	6.25	5.25
101/40	2.00	4.50	2.00	2.00
Average	4.75	5.53	4.41	3.33
Grand Average	4.82	5.57	3.98	3.14

Sukunya Dhammaphonphilas
Peter A. Peterson

4. Isozymes of four enzyme types among three tissues (meiotic material, leaves and roots) of seven inbred lines.

The four enzyme types tested are esterases, peroxidases, phosphatases and leucine amino peptidase. Bands found in starch gels were either tissue limited or general (found in each of the three tissues). Of the 10 esterase bands, none were limited to meiosis and only one was tissue limited--i.e., one appeared in the leaf only of several inbreds. Some of the peroxidase bands were tissue limited to the leaf but none was limited to meiotic tissue or roots. None of the three phosphatase bands nor the one leucine amino peptidase band was limited to any of the three tissues.

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5. Three C^I alleles.

In MGCNL 42:84, it was reported that three C^I alleles could be distinguished. These were $C^{I(m. coop)}$ from the Maize Genetics Cooperative, $C^{I(mc)}$ from Maiz Chapolote and $C^{I(ZC)}$ from Zapolote Chico. The distinction in the earlier report was by a color matching test.

In a reexamination of this material using isogenic stocks and a colorimetric test this distinction has been confirmed. There are three distinguishable color-suppressing C^I alleles. Isogenicity was accomplished by successively crossing each of the alleles into the color converted W-22. The kernels for each of these isolated lines were obtained from testcrosses onto two color lines, W-22 and an early flint.

Peter A. Peterson

6. Carbohydrases of sh_1.

The relative activities of some carbohydrases in developing endosperm tissue of maize varying in gene dosage of the shrunken-1 allele were studied. The activities of ADP-glucose pyrophosphorylase, soluble ADP-glucose:starch synthetase, and α-amylase in shrunken ($sh_1 sh_1 sh_1$) endosperm approximately equaled those activities in normal ($Sh_1 Sh_1 Sh_1$) endosperm 18 days after pollination. The amylase activities in endosperm

controlled by all four gene dosage levels of the shrunken-1 allele decreased with the age of the kernel. Glucosidase activity, present in normal endosperm, was missing from developing shrunken endosperm, and granular bound ADP-glucose:starch synthetase had higher activity in normal than in shrunken endosperm.

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7. Diversity of germinal derivatives of $a_2^{m(r-pa-pu)}$.

As reported in MGCNL 45:77-78, the $\underline{a}_2^{m(r-pa-pu)}$ allele is stable pale in the absence of En; in the presence of En, the phenotype is colorless but is mutable expressing colorless, pale and deep purple sectors in the aleurone. Full mutant colorless and colored kernels not responsive to the presence of En are recovered in the testcross progeny of $\underline{a}_2^{m(r-pa-pu)}$. The colored mutations occur as single kernels on the progeny ear and only one occurrence of an ear sector has been recovered. Intensity of the aleurone pigment of these mutants varies from a dark pale color to full $\underline{A}_2$ expression.

In order to verify the visual distinction of these derivatives, a quantitative analysis of the pigment was made. Four kernel types were examined. These included: uniformly pale colored ($\underline{a}_2^{m(r-pa-pu)}$ without En) and full colored (independent germinal mutations of the $\underline{a}_2^{m(r-pa-pu)}$ allele) kernels and, for comparative purposes, the control included full colored and colorless types. The pale and full colored derivatives were isolated from testcrosses.

Following methanol extraction of the ground kernels, a colorimetric reading of the pigment was made on a Beckman Model DB Spectrophotometer (510 or 530 mu - depending upon the Pr genotype). The mean was determined from three samples from each ear and the results are shown in Table 1.

Table 1. Pigment content of pale kernels of $\underline{a}_2^{m(r-pa-pu)}$/ $\underline{a}_2^{m(r-pa-pu)}$/$\underline{a}_2$ constitution, colored germinal mutations of the $\underline{a}_2^{m(r-pa-pu)}$ allele, and colored and colorless controls.

Sample	Phenotype	Genotype	Optical Density
A. Control (colored)			
1	full colored	$\underline{A}_2/\underline{A}_2/\underline{a}_2$	.71
2	full colored	$\underline{A}_2/\underline{A}_2/\underline{A}_2$	.76
B. Germinal mutants			
3	full colored	$\underline{A}_2/\underline{A}_2/\underline{a}_2$	.70
4	full colored	$\underline{A}_2/\underline{A}_2/\underline{a}_2$	.38
5	full colored	$\underline{A}_2/\underline{A}_2/\underline{a}_2$	.13
C. Pales			
6	pale	$\underline{a}_2^{m(r-pa-pu)}/\underline{a}_2^{m(r-pa-pu)}/\underline{a}_2$	.07
7	pale	" "	.05
8	pale	" "	.05
D. Control colorless			
9	colorless	$\underline{a}_2/\underline{a}_2/\underline{a}_2$	.02
10	colorless	"	.03
11	colorless	"	.02
12	colorless	"	.02

The pale kernels, though low in anthocyanin content, were statistically differentiated from the colorless control.

The three colored germinal mutations are decidedly different showing a wide range of anthocyanin content (70, 38 and 13). This is consistent with their variable phenotypes. One has a value similar to that of the colored control. This confirms that germinal mutant derivatives of the $\underline{a}_2^{m(r-pa-pu)}$ allele vary from colorless to full color $\underline{A}_2$ alleles including alleles showing variable intermediate levels of color.

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1. Disjunction and preferential fertilization in TB-9b.

Several studies have been made in which it has been possible to estimate the rate of disjunction and preferential fertilization of the B^9 chromosome in the A-B translocations B-9b. Roman[4] found normal disjunction only occurred in a frequency of 1.8% and that preferential fertilization occurred in 66.3% of the pollinations involving pollen grains in which nondisjunction had occurred. Bianchi, Bellini, Contin and Ottaviano[3] found normal disjunction in frequencies of 33.3% and 22.1% in two sets of crosses and preferential fertilization 59.5% and 65.3%, respectively. Carlson[1] found preferential fertilization values ranging from 64% to 69%. However, he did find in some crosses that if one particular stock was used as a female parent no preferential fertilization was observed. The rates of normal disjunction ranged from 2% to 18%.

In recent crosses to test for the presence of I on the B^9 chromosome, plants of the putative genotype B^9 (I) 9^B/9(C) were crossed as males onto a homozygous purple aleurone stock which was homozygous for the R_2^{scm} allele. This r allele is not only responsible for colored aleurone but also produces color in the scutellum. If the genotype of the male parents is correct then it should be possible to determine the following facts from the resulting seeds: 1) the frequency with which pollen grains carrying a normal chromosome nine and those carrying the translocated chromosomes participated in fertilizations, 2) the rate of normal disjunction of the B^9 chromosome and 3) the rate of preferential fertilization. The results of the above crosses are given in Table 1.

Before considering the results, two characteristics of the I allele should be reviewed. First, in crosses of I to CC plants, heterozygous seeds will frequently not be completely devoid of aleurone color but will show a tinge of pigment. Secondly, seeds heterozygous for I in such crosses will have spots of color where I has been lost

Table 1. Classes of seeds produced from the cross purple aleurone $(\underline{R}_2^{scm}\ \underline{R}_2^{scm})$ X $B^9(\underline{I})9^B/9(\underline{C})$

Phenotypic Classes Observed	Purple Pl.scut	Purple Yel.scut	Pl.tinged spotted Pl.scut	Yel.-spotted Pl.scut	Yel.non-spotted Pl.scut	Pl.tinged spotted Yel.scut	Pl.tinged non-spotted Yel.scut	Yel. spotted Yel.scut	Yel.non-spotted Yel.scut	Total
71-9187-2/8181-2	97	72	2	1	26	17	1	14	5	235
71-8184-4/8181-2	113	66	0	3	32	23	0	16	3	256
71-8189-3/9181-1	165	86	5	3	44	28	0	37	8	376*
71-9183-4/9181-3	138	50	1	9	25	12	3	33	5	276
71-8182-1/9181-3	151	71	0	1	44	24	6	14	8	319
71-8182-2/9181-5	134	64	0	7	34	31	3	17	1	291
71-8182-4/9181-5	121	67	6	1	28	26	0	22	2	273
71-8182-3/9181-5	110	51	0	3	19	29	1	13	2	228
71-9185-6/9181.1-5	140	57	0	3	21	45	0	39	3	308**
71-8186-2/9192-6	106	62	0	6	36	11	0	17	2	240**
	1275	646	14	37	309	246	14	222	39	2,802

*3 seeds questionable classification not included in total.

**2 seeds questionable classification not included in total.

from a cell lineage. The number of spots expected is inversely proportional to the number of _I_ alleles present.

In Table 2, the probable genotypes of the phenotypes listed in Table 1 are given. The class A seeds are the result of the functioning of pollen grains carrying normal (non-translocated) chromosomes. Class

Table 2. Probable genotypes of the phenotypes shown in Table 1.

Phenotype	Genotype		Class
	Endosperm	Embryo	
Purple endosperm; purple scutellum	999 ($\underline{CCC}$)	99 ($\underline{CC}$)	A
Purple endosperm; yellow scutellum	9^B99 ($\underline{CC}$)	$B^9B^99^B9$ ($\underline{IIC}$)	B
Purple tinged, spotted endosperm; purple scutellum yellow, spotted endosperm; purple scutellum yellow, non-spotted endosperm; purple scutellum	$B^9B^99^B99$ ($\underline{IICC}$)	9^B9 ($\underline{C}$)	C
Purple tinged, spotted endosperm; yellow scutellum Purple tinged, non-spotted endosperm; yellow scutellum yellow, spotted endosperm; yellow scutellum yellow, nonspotted endosperm; yellow scutellum	B^99^B99 ($\underline{ICC}$)	B^99^B9 ($\underline{IC}$)	D

B seeds have deficient endosperms and hyperploid embryos and thus are the result of nondisjunction. The class C seeds have a hyperploid endosperm and a deficient embryo. Notice that in this class there is a low frequency of purple-tinged seeds and seeds with purple spots. (Spots were counted by using a binocular microscope and a magnification of 19.5 x). This is as expected if these seeds have two _I_ alleles in the endosperm. This class is also the result of nondisjunction. Seeds of D class result

from the fertilization by pollen grains in which nondisjunction did not take place and thus the endosperm and embryo have only one I. This is shown in the embryo by yellow scutellum color and in the endosperm by a higher frequency of purple-tinged seeds and spotted seeds than observed in class C. The higher frequency of purple-tinged and spotted seeds is expected because only one I allele is present.

From Table 3 it can be seen that pollen grains carrying the A-B translocation function more frequently (54.5%) than those that had a normal chromosome (45.5%). This is a very significant difference (X^2 = 22.6). Purple scutellum in the seeds with the normal chromosome was determined by cutting the germ. Why translocation bearing pollen grains should be more successful in accomplishing fertilizations is not obvious.

Table 3. An analysis of the data presented in Table 1.

Types of fertilizations	Phenotypic class (see Table 2)				Total
	A	B	C	D	
All classes of fertilizations	1275	646	360	521	2802
Fertilizations involving translocation and normal gametes	1275 (45.5%)		1527 (54.5%)		2802
Translocation fertilizations only		646 (42.3%)	360 (23.6%)	521 (34.1%)	1527
Translocation fertilizations involving nondisjunction		646 (64.2%)	360 (35.8%)		1006

If only the fertilizations which resulted from pollen grains with TB-9b are considered, it can be seen from Table 3 that normal disjunction is occurring 34.1% of the time (Class D). Table 4 summarizes the rates obtained for normal disjunction of TB-9b from several workers. It is obvious that the rate with which normal disjunction occurs is very variable and probably depends upon the genotype of the male parent although environmental factors can not be ruled out. In Carlson's paper,[1] two different TB-9b pollen sources were used to pollinate the same two female lines. In one source (678-5) the pollination on the two female lines revealed normal disjunction in 2% and 4% of the progeny. In crosses involving the second line (808-1) the values of 16% and 18% were observed. The different rates may reflect genotypic differences in the two male lines. However, environmental influences can not be ruled out since nothing is reported on the differences, if any, in environmental conditions surrounding the growth of these plants (e.g., planting dates, position in field with respect to each other, maturity dates, etc.).

Table 4. A summary of rates of normal disjunction and preferential fertilization of TB-9b from several studies.

Source	Rate of normal disjunction	Rate of preferential fertilization
Roman[4]	1.8%	66.3%
Bianchi, et al.[3]	33.3% & 22.1%	59.5% and 65.3%
Carlson[1]	range from 2% to 18%	64% to 69%
Carlson[2]	18%	67%
This report	34.1%	64.2%

The rate of preferential fertilization in Table 3 is 64.2% (Class B). Table 4 gives the rates of preferential fertilization from several sources. It is obvious that the rate of preferential fertilization is relatively constant and not greatly influenced by the environment. However, Carlson[1] found a female tester line which, when used in crosses

with TB-9b plants, did not show preferential fertilization. This would seem to indicate that there is a genetic basis for determining whether or not preferential fertilization will occur.

References:

1. Carlson, W. R. Genetics 62:543-554, 1969.
2. Carlson, W. R. Maize Genetics Cooperation News Letter 44:91-92, 1970.
3. Bianchi, A., Bellini, G., Contin, M. and Ottaviano, E. Z. Vererb. 92:213-232, 1961.
4. Roman, H. Proc. Nat. Acad. Sci. U.S. 34:36-42, 1948.

Donald S. Robertson

2. Location of the modifier gene of the $\underline{cl_1}$ locus.

The white-albino mutant $\underline{cl_1}$ is located on chromosome three. Two alleles of this mutant are known $\underline{w_{7716}}$ and $\underline{cl_p}$. These mutants have the white (or pale yellow) endosperms and albino seedlings typical of this class of mutants. Four dominant, allelic modifiers of these genes have been described (Heredity 21:1-7, 1966) which, when present, partially or completely suppress the albino phenotype. Depending upon the modifier present, the seedling can be pale green (pastel) or green. The modifiers do not alter the endosperm phenotype.

Attempts to locate the locus of the modifier alleles have been frustrated by the rather widespread occurrence of modifier genes in genetic stocks. In the F_2's of crosses of the $\underline{cl_1}$ alleles to the inbred M14, pale green (pastel) or green seedlings segregated in the white endosperm class. These results indicate that this inbred carries two modifiers, one responsible for pale green seedlings and the other for green seedlings. To verify that the green M14 modifier was allelic to the other known modifiers of the $\underline{cl_1}$ locus, plants of the following genotypes were self pollinated: $\underline{w_{7716}}\ \underline{Cl_M^{M14}} / \underline{+}\ \underline{Cl_M^4}$, $\underline{+}\ \underline{cl_M^{M14}} / \underline{cl_p}\ \underline{Cl_M^4}$ and $\underline{w_{7716}}\ \underline{Cl_M^{M14}} / \underline{cl_p}\ \underline{Cl_M^4}$. From these selfs, the white or pale yellow seeds were planted in a seedling bench. If $\underline{Cl_M^{M14}}$ is allelic to $\underline{Cl_M^4}$, no albino seedlings will be observed. Out of 2,221 seedlings grown, no albinos were found. Another allele test was made involving the $\underline{Cl_M^3}$ modifier.

In this test the white or pale yellow seeds from the selfs of the following genotypes were grown: $\underline{+}\ \underline{Cl}_{M}^{M14} / \underline{cl}_{1}\ \underline{Cl}_{M}^{3}$ and $\underline{w}_{7716}\ \underline{Cl}_{M}^{M14} / \underline{cl}_{1}\ \underline{Cl}_{M}^{3}$. Out of 2,438 seedlings tested no albinos were observed. From the two tests a total of 4,659 seedlings were grown without the production of a single albino. This would indicate that the $\underline{Cl}_{M}^{M14}$ allele is allelic to the other modifiers at the $\underline{Cl}_{M}$ locus.

Since the inbred M14 carries a modifier allelic to the other known modifiers of the $\underline{Cl}_{1}$ alleles, a series of waxy translocations which had been converted to the M14 background were crossed to stocks carrying $\underline{cl}_{1}$ or $\underline{w}_{7716}$ without the modifiers. The F_1's of these crosses were self pollinated and starchy and waxy pale yellow and/or white seeds planted. Linkage with a particular translocation should result in a surplus of albino seedlings in the starchy class and a corresponding deficiency in the waxy class. These conditions were found for only T 8-9_{6673} (Table 1).

In spite of the deficiency in the waxy class, there is a definite indication of linkage with T8-9_{6673} (breakpoint at 8 L.35). To obtain more reliable linkage data, a modified testcross will be made by crossing the F_1 to a waxy OH43 line that does not carry any $\underline{cl}_{1}$ modifiers. The plants from the starchy and waxy testcross seeds will be grown, classified for pollen sterility and self pollinated. Plants segregating for pale yellow or white seeds will be tested for the presence of the modifier gene to determine the association between the translocation, waxy and the modifier locus.

As mentioned above, the inbred M14 carries two modifiers of $\underline{cl}_{1}$ expression (i.e., one responsible for green seedlings and the other for pale green seedlings). The allele tests reported above with $\underline{Cl}_{M}^{4}$ and $\underline{Cl}_{M}^{3}$ involved the green modifier from M14, while the translocation used in the linkage test carried the pale green modifier. Since this latter modifier has not been allele tested with the known modifiers there is a chance that the gene carried on chromosome 8 might not belong to the same locus as the others. This seems unlikely since so far five independently occurring modifiers have proven to be allelic. However, to be sure that the same locus is involved, the pale green modifier from M14 will be allele tested with one or more of the other modifiers.

Table 1. F_2 seedling data involving the pale yellow and/or white seeds from the F_1 between $\underline{wx}$T8-9$_{6673}$ and $\underline{w}_{7716}$

Plant	Wx		wx	
	Pale green (pastel)	Albino	Pale green (pastel)	Albino
66-7149-3	24	8	3	0
-6	20	12	13	1
70-3211-1	17	5	7	0
-4	18	12	7	1
-8	19	10	5	0
-12	23	4	8	0
-13	16	7	2	0
-15	10	5	3	1
-17	13	7	3	1
-20	15	6	7	0
-26	27	10	7	0
-28	9	11	3	1
-29	8	5	0	1
	219	102	68	6

Another series of tests is being made to confirm the location of the modifier locus. This involves crosses of $\underline{cl}_1$ $\underline{cl}_1$ $\underline{Cl}_M^3$ $\underline{Cl}_M^3$ plants with a series of waxy-chromosome nine translocations in the background of the inbreds OH43 or N25. Since neither of these inbreds carry $\underline{cl}_1$ modifiers, the F_1 plants should be heterozygous for the modifier locus, waxy and the translocations. It, therefore, should be possible to obtain evidence of linkage from the F_2 populations of these crosses.

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1. Selecting mutants of mitotic nondisjunction with TB-9b.

Nondisjunction of the B chromosome is under genetic control (Roman, 1949) and the isolation of mutants of nondisjunction should, therefore, be possible. Mutants lacking the ability to undergo nondisjunction should be the easiest class of mutants to detect, but there are problems in identifying such mutants. Rates of spontaneous mutation are extremely low, requiring large population sizes. In addition, classification of the mutants requires testcrossing each individual to determine its rate of nondisjunction. A partial answer to these problems has been found. Selection for chromosomal mutation, rather than point mutation, greatly reduces the number of individuals that need be screened. Chromosomal mutations occur at a fairly high frequency for the B chromosome, and they have the advantage over point mutations of visibility. Classification problems can be simplified by selecting mutants from the progeny of TB-9b plants that show a very high rate of nondisjunction (95% or more). Only kernels resulting from normal disjunction of the B^9 need be tested for mutation, and these are few in number. To test these ideas, an inbred TB-9b line with a high rate of nondisjunction was selected and crossed to a bz tester.

$$\underline{sh}\ \underline{bz}\ \underline{wx}\ \underline{B}\ \underline{Pl} \quad X \quad 9^{B^{Wx}}\ 9^{B^{Wx}}\ B^{9^{Sh\ Bz}}$$

The Bz seeds from the progeny were grown and Bz plants selected for testing. Of 2,161 progeny, only 57 were Bz in both endosperm and sporophyte. A further reduction in effort was made by analyzing nondisjunction from self pollinations, rather than testcrosses. From the 57 self pollinations, four apparent mutations were found. Two of these were found to be new isolations of the B^9 isochromosome. The other two have not shown any easily identifiable abnormality in mitosis, and pachytene analysis will be needed. Selection of the isochromosome here depended on two factors: 1) The isochromosome generally has a low rate of nondisjunction. 2) Self pollination does not discriminate between transmission of

the chromosome through the male vs. the female parent. Because of pollen competition, the isochromosome is transmitted mainly through the female parent and cannot undergo nondisjunction. The finding of the isochromosome suggests that selection of chromosome abnormalities is possible. In addition, the highly effective mutagen, ethyl methane sulfonate, might allow screening of point mutations. While a $9^B\ 9^B\ B^9$ male was used in the present experiment to encourage chromosome abnormalities, a $9^B\ 9^B\ B^9\ B^9$ parent would be suitable with EMS.

Reference:

Roman, H., 1949. (Abstract). Records of the Genetics Society of America, no. 18, p. 112.

Wayne Carlson

2. An unselected "mutant" affecting nondisjunction.

This summer, a series of crosses were made between an inbred TB-9b stock and the F_2 of two inbred *c sh wx* testers. The F_2 plants were segregating for many different traits, but were homozygous for *c sh wx*. Plants selected from the TB-9b line were hyperploid ($9^{c\ sh\ wx}\ 9^{B^{Wx}}\ B^{9^{C\ Sh}}\ B^{9^{C\ Sh}}$). Of several hundred ears produced in the cross (*c sh wx* ♀ X TB-9b ♂) all were typical except one. The abnormal ear contained an extremely high rate of *C-c* multiple sectored kernels. Classification of the ear was as follows:

C Wx =	78
C/c Wx =	35
C wx =	27
C/c wx =	15
c Wx =	103
c wx =	5

of the total colored seeds, 50/155 are variegated. The ear with this high proportion of sectored kernels was produced in a cross (1818 X 1819J) in which one pollen shedding from a TB-9b plant was crossed onto 10-15 ears of the F_2 *c sh wx*. Since only one ear was abnormal, the "mutation" must be attributed to the female parent. This "mutation" is interesting because it affects B^9 stability, but is not located on the B-9b translocation. If the "mutation" acts by inducing nondisjunction of the B^9, it is acting at the wrong time (during endosperm

development) and without the aid of the 9^B chromosome (note effect on C wx kernels). The immediate question is whether the "mutation" is real or the product of a rare combination of genes from the F_2 segregation. The answer is not yet known.

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1. Genes for spikelet bearing two fertile pistillate flowers.

The cultivated varieties and hybrids of maize normally develop a pistillate inflorescence bearing spikelets with a single fertile flower. The second flower present in the spikelet aborts at an early stage. A few varieties with a fertile second flower and a spikelet producing two grains have been described.

In 1966, we isolated from a plot sown with an open pollinated variety some plants having ears with two kernels in each spikelet. From the preliminary morphological and genetical analysis of this character the following conclusions have been drawn:

1) The appearance of two kernels per spikelet is associated with the development of a second flower with functional pistil. The homozygous mutant ear has about 90% of spikelets with two flowers.
2) In the F_1 ears obtained from crosses between mutant plants and normal inbred lines, some spikelets (5% or less) located at the top part of the ear bear two fertile flowers. This suggests that at least one of the factors controlling the character is partially dominant.
3) The phenotype of the F_2 ears is variable. About 50% of the ears are normal (group 4), 40% show intermediate phenotypes classifiable into at least two groups (groups 3 and 2), and 10% fully express the mutant phenotype (group 1).

4) The F_3 progenies obtained from group 1 reproduce the mutant phenotype, with some exceptions possibly due to incorrect F_2 classification.
5) The F_3 ears derived from F_2 intermediate groups segregate for normal, intermediate and mutant phenotypes. The progenies from F_2 group 4 contain phenotypically normal and intermediate ears. From the data at hand, it is possible to hypothesize that two factors control the character.
6) In the F_3 progenies studied, mutant ears bear more seeds than the normal ones (404 versus 289), with a slightly higher total kernel weight (69 versus 64 g per ear); the average kernel weight is lower (17 versus 21 g).

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2. Gametophyte factors in chromosome 9 of inbred lines.

The genetic stock marked with yg_2 sh_1 wx Ga_8 has been crossed with 60 inbred lines and the ensuing hybrids have been self-pollinated. The ears obtained have been analyzed (in number, about six) as to the segregation ratios for the markers mentioned. The following table reports the cases in which the data suggest the presence in the inbred lines of ga factors, with the exception of the line H 21 in which there is indication of a super-Ga_8 factor. Obviously, in general, all the

Line tested	Marker rate significantly deviating from .25			Ears deviating/ Total ears
	sh	wx	yg	
H 21	.29	.29		4/8
MIBO 4	.17			3/15
R 157	.16	.17		1/4
R 158	.04	.00		1/4
W 32H	.20	.17		3/3
W 64A		.18		3/6
L 1047	.20	.17		3/3
L 1057	.14	.01		1/5
L 1058	.15		.00	1/6

cases reported in the table may also be interpreted as indicative of other Ga/ga differences besides Ga_8, but all giving rise to significant deviations in the Mendelian ratios of markers in chromosome 9. In the F_2 involving the line L 1047, a 4% frequency of colored kernels was observed in one ear which, however, showed normal ratios for the other markers. The inbred lines in which no significantly deviating values have been obtained are the following: A 90, A 158, A 239, A 251, A 364, A 374, B 2, B 6, B 14, C 103, Lo 5, Lo 11, Lo 12, Lo 22, Lo 32, Lo 38, Lo 58, Lo 289, MIBO 6, MIBO 7, MIBO 9, OH 7, R 87, R 117, RNY, Sel 224, W 9, W 15, W 22, W 23, W 37A, W 75, W 79A, W 85, W 153R, W 187d, W 324, W 374, WF 9, WM 13, WM 13R, WR 3, W 374R, M 14, Minn C_1, Minn C_6, SG 14, C 123, OH 41, L 1038, L 1111.

A. Bianchi

3. Inbred mutations on prolific type of maize.

E.M.S. (ethyl-methane-sulphonate) induced mutations were studied in a pop line. Dry kernels were treated, just before sowing, with a 1.4% water solution of E.M.S. for 12 hours. The plants obtained were pollinated by a stock homozygous for several recessive markers. The female parent possesses the corresponding dominant alleles.

The results obtained are reported in the table:

Treatment	Examined plants	Plants with mutations	
		on 1 ear (1)	on more ears (2)
0	1077	0	0
E.M.S. 1.4%	2290	53	29

(1) Position of the mutated ear

Position	1	2	3	4	5	6
Frequency	18	16	9	3	4	3

(2) Position of the mutated ears

Position	1-3, 2-4, 1-3-5 ..	1-2, 2-3, 1-3-4 ...	all
Frequency	15	6	8

The ear position number is 1 for the lower ear on the stem. Even numbered ears, in a plant, are located on one side of the stem, the odd ones on the other. The ears segregating for the markers of the pollinating stock are classified as mutated. In some cases the mutation is limited to a sector of the ear.

From the reported data, the following conclusions may be drawn:

1) The treatment is effective in inducing mutations;
2) The frequency of ears showing mutations decreases with the ear insertion height;
3) When two or more ears in a plant are mutated, they are frequently located on the same side of the stem. This suggests a common origin of these ears from a single mutated cell line.

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1. Changes in weight, protein and lysine content in opaque-2 kernels of corn during backcrossing.

