MAIZE GENETICS COOPERATION

NEWS LETTER

54

March 31, 1980

Department of Agronomy
and
U. S. Department of Agriculture
University of Missouri
Columbia, Missouri

This is an informal news letter by which working research information on the genetics and cytogenetics of maize is shared. Communications are received and assembled with minimum editing. Specific data, methods and observations are appropriate.

The text should be double-spaced.
Tables and Figures should be compact and ready for the camera.
References should be used sparingly; when needed, they should be identified in abbreviated form in the text (parenthetically), including authors' initials to facilitate indexing.
Deadline for contributions for the next issue (number 55, 1981) is January 1, 1981.

Some sources of general information on maize genetics and cytogenetics:

Emerson, R. A., G. W. Beadle and A. C. Fraser, 1935. A summary of linkage studies in maize. Cornell Univ. Agric. Exp. Sta. Memoir 180.

The Mutants of Maize. M. G. Neuffer, L. M. Jones and M. S. Zuber, Crop Sci. Soc. Am., Madison, Wisc., 1968.

Handbook of Genetics, vol. 2, pp. 3-30. R. C. King, ed., Plenum Press, New York, 1974.

Handbook of Biochemistry and Molecular Biology, 3d edition, vol. II, pp. 833-847. G. D. Fasman, ed., CRC Press, Cleveland, Ohio, 1976.

Evolution of Crop Plants, Chap. 37, pp. 128-136. N. W. Simmonds, ed., Longman, N.Y., 1976.

Maize Research and Breeders Manual No. VIII. C. B. Henderson, Illinois Foundation Seeds, Inc., Champaign, Illinois, 1976.

Corn and Corn Improvement, 2d edition, G. F. Sprague, ed., Amer. Soc. Agron., 1977.

Maize Breeding and Genetics. D. B. Walden, ed., Wiley, N.Y., 1978.

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I. FOREWORD

The notes are again arranged in order by city this year; if this has been helpful in locating and in reading, it is because it is a good idea that was used by the early editors of the News Letter.

50 years ago (Dec. 19, 1929; February 5, 1930; April 17, 1930; July 26, 1930) lists of linkage groups, revised "rainbow" maps, linkage data and references were distributed from Cornell. These are reproduced in this issue from the copy of E. G. Anderson.

About 800 copies of this issue will be sent to research workers, laboratories and libraries around the world. The costs of preparation, reproduction and mailing continue to be borne by National Science Foundation grant funds to the University of Illinois for the Stock Center. The year-round office workload for the News Letter is supported by the U. S. Department of Agriculture, and facilities are provided by the University of Missouri. Their support is indispensable and we all owe a debt of gratitude to them.

Mapping studies are increasing. Several cooperators have suggested that organized mapping needs to be done by the Coop (or perhaps by a specific center, supported by a national agency); some suggest that the News Letter (i.e., your editor) make compilations and coordination; some that a committee be formed; some that cooperation simply be encouraged. Responding to a call for cooperators to identify interest in mapping particular chromosomes, D. S. Robertson indicates active mapping of chlorophyll factors on chromosome 6; R. H. Whalen tenders interest in factors on chromosome 7; and W. R. Carlson in factors on chromosome 9.

In this News Letter, "Zealand 1980" is an attempt to bring together new factors and linkage information in the formal literature and in the notes for the year just past; perhaps this will be a useful device (please give reactions). A brave, new working map for chromosome 3, constructed from the ground up by review of data in Emerson, Beadle and Fraser and the News Letter, is included; new data and clarifications would be most welcome.

An index of genetic and cytogenetic symbols in Corn and Corn Improvement, 2d edition (G. F. Sprague, ed.) is available upon request.

Back issues can be supplied on request.

A microfilm of volumes 1-29 and 33 is available for $9.50 U.S.; checks should be made out to E. H. Coe, Jr.

Airmail service to addresses outside the U.S. will be provided for $3.00 if received by January 1st.

Deadline for the next issue is January 1, 1981; see inside front cover.

I appreciate the encouragement and support of M. G. Neuffer, J. B. Beckett and G. G. Doyle in planning and developing this volume; Ming-Tang Chang, Christine Curtis, Man Mohan Johri, Kathryn Kind, Stephen Modena and Manh Nguyen aided in editing and proofing of copy; Pat Berry and Shirley Kowalewski carried out the office and bibliographic work; Mary Nelson once again applied her thorough, precise and diligent attention to the composition work and to the production of final copy.

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II. REPORTS FROM COOPERATORS

AMES, IOWA
Iowa State University

The Ub controlling element system

A mutable kernel type showing purple or red spots on a colorless background was found by Dr. G. F. Sprague at the University of Illinois. This kernel type arose from corn lines with aberrant ratios for the A gene (Sprague and McKinney, 1971). Control of this spotting is associated with the A1 locus.

Relationship of the mutability to other controlling element systems: In order to test the relationship between this mutable kernel type and presently known controlling element systems experiments were conducted with the receptor alleles of the En, Ac, Dt and Fcu systems. The general nature of this cross with the new mutable a1 allele (a1-m*):

a1-m* a1-m* A2 A2 [mutable] x A1 A1 a2-m(r) a2-m(r) [colorless]

↓

Colored seed [a1-m*/A1 A2/a2-m(r)] x A1 A1 a2 bt/a2 bt

↓

Colorless, no spots x a1 sh2/a1 sh2 A2 A2

↓

1/2 of progeny ears show spotting

This type of test confirms that the En receptor allele, a2-m(r), is not triggered to show spots and further confirms that the a1-m* allele was present. Thus, the mutability of the a1-m* allele does not contain an En element. Similar procedures conducted with the receptor alleles of the regulatory elements Dt, Ac, and Fcu indicated that the component triggering mutability for a1-m* is not one of these regulatory elements:

Receptor elements	System tested	Presence (+) or absence (-) of mutability
a1-m(r)	(En)	-
a2-m(r)	(En)	-
r-cu	(Fcu)	-
a1-m(dt)	(Dt)	-
C-I(Ds)	(Ac)	-

A two-unit system is uncovered: In a number of crosses of this mutable kernel type by an a1 tester (a1-m* Sh2/a1-m* Sh2 x a1 sh2/a1 sh2, all other color genes dominant; the a1 allele linked to sh2 is a non-mutating allele) completely colorless kernels arose. Repeated selection and testing of mutable kernel progeny (a1-m* Sh2/a1 sh2 x a1 sh2/a1 sh2) yielded colorless kernels among the round progeny. When these colorless kernels were tested with the sib colorless shrunken sibs from the same ear, mutability resulted. The segregation of mutable and colorless kernels among the round progeny (1/2:1/2) leads to the conclusion that a separable factor has been uncovered that triggers the mutability of a colorless allele. Because of its non-relationship to the other systems, this finding establishes a new system of mutability to be added to the previously described systems.

This system is designated with a regulatory element, Ub, (Ubiquitous--basis described below) and a receptor element, Rub, for receptor of Ub signals. The colorless a1 allele responding to Ub is a1-Rub. Thus,

Ub + a1-Rub = mutable--purple or red spots on colorless background

a1-Rub = colorless

Ub + a1 sh2 = colorless--an a1 allele that does not respond to any regulatory element.

The prevalence of Ub: In outcrosses of a1-Rub plants (without Ub) to unrelated a1 tester lines (unrelated in having no history of crosses with plants containing Ub), an unexpected result was observed. In every case in crosses with these unrelated a1 tester lines, mutability was found, indicating that Ub is present in these unrelated lines. The pervasiveness of this regulatory element prompted the naming of this new system Ubiquitous (Ub).

Crosses to assorted lines are now being tested to explore the prevalence of Ub in many unrelated inbred lines. It should be noted that the presence of Ub would escape detection without the availability of the a1-Rub tester.

Peter F. Friedemann and Peter A. Peterson

The diversity of En states arising from two autonomous alleles

With controlling elements the pattern of variegation is a reflection of the time and frequency of gene activation during kernel development resulting in differences in the size and frequency of colored sectors. This pattern of variegation is under the precise and heritable control of the regulatory element acting on the receptor elements of a two-element system. The pattern produced by a regulatory element is referred to as its state and frequent changes in state occur. With a constant receptor element, diverse En regulatory element activity can be observed.

The regulatory element can be located at many sites within the maize genome and it can transpose from one position to another. Changes in state are often associated with transposition (Peterson, Genetics, 1970; Brink and Williams, Genetics, 1973). The state of the controlling element does not appear to be an intrinsic property of the element, but due to the position of the controlling element within the maize chromosome (Peterson, in DNA Insertion Elements, 1977, CSH).

Two unstable a1 alleles (a1-m) were selected for study. Each was determined to be associated with En at this locus, thus mutability was autonomously controlled. Transpositions of En from those two unstable a1 alleles were isolated. The timing and frequency of sectoring produced by 189 transposed En's on standard responsive tester lines were visually rated against a standard set of kernels. The linkage position of each of these En's relative to a1 was determined using standard three-point linkage tests (a1 En et).

Although the two source a1-m alleles had unique and easily distinguishable patterns of variegation while the En was a component of the source a1-m allele, the transposed En's produced identical arrays of states after transposition. However, no correlation or association was found between either the timing or the frequency of sectoring and the distance from the a1 receptor allele.

There is no correlation between the distance of En from the receptor allele and the intensity of the signal (as determined by the number and frequency of colored sectors). This indicates that the diffusion of the En gene product to the receptor allele is not the limiting factor determining the state of the En. These results

support the position hypothesis (Peterson, 1977) for the state of a controlling element because En's from different sources do not differ in the array of patterns that they yield following transposition.

Elaine Nowick and Peter A. Peterson

Request for stock

I would be interested in obtaining seeds of stocks of established inbred lines which during propagation have undergone deterioration (i.e., did not breed true to the expected phenotype of the inbred). Instances where small, runty plants or other offtypes segregate are of particular interest. Please send seeds to Donald S. Robertson, Department of Genetics, Iowa State University, Ames, Iowa 50011.

Donald S. Robertson

A new r mutant

In 1976, a selfed ear from the progeny of an outcross of a homozygous purple aleurone Mu plant to a purple aleurone stock segregated for sectored seeds. The sectored seeds had a pattern of aleurone color similar to that of R-st. In 1977 the sectored seeds were crossed as males to all of the aleurone testers. Only in crosses to the r tester did anything other than purple seeds result. The cross to r produced completely non-purple seeds or seeds with only one or two very small flecks of purple (near yellow seeds). Selfs or sibs of plants from sectored seeds resulted in ears that had predominantly sectored seeds with a few full colored purple and a few yellow or near yellow seeds.

In 1978, reciprocal crosses of plants from sectored seeds were made with r tester. Again, when sectored plants were used as males the outcross seeds were yellow or near yellow. However, the ears from the reciprocal cross (sector plants as females) produced ears with mostly sectored seeds and a few full-colored purple seeds and a few yellow or near yellow seeds. Twenty selfs of plants from yellow or near yellow seeds on homozygous sectored ears produced ears that showed the typical sectored pattern (i.e., mostly sectored seeds with occasional full colored and yellow or near yellow seeds). These same plants crossed as males to r testers gave mostly yellow seeds with an occasional near yellow one. Full colored purple seeds from homozygous sectored ears gave plants that when selfed produced the typical homozygous sectored ears. Outcrosses of plants from full colored seeds as males to r tester produce ears with predominantly yellow seeds and a few near yellows. The reciprocal cross gave ears with predominantly sectored seeds and a few full colored and yellow or near yellow seeds. To date, no true stable yellow or stable purple stock has been derived from this r-sector mutant.

In 1978, yellow seeds from homozygous sectored ears were selfed and crossed to a purple aleurone stock or reciprocally crossed to the purple aleurone line. All selfs gave homozygous sectored seeds. All outcrosses of the sector stock as males gave homozygous purple ears. All crosses with sector stock as female segregated 1:1 for purple and mottled seeds, typical of r mottling. The purple aleurone stock was heterozygous for R-scm2, an R allele that does not mottle when crossed as a male with a r stock. These results suggest that R-standard r-sec r-sec seeds are mottled and R-scm2 r-sec r-sec seeds are purple. This was confirmed by crossing plants from the purple and mottled seeds as males to r testers. The cross of the plants from mottled seeds gave the expected ears with mottled (R r r) and yellow seeds (r-sec r r). Also, homozygous sector plants pollinated by pollen from homozygous R-scm2 plants produced ears with only purple seeds.

In summary, this new r allele (r-sec) when homozygous shows an aleurone pattern similar to R-st. When outcrossed to r stocks as male, little or no pigmentation is observed. However, when crossed as a female with r tester stocks, the r-sec

phenotype is observed. Homozygous r-sec ears have a few full color and colorless seeds but these phenotypes have not been found to be transmitted as yet. This new allele behaves like a recessive r when crossed with R stocks (i.e., R r-sec r-sec seeds are mottled while R R r-sec are purple).

Donald S. Robertson

Testing Ac-Ds controlling element system for mutator activity

In 1977 (MGCNL 51:37) we reported on tests of controlling element systems for mutator activity. A variegated pericarp stock with Mp was included in these tests. This active Mp stock did not show any mutator activity. Brink has shown that Mp has Ac activity. Thus this test would suggest that Ac also is lacking measurable mutator activity. To confirm this, an active Ac Ds system was obtained from Dr. Neuffer (Univ. Missouri). The seeds used as a source of Ac Ds were a/A·Ds, Ac/- and had purple or red aleurone sectors. The plants from these seeds were weak and it was not possible to self pollinate them because the silks were delayed until after the pollen had finished shedding. Thus, the Ac Ds plants were sib pollinated and the parents crossed to standards. In the standard test for mutator activity, the tested plants are selfed and outcrossed to standard. The self is necessary to establish that the putative mutator stock is not carrying any mutants. In the standard test, the outcross progeny are self pollinated and the selfs tested for seedling mutants. The frequency of plants segregating for seedling mutants is used to calculate the mutation rate. In these Ac Ds tests, we were not able to use a self to determine if the Ac Ds pollen parents carried a mutant. However, since the pollen parent was crossed with a sibling plant, seeds from these crosses were planted and the resulting plants self pollinated and the self progeny screened for seedling mutants. At the same time seeds of outcrosses of one or both of the sib parents were planted and the resulting plants self pollinated and the self progeny scored for seedling mutants. If one or both of the Ac Ds parents carried mutants they would show up in the progeny of the Ac Ds cross and also in the appropriate standard outcross progeny. Results of these crosses are given in Table 1. It is obvious that these Ac Ds stocks do not have

Table 1. Test of Ac Ds stock for mutator activity.

1978 Family No.	1977 Parent Numbers	Parental Mutants	New Mutants	Total Plants	% New Mutants
1703	77-1345-15/B45-10	0	0	30	0
1704	Stand/1345-10	0	0	47	0
1705	77-1345-8/1344-2	0	0	34	0
1706	Stand/1344-2	0	0	49	0
1707	Stand/1345-8	0	0	41	0
1708	77-1345-12/1345-6	v*	0	34	0
1709	Stand/1345-6	0	0	47	0
1710	Stand/1345-12	v	w* (one self only)	46	2.1
1711	77-1345-14/1345-6	0	0	29	0
1712	Stand/1345-14	0	0	43	0
TOTAL			1	400	0.25

*v = virescent, w = albino

significant mutator activity. The 0.25 percent mutation rate is comparable to those of our control (Non-Mu) stocks. In reality the true mutation rate of this Ac Ds stock is lower than the 0.25 percent value since in the sib crosses tested each parent was Ac Ds. Thus, for each plant selfed in a sib cross progeny, two Ac Ds gametes were tested thus each should be counted twice. The total number of Ac Ds gametes tested in Table 1 thus is 527 and the resulting mutation rate is 0.19 percent.

To date, no controlling element system has a mutation rate that approximates that of Mu. This is an interesting observation in light of the well documented instances of the movement of controlling elements which have resulted in new loci coming under their control. Such movement to a locus controlling a seedling trait would show up as a new mutant in our tests. Since such mutants are rare, it must be concluded that the controlling element systems so far tested are not very efficient mutators.

Donald S. Robertson

Mu activity in pollen samples collected on consecutive days

Plants with the Mu mutator system have a mutation rate 30-50 times higher than non-Mu plants. The standard test for Mu activity is made by outcrossing Mu plants to a standard (non-Mu) line and selfing the outcross progeny. The frequency of selfed ears that segregate for seedling mutants is used to calculate the mutation rate.

It is possible that Mu activity may not be uniformly expressed at all times in all tissues of a plant. If this were so, samples of pollens taken from different days from the same plant may result in outcross progeny with different mutation

Table 1. Mutation rates in three serial outcrosses of plants sampled on 5-7 consecutive days of pollen shedding.

Plant No.	Day	Total Plants Selfed	Total Different Mutants	% Different Mutants	Heterogeneity χ^2 Calculated Over Days (and P)
5062-3	1	77	4	5.2	
	2	63	5	7.9	
	3	52	8	15.4	
	4	47	8	17.0	
	5	60	7	11.7	
	6	71	8	11.3	
	7	57	4	7.0	7.1615 (P=.30-.50)
5061-9	1	49	5	10.2	
	2	51	6	11.8	
	3	40	4	10.0	
	4	44	5	11.4	
	5	55	5	9.1	
	6	52	6	11.5	0.3017 (P = > .99)
5062-4	1	51	4	7.8	
	2	53	2	3.8	
	3	46	4	8.7	
	4	64	5	7.8	
	5	52	3	5.8	1.3105 (P=.80-.90)

rates. To test this, Mu bearing plants were bagged as soon as the central spike began to shed pollen. An outcross was made the next day and each consecutive day as long as plants kept shedding pollen. The mutation rates in three of these outcross series are given in Table 1. Although there is some variation in mutation rates in pollen samples taken on different days it is no greater than that expected from sampling error.

In Table 2, the mutation rates for each cross for each day were combined to determine if a consistent pattern of Mu activity relative to days after the initia-

Table 2. Mutation rates combined by days for three serial outcrosses.

Day	Plant No.	Total Plants Selfed	Total Different Mutants	% Different Mutants	Heterogeneity χ^2 for Each Day (and P)
1	5062-3	77	4	5.2	
	5061-9	49	5	10.2	
	5062-4	51	4	7.8	
	Total	177	13	7.3	1.1303 (P=.50-.70)
2	5062-3	63	5	7.9	
	5061-9	51	6	11.8	
	5062-4	53	2	3.8	
	Total	167	13	7.8	2.3153 (P=.30-.50)
3	5062-3	52	8	15.4	
	5061-9	40	4	10.0	
	5062-1	46	4	8.7	
	Total	138	16	11.6	1.2051 (P=.50-.70)
4	5062-3	47	8	17.0	
	5061-9	44	5	11.4	
	5062-1	64	5	7.8	
	Total	155	18	11.6	2.2426 (P=.30-.50)
5	5062-3	60	7	11.7	
	5061-9	55	5	9.1	
	5062-1	52	3	5.8	
	Total	167	15	9.0	1.1863 (P=.30-.50)

Heterogeneity χ^2 for totals of each day = 3.1119 (P = .50 - .70)

tion of pollen shedding is present. No significant difference is seen between crosses within days nor is any significant difference in the combined mutation rates indicated between days.

The results of these tests are consistent with the view that Mu activity is uniformly expressed in all sporophytic tissue of the tassel over the 5-7 day interval of pollen shedding tested.

Donald S. Robertson

BASEL, SWITZERLAND
Friedrich Miescher Institute

Maize anther culture

Following the disappointing results in many laboratories with attempts to repeat the success in maize anther culture reported by Chinese workers (Scientia Sinica 22:237-247, 1979), a small-scale experiment was set up in July 1979 using field-grown material. 8,686 anthers were plated on modifications of the Chinese medium, and some encouraging results were obtained from two of the genotypes tested:

	Anthers Cultured	Anthers Producing Embryoids	Plants Obtained
Seneca 60	1716	3	3 (two diploid, one haploid)
F2 hybrid Chinese (seed supplied by Y. C. Ting)	1284	8	2 (one diploid, one not determined)

The best results were achieved using N6-medium with sucrose (12% w/v), casein hydrolysate (500 mg/l) and triiodobenzoic acid (0.35 mg/l), and culturing anthers at the uninucleate vacuolate stage of pollen development.

Of the five plants obtained only one has so far been brought to flowering. This diploid plant from Seneca 60 reached a height of less than 30 cm, but produced an apical tassel and a single lateral cob. The anthers contained very little fertile pollen (less than 2% by iodine-potassium iodide staining), but it remains to be seen whether this low fertility is genetic in origin or simply a consequence of the poor conditions (greenhouse) under which this plant was grown.

Richard Brettell

BLOOMINGTON, INDIANA
Indiana University

Genic content and structure of abnormal chromosome 10

Abnormal chromosome 10 (K10), first described by Longley, differs morphologically from normal 10 in two respects. It is longer by virtue of possessing an extra segment of chromatin at the end of the long arm, whose length at pachynema is approximately equal to that of 10S. This segment contains a proximal euchromatic region, a conspicuous heterochromatic knob, and a short euchromatic tip. Normal 10 not only lacks the extra piece, but differs from K10 in the chromeric structure of the distal one-sixth of its long arm. The corresponding segment in K10 (hereafter referred to as the differential segment) has three small knobs which are not present in N10. The R locus in K10 is situated to the left of the most proximal of the three small knobs. According to Coe's summary, the linear order and map positions of loci in distal 10L are: centromere - R(57) - W2(73) - O7(80) - Sr2(92). These four loci are also carried in the long arm of K10 but aside from the location of R, which is similarly placed in K10 and N10, nothing is known about their order. That the distal one-sixth of N10 differs structurally from K10 was strongly indicated by Kikudome's finding that the 35% recombination between R and Sr2 in N10/N10 homozygotes was reduced to 1% in K10/N10 heterozygotes and that all crossovers

between R and Sr2 in K10/N10 plants occurred between R and the leftmost of the three small knobs in the differential segment. It could be argued (1) that the differential segment of K10 is foreign chromatin of unknown origin and that the W2, O7, and Sr2 loci are situated in the portion of K10 extending beyond the tip of N10 or (2) that the differential segment contains the three loci but a rearrangement within the segment reduced crossing over in K10/N10 heterozygotes. On either alternative, the low percentage of R - Sr2 recombination is dependent on a lack of homology between the distal one-sixth of N10 and the corresponding segment of K10. This dissimilarity should be revealed by the pattern of pairing at pachynema in K10/N10 heterozygotes. Somewhat surprising was the observation that pairing of the long arms of the heteromorphic pair was usually intimate, although occasionally asynapsis of the tip of 10L was observed. The data reported in this note demonstrate the correctness of alternative (1) above.

Inasmuch as the K10 chromosome is responsible for the preferential recovery in megasporogenesis of the knobbed chromosome in knobbed/knobless heterozygotes, for neocentromere formation by knobs, and for an enhancement of crossing over in structural heterozygotes and in centric heterochromatin, it is of uncommon cytogenetic interest. We decided to probe the structure of K10 by studying deficient K10 chromosomes resulting from the breakage of dicentric bridges. As we have previously shown in our studies of the high-loss phenomenon, dicentric bridges are produced at the second microspore division because of a delayed replication of the heterochromatic knobs. The K10 knob is similar to knobs on other chromosomes in that it too undergoes delayed replication and chromatin elimination by the above mentioned mechanism. The K10 knob is not completely homologous to other knobs but they all share in common a delayed replication, induced by B chromosomes, at the second microspore mitosis.

When pollen from K10 G R Sr2/K10 G R Sr2 plants with several B chromosomes was used on g r sr2 testers, approximately 80% of the kernels had the anticipated colored aleurone since they received a K10 chromosome carrying the R allele. Sixteen percent of the kernels were colorless having lost the R allele as a consequence of a break in 10L proximal to R and 4% were mosaic for colored and colorless aleurone due to the bridge-breakage-fusion cycle undergone by a chromosome 10 arising from a break distal to R. All of the seedlings from colorless and mosaic kernels were green, indicating the presence of the dominant G and Sr2 alleles in the embryos. However, among the seedlings arising from the colored (R) kernels, some were hemizygous for sr2 or for g sr2 and were phenotypically striate. The g sr2 hemizygotes are grossly deficient for most of 10L and the modified chromosomes were not transmissible through the gametophyte. The hemizygous sr2 plants were tested for the presence of the R allele and for male and female transmissibility of the deficient chromosome. Eleven Df K10 chromosomes have been isolated and are currently being investigated. Our studies are incomplete at this time, but sufficient information has been gathered to permit certain conclusions regarding the structure of K10. The accompanying table summarizes our results to date.

All of the eleven Df K10 chromosomes listed were tested for the extent of the deficient segment by combining each with strains carrying the recessive alleles of w2, o7, and sr2. If the F1 aleurone or seedlings expressed the recessive phenotype, the deficiency was considered to include that locus. As Brink and McWhirter have shown the recessive opaque-7 trait is subject to modifying genes and consequently has a low penetrance. It is difficult at times to know if the apparent normal phenotype is due to presence of the dominant O7 allele or if O7 has been lost and the pseudo-normal phenotype results from modifiers. It is, in short, a mutant which should be avoided if unambiguous results are to be easily obtained (except when the proper modifiers are present). Since the status of the O7 locus has not been determined for most of the deficient K10 chromosomes, we have not included it in the following tabulation.

Deficient Chromosome	Deleted Loci	Transmissibility	Cytology
Df K10 (A)	W2 Sr2	Female only	Half T*
Df K10 (B)	W2 Sr2	Female only	Half T
Df K10 (C)	W2 Sr2	Female only	Unknown
Df K10 (D)	Sr2	Female only	Simple Df?
Df K10 (E)	W2 Sr2	Female only	Half T
Df K10 (F)	W2 Sr2	Female and male	Simple Df
Df K10 (G)	W2 Sr2	Female only	Half T
Df K10 (H)	Sr2	Female and male	Unknown
Df K10 (I)	W2 Sr2	Female only	Unknown
Df K10 (J)	W2 Sr2	Female, low in male	Unknown
Df K10 (K)	Sr2	Female and male	Unknown

*A translocated chromosome involving K10. The complementary translocated chromosome is not present since reciprocal translocations do not occur (Saraiva, 1979).

The Df K10 (F) chromosome has been most extensively studied to date. Df K10 (F) pollen grains achieve considerable success in functioning in competition with N10 pollen with the percentage of functioning Df pollen in different crosses ranging from 18 to 40. The progeny from selfing Df K10 (F) R df/N10 r sr2 plants had, in addition to the expected plump-colored and plump-colorless kernels, an unexpected class with numerous spots of anthocyanin on a colorless background. The spotted phenotype simulated that expected from an unstable r allele mutating to dominant R during endosperm development. Many of the spotted kernels were also mosaics of plump and defective endosperm sectors. The cells with colorless aleurone appeared to coincide with areas having defective endosperm while cells with colored aleurone were over regions with normal endosperm development. The colorless sectors possessed an aleurone layer so the failure of anthocyanin formation cannot be ascribed to absence of the aleurone. The spotted aleurone trait could be accurately classified on most of the ears but considerable variation was found in the degree and extent of defective endosperm development. Some spotted kernels had nearly normal endosperms but the majority were clearly mosaic for normal and abnormal endosperm sectors.

Most of the spotted kernels (R R R) had viable embryos which upon germination gave rise to pure albino seedlings having no trace of green tissue. No albinos came from white (r r r), from mottled (R r r), or from self colored (R R r) kernels, all of which had normal endosperms. In short, the albino seedlings, the failure to synthesize aleurone color, and the abnormal endosperm development were found only when the Df K10 (F) chromosome was homozygous. It may be surmised that the Df K10 (F) chromosome is deficient for a locus involved in regulation of anthocyanin synthesis, for a locus concerned with endosperm development, and for a gene affecting chlorophyll formation, as well as for the Sr2 locus. Presumably separate loci are involved.

Lindstrom (Genetics 1925) stated that the w2 allele, which lies ca. 19 recombination units to the left of Sr2, frequently gave a defective endosperm when homozygous, but this character was sensitive to modifiers since there was great variation in the degree of defectiveness. The twofold effect of the w2 mutation was ascribed by Lindstrom to one pleiotropic or to two closely linked genes. Since the Df K10 (F) chromosome likewise affected both endosperm and chlorophyll, crosses were made of Df K10 (F) R df/N10 r W2 plants with pollen from r w2/r W2 individuals. Self-colored, R-r spotted, and colorless kernels occurred in a ratio of 1:1:2. The plump, self-colored kernels were R df/R df/r W2, the spotted kernels

(which were also mosaic for plump and defective endosperm sectors) were R df/R df/r w2, and the plump colorless kernels were either r W2/r W2/r W2 or r W2/r W2/r w2 in constitution. The self-colored kernels yielded green seedlings, the R - r spotted kernels only white seedlings and the colorless kernels only green seedlings, indicating no or very low crossing over between R and the Df. The Df K10 (F) chromosome was deficient for the W2 locus. Apparently, the w2 chromosome isolated by Lindstrom over 55 years ago has a mutation (or deficiency) for loci controlling aleurone color synthesis as well as endosperm development and chlorophyll synthesis, none of which are complemented by the Df K10 (F) chromosome. The spotted R df/R df/R df kernels from self pollination and the R df/R df/r w2 kernels have identical phenotypes. No homozygous R w2 kernels have as yet been produced in our studies. Our prediction is that they will be phenotypically similar to the above two classes of kernels.