Changes in weight in opaque-2 corn kernels as well as the changes in protein and lysine content were studied on segregating ears from selfed plants, phenotypically normal, but genotypically heterozygous. Studies were carried out in successive generations of backcrossing planted in one season. Segregation in every generation was considered on 7-10 selfed ears.

Lines A344, A198, Sg25, W155, Sg2, and WF9 were included in the experiments, and $\underline{o}_2\underline{ra}_1\underline{gl}_1$ and $\underline{o}_2$Syn A were included as opaque-2 gene sources having protein content of 9.75% and 11.0% and lysine content of 4.32% and 4.50%, respectively.

To eliminate possible size differences in kernels from top and bottom parts of the ears, adjacent translucent kernels up or down in the row were taken as controls. These two classes were weighed and

the mean weight of opaque-2 kernels was determined in per cent relative to the translucent kernels.

Protein content was determined on the whole kernel basis by the Kjeldahl micromethod. Lysine content in hydrolysates was determined by ion exchange chromatography on the Hitachi KLA-3B automatic amino acid analyzer. Each sample was a composite of several ears in each generation.

Weight depression rate of opaque-2 kernels in per cent of the normals during successive backcrossing is illustrated in Table 1. Weight reduction of opaque-2 kernels is significantly differentiated among the lines; e.g., in A344 it amounts to 24.2% while in WF9 it is only 6.6% in comparable BC3 generations. This confirms available data on differential reaction of separate line genotypes to the introduction of the opaque-2 gene.

Table 1. Depression rate in weight of opaque-2 kernels during various generations of backcrossing.
Weight of opaque-2 kernel expressed as per cent of normal weight.

Line	Backcross generation of a selfed plant				
	F_1	BC_1	BC_2	BC_3	BC_4
A 344	-	78.7	77.8	75.8(6)	72.2(7;9)
W 155	-	84.6	83.4	81.5(6)	79.3(7;9)
A 198	88.1	95.3	93.6(2)	89.1(3;6)	90.6(4;7;9)
Sg 2	82.9	91.0(1)	87.5(2;5)	89.7(3;6)	-
Sg 25	90.6	88.8	85.5(2)	89.5(3;8)	-
WF 9	91.1	93.6	93.7(2)	93.4(3)	-

Significant at P = 0.05

In parentheses:

Significant when comparing

(1) F_1-BC_1
(2) F_1-BC_2
(3) F_1-BC_3
(4) F_1-BC_4
(5) BC_1-BC_2
(6) BC_1-BC_3
(7) BC_1-BC_4
(8) BC_2-BC_3
(9) BC_2-BC_4
(10) BC_3-BC_4

Table 2. Protein and lysine content of opaque-2 kernels in successive generations of backcrossing

Line	Original line		Generation of selfed plants										Mean of generations to the original in %	
			F_1		BC_1		BC_2		BC_3		BC_4			
	Protein	Lysine	Protein	Lysine	Protein	Lysine	Protein	Lysine	Protein	Lysine	Protein	Lysine	Protein	Lysine
A 344	12.93	2.83	-	-	10.18	4.68	10.87	5.20	11.18	4.87	11.62	4.98	84.8	174.2
A 198	11.87	2.74	10.37	4.70	10.06	4.57	11.37	3.5	11.62	4.93	11.75	4.19	92.9	159.8
Sg-2	10.75	2.55	10.87	4.37	10.69	4.68	10.37	4.28	10.31	4.62	-	-	98.2	172.9
Sg-25	11.94	2.56	11.12	4.18	11.12	3.86	11.94	3.76	11.31	4.72	-	-	95.3	161.3
W-155	13.00	2.78	-	-	12.00	4.48	12.37	4.02	12.62	3.57	13.00	4.36	96.0	147.5
WF_9	11.06	2.78	13.06	4.34	12.12	4.36	11.18	4.64	10.81	4.05	-	-	106.6	156.0

There is a tendency in some lines toward augmentation of the depression rate in weight of opaque-2 kernels from lower to higher generations (A344, W155, Sg25), while in others the reduction is maintained at the same level (A198, Sg2, WF9). Thus, it may be suggested that there are differences in modifiers in some genotypes. Differences in depression rates were significant between non-adjacent backcross generations of the same line. These results suggest that the backcrossing line for which the opaque-2 counterpart is developed plays the primary role in determining the depression rate.

The protein content of opaque-2 kernels of backcross generations in all genotypes was somewhat lower than in the original lines. Significant differences were noted only for line A344 (Table 2).

In the course of backcrossing, the protein content in opaque-2 kernels comes close to the level of the original line. It may be concluded that the reduced protein content in opaque-2 kernels is not controlled by the specific activity of the $\underline{o}_2$ gene but by the possible influence of the opaque-2 genotype source, by dominance of low protein content, and by reduction of protein content in hybrid F_1 compared with the parental lines.

The lysine content in opaque-2 kernels exceeds that in the original line by 47-74% (Table 2), and that is associated with the specific action of the opaque-2 gene and is not dependent on the protein level of the original line.

The lysine content in opaque-2 kernels of the same genotype changes very little through generations of backcrossing. In our material, the lysine content of the protein in opaque-2 kernels in various counterparts is only slightly different; however, it may be assumed that with a wider source of material, greater differences would have been found.

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1. Sterility and other seed characteristics in naturally occurring populations of teosinte.

In the fall of 1971 a hunt searching for useful mutants of teosinte in naturally occurring populations was headed by George Beadle and myself in Guerrero, Mexico. This opportunity to collect extensively for seven days a population over a 40 km transect near Teloloapan, Guerrero enabled me to collect data on sterility in a wild population of teosinte. The data reported below are derived from a sample for each plant based on the total number of fruitcases found in the third from the tassel (usually the most productive) fruiting node. This node bears 3-18 spikes, usually 5 to 10, with an average of 7 or 8 fruitcases per spike.

The seed in teosinte is enclosed in a rachis segment and the seed and rachis segment are referred to as a fruitcase. If the rachis segment is totally white there was no pollination and no development of the seed. The causes for this condition are numerous; examples are: late flowering, where the silks emerged but no pollen fell on the silks, the silks failed to emerge from the enclosing shucks, an insect ate the emerging silks, etc. The white fruitcases are most abundant at the last nodes to flower (i.e., the nodes closest to the tassel and the most basal). The first node to flower is usually the third node from the tassel and in this node only the last of the spikes to develop bear white fruitcases with usually the entire spike being white.

If a single seed in a spike is unpollinated but the seed above and below are pollinated then the rachis tissue in the area of the vascular traces is colored but the rachis flaps and enclosing lower glume are white. In these fruitcases no trace of the seed or arrested seed is visible and these are recorded as non-fertilized fruitcases.

The last class of fruitcases includes those in which the rachis segment is fully pigmented and only the enclosing lower glume is white. Such fruitcases contain a shrunken seed which is defective and to date I've not been able to germinate any of these recovered defective seed.

These are recorded as defective seed in the chart. The data for teosinte growing wild in Mexico are to a degree comparable with those for maize reported by Mangelsdorf (1926) and reviewed by Crumpacker (1967).

Site number	Number of plants scored	Number of fruitcases	Number of white fruitcases	Number of partial white fruitcases	Number of defective seed in fruitcases
1	187	3253	443	77	108
2	344	3175	425	129	41
3	1079	6005	875	212	103
6	969	9229	1290	261	118
7	908	4203	623	262	78
9	855	7141	1035	99	82
10	751	8071	1095	211	107
11	1250	7917	1320	370	92
13	552	7082	992	112	123

During the intensive look at teosinte fruitcases, several further observations about the shape, size, and coloring of the fruitcases were made. These observations and conclusions have been made over a ten year period, but this large collection of seed was an opportunity to test these conclusions. The fruitcase color of a single plant is constant but seldom do surrounding plants exhibit the same color. The color varies from ebony to a bluish steel grey and appears to be due to the interaction of a two color system--one for brown/white and the other for grey/white, which are inherited as incompletely dominant factors. The single seed per plant collections can be sorted into eight different classes and support my observations. The selective advantage of a diversity of fruitcase color classes is obvious for a dispersal unit as large and heavy as that of teosinte, which when it falls to the ground is vulnerable to ground feeding animals, especially birds. The only birds observed to actually feed on teosinte were *Cassidix mexicana* (Boat-

Tailed Grackle), which take insects and occasionally seed from the node of the plant.

The fruitcase of teosinte is so heavy that there is good reason for it to be limited to hillsides where downhill dispersal is gravity affected and the triangular shape prevents rolling and promotes settling in cracks or behind rocks. There also is a fruitcase polymorphism of medium-sized (as distinct from the large fruitcase types of the race Chalco) and smaller fruitcase types in the population. This polymorphism is not correlated with the vigor of the parent plant. It is true that large vigorous plants producing over a thousand seeds possess the larger seed, but so do some of the small plants producing less than a hundred seed per plant.

These observations lend support to the thesis that teosinte in the Balsas basin is a wild plant adapted to its surroundings and quite distinct from teosinte of maize fields in the Valley of Mexico or Central Plateau of Mexico.

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1. Common ancestry of the primitive races of maize indigenous to the Ayacucho area in Peru.

We have studied an important collection of archaeological cobs extending back almost 4000 years from several sites (Ac 100, Ac 117, Ac 244) at Ayacucho, Peru excavated by Dr. R. S. MacNeish. The material comes from the type locality of Confite Morocho, an ancient race that Grobman *et al.* (1961) consider to be the most primitive living race that is ancestral to the more advanced races of both North and South America.

A preliminary inspection of the cobs revealed that some of the cobs fit Grobman's taxonomic data for the primitive races Confite

Puneno, Confite Morocho and Morocho still grown in the area. However, at the time it seemed that a majority of the cobs should be classified as hybrid derivatives such as Confite Morocho introgressed by Confite Puneno on a basis of Grobman's data. But when the data on the age of the various levels in the excavations were received from Dr. Barbara Pickersgill, who gathered the plant remains from the dig, the reason for the intermediate nature of most of the cobs became apparent. The intermediate types extended back a thousand years further in this material to 4000 B.P. than the so-called primitive races. Thus it seems that the oldest cobs represent a common ancestor to these primitive races rather than being their hybrid derivative. We propose to name this ancestral race Ayacucho after the archaeological area. Grobman _et al._ (1961) had proposed an ancestral race, Confite Chavinense, suggested by some ceramic replicas, that led to Confite Puneno but their presumed race was fasciated and, thereby, unlike the oldest cobs from Ayacucho. Previously the race Confite Morocho has been considered as being close to the "wild state." It would now seem that the Ayacucho race was the more primitive and ancestral to several indigenous races in Peru.

W. C. Galinat

2. A heritable phenotype for two-ranked ears in maize allelic to the same trait in teosinte.

A mutation with a relatively stable phenotype for two-ranked ears was discovered in a single plant in the F_3 from a cross between an old inbred line of Wilburs Flint and Siberian Red Flint. Unlike the depauperate phenocopies for two-ranked ear frequently found in stunted eight-rowed maize, this two-ranked type found in our "Waltham Flint" is relatively stable in phenotype and has been inherited through three generations. Although the trait is 100% heritable, some variations in the time of gene action are shown by a few ears with four-ranked butts immediately changing to the two-ranked phenotype.

The poorly programmed action of genes in maize controlling this and certain other teosinte-like traits (_i.e._, single female spikelets) indicates an unadapted genetic background. One result of such unstable

phenotypes is to distort the segregation ratios and to obscure the mode of inheritance. The unstable phenotype characterizes both the mutant and teosinte derived traits.

On outcrossing of the two-ranked Waltham Flint to a two-ranked derivative from a maize-teosinte hybrid, all ears (36) in the F_1 and F_2 were two-ranked, indicating allelism of the genes controlling this trait in the maize and teosinte parents.

Segregations from maize-teosinte hybrids usually indicate that the two-ranked trait is controlled by two independently inherited units. The origin of the two-ranked condition in the Waltham Flint may stem in part from the bringing together of the necessary recessives during the recent hybrid origin of this variety and in part from successive mutations. In any case, the recessive alleles for this trait in maize matched off in hybrid combination with the corresponding recessive alleles from teosinte.

W. C. Galinat

3. A possible role of condensation in a domestication of teosinte.

Teosinte is highly variable in the development of its lateral branches on which its female spikes are usually borne. In some plants these upper branches are elongate and terminated by a tassel with the female spikes dispersed singly in the axils of its leaves. At the other extreme, a telescoping of the branch aggregates its spikes in tight clusters close to the main culm and all are female. In collecting seed from thousands of teosinte plants on a recent expedition in Mexico, we found that the harvesting of bulk seed was much easier from plants with clustered spikes because of the greater concentration of spikes and resultant accumulation of fruit cases within their overlapping and, thereby, mutually protective husks. This suggests that an important, if not the first, step in a possible domestication of teosinte, if this occurred, could have been selection perhaps unconsciously applied for a condensation of spikes into tight clusters. At first condensation in teosinte would serve something of the same purpose as the rigid rachis character in the domestication of other cereals. Once cultivation

(planting and harvesting) began, the more condensed forms would automatically take over.

Selection for higher levels of condensation would go beyond the clustering of spikes and associated traits of reduced shattering of fruit cases and triangularization of their shape in the lower more condensed positions. It would tend to force the developing spikelets out of their vertically compressed cupules as well as promote a proliferation in ranking. Condensation of secondary branches onto the main axis may represent one system for the origin of yolking and whorling, as suggested by Anderson and Brown (1948). These authors did demonstrate that condensation is a factor in the development of higher orders of polystichy. The high degree of secondary branching apparent in the teosinte tassel might reflect a potential for polystichy through such branch condensation. Furthermore, maize that is considered to lack condensation in the tassel according to Anderson, such as the northern flints and Confite Morocho, still has more condensation in the female spike than teosinte, as shown in its hybrids with teosinte. Distortions in the transition between two states of phyllotaxy may result from primordial slippage. This slippage should be expected in the maize cob under the stress of compaction, combined with a reduced nodal network.

The carry-over in maize of the condensation that clusters the spikes in teosinte would result in the multi-husk enclosure of an ear terminating a telescoped branch.

David W. Galinat
W. C. Galinat

4. <u>A possible inverse relation between degree of tassel branching and kernel row number in certain strains of corn.</u>

In a small population (20 plants) of string cob sweet corn characterized by a high degree of tassel branching, an estimate of the proportion of the tassel that was included in the branching zone was made and recorded on the tassel bag at pollination time. Later at harvest time we were surprised to find that the most highly branched tassels were on plants tending to have ears with lower kernel-row numbers (see Table).

In this population (71-241-250), a reduction in tassel branching appears to be associated with an increase in kernel row number. The data could be interpreted as support for the suggestion of Anderson and Brown (1948) that a condensation of tassel branches increases kernel row number or is involved in the origin of whorling. More extensive data are necessary.

Degree of tassel branching vs kernel row number		
Proportion of tassel branched	Number of plants	Average kernel row no.
60%	3	12.7
70%	5	12.0
75%	3	10.0
80%	8	9.75
85%	1	10.0

W. C. Galinat

5. Preliminary studies of a Tripsacum chromosome partially homoeologous to maize chromosome 1.

A chromosome from Tripsacum dactyloides carrying the Bm_2 locus in common with maize chromosome 1 but not several other loci on maize chromosome 1, including sr, br, and an, has finally been isolated on a marker gene stock of maize after repeated failures to accomplish this in the past.

As an addition monosomic (20 + 1) on maize, it failed to show any pairing associations with the maize complement at diakinesis and metaphase I in 40 plants examined from two families.

Preliminary measurements were made on the univalent as a precaution against its possible alteration before isolation as a bivalent. Morphological data on the univalent are often unreliable because of fold-backs and distortions from stretching. Previously the bivalent condition has been selected eventually, following self-pollination of such

monosomic stocks in some cases (tripsacum chromosome Tr 9 and Tr 7), or following nondisjunction in other cases (Tr 5 and Tr 13). We should identify such a bivalent for the $\underline{Bm_2}$ chromosome from Tripsacum in the crop to be grown during the summer of 1972.

From some 250 observations at pachytene often coursing around foldbacks, the length of the $\underline{Bm_2}$ chromosome averaged 34.7 microns. In 10 observations, the position of its centromere was located and an arm ratio of 3.5:1 determined. A terminal knob on the long arm was observed.

On a basis of the above morphological features, this $\underline{Bm_2}$ chromosome was tentatively identified as chromosome Tr 3 in the complement of T. dactyloides. The corresponding data from Chandravadana et al. (1971) give Tr 3 an average length of 40.3 u, an arm ratio of 3.1:1 and a terminal knob in the long arm. Their idiogram representing the original complement of the T. dactyloides used in these studies is the basis for identifications in subsequent items.

W. C. Galinat
R. V. Tantravahi
P. Chandravadana

6. Preliminary studies of a Tripsacum chromosome partially homoeologous to maize chromosome 6.

A chromosome from T. dactyloides carrying the Py locus and possibly the Sm locus in common with maize chromosome 6 but not the nucleolus organizer of this maize chromosome has been isolated. A different tripsacum chromosome, at the 16th position in its complement, carries the nucleolus organizer. Chromosome Tr 16 from tripsacum is still in the process of isolation (see next item). Nothing is known as yet of its gene content relative to that of maize.

Again preliminary measurements were made on the univalent in the absence of the bivalent condition and with recognition that eventual confirmation with data on the bivalent is necessary. From 27 observations at pachytene of the Py tripsacum chromosome from 4 plants, the length averaged 41.7 u. The centromere was located in 3 observations giving an arm ratio of 2.5:1. There is a terminal knob on the long arm. This tentative data on the univalent of the Py marked chromosome suggests the fourth position in the original complement of T. dactyloides.

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7. Progress towards isolating the Tripsacum homoeolog to maize chromosome 3.

Previously the tripsacum homoeolog to maize chromosome 3 has always immediately dropped out from the progeny of the second backcross to the marker stock maize. In a single plant it has now survived to the third backcross to maize, although unexpectedly captured together with three other extra tripsacum chromosomes. The four extra chromosomes of this plant (2n = 20 + 4) appeared throughout meiosis as univalents, indicating they are different from each other. At least one of them may carry A_1, Sh_2, Lg_2 loci corresponding to maize chromosome 3.

From 56 observations made at pachytene, it was possible to tentatively identify two out of the four univalents. One is a very short knobless chromosome averaging only 12.9 u in length, or similar to that of chromosome 18, the smallest in the complement of T. dactyloides. The other is the important nucleolus organizing chromosome, Tr 16, of tripsacum. Tr 16 as a univalent was observed to associate with the maize nucleolus along with the chromosome 6 bivalent of maize. The remaining two chromosomes each have a terminal knob. They could not be classified.

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8. Trivalent frequencies in one of the control crosses for the triple heterozygote of maize chromosome M4, teosinte segment t4s and tripsacum partial homoeolog Tr 7.

In last year's MNL (45:101) we reported that when tripsacum chromosome Tr7 marked by the Su_1 locus was added to the heterozygous fourth chromosome segment of teosinte to give the triple heterozygote M4, t4s, Tr7 a high frequency of trivalency of 60 to 70% was observed at diakinesis and metaphase I. One of the two isogenic controls, M4, M4, Tr7, has now been produced and studied. The second control t4s, t4s, Tr7 has not been studied.

In the first control, M_4, M_4, Tr7, 65 cells examined at diakinesis showed 24.6% trivalency and 30 cells at metaphase I had 20% trivalency.

In addition to the true trivalency, 33% of cells at diakinesis and 20.3% of cells at metaphase I showed a false association of the tripsacum univalent with one of the maize bivalents. In these cases the univalent was positioned in such a way that a chiasma could not be inferred.

Thus, it could be that the higher trivalency in the triple heterozygote (65%) over that of one control (23%) was due to the presence of the teosinte segment. On the other hand, it is possible that mere heterozygosity for this segment had an effect. This possibility will be tested by combining Tr7 with the homozygous t4s, t4s teosinte segment.

In the triple heterozygote M_4, t4s, Tr7 reported last year, the pachytene spread was generally very poor. Whenever we could identify the tripsacum univalent in a small sample of analyzable cells, it either appeared as a univalent or it was clearly "hooked" onto the maize-teosinte fourth chromosome bivalent in the long arm and not with the short arm where the essential segment of teosinte has been assumed to be located. Additional linkage studies of this teosinte chromosome segment are necessary and are in progress.

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P. Chandravadana

9. Altered morphology of the Gl_3 chromosome in progenies showing a higher transmission rate.

During a cytological study of a family of plants showing a higher transmission rate of the Gl_3 chromosome (Tr 13) in progenies of 20 + 1 plants, a single plant was found where the original Tr 13 chromosome seems to have suffered a morphological change. This chromosome, which originally had a knob in its long arm, lost it and appeared as a small fragment at pachytene. In 10 of the 15 observations made at pachytene, the fragment was found to be attached to the centromere of a maize bivalent. In three cases it was found lying free and in two other cases it was found on a maize bivalent. A somewhat similar fragmentation of the Su^d chromosome (Tr 7) has been reported earlier by Rao and Galinat (MNL 42:105-106). It is not known if the fragment represents the knobless arm of the original Tr 13 chromosome, derived as a result of breakage at

the centromere and the centromere of the fractured chromosome sticking to the centromere of a maize bivalent (non-homologous centromere association), or an acentric fragment which would be lost in the next generation. A large number of cells examined at diakinesis and metaphase I showed the fragment appearing separately from the rest of the bivalents and at anaphase I it showed a tendency to divide with the two sister chromatids attached by a "fiber."

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10. Comparative studies of American Maydeae and the Andropogoneae: III Morphology of the pachytene chromosomes of Manisuris cylindrica (2n = 18).

The cytology of Manisuris cylindrica is of special interest in our cytological comparisons of the Andropogoneae to their close relatives in the American Maydeae because of the speculations that Manisuris is both one parent of Tripsacum and the evolutionary link connecting their respective tribes.

From about 250 observations made on individual Manisuris chromosomes at pachytene, it was possible to identify each of the nine members of the complement by their relative lengths and arm ratios (see Table). Due to poor spreading, not all chromosomes could be identified individually in any single cell.

The chromosomes are knobless. The position of their centromeres is median to submedian except for chromosomes 3 and 8 in which it is subterminal. The centromeres are oval achromatic regions with deeply stained heterochromatic areas on either size, as in Coelorachis and Tripsacum. Manisuris (n = 9) has half of the number of chromosomes and, on the average, shorter chromosomes than those of the other two genera (n = 18).

The nucleolar chromosome is assigned the 8th position. The organizing body itself is subterminal in the short arm as in Coelorachis and maize but not in the species of Tripsacum studied so far.

Morphology of the pachytene chromosomes of Manisuris cylindrica (2n = 18)

Chromosome No.	Long arm (microns)	Short arm (microns)	Total length (microns)	Arm ratio
1	26.3	19.8	47.9	1.4
2	21.6	16.6	39.6	1.3
3	23.4	9.4	38.6	2.5
4	18.4	13.0	33.1	1.4
5	17.3	9.4	28.1	1.9
6	15.1	10.8	27.4	1.5
7	14.4	10.8	27.0	1.4
8*	15.8	10.8	21.9	3.5
9	10.1	7.2	18.4	1.4

*Nucleolus organizing chromosome.

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11. Comparative studies of American Maydeae and the Andropogoneae: IV Morphology of the pachytene chromosomes of Coelorachis racemosa (2n = 36).

The basic chromosome number in Coelorachis is 18, the same as the genus Tripsacum. Meiosis has been found to be regular, 18 bivalents being formed in almost all cells. Occasionally there are cells with 17 bivalents and 2 univalents. Extensive studies of chromosomes at the pachytene stage of meiosis in pollen mother cells have been made.

Most of the Coelorachis chromosomes can be identified by their relative lengths and differences in arm ratios (see Table 1). In cases where their lengths and arm ratios are similar, they could be distinguished by comparing them together in the same cell.

The general range in chromosome lengths and arm ratios is similar to that of some species of Tripsacum.

Table 1. Pachytene chromosomes of Coelorachis racemosa
(2n = 36)

Chromosome No.	Long arm (microns)	Short arm (microns)	Total length (microns)	Arm ratio
1	50.4	23.4	74.9	2.2
2	37.4	24.1	63.0	1.6
3	48.6	11.5	61.9	4.3
4	26.6	22.7	51.1	1.2
5	28.4	14.0	44.3	2.1
6	22.7	17.6	41.8	1.3
7	22.3	12.6	37.1	1.8
8	18.4	15.8	36.0	1.2
9	25.9	6.8	34.2	3.9
10	42.3	9.0	33.1	2.5
11	17.6	12.6	32.0	1.4
12*	22.7	6.5	30.2	3.6
13	14.0	12.2	27.7	1.2
14	19.8	6.5	27.7	3.2
15	16.6	8.6	26.6	2.0
16	12.6	10.8	24.8	1.2
17	10.4	8.6	20.9	1.2
18	10.1	4.7	16.2	2.2

*Nucleolus organizing chromosome.

All 18 Coelorachis chromosomes are uniformly marked by heterochromatic regions on either side of the centromere as in Tripsacum. There are no distinctive features as knobs or chromomeres that distinguish one chromosome from the other except for the nucleolus organizing chromosome. Its nucleolus organizing body is located subterminally on the short arm of chromosome 12 in contrast to Tripsacum where it is on the 10th or the 16th chromosome. The nucleolus organizing body is also subterminal in maize although it is internal in the Tripsacum species reported on so far.

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1. Progeny test of spontaneous chromosome aberrations involving chromosome 1.

The detection of chromosome aberrations caused by events of non-disjunction and breakage of chromosome 1 taking place in the male gametophyte was reported in last year's MNL (45:119-123). The chromosomes were counted and a preliminary genetic analysis was done on exceptional F_1 individuals obtained in the cross bz_2 x Bz_2 Bz_2.

Among different classes of chromosome aberrations, one group of 15 individuals was given the most attention, since 21 chromosomes were counted in each of the plants and odd ratios (far from disomic) were obtained in testcrosses to bz_2. A high percentage (30-40%) of shriveled pollen grains was produced by these plants.

Samples of colored kernels (Bz/) taken from ears developed on some of these plants after pollination by the bz_2 tester were planted last summer and reciprocally testcrossed to bz_2. The data are summarized in Table 1. In many plants non-disomic ratios for the marker bz_2 were observed, mostly associated with a high pollen sterility (30-50%). On the other hand, the majority of plants giving disomic ratios had normal pollen. Some near-disomic ratios are associated with pollen sterility, but in most of these cases reciprocal crosses differ in this regard (disomic vs. nondisomic) suggesting that a chromosomal aberration is still present.

Differences in reciprocal crosses were often observed with plants showing high pollen sterility, with regard to the ratio Bz : bz. In Table 2 the plants tested in reciprocal crosses are classified according to the ratios shown for the marker bz_2. The majority of non-disomic ratios with a large excess of bz are found when the plants were tested as the pollen parents, while non-disomic ratios with a large excess of Bz were found more often when the plants were the pistillate parents.

Table 1. Segregation types found in reciprocal testcrosses to $\underline{bz_2}$ involving $\underline{Bz}$/ plants some of which are trisomic for chromosome 1.