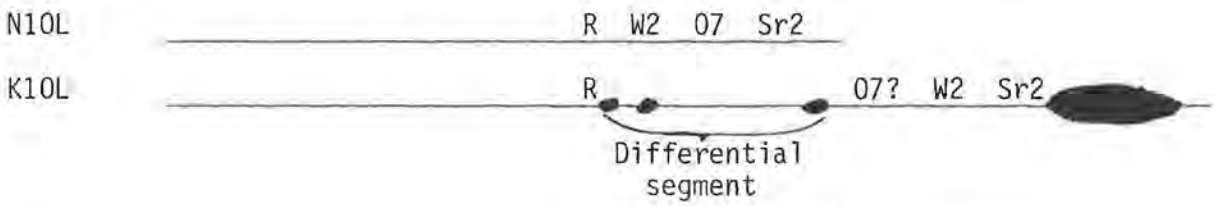
Some of the Df K10 chromosomes do not have a deficiency for the W2 locus. In these cases neither spotted kernels nor white seedlings are produced in F2 populations or in crosses with r W2/r w2 testers.

Although the cytological studies have not been completed, we have found two Df K10 chromosomes lacking the Sr2 and W2 loci which are longer than the normal 10 in Df K10/N10 microsporocytes. Although the Df K10 chromosomes lack the conspicuous K10 knob, they can be distinguished from N10 because they possess the three small knobs in the differential segment. When there is asynapsis of the ends, it is clear that the longer chromosome of the pair is the Df K10. Therefore, the W2 and Sr2 loci must be in the chromatin segment of K10 beyond the end of N10. It should be emphasized that the K10 chromosomes which lack W2 and Sr2 but exceed N10 in length are simple terminal deficiencies. They had little opportunity to accumulate duplicated chromatin by undergoing a series of bridge-breakage-fusion cycles since they arose by breakage of a dicentric bridge at anaphase of the second microspore mitosis. The telophasic products give rise to the two sperm cells. When the sperm nucleus with a freshly broken end unites with the egg, healing of the broken end takes place in the zygotic nucleus.

W2 must lie proximal to the knob since deficient K10 chromosomes have been isolated which are knobless and deficient for Sr2 but still possess W2. Inasmuch as Df K10 chromosomes lacking Sr2 arose from breaks in the proximal euchromatic segment of the extra piece, Sr2 could be in the distal euchromatic tip, in the knob, or in the euchromatin to the right of the breakpoint. A more precise assignment of the cytological location of Sr2 comes from studies by Judith Miles (Indiana University Ph.D. thesis, 1970). She obtained a modified K10 chromosome, here designated K^o, which has the three small knobs of the differential segment and the proximal euchromatin of the extra piece. It was, however, deficient for the knob and the euchromatic tip of K10. Her K^o chromosome had the Sr2 allele. Therefore, the physical location of Sr2 cannot be in the knob or in the distal tip of K10. Since we have chromosomes deficient for Sr2 and doubly deficient for W2 and Sr2 but not for W2 alone, we conclude that the linear order in K10 is centromere - differential segment - W2 - Sr2 - Knob. Although displaced from its normal location, the segment containing W2 and Sr2 has the same orientation relative to the centromere in K10 and N10.

Df K10 (F) may possess the dominant O7 allele, although as stated earlier this trait has a poor penetrance. If this locus has been retained, we have isolated a chromosome deficient for W2 and Sr2 but carrying O7, which lies between these loci. Irrespective of the status of O7, the cytogenetic evidence places the W2 and Sr2 loci in the extra chromatin segment extending beyond the tip of the long arm of N10. If O7 proves to be in the Df K10 (F) chromosome, the linear order in the K10 chromosome has been structurally altered since it would be O7 - W2 - Sr2 - Knob. The origin and constitution of the differential segment has not been established but no genes have been assigned to this segment and our studies indicate that it

differs in gene content from the corresponding segment of N10. The differences between N10 and K10 are diagrammatically shown below:



The great reduction in recombination between R and Sr2 in K10/N10 heterozygotes is intelligible by virtue of the transposition of the terminal portion of 10L reported in this note.

M. M. Rhoades and Ellen Dempsey

The functioning of a mutable alleles in the absence of a conventional Dotted gene

It has generally been considered that a controlled locus is completely stable in the absence of the controlling gene (or at least the instability must be initiated by a controlling locus) but produces a mosaic array of cells with functioning alleles in its presence. During the course of the construction of anthocyanin R self color testers (MNL 53), observations were made on the a locus, which suggest that the a mutable alleles of the Dotted system can function in a very restricted set of cells in the absence of a Dotted gene or at least a conventional Dotted gene.

The a-m (normal frequency of dots), a-m-1 (high frequency of dots) and a-st (stable in the presence of Dt) alleles were converted to lines which were homozygous for R-sc in order to allow anthocyanin production in the scutellar tissue. The aleurone in all three stocks is completely without pigment, unless the dominant A allele is introduced or unless one of the Dotted loci is present, in which case the a-m and a-m-1 lines exhibit their characteristic response of dots. The unusual feature of these stocks is a halo of pigment in the scutellum around the plumule of the embryo. This effect radiates farther in the a-m-1 material than with a-m but is completely absent in the a-st line. The pigment is most intense adjacent to the plumule and decreases to none within a few cell layers. This expression is not in the form of dots but is a continuous one.

There are several possible interpretations of these observations, which point to some unique properties of the system. Firstly, the "mutable" a alleles may be functioning of their own accord, but their action is limited to a small portion of the scutellum or alternatively to the plumule. If the latter is true, the factors (Pu genes) necessary for anthocyanin expression in the plumule are not present and therefore this tissue is colorless. The pigment precursors would diffuse from the plumule into the scutellar tissue to complete the anthocyanin pathway. If these genes are indeed functioning of their own accord, it is interesting to note that the level of expression is correlated with the frequency of dots as when a Dt allele is present in the genome.

An alternative might be that a highly tissue specific Dotted locus is present in these stocks. Such a locus would be active only in the plumule, producing sectors of A tissue. This would result in the production of anthocyanin precursor which upon diffusion into the scutellum would be utilized in the remainder of the pathway. The correlation between the halo size and dotting frequency would be due to the number of presumptive "dots" in the plumule.

The possibility that the anthocyanin production is due to a duplicate A gene with altered tissue specificity is not favored because of the correlation between the halo size and the "mutability" of the a alleles used.

James A. Birchler

A proposal for a uniform genetic marking of the maize genome

The ability to vary the dosage of chromosomes and chromosomal segments is useful in a variety of studies. An optimal situation would be one in which the maize geneticist could manipulate the dosage of any region of the genome using but a single genetic marker for all regions and using one which could be reliably classified at the mature kernel stage. Such a situation would allow analyses on regions not presently amenable to such studies and greatly conserve time and space for field operations. The potential for this exists with the TB-10L18 translocation, induced by B-Y. Lin (Genetics 92:931). This chromosome differs from the usual B-A translocation in that the break in the B chromosome is in the short arm of the supernumerary chromosome, leaving the major long arm unaffected. The A chromatin is broken in 10L thus producing a metacentric with the B centromere, the BL and 10L being the respective arms. This leaves the B short arm appended to 10S on the 10 centromere. The 10L portion of the BL·10L chromosome is marked by an R self color (R-sc) allele.

If this chromosome were now used to induce translocations with the various arms of chromosomes 1-9, the respective arms would be linked to the B centromere with the property of nondisjunction at the second microspore division and simultaneously be genetically marked by the R-scm allele which is also linked to the B. Thus regardless of the particular chromosome involved in this hypothetical type of compound B-A translocation, it could be used as a male onto silks of plants of an r-g tester and the dosage of any chromosome arm could be detected on the basis of the R-scm phenotype.

It may be possible to convert the existing B-A translocations to this system. The necessary contingent is that recombination occur in the B chromosome, for which Lin's TB-10L18 will allow a genetic test. If such is the case, recombination in the BL region between TB-10L18 and any other particular TB-A (all with breakpoints in BL) would give a product which now links the B centromere to both 10L and the respective portion of the other chromosome involved in the original TBA. The resultant chromosomes would be A·BL distal, A·BL prox·B10L, and 10·BS, which collectively contain all portions of the B chromosome.

Once isolated, these translocations could be maintained in homozygous condition by self pollination and crossed as males onto an r-g tester to produce the phenotypically (R-scm) marked dosage series as described by Beckett (1978, J. Hered.). Such translocations could also be maintained as hyperploid heterozygotes. In this case, it is necessary to alternate generations of crossing the stocks to R-nj and R-st to be able to completely distinguish duplicate gamete transmission and cases of recombination between centromere 10 and the R locus. The details are complex and are not included here.

In each dosage analysis, the TB-10L18 can serve as a control on any effects produced by this chromosome arm. Finally, it is noted that chromosome arm 10S can not be included in this scheme and some other marker will be required in that case.

James A. Birchler

Mapping of three independently inherited genes encoding mitochondrial malate dehydrogenase isozymes

The mitochondrial malate dehydrogenase (m-MDH) isozymes are encoded by three independently inherited nuclear genes in seedlings (Goodman et al., MNL 52:99, 1978; Genetics, in press) and in the scutellum of the mature kernel (Newton, MNL 53:16-24, 1979).

Mdh1 is located on chromosome 8. It is linked to the 8L breakpoints of two waxy-marked reciprocal translocations between chromosomes 8 and 9: T8-9d (8L.09; 9L.16) and T8-9 (6673) (8L.35; 9S.31). Mdh1 is not linked to waxy in the absence of these translocations.

Mdh3 is located in the distal region of the long arm of chromosome 3 (Newton, 1979), exhibiting approximately 2.6% recombination with sh2.

Mdh2 was originally reported by Goodman et al. (1978) to be on chromosome 6 following trisomic analyses. Crosses with TB-6Lc confirmed and extended this localization to the long arm of chromosome 6 (Newton, 1979). Since linkage of Mdh2 with Y1 (6-17) was NOT observed, we hypothesized that Mdh2 was located in the distal region of the long arm of chromosome 6. TB-6Lb uncovers genes in distal 6L: its breakpoint lies between Pt (6-59) and py (6-68)--see Beckett, J. Hered. 69:27-36. Jack Beckett generously supplied the TB-6Lb stock used to demonstrate uncovering of Mdh2. Thus, we conclude that Mdh2 is located in the distal region of the long arm of chromosome 6.

Using different lines, McMillin, Roupakias and Scandalios (Genetics 92:1241) recently reported evidence which confirms the previous trisomy 6 analysis of Goodman and the TB-6Lc work of Newton. They, however, interpret their results differently--claiming that two linked genes coding for m-MDH isozymes are in this chromosomal region. On the other hand, the results of extensive testcross analyses (Goodman et al., Genetics, in press) and biochemical studies (Newton and Schwartz, Genetics, in press) support the hypothesis that three independently inherited genes encode the m-MDH isozymes. The mapping of Mdh1, Mdh2 and Mdh3 to separate chromosomes is also supportive of the latter model.

Kathleen J. Newton

Localizations of the independently inherited duplicate genes encoding the soluble malate dehydrogenase isozymes

The cytosolic or soluble malate dehydrogenase (s-MDH) isozymes are encoded by independently inherited duplicate genes, Mdh4 and Mdh5 (Goodman et al., MNL 52:99; Goodman et al., Genetics, in press; Newton, MNL 53:17-18). Mdh4 is on chromosome 1: it is included in TB-1La and TB-1La-5S8041 (Newton, Genetics 91:s88-89), mapping approximately 29 recombination units proximal to Adh1. Mdh5 is also included in TB-1La-5S8041 but not in TB-1La. Approximately 20% recombination between Mdh5 and a2 is observed. The fact that TB-1La-5S8041 uncovers Mdh5 suggests that this gene lies distal to a2 in the short arm of chromosome 5.

Kathleen J. Newton

A further cytogenetic localization of bz2

The bz2 locus has been further localized relative to translocations with breakpoints in 1L. It was previously known that bz2 is uncovered by TB-1La (see Beckett, 1978) and TB-1La-5S8041 (Robertson, MNL 49:79). To extend this work, the bz2 R-scm tester stock of Birchler (MNL 53:103) was crossed as females by a series of compound B-A translocations involving varying lengths of 1L and terminally replaced by distal 3L. The results are summarized below:

TB-A	1L Breakpt.	bz2	Bz2
TB-1La-3L4759-3	0.39	0	75
TB-1La-3Le	0.58	0	330
TB-1La-3L5267	0.72	62	233
TB-1La		26	74

Thus bz2 lies between the 1L breakpoints of T1-3e and T1-3-5267, which cytologically corresponds to the region of 0.58-0.72.

Kathleen J. Newton and James A. Birchler

Induction of alcohol dehydrogenase by amino acids

ADH can be induced in seedling roots by a variety of methods including anaerobic stress and treatment with 2,4-D. We present here evidence that addition of exogenous amino acids can induce ADH1 and ADH2 under aerobic conditions, as well as enhance the induction of ADH during anaerobic stress.

Typically anaerobic induction of ADH is accomplished by totally immersing seedlings in .005 M phosphate buffer. When this buffer is made .3 mg/ml with respect to casein amino acids a 15-40% enhancement of ADH induction is observed. If just the tips of seedling roots (1 cm) are immersed in a 5 mg/ml solution of casein amino acids (or any number of single amino acid combinations) these roots show a 200-300% increase in ADH activity over control seedlings whose root tips were immersed in the buffer without amino acids.

Single amino acids also cause induction. When seedlings were grown anaerobically on blotting paper saturated with various amino acid solutions, all of the 15 amino acids tested gave induction of ADH. The ADH levels in seedlings grown on .005 M amino acids varied from 3-19% above control seedlings grown on buffer saturated paper, depending upon the particular amino acid used. Amino acid concentrations as low as .0005 M showed induction of ADH. On starch gels, bands for both ADH1 and ADH2 were observed in extracts from amino acid induced roots.

These results explain an interesting problem we've experienced in studies of the process of ADH induction. In vitro translation fails to detect any trace of ADH mRNA in aerobically grown roots, yet in vivo pulse labelling with labelled amino acids consistently detected small amounts of ADH protein synthesis which seemed to indicate presence of the mRNA.

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Inheritance and linkages of multiple aleurone layering

S. Duangploy, M. S. Zuber and B. G. Cumbie (MGCNL 50:90-91, 1976) found that the inheritance of multiple aleurone layering is controlled by possibly two genes with partial dominance where both dominant genes are necessary. The results of the backcrosses agreed with the model proposed although their reciprocals didn't. O. E. Nelson and M. T. Chang (Crop Sci. 14:374, 1974) also found conflicting results in different F2 families.

We conducted a backcross study of linkage. The marker source was an advanced generation of the F1 of Mangelsdorf Tester crossed to IAC Maya, a mostly Yellow Tuxpeño cultivar. The source of multiple aleurone was ACRE 134, from the Brazilian Germplasm Bank, crossed and backcrossed once to IAC Maya o2 before concentrating the multiple aleurone character. Both materials aren't lines. This IAC Maya with multiple aleurone was pollinated by the marker, as was the resulting F1 hybrid. The criterion of classification was single layer (mal), and more than one layer, multiple aleurone (Mal). There was difficulty in classifying wx in su background. The results and chi-square analysis are presented in Tables 1 and 2.

Inspection of Table 1 shows at first glance that two complementary dominant genes would explain most of the inheritance of multiple aleurone layering. Note that for waxy the cross or backcross was probably made with an heterozygous marker. By Table 2 we see that there is linkage of one of the dominant complementary genes with Su for both families without heterogeneity. With Y there was no sign of linkage. With wx although the total showed strong evidence of linkage, with $P < 0.01$, there was also an almost equally strong heterogeneity. To see the reason

Table 1. Phenotypic frequencies observed in two families of backcrosses whose origin is described in the text.

	Markers				Families		Total
	Mal	Y	Su	Wx	I	II	I + II
	+	+	+	+	4	9	13
	+	+	+	-	5	5	10
	+	+	-	+	1	3	4
	+	+	-	-	6	4	10
	+	-	+	+	9	8	17
	+	-	+	-	4	4	8
	+	-	-	+	2	6	8
	+	-	-	-	1	2	3
	-	+	+	+	29	21	50
	-	+	+	-	4	9	13
	-	+	-	+	33	12	45
	-	+	-	-	8	14	22
	-	-	+	+	22	26	48
	-	-	+	-	5	4	9
	-	-	-	+	20	17	37
	-	-	-	-	4	11	15
I (+)	32	90	82	120			
I (-)	125	67	75	37			
II (+)	41	77	86	102			
II (-)	114	78	69	53			
I + II (+)	73	167	168	222			
I + II (-)	239	145	144	90			
Total	312	312	312	312			

Table 2. Results from both families pooled. Phenotype, frequency, and χ^2 tests for the segregations indicated. Note that with wx the marker is heterozygous. The interactions are the exact ones; below it is the heterogeneity between families.

	Phenotype (M=marker)				χ^2			
Marker	M Mal	M mal	m Mal	m mal	Mal 1:3	Marker 1:1	Interaction / Heterogeneity	P
su	48	120	25	119	0.427	1.846	5.437	0.02-0.01
							0.379	0.70-0.50
y	37	130	36	109	0.427	1.551	0.309	0.70-0.50
							0.625	0.50-0.30
wx	42	180	31	59	0.427	1:3 2.495	8.612	< 0.01
							7.120	< 0.01

for this heterogeneity Table 3 was mounted. In it we present for both families I and II, within Wx and wx separately, the segregation for Mal and Su. It is seen that in Family I within Wx there is a 1:7 segregation of Mal:mal, within wx a 1:1 segregation. In Family II the segregation in both Wx and wx remained the same, 1:3. It suggests that linked to wx in Family I there was one recessive gene complementary to the dominants that are complementary for Mal. In Table 4 is shown the

Table 3. Hierarchical analysis showing segregation within Wx and within wx separately, for su marker gene with Mal. In Family I the 1:3 segregation breaks down in a 1:7 within Wx and 1:1 within wx. In Family II there is no change.

	Genotype				Chi-square value			
	Su Mal	Su mal	su Mal	su mal	Multiple aleurone	Marker	Exact Interaction	P
Family I								
Wx	13	51	3	53	1:7 0.076	1:1 1.200	5.781	0.02-0.01
wx	9	9	7	12	1:1 0.676	1:1 0.027	1.275	0.30-0.20
Family II								
Wx	17	47	9	29	1:3 0.013	1:1 6.627	0.104	0.80-0.70
wx	9	13	6	25	1:3 0.308	1:1 1.528	2.774	0.10-0.05

Table 4. Phenotypes, models applied to the calculation of p for an approximate solution of the results, frequencies observed and calculated, p and their errors and chi-square of deviations from fitting.

Coupling	Su Mal ¼ (1-p)	Su mal ¼ (1+p)	su Mal ¼ p	su mal ¼ (2-p)	p	χ^2 Deviation
I + II						
Observed[a]	48	120	25	119		6.41
Expected[a]	40.4	115.6	37.6	118.4	48.2±5.36	
Observed[b]	48	120	(30)	(138)		2.31
Expected[b]	45.2	122.8	38.8	129.9	46.2±5.09	
Repulsion	Wx Mal ¼ p	Wx mal ¼ (2-p)	wx Mal (1-p)	wx mal (1+p)		
I only						
Observed[c]	16	104	(48)	(63)		6.89
Expected[c]	8.51	107.0	49.3	66.2	14.7±7.47	
Observed[d]	16	104	(52)	(68)		6.38
Expected[d]	8.8	111.2	51.2	68.8	14.6±7.58	

[a]With the original observations.
[b]Correcting the observations for a perfect 1:1, Su:su segregation.
[c]Multiplying by three the wx frequencies observed.
[d]Correcting the observations for a perfect 1:1, Wx:wx segregation.

calculation of p. With su and a coupling situation and the model shown by maximum likelihood the value of p obtained was 48.2 ± 5.36 (a). This value is not coherent with the significance of the chi-square interaction. To get a better fit the values of Su:su were adjusted to a perfect 1:1 segregation before calculating p, 46.2 ± 5.09 (b). The value of n to calculate the error was taken as double the su class, the smaller class. The chi-square deviations dropped sharply. With Wx and a repulsion situation the linkage was calculated for Family I only. First we multiplied by three the wx frequencies to get nearer 1:1, Wx:wx segregation. The value of p obtained 14.7 ± 7.47 (c). Adjusted to a perfect 1:1 the value was p = 14.6 ± 7.58 (d) with a little improvement in fit. The value of n to calculate the error was double the wx class. Since there are clearly at least three genes involved for multiple aleurone and we calculated the solutions for a two gene model, these are only rough approximations to show linkages and phases.

Our results suggest that the multiple aleurone layering can be controlled by three genes. There is a pair of complementary dominants. Another recessive gene is complementary to these dominants in some way. One of the dominants should be loosely linked to Su; we propose for it the symbol Mal2. The recessive complementary gene is strongly linked to wx; we propose for it the symbol mal1. It seems more widespread in non-multiple aleurone maize. Not excluded is the possibility of a colored scutellum type of inheritance including inhibitors and linkages between multiple aleurone factors.

Luiz Torres de Miranda

Inheritance and linkage of root characteristic from Pueblo maize

G. N. Collins (J. Agric. Res. 1:293-302) reported on root characteristics of Hopi maize which make it more adapted for suboptimal conditions. Our source was Navajo, received from the Germplasm Resources Laboratory, Beltsville, Maryland, USA. The marker was the same described in the preceding work.

Whole ears of segregating F2 selfed and siblings of the cross on different opportunities were planted 15-20 cm deep in a sand pool dug within a greenhouse floor. A few seedlings that emerged proved on digging to be "scapes" having not dropped to the desired depth. After a few unsuccessful attempts we put F2 families to germinate in paper dolls in a standard germinator at about 25° C. After six days the seedlings were classified in two classes: absence of seminal roots (Asr), and presence of seminal roots (asr). The first is characteristic of Navajo, the second of common maize including the marker. The results of three families segregating su are presented in Tables 1 and 2. They must be somewhat disturbed by bad

Table 1. F2 phenotypes observed derived from the cross of adapted Mangelsdorf Tester (asr) x Navajo (Asr). Asr stands for Navajo type of root with absence of seminal roots, and asr for presence.

Families	Su Asr	Su asr	su Asr	su asr	Segregation Asr:asr	p*
I	114	39	26	21	3:1	38.0 ± 3.1
II	129	50	35	16	3:1	47.5 ± 3.2
I + II	243	89	61	37	3:1	43.0 ± 2.2
III	70	9	61	21	9:7	30.0 ± 4.3

*p calculated by the product method for the segregations indicated.

Table 2. Chi-square analysis of data in Table 1.

Families	χ^2 Su su	Asr asr	Exact Interaction
I	3:1 0.240	3:1 2.667	6.306*
II	0.980	1.675	0.230
Sum	1.220	4.342ns	6.536*
I + II	1.119	4.245*	4.378*
Heterogeneity	0.101	0.097	2.158
III	3:1 5.061*	9:7 3.372	5.364*

adaptation of material. For the first two families there is a little deficiency in Asr for fitting a 3:1 segregation, 304 observed versus 322.5 expected, which is detected for the total, not for each family individually, although the deviation is consistent. For the third family there isn't significant deviation from a 9:7 ratio of Asr:asr. The results suggest that depending on environmental conditions or genetic background the absence of seminal roots segregates as a single dominant, or as a pair of complementary dominants. One of these genes has a linkage with Su. We propose for it the symbol Asr1 (absence of seminal roots 1).

By the product method with the first two families, which gave a 3:1 ratio of Asr:asr, the value calculated was $p = 43.0 \pm 2.2$. For the family that gave a 9:7 ratio the value was $p = 30.0 \pm 4.3$.

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Cytological stability of maize anther calli

Anther calli of maize strains King Huang 13 and King Huang 9, Chun-Dan, Lai-Ping Bai, and Shu-Ke-chuang were employed. These calli grew about two months on N6 medium from the time of inoculation to the time of collection. Most of the collections and fixations were made at 3 o'clock in the afternoon. Materials fixed at this time were found to have the highest mitotic index. The fixative was aceto-alcohol (1:3) and the squash was done in a drop of haemotoxylin.

When over 150 pieces of calli from the above five different maize strains were cytologically examined, it was observed that the frequency of the occurrence of mitotic divisions was very low. Only 178 dividing cells were found in these calli. The variations in chromosome numbers and their percent of the total were as follows:

	Chromosome No.									
	5	6	7	8	9	10	15	16	19	20
No. cells	14	1	1	2	1	132	1	2	1	23
Percent	8	0.5	0.5	1	0.5	74	0.5	1	0.5	13

It is clear that most of the callus cells had 10 chromosomes. However, some of the cells had 20 chromosomes. Very few hypodiploid or hyperhaploid cells were observed. This relatively stable haploid condition might be accounted for by the fact that these calli were cultured only for a short period of time. It is known that long-term culture of plant tissue might produce more alterations in chromosome constitutions than short-term as reported by Torrey (1967). It can also be seen that the stability of chromosome constitutions varies among the calli of different maize strains. This observation is in agreement with that of Inomata et al. (1976), who found different chromosome stabilities in callus tissue of lines 3B54 and 3B58 of Chinese spring wheat (Triticum aestivum).

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Cytological stability of maize pollen (H1) plants

Root-tip meristems of the pollen (H1) plants of maize strain 592, Chun-Dan 105, King Huang 13, King Huang 9, Lai-Ping-Bai, Shwei-Bai, Ba-Tang-Bai, and two hybrids of 592 x Lai-Ping-Bai and 592 x Eh-Bai were used for studies. These root-tips were also fixed with aceto-alcohol (1:3) and slides were prepared by following standard squash technique and doubly stained with Feulgen and aceto-carmine.

Variations in chromosome number: Chromosome counts were made with the root-tip cells of the H1 plants of maize strains 592, Chun-Dan 105, King Huang 13, Lai-Ping-Bai, King Huang 9, Ba-Tang-Bai, Shwei-Bai and two F1 hybrids of 592 x Eh-Bai, 592 x Lai-Ping-Bai. A pooled total of 352 cells at either metaphase or late prophase were examined:

	Chromosome Number																			
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	25	40
No. Cells	1	5	2	1	5	2	5	197	3	2	3	4	7	7	3	5	2	96	1	1
Percent				6				56					10.3					27.3	0.5	

The chromosome numbers ranged from three to 40 per cell. Among these numbers, haploid cells (n = 10) were counted to be 197 (56%), diploid cells (20) to be 96 (27%), hypohaploid (< 10) to be 21 (6%), between haploid and diploid (11-19) to be 30 (10%), hyperdiploid (> 20) to be 2 (0.5%). It was surprising to see a cell with three intact chromosomes undergoing active mitotic division. It appears agreeable to Torrey's (1967) report that in tissue culture, only a portion of the plant genome might be necessary for normal mitosis.

When consideration is made on the basis of individual plants of the above six varieties and two hybrids, it has a total number of 29 plants. Among them, plants with root-tip cells having exclusively 10 chromosomes were scored to be 9 (31%); plants having exclusively 20 chromosomes to be 2 (7%); plants having chromosome numbers other than 10 and 20 (hypohaploids, hypodiploids and hyperdiploids) to be 18 (62%). Among these 18 plants, eight had in most of their cells 10 chromosomes, five had in most of the cells 20 chromosomes; and the remaining five had neither 10 nor 20 chromosomes as a predominant number.

Changes in chromosome structure: In general, alterations in chromosome structure were not so frequently found as those in chromosome number. However, at metaphase and anaphase of mitosis, fragments, bridges, tripolar separations, and early parallel splitting of chromatids were occasionally observed. These irregularities may account for, at least partly, the wide range of variations in chromosome number. Even though little study has been done on the cause of these irregu-

larities, it might be hypothesized that chemical as well as physical components of the culture may play some role.

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Regeneration from maize anther calli

During the last year we had encouraging developments with our maize anther culture. For the first time in many years we obtained two plantlets from regeneration of calli. Maize genotypes of King Huang 9 and King Huang 13, both from China, were employed in this experiment. Anthers were grown in both MS and N6 (Chu's) media for six weeks and they were then transferred to regeneration medium without any 2,4-D or TIBA. Three weeks later, two regenerations appeared. However, both of them were finicky and failed to grow into mature plants. Now further experiments are being carried on with refined techniques. It is hoped to have more pollen plants developed in the near future.