Family	Crossed as:	Frequency of ears showing the following ratios:				Total
		disomic (or near)		non-disomic		
		N*	⍏*	N	⍏	
1990	♀	9	1	0	3	13
	♂	9	1	0	3	
1991	♀	7	1	0	3	11
	♂	7	0	0	4	
1992	♀	6	4	0	6	16
	♂	6	5	0	5	
1993	♀	1	2	0	3	6
	♂	1	1	0	4	
1994	♀	6	5	0	0	11
	♂	6	0	0	5	
1995	♀	10	0	2	0	12
	♂	9	0	3	0	
1996	♀	1	1	0	5	7
	♂	1	0	0	6	
Totals	♀	40	14	2	20	76
	♂	39	7	3	27	

*N = normal pollen
⍏ = pollen with high sterility (30-50%).

Many points of interest are emerging from the development of the present study. First of all, pollen sterility is found in the progeny of six out of seven families tested, suggesting that chromosome 1 was originally involved in events of nondisjunction and breakage at the same time. Moreover, if nondisjunction was common to all cases, the location of breakages is likely to be different from case to case (which arose independently). Obviously, pollen sterility would be transmitted from one generation to the other, if the interpretation of the data is correct, when a broken chromosome 1 is present in a gamete where a normal

Table 2. Analysis of the segregation types found in reciprocal testcrosses to bz_2 of the Bz/ plants shown in Table 1.

Family	Ratios (Bz:bz) obtained when the Bz/ plants were crossed: as ♀ x bz_2				as ♂ x bz_2			
	near 1:1 ♀ and ♂	near 1:1 ♀ only	large excess Bz	large excess bz	near 1:1 ♀ and ♂	near 1:1 ♂ only	large excess Bz	large excess bz
1990	9	1	2	1	9	1	1	2
1991	7	1	3	0	7	0	3	1
1992	6	4	5	1	6	5	0	5
1993	1	2	2	1	1	1	0	4
1994	6	5	0	0	6	0	0	5
1995	9	1	2	0	9	0	2	1
1996	1	1	2	3	1	0	0	6
Totals	39	15	16	6	39	7	6	24

Note: Ears with a large excess of Bz or bz are those giving significant χ^2 deviations from the 1:1 ratio ($P < 0.01$).

chromosome 1 is also present, or when two chromosomes 1 are deficient for different regions in the same gamete. However, a possibility exists that pollen sterility is present in trisomic 1 plants regardless of chromosome breakages, since non-disomic ratios are not found in plants with normal pollen, except for family 1995.

Achille Ghidoni

2. Genetic and cytological investigation of nonrandomly transmitted chromosomes in trisomic 10 plants.

An instance of nonrandom transmission of chromosomes in trisomic 10 plants was reported in last year's Maize Genetics News Letter (45: 115-119). Among the progeny of the cross $R^{nj}R^{st}r$ x rr the R^{st} class was significantly less than the R^{nj} class. Moreover, the $R^{nj}R^{st}$ class was

also deficient. After making reciprocal crosses to an *r* tester, a greater discrepancy in the recovery of the same classes appeared when the trisomic plants furnished the pollen.

As an interpretation of the data, it was suggested that a chromosomal condition linked to $\underline{R}^{st}$ affected its ability to be inherited. Accordingly, root tips were taken from samples of the $\underline{R}^{st}$ and $\underline{R}^{nj}$ classes obtained in the cross cited above. The expectation was that most $\underline{R}^{nj}$ individuals would be disomic ($\underline{R}^{nj}\underline{r}$) and that few would be trisomic ($\underline{R}^{nj}\underline{rr}$). On the other hand, most $\underline{R}^{st}$ individuals were expected to be trisomic if a chromosome condition linked to $\underline{R}^{st}$ negatively affects the transmission of this chromosome 10 alone. Thus, the chromosome bearing $\underline{R}^{st}$ would usually be transmitted in the presence of a normal chromosome 10 (which in this case carried *r*), or without the second chromosome 10 when a crossover separated $\underline{R}^{st}$ from the unfavorable chromosomal condition.

Table 1 shows the frequency of trisomic and disomic individuals in the $\underline{R}^{nj}$ and $\underline{R}^{st}$ classes.

Table 1. Frequency of trisomic and disomic individuals in the $\underline{R}^{nj}$ and $\underline{R}^{st}$ classes obtained by counting chromosomes in root tips.

Chromosome numbers	20	21	Total
$\underline{R}^{nj}$ Class	36	13	49
$\underline{R}^{st}$ Class	23	80	103

The cytological data fit well with the expectation indicated above. Other samples of the same classes were progeny tested by crossing reciprocally to an *r* tester. The results are summarized in Table 2.

Table 2. Frequency of ears showing disomic and non-disomic ratios after crossing $\underline{R}^{nj}/$ and $\underline{R}^{st}/$ plants to an $\underline{r}$ tester.

	Ears with disomic ratios	Ears with non-disomic ratios
$\underline{R}^{nj}$ Class	9	3
$\underline{R}^{st}$ Class	1	55

While the result for the $\underline{R}^{nj}$ class fits with the expectation (as was confirmed also by the cytological finding), the $\underline{R}^{st}$ class shows a remarkable deficiency of ears with disomic ratios. This suggests that a crossover separating the gene $\underline{R}^{st}$ from the linked chromosome condition is infrequent. It is obvious from a comparison of the genetic data with the cytological data reported in Table 1 that many individuals giving non-disomic ratios for $\underline{R}^{st}:\underline{r}$ had 20 chromosomes.

A deficiency in the chromosome 10 carrying $\underline{R}^{st}$ cannot entirely explain the phenomenon, unless the deficient chromosome is consistently excluded from pairing configurations and is therefore preferentially lost during meiosis. If the deficiency is small, it is unlikely to drastically affect the pairing ability of this chromosome. On the other hand, if it is a large deficiency, the chromosome may be transmissible only in the presence of a normal chromosome 10, and this does not account for the many plants with 20 chromosomes still giving non-disomic ratios. The problem requires further investigation.

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1. Cytological localization of interchange breakpoints to the nucleolus organizer region or satellite.

Longley (ARS-34-16:1-40, 1961) lists the interchanges involving the short arm of chromosome 6 according to the relative location of the breakpoint between the centromere and the end of the arm. For many studies it is desirable to know whether the breakpoint is in the nucleolus organizer region or in the satellite. Thus, we are listing below the interchanges with breaks in these two cytologically distinct regions.

Homozygous interchange stocks were used in identifying the breakpoints. The interchanges with a break in the satellite have been reported previously (Phillips, *et al.*, Crop Science 11:525-528).

Breakpoints	Stocks
Nucleolus organizer region	1-6 Li (formerly 4-6 Li), 1-6(5495), 1-6(4986), 1-6(6189), 1-6(8415) 2-6(8786), 2-6(027-4), 2-6(5419), 2-6(8441) 3-6(032-3), 3-6(030-8) 4-6(4341) 5-6 f, 5-6(8696) 6-7(5181), 6-7(4964), 6-7(035-3) 6-9 a, 6-9 d 6-10(5519)
Satellite	1-6 b 2-6(001-15) 3-6 b 4-6 c, 4-6(5227), 4-6(7328), 4-6(003-16) 5-6 b, 5-6 d, 5-6(8219) 6-7(7036) 6-9(017-14) 6-10 f

R. L. Phillips
S. S. Wang

2. A cytogenetic method for utilizing nuclear male-sterility in hybrid corn production.

Until recently, use of the "T" male-sterile cytoplasm has aided the efficient and economical production of hybrid corn. High susceptibility to Southern Corn Leaf Blight of varieties produced by means of "T" type cytoplasmic male-sterility has led to a return to costly detasseling procedures. An attempt is currently in progress to develop and test a method of using nuclear (rather than cytoplasmic) male-sterility for the production of lines with all male-sterile plants; current methods only allow for the production of lines with 50% male-sterile plants. Utilization of such a method (which we term the "double duplication method") would eliminate the need for detasseling and avoid potential problems associated with planting large acreages to varieties with a single source of cytoplasm. The double duplication method also should be immediately applicable to various other agriculturally important species.

The method consists of selecting pairs of chromosomal interchanges (designated by "a" and "b" below) from currently available stocks according to the following criteria. First, the breakpoints of each of the interchanges must occur in the same arm in each of the chromosomes. Next, the order of the breakpoints must be reversed in the two chromosomes with respect to their centromeres. Also, a male-sterile (ms) locus must be located in the arm containing the breakpoints in one of the chromosomes. The male-sterile locus ideally should be near one of the breakpoints. A simple representation is diagrammed below.

Stocks homozygous for each of the two chromosomal interchanges and for the normal male-sterile allele are crossed. The chromosome constitution of progeny resulting from such a cross is represented below.

The progeny (each heterozygous for the two interchanges) are crossed, as the female parent, with a stock possessing a chromosome complement that is normal but carrying the desired male-sterile gene in the heterozygous condition. One-sixth of the total progeny from the previous cross should be of the desired genotype. The desired progeny contain a duplication for the "between breakpoints" region of each of the two chromosomes involved (a double duplication) and a normal set of chromosomes carrying the recessive male-sterile allele. This can be represented as below.

The only chromosome combination to successfully be transmitted through the pollen is 2 & 4. Chromosome combinations 1 & 3, 1 & 4, and 2 & 3 all result in aborted pollen grains or ones that are unable to compete with normal pollen. The line diagrammed above is crossed, as the male parent, to plants homozygous for the recessive male-sterile allele and with a normal chromosome complement. All the progeny from such a cross should be male-sterile and the type to be used in commercial seed production.

A Donald F. Jones Scholarship has been awarded to carry out the above research.

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3. Position of bm_1 in chromosome 5.

The T1-5 (8041) interchange was shown by diakinesis observations on intercrosses with the other T1-5 interchange stocks to have the

breakpoints either in the short arm of 1 and the long arm of 5, i.e. SL, or in LS. Linkage tests with markers show that the break in chromosome 1 was in the long arm, indicating it is an LS interchange. The break-point in 5 is close to the centromere. A linkage test in a stock homozygous for the interchange shows that bm_1 and pr are now independent. Hence, bm_1 is not as close to the centromere as we had formerly believed or hoped, and is not absolutely reliable as a centromere marker. We list the breakpoints as being at 1L.80-5S.10. The break was in 5L in Longley's original list.

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C. R. Burnham

4. A 3-chromosome triple interchange stock.

The interchange stocks T8-9b (8S.67-9L.75), T8-10 (5944) (8L.75-10L.40), and T9-10b (9S.13-10S.40) were used for the three possible intercrosses. In each intercross, the breakpoints in the common chromosome were in opposite arms in the two parents. The permanent ⊙ 6 that arose by crossing over in the differential segment to produce a tripartite chromosome was established from each of the three intercrosses. The studies of chromosome pairing in intercrosses between the ⊙ 6 stocks will be reported elsewhere.

By intercrossing two of the permanent ⊙ 6 stocks, backcrossing to one of the parent ⊙ 6 stocks, followed by selection of plants whose sterility suggested they carried the three different tripartite chromosomes, a stock has been selected which is homozygous for those three chromosomes. The following testcross results verify this conclusion:

1. cross with standard normal = ⊙ 6 + 7II
2. cross with each of the 3 permanent ⊙ 6 = ⊙ 4 + 8II.

In this stock in which the three interchanges are combined, chromosomes 8, 9, and 10 are marked by an interchange breakpoint in each arm. The efficiency of this 3-chromosome, triple interchange stock remains to be tested.

C. R. Burnham

5. The synthesis of two-chromosome double interchanges.

Two-chromosome double interchange stocks were synthesized in maize by intercrossing single interchange stocks, each with breakpoints that involved the same two chromosomes. Combinations that combined both of the single interchanges into the two pairs of chromosomes were established presumably by simultaneous crossovers that occurred in the two differential segments.

A series of interchanges involving chromosomes 9 + (1 through 10) were employed along with 1-5's and 2-6's. Nine different opposite-arms double interchange stocks were obtained in maize involving the following chromosomes: 1-9, 2-9, 4-9, 5-9, 6-9, and 9-10 from 9 + (1 through 10) series, one 2-6, and two different 1-5's. The series involving 9 covers all chromosomes except 3, 7, and 8. Five different I-IV same-arms double interchange stocks were also synthesized in *Neurospora crassa*.

Several of the synthesized two-chromosome double interchange stocks in both maize and *Neurospora* were tested for their effectiveness as linkage detectors by crossing them with multiple marker stocks. It appears that such stocks can be more effective than other interchange techniques in locating unplaced genes.

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1. A rapid screening technique for photosynthetic mutants.*

Photosynthetic mutants have provided a valuable approach to the resolution of questions concerning photosynthetic mechanisms (Levine, R. P., 1969, Ann. Rev. Pl. Physiol. 20:523-540). As the use of mutants necessitates their rapid identification, an *in vivo* screening technique was developed to locate photosynthetic mutants that have normal pigment

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and structural appearance. This technique has been used to locate Zea mays mutants of the above type.

A screening technique was developed by Levine for algal mutants which compared levels of chlorophyll fluorescence. Colonies which were blocked in photosynthetic electron transport, either by chemical inhibition or by mutation, showed higher visual fluorescence than normal types (Bennoun, P. and R. P. Levine, 1967, Plant Physiol. 42:1284-1287; Levine, R. P., 1971, In: A. San Pietro, ed. Methods of Enzymology, XXIII, Part A. Academic Press, N.Y., pp. 119-129). The feasibility of a similar technique for higher plants was suggested since in vivo fluorescence of whole plant leaves could be observed and increased with photosynthetic inhibitors (Stokes, G. G., 1852, Phil. Trans. Roy. Soc. London 1852: 463-562; Kantsky, J. and A. Hirst, 1931, Naturwissenchaften 19:964).

Young leaves of tomato, spinach, the plastome mutant of Oenothera hookeri (Stubbe, W., 1959, Z. Vererbungslehre 90:288-298) and suspect mutants of Zea mays were used.

Whole leaf fluorescence could be observed and photographed in the dark through a Corning 2030 red filter which transmits wavelengths above 640 nm. Fluorescence was excited by a tungsten light (2×10^4 ergs/cm^2. sec.) passed through a 6 mm heat absorbing glass (or 10 mm water) and a Corning 4305 blue filter. This filter had a peak transmission of 473 nm and a range from 320 to 640 nm. Leaves were placed directly on the blue filter and covered by the red. An alternate method employed a spectroline SL-3660 long wave ultraviolet lamp for excitation of fluorescence. This lamp had a peak output at 360 nm and a range from 315 to 420 nm at an intensity of 1×10^4 ergs/cm^2·sec. The plant leaves were suspended 7 mm from the lamp by a thin polyethylene sheet and viewed through a red acrylic cutoff filter (Rohm and Hass 2444) that transmits light above 605 nm.

In order to show that a variation in fluorescence was indeed correlated with functionality of the photosynthetic apparatus, a comparison of the level of fluorescence was made between normal leaves and those treated with photosynthesis inhibitors. Quite striking differences were noted in the visual fluorescence when plants were treated with these

inhibitors. As a further proof, the plastome mutants of Oenothera, in which variegated (mutant-normal) leaves are produced, were also examined. Mutant sections fluoresced intensely compared to normal sections. When treated with electron transport inhibitors normal leaf parts fluoresced as brightly as the mutant sections, but the fluorescence of the mutant areas was no further increased by chemical inhibition. These plants were reported to be PS-II mutants (Fork, C. D. and U. W. Heber, 1968, Pl. Physiol. 43:606-612).

These results indicate that when electron transport is blocked between the two photosystems, whether by chemical inhibition or mutation, the affected plant tissue can be identified visually by increased fluorescence. As further proof that the fluorescence technique is useful for screening higher plants, we have isolated suspected PS-I and PS-II mutants of Zea mays seedlings due to their high in vivo leaf fluorescence. A more detailed report has been submitted to Plant Physiology and additional work is now underway.

As a practical note, care must be taken that there is little variation in chlorophyll content or in thickness of leaves which are scanned. These variations will alter fluorescence since more pigment or a thicker cross section would allow more re-absorption by chlorophyll.

We acknowledge the kindness of M. G. Neuffer, University of Missouri, who supplied Zea mays seeds used for screening.

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1. Two new B-type translocations involving chromosome 10.

X-ray-induced A-B translocations involving both arms of chromosome 10 have been identified. TB-10b, located on the long arm, is proximal to li, g_1, r and sr_2. The TB-10S mentioned in MNL 45:144 is

now verified and can be designated TB-10c; the breakpoint is on the short arm proximal to nl and oy.

J. B. Beckett

2. Location of new mutants by the A-B translocation method.

Following the procedure outlined earlier (MNL 45:144), 161 mutants were tested this year with a slightly modified and improved set of A-B translocations. The collection included 113 selected new mutants from EMS and NG treatments as well as 48 old cases that had received an inadequate test last year. The translocations used were the same as last year except that TB-1a was substituted for TB-1c, and TB-2L, $3L_{7285}$ and TB-6a were omitted. Translocation 10S has also been verified and designated TB-10c (see Beckett, above).

Fifty-nine of the 161 mutants tested have been tentatively located to chromosome. They have been added to those found last year and placed on a revised chromosome map (figure 1). Temporary symbols are used on the map as follows: w (white), wl (yellowish white), l (yellow), v (virescent), pg (pale green), pgs (pale green spotted), yg (yellow green), cb (crossbanded), pb (piebald), str (striped), gs (green stripe), ys (yellow stripe), wlb (white leaf blade), alb (albescent), spk (speckled), nl (narrow leaf), ad (adherent), d (dwarf), nec (necrotic), gl (glossy), bf (blue fluorescent), et (etched endosperm), sh (shrunken endosperm).

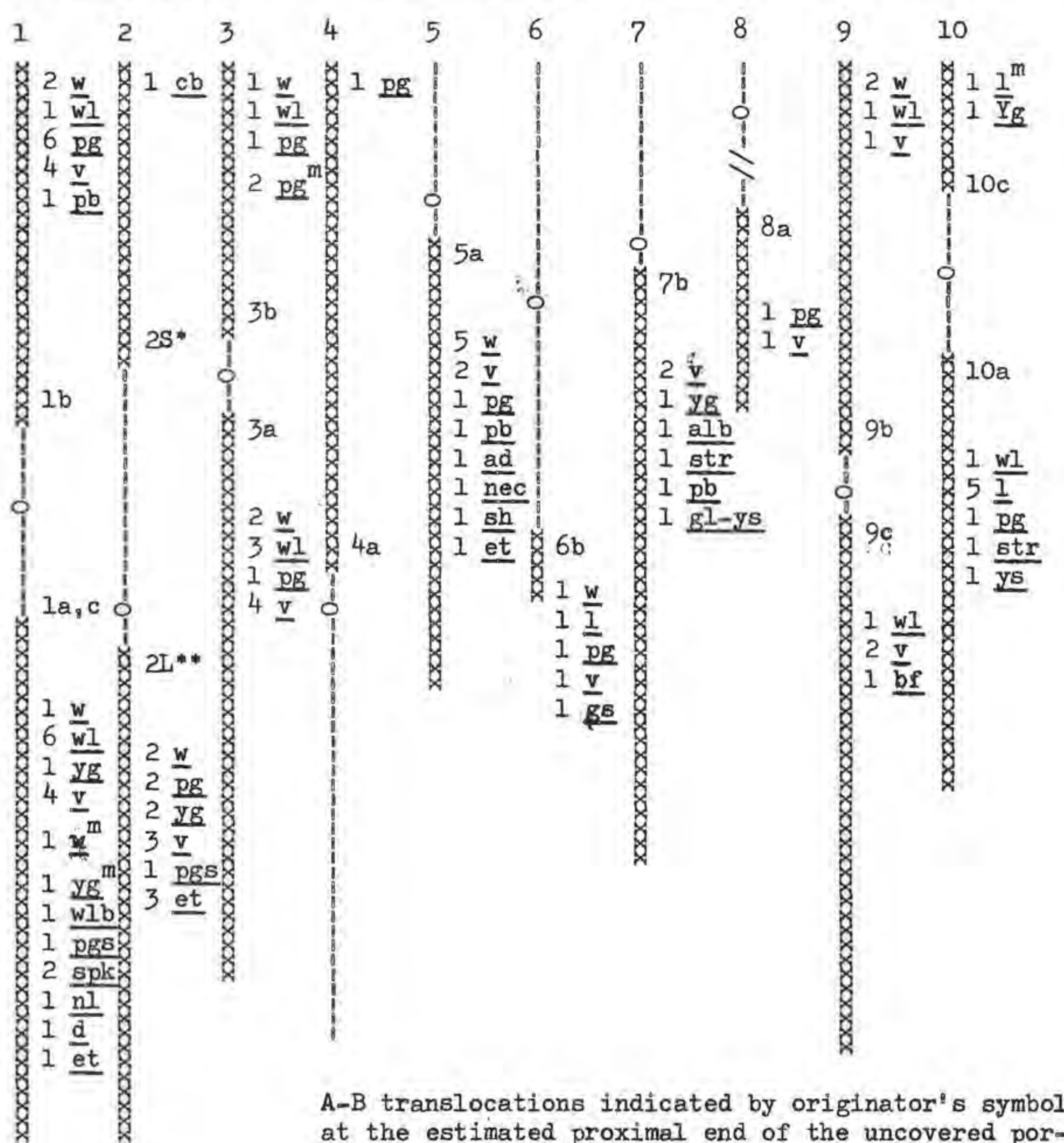
M. G. Neuffer
J. B. Beckett

3. New mutants induced by ethylmethanesulfonate and nitrosoguanidine.

Following procedures outlined in MNL 45:146, ears of vigorous genetic stocks were crossed by similar pollen treated with ethylmethanesulfonate (EMS) or nitrosoguanidine (NG). The resulting kernels were planted, the seedlings were noted for mutants, and the mature plants noted and selfed. The selfed ears were observed for segregation of endosperm texture and morphology mutants (not for aleurone color, as r and c were segregating in the initial parents), and a sample was planted in sand benches to test for seedling mutants. Excluding mature plant

Figure 1

Linkage map with A-B translocations and tentatively located mutants.



A-B translocations indicated by originator's symbol at the estimated proximal end of the uncovered portion (xxxx). The numbers and types of mutants uncovered are listed beside each region.

* TB 2S, $3L_{6270}$

** TB 2L, $1S_{4464}$ or TB 2L, $3L_{7285}$

characters, a total of 1208 new mutants was found. The results of this experiment are summarized in Table 1.

Table 1. Summary of results from progeny tests of kernels produced from pollen treated with ethylmethanesulfonate (EMS) or nitrosoguanidine (NG) in paraffin oil. Frequency x 10^{-3} in parentheses.

	kernels planted	surviving plants*	selfed ears tested	endosperm mutants		seedling mutants	
Control	587	523	414	0	(0)	3	(0.7)
EMS	7645	6007	4277	259	(61)	860	(201)
NG	1130	493	160	13	(81)	73	(456)

*These figures are low because of poor field conditions.

In spite of poor field conditions and problems of handling that are reflected in the data, there are distinct differences in survival and ear production between treatments. The NG treatment caused a striking reduction in germination and viability of surviving plants, while the EMS treatment did not. This difference was clearly seen when comparing the growing plants. Plants of the control and EMS progenies were vigorous and uniform, while those of the NG progenies were slow and extremely variable. Many did not survive till flowering, and only a few of those that did approached normal vigor and appearance.

Examination of F_1 seedlings and growing plants for probable dominant mutants yielded 24 pale green (pg), eight pale or yellow green sectored, one narrow leaf (nl) and one yellow green (yg) in the EMS-treated families, and three pg and one sectored in the NG-treated material. None was found in the control families. All of these cases (except one) either failed to produce ears or were not transmitted. The single exception was the yellow green case, which proved to be an excellent dominant yellow green mutant. This mutant will be described later.

The selfed ears included many that were segregating for various types of endosperm texture and morphology mutants, the analysis of which is presently being deferred.

A sample of thirty kernels from each selfed ear was planted in the sand bench, and the seedlings were examined for mutant types. The yield of seedling cases was much higher than expected when compared to the frequency of endosperm cases. The mutants included many of the known types as well as some that had not been seen before. A breakdown of seedling mutants into broad categories is presented in Table 2. Each category includes a wide range of variant types.

The white (w) seedlings include types with narrow stiff leaves, some with broad leaves, some that die quickly and others that grow normally to the 3-4 leaf stage. Some are chalky white, some almost translucent; some are bluish white, and some have patches of cells that become transparent. The yellowish white (wl) mutants have similar variations but also have varying amounts of yellow pigment; the narrow stiff-leaf type is rarely seen. The yellow (l) seedling types are more uniform and mostly normal in early development. Some are bright yellow, some faintly green and some a dull deep yellow. Some bleach to white rather quickly, and others remain yellow until the endosperm nutritional source is depleted. All the w, wl and l mutants are seedling lethals.

The virescent (v) class is highly variable in terms of chlorophyll expression but not for leaf texture and morphology. In all cases the mutant seedlings emerge with either reduced, defective or absent chlorophyll. After emergence they change at various speeds and in various patterns to something like normal appearance. The background or initial color differs from case to case including white, yellow, pale green and yellow green. Some turn green from leaf tip toward the base, others in the reverse order. Some turn green uniformly over the leaf, and others do so in small streaks, giving the leaf a grainy appearance; still others turn green in large irregular streaks and stripes. Many show indications of being sensitive to variations in light and temperature.

The pale green (pg) mutants have a reduced amount of chlorophyll, which remains uniform during the life of the plant. Some are faintly

Table 2. Breakdown of seedling mutants obtained in F_2 from crosses involving pollen treated with the chemical mutagens ethylmethanesulfonate (EMS) and nitrosoguanidine in oil

	EMS	freq. x 10^{-3}	NG	freq. x 10^{-3}	control oil	freq. x 10^{-3}
F_2 ears tested	4277		160		414	
white (w)	53	12	6	38	0	0
yellow white (wl)	60	14	8	50	0	0
luteus (l)	32	7	5	31	2	0.5
virescent (v)	99	23	9	56	0	0
yellow green (yg)	14	3	1	6	0	0
pale green (pg)*	131	31	17	106	0	0
Zebra stripe (zb)-piebald (pb)	28	6	1	6	0	0
necrotic (nec)	81	19	1	6	0	0
lethal (ll)	21	5	0	0	0	0
dwarf (d)-small*	181	42	17	106	1	0.2
adherent (ad)	21	5	0	0	0	0
streaked and speckled	46	11	3	19	0	0
striped (str)	15	4	1	6	0	0
yellow stripe (ys)	15	4	2	13	0	0
glossy (gl)	13	3	1	6	0	0
other	50	12	1	6	0	0
Total	860	201	73	455	3	0.7

*These classes are inflated because of difficulties of classification and the frequent occurrence of phenocopies.

green and die after endosperm depletion; others are darker green and live longer; some survive to maturity. Leaf texture and morphology is generally nearly normal. The yellow green (yg) mutants resemble the pg mutants but have varying amounts of yellow pigment. This class varies

in viability, but in most cases the mutants survive to maturity. Included are some which grow more vigorously than normal seedlings under winter greenhouse conditions. There are some mutants in this class that develop necrotic patches that cause withering of parts of the leaves but no lethal damage. There is also one dominant yellow green mutant.

The zebra stripe (zb)-piebald (pb) class includes those green and pale green seedlings that have diurnal crossbands or patches of lighter tissue. In some cases, the bands are regular, with sequences of two or more shades of green, yellow or white; in others, the banding is irregular and occurs in patches along the midrib or on the leaf blade. Also included here are a group of seedlings called white tip (wt), which are of two types: (1) those which emerge as a green seedling with white leaf tips, and (2) those which are initially observed as a white seedling with a faintly green leaf base, with subsequent development of chlorophyll in the direction of the leaf tip.