Y. C. Ting and Margaret Yu

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Mutation for earliness

An early mutant was observed in 1978 in the well-known French inbred line F7, within an ear to row nursery. Within the segregating progenies from selfing, the results of countings quite clearly indicate that the mutation has a Mendelian type of inheritance and it is recessive in the F7 genetic background:

	Observed		3:1 expected					
Progeny	Normal	Early	Normal	Early	Total	d.f.	χ^2	P Value
1	72	23	71.25	23.75	95	1	0.032	0.75-0.90
2	70	22	69	23	92	1	0.057	0.75-0.90
3	68	27	71.25	23.75	95	1	0.285	0.50-0.75
Total	210	72	211.5	70.50	282	2	0.043	

Measurements of plant height and leaf number are in agreement with the significant gain of 8 days for silking, due to a decrease of the internode number:

	Ear Height cm	Plant Height cm	Leaves Above Ear	Total Leaves	100 Kernel Weight gm	Silking Day
F7 N	29.8±1.7	76.7±3.1	3.7±1	13.4±2.0	35.2±1.0	20.8 July ± 1.6
F7 Early	25.3±1.7	65.7±1.5	3.1±0.3	10.3±0.3	28.7±3.0	12.5 July ± 3.4

Standard errors are of the mean of 10 plants at P = 0.01 level; all measurements are significantly different at the 0.01 level.

Photoperiodic reaction will be tested to determine the physiological basis of the mutation. The decrease of the internode number seems to be different from that reported by Blanco (MGCNL 53:8-9, 1979), in which the similar decrease is

associated with the pale green system pg11 pg12. No visual difference can be seen between normal and early F7 about chlorophyll content.

The usefulness is subject to the inheritance in different backgrounds. Because many genes are segregating, it seems difficult to compare the ranges of the F2 generations from F7 normal and F7 early crossed with each inbred line. In the breeding of conversion, the inheritance will be better known only after three backcrosses at a level of 93.75% homozygosity. These backcrosses will be made without intermediary selfings, taking from the different generations the earliest silking plants. In each generation of backcross and in each progeny, n plants have to be backcrossed. With a probability of 0.01 to lack one gene, n is computed from $(1/2)^n \leq 0.01$. At the third backcross, i.e., for each 7^2 progenies 7 plants have to be backcrossed and then 343 plants have to be selfed. Another limitation is the decrease of yield correlated with the earliness increase, inasmuch as the kernel weight is affected.

M. Pollacsek and M. Caenen

Looking for mutations affecting crossing over

The recovery of parental gametes in homozygous stage from selfed F1 hybrids, giving directly a number of inbred lines, is supposed to result from association of a general suppression of crossing over and a directional segregation of parental gametes (Oenothera method imagined by Burnham, 1946). A preliminary search for a suppression of crossing-over other than an inversion system was carried out for the fl2 su1 region located on the fourth chromosome. The need for a large screening was found using kernel traits according to the following procedure.

Eighty-five flint local varieties were crossed in an isolated field with a homozygous strain for fl2 and su1 as a male parent in 1978. The F1 plants were detasseled in 1979 and pollinated in an isolated field by a su1 strain. Therefore the ears were screened for their lack of floury kernels, which are recombinants:

	Female Gametes				Kernel Genotypes						Phenotypes
Par.	fl2	fl2	su1	su1	fl2	fl2	+	su1	su1	su1	su1
Par.	+	+	+	+	+	+	+	+	+	su1	+
Rec.	fl2	fl2	+	+	fl2	fl2	+	+	+	su1	fl2
Rec.	+	+	su1	su1	+	+	+	su1	su1	su1	su1

Among 15,000 screened ears, only one desirable ear with normal and sugary kernels was found in the population of Barisis (Aisne) France. In order to eliminate the possibility of an inversion (the collected ear was not well filled), or a reverse mutation in 1978 in the pollen (fl2 to +), the plants from sugary kernels will be pollinated by a normal type. All kernels should have a floury 2 appearance if we have detected a new system of suppression of crossing over. In case of success, we will have to check this system for other regions and chromosomes.

M. Pollacsek

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Determination of chromosome knob number in Mexican races of maize

Observations of chromosome knobs were made in 45 collections of Mexican maize representing 23 recognized races of Zea mays L. Pollen mother cells were collected and fixed from 5 randomly selected plants within each of the 45 populations.

Observations of the pachytene stage of meiosis were made on 10 cells from each plant. Data were recorded concerning number and size of knobs, characteristics of individual knobs and any anomalous knob behavior. A statistical analysis was performed with the mean number, variance and standard error being calculated for plants and populations (see table). Knob number variability was quite low within plants and within the range of ± 1 knob among plants within populations. In most

MEXICAN RACES	POPULATION	MEAN KNOB NUMBER	VARIATION	STANDARD ERROR
ARROCILLO AMARILLO	PUEBLA 91	7.86	.08	.13
BOLITA	OAXACA 28	7.34	.88	.42
" "	OAXACA 40	6.72	.14	.17
" "	OAXACA 44	8.10	.22	.21
CELAYA	GUANAJUATO 28	7.42	.79	.40
" "	GUANAJUATO 29	8.94	.10	.14
CHALQUENO	HILDAGO 7	7.64	.15	.17
" "	MEXICO 48	7.72	.17	.19
" "	ZACATECAS 4	7.36	.70	.37
CHAPALOTE	SINALOA 2	10.76	.01	.05
COMITECO	CHIAPAS 206	8.4	.20	.20
CONICO	MEXICO 72	4.78	.65	.36
CONICO NORTENO	AGUAS CALIENTES 8	7.56	.77	.39
" " " "	AGUAS CALIENTES 14	6.28	.73	.38
" " "	AGUAS CALIENTES 15	5.8	.17	.19
" " " "	GUANAJUATO 34	9.18	.35	.26
" " " "	GUANAJUATO 49	9.16	.89	.42
" " " "	GUANAJUATO 56	6.82	.79	.40
" " " "	GUANAJUATO 68	6.12	.04	.09
" " " "	QUERETARO 1	8.80	.37	.27
" " " "	QUERETARO 3	9.38	.34	.26
ELOTES OCCIDENTALES	NAYARIT 29	7.38	.11	.15
" " " "	NAYARIT 38	7.02	.98	.44
HARINOSO DE OCHO	NAYARIT 24	4.5	.16	.18
JALA	NAYARIT 6	7.30	.14	.16
NAL-TEL	YUCATON 7	6.26	.15	.17
OLOTON	CHIAPAS 92	4.92	.23	.21
REVENTADOR	NAYARIT 15	5.18	.43	.29
TABLONCILLO	JALISCO 42	7.14	.18	.19
" "	JALISCO 43	10.18	.13	.16
" "	JALISCO 87	6.56	.43	.29
" "	JALISCO 103	8.60	.09	.13
TABLONCILLO	NAYARIT 12	6.82	.42	.29
TEHUA	CHIAPAS 29	6.5	.40	.28
" "	CHIAPAS 204	13.92	.76	.39
TEPECINTLE	CHIAPAS 76	8.72	.20	.20
TUXPENO	OAXACA 7	6.94	.57	.33
" "	VERACRUZ 39	7.44	.19	.20
VANDENO	GUERRERO 96	7.96	.11	.15
ZAPALOTE CHICO	OAXACA 50	12.72	.50	.32
ZAPALOTE GRANDE	CHIAPAS 224	7.4	.57	.34

instances mean knob number determinations among populations within a race were very similar. However, appreciable variation in mean knob number was observed among the different races examined, ranging from 4.5 knobs in Chapalote to 13.92 knobs in Tehua. Knob size also varied greatly among populations, with size generally showing an inverse relationship to number. In a few races such as Zapalote Chico, an obvious mixture of both large and small knobs was observed.

A. L. Rayburn III, J. D. Smith, and H. J. Price

Procedure for Giemsa staining Zea mays pachytene chromosomes

Giemsa dye, when used according to modified C-band techniques, gives better resolution of the pachytene chromosome knobs of Zea mays than does acetocarmine. With Giemsa the knobs seem to have a more distinct shape and structure than with acetocarmine. These shapes are consistent from cell to cell. The problems of

overlapping chromosomes, chromomeres, etc. were overcome by the Giemsa method. Giemsa staining permits heterozygous vs. homozygous knob recognition, a distinction which is difficult using acetocarmine. Also noted was the absence of the nucleolus when using the Giemsa technique.

This method gives better resolution of knobs and their structure yet is still relatively fast and results in a permanent slide. This technique is most useful when dealing with corn lines with characteristics which result in poor acetocarmine preparations, e.g., lines with large numbers of knobs, fused knobs, poor chromosome spreading, etc.

The florets were collected and fixed in cold (4° C) 3:1, Farmers Solution of 3 absolute alcohol:1 glacial acetic acid for 24 hours and stored in 70% alcohol until stained. The squashing and staining series is as follows:

1. Hydrate the florets in distilled water for 30 minutes.
2. Remove the anthers and place on a subbed slide (subbing agent: 5 g gelatin, .1 g chrome alum in 100 ml distilled water.
3. Squash the anthers with a coverslip in distilled water.
4. Place slide on slide warmer at 37° C for 15 minutes. Remove coverslip and return to the slide warmer until dry.
5. Immerse slides in a saturated solution of barium hydroxide (pH 13.5) for 170 minutes.
6. Remove slides and rinse 3 times in distilled water.
7. Place in Giemsa stain (2% Gurr improved Giemsa stain R66 in .1 M phosphate buffer, pH 6.8) for 7 minutes.
8. Rinse twice in distilled water, air dry and mount coverslips over permount.

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A breeding strategy for the allotetraploidization of maize

Allotetraploid maize would be a true-breeding hybrid and would not have the reduction in fertility and vigor caused by aneuploidy in autotetraploid populations.

The allotetraploidization of maize can be achieved by restructuring a maize genome so that its chromosomes will not pair with those of the normal maize genome. This restructuring can be done by concentrating induced and naturally occurring cryptic and visible chromosome aberrations, qualitatively and quantitatively different pairing factors, and genes affecting the expression of differential pairing affinity (like the Ph gene in wheat) into a single line by a recurrent selection type of breeding program.

It has been shown experimentally (Theor. Appl. Genet. 54:103-112, 1979) that differential pairing affinity (DPA) factors are abundant and that they may be readily induced by X-irradiation and chemical mutagens. The assembly of a new genome containing enough DPA factors tc produce almost complete autosyndetic pairing presents many problems.

Kind of germ plasm. At one time it was thought desirable to use much exotic germ plasm in the hope of obtaining more naturally occurring DPA factors. This would have the drawback of incorporating much non-adapted material. However, experiments indicate that Corn Belt maize is as variable as that from other parts of the world, and therefore the inclusion of exotic material is not advantageous.

The type of DPA. The DPA could be based on cryptic or visible structural aberrations, or on qualitative or quantitative changes in the pairing code. Inversions

are effective in producing DPA, but they pose many problems. They prevent the recombination of genetic material inside the inverted region (except for 4 strand double exchanges) and thus restrict the formation of new combinations of DPA factors. Duplicate-deficient and deficient chromosomes are produced from crossing over in the inverted region. These will persist in tetraploid populations. Reciprocal translocations are not effective in producing DPA according to Sybenga (1973, Genetica 44:270-282). Duplications and deficiencies disrupt the genic balance and are to be avoided.

Thus, it is better to rely on cryptic aberrations; small inversions; and changes in the number of pairing units in the pairing initiation sites if these are repetitive.

Restructuring on the diploid or tetraploid level. It will be done on the tetraploid level for the following reasons. Selection for agronomic traits should be made on the level where the genetic material will be used. The amount of DPA is more easily assessed on the tetraploid level.

Assessment of DPA. Cytological methods of assessing DPA such as determination of quadrivalent frequencies are less efficient than genetic methods. As a plant with the duplex constitution of AAaa approaches allotetraploidy the frequency of aa gametes as determined in a test cross declines from 1/6 (chromosome segregation) to 0. In an allotetraploid only Aa gametes are formed.

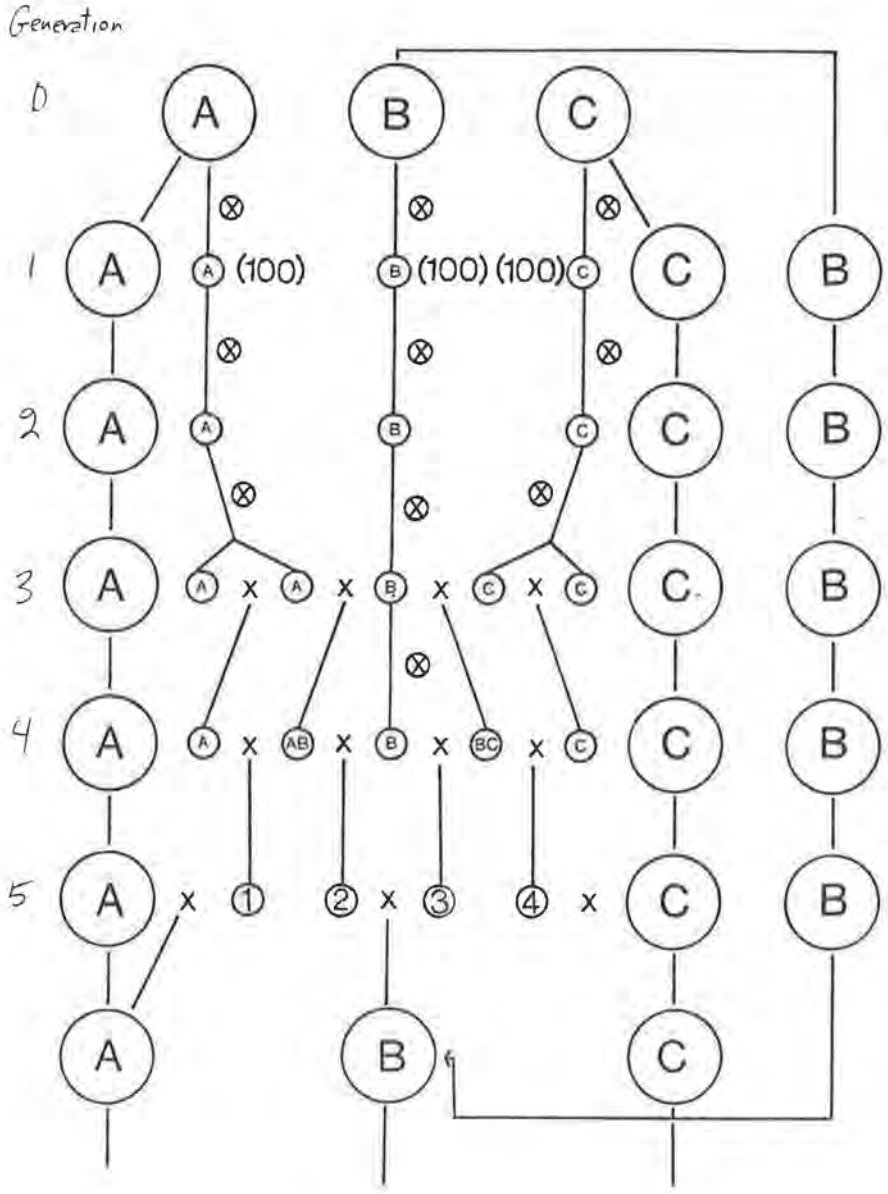
A breeding system. The idea expressed by Stebbins and others that an autotetraploid or a segmental allotetraploid can evolve into a true allotetraploid by selection for DPA mutant factors which would produce a more regular meiosis and greater fertility is questionable. Chromosome assortment and crossing over between homoeologues would prevent the fixation of two different pairs of genomes. The basic requirement for speciation is isolation. Consequently, any allotetraploidizing breeding program must keep the population being restructured reproductively isolated from normal maize populations.