The necrotic (nec) class includes those that have an abrupt wilting or browning of the leaf tips which advances down the leaf, usually causing death of the seedling. Sometimes these areas are localized on the terminal third of each leaf or in zebra-like stripes, in which case the mutant is not lethal. In some the necrotic tissue gives off a brown exudate; in others the tissue wilts dry and turns white.

The lethal (ll) class includes all those that die abruptly from various unclassified causes; closer observation may move many of these into the necrotic class.

The dwarf (d)-small class includes all the small seedling mutants seen. A large number are typical broad leaf andromonoecious dwarfs which respond to gibberellic acid; others have stiff narrow leaves, some with pale green flecking; some are dark green. Some are intermediate in growth; others are extremely small, being only three cm tall after two months growth. Some have large leaves with shortened internodes. Others have miniature parts and can be described as tiny or pigmy.

The adherent (ad) class includes a wide range of types that have the common characteristic of having some leaf or coleoptile tissue adhering together. In some cases this is extreme, and the seedling bunches

up in a knot. In other cases only the first two leaves are stuck together, and the plant grows normally. In some cases the leaves are all rolled tightly, forming a smooth tube; in others, the leaves are bunched up and crinkled.

The streaked and speckled class includes wide variations of green with small streaks or specks of lighter (including white and yellow) tissue or lighter green leaves with streaks and specks of darker green tissue. In some cases the leaves are narrow and stiff. In others they have normal shape and texture.

The striped (str) class includes all variations of white, yellow and pale green striping, ranging from an occasional stripe to those as extreme as striate (sr_2). Some are associated with morphological differences, and others are not.

The yellow stripe (ys) class is quite narrow, including only individuals which resemble the known ys mutants. The phenotype is that of normal green leaf veins and light yellow green tissues between the veins.

The glossy (gl) class includes all those which have a glossy phenotype at the 1-4 leaf stage. Some are associated with changes in leaf morphology, and others are not.

The "other" class includes a miscellaneous lot of interesting cases which were hard to classify in terms of known mutants.

M. G. Neuffer

4. Dominant yellow green.

A single yellow green seedling appeared among 56 normal seedlings in the F_1 following EMS treatment. The plant, which remained yellow green till maturity, was selfed. Sixty kernels planted from the selfed ear produced ten normal green, 33 bright yellow green and eight pale yellow seedlings. The yellow seedlings died as soon as the endosperm reserves were depleted. The yellow green seedlings grew more rapidly than the green and produced normal tassels and ears. (This rapid growth occurs only in the winter greenhouse; in the field, the yellow green plants are much smaller than normal.) Yellow green plants were crossed on normal sibs and other genetic testers. In all cases, seedling tests of the sib

and testcross ears gave a 1:1 segregation for yellow green and green seedlings.

Yellow green plants were crossed by each of the A-B translocations (MNL 45:144) and plantings made from the resulting seeds. All of the ears gave a 1:1 segregation for yellow green except the cross by TB-10c, which had 69 green, 29 yellow green and ten pale yellow seedlings. The pale yellow seedlings appeared to be hypoploids, thus indicating that the mutant has a yellow seedling phenotype when hemizygous.

These results indicate that the mutant is a dominant yellow green in heterozygotes and a lethal yellow in homozygotes and hemizygotes and that it is located on the short arm of chromosome 10. It is tentatively designated as $\underline{Yg_4}$.

M. G. Neuffer

5. Tan necrotic.

Two cases in which the mutant seedlings emerged with tightly rolled leaves were found in the EMS progenies. When the leaves were unrolled, they were found to be tan in color with uniformly spaced bands of dark brown tissue. A slight amount of chlorophyll appeared on the coleoptile and underlying leaf sheath at soil level. The seedlings grew very little and died in a few days. A good but not exclusive test by existing A-B translocations failed to uncover either mutant.

M. G. Neuffer

6. Pale green spotted.

Several cases characterized as pale green with fuzzy dark green spots have been found in EMS, NG and mutator system progenies. One of these (pgs, E-464), which was found in an EMS-treated culture and has been located on the long arm of chromosome 2, can be described as an example. The seedlings emerge as a moderate pale green with good vigor. At about the 2 leaf stage, small fuzzy spots of dark green (slightly larger than a pin head) appear and increase in number until there may be 40-100 on a leaf. Occasionally a spot may be much larger, in which case it will be elongated, conforming to the pattern of cell lineage of the

leaf. The border of the spot, however, is still fuzzy, as though a precursor for normal chlorophyll were diffusing into the light green tissue. Mutant seedlings lack vigor and rarely grow to maturity even under the best of culture conditions. A second such mutant (pgs, M-21) appeared in a mutator system progeny and has been located in the long arm of chromosome 1.

M. G. Neuffer

7. A tandem duplication and an intrachromosomal displaced duplication induced by irradiation.

This project has been discussed in detail in previous reports. Simply, the procedure to obtain duplications is to irradiate diploid material which is heterozygous for two very closely linked markers in the repulsion phase and to select testcross progeny which have both dominant markers. This was done with A sh/a Sh kernels which were planted and crossed with a sh/a sh plants. The A Sh kernels produced were tested genetically for the presence of duplications. These kernels are of three types: (1) crossover cases, (2) trisomes--in which there has been nondisjunction and the constitution of the kernels is A sh/ a Sh/a sh, and (3) duplications.

It was found that most of the A Sh cases were crossovers or trisomes. Irradiation greatly increases the frequency of nondisjunction. However, two cases of duplications have been isolated and cytologically identified.

The first is a tandem duplication (tDp3L a), which arose from a translocation between homologous chromosomes. It is a duplication of about 20% of the long arm of chromosome 3. There is generally a large buckle in the chromosome 3 pachytene bivalent. The exact nature of the duplication is unknown--i.e., whether the proximal segment carries the A sh markers and the distal segment carries the a Sh markers or vice versa. Genetic data for this duplication are presented in Table 1.

Table 1

Cross	No. of plants	No. of gametes	Percent			
			A Sh	A sh	a Sh	a sh
1. A sh-a Sh/a sh X a sh/a sh	7	2,256	36.17	13.34	11.97	38.52
2. a sh/a sh X A sh-a Sh/a sh	28	35,402	2.71	34.23	2.07	60.99
3. A sh-a Sh/a Sh X a sh/a sh	10	3,381	38.57	9.41	52.03	0.00
4. a sh/a sh X A sh-a Sh/a Sh	8	9,322	5.59	26.91	67.50	0.00

It may be seen from the data in which the duplication heterozygote was the female parent that A sh and a Sh gametes are formed in about equal numbers. The data from the reciprocal crosses indicate that the duplication is poorly transmitted through the pollen. In cross 2 there is a great excess of A sh gametes over a Sh gametes. This is because most of the a Sh gametes now carry the duplication; they are actually a Sh-a sh. The relative proportions of A sh, A sh-a sh, a Sh, and a Sh-a sh gametes depend on where the markers are positioned in the duplicated segment and also depend on which markers are in the distal and proximal segments if there is polarity in pairing. There may be a greater tendency for the distal element to be paired and the proximal element unpaired (in the buckle) or vice versa. Polarity in pairing cannot be determined by genetic data without knowing the placement of the markers in the duplicated segments and may not be determined by cytological data, as the buckle may shift after the time of crossing over as in the case of the displaced duplication of 3 in chromosome 9. This is explained in Table 2.

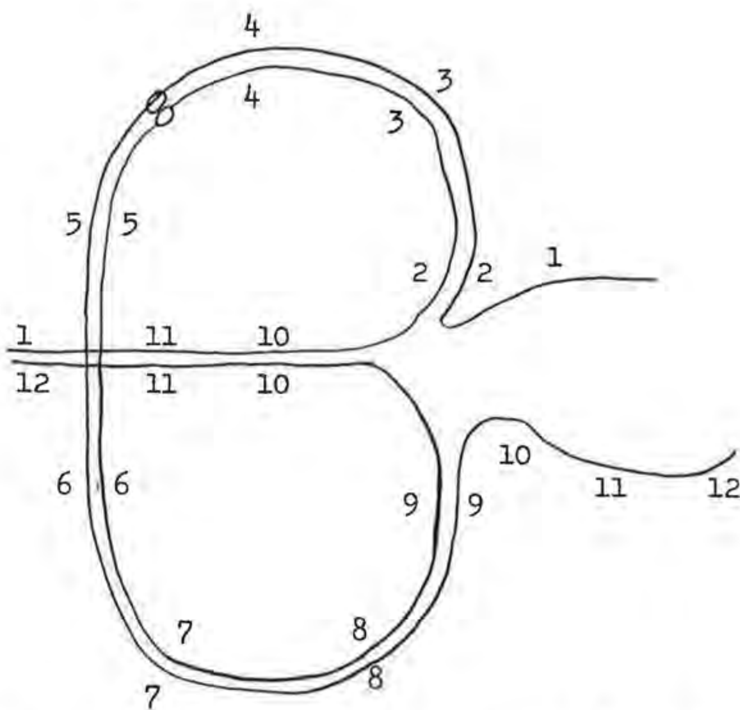
Table 2. Effects of different modes of pairing and crossing over on the frequency of recombinational gametes

	Recombinational gametes			
	A sh	A sh-a sh	a Sh	a Sh-a sh
A sh / a Sh / I a sh II — c.o. in I	-	X	X	-
a Sh / A sh / I a sh II — c.o. in II	X	-	-	X
a Sh / A sh / I a sh II — c.o. in I	X	-	-	X
A sh / a Sh / I a sh II — c.o. in II	-	X	X	-

From the genetic data there must be a greater frequency of modes 2 or 3 than of 1 or 4. The position of the $a_1 sh_2$ loci in the duplication can be easily determined by the use of outside markers such as lg_2 and et.

The second duplication is an intrachromosomal displaced duplication (dDp3L-3S); a chromosome segment containing the a Sh loci has been interpolated into the short arm of chromosome 3. If the sequence of normal chromosome 3 is 1 2 3 4 ctr 5 6 7 8 9 10 11 12 the sequence of the

dDp3L-3S chromosome is 1 11 10 2 3 4 ctr 5 6 7 8 9 10 11 12. A pairing configuration often seen at pachynema is shown below:



The genetic data on this duplication are given in Table 3.

Table 3

Cross	No. of plants	No. of gametes	Percent			
			A Sh	A sh	a Sh	a sh
A sh-a Sh/a sh X a sh/a sh	21	8,029	24.54	23.90	24.21	27.35
a sh/a sh X A sh-a Sh/a sh	2	1,961	10.61	35.80	14.33	39.26

As may be seen from the cross where the female plants were the duplication heterozygotes, the frequencies of the different types of gametes are about equal. This indicates that there is 50% recombination between the two elements of the duplication, a frequency expected on the basis of cytological information. When the duplication heterozygote is the male parent, the data indicate that the duplication bearing pollen

does not compete on equal terms with the normal pollen. The depression of the a Sh class relative to the A sh class is probably because the a Sh markers are in the duplication segment in the short arm and generally the a Sh gametes are actually a Sh-a sh.

G. G. Doyle

8. A telocentric trisome and its potential use in the production of commercial hybrid corn using genic male sterility.

A telocentric trisome (2n + t6L) arose spontaneously in a culture of primary trisome 6 probably by the transverse division of a univalent chromosome 6 at meiosis. One telocentric trisome in an otherwise normal progeny was recognized by a peculiar ratio of Y kernels to y kernels on the ear. There were 90 Y kernels or 25.9% and 248 y kernels or 74.1% instead of 38.2% Y and 61.8% y as found in a simplex primary trisome. In addition all the Y kernels were noticeably smaller than most of the y kernels. Cytological examination of this progeny revealed the presence of a telocentric chromosome consisting of the long arm of chromosome 6, along with the normal complement.

At the pachytene stage of meiosis this telocentric chromosome is frequently paired nonhomologously with itself. At diakinesis the trivalent frequency has been found to be 34.6%. Only 133 cells have been observed so this is a rough estimate. The pattern of chromosome disjunction can be determined by examining the quartet stage of meiosis. Since the telocentric chromosome 6L does not have a nucleolar organizer, spores which have only this chromosome instead of a normal chromosome 6 have a diffuse nucleolus. The frequency of quartets with two spores with diffuse nucleoli has been found to be only 3.15% (50 out of 1,585 quartets). This indicates that the two normal chromosomes 6 generally disjoin from each other. If the disjunction of the chromosomes of the trivalent were at random then we would expect the frequency of quartets with two spores with diffuse nucleoli to be 11.5% (1/3 X 34.6).

Spores with only the telocentric are inviable. The resulting pollen abortion is very small (1/2 X 3.15% or 1.58%). Background pollen abortion would prevent the identification of the telocentric trisome by pollen abortion rate. There is no noticeable semi-sterility on the ears

of telocentric trisome plants.

The telocentric chromosome (t6L) is transmitted when a normal chromosome 6 is also present. The transmission rates can be studied easily because the telocentric is marked with Y and the normal chromosomes are marked with y. The Y_1 locus is very close to the centromere and, since there is reduced pairing of the telocentric and the normal chromosome, there is less chance of crossing over. See Tables 4 and 5.

Table 4. Transmission rates of hyperploid gametes n + t6L

Cross	No. of plants	Number of kernels				Transmission rates	
		Y	Y-y mosaics	y	Total	% Y	% Y-y mosaics
y/y X t6L Y/y/y	36	331	30	19,149	19,510	1.70	0.15
t6L Y/y/y X y/y	90	4,774	3	18,494	23,271	20.51	0.01

There were a number of kernels which were mosaic for Y and y (generally half and half). The telocentric chromosome is apparently frequently lost in the development of the endosperm. The difference in the frequency of mosaic kernels in the reciprocal crosses reflects the different constitutions of the two endosperms, of course. In the first case it is t6L Y/ y/ y/ y and in the second case it is t6L Y/t6L Y/ y/ y/ y/. The frequency of mosaic kernels when the female parent is the telocentric trisome theoretically should be the square of the frequency of mosaic kernels when the telocentric trisome is the male parent.

The results of progeny tests of plants grown from Y kernels are given in Table 5.

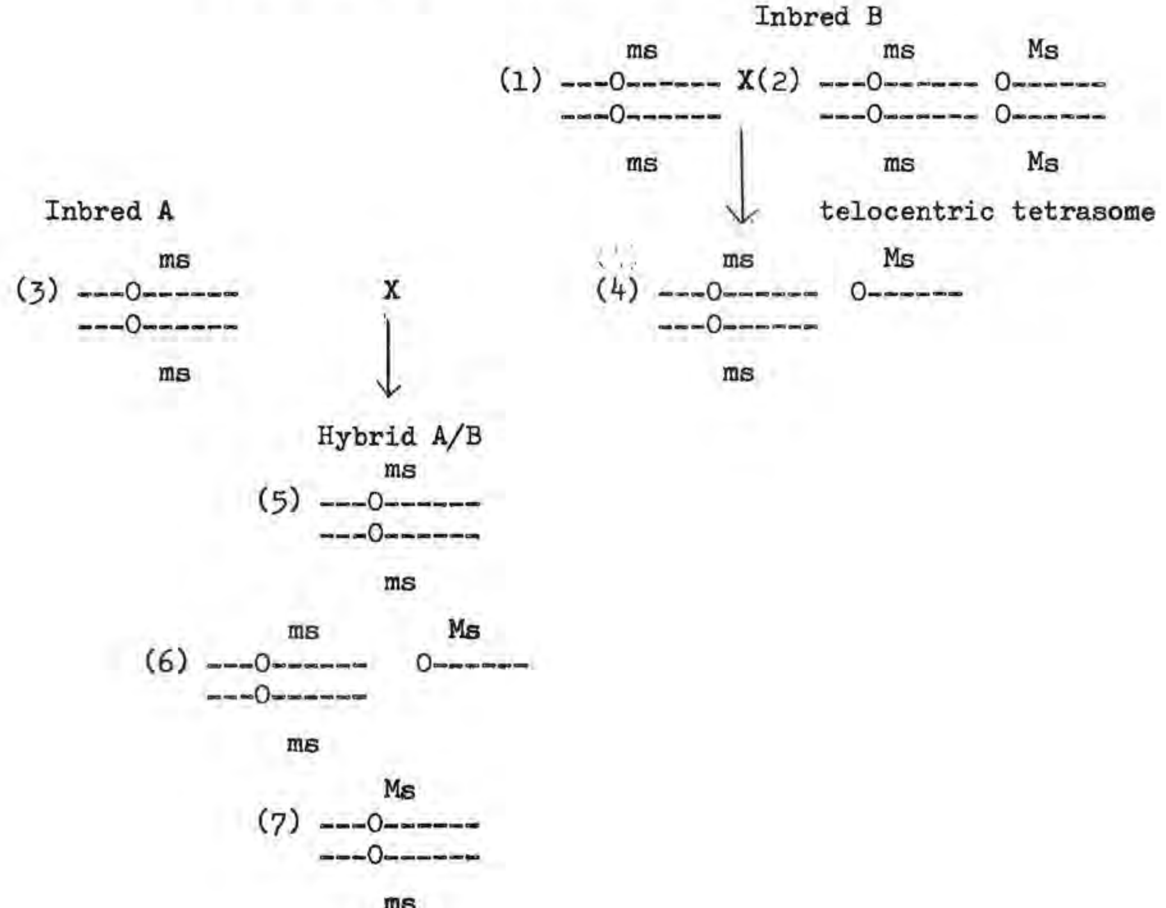
Table 5

Cross	Number of plants with constitutions of					% "cross-overs"
	t6L Y/y/y	Y/y/y	Y/y	y/y	Total	
(t6L Y/y/y X y/y) X y/y	108	0	1	2	111	0.92
(y/y X t6L Y/y/y) X y/y	21	0	2	0	23	8.70

There were two cases when the telocentric trisome was the female parent in which the progeny of Y kernels was all y. Probably the telocentric was lost somatically. The data are inadequate but it appears that there is a very low crossover rate between the Y locus and the centromere when the telocentric trisome was the female parent. When it was the male parent, there is a much higher apparent crossover rate, but this is not accurate because we are selecting for crossover events when Y kernels are used. The Y gene can be transmitted through the pollen only when it has crossed over on to a normal chromosome or is in hyperploid gametes which seldom function. If we multiply the frequencies of crossover events in the Y kernels times the frequencies of Y kernels in the total progeny and multiply this times two, the crossover frequencies are 0.38% for the female (20.52 X 0.92 X 2) and 0.32% for the male (1.85 X 8.70 X 2).

These data suggest the possibility of using this telocentric trisome in the commercial production of hybrid corn involving genic male sterility. A male sterile locus (ms_1) is very closely linked to the Y locus; the crossover rate is less than 1%. Since the hyperploid gametes are transmissible through the pollen, it is possible to get the telocentric trisome in different cytoplasms. Commercial hybrid corn could be produced by the following procedure.

Procedure for producing hybrid corn



Stock (1) can be maintained by crossing it as the female with stock (4), the telocentric trisome. Stock (2) can be produced by selfing the telocentric trisome. The telocentric tetrasome should be fairly stable. It probably can be recognized by a distinctive phenotype. It has not been isolated yet. The progeny (4) of a tetrasome and a disome should be mostly trisomic. The genic male sterile inbred A (stock 3) [which is maintained in the same fashion as stock (1)] is crossed with the telocentric trisome of inbred B (stock 4). The resulting hybrid should be mostly stock (5), which can be used as the female parent in a cross with another inbred for a three way cross, or with a hybrid produced by detasseling, by cytoplasmic male sterility, or by one using another genic male sterile and another system for maintaining male sterile lines. The double cross hybrids would all be fertile. The

frequency of stock (7) is so low as to be tolerable. The telocentric trisome, stock (6), which would also occur in stocks (1) and (3), could probably be removed from the field before pollination. If its phenotype is not distinctive enough to be recognized, then it is possible to translocate any dominant gene marker onto the telocentric. If white hybrids are desired, it is possible to eliminate most of the trisomes by using the $\underline{Y}_1$ gene marker. Some of the telocentric trisomes could be eliminated by using only the heavier seed.

This procedure has some advantages over the method proposed by Dr. Earl Patterson in which a duplicate-deficient chromosome is used to carry the Ms allele. The duplicate-deficient chromosome is not transmitted through the pollen and it remains in the cytoplasm in which it was produced. Thus, if this method is widely used, it would lead to homogeneity of cytoplasms which would be dangerous since a new mutant form of a pathogen could arise to attack lines with this cytoplasm. (This difficulty could be overcome by crossing the duplicate-deficient line with a tetraploid. The resulting triploid could then be crossed as the male parent onto diploids and after a few generations the trisomic progeny could be removed from the population leaving the duplicate-deficient chromosome in new cytoplasmic backgrounds.) Since the telocentric is transmitted at a low frequency through the pollen we do not have this problem.

However, the main advantage of the telocentric trisome system is that the pollen parent (4) of the initial commercial cross would be almost all of the desired type, whereas in the duplicate-deficient system only half of the plants in the pollen parent rows would be male fertile.

The disadvantage of the telocentric system is the transmission of the hyperploid gametes through the pollen; while the frequency is low (1.85%), it is not tolerable. It should be possible by selection and structural modification of the telocentric by irradiation to lower this frequency.

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1. Evaluation of mass-selected populations based on performance of selected S_2 line topcrosses.

In 1968, approximately 1000 plants of the Hays Golden variety (HG) and of each of three improved mass-selected populations were grown in the nursery. The three improved populations were derived from HG by (1) mass selection for high grain yield for 12 generations (C12), (2) thermal neutron irradiation of seeds plus mass selection for high grain yield for 13 generations (I13), and (3) mass selection for prolificacy for 7 generations (P7). Approximately 300 of the best-appearing plants were self-pollinated in each population, and seed was saved from those that were disease-free and standing well at harvest. In 1969, selection was practiced between and within S_1 lines of each population, and selfed seed was saved from the best plant of each selected line. Further selection between and within S_2 lines was practiced in 1970. Selected S_2 lines were also topcrossed to Oh43 and to the single cross N7A x N7B.

Table 1. Grain yield (q/ha) of selected S_2 line topcrosses.

Tester	Popn.	No. of lines	Grain yield q/ha					
			Mean	Range		Best lines		
				Low	High	Top 5	Top 10	Top 20
Oh43	HG	100	88	67	101	99	98	97
	C12	90	98	82	117	112	111	109
	I13	80	96	74	114	109	107	105
	P7	72	97	77	114	110	108	105
	Checks	9	94	72	114	106		
N7AxN7B	HG	99	90	69	108	104	101	99
	C12	119	96	70	114	112	109	107
	I13	92	95	70	110	109	107	105
	P7	81	94	70	119	109	106	104
	Checks	9	84	69	107	93		

The hybrids developed by topcrossing were grown in yield trials in 1971. Plot size was 5.8 M^2 and plant density was 51,666 plants per hectare. Preliminary yield results are presented in Table 1.

Hybrids involving lines from selected populations show a definite superiority over those from the parent population whether you look at the mean of all lines, the highest yielding line or some subset of the highest yielding lines. Although lines from the three selected populations performed somewhat the same, the C12 lines appear to have a slight advantage over I13 lines. We can also conclude that 7 generations of mass selection for prolificacy was about as effective as 12 or 13 generations of mass selection for high grain yield. Hybrids involving lines from improved populations compared very favorably in yield with the best Nebraska Experiment Station hybrids included as checks. One hybrid check, a cross between two related lines (N7A x N7B) was a relatively low yielder as shown in Table 1.

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1. Effects of genetic and environmental factors on production of phytoalexin from *Helminthosporium turcicum* of *Zea mays*.

Genotypes used were *Ht Ht Bx Bx*, *Ht ht Bx Bx*, *Ht Ht bx bx*, *ht ht Bx Bx*, and *ht ht bx bx* (see MGCNL 45).

Production of inhibitory substances (presumably phytoalexin) decreased in the following order, as determined by a bioassay test with leaf diffusates on spore germination: *Ht Ht Bx Bx*, *Ht Ht bx bx*, *Ht ht Bx Bx*, *ht ht Bx Bx*, *ht ht bx bx*, and control (sprayed with water only). Differences between genotypes were all highly significant. *Ht ht Bx Bx* was much less inhibitory than *Ht Ht Bx Bx*.

Environmental factors studied were: attached or detached leaf, inoculum concentration, predisposing temperature, seedling age, and days from inoculation until collection of diffusate. These all significantly affected production of phytoalexin.

Much more phytoalexin was produced by the attached than by the detached leaf. A high spore concentration increased both the rate and amount of phytoalexin over a low concentration. A predisposing temperature of 70° F produced more inhibitory substances than did 80-90° F. Diffusates from seedlings inoculated at the fifth and sixth leaf stage inhibited spore germination more than seedlings inoculated at later stages. Production of phytoalexin increased up to the third, fourth or occasionally the fifth day after inoculation. After this time, the inhibitory effect gradually disappeared.

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1. A new anthocyanidin in maize: luteolinidin.

The gene sm (salmon silk) in the presence of red pericarp (P^{rr}, etc.) results in silks which are salmon in color. The P locus determines pericarp and cob color. Of particular interest is the P^{rr} allele which gives red pericarp and cob color (Emerson et al., 1935). This study was directed to the identification of pigments which cause salmon silk and red pericarp color in the genotype P^{rr} sm/P^{rr} sm.

A genetic marker stock, P^{rr}Y Pl sm py/P^{rr} Y Pl sm +, which has salmon silks, red pericarp, and red cob was used for this study. Silks from this stock about 5 days after emergence were removed from the ear and ground in acidified 80% methanol. Pericarp from mature kernels of the same stock was obtained by soaking kernels for 4 hours and hand-peeling the pericarp. Similarly, pericarp was ground in acidified 80% methanol. The pericarp and silk samples were allowed to stand for 24 hours, filtered, and reduced at 40° C with a rotary evaporator. Separation and identification of anthocyanins was accomplished by the usual techniques, paper chromatography, acid hydrolysis, and light and UV

spectrophotometry (Harborne, 1967). Four solvent systems were employed for paper chromatography with No. 1 Whatman paper. The solvents were: BAW, n-butanol-acetic acid-water (4:1:5, top layer); 1% HCl, water-conc. HCl (97:3); HOAc-HCl, acetic acid-conc. HCl-water (15:3:82); and Forestal, acetic acid-conc. HCl-water (30:3:10). Spectral determinations first were made in methanol containing .01% conc. HCl and then after the addition of 6 drops of a 5% $AlCl_3$ solution.

Acid hydrolysis of salmon silk extracts yielded one anthocyanidin which was orange in color. R_f values and spectral maxima are presented in Table 1. For comparison, R_f values and spectral maxima for luteolinidin are cited (Harborne, 1967). R_f values for the salmon silk anthocyanidin and luteolinidin are similar in Forestal and BAW solvents. Spectral maxima for the two pigments were also similar in MeOH-HCl as were the bathochromic shifts due to the $AlCl_3$ reagent. Based upon these similarities, the unknown anthocyanidin derived from salmon silks is identified as luteolinidin.

Table 1. Colors, R_f Values and Spectral Maxima of Salmon Silk Pigments

Anthocyanidin	Visible color	R_f values (x 100) in				MeOH-HCl	$AlCl_3$
		Forestal	BAW	1% HCl	HOAC-HCl	λmax(nm)	$\Delta\lambda$ (nm)
Unknown Anthocyanidin (hydrolysate)	orange	63	61	4	17	499	50
Luteolinidin*	orange	61	56	--	--	493	52
Anthocyanin							
No. 1	orange	--	27	17	39	--	--
No. 2	orange	--	57	33	42	--	--

*Values as cited by Harborne (1967).

Two anthocyanins based on luteolinidin have been isolated from salmon silks. Color and R_f values are reported in Table 1. No. 1 has

R_f values like luteolinidin 5-glucoside (Harborne, 1967) and is the most abundant. The identity of No. 2 is unknown.

The same pigments were found in the red pericarp ($\underline{P}^{rr}$) as in salmon silks. Results given in Table 1 apply equally well for red pericarp and are not repeated. Red pericarp color is, consequently, due to two anthocyanins based on luteolinidin.

Red silk color is common in corn and is easily distinguished from salmon. This red pigment was isolated from the silks of the inbred line NC 236 by the methods previously described. The anthocyanidin was prepared by acid hydrolysis and purified by paper chromatography. Two anthocyanidins, cyanidin and pelargonidin, were identified by co-chromatography with authenticated anthocyanidins in two solvent systems. These two anthocyanidins have previously been reported to be responsible for plant and aleurone color in corn.

It, thus, appears that two distinct pigment systems exist for the determination of silk color. The first is red silk color, which is based upon anthocyanins of cyanidin and perlargonidin. Red silks are determined by certain R alleles ($\underline{R}^{rr}$, $\underline{r}^{rr}$, etc.) when $\underline{A}_1$ is present (Emerson et al., 1935). The second is salmon silk color, which is based upon anthocyanins of luteolinidin. Salmon silk is determined by the sm allele when certain P alleles ($\underline{P}^{rr}$, etc.) are present.

A structural comparison of luteolinidin versus cyanidin and pelargonidin is revealing. Luteolinidin is deoxy for the 3 position while cyanidin and pelargonidin are hydroxylated. This suggests that 3-deoxy compounds, flavonones or flavones, would be likely precursors of luteolinidin. On the other hand, 3-hydroxyl compounds, dihydroflavonol or flavonol, would be likely precursors of cyanidin and perlargonidin. The need for different precursors could account for the two distinct genetic systems controlling salmon and red silk color.

References:

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C. S. Levings, III

2. Nonrandom fertilization by pollen in mixtures.

Experiments have been underway to investigate selective fertilization effects involving pollen of strains with contrasting endosperm color. The varieties chosen for an investigation of the hereditary characteristics of the phenomena are Jarvis, which has yellow endosperm, and Weekley, which has white endosperm. The technique used to measure the trait is to pollinate pairs of plants of each variety which flower at the same time with mixtures of their pollen. At harvest time, 100 kernels of each ear are classified for endosperm color. Table 1, which gives the results expected if fertilization by the two kinds of pollen in the mixture is random, shows the relationship between endosperm color and mating type on each ear. Considering a pair of plants as a unit, the expected proportion of self-pollinated seed is given by the expected proportion of pure yellow seed + pure white seed as follows:

$$[p(100) + (1-p)(100)]/200 = 1/2.$$

In other words, in the absence of selective fertilization, the ratio of self:cross seed is expected to be 1:1 regardless of the relative proportion of yellow:white pollen in the mixture.

Two samples of the original varieties, Jarvis and Weekley, have been examined for possible selective fertilization effects (Table 2). In the first test, satisfactory seed set was obtained on 42 pairs of ears. The percentage of selfed kernels was 50.52% when averaged over all pairs. The heterogeneity chi-square was significant, however, which suggests that variability exists among the pairs for percentage of self seed. Nineteen pairs showed significant deviations from the expected 1:1 ratio; 9 pairs had more self seed than expected (inbreeders) and 10 had fewer than expected (outbreeders).

Out of the 42 pairs, 18 pairs were selected for additional study. Self seed of these were planted in a winter nursery in 10 plant rows, and each plant was self-pollinated to reveal misclassified seed. Segregating ears were discarded. Nonsegregating ears were shelled in bulk to give S_2 seed of each progeny. These were tested in 1967 as paired progeny. Pollinations were with mixtures of pollen of individually paired plants within each progeny pair. Seed was obtained on 16 of the 18 progeny

Table 1. Expectations of random fertilization by mixed pollen of a contrasting pair of parent plants.

Parental genotype	Number of seeds classified	Pollination by mixed pollen with "<u>Y</u>" and "<u>y</u>" gametes in frequencies p and 1-p, respectively			
		Endosperm		Expected number of seeds	Mating type
		Color	Genotype		
YY	100	Yellow Cream	YYY YYy	p(100) 1-p(100)	Self Cross
yy	100	Cream White	yyY yyy	p(100) 1-p(100)	Cross Self
Total No. kernels	200			200	

Table 2. Results of pollination of two samples of paired plants and their inbred progeny with mixtures of their pollen.

Year	Generation	No. pairs tested	Average percentage of self seed	Chi-square tests*		Parent-offspring regression
				1:1	Heterogeneity	
1966	S_0 Parents	42	50.52	N.S.	**	.293
1967	S_2 Progeny	16	54.59	*	**	
1970	S_0 Parents	25	50.34	N.S.	**	.290
1971	S_1 Progeny	18	49.74	N.S.	**	

*Goodness of fit test for 1:1 ratio of self:cross seed and the corresponding test for heterogeneous ratios among individual pairs of plants or progeny.

pairs, as indicated in Table 2, and the parent-offspring regression was estimated to be .293. The heterogeneity chi-square shows that significant differences exist among progeny pairs for percentage of self seed.

The original varieties were again evaluated in 1970 and 1971 in the same way as before. Out of the 25 pairs of plants classified, there were 6 which showed a significant deviation from 50% selfed seed; 3 gave more than 50% self seed (inbreeders) and 3 gave less than 50% self seed (outbreeders). The self progeny of all 25 pairs were tested in paired progeny rows in 1971. Of these, 18 progeny pairs could be evaluated by pollen mixtures. Those not represented were eliminated because of differences in flowering time.

Note the excellent agreement between the results of the two samples in terms of average percent selfing and in terms of parent-offspring regression.

The progeny tested in 1967 were grouped into one of three categories based upon the percentage of self seed. These are: (1) pairs with more than 50% self seed (inbreeders); (2) pairs with very nearly a 1:1 ratio of selfs:crosses (neutrals); and (3) pairs with more than 50% crossed seed (outbreeders). Seed which has been classified as self seed of each pair was planted and the progeny self-pollinated to reveal misclassification and assure purity of the yellow and white strains. This resulted in S_4 seed of 4 pairs of lines in the inbreeder class and 5 pairs of lines in the neutral class and in the outbreeder class. These S_4 lines were then inter-mated within classes and strains to form subpopulations of each variety representing each of the three categories.

The subpopulations, which were the result of one selection cycle, were evaluated in 1969 and their progeny in 1970 by the techniques already described. The responses to selection, summarized in Table 3, provide estimates of realized heritability. These estimates are of the same order of magnitude and agree very well with heritabilities indicated by parent-offspring regression (Table 2). This indicates that the response to divergent selection is essentially symmetrical and is in excellent agreement with expectations based upon parent-offspring covariances in the original populations.

Table 3. Results of divergent selection for percentage of self seed on pairs of plants pollinated with mixtures of their pollen.

Direction of selection	Average percentage of self seed		
	Selection differential	Selection response	Realized* heritability
Inbreeders	19.73	6.53	.331
Outbreeders	11.12	3.07	.276

*Computed as Selection Response/Selection Differential.

Table 4. Evaluation of subpopulations resulting from divergent and canalizing selection for percentage of self seed on pairs of plants pollinated with mixtures of their pollen.

Sub-population	Generation	No. pairs tested	Average percent-age of self seed	Chi-square tests‡		Parent-offspring regression
				1:1	Hetero-geneity	
Inbreeders	S_0 Parents	19	57.05	**	**	
	S_1 Progeny	14	53.72	**	**	.015
Neutrals	S_0 Parents	19	50.82	N.S.	**	
	S_1 Progeny	7	50.06	N.S.	N.S.	.096
Outbreeders	S_0 Parents	30	47.45	**	**	
	S_1 Progeny	26	47.78	**	**	-.166

‡Goodness of fit test for 1:1 ratio of self:cross seed and the corresponding test for heterogeneous ratios among individual pairs of plants or progeny.

Data of each of the 3 subpopulation pairs are summarized in Table 4. The 19 pairs of ears representing the inbreeder class average 57% self seed, which is a significant deviation from the 1:1 ratio of selfs:crosses. Eight pairs of the 19 pairs tested had significantly more than 50% self seed and none had significantly less than 50%. In 1970 the 14 progeny pairs averaged significantly more than 50% self seed. Heterogeneity among progeny pairs is indicated; 8 of the progeny pairs had significantly more than 50% self seed and none had significantly less than 50%.

The neutral populations averaged approximately 50% selfing in both years of the test.

The outbreeder class, represented by 30 pairs in 1969, had significantly less than 50% self seed on the average. Heterogeneity is indicated and 2 pairs of the 30 had significantly more than 50% self seed while 9 had significantly less. The progeny pairs evaluated in 1970 show essentially the same pattern, with only one pair with significantly more than 50% selfing and 10 pairs with significantly less.

These data show quite conclusively that divergent selection was effective, and that populations which show a degree of selective fertilization have been developed. The parent-offspring regressions computed within each selected population suggest that heritable variance for the trait has been exhausted. This could be due to the effectiveness of selection, but a more likely cause is inbreeding resulting from small effective populations.

In order to study the mechanism governing this trait in more detail, inbred lines are being developed to represent the two divergent classes; viz. inbreeders and outbreeders. The lines, which originated in the selection study described above, were developed as paired progeny by selection within the inbred pairs through the S_4 generation. Data for pairs of lines which were eliminated because of differential flowering time, difficulty in seed classification, or variable expression of the trait are not included (Table 5).

Table 5. Pairs of inbred lines selected for nonrandom fertilization effects of mixtures of their pollen.

Designation of inbred pairs		Percent self seed from pollen mixture				
		Generation of inbreeding				
Yellow	White	S_0	S_1	S_2	S_4	S_6
P1	P2	79.5	--	82.5	92.0	84.0
P3	P4	79.5	--	82.5	97.2	95.1
P5	P6	79.5	--	71.5	98.5	81.4
P7	P8	63.2	--	56.5	93.2	42.5
P11	P12	39.2	--	20.2	49.5	--
P19	P20	63.2	--	56.5	36.5	--
P101	P102	47.0	42.0	31.5	--	--
P103	P104	47.0	38.0	35.0	--	--

Table 6. Percentage of self seed from pollen mixtures of related pairs of inbred lines.

White inbreds	"Yellow" inbreds			Mean
	P1	P3	P5	
P2	84	92	65	80
P4	--	95	55	75
P6	64	87	81	77
Mean	74	91	67	78

Mean of diagonals = 87

Mean of off diagonals = 73

The data show that the development of pairs of lines for the inbreeder class has been more successful than for the outbreeder class. Note, however, that three of the pairs which are distinct inbreeders are descendants of the same pair of S_0 plants. The two pairs of S_2 lines which appear to be in the outbreeder class are also closely related. The rather wide fluctuations from generation to generation seen in some of the pairs, like P7-P8 for example, are probably due primarily to environmental variations although genetic sampling error may also contribute.

Since three of the inbreeder pairs are closely related, the possibility that major loci are involved will be considered in crosses with unrelated lines to be evaluated in the future. Preliminary evidence which bears upon this question was obtained by testing them in all possible pairs of contrasting endosperm color (Table 6). The diagonals of Table 6 represent the pairwise combinations in which the lines were developed. The off-diagonals represent combinations not considered in the development of the lines. The agreement between the two means shows that the selective fertilization effect is nearly as great in the unselected combinations as it is in the selected combinations, and suggests considerable genetic similarity among the inbreds of each endosperm type. The greatest difference observed involves line P3, which appears to result in significantly greater selective fertilization effects in combination with all 3 of the white lines tested.

It should be mentioned that an examination of the pairs of ears of these inbreds, where the degree of selective fertilization is much greater than in the varietal material, shows convincingly that the effect is essentially symmetrical. That is to say, in the inbreeder class for example, the yellow line discriminates against the white pollen just as strongly as the white line discriminates against the yellow pollen. In all of the cases tried, however, the two inbreds will set crossbred seed normally when the pollens are not mixed together. The pattern observed here appears to be in contrast with patterns reported for known gametophyte factors.

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1. Behaviour of half-opaque maize.

Eleven inbred lines have been selected for incorporation of the opaque-2 gene. After two backcrosses, the opaque kernels from the different lines were utilized in developing an opaque-2 synthetic. In the second generation of the synthetic opaque-2, several sectored kernels with normal (translucent) tissue were observed. These were classified into seven distinct types (S_2 to S_8). Diallele crosses were made among these including complete opaque (S_1). After two generations of selfing, certain crosses in the F_3 gave mainly half opaque kernels (S_5).

Table 1. Half opaque maize from certain diallele crosses

Cross	F_1	F_2	F_3
S_2 x S_4	S_5	S_5, S_5^*	S_5
S_4 x S_3	S_5	S_5^*	S_5
S_4 x S_7	S_2	S_5, S_5^*	S_5
S_4 x S_7	S_6	S_5^*	S_5
S_4 x S_7	S_5	S_5, S_5^*	S_5
S_4 x S_8	S_5	S_5, S_5^*	S_5
S_5 x S_6	S_8	S_5, S_5^*	S_5
S_6 x S_4	S_5	S_5	S_5

Note: S_5^* = 1/3 / 3/4 $\underline{o}_2$

S_5 = 1/2 $\underline{o}_2$

The lysine content of the sectored seed has been analyzed and it was found to be similar in all the types including half opaque suggesting that the sector size may not alter the lysine content. The modified opaque may be more useful in breeding high lysine maize and also may be more acceptable for direct consumption.

S. Annapurna
G. M. Reddy

2. Electrophoretic studies of half opaque endosperm (S_5).

One of the S_5 cobs from the cross S_4 x S_7 was selected for biochemical studies. The normal half, $S_5(\underline{+})$, and opaque half, S_5 ($\underline{o_2}$), were separated and the soluble proteins extracted with .01 M sodium pyrophosphate buffer containing 10^{-4} M EDTA and 0.7 ml of mercaptoethanol. The S_5 ($\underline{+}$) and S_5 ($\underline{o_2}$) tissues were also subjected to three consecutive extractions with water, 5% NaCl and 70% ethanol. All these protein extracts were subjected to electrophoretic separation in 7.5% polyacrylamide gels. The saline extract was dialysed before electrophoresis. Table 1 gives the pattern of protein bands in both translucent and opaque tissues of S_5.

Table 1. Endosperm protein pattern of S_5 $\underline{+}$ and S_5 $\underline{o_2}$

Extract	Tissue	1	2	3	4	5	6	7	8
Na Pyrophosphate	S_5 (+)	I	I	M	M	A	I	M	F
	S_5 (o_2)	A	M	A	M	M	M	M	M
Water	S_5 (+)	F	A	I	M	F	F	F	
	S_5 (o_2)	M	M	M	F	F	F	A	
5% Na Cl	S_5 (+)	F	M	F	M				
	S_5 (o_2)	F	F	A	A				
70% Ethanol	S_5 (+)	F	F	F					
	S_5 (o_2)	A	A	A					

(I = Intense, M = Medium, F = Faint, A = Absent)

Though both opaque and normal tissues are from S_5 kernels, they showed a significant difference in the protein pattern. The pyrophosphate extract of S_5 (+) shows the maximum number of bands. Also S_5 (+) showed a greater number of bands than S_5 (o_2) in all the extracts except the water fraction. The differences between these tissues were observed to be maximum in the ethanol extract where S_5 (o_2) is devoid of any protein bands. But in both tissues the intensity of the bands decreased with consecutive extractions.

S. Annapurna
G. M. Reddy

3. Induction of seedling and endosperm mutations with DES.

A homozygous dominant multiple stock, Bm_2 Lg_1 A_1 Su_1 Pr Y_1 Gl_1 J_1 Wx G_1, was treated with three different concentrations of DES (MNL 44:178). Seedling and endosperm mutations were observed in 0.006M treatment in M_2 and M_3, respectively (Table 1). The mutation frequency was calculated on the basis of the total number of independent mutations divided by the total number of M_1 ears.

Table 1. Mutation frequency observed for various seedling and endosperm characters.

No. of loci mutated	Type of mutation			Mutation frequency
	Seedling	Endosperm	New mutations	
1	-	a_1	-	0.01
2	-	$a_1 y_1$	-	0.02
6	bm_2, lg_1	a_1, y, wx	Salmon silk	0.06
8	lg_1, g_1	a_1, su, y, wx	White leaf sheath	0.08
14	bm_2, lg_1 gl, g_1	a_1, su, pr, y_1, wx	White leaf sheath, unbranched tassel, salmon silk, dwarf, albino.	0.14

The recessive mutations for the ten known markers were found to be allelic, with the exception of $\underline{g}_1$ and $\underline{gl}_1$ which need to be tested. The recovered new mutants were found to breed true and allelic studies are in progress.

V. S. Bharathi
G. M. Reddy

4. High protein opaque-shrunken endosperm.

Induced opaque-shrunken endosperm (MNL 44:178) was found to have high protein (18.0%). Preliminary studies suggest that the shrunken-opaque is not allelic to either $\underline{sh}_1$, $\underline{sh}_2$, $\underline{sh}_4$ or $\underline{bt}_2$.

V. S. Bharathi
G. M. Reddy

5. Biochemical nature of bz_1 and bz_2 mutants.

The chemical nature of the accumulated substance in $\underline{a}_2$ mutant aleurone was reported earlier (MNL 45:169-171). Similar studies were conducted with $\underline{bz}_1$ and $\underline{bz}_2$ along with certain other double mutant combinations.

The characterization of the isolated substances was made by the following: 1) Rf values; 2) absorption maxima; 3) visible color; 4) color reactions; 5) response to various diagnostic spraying reagents; 6) thin layer chromatography (Silicagel); 7) paper chromatography. Absorption maxima of chromatographically pure compounds were recorded in 5% methanol-hydrochloric-acid solution on UV specord VIS. The relative quantities of the pigments were determined on a Klett-Summerson photoelectric colorimeter.

Table 1. Identification of substances accumulated in different genotypes.

Genotype	Leucoanthocyanidin	cyanidin	cyanidin-3-glucoside
bz_1	P	P	A
bz_1 pr	P	A	A
bz_1 in	P	P	A
bz_1 a_1	A	A	A
bz_1 a_2	P	A	A
bz_2	A	TA	P
bz_2 in	A	TA	P
bz_2 a_1	A	A	A
bz_2 a_2	P	A	A

(P = Present; A = Absent; TA = Trace amounts)

These studies suggest that bz_1 and bz_2 accumulate cyanidin and cyanidin-3-glucoside, respectively, indicating that the Bz_1 gene may control a glycosidation step. The double mutants, a_1 bz_1, a_1 bz_2, a_2 bz_1, and a_2 bz_2, lack these pigments.

A. R. Reddy
G. M. Reddy

6. The role of the modifying factors, In/in and Pr/pr.

Colorimetric analysis of the pigment levels in bz_1 in and bz_2 in suggests that the homozygous recessive in enhances the production of cyanidin in bz_1 and cyanidin-3-glucoside in bz_2 tissue. The mutant bz_1 Pr accumulates cyanidin and bz_1 pr pelargonidin. The accumulation of cyanidin in bz_1 and cyanidin-3-glucoside in bz_2 indicates that Bz_1 might be involved in glycosidation. Further the Bz_1 gene may act prior to Bz_2 and both of them act after In, Pr, A_1 and A_2. These observations independently confirm the sequence of gene action proposed earlier (MNL 35:95).

A. R. Reddy
G. M. Reddy

7. Action of c_2 and Pr/pr.

Seeds of c_2 in pr were germinated under incandescent light. The aleurone of the triple mutant c_2 in pr developed a small quantity of red pigment, pelargonidin-3-glucoside. Also, the nonilluminated c_2 in pr seed had a faint red pigment (pelargonidin-3-glucoside) indicating that the Pr/pr gene might act before the c_2 gene in the gene action sequence.

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1. Protein electrophoretic patterns of maize, teosinte, and Tripsacum dactyloides.

Electrophoretic patterns of 70% ethanol extracts of ground seed of maize and teosinte are similar, but differ from that of *Tripsacum dactyloides*. The maize and teosinte bands have homologous migration velocities. The electrophoretic technique was similar to that of Johnson (1967). The nonspecific protein stain was naphthalene black.

Extract with 0.5 M NaCl (Paulis & Wall 1969) of maize and teosinte gave almost identical electrophoretic patterns, using Johnson's disc electrophoresis technique. There are at least 8 bands with homologous migration velocities. The maize and teosinte patterns are different from that of *T. dactyloides*. There is slight pattern variation among different races of maize and among different races of teosinte, but over all, teosinte does not appear to have any bands not found in maize. Primitive races of maize from Peru have similar patterns to primitive races of maize from Mexico.

Using this technique, the seed protein patterns of wild and cultivated diploid and tetraploid wheat, and wild and cultivated diploid and tetraploid cotton were shown to be almost identical (Johnson & Hall, 1965; Johnson, Barnhart & Hall, 1967; Johnson, 1967; Thein, 1967; Johnson & Thein, 1970). Even though more tropical species of *Tripsacum*

and other maize relatives have yet to be investigated, the above data support the hypothesis that maize is domesticated teosinte.

This work was begun at the Genetics Department, University of Missouri, Columbia, Missouri, U.S.A.

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J. Giles Waines

2. Leaf phenolics of Zea mays, Zea mexicana and Tripsacum species.

A project is underway to investigate leaf phenolic constituents of primitive races of _Zea mays_, geographically diverse collections of _Zea mexicana_ and several biotypes of each species of _Tripsacum_.

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3. New chromosome techniques for knob detection in mitotic chromosomes in maize and teosinte.

Recent advances in cytological techniques have made possible the linear differentiation of mitotic chromosomes in many plant and animal species (Caspersson et al. 1969; Vosa, 1970, 1971; Pardue and Gall, 1970; Arrighi and Hsu 1971).

There are now two new main cytological methods; one exploits the differential DNA binding specificity of certain fluorochromes of the acridine group and the other the property of the Giemsa stain to differentiate, after various kinds of denaturation and reannealing, between repetitive and less repetitive DNA sequences in the chromosomes. The

exact biochemical implications of both methods are not fully known at present.

The present note relates to a series of experiments carried out with both methods on the chromosomes of some varieties of *Zea mays* and *Zea mexicana*.

Fluorochrome method

The technique used has been that suggested by Vosa involving the use of quinacrine dihydrochloride and quinacrine mustard as well as ethidium bromide. The results showed that in maize and teosinte there are no highly fluorescent bands or bands of reduced fluorescence and that in both species the chromosomes show uniform fluorescence along their length. The chromocentres, when present, are visible and show normal fluorescence.

Giemsa method

Several techniques were tried with variable results. The more consistent was a modification of the technique suggested by Sumner et al. (1971) using barium hydroxide as denaturing agent and a saline buffer (SSC) for reannealing (Vosa and Marchi, 1972). The results show dark staining bands in several positions in the chromosomes of maize and teosinte. In maize these bands seem to correspond in number and location to the knobs.

Good agreement in band and knob position was found in two varieties of maize from Brazil. The teosinte varieties used were from Guatemala, Mexico and Honduras.

The Giemsa technique as outlined above should prove itself to be an important tool in the study of knob polymorphism in maize and teosinte.

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1. The use of linear regression graphs in the determination and prediction of yield behavior in maize.

Since the development of this method by Robbertse (unpublished D.Sc. (Agric.) thesis, University of Pretoria, 1969 and MNL 44:180), it has been extensively studied and used in practice. The results to date show it to be appreciably more useful in breeding and cultivar choice than any other known statistical determination.

Due to the very high genotype-environment interaction in maize in Southern Africa, single trial averages are extremely unstable and relatively useless. Global averages over a large number of trials, although more stable, have little predictive value for the varying conditions under which any maize cultivar will be grown. As Robbertse showed, grouping of trials in order to reduce genotype-environment interaction is so unstable over years, that its value is highly suspect.

These conclusions were strongly supported by the work of Wickens (unpublished D.Sc. (Agric.) thesis, University of Pretoria, 1971) on double hybrid predictions, using the above statistics as well as regression graphs.

The results of Robbertse and of later workers have shown that the regression of specific cultivar yields on average trial yields is highly linear with R^2 values in the region of 90%. Only with very large numbers of trials ($\pm$100) do some cultivars give a significant although very slight curvature. Furthermore, when using the average of

the same entries as the independent variable, the linear regression graphs are amazingly stable over years so long as the variance of the independent variable is sufficiently large.

The indications are that mean yield (the independent variable) is a sufficiently complete measure of the factors that influence specific cultivar yield. As a result, the regression lines are highly linear and stable. Furthermore, they give an extensive and easily seen indication of the adaptability of the cultivars over the range of conditions that have been sampled in the trials.

It has been found by Nelson (personal communication) that in Rhodesia under the pertaining high yield potential, the graphs are sensitive to population density. This aspect is being studied and may have to be taken into consideration in the practical application. It would also affect other existing methods. Nevertheless, the method allows a uniquely high and acceptable degree of predictive accuracy in regard to yield. In extensive practical use in Southern Africa it would seem to be a very important breakthrough in maize breeding. Further research into the application of the method is under way.

It is interesting to note that all the arguments in favor of the use of regression coefficients as stability selection criteria, as suggested by Finlay and Wilkinson (Austr. J. Agric. Res. 14:742-754) and Eberhart and Russell (Crop Sci. 6:36-40), also apply to this use of regression, with the important expansion that this method not only allows the use of nearly all the definitions of stability, but also gives an extensive indication of the yield performance characteristics of the cultivars in the case of maize. Its use for other characteristics and other crops has not as yet been tested.

The one known disadvantage is that this method contains all the problems of common linear regression analyses.

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1. X-ray induced reversion of sh-bz-x2?

The two genes involves in the x-ray-induced double mutant sh-bz-x2 revert to the dominant state simultaneously but at an extremely low frequency (MNL 44:183-185). In an attempt to increase the reversion rate, stocks homozygous for sh-bz-x2 were x-rayed and testcrossed.

Two experiments were performed in which the radiation was applied at different stages. In the first, sh-bz-x2/sh-bz-x2 individuals were treated with ca. 1000r at a stage just prior to the onset of meiosis. The proper stage was determined by sampling the sporocytes of a few plants. Pollen from 28 treated individuals was applied to silks of sh bz plants in an isolation field to eliminate the possibility of contamination.

In the second experiment, seeds of Yg sh-bz-x2 pr homozygotes were x-rayed with ca. 1000 r, planted and pollinated by a yg sh bz Pr stock. Both yg and Pr served as contamination markers. This experiment was performed for the following reasons. The two original cases of reversion are the only ones to date in which the source of the dominant phenotypes is certain; contamination and heterofertilization have been ruled out. In both of these cases the revertants segregated on the ears rather than appearing as single kernels, indicating that the causal event occurred early in the development of the plant. It was felt that the change giving rise to the dominant phenotypes might be prone to induction at the embryo stage.

Experiment #1 yielded a total of 75,323 kernels, none of which was Sh Bz in phenotype. Two possible Sh bz seeds were recovered but one of these did not germinate when planted and thus, cannot be tested. It is probable that the plump phenotypes were spurious and the kernels were genotypically sh bz/sh bz. The genotype of the plant which survived will be confirmed in a testcross.