This isolation poses a problem. We can grow a population of material which is subjected to X-irradiation and chemical mutagens and take samples from it and cross them with genetic marker stocks. Plants from those crosses which show lower frequencies of recessive segregants (from a higher level of DPA) cannot be used to form an elite population because the restructured material has been mixed with normal material. The use of seed from siblings requires high correlation between it and the material that went into the test cross. Ideally, it should be an inbred line. However, the progress toward homozygosity is very slow in autotetraploid populations (and even slower in segmental allotetraploids)--after 10 generations of self fertilization, the heterozygosity is about 19%. Thus genetic testing would appear not to be feasible.

Nevertheless, there is a solution to this problem. It is simply to restructure the genetic markers as well. The breeding system is shown in the diagram.

Three synthetics (A, B, and C) are maintained by random crossing within themselves and are subjected to X-irradiation (10,000 r to the dry kernels) every generation. Synthetic B was derived from 20 diploid maize lines which were subjected to X-irradiation (5,000 r) for 10 generations, 8 exotic lines, various open pollinated varieties which have been incorporated in the tetraploid level via the el gene. This synthetic has a large proportion of Argentine Flint, and Alexander's Synthetic B (a very good source material which was derived from over 30 inbred lines) which were also subjected to recurrent X-irradiation. Synthetic B has all dominant genes.

The other two lines (A and C) are homozygous for a different group of 5 recessive markers: bz2, lg y v16 wx and a su pr gl g. There is one marker for each of the 10 chromosomes.



About 300 plants in each synthetic are grown each year. A random sample of seed from 100 of the best ears is used to produce the next generation. After an initial mixing period (which has been completed) a sample of 100 kernels will be taken to produce test lines. After a few generations of self fertilization, these lines are crossed with each other in the manner shown in the diagram. At generation 4 the test cross is made and the genetic ratios for all ten genes will be determined. A value called the allosyndetic index is computed which is simply the sum of the percentages of recessive gametes. Progenies whose allosyndetic indices are in the 10% lowest group will be selected and backcrossed to the synthetics and added to them. Progenies giving higher allosyndetic indices are discarded.

The ratio of old material to new material in the new synthetic will probably be 1:1. This method carries dominant genes into the A and C synthetics. These can be eliminated easily in future generations. The introduction of recessive genes into the B population may require the use of test crosses in future generations to get rid of them.

Eventually, enough DPA factor will accumulate in the B synthetic, so that samples of it can be taken to be crossed with normal 4n maize lines. It is hoped that one of these hybrids will have 20 pairs of bivalents and be an allotetraploid.

G. G. Doyle

An efficient method for producing trisomic and telotrisomic plants in uniform backgrounds

Self- and sib-pollinated ears of some inbred lines produce occasional grains that are clearly smaller than their neighbors. Following are data obtained from cytological examination of mitoses from root tips of such small kernels germinated in petri dishes:

Inbred lines	Kernels (no.)	Normal seedlings (no.)	Primary trisomics (no.)	Monotelo-trisomics (no.)	Monotelo-disomics (no.)
W23 and 3 close derivatives	28	14	4	3	1
N6	8	4	0	2	0

Of the 22 "W23" plants examined, 14 (64%) were normal, 4 (18%) were primary trisomics, 3 (14%) were telotrisomics, and one (5%) was monotelodisomic (i.e., diploid but lacking an arm of one chromosome). Only 6 N6 plants were examined; 2 (33%) were telotrisomic. The trisomic and telocentric chromosomes varied greatly in length, so several chromosomes were likely represented; chromosome 1 was definitely identified.

It appears that the simple procedure of selecting small kernels from inbred ears provides an efficient method for developing trisomic and telotrisomic stocks in uniform backgrounds. If the small kernels have aneuploid endosperms, as seems likely, then it is probable that trisomics of certain chromosomes and chromosome arms will not be selected by this method, because aneuploid endosperms produced by some B-A translocations are approximately normal in size.

The expert assistance of Percy Sallee in all aspects of fixing, staining, and cytological examination of the preparations is gratefully acknowledged.

Jack B. Beckett

Dominant dwarf D8 is between bz2 and gs on chromosome 1

Testcross data from + D8 +/bz2 + gs:

Parentals	200 + 207	407	
Region 1	29 + 38	67	13.8%
Region 2	8 + 4	12	2.5%
Doubles	0	0	
	Total	486	

Thus, D8 is close to gs (2.5% recombination), probably between gs and the group of lw, Adh, and Kn, 7-8 units to the left of gs.

E. H. Coe, Jr.

Recessive plant color intensifier a3 recombines with a1

The a3 factor (see MNL 53:27), which confers intense color in combination with a barred allele at the B locus, is uncovered by TB-3La. To test for linkage with factors in this arm, colored (A1) seeds were selected from F2 ears from a3 + +/+ a1 et, classified for a3 and self-pollinated. Of 19 plants that were A1 A1 (out of 79 tested), 13 were a3 a3; 2 of the 6 A3 recombinants were +/et and 4 were +/+. Among 14 a3 a3 plants tested, all but one was A1 A1: the recombinant was a3 + +/a3 a1 et. Apparently a3 is to the left of a1, 4 to 16 units away (calculating 6 a3-A1 recombinant strands among 2 x 19 = 38 A1 strands, 16%; 1 a3 a1 among 28 a3, 4%).

E. H. Coe, Jr.

Exceptional seedlings from iojap and chloroplast mutator

Exceptional white or yellow seedlings from the cross of ij ij or cm cm ear parents by normal pollen parents occur in clustered locations on the ear, demonstrated by "ear map" plantings. A number of ear maps have been derived to ask certain questions: How often do ears show such sectors? Do sectors occur in 1/2, 1/4, 1/8, etc. of the ear? Are some ears more "unstable" than others? In addition to the white seedlings, the occurrence of sectorial (i.e., heteroplasmic) individuals might be within white clones (perhaps arising by paternal transmission of normal plastids) or independently of white clones (perhaps arising by late origination of the heteroplasmic state in the meiotic or pre-meiotic lineages).

From a group of 17 ears of ij ij and 21 of cm cm crossed by Oh51a pollen parent, the following ear-by-ear results were found:

	Green	Sectored	White		Green	Sectored	White
ij ij	143	4	48	cm cm	221	0	1
	104	0	12		82	1	0
	47	0	16		183	1	0
	109	4	2		0	0	20
	141	0	5		40	1	0
	156	2	17		160	7	2
	189	0	5		172	0	0
	109	0	0		44	0	0
	32	0	0		293	0	0
	46	0	0		59	1	5
	12	0	2		233	5	7
	43	0	0		119	6	12
	84	0	0		151	1	2
	70	1	9		30	0	0
	145	3	10		74	1	0
	119	7	3		97	0	5
	330	0	10		15	3	1
					35	0	0
					62	0	0
					57	0	0
					83	0	0

The distribution by events is as follows:

	0	1	2	3	4	5	6	7	8	9	10+
Sectored from ij	11	1	1	1	2			1			
Sectored from cm	11	6		1		1	1	1			
White from ij	5		2	1		2				1	6
White from cm	12	2	2			2		1			2

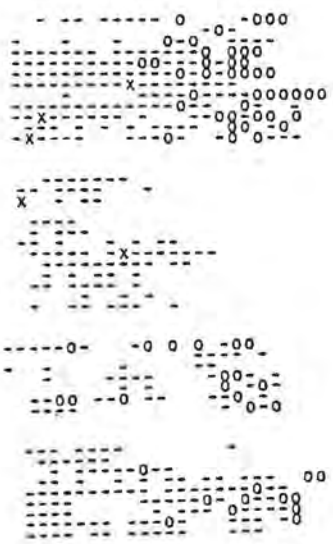
White seedlings appear to occur in a non-Poisson series, while sectorial seedlings appear to be more nearly individual in origin.

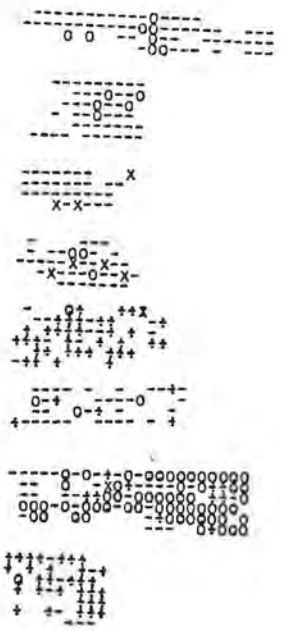
The accompanying ear maps (17 from ij, 15 from cm) include the same ears as above (crossed by Oh51a) and some others crossed by other pollen parents. Many of the maps show scattered, isolated white seedlings, and only a few show groupings that may be clonally related. Sectorial seedlings occur independently of whites for the most part.

ij ij X ++

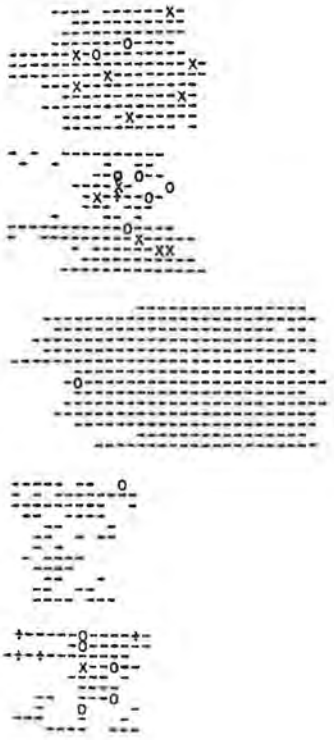
Key:

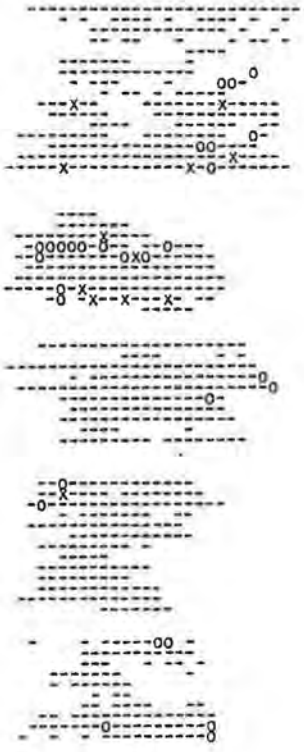
-	green
x	sectored
o	white or yellow
:	purple aleurone
blank	no seed or seedling





cm cm X ++





White seedlings, arising from early or late events during ear development, appear most often to reflect high instability in the ear (i.e., extended sorting out of the heteroplasmic state) rather than homogenous clonal groups. Sectorial seedlings, on the other hand, appear to reflect late, isolated events (new origins of the heteroplasmic state?), and not biparental zygotes.

E. H. Coe, Jr.

Clonal analysis of development in corn

In the corn plant the tassel, ear and each node develop from a small group of embryonal cells. Based on the analysis of clones, the shoot apex of the dormant embryo has been visualized to consist of 2-4 cells at the top set off to become the tassel, followed by 16 cells to become the 4-7 upper nodes (above the ear), and finally three levels of 32-cells-each representing the remaining nodes (Coe and Neuffer, 1978, pp. 113 ff. in The Clonal Basis of Development, eds. Subtelny and Sussex, Academic Press). The 32 cells at a given level develop into 2-3 nodes. The ear shoot develops from 2-4 cells which represent a subset of the 32 cells at that level.

The technique of marking cells through x-ray induced elimination of a dominant allele was used to investigate the elaboration of tassel, ear shoot and various nodes from embryonal cells. The ultimate aim is to arrive at a dynamic picture of corn plant development from the dormant embryo. Dry seeds heterozygous for color markers or mutations affecting the morphology of tassel and ear were x-rayed and grown, and sectors were scored in the mature plants.

Development of the tassel: Among over 3,000 plants examined (marked for one or more mutations, such as +/Vg, +/bz2, B Pl/b pl, +/Tu, +/Ts6, +/ra, R-r/r-g), 41 tassel sectors were observed. The majority of tassels (60%) developed from 4 ± 1 cells, the remainder from 2 to 14 cells. When the sector included the central spike, the latter was divided vertically into two halves showing that the subset of cells developing into the central spike comes from two separate cells. A vivid expression of this was observed in -/ra sectors where all the additional branch spikes were arranged only on one half of the central spike.

At the border of a sector, some of the male florets were also half sectored, but all the three anthers in such florets were either purple (R-r) or green (r-g). A single spikelet can develop from 2 cells but the stamens of a floret share a common cell. The mutations Vg, Tu, Ts6 and ra were found to be cell autonomous for expressivity in the tassel, and therefore their products must be cell limited. No sectors in tassel or ear were found among over 2,000 plants heterozygous for ts1, ts2, ts4, Tp1, Tp2, sk or D8.

Determination and development of nodes: The 1979 data on the apparent cell number (ACN) and the extent of sectors (Figs. 1 and 2) using a different strain of corn are similar to those reported by Coe and Neuffer (1978). The absolute ACN seems to depend on a particular strain, but invariably the nodes above the ear (nodes 15-20) show half the ACN of the lower nodes (nodes 8-15).

Node Level		Dry Seed	2 Days	8 Days
21		10	-	-
20		12	11	20
19		7	10	30
18		12	13	25
17		11	13	18
16		21	18	26
15		27	23	35
14	E	30	22	31
13	A	43	20	42
12	R	49	25	47
11	S	42	24	67
10		39	26	61
9		35	30	67
8		-	30	149
7		13	26	107

Fig. 1. Apparent cell number at each node level for material x-rayed at dry seed stage and 2 and 8 days after sowing.

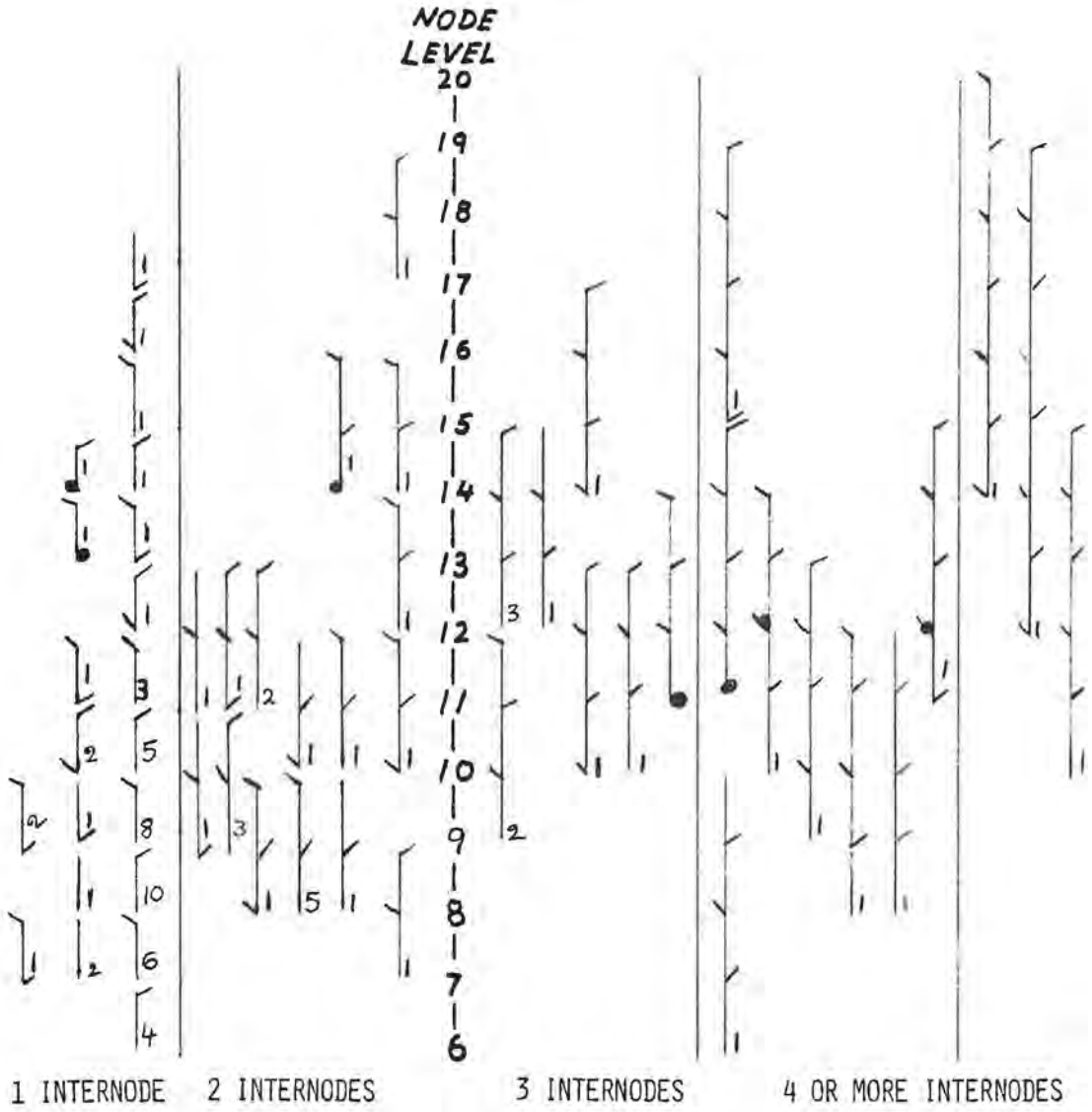


Fig. 2. Extent of sectors at each node level for material x-rayed at dry seed stage. Leaf is represented by a lateral projection (/), while an ear is designated by filled circles (●). The numbers (1-10) represent the number of sectors observed at a given node.

Unlike some of the ferns, in the shoot apex of corn all cells divide. At the dormant embryo stage (except for the 2-4 cells destined to produce tassel) all the cells behave as independent components because the individual sectors extend 1, 2, 3, 4 or more nodes (Fig. 2). In a strict sense cells at the dormant embryo stage have not become destined to produce a particular node. As the development proceeds, the 32 meristematic cells at a level divide to produce nodal initials and another 32 cells representing the two remaining nodes. Each node initial cell is no longer an independent component and collectively the nodal initials become destined to produce a particular single node. The process of determination thus involves specifying the destiny of a group of cells to a specific node. In the plants x-rayed 8 days post-sowing (Fig. 3), the sectors extend for one node only

Node Level	Dry Seed	2 Days	8 Days	13 Days
20	6.0	7.6	5.0	4.0
19	4.3	4.3	3.3	-
18	1.0	2.5	4.5	-
17	4.0	3.5	3.0	2.0
16	1.7	2.5	2.1	1.0
15	2.4	2.3	2.0	1.0*
14 E	2.2	5.3	1.5	1.5
13 A	2.4	3.1	1.2	1.3
12 R	2.4	2.0	1.1	1.0
11 S	1.5	2.0	1.0	1.0
10	1.5	1.4	1.0	1.0
9	1.3	1.2	1.0	1.0
8	1.0	1.2	1.0	1.0
7	1.0	1.0	1.0	1.0

*Sector only in bract or husks

Fig. 3. Extent of sectors (in nodes) at each node level for material x-rayed at dry seed stage and 2, 8 and 13 days after sowing.

between nodes 7 and 11 and 1.1 to 5 nodes at nodes 12 through 20. Groups of cells thus seem to become determined at successively higher levels and determination progresses from the base of the plant toward ear-bearing nodes. In the plants x-rayed 13 days post-sowing, determination is not only progressing at the base but is also initiated from nodes 15 toward the top (Fig. 3). This finding is consistent with the notion that at this time (13 days after sowing), the corn plant has been separated into two compartments, the upper one-third and the lower two-thirds.

The majority of sectors induced at the dry seed stage started at the base of an internode, extended up through one or more nodes and terminated in a leaf. At the ear-bearing nodes, the sector started in the bract or husk and ended in the leaf situated one or two nodes above (Fig. 2). These results confirm the observations of Sharman (Ann. Bot. 6:245, 1942). The clonal analysis as well as the developmental anatomy both show that an internode corresponds to the lower half of a developing node, and that the ear shoot represents an axillary bud associated with the leaf above and not with the leaf in whose axil it appears.

Further development involves the formation of leaf and internode initials from nodal initials. While the leaf primordia are developing, the 32 internode initials divide leading to a widening of the axis: clones induced 8 days after sowing measured 1/64th at nodes 9 to 11 and 1/107 to 1/149th at nodes 7 and 8. In the plants x-rayed still later (13 days) the sectors at nodes 7-12 extended a single but entire internode. The internodes are therefore represented by a single layer of cells. Cell divisions leading to an increase of cell number in the vertical direction occur much later.

The results obtained thus far strongly suggest that the ground plan for all the nodes is laid down first while the shoot apex is still situated at the base of a corn seedling. The burst of growth occurring later mostly involves cell divisions and cell expansion in the internode initials.

Development of the ear shoot: Among over 6,000 ears examined, 138 ear sectors arising due to a loss of Bz2, P-WR, B, Pl or fertility factors were found. Only 28 of these entered the cob. An analysis shows that the ear shoot is derived from 4-6 cells which constitute a subset of 32 cells and, further, only two cell lineages extend and contribute to the cob and florets. The remaining two to four clones occur only in the husks and can terminate in any of the twelve or fourteen husks. Though the cob size in a given family is more or less constant, the relative contribution of two cells to the cob is highly variable. One cell can generate anywhere between 5 to 50% of cob and less frequently only a single cell extends into the cob. The extreme plasticity of the two cell lineages extending into the cob seems more or less a general rule and this feature can account for

the unexpected ratio of green vs. white seedlings in a cross of half-white ij/+ ♀ x +/+ ♂ (see Rhoades, 1946, Cold Spring Harb. Symp. Quant. Biol. 11:202).

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Effect of growth regulators on the expression of Pt, Tu, sk and bk2

Several mutants of corn--Pt, Tu, sk and bk2--were treated with growth regulators in an attempt to normalize the plants. The long glumes in the female spikelets (tunicate) and the proliferation of pistillate tissue (polytypic) could be due to an excessive accumulation of endogenous gibberellins or auxin, while lack of silk formation in silkless might be due to an inadequate endogenous cytokinin or auxin. Since NAA is reported to stimulate stalk stiffness (Nickerson and Lindahl, 1962, MGN 36:97), brittle stalk (bk2) plants were treated with NAA.

The dose and application schedule for various families is summarized below:

Genotype	Growth Regulator	Dose and number of applications
Pt/+, Pt/Pt ♂ ♀ Tu/+ ♂	AMO 1618 TIBA	0.01, 0.1 and 1 mM 17 applications, 0.5 ml each from June 25 to July 19
sk/+, sk/sk	BA, IPA, NAA	5, 10 and 100 µM (BA and IPA), 50, 100 and 500 µM (NAA) 17 applications from June 25 to July 19, first four applications 0.25 ml each, remaining 0.5 ml each
bk2/bk2, bk2/+ and +/+	NAA	50, 100 and 500 µM 21 applications, 0.25 ml each from May 29 to July 18

With the help of a 0.5 or 1 ml pipette, the solutions were introduced below the ligule in the axil of the tenth leaf of 40-day-old Pt, Tu and sk plants. The solution was retained in the space formed due to the encirclement of culm by sheath. At the time of first application, the ear shoot at node 10 was less than 1 mm long and female florets had not been initiated. In the bk2 family, NAA solution was dropped in the apical cup starting with 14-day-old plants. Each treatment included 5 to 8 plants.

The expression of tunicate and polytypic was not suppressed in any of the treatments. In the tunicate stock, in the plants receiving 0.1 and 1 mM TIBA the ear shoot at node 10 remained short or failed to develop and functional ears developed one or two nodes higher than in untreated plants. In the polytypic plants receiving 1 mM AMO 1618, growth of 12-14 axillary shoots per plant (one per node) was observed. But only one or two of these at nodes 12-15 developed into functional ears.

In none of the treatments were silks restored and the ratio of silkless:normal was close to 1:1 in the treated family (the plants in this family were derived from a cross between sk/+ x sk/sk). Similarly NAA did not restore normal stalk strength in the brittle stalk family. NAA-treated and untreated plants were equally brittle.

These negative results indicate that in the mutants tested, endogenous hormonal imbalance may not be involved. The mutant phenotype may be due to specific cell

limited gene products. At present it is not known if the expression of Pt, Tu and sk is cell autonomous in ear shoots. However, brittle stalk seems to be cell autonomous and a single sectored plant (half brittle, half normal) has been recorded earlier (Coe, 1960, MGN 34:62).

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Dominant disease lesion mutants

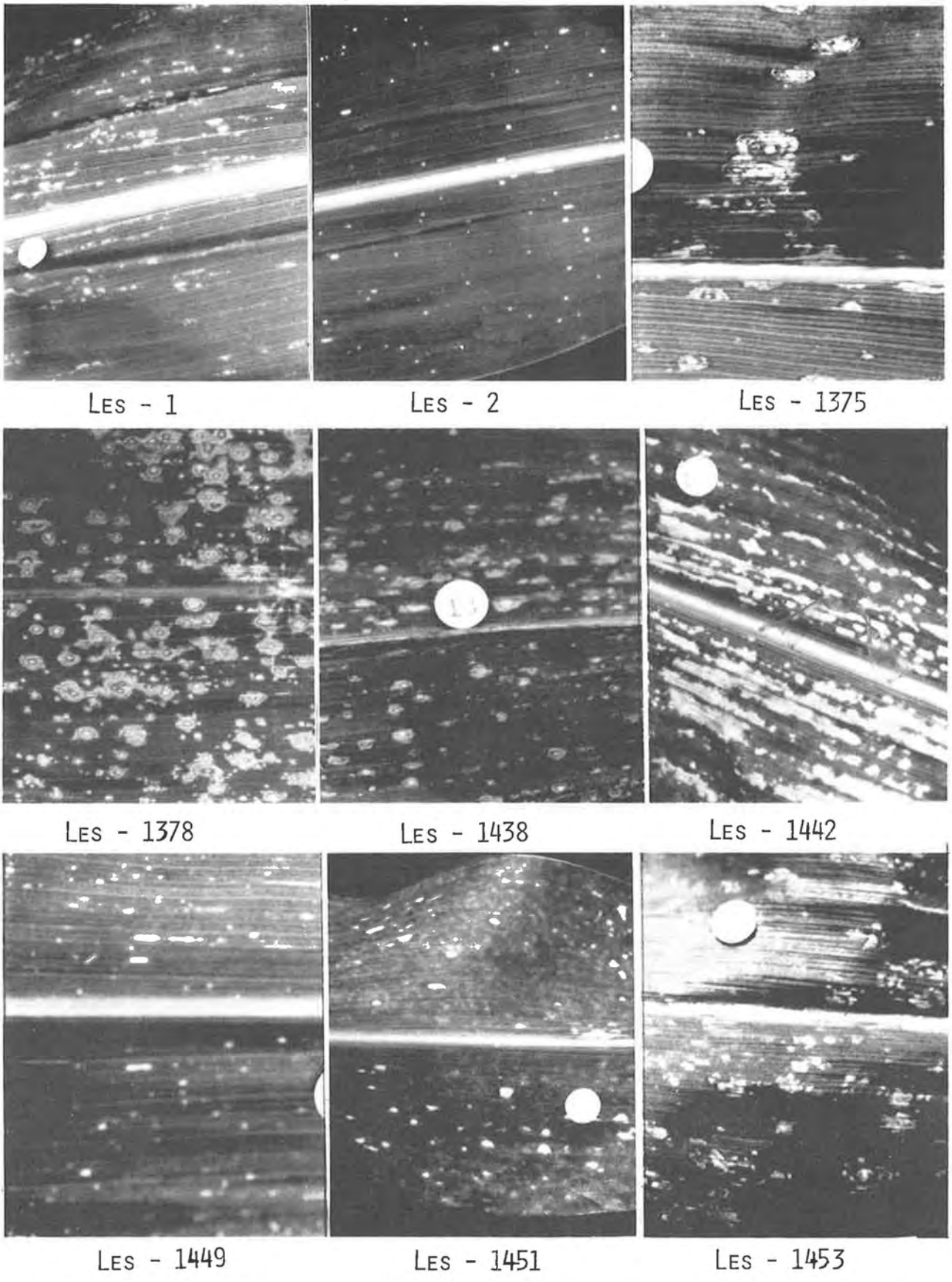
Eleven dominant disease lesion mutants were isolated in plantings of kernels from crosses by pollen treated with ethylmethane-sulfonate using the paraffin oil technique (Neuffer 1978). All eleven mutants were isolated as single plants in the M1 population. These plants were selfed and outcrossed to normal in succeeding generations using lesion mutants as a male parent. In the outcross population the segregation for mutant to normal was always found to be 1 mutant:1 normal indicating dominance.