In experiment #2, 1221 testcross ears from treated seeds were harvested. If reversion was induced at the embryo stage in one of the

homologs, ears segregating for the Sh Bz and sh bz phenotypes would be expected. None was found but a total of 48 ears contained kernels of the following phenotypes: 33 Pr Sh Bz; 41 pr Sh Bz; 4 Pr sh Bz; 4 pr sh Bz; 1 pr Sh bz; and 4 Sh colorless. The pr classes are most likely the result of fertilization by foreign pollen. Rhode Island summers are generally quite breezy, a condition which raises the comfort factor appreciably but also increases the likelihood of contamination. The alternative of simultaneous reversion of sh-bz-x2 and mutation of Pr to pr is highly unlikely. The origin of the remaining classes will be determined by testing for the presence of yg. The four colorless Sh kernels could have arisen from Sh a pollen since some of the sh-bz-x2 homozygotes used in this study were A/a in constitution.

Since the above exceptional kernels occurred as single cases rather than segregating populations, it is unlikely that they represent reversions induced by the x-ray treatment. It is conceivable that the events which gave rise to the original reversions were discrete changes which might not be readily induced by ionizing radiation. Since EMS is known to induce genetic changes at the molecular level at a detectable frequency in maize (Chourey, MNL 43:53-54), treatment of sh-bz-x2 with this mutagen will be performed next summer.

John P. Mottinger

2. Tests of bz-x3, bz-x4 and bz-x5 with the Ac Ds and Spm systems.

The x-ray-induced mutants bz-x3, bz-x4 and bz-x5 are mutable alleles which revert to the dominant state somatically in both endosperm and plant tissue. (For background, see MNL 44:182-183). Tests have been conducted to determine if the mutability is due to the presence of either Ac or Spm.

Plants of the constitution bz-x3 wx/bz wx, bz-x4 wx/bz wx or bz-x5 wx/bz wx which exhibited reversion activity due to the presence of the bz-x alleles were crossed with a stock homozygous for wx^{m-8}, an allele which responds to Spm. In the progeny of these crosses, no kernels with Wx tissue were observed indicating that Spm was not present in the bz-x heterozygotes.

Tests for the presence of Ac were performed using bz^{m-1}. From crosses of bz-x3, bz-x4 or bz-x5 heterozygotes with bz^{m-1} homozygotes, usable progeny were recovered only from bz-x3 crosses due to severe ear rot. Since the reversion patterns of bz^{m-1} and the bz-x alleles are quite distinct, there was no problem in distinguishing their respective activities. No kernels were observed with reversion patterns resembling that of bz^{m-1} indicating that Ac was not present in the bz-x3 stock.

Preliminary tests indicate that mutability of the bz-x alleles is either autonomous or due to a tightly linked regulating element. Distinction between these two alternatives and information on the nature of these systems await further tests.

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1. Variation in pollen grain size of inbred maize lines.

Pollen grain diameter was measured on a number of inbred maize lines in 1970 and 1971. The lines were agronomic stocks grown in the field at Brookings, South Dakota. Pollen collected in petri dishes throughout the day was stained with carmine and at least 50 grains measured for each sample. A total of 172 diploid lines were tested and significant differences among them detected. A frequency distribution is shown in Table 1. The distribution was quite normal with a median diameter of 0.0960 mm and a range of 0.0216 mm.

Similar measurements were obtained for five homozygous autotetraploid lines. Mean diameters of these lines ranged from a low of 0.1020 mm to a high of 0.1200 mm. Only one 4N line fell within the range of the diploids. The difference between diploid and tetraploid means was highly significant ($P < .01$). Differences among the five 4N means also were highly significant.

Banerjee and Barghoorn (Maize Genetics Coop. News Letter 45:244-245, 1971) reported that position of the flower on the tassel, size of

Table 1. Frequency of average pollen grain diameters of diploid maize lines.

Pollen diameter (mm)	Number of lines
.0840	1
.0864	3
.0888	11
.0912	32
.0936	41
.0960	44
.0984	22
.1008	15
.1032	2
.1056	1

the anthers, time of anthesis and anther dehiscence, and water deprivation cause variability in maize pollen grain size. Our system of bulk sampling of pollen by tapping the tassel over a petri dish made it impossible to test these factors. We did detect real differences among plants within inbred lines and among days of sampling of the same plants. These observed differences are assumed to be due to the biological factors listed by Banerjee and Barghoorn.

Simple correlation among the two year's data for the 10 lines most extensively sampled was r = 0.88**.

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1. Relative amounts of DNA in mouse sperm and maize spores at late telophase II.

Freshly dissected mouse sperm were suspended in .2M sucrose and air dried on microscope slides. Anthers containing maize spores at

early quartet stage were squashed in .2M sucrose and also air dried on microscope slides. Mouse and maize slides were fixed and stained in the same lot by the following procedure: fix 20 minutes neutral 50% formalin, 4 washes (5 minutes each) distilled water, 1N HCl room temperature (1 minute), 1N HCl 60°C (14 minutes), 1N HCl room temperature (1 minute), 4 washes (1 minute each) distilled water, stain basic Fuchsin Schiff's reagent (7 minutes), 3 rinses (5 minutes each) mixture 90 ml. distilled water; 5 ml. 1N HCl; 5 ml 10% aqueous potassium metabisulfite, 4 washes (2 minutes each) distilled water, graded alcohol series to xylene, mounting in index of refraction immersion oil matched (as nearly as possible) to the index of refraction of the cell background. Mean nuclear DNA values in arbitrary units as measured with a Canalco-Zeiss Microspectrophotometer by the two wave length method in 123 cells each, mouse sperm and maize spores, were: mouse 264, maize 524. Estimated ratio of DNA per genome corn/mouse was 1.7681 ± S.E. 0.0612. Measurements of nuclei from a few cells each of maize telophase I and mouse gonial cells, mouse secondary spermatocytes, and mouse spermatids were reasonably consistent with these estimates.

M. P. Maguire

2. Experimentally produced meiotic abnormalities.

Meiotic abnormalities of undetermined cause in maize microsporocytes were reported in this Newsletter last year. These have now included synaptic failure, failure of chiasmate association to persist until metaphase, irregular chromosome contraction at diplotene, presence of multiple nucleolar-like bodies at diakinesis, end-to-end association of diakinesis bivalents, cytokinetic failure at first and second meiotic division, and reorientation and abnormal separation of metaphase I bivalents. In this latter case sister centromeres of previously normal appearing metaphase I bivalents seem to separate; then these sister centromeres seem to become cooriented on the metaphase plate and simultaneously associated with homologous sister centromeres, similarly cooriented. Anaphase I then seems to produce equational separation, anaphase II disjunctional separation with occasional resolution of

chiasmata. Bivalents also sometimes separate completely into 40 monads at metaphase I. Following numerous tests it was discovered that these abnormalities were correlated with the use of 3 X 5 filing cards to support tassels of Zea whose stalks had been incised. In response to inquiries to the manufacturers of the cards as to changes in their manufacturing procedure (since the cards had been previously and often used without effect) we received samples of two different kinds of modified starch used by them for sizing in their cards. Starch from one of these samples (which had been treated with ethylene oxide) consistently produced the abnormalities in several different maize stocks. We have now isolated the active substance in crystalline form in small quantity. It is water soluble and unsuitable for gas chromatograph or mass spectrograph analysis without modification. We are now hoping to obtain the biologically active, modified starch in sufficient supply for conventional chemical analysis and are planning studies of the mechanism of its action.

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1. Pigments in hydrolyzed methanol extracts of maize tissues.

Anthocyanidins.

Seah and Styles (M.G.C.N.L. 43:183-184) reported that seven anthocyanidin spots were present on thin-layer chromatograms of the hydrolysates of pigments extracted from various pigmented Pr strains of W22. Although cyanidin was the predominant pigment, lesser amounts of pelargonidin, peonidin, and four other unknown anthocyanidin-like pigments were also found. One of the unknowns was an orange pigment, and this has now been characterized as luteolinidin (3-deoxycyanidin). The colours, Rf values, and spectral data of the other three pigments and of two other pigments since found are shown in Table 1. Their properties do not match those of any of the previously reported

Table 1. Properties of five anthocyanidin pigments.

Spot No.	Colour		Rf x 100		λ max (mu)	$E_{440}/E_{max.}$	$\Delta\lambda$(mu)
	Visible	U.V.	Forestal	FHW[1]	MeOH,HCl	x100	$AlCl_3$ in MeOH
5.	Purple	Dull red	74(7)[2]	48(2)	275,544 (6)	38 (6)	40 (3)
6.	Purple	Dull red	84(2)	54(2)	265,546 (6)	48 (6)	34 (4)
7.	Purple	Dull red	82(2)	52(1)	274,539 (3)	55 (3)	39 (2)
8.	Purple	Dull red	36(5)	9(1)	275,540 (6)	35 (6)	39 (3)
9.	Purple	Dull red	39(5)		538 (2)	32 (2)	33 (1)

[1]Formic acid - conc. HCl - water (5:2:3)

[2]Figures in parentheses indicate number of chromatograms or spectra from which mean values shown were derived.

anthocyanidins. The fact that they undergo a bathochromic shift in the presence of aluminum ion indicates that they have at least one catechol group in their structure. It is not known whether they exist in the plant as glycosides, or whether they are a product of the conversion of some leuco substance. We have good reason to believe, however, that they are not artifacts.

Luteolinidin (3-deoxycyanidin)

Luteolinidin can be isolated from hydrolyzed extracts of anthers, silks, tassel glumes, and in some cases leaf sheaths of pigmented Pr plants. It can also be found, in approximately the same amount, in r^g b plants with no other detectable anthocyanidins, and in a_2 plants that have only trace amounts of cyanidin resulting from the conversion of leucoanthocyanidin. It is present in the same amounts also in pr plants, even in the anthers where the predominant anthocyanidin is pelargonidin. No apigeninidin (3-deoxypelargonidin) is found in pr anthers as might be expected if the 3-deoxy anthocyanidins were under the control of the Pr gene. From this evidence, therefore, it would seem that the pathway to the 3-deoxyanthocyanidins may be separate from the pathway to the other anthocyanidins. That the two pathways may not be completely independent is shown by the complete absence of all anthocyanidins (3-deoxy anthocyanidins included) in a_1 plants. Reddy's proposed gene action sequence for the pathway to anthocyanin in maize places the A_1 gene after R, but before A_2. This presumably means that the Pr, R, and A_2 actions are required only for the pathway to the common anthocyanins, whereas the A_1 action is required for both pathways.

Probable origin of luteolinidin

Luteolinidin is present in moderate amounts in the hydrolyzed extracts from silks of all genotypes tested except a_1. Chromatography of unhydrolyzed silk extracts does not yield an orange spot as expected from a luteolinidin glycoside, but a test for the presence of luteoforol (leucoluteolinidin) is positive. Thus it appears that the silks, and probably other tissues also, contain luteoforol which converts to luteolinidin upon hydrolysis of the methanol extracts.

Probable origin of bz_1 pigment

Hydrolyzed extracts of bz_1 silks yield a relatively large luteolinidin spot, but no other anthocyanidins. When bz_1 silks are extracted in 1% HCl in MeOH prior to their emergence from the leaf sheath, the extract is light green and tests positive for luteoforol. After the extract has been in the refrigerator for a period of time (two or three weeks), it becomes orange-brown. When chromatographed, a brown pigment is obtained that behaves in the same manner as the brown pigment which is obtained by extracting bronze coloured tissues of mature bz_1 plants. It seems probable, therefore, that the brown coloured bz_1 pigment is a phlobaphene formed largely if not solely from luteoforol.

E. Derek Styles
Oldriska Ceska

2. Repression of anthocyanin pigmentation in young seedlings by Pl.

We have repeatedly observed that when our W22 r^g B pl and r^g B Pl strains are grown together under the same conditions, the r^g B pl seedlings are always the first to become pigmented. At the second or third internode stages, plants of the two genotypes are virtually indistinguishable, and it is not until the fourth or fifth internode stages that the r^g B Pl strains are clearly darker than the r^g B pl. We have recently compared O.D. readings of extracts from several Pl and pl strains, and have found that Pl not only represses B pigment in the seedlings, but also pigment conditioned by an R^r factor (specifically, R^r Ecuador 1172). The effect is most marked at the first internode stage, and becomes progressively less as the seedling matures. In one experiment, measuring only the first internode plus the ligule region of the first leaf, significantly lower O.D. readings were obtained from r^g B Pl plants as compared to r^g B pl plants in samples taken every day for a period of 10 days. In another group of seedlings at the early first leaf stage, Ecuador R^r B^b pl seedlings were strongly pigmented in contrast to Ecuador R^r B^b Pl seedlings, which had little or no pigment and were indistinguishable from r^g B^b Pl and r^g B^b pl plants of the same stage. The Pl seedlings did develop pigment later, but differences were still measurable even at the

third leaf stage, particularly in the younger (most recently developed) tissues. "Repression" may not be the right word to use for this Pl effect, but it seems clear that Pl can prevent or retard pigment formation in plant parts capable of producing pigment in the absence of Pl, just as it can condition or enhance pigment production in other parts of the same plant (e.g. cob, anthers, etc.).

E. Derek Styles
David J. Kyle

3. C-glycosylflavones.

Levings and Stuber (Genetics 69: 491-498, 1971) have recently reported that luteolin derivatives have been found in silks that respond to cutting by turning brown at the point of injury. One of these derivatives was identified as an isoorientin derivative, a C-glycosylflavone.

We have found that, in our W22 strains, there is an abundance of C-glycosylflavones in the hydrolyzed extracts of the silks, anthers, and tassel glumes of a_1 A_2 R^r plants, and moderate amounts in hydrolyzed extracts of silks and tassel glumes (but not anthers) of bz_1 and A_1 a_2 R^r plants. We have found C-glycosylflavones in the hydrolyzed extract of tassel glumes from all stocks tested thus far, but we have not yet detected any in the extracts of leaf sheaths.

Two of these compounds have been tentatively identified as C-glycosylflavones based on luteolin from the following spectral properties and Rf values:

	λ max in MeOH	Rf values in	
		BAW	15% HOAc
#1	256, 271, 349	15	14
#2	258, 269, 350	24	26

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1. Estimation of S period by different methods.

In previous News Letters, we have reported on the nuclear cycle in maize. The nuclear cycle calculations depend, at least in part, on the ability to estimate accurately one or more component and the total time. In earlier studies, estimates for tS (the duration of the DNA Synthesis period) have been extrapolated from the histogram plot (at the 50 percent intercept) of the frequency of labelled prophases. Such a measure is valid for all populations possessing the following constraints (Quastler and Sherman, 1959):

(1) The cycle is in a steady state;
(2) The cells are proliferating asynchronously;
(3) The DNA Synthesis time (tS) shows no variation from cell to cell.

However, the complete absence of variation from cell to cell in the duration of the component phases of the nuclear cycle is never or rarely found in proliferating cells. As a consequence of such variation, the 100% plateau of the percent labelled prophase curve is shortened. In 1970, Gerecke introduced a new method for estimating the S period. The advantage of his method is the fact that it allows for any variation of tS, tG_2, and tM so that the constraints about the cell system under observation can be reduced. The aim of this note is to report the application of Gerecke's method to our data. The following equations were proposed by Gerecke (1970a, 1970b):

$$D. \ (\bar{t}S + ta) = D. \int_{t_1}^{t_2} p\ (t).\ dt \qquad (1)$$

Therefore:

$$\bar{t}S + ta = \int_{t_1}^{t_2} p\ (t).\ dt \qquad (2)$$

Where

p (t) = the percentage of labelled cells seen at different times after ^3H - TdR incubation,

D = the absolute number of cells in prophase (cells/unit time).

$\int_{t_1}^{t_2}$ p (t).dt= the area under the percent labelled prophase curve.

According to equation 2, the area under the curve is a direct measure of the sum of the mean DNA Synthesis period ($\bar{t}S$) and incubation time (ta = 30 minutes). A third method has also been introduced in this study. The area under curve was calculated from a determination of the perimeter by the use of a planimeter.

The estimates of the duration of the S period calculated by the three methods are presented in Table 1. Harvey's (1970) method employing the F-test was performed to test for differences among methods. An $F_{(2,6)}$=0.098 (ns) was ascertained. It was concluded that the three methods yielded similar results. It is presumed that the accuracy of estimating tS by any of three methods depends on the sample size and the mechanics of plotting the curve.

Table 1. The results of using different methods for estimating the DNA synthesis period (tS, in hours) in several stocks of Zea mays L. at 25°C.

Stocks	Methods		
	Gerecke (1970a)	Planimeter	Q & S (1959)*
Seneca 60	4.5	4.5	5.5
W-23	5.8	5.8	6.0
9-tester	5.0	5.5	5.0
KYS	5.4	5.4	5.5

*Quastler and Sherman (1959); (at the 50% intercept).

References:

1. Gerecke, D. 1970a. Die Naturwissenschaften 7:360-361.
2. ________ 1970b. Exptl. Cell Res. 62:487-489.
3. Harvey, W. R. 1970. Biometrics. 26(3):485-504.
4. Quastler, H., and F. G. Sherman. 1959. Exptl. Cell Res. 17:420-438.

Ram S. Verma

2. Induction of mutations in maize with mitomycin C.

Mitomycin C (MC) is a mutagen in some strains of *E. coli* in which it also increases the frequency of recombination (Iijima and Hagiwara, 1960). In *Ustilago* and *Saccharomyces*, Holliday (1964) indicated that MC is nonmutagenic in these organisms although it does increase the frequency of mitotic crossing over. The purpose of the present study was to examine the effect of MC on mutations in maize.

In the first experiment, homozygous triple dominant stock of "Seneca - 60" (S-60), Yg_2, Sh_1, and *Wx*, and homozygous recessive No. 9 tester were used. The experiment was carried out in the field. Before crossing, tassels of the S-60 male parent were treated with 0.0005% MC for 6 hrs. The time for treatment was 4-6 days before pollen shedding. The leaves surrounding the shoot were slit open with a razor blade. The tassel branches individually were imbedded tightly in cotton. Leaves were closed and wrapped with masking tape. A 0.0005% solution of MC was injected into the cotton with a hypodermic syringe until saturation was reached (about 20-25 ml per tassel). The cotton and the masking tape were removed after 6 hrs. of treatment. During flowering, the pollen from treated plants was collected and used to cross on to the No. 9 tester plants. Mutation frequencies of the sh_1 *wx* loci were determined from the F_1 seeds.

The total mutation frequency (Table 1) induced by MC was 0.123% for the sh_1 locus and 0.090% for the *wx* locus, as compared to 0.012% for shrunken and for waxy in the control, an increase of almost X10.

Table 1. Frequency of mutants obtained in a cross of
$\underline{yg_2}$ $\underline{sh_1}$ $\underline{wx}$ X $\underline{Yg_2}$ $\underline{Sh_1}$ $\underline{Wx}$ following MC treatment.

Treatment	Population (no. of seeds)	No. of mutants			Total mutants			
		Single		Double				
		sh_1	wx	sh_1 wx	sh_1	frequency %	wx	frequency %
Control	7877	1	1	0	1	0.0126	1	0.0126
0.0005% MC	8915	4	1	7	11	0.123	8	0.0897

In the second experiment, F_1 seeds (No. 9 tester X S-60) were soaked in one of three concentrations of MC (0.0005, 0.001 or 0.004%) at 22 ± 2°C (room temp.) for 12 hrs. The numbers of seeds used for each treatment are shown in Table 2. In order to facilitate uniform absorption during the treatment, the flasks containing the seeds were shaken every 30 minutes.

The seeds were germinated on moist filter paper in Petri dishes at room temperature. Three days after treatment, six root tips were selected randomly from each treatment and fixed for cytological studies. The percentage of germination and the root length were also scored at that time. The germinated seeds were sown in the greenhouse. Seedling height was determined from 14 day old seedlings grown in the greenhouse; then they were transplanted to the field. Viable chlorophyll mutations of M_1 plants were scored in the field during the entire life cycle of plants.

The effects of MC were studied on seed germination, seedling growth, root growth, mutation rate and chromosomal breakages. In Table 2, seeds treated with one of these three concentrations showed that there was no effect on germination as compared to the control, but survival decreased as the concentration was increased. There was no significant difference in the mean height of seedlings in solutions of 0.0005% and 0.001%, but in the 0.004% solution, the mean seedling height was significantly lower. Seedling height and root length were drastically

Table 2. Effect of the treatment of F_1 maize seeds (No. 9 x S-60) with MC for 12 hrs. at room temperature on germination, seedling growth, and viable chlorophyll mutation rate.

Treatment	Condition	No. of seeds	% of germination	Root length (3 days after treatment)		Plant height (14 days)		Survival after 30 days (%)	Viable chlorophyll mutation (M_1 plant basis)	
				Mean length (cm)	% reduction of control	Mean height (cm)	% reduction of control			
Control	H_2O	100	94	6.6	-	24.7	-	100	0	-
MC	0.0005%	150	88.7	4.6	30.3	20.7	16.2	90.2	14	10.5%
MC	0.001%	150	92	4.2	36.4	21.2	14.2	87.7	19	13.7%
MC	0.004%	200	91	2.7	59.1	17.9	27.5	85.7	23	12.6%

Table 3. Effect of the treatment of F_1 maize seeds (No. 9 x S-60) with MC for 12 hrs. at room temperature on chromosome breakage, as studied in first root tip mitosis 3 days after treatment.

Treatment	Concentration	No. of anaphase cells scored	No. of abnormal anaphases	% of abnormal anaphases	No. of bridges and pseudo-chiasmata	No. of fragments	No. of lagging chromosomes
Control	H_2O	413	3	0.7	2	1	2
MC	0.0005%	233	20	8.58	15	14	1
MC	0.001%	242	31	12.81	14	26	5
MC	0.004%	195	49	25.13	20	43	15

reduced at the high concentrations. The root length in the highest concentration (0.004%) produced at 59.1% reduction over the control value.

The various types of cytological abnormalities of root tip mitoses and their frequencies are shown in Table 3. Anaphase bridges and fragments occurred frequently in the treated materials, although very few aberrations were found in the control material. The frequency of chromosomal aberration was proportional to the concentration. The reduction of root length as well as the percentage of abnormal cells showed a correlation with the concentration.

The most striking phenotypic changes in the MC-treated M_1 plants were yellow, albino, and pale-green longitudinal stripes of various sizes in the leaves. The frequency of viable chlorophyll mutations is shown in Table 2. One albino plant was observed in this experiment. No chlorophyll mutants were found in the control. These experiments suggest that MC is also a mutagen in maize.

References:

Holliday, R., 1964. The induction of mitotic recombination by mitomycin C in Ustilago and Saccharomyces. Genetics 50: 323-335.

Iijima, T., and A. Hagiwara, 1960. Mutagenic action of mitomycin C on Escherichia coli. Nature 185: 395-396.

M. S. Lin

3. The effects of hydroxylamine sulfate on the nuclear cycle and endoreduplication in maize root tips.

Two experiments have been conducted to study the effects of hydroxylamine sulfate (HAS) on the nuclear cycle and endoreduplication. Intact roots of "Seneca - 60" were exposed to ^{3}H-thymidine (1 uc/ml final concentration) for 30 min., followed by a 0.05% HAS treatment for 2 hrs. After washing, the intact roots were returned to the germination chamber (24±1°C) for further growth and fixed at 2-hour intervals up to 32 hrs. post-treatment. Autoradiographs were prepared according to the schedule of Douglas (MGCNL 42: 175-178, 1969) and from Feulgen squashes of this material. For each treatment and control, the mitotic index and prophase labelling index were determined.

Table 1. Relation between the mitotic index and the proportion of prophases labelled at various times after a 2 hour treatment with 0.05% HAS.

Time after treatment (hr.)	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32
Control	9.53	-	-	-	-	-	-	-	8.30	-	-	-	-	-	-	-	9.34
Mitotic index (%)	10.01	7.37	1.84	0.85	1.24	0.77	9.04	11.31	9.65	9.78	9.56	11.08	8.67	11.25	8.00	10.19	9.95
Prophases labelled (%)	0	3.62	5.56	9.09	13.64	21.21	64.04	82.44	74.14	62.25	37.54	34.67	38.92	53.92	61.23	42.24	33.24

The results indicated that the mitotic index was affected immediately, during the incubation period. The relation between mitotic index and prophase labelling at various time intervals after HAS treatment indicated that the mitotic index had decreased to about 0.7% - 1.8% during the 4 to 10-hour period after HAS treatment, which in turn indicated that those nuclei were in G_2 and at the end of S period during HAS treatment. The mitotic index returned to the control value at 12 hrs. The data showed that the effect of HAS on the nuclear cycle was to inhibit and prolong the duration of G_2 and to inhibit the transition of late S to G_2 (treatment: $G_2 + P = 12.5$ hr.; control: $G_2 + P = 2.1$ hr.). The S period was also increased 2.5 hr. by this drug (treatment = 7.5 hr.; control = 5 hr.).

In the second experiment, intact roots were treated with HAS (0.05%) for 2 hr., washed thoroughly, returned to the germination chamber (24 ± 1°C) for further growth, and fixed at 4-hour intervals up to 32 hr. post-treatment. One group of the intact roots was immersed in a 0.03% solution of 8-hydroxyquinoline for 2.5 hr. prior to fixation.

A cytological feature of endoreduplicated cells is the presence during prophase and metaphase of the subsequent mitosis. At prophase, the chromosomes show a quadripartite structure instead of the usual bipartite structure. The four threads of chromatids, coiled 2 by 2, form two major strands (each strand with 2 chromatids). Each centromere joins 4 chromatids (2 major strands). The centromere divides into two during late prophase or metaphase. The chromosomes reach their greatest contraction and the four chromatids lie in parallel. The number of chromosomes doubles and they remain arranged in pairs. These are called "diplochromosomes." Immediately afterwards the centromeres divide once more and the anaphase movement begins. The cytological behaviour at anaphase and telophase is similar in diplochromosomes and in a tetraploid nucleus.

The frequencies of endoreduplicated cells at metaphase are presented in Table 2. These results show that the cells with diplochromosomes were first seen at 20 hr. after treatment. There was an increase in the frequency between 24 hr. and 28 hr. after treatment.

Table 2. Frequencies of endoreduplicated cells (at metaphase) at various times after the intact roots were given a 2 hour treatment with HAS at 24 ± 1°C.

Treatment (conc.)	Hour after treatment	No. of metaphases scored	No. of metaphase cells with diplochromosomes	% of cells with diplochromosomes
0.05%	20	71	2	2.82
0.05%	24	227	12	5.29
0.05%	28	266	19	7.14
0.05%	32	225	0	-
0.2%	28	353	36	10.20

At 32 hr. after treatment, no cells with diplochromosomes were observed. Apparently, the induction of endoreduplication by this drug occurs at a certain stage in the nuclear cycle. If we compared the duration of endoreduplication with that of the nuclear cycle (Table 1) after HAS treatment, the endoreduplication might take place after (G_2) and/or during (S) DNA synthesis at the time of HAS treatment (G_2, because of a complete omission of mitosis between two DNA doublings; S, because of successive DNA doublings). Cells with endoreduplication should undergo two series of DNA replication in interphase before entering mitosis. Therefore the following question arose. During which stage of the nuclear cycle (S or G_2) can cells be induced to undergo the second series of DNA replication by HAS at the time of treatment? With a view to answering this question, ^{3}H-thymidine and autoradiographs will be used for this study.

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1. The effects of sexual differentiation and B-chromosomes on the rate of transposition of modulator from the Wx locus in maize.

This article describes the results of tests for possible interaction between the heterochromatic B-chromosomes of maize, and the transposable non-specific repressor element Modulator (Mp) which has been shown to interact with the partially heterochromatic abnormal chromosome 10 (K10) segment (Williams & Brink, 1972).

Numbers of B-chromosomes ranging from 1 to 5 were introduced into W23 x W22 F_1 hybrids carrying an unstable waxy allele $\widehat{WxMp}$ (wx^{m-1}, Ashman) heterozygous with the stable recessive wx. To test transposition in sporophytic tissues, equivalent numbers of plants carrying B-chromosomes and controls without B-chromosomes were crossed reciprocally with a W23 homozygous recessive stable wx/wx line. Numbers of whole kernel Wx selections on the resulting ears were tabulated, together

Fig. 1

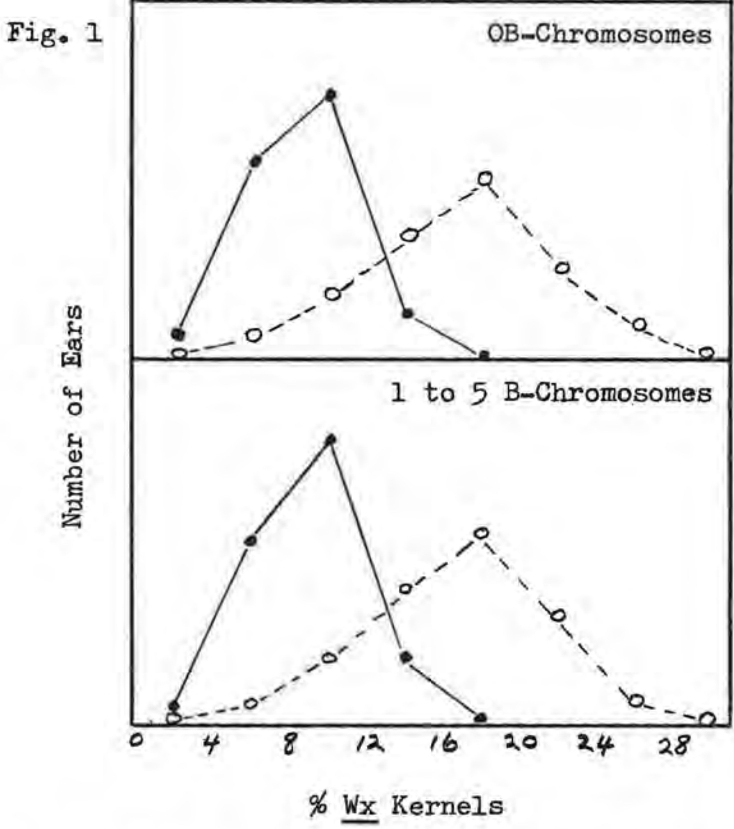
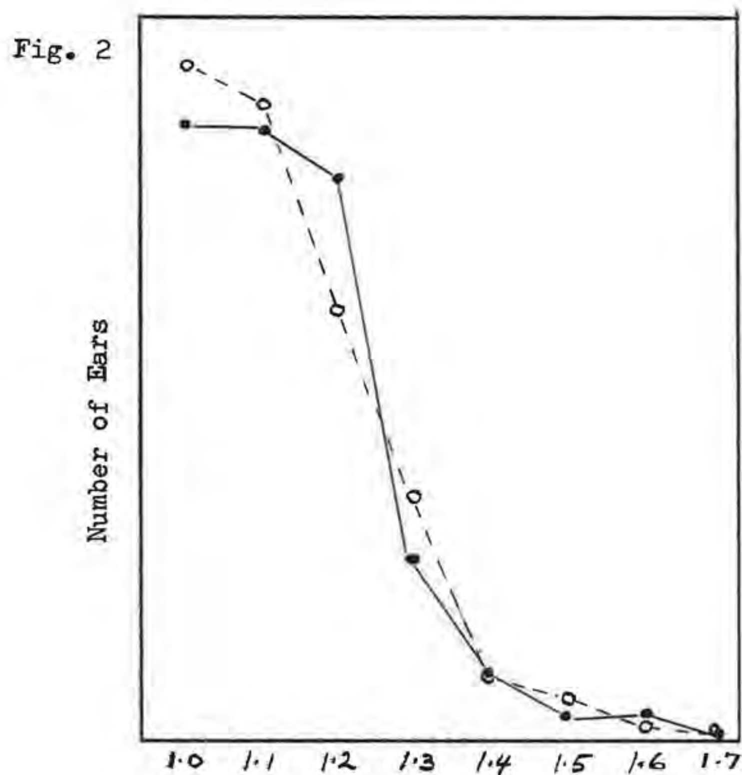


Fig. 1 Frequency distributions of the percentage of Wx kernels on ears derived from B-chromosome containing plants or OB controls used as female and as male parents.

•——• Female-derived WxMp (375 control ears and 375 ears with B-chromosomes)

o- - -o Male-derived WxMp (76 control ears and 78 ears with B-chromosomes)

Fig. 2



Mean no. Kernels per Sector

Fig. 2 The effect of B-chromosomes on the mean number of kernels per somatic sector of Wx mutant tissue on ears derived from Wx Mp/wx female parents.

•——• Plants with B-chromosomes

o- - -o Controls without B-chromosomes

with somatic sector size data for ears from WxMp/wx female parents.

Fig. 1 shows the frequency distributions of the percentage of Wx kernels on ears derived from B-chromosome-containing plants or OB controls used as female and male parents. Fig. 2 shows the frequency distributions of the mean somatic sector size on ears derived from WxMp/wx female parents. Numbers of B-chromosomes in the range 1 to 5 do not detectably affect the frequencies of transposition mutations through the male or female side of crosses, and do not affect the timing of transposition (sector size) through the female side. Since the production of whole kernel mutants in crosses of this type is mainly dependent on transpositions occurring in sporophytic tissues up to meiosis and in the functional spores before replication, it can be concluded that low numbers of B-chromosomes do not affect the transposition of Modulator in sporophytic tissues differentiating as male or female.

Fig. 1 also shows that the frequency of Wx mutant kernels is significantly higher when WxMp is derived from the male side of crosses, regardless of B-chromosome constitution ($P < 0.001$, Mann-Whitney-Wilcoxon non-parametric test, Steel & Torrie, 1960, p 405). Such an effect might result from either an increase in the rate of transposition during tassel differentiation, or a constant transposition rate maintained over a greater number of cell cycles than occurs during ear shoot differentiation.

To estimate gametophytic transpositions the concordance of embryo and endosperm for kernels selected as whole endosperm Wx mutants was tested as follows: Samples of Wx mutant selections derived from male or female WxMp/wx parents carrying OB-, 4B- or 5B-chromosomes were selected from the ears obtained in the previous test, grown out and pollinated with W23 homozygous recessive stable wx/wx. Resulting ears were scored for segregation of Wx/wx (concordant) or WxMp/wx (non-concordant).

Table 1 shows the results of concordance tests. Non-concordance is a result of certain patterns of transposition during development of gametophytes. For both 1970 and 1971 the incidence of non-concordance is significantly higher in OB controls when WxMp is derived through female gametophytes (X^2 test; 1970, $P < 0.025$; 1971, $P < 0.005$). An effect of

this type is expected on theoretical grounds from the differences between female and male gametophytic developmental pathways. If it is assumed that the transposition rate per mitotic cycle is constant and identical for male and female gametophytes, and that the two synergids of the embryo sac contain sister nuclei, it can be calculated that non-concordant mutant selections with Wx endosperm and WxMp embryo should be 4 times as frequent through the female gametophyte. The data of Table 1 indicate non-concordance was 3·43 times as frequent through the female gametophyte for 1970, and 6·24 times as frequent for 1971.

Table 1

Year	Derivation of WxMp	B-chromosome constitution of WxMp/wx parents	% non-concordant kernels	No. kernels tested
1971	♂	0	2.81	178
	♂	4	0.70	143
	♂	5	0.00	29
	♀	0	17.53	194
	♀	4	29.25	147
	♀	5	25.00	16
1970	♂	0	14	21
	♀	0	48	21

(Bracket 1: ♂ values 2.81, 0.70, 0.00 vs. ♀ values 17.53, 29.25, 25.00; bracket 2: 14 vs. 48; bracket 3: 17.53 vs. 29.25 and 25.00.)

1. Significantly different; $P < 0.005$; X^2 test
2. Significantly different; $P < 0.025$; X^2 test
3. Significantly different; $P < 0.025$; X^2 test

The higher incidence of non-concordance for female-derived WxMp means that a greater fraction of Wx selections result from gametophytic transpositions when WxMp/wx plants are used as female parents than when the same plants are used as male parents. Allowance for this fact increases rather than decreases the significance of the higher rate of sporophytic transposition for male-derived WxMp shown in the previous test (Fig. 1).

Table 1 also shows that for 1971 the frequency of non-concordance for female-derived WxMp is significantly higher among selections derived from 4B- and 5B-chromosome parents than among corresponding selections from 0B controls (X^2 test; $P < 0.025$). This indicates that although low numbers of B-chromosomes have no effect on Mp transposition from WxMp during sporophytic development, they may increase the rate of transposition during development of the female gametophyte. There is no detectable difference in the frequency of non-concordance among the different B-chromosome levels when WxMp is derived through male gametes.

In view of the fact that the Wx locus is overtly expressed only in the gametophytes and endosperm, it is of possible significance that the female gametophyte is the only tissue in which an interaction of the abnormally-repressed WxMp compound with B-chromosomes has been detected.

References:

Steel, R. G. D. & J. H. Torrie (1960) Principles and Procedures of Statistics. McGraw-Hill Book Co. Inc. N.Y.

Williams, E. and R. A. Brink (1972) The Effect of Abnormal Chromosome 10 on Transposition of Modulator from the R Locus in Maize. Genetics (In press).

Elizabeth Williams

2. Synthesis of a set of B-A translocations involving a given segment of chromosome 10.

Because of their utility in various cytogenetic investigations, a set of B-10 translocations was sought representing breakpoints in chromosome 10 at various positions between the centromere and the R locus. Toward this end tassels of plants in an R^{scm} (self-colored mutant of R-marbled) subline of Inbred W22 carrying 7 to 10 B chromosomes were irradiated following the first pollen mitosis and then crossed to $r^g r^g$ females. If the irradiation induced an interchange between an A and a B chromosome, the B^A chromosome so formed should nondisjoin at the succeeding pollen mitosis, providing that newly formed translocations behave immediately in the manner of previously established ones. When the break in the A chromosome involved that portion of chromosome 10's long arm proximal to R, and the $B^{10}B^{10}$ sperm resulting from nondisjunction

fertilized the egg, a kernel having colorless aleurone ($r^g r^g$/-) but the strongly colored embryo characteristic of R^{scm} should result.

Extensive matings to $r^g r^g$ (Inbred W22) females of forty plants treated with 500 R of X-irradiation yielded 102 colorless aleurone but colored embryo kernels. When grown and tested as staminate parents to $r^g r^g$ the following year, all but 38 segregated self-colored and colorless aleurone in a 1:1 ratio and possessed corresponding embryo phenotypes. Loss of R^{scm} from one sperm in these instances had not lead to detectable alteration in the second. The remaining 38 when similarly tested produced kernels of the selected parental phenotype in a high frequency, indicative of B-10 translocation. This experiment netted, therefore, nearly one translocation of the particular sort desired per irradiated plant, or, in terms of kernels screened, about 3×10^{-4}.

Bor-Yaw Lin

3. Effect of M^{st} on unstable plant color derivatives of $R^{st}R^r$ heterozygotes.

Among the progeny of $R^{st}R^r$ heterozygotes, near-colorless aleurone derivatives with unstable plant color occur with a frequency of approximately 5×10^{-5}. The phenotype and outside marker configuration of these new forms suggest that they arise by an intralocus recombination event which places the instability component associated with seed spotting of R^{st} into cis relation with the plant pigmenting determiner (P) of R^r. The net effect is that (P) replaces the seed pigmenting component (Sc) of the stippled complex ($ScI^R Nc$), yielding ($PI^R Nc$). The present report presents data showing that M^{st}, an enhancing modifier of stippling, located 5.7 units distal to R, also increases the plant color instability of ($PI^R Nc$) forms.

The plant color gene (P) is expressed most conspicuously in the young seedling, where it conditions colored coleoptile and roots, and in the tassel, where it conditions pigmented anthers. The effect of M^{st} on unstable expression of (P) was investigated at both stages of development, in separate studies. Three ($PI^R Nc$) selections of independent origin, isolated by K. V. Satyanarayana, were grown in each case as

heterozygotes with $\underline{r}^g\underline{M}^{st}$ (test) and $\underline{r}^g\underline{+}$ (control). Because the three selections gave similar results the data have been bulked.

(a) Instability in the seedling. Five hundred seedlings of genotype $(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{M}^{st}$ and 500 of genotype $(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{+}$ were scored for presence of pigmented sectors in coleoptile and roots:

Genotype	Seedlings with red sectors	
	Number	%
$(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{M}^{st}$	77	15.4
$(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{+}$	21	4.2

The effect of $\underline{M}^{st}$ was significant ($P < 0.01$).

(b) Instability in the tassel. Separate populations of plants with genotypes identical to those in Part (a) were grown to maturity and the anthers scored for presence or absence of pigmented sectors:

Genotype	Fraction of plants with anther sectors
$(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{M}^{st}$	46/48
$(\underline{PI}^R\underline{Nc})\underline{+}/\underline{r}^g\underline{+}$	0/93

Anther sectoring occurred exclusively in the $\underline{M}^{st}$ class. This supports the seedling observations in confirming that plant color instability of $(\underline{PI}^R\underline{Nc})$ is of the same fundamental nature as seed spotting of $\underline{R}^{st}$.

Although anther sectors were small, encompassing four anthers at most, a one-generation test for $\underline{M}^{st}$ in $\underline{R}^g$ stocks is now available.

W. M. Williams

4. Effect of hemizygosity on germinal mutation in the R-stippled and mutable R-Navajo systems.

In a limited test of plants hemizygous for $\underline{R}^{st}$ (i.e., those having an $\underline{R}^{st}$-bearing standard chromosome 10 but the 10^B chromosome of translocation B-10a in place of the normal homologue) Kermicle (1970*) obtained a self-colored ($\underline{R}^{sc}$) mutation frequency of 39×10^{-4}, while plants heterozygous $\underline{R}^{st}/\underline{r}^r$ (W22 source) gave a value of only 16.2×10^{-4}. In neither case was mutation to $\underline{R}^{sc}$ related to crossing over at meiosis.

*Genetics 64:247-258

This suggested that hemizygosity may lead to an increased rate of transposition of the element $\underline{I}^{R}$ away from the $\underline{R}$-locus and, conceivably, this could be a general characteristic of transposable elements. Thus, an experiment was performed to compare the effect of hemizygosity on $\underline{R}^{st}$ with that on the mutable-Navajo ($\underline{mR}^{nj}$) system which is controlled by the transposable element, Modulator (I. M. Greenblatt, pers. comm.). The systems were tested in hemizygous condition and in heterozygotes with $\underline{r}^{g}$.

Plants hemizygous for the respective alleles were derived by pollinating $\underline{R}^{st}\underline{M}^{st}$ and $\underline{mR}^{nj}$ stocks of inbred W23 with material homozygous for translocation B-10a carrying $\underline{R}^{g}_{6}$. In the inbred W22 strain of B-10a employed, nondisjunction of the B^{10} element of the translocation occurs regularly at second pollen grain mitosis, giving one hypoploid and one hyperploid male gamete within the same male gametophyte. Since the $\underline{R}$ locus is carried by B^{10}, one sperm lacks $\underline{R}$ while the other carries two doses. Recognition of progeny kernels carrying hypoploid $\underline{R}^{st}$/- and $\underline{mR}^{nj}$/- embryos was facilitated by observation of their associated hyperploid endosperms marked by $\underline{R}^{g}_{6}$. Because the hypoploid plants so generated were W23 x W22 hybrids they were vigorous and, although retarded relative to normal plants and semi-sterile, nevertheless yielded on the average more than 225 kernels per ear.

Corresponding $\underline{R}^{st}/\underline{r}^{g}$ and $\underline{mR}^{nj}/\underline{r}^{g}$ heterozygotes were derived in a parallel fashion by use of W22 $\underline{r}^{g}$ pollen parents.

The hemizygous and heterozygous combinations were hand-pollinated with a W23 $\underline{ACr}^{g}$ stock. $\underline{R}^{sc}$ and $\underline{R}^{nj}$ selections from the resulting kernel population were grown and the mutant phenotypes tested for heritability by pollinating with a $\underline{r}^{g}$ stock.

$\underline{R}^{st}$ hemizygous plants ($\underline{R}^{st}$/-) yielded $\underline{R}^{sc}$ mutants at a frequency of 37 per 10^{4} gametes, while $\underline{R}^{st}/\underline{r}^{g}$ material produced 16.5 per 10^{4} gametes. The difference was statistically significant ($P < 0.001$):

Parental genotype	Number of $\underline{R}^{st}$ gametes tested	Number of confirmed R^{sc} derivatives	Frequency of $\underline{R}^{sc}$ mutation
$\underline{R}^{st}$/-	37,940	142	37.4×10^{-4}
$\underline{R}^{st}/\underline{r}^{g}$	46,560	77	16.5×10^{-4}

As with $\underline{R}^{st}$, mutable-Navajo showed a higher yield of germinal mutants per gamete tested in the hemizygous state than in the heterozygous state although the relative difference was not as large. Analysis of the mutable $\underline{R}^{nj}$ data was complicated by two factors not encountered in the $\underline{R}^{st}$ study. First, a number of somatic sectors involving mutation from $\underline{mR}^{nj}$ to $\underline{R}^{nj}$ occurred. Any confirmed sector of three or more kernels in size was counted as a single event. Associations of two kernels were not regarded as sectors but were considered, for the purposes of this experiment, as two independent events. Fewer than five sectors occurred in each genotype. Secondly, besides parental-type kernels and $\underline{R}^{nj}$ revertants there was, on each ear, a class of 'light' mutable-Navajo kernels. No quantitative separation of the 'light' $\underline{mR}^{nj}$ kernels was made because the phenotype overlapped with the parental types. A sample was progeny tested and found to be a heterogeneous collection of types, mostly lighter in aleurone phenotype than standard $\underline{mR}^{nj}$. Tests of their capacities to cause Ds-induced breakage in an IDs tester stock revealed that such 'light' $\underline{mR}^{nj}$ types carried a second dose of Modulator in their genomes and are thus the counterpart of light variegated pericarp in this respect. For the purposes of the present experiment these derivatives were included as part of the total population of gametes tested. No attempt was made to determine whether they were equally represented in the two test groups.

The material was grown in two separate tests in different years. X^2 tests indicated that the $\underline{R}^{nj}$ frequencies for each genotype in the two years were not significantly different. The data for the two tests were thus bulked. Hemizygous $\underline{mR}^{nj}/-$ produced a significantly higher frequency of $\underline{R}^{nj}$ mutants than did heterozygous $\underline{mR}^{nj}/\underline{r}^{g}$ ($X_1^2 = 6.55$; $P < 0.025$):

	Parental genotype	Number of mR^{nj} gametes tested	Number of confirmed R^{nj} mutations	Frequency of R^{nj} mutation
First test	$\underline{mR}^{nj}/-$	3,280	182	5.6×10^{-2}
	$\underline{mR}^{nj}/\underline{r}^{g}$	4,000	180	4.5×10^{-2}
Second test	$\underline{mR}^{nj}/-$	2,437	110	4.5×10^{-2}
	$\underline{mR}^{nj}/\underline{r}^{g}$	5,200	206	4.0×10^{-2}
Total	$\underline{mR}^{nj}/-$	5,717	292	5.1×10^{-2}
	$\underline{mR}^{nj}/\underline{r}^{g}$	9,200	386	4.2×10^{-2}

It is apparent that hemizygosity has a marked effect on mutation of $\underline{R}^{st}$ to $\underline{R}^{sc}$, and probably also causes an increase in mutation of $\underline{mR}^{nj}$ to $\underline{R}^{nj}$. Further study to determine whether this is a response common to autonomous transposable elements would seem to be justified.

We do not know what property of hemizygosity is responsible for the observed effect. The mutations under study were mostly single kernel events - implying transposition at, or very near, meiosis. Conceivably then, the processes of meiotic chromosome pairing may be involved in some way. Further information on this point may be obtainable from more extensive study of the $\underline{mR}^{nj}$ system, which gives a significant frequency of somatic sectors. If only meiotic chromosome pairing is involved then no effect of hemizygosity on somatic mutation rate should be found.

W. M. Williams

5. Tandem and displaced duplications in the distal end of 10L.

The R locus, which is essential for anthocyanin pigmentation in certain plant and seed tissues, is located in the distal one-fifth of the long arm of chromosome 10. The first allele of this locus to be extensively studied, $\underline{R}^{r}$ (Cornell or standard), was found to be associated with a tandem duplication. The proximal member of the duplication carries P, the plant pigmenting determiner, while the distal member carries S, the seed pigmenting determiner.

Lc is the designation given to a leaf color factor extracted from the $\underline{R}^{r}$-Ecuador 1172 strain. Lc maps distal to the R locus, and shows between 1 and 2% recombination with it. A large number of seedling and plant tissues are pigmented by the action of Lc: coleoptile, blade joint, roots (weakly), nodes, silks, pericarp, and leaf blade. Strong pigmentation of the first blade joint allows one to screen for the presence or absence of Lc at the seedling stage, even in the presence of P of $\underline{R}^{r}$. One of the adult plant tissues, on the other hand, that is most conspicuously pigmented by Lc is the leaf blade. Hence its name Lc (leaf color). An extensive study aimed at fractionating the Lc compound phenotype yielded negative results.

Lc was first suspected of being borne on a segment sharing homology with the R^r:standard duplicated segment when, from the heterozygote + R^{nj} Lc/g R^r lc, a + Lc-marked derivative carrying Nj (R^{nj}) and the S component of R^r was isolated. On subsequent analysis this derivative was found to be Nj Lc : S lc in constitution. This strand carries an extensive tandem duplication (the colon represents the junction between the proximal and distal members of the duplication) and therefore is quite unstable. It arose presumably by an exchange within the obliquely paired P-bearing segment of R^r and Lc-bearing segment of R^{nj}.

To test for homology between the P- and Lc-bearing segments, the following simple test was designed. The progeny from the cross R^rLc/R^rLc ♀♀ X r^glc/r^glc ♂♂ was screened for r^rlc and r^gLc exceptional derivatives, in addition to r^rLc cases expected from exchange between P and S elements of R^r. r^rlc derivatives would occur if the P- and Lc-bearing segments pair with each other and an exchange occurs distal to the anthocyanin gene in the respective segments. An exchange proximal to the anthocyanin genes would result in a r^gLc derivative (see Fig. 1).

Table 1 gives the numbers and frequencies of the different classes of r derivatives obtained from pollinating R^rLc homozygotes with r^glc. The only types of derivatives recovered were r^rLc and r^rlc, which occurred in approximately equal numbers. From these results it is possible to conclude that there is indeed a chromosomal segment distal to Lc that is homologous with a portion of the R^r duplicated segment distal to the anthocyanin markers. The homology between the two segments does not appear to extend proximally beyond the anthocyanin genes, since no r^gLc derivatives were obtained. The recombinational origin of the r^rlc derivatives was confirmed in an additional experiment that incorporated M^{st} as a marker located distal to Lc.

Peculiarly, the r^rlc derivatives from R^rLc homozygotes were not associated with reduced fertility. Since the region between R and Lc has been deleted in these derivatives, one would have expected them to show the typical transmission behavior of large deficiencies. Yet, both male and female transmission was found to be normal. Furthermore, r^rlc

Table 1. Colorless seed derivatives from $R^r Lc$ homozygotes crosses to $r^g lc$ males (Population: 124,000).

Type of derivative	Number	Freq. (x 10^{-4})
$r^r Lc$	69	5.6
$r^r lc$	62	5.0
$r^g Lc$	0	NIL

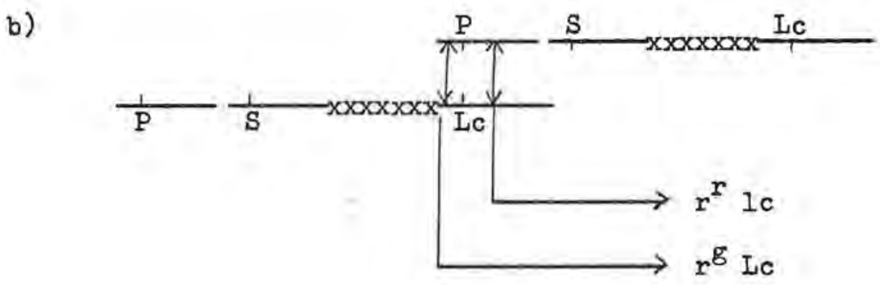
Figure 1. Test of homology between Lc and R^r: types of crossover colorless seed derivatives that can arise in R^r Lc homozygotes if the P- and Lc-bearing segments are coextensive and can pair with each other (xxxxxxx = dispensable chromosome segment).

a)

P S xxxxxxx Lc

P S xxxxxxx Lc → r^r Lc

b)



homozygotes occurred in the expected frequency among the progenies of the original $r^r lc/r^g lc$ selections, ruling out the possibility of a zygotic recessive lethal being associated with the deficiency. Therefore, it appears as if the region between R and Lc--one to two units long--is completely dispensable; its deletion from the genome seems to have no discernible effect.

The R-Lc segment could be duplicated elsewhere in the genome. If one thinks of Lc as an R factor, then this segment could conceivably be duplicated either immediately proximal to R or immediately distal to Lc in a standard chromosome 10. If the R-Lc segment occurs also proximal to R, then one would have expected several $r^g Lc$ derivatives from $R^r Lc$ homozygotes (see Fig. 2a). Yet none were found. If the segment is also present distal to Lc one would expect frequent losses of Lc in Lc homozygotes (see Fig. 2b). $R_1^g Lc$ (R_1^g = S) homozygotes were pollinated with $r^g lc$ and the seedling progeny screened for the absence of Lc traits. From a population of 12,400 seedlings, 7 $R^g lc$ derivatives were found: the lc phenotype of these selections was confirmed in the respective mature plants. This fraction represents a frequency of 5.6×10^{-4}, which compares favorably with the frequency of $r^r lc$ derivatives obtained from $R^r Lc$ homozygotes (5.0×10^{-4}), suggesting that the region of exchange in $R_1^g Lc$ homozygotes is small and very possibly restricted to that half of the R^r duplication present in R_1^g.

Figure 2. Types of crossover derivatives expected from (a) R^r Lc homozygotes if the R-Lc region occurs also proximal to R, or (b) R_1^g Lc homozygotes if the R-Lc region is duplicated distal to Lc.

a) R-Lc region duplicated proximal to R

```
          xxxxxx P ______ S ______xxxxxxx Lc ______
______  ______xxxxxxx______
  P       S          Lc              ————————> r^g Lc
```

b) R-Lc region duplicated distal to Lc

```
          S ______xxxxxxx Lc ______xxxxxxx
______xxxxxxx________xxxxxxx
  S             Lc                   ————————> R^g lc
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In conclusion, the R-Lc region does not appear to be duplicated in the immediate vicinity of the R locus. The Lc-marked segment and either the P- or the S-marked segment would therefore constitute a direct but displaced duplication, just as the P- and the S-marked segments comprise a direct, tandem duplication.

Hugo K. Dooner

6. Induction and maintenance of maize callus tissue.

Yamada, et al. (Proc. Japan Acad. 43: 156, 1967) and Carter, et al. (Nature 214: 1029, 1967) demonstrated that callus could readily be induced in rice and wheat by germinating the seeds on a medium which contained greater than 5 mg/l 2,4-D. We have used this method for maize and have obtained nearly 100% success regardless of the strain used.

Maize seeds are surface sterilized by stirring in detergent and 5% Chlorox, rinsed, and soaked overnight in aerated water. The seeds are again sterilized with 5% Chlorox and the embryos with a portion of the scutellum are removed under sterile conditions. These are planted on Murashige and Skoog medium (Physiol. Plant. 15: 473, 1962) containing 10 mg/l IAA, 0.04 mg/l kinetin, 25 mg/l 2,4-D and 10 g/l agar. The cultures are grown under continuous low light at 25° to 30°C. On this medium the primary root of the germinated seedling thickens and grows only several millimeters. The shoot grows a few centimeters and dies. The mesocotyl swells and unorganized callus proliferates from this region. Under the best conditions a cubic centimeter of callus is formed in six weeks. This callus may be divided and subcultured on Murashige and Skoog solid medium without 2, 4-D. Callus induced last March is still growing after being subcultured several times on this medium. Particularly rapid growth of maize callus can be obtained in liquid shake culture. Again, Murashige and Skoog medium is used, but without agar. The cultures are shaken at 120 rpm at 30°C.

We have not obtained complete differentiation of the callus in culture. Under the levels of hormone employed, normal appearing roots are often initiated, but other than occasional green buds, no shoots are formed.

The rate of callus growth, but not its induction, appears to be strain dependent. Single cross hybrids grow faster than inbreds, and some inbreds do better than others. One inbred which has performed well in our hands is A632. Callus has also been induced in putative androgenic haploid seed obtained from Dr. J. L. Kermicle. These are particularly slow growing.

Corn callus from other than endosperm origin has also been reported by others (cited in Masteller and Holden, Pl. Phys. 45: 362, 1970). Dr. Ed Green is also conducting extensive studies on maize tissue in culture at the University of Minnesota.

Ben Burr
Oliver Nelson

7. A recently isolated mutant with an opaque phenotype.

The designation, opaque-6, is assigned to a recently isolated mutant with an opaque phenotype inherited as a Mendelian recessive. The mutant, which has good expressivity, is not allelic to opaque-1, opaque-2, opaque-4, opaque-5, or horny. The homozygous mutant plants die when about 2" tall. The only plants from mutant seeds surviving to maturity are heterozygotes resulting from heterofertilization. When compared to normal maize, there is no change in the amino acid profile of the collective endosperm proteins. The mutation was detected in a popcorn line by R. B. Ashman (his number, ASX 566).

It is my understanding that the mutant (floury-10) reported by McWhirter (MNL 45:184) last year will now be designated opaque-7.

Oliver Nelson

8. The location of lo_2.

The lethal ovule mutant, lo_x, reported in MNL 43: 145 as being 6 map units from wx on chromosome 9, is located distal to wx. The data leading to this conclusion are derived from the following cross:

$$\frac{c\ sh\ +\ wx\ gl_{15}}{C\ Sh\ lo\ Wx\ Gl_{15}} \times \frac{c\ sh\ +\ wx\ gl_{15}}{c\ sh\ +\ wx\ gl_{15}}.$$

Table 1. The progeny derived from the cross c sh + wx gl_{15}/C Sh lo Wx Gl X c sh + wx gl/c sh + wx gl.

Plant No.	C Sh Wx			c sh wx			C sh wx			c Sh Wx			C Sh wx			c sh Wx			C sh Wx			c Sh wx			Σ
		Gl	gl		Gl	gl		Gl	gl		Gl	gl		Gl	gl		Gl	gl		Gl	gl		Gl	gl	
44123-1 / 43075	0	--	--	157	2	132	7	0	6	1	1	0	25	1	19	6	3	1	0	-	-	0	-	-	196
44123-2 / 43075	6	4	0	168	7	117	14	0	12	0	-	-	18	0	16	14	8	3	1	1	0	0	-	-	221
44123-3 / 43075	0	-	-	155	11	91	4	0	3	0	-	-	33	0	28	10	4	-	0	-	-	0	-	-	202
Total	6	4	0	480	21	340	25	0	21	1	1	0	76	1	63	30	15	4	1	1	0	0	0	0	619

Three ears were scored, and the data are given in Table 1.

On the assumption that no $\underline{lo}_x$ megaspores are functional, the percentage of recombination between $\underline{Wx}$ and $\underline{lo}_x$ is 6.1. This agrees with the previous estimate of 6 percent recombination (MNL 43). The percentage of recombination between $\underline{Sh}$ and $\underline{lo}_x$ is 13.4.

The mutants at this locus are being designated as lethal ovule-2 ($\underline{lo}_2$).

Oliver Nelson

ADDENDUM:

UNIVERSITY OF MINNESOTA
St. Paul, Minnesota

1. A note on field classification of plants for pollen sterility.

I have been puzzled by reports of difficulties in classification of pollen for sterility found in heterozygotes for chromosomal interchanges in maize. Recently, when I was told about the difficulty, I found that the slide was prepared for examination with the pocket microscope by shaking pollen from a tassel on to the slide. This probably would give inconsistent readings, since varying proportions of old, shriveled pollen would be included with the newly shed pollen. Use of a fresh, nondehisced anther solves this problem.

The small pocket microscope with 40X magnification, formerly made by Leitz, is excellent, but is no longer manufactured. One similar in size (cylindrical in shape, 2.8 cm in diameter x 5 cm) and similar in operational features with slightly lower magnification was available two years ago from: Nippon Microscope Works, Ltd.,
No. 4-16, 2-chome Minami Aoyama,
Minato-Ku, Tokyo, Japan

A minimum of 12 may have to be ordered, but the cost is low. Enlarging the opening in the base with a metal reamer increases the amount of light that enters and improves its performance. This microscope is small enough to carry in one hand, holding the small glass slide between the second and third fingers of the same hand. This leaves both hands free

enough to do the needed manipulations, which may include holding the tassel while selecting the anther for the pollen sample.

Pollen classification of maize can be done rapidly in the field. The anthers begin to extrude from the glumes as the temperature rises in the morning. If too cool, extrusion can be induced by taking a floret with mature anthers and warming it in one's hand or by breathing on it. Pollen soon begins to shed normally. Nondehisced anthers full of mature pollen are easily distinguished from ones already shed. The length of time classification is possible each day depends on temperature, humidity, and wind velocity.

To prepare the slide, pick off a mature, nondehisced anther between the thumb and forefinger of one hand, e.g. the right hand, pinch off the tip of the anther with the thumb nail and forefinger of the other hand. The anther contents can be placed on the slide by squeezing the anther or by rolling it between the tips of the thumb and forefinger of the right hand. The pollen will sift out very easily. A gentle tap on the slide will spread the pollen if it is in a clump. Use the sky as the light source if needed. The top lens assembly can be screwed in or out to focus on the pollen. With practice, which includes making sterility counts under a compound microscope, estimates can be made of the degree of sterility. If the sterility is low, separate samples from additional anthers should be checked for consistency of the degree of sterility. Anthers too young but close to shedding can be classified by crushing the anther between thumb and finger and smearing it on the slide.

We mark the fertile plants by tearing off all but 2 to 3 inches of the two top leaves, and the semisterile ones with a string about two feet long looped around the top internode or by breaking off the tassel, leaving only the lower 2 or 3 branches. We mark plants that have higher or lower sterility with a white tag on which the degree of sterility is recorded.

Chas. R. Burnham

2. A method of using tags to mark crossed ears at pollination and at harvest in maize.

Before the pollination season begins, we staple a tag, 4.5 cm x 7.5 cm, from 200 lb. tagboard, on the inside of the fold at one side and between the middle and the closed end of each pollination bag. When a cross is made, the culture and plant number of the male parent and the date are written on the lower half of the tag, together with any information needed to describe the female and the male parents. The bag is then placed over the ear and stapled around the stalk. We usually omit the culture number of the female parent at the time the cross is made, or add only the plant number of the female parent in the upper right corner of the tag. The pencil we use is: Eagle Veriblack #315. It is a soft pencil with a thick lead, but many tags can be written before sharpening is needed. As soon as the crossing is completed, the culture numbers for the female parent are stamped on the upper half of the tag.

At the time of harvest, the tag is removed from the tassel bag and nailed on the ear, using a common lath nail, or a brad with a somewhat larger head. A small oval-shaped stone that is easy to carry substitutes for a hammer. The ears should be laid out on trays for drying. If placed in a bag, the tags may come off in handling.

The method described has several advantages: 1. Stapling the tag on the inside fold of the tassel bag usually protects the tag from weathering and rubbing against other plants which might make the numbers illegible. Very few are lost from that source. After the female culture and plant numbers are added, a tassel bag that is blown off but not lost can be returned to the proper plant. 2. The method avoids the need for copying to transfer information to the ear at the time of harvest. This avoids one source of errors. 3. The nail can be driven into the moist cob easily at the time of harvest. Rubber bands were used in some laboratories, but these disintegrate after a few years.

Chas. R. Burnham

IV. REPORT ON MAIZE COOPERATIVE

A total of 153 seed requests were received by the Maize Cooperative in 1971 and 1,438 packets were sent to supply the requests. Domestic requests accounted for 74 percent of the total, and foreign requests the remaining 26 percent. A further breakdown shows that 58 percent of the requests were from Geneticists, 17 percent from Plant Breeders, 16 percent from Physiologists and stocks used for educational purposes accounted for 9 percent of the total requests.

During 1971, chromosomes 1 and 8 were increased and stocks of these two chromosomes were also grown to confirm mature plant pedigrees. In addition, certain multiple tester combinations for chromosomes 2, 3, 4, 5, 6, and 7 were grown for increase or to get new gene combinations, test linkage, or confirm mature plant pedigrees. The basic series of 20 chromosomal rearrangements (a waxy and non-waxy set) used for locating unplaced genes has been backcrossed into two inbreds, W23 and M14. This project nears completion and considerable nursery work was done setting up homozygosis tests to be grown in 1972. Also a backcrossing program nears completion putting aleurone plus plant color genes into M14 and W23 backgrounds. Most of this material will be grown in 1972, for final pedigree confirmation and increase. Also certain endosperm loci that have not been backcrossed into standard inbred lines by other geneticists are being backcrossed so that all endosperm loci will be in a common genetic background. All the inversions in our collection were grown in 1972 either for homozygosis tests or increase, and an increase was made of the most commonly requested tetraploid stocks.

We received 204 stocks from Dr. W. R. Singleton this past year. Most of the stocks include material from his irradiation studies along with certain types of mutants he has obtained that are allelic to other known loci. The collection also contains cultures which show pollen and ear sterility. All stocks will be tested to determine what traits are involved and their usefulness.

All stocks in the Maize Cooperative collection are now stored in our new cold storage facility. Chromosomes 1, 3, 4, 5, 6, and 8 have

been re-filed and newly revised lists of stocks available for these chromosomes appear at the end of this report. We are working at rearranging and filing stocks of the remaining four chromosomes and revisions of the stock lists for these chromosomes will be included in next year's News Letter.

The list of translocations available from the Co-op is published in the Co-op Report in News Letter volume 43, 1969.

Requests for seed or correspondence relative to the stock collection should be addressed to:

Dr. R. J. Lambert
S-116 Turner Hall
Department of Agronomy
University of Illinois
Urbana, Illinois 61801

Catalogue of Stocks

Chromosome 1

sr_1 zb_4 P^{WW}

sr_1 P^{WR}

sr_1 P^{RR} an_1 ad_1 bm_2

sr_1 P^{WR} an_1 gs_1 bm_2

sr_1 P^{WR} an_1 bm_2

sr_1 P^{RR} gs_1 bm_2

sr_1 P^{WR} bm_2

vp_5

zb_4 ms_{17} P^{WW}

zb_4 ts_2 P^{WW} br_1 f_1 bm_2

zb_4 ts_2 P^{WW} bm_2

zb_4 P^{WW}

zb_4 P^{WW} br_1

zb_4 P^{WW} br_1 f_1 bm_2

zb_4 P^{WW} bm_2

ts_2 P^{RR}

ts_2 sk

ts_2 P^{WW} br_1 bm_2

P^{CR}

P^{RR}

P^{RW}

P^{CW}

P^{MO}

P^{VV}

Chromosome 1 (Continued)

P^{RR} as br_1 f_1 an_1 bm_2

P^{RR} br_1 f_1 an_1 gs_1 bm_2

P^{RR} an_1 ad_1 bm_2

P^{RR} an_1 gs_1 bm_2

P^{RR} ad_1 bm_2

P^{WR} an_1 Kn bm_2

P^{WR} an_1 ad_1 bm_2

P^{WR} an_1 br_2 bm_2

P^{WR} an_1 bm_2

P^{WR} ad_1 bm_2

P^{WR} br_1 Vg

P^{WR} br_1 f_1 gs_1 bm_2

P^{WW} rs_2

P^{WW} rs_2 br_1 f_1

P^{WW} as br_1 f_1 bm_2

P^{WW} hm_1 br_1 f_1

P^{WW} br_1 f_1 ad_1 bm_2

P^{WW} br_1 f_1 bm_2

P^{WW} br_1 f_1 an_1 gs_1 bm_2

as

as rs_2

rd-Hy

br_1 f_1

br_1 f_1 bm_2

Chromosome 1 (Continued)

br_1 f_1 Kn

br_1 f_1 Kn Ts_6

br_1 f_1 Kn bm_2

br_1 bm_2

Vg

Vg an_1 bm_2

Vg br_2 bm_2

bz_2^m m

bz_2^m M

an_1 bm_2

an_1 bz_2 6923 (apparent deficiency including an_1 and bz_2)

br_2

br_2 an_1 bm_2

br_2 bm_2

tb_{8963}

Kn

Kn Ts_6

lw_1

vp_8

gs_1 bm_2

Ts_6

bm_2

id

nec_{8147}

ms_9

Chromosome 1 (Continued)

ms_{12}

ms_{14}

fg

$mi_{8043} = mi_1$

D_8

TB-1a (1L.20)

TB-1b (1S.05)

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

lg_1 gl_2 b fl_1 v_4 Ch

lg_1 gl_2 B gs_2

Chromosome 2 (Continued)

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

cr_1

Chromosome 3 (Continued)

cr_1 d_1

cr_1 d_1 Lg_3

cr_1 pm ts_4 lg_2 na_1

cr_1 ts_4 ba_1 na_1

cr_1 ts_4 na_1

d_1Tall = d_{6016} = tn

d_1 rt_1

d_1 rt_1 Lg_3

d_1 rt_1 Rg ts_4 lg_2

d_1 rt_1 pm

d_1 Rf_1 lg_2

d_1 ys_3

d_1 ys_3 Rg

d_1 Lg_3

d_1 Rg ts_4 lg_2

d_1 pm

d_1 ts_4 lg_2

d_1 ts_4 lg_2 a_1^m; A_2 C R Dt_1

ra_2

ra_2 ys_3 Lg_3 Rg

ra_2 ys_3 Rg

ra_2 Rg pm ts_4 lg_2

ra_2 Rg lg_2

ra_2 pm lg_2

ra_2 lg_2

Chromosome 3 (Continued)

Cg

cl_1

cl_1 Cl_2

cl_1 Cl_3

clp Cl_4

rt_1

ys_3

ys_3 Lg_3

ys_3 gl_6 lg_2 a_1^m et; A_2 C R Dt_1

ys_3 ts_4

Lg_3

Lg_3 Rg

Rg gl_6 lg_2

gl_6 pm lg_2 a_1^m et; A_2 C R Dt_1

gl_6 lg_2 A_1; A_2 C R

gl_6 lg_2 A^b et; A_2 C R Dt_1

gl_6 lg_2 a_1^m et; A_2 C R dt_1

gl_6 lg_2 a_1^m et; A_2 C R Dt_1

ts_4

ts_4 ba_1 na_1

ts_4 lg_2 a_1^m; A_2 C R Dt_1

ts_4 lg_2 gl_7

ts_4 na_1 a_1^m et; A_2 C R Dt_1

ts_4 a_1^m; A_2 C R Dt_1

ba_1

Chromosome 3 (Continued)

lg_2 na_1

lg_2 A^b et; A_2 C R Dt_1

lg_2 a_1^m sh_2 et; A_2 C R Dt_1

lg_2 a_1^m et; A_2 C R dt_1

lg_2 a_1^m et; A_2 C R Dt_1

lg_2 a_1^{st} sh_2 et; A_2 C R Dt_1

lg_2 a_1^{st} et; A_2 C R Dt_1

na_1

A_1 sh_2; A_2 C R B Pl dt_1

A_1 ga_7; A_2 C R B Pl dt_1

$A_1{}^d$-31; A_2 C R

$A_1{}^d$-31; A_2 C R pr dt_1

$A_1{}^d$-31; A_2 C R pr B Pl dt_1

$A_1{}^d$-31; A_2 C R B Pl dt_1

$A_1{}^d$-31; A_2 C R Dt_1

$A_1{}^d$-31; A_2 C R pr Dt_1

$A_1{}^d$-31; A_2 C R pr B Pl Dt_1

$A_1{}^d$-31; A_2 C R pr B pl Dt_1

$A_1{}^d$-31 sh_2; A_2 C R B Pl dt_1

$A_1{}^d$-31 sh_2; A_2 C R Dt_1

$A_1{}^d$-31 sh_2; A_2 C R B Pl Dt_1

$A_1{}^d$-31 sh_2 et; A_2 C R Dt_1

$A_1{}^d$-31 et; A_2 C R Dt_1

a_1^m; A_2 C R dt_1

a_1^m; A_2 C R pr dt_1

Chromosome 3 (Continued)

a_1^m; A_2 C R pr B Pl dt_1

a_1^m; A_2 C R B Pl dt_1

a_1^m; A_2 C R Dt_1

a_1^m; A_2 C R pr Dt_1

a_1^m; A_2 C R B Pl Dt_1

a_1^m sh_2; A_2 C R B Pl dt_1

a_1^m sh_2; A_2 C R B Pl Dt_1

a_1^m sh_2 et; A_2 C R Dt_1

a_1^m et; A_2 C R Dt_1

a_1^{st}; 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 B Pl Dt_1

a_1^{st} sh_2 et; A_2 C R Dt_1

a_1^{st} et; A_2 C R Dt_1

a_1^{st} et; A_2 C R pr Dt_1

a_1^{st} et; A_2 C R B Pl Dt_1

a_1^p et; A_2 C R dt_1

a_1^p et; A_2 C R B Pl dt_1

a_1^p et; A_2 C R Dt_1

a_1^p et; A_2 C R B Pl Dt_1

$a\text{-}x_1$

a_1 Ga_7; A_2 C R

$sh_2 = bt_{60\text{-}156} = sh_{Garwood}$

vp_1

Rp_3

Chromosome 3 (Continued)

gl_7

gl_{12}

TB-3a (3L.10)

TB-3b (3S.50)

Primary Trisomic 3

Chromosome 4

Rp_4

Ga_1

Ga_1 su_1

Ga_1^S

Ga_1^S bt_2

st

st Ts_5

st fl_2

st Ts_5 su_1

Ts_5

Ts_5 la su_1 bm_3 gl_3

Ts_5 fl_2

Ts_5 fl_2 su_1

Ts_5 su_1

Ts_5 su_1 zb_6

Ts_5 su_1 zb_6 o_1

Ts_5 su_1 gl_3 o_1

Ts_5 Tu

la su_1 Tu gl_3

Chromosome 4 (Continued)

la su_1 gl_3

la su_1 gl_3 c_2; A_1 A_2 C_1 R

la su_1 gl_3 o_1

fl_2

fl_2 su_1

fl_2 su_1 bm_3

su_1

su_1^{am}

su_1 bm_3

su_1 bt_2 zb_6

su_1 bt_2 gl_4

su_1 zb_6

su_1 zb_6 Tu

su_1 zb_6 Tu gl_3

su_1 zb_6 $C_2^{Idf\ (Active-1)}$; A_1 A_2 C_1 R

su_1 gl_4

su_1 gl_4 Tu

su_1 gl_4 Tu o_1

su_1 gl_4 j_2

su_1 gl_4 o_1

su_1 j_2

su_1 gl_3

su_1 gl_3 o_1

su_1 o_1

$bt_2 = bt_4 = bt_{60-158} = bt_{williams}$

Chromosome 4 (Continued)

bt_2 gl_4

bt_2 gl_4 j_2

$gl_4 = gl_{16} = gl_{stadler}$

Tu

$Tu^1$1st

$Tu^1$2nd

Tu^d

Tu^{md}

Tu gl_3

j_2

j_2 c_2; A_1 A_2 C_1 R

j_2 C_2; A_1 A_2 C_1 R

v_8

gl_3

gl_3 dp

c_2; A_1 A_2 C_1 R

C_2; A_1 A_2 C_1 R

C_2^{Idf} (Active-1); A_1 A_2 C_1 R

v_{17}

gl_7

o_1

ra_3

TB-4a (4S.20)

Primary Trisomic 4

Chromosome 5

lu_1

$lu_1\ sh_4$

ms_{13}

gl_{17}

$gl_{17}\ A_2\ pr;\ A_1\ C\ R$

$gl_{17}\ a_2;\ A_1\ C\ R$

$A_2\ vp_7\ pr;\ A_1\ C\ R$

$A_2\ bm_1\ pr;\ A_1\ C\ R$

$A_2\ bm_1\ pr\ ys_1;\ A_1\ C\ R$

$A_2\ bm_1\ pr\ ys_1\ eg;\ A_1\ C\ R$

$A_2\ bm_1\ pr\ v_2;\ A_1\ C\ R$

$A_2\ bt_1\ pr;\ A_1\ C\ R$

$A_2\ sh_3\ pr\ ys_1;\ in\ A_1\ C\ R$

$A_2\ v_3\ pr;\ A_1\ C\ R$

$A_2\ pr\ na_2;\ A_1\ C\ R$

$A_2\ pr\ ys_1;\ A_1\ C\ R$

$a_2;\ A_1\ C\ R$

$a_2;\ A_1\ C\ R\ B\ Pl$

$a_2\ bm_1\ bt_1\ bv_1\ pr;\ A_1\ C\ R$

$a_2\ bm_1\ bt_1\ pr;\ A_1\ C\ R$

$a_2\ bm_1\ bt_1\ pr\ ys_1;\ A_1\ C\ R$

$a_2\ bm_1\ gl_8\ pr\ v_2;\ A_1\ C\ R$

$a_2\ bm_1\ sh_4\ pr\ v_2;\ A_1\ C\ R$

$a_2\ bm_1\ pr\ na_2;\ A_1\ C\ R$

$a_2\ bm_1\ pr\ ys_1;\ A_1\ C\ R$

Chromosome 5 (Continued)

$a_2\ bm_1\ pr\ ys_1\ eg;\ A_1\ C\ R$

$a_2\ bm_1\ pr\ ys_1\ v_{12};\ A_1\ C\ R$

$a_2\ bm_1\ pr\ v_2;\ A_1\ C\ R$

$a_2\ bt_1\ v_3\ Pr;\ A_1\ C\ R$

$a_2\ bt_1\ v_3\ pr;\ A_1\ C\ R$

$a_2\ bt_1\ pr;\ A_1\ C\ R$

$a_2\ bt_1\ v_2;\ A_1\ C\ R$

$a_2\ v_3\ pr;\ A_1\ C\ R$

$a_2\ pr;\ A_1\ C\ R$

$a_2\ pr\ v_2;\ A_1\ C\ R$

vp_2

$vp_2\ gl_8$

vp_7

$bm_1\ yg_1$

$bt_1 = bt_{Alex\text{-}Krug} = bt_{Krug6\text{-}1303\text{-}2} = bt_{Vineyard} = bt_{6\text{-}783\text{-}7} = sh_{Eldridge} = bt_{C103} = sh_3 = sh_5$

ms_5

$v_3 = v_{8983}$

td ae

ae

sh_4

$gl_8 = gl_{10}$

na_2

lw_2

Chromosome 5 (Continued)

ys_1

eg

v_2

yg_1

gl_5

ms_{13}

v_{12}

lw_3 lw_4

Primary Trisomic 5

Chromosome 6

rgd po y_1

rgd Y_1

ms_6 = po

po y_1 pl

po Y_1 pl

$y_1 = pb_1 = w^m$

y_1 l_{10}

y_1 l_{4920}

y_1 w_{8896}

y_1 pb_4

y_1 pb_4 pl

y_1 pb_4 Pl

y_1 ms-si

y_1 at-si = ms-si

y_1 wi Pl

Chromosome 6 (Continued)

y_1 pg_{11}; Wx pg_{12}

y_1 pg_{11}; wx pg_{12}

Y_1 pg_{11}; Wx pg_{12}

Y_1 pg_{11}; wx pg_{12}

y_1 pl

y_1 pl su_2

y_1 Pl

y_1 Pl Bh; c sh_1 wx A_1 A_2 R

y_1 su_2

y_1 l_{4120}

Y_1 l_{10}

Y_1 pb_4

Y_1 wi pl

Y_1 wi Pl

Y_1 pl su_2

Y_1 su_2

wi

$pg_{48-040-8}$ = pg_{11} pg_{12}

pg_{6656} = pg_{11} pg_{12}

yg_{6853} = pg_{11} pg_{12}

Pl Dt_2; a_1 A_2 C R

pl sm

Pl sm

Pl sm Pt py

Pl sm py

Chromosome 6 (Continued)

Pt

w_1

$w_{8657} = w_{025-12} = w_{035-2} =$
$w_{5946} = w_{8050} = w_{6853} =$
$w_{1-7_{4302}}$

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

Chromosome 7 (Continued)

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

Tp_1

vp_9 gl_1

Dt_3; a_1 A_2 C R

Primary trisomic 7

Chromosome 8

gl_g

$v_{16} = v_{8661}$

v_{16} j_1

v_{16} ms_8 j_1

$nec_{6697} = sie_{7748} = nec_{025-4}$

v_{16} ms_8 j_1 gl_g

TB-8a (8L.70)

Primary Trisomic 8

Chromosome 9

Bf_1

Bf_1 bm_4

bm_4

bp Wx; P^{RR}

Chromosome 9 (Continued)

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}

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

Chromosome 9 (Continued)

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

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

TB-9a (9L.40)

TB-9b (9S.40)

Primary trisomic 9

Chromosome 10

bf_2

du_1

g_1

$g_1\ Tp_2$

$g_1\ r^g;\ A_1\ A_2\ C$

$g_1\ r^{ch}$

$g_1\ r;\ A_1\ A_2\ C\ wx$

$g_1\ R^r\ sr_2;\ A_1\ A_2\ C$

$g_1\ R^g\ sr_2;\ A_1\ A_2\ C$

$g_1\ r\ sr_2;\ A_1\ A_2\ C$

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

$r^g;\ A_1\ A_2\ C$

$r^r;\ A_1\ A_2\ C$

$r^r \cdot E^j;\ A_1\ A_2\ C$

$r\ K^{10};\ A_1\ A_2\ C$

$R^r\ K^{10}\ g_1;\ A_1\ A_2\ C$

$R^g\ sr_2;\ A_1\ A_2\ C$

$r^r\ sr_2;\ A_1\ A_2\ C$

$r^g\ wx;\ A_1\ A_2\ C$

Chromosome 10 (Continued)

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_1

TB-10a (10L.35)

Primary trisomic 10

Unplaced Genes

dv

dy

el

gl_{12}

gl_{14}

h

l_3

l_4

Rs_1

v_{13}

w_{11}

$ws_1\ ws_2$

ub

Unplaced Genes (Continued)

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

a_1 su_1 A_2 C R

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

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

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.

V. RECENT MAIZE PUBLICATIONS

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