Characterization: The sequence of events that leads to lesion formation following infection of a susceptible host by a pathogen and the basic phenomena behind these events in plants have been extensively studied and are thought to be fairly well understood. In simplistic fashion we may say the pathogen produces a toxin which destroys the integrity of cell membranes and allows the successive invasion of surrounding cells. As a consequence spots with a center of dead cells and concentric rings of dying and newly interrupted cells occur on the leaves and other parts of the host plant. The frequency, size, shape, texture, color and intensity of lesions depends upon the genotypes of the host and the pathogen and in a different way upon the conditions at the time of infection. The disease lesion mutants reported by Neuffer and Calvert (J.H. 66:265-271, 1975) and those reported here produce a phenotype that mimics the symptoms of a particular disease under particular conditions. Sometimes the resemblance is so precise that the mimic cannot be distinguished from the disease except by testing for the presence or absence of the pathogen in the plant in question. Figure 1 presents sections of the 8th leaf of 45-day-old plants from 9 of the 11 mutants. Les*-1376 and Les*-1461 were not included because conditions were not ideal for their expression in the 1979 plantings used for photographing. Note differences in size, shape, intensity and distribution. For example Les1, Les*-1375 and Les*-1453 have large spreading lesions that closely resemble infection of susceptible lines of corn with several Helminthosporium species.

Les2, Les*-1442, Les*-1449 and Les*-1461 have small lesions; Les2 and Les*-1449 resembling fungal infection of a "hypersensitive" resistant host while Les*-1461 has small chlorotic spots resembling certain bacterial diseases. Les*-1378 shows a distinctive clustering of both large and small lesions.

Mutant	Tissue Affected	First Expression	Temperature for Expression	Other Characteristics
Les1	leaf, sheath	10-12	20° C	-
Les2	leaf	12-20	-	hypersensitive
Les*-1375	leaf, sheath	12-40	-	large
Les*-1376	leaf	40	-	like viral infection
Les*-1378	leaf, sheath	12-40	-	random clusters
Les*-1438	leaf, sheath	12-20	20° C	-
Les*-1442	leaf, sheath	25-40	-	follows vein; extreme necrosis
Les*-1449	leaf	25-40	32° C	hypersensitive
Les*-1451	leaf, sheath	12-40	20° C	chlorotic/necrotic spots
Les*-1453	leaf, sheath	12-40	20° C	large
Les*-1461	leaf	-	-	chlorotic spots

Fig. 1. Lesion mutants



The accompanying is a list of all 11 mutants with some important distinguishing characteristics. The first expression (listed as numbers of days from planting)was taken under field conditions at Columbia, Missouri in June 1979; notes were taken at weekly intervals and individual plants varied a great deal, hence the generalized numbers. Temperature expression was obtained by growing in growth chambers with 14 hours moderate light and 10 hours of dark with constant temperatures of 20°, 27° and 32° centigrade for 30 days. Those designated (-) did not express lesions during the experiment. This is probably due to the fact that other factors such as humidity, temperature variation, etc. may be necessary for expression of these mutants.

Location to chromosome: The mutants were crossed with the T wx reciprocal translocation series available from the Coop. Stock Center. The F1's were backcrossed to a homozygous wx non-mutant stock. The resulting waxy and non-waxy kernels were separated and sown and the resulting plants were noted for lesion and normal types. Backcross progenies of most of the translocation stocks with the mutants gave random distribution of wx and lesion characters. Following are those backcross progenies that gave some indication of linkage:

			Backcross Classes				
Mutant	Family	Translocation	Lesion Wx	Normal Wx	Lesion wx	Normal wx	Approx. Location
Les1	17:531	2-9b	39	7	5	22	2S
Les2	27:2001	1-9c	10	4	2	17	1S
	27:2002		13	7	3	16	
Les*-1375	27:2008	4-9g	8	4	4	10	4S
Les*-1376	22:467	3-9c	16	2	3	7	3L
Les*-1378	-	-	-	-	-	-	-
Les*-1438	24:39	9-10b	12	7	8	12	10S
	27:2016		16	9	11	21	
Les*-1442	-	-	-	-	-	-	-
Les*-1449	27:2019	1-9(4997)	15	4	5	15	1L
Les*-1451	26:48	5-9a	22	17	15	22	5L
	27:2027		23	14	8	20	
Les*-1453	-	-	-	-	-	-	-
Les*-1461	24:75	1-9(8389)	16	4	4	15	1L

Location of these mutants on chromosome 9 can be ruled out in most cases because all the other crosses were random. A more accurate location of Lesion-1 on chromosome 2 has already been reported (MNL 51:59-60).

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Possible relation between level of cyclic hydroxamate and lesion formation

The presence of glucoside of the cyclic hydroxamate 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and its role in resistance to many pathogens and insects has been reported by several workers. The concentration of DIMBOA was correlated with lesion development in the plant during pathogenesis. The dominant disease lesion mutants which mimic disease symptoms would be a model system to study the role of this glucoside in lesion formation. The three lesion mutants, Les1, Les*-1438 and Les*-1453, which show lesion development at 20° C, were used for estimation of DIMBOA. The plants were grown either in growth chambers maintained at 20° C with 14 hr day and 10 hr night or in the greenhouse for 21 days and then

transferred to a 20° growth chamber. Initiation of lesions was observed after 4 to 5 days. Stem tissue (200-400 mg) from single plants was used in glucoside analysis. The DIMBOA analysis was done by the rapid procedure developed by Long et al. (Crop Science 14:601-603). The results are given below:

	Mean DIMBOA concentration in mg/g fresh weight			
Expt. No.	Sample Number	Lesion sib	Sample Number	Normal sib
		Les1		
1	3	0.016	2	0.832
2	3	0.508	3	0.419
3	3	0.377	3	0.218
4	1	0.622	3	0.865
5	3	0.578	4	0.698
6	2	0.570	4	0.521
7	4	0.549	4	0.550
	19	Av. 0.460 ± 0.079	23	0.584 ± 0.086
		Les*-1438		
1	1	0.615	1	0.959
2	3	0.822	3	0.830
3	5	0.541	3	0.554
	9	Av. 0.659 ± 0.084	7	0.781 ± 0.119
		Les*-1453		
1	2	0.430	2	0.909
2	2	0.319	2	0.651
	4	Av. 0.374 ± 0.055	4	0.780 ± 0.129

Our initial results (experiment 1 with each) were striking and highly significant. Clearly, normal sibs had almost twice as much DIMBOA as did the mutant sibs. Succeeding trials were erratic and less instructive although still showing the same trend. The reasons for this ambiguity are not known but one factor involved may be the age and general health of the plants used. Initially we were forced to use the same material which was overgrown and distinctly unhealthy from culture conditions. Other causes for variation in results may be (1) undetected day to day fluctuation in glucoside level, (2) individual plant differences and (3) variations due to environmental conditions beyond our control. In regard to item 3 we found that even though we can regulate lesion formation by varying temperature, this control is not as precise as we would like. Other factors such as humidity, light and daily temperature range which we did not properly control may be involved. However, it does appear that the level of DIMBOA is higher in normal sibs than in mutant plants at some stage in development. The level of DIMBOA concentration may be one of the factors responsible for the lesion initiation.

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Anther culture studies

During this past summer, we undertook anther culture studies in Columbia, Missouri. During the course of the summer, we plated about 40,000 anthers from 28 different maize genotypes on 45 variations of media. The results described below pertain to the 20,000 anthers evaluated in North Dakota.

The three basic types of media tested were the N6, the Yu Pei, and Murashige and Skoog (M+S) media. There were 6 variations of M+S, 14 variations of Yu Pei, and 25 variations of the N6 media. All of the media contained 0.5% activated charcoal, and all of the media contained 3% sucrose except for 11 variations of the N6 medium which contained 12% sucrose. This modification turned out to be important since all but one of the 15 plates yielding embryos or callus contained one of the variations of N6 medium containing 12% sucrose. The hormone content of the medium did not appear crucial since 7 of the 11 variations of N6 media containing 12% sucrose were effective including media supplemented only with 0.1 mg of TIBA, with 2,4-D and TIBA, with 2,4-D only, with TIBA and 6 benzylaminopurine, or with kinetin only.

There was a degree of genotype specificity for responding to the media. Among the 14 genotypes tested on N6 media containing 12% sucrose, success was obtained with 7 of them. These were Black Mexican Sweet, 1 dish; Illinois Hi Oil x Black Mexican Sweet (F1), 2 dishes; W23 x Black Mexican Sweet (F1), 1 dish; Illinois Hi Oil x Longfellow flint (F1), 3 dishes; Golden 113, 3 dishes; Lai Pin Pai x Golden 113 (F1), 3 dishes; (Lai Pin Pai x Golden 113, F1) x Golden 113 (backcross), 2 dishes. It should be noted that the Golden 113 and Lai Pin Pai are genotypes that were found to be well suited for anther culture by the Chinese workers.

Both callus and embryos emerged from inside the cultured anthers after 30 to 45 days in culture. These continued to develop for a while on the 12% sucrose containing medium but were usually transferred to a 3% sucrose containing medium. When this was done, development ceased except in the case of the embryo produced on the kinetin supplemented medium. This embryo germinated and grew into a plant. Pictures of the anther cultures showing callus, embryos and the young plant are shown in Figure 1.

Our success rate of 15 dishes producing embryo or callus out of about 450 dishes total or about 20 anthers responding out of about 20,000 plated may appear discouraging because of the low frequency of success. Actually, we are pleased and encouraged inasmuch as only about one-fourth, or 5,000 anthers were plated on media containing 12% sucrose, an important feature for success. Furthermore, among these 5,000 anthers, about half were from genotypes that are apparently not responsive to anther culturing on the N6 medium, a result in complete agreement with the genotype specificity observed in China. Finally, among the 2,500 anthers plated from responsive genotypes, about one-third were plated on media that produced no positive response. Therefore, a success rate of 20 anthers out of 1,700 or so is close to a 1% success rate which is comparable to that obtained in the Chinese laboratories.

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Ill. Hi Oil x Long. flint

Lai Pin Pai x Golden 113

(Lai Pin Pai x Gold. 113) x Gold. 113

Lai Pin Pai x Golden 113

Golden 113

Ill. Hi Oil x L.F.

Lai Pin Pai x Golden 113

Lai Pin Pai x Golden 113

Plant from embryo in adjacent picture

FIGURE 1. Anther cultures of different strains of maize on N6 medium containing 12% sucrose. The six upper photographs were taken 40 to 50 days after plating the anthers. The lower three (#1,#2, and #3) are of the same anther taken 49, 67, and 81 days after plating. Photograph #3 shows the young plant produced when the anther and attached embryo of #2 were transferred to a medium containing 3% sucrose. All photographs are 20X except for #3 which is 10X.

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Cytological observations of several B-A translocation hyperploid stocks

Cytological studies of the meiotic behavior of several hyperploid stocks that arise from B-A chromosome translocation stocks have been initiated. These are preliminary observations of B-A translocations relative to an eventual determination of breakpoint positions and characterizations of their meiotic behavior. At this time, observations are organized into three categories: (1) diakinesis configurations, (2) quartet analysis using the nucleolus as a cytological marker, and (3) the frequency of "bridge-like" structures at anaphase-I of meiosis.

A number of different reciprocal B-A translocation stocks now exist. Since the B centromeres of the B^A chromatids often non-disjoin at the second mitotic division of the microspore, two different spermatozoa will result. One will be hyperploid, with two B^A chromosomes. The other will by hypoploid, without any B^A chromosomes. This report primarily discusses observations of the hyperploid plants. These hyperploid plants were selected through genetic tests and cytologically confirmed by pachytene analyses.

Analysis of configuration frequencies at late diakinesis has been initiated in several hyperploid stocks. Eleven diakinesis figures were deemed to be either 9II (bivalents) + AA^BB^A + B^A or 9II + AA^B + B^AB^A. The cells that showed only ten diakinesis figures were evidently 9II + an $AA^BB^AB^A$ complex. It appears that pairing relationships among the $AA^BB^AB^A$ chromosomes differ considerably from one hyperploid stock to another. Much additional information is needed, including breakpoint locations, before forming any conclusions.

Hyperploid Stocks	Diakinesis Configurations		Total Cells
	11 figures	10 figures	
TB-6Lc	16	25	41
TB-9Sd	79	40	119
TB-3Sb	23	12	35
TB-3Lc	20	94	114
TB-10Lb	13	48	61

Quartets of microspores were analyzed for meiotic nondisjunction of the A chromosome 6. This choice is facilitated by the use of the nucleolus as a cytological marker. Five different hyperploid stocks and the L289 normal stock were observed. All of the hyperploid stocks have an L289 background. The data are presented at the top of the next page.

It is of interest that only one of the two hyperploid stocks involving chromosome 6 displayed an appreciable frequency of nondisjunction of the A centromeres at meiosis-I. The other did not. Also, hyperploid stocks involving B-A translocated chromosomes other than 6 did not show any nondisjunction of the chromosome 6 centromeres. Chromosomes 3 and 9, of course, cannot be tested in this manner. Also, L289 normal was without any nondisjunction in this test. Other B-A translocations involving chromosome 6 will be tested. At any rate, the presence of the B-A translocation in the TB-6Lc stock (1) causes significant nondisjunction of the A centromeres of 6, and (2) takes place in meiosis.

Stocks	Normal disjunction of chromosome 6	Nondisjunction of chromosome 6 at meiosis-I	Nondisjunction of chromosome 6 at meiosis-II
			
hyperploid TB-6Lc	1195	79	0
hyperploid TB-6Lb	1418	3	1
hyperploid TB-9Sd	96	0	0
hyperploid TB-3Sb	131	0	0
hyperploid TB-3Lc	332	0	0
L289 normal	1019	0	0

Lastly, a significant frequency of bridge-like structures is present in anaphase-I of meiosis in the hyperploid stocks. Although normal stocks show some of these bridge structures, there is a statistically significant difference between their frequencies and that of the hyperploid stocks (contingency Chi-square test with P = .001). Feulgen tests were carried out on cells showing these bridge structures and they were shown to be Feulgen-positive. Cytologically, they take the appearance of typical chromatid bridges, but no acentric fragments were ever found in conjunction with them.

	Anaphase-I bridges					Total Cells
	0	1	2	3	4	
Hyperploid stocks with L289 background						
TB-3Lc	15	2	4	1	0	22
TB-3Ld	8	3	0	0	0	11
TB-3Sb	16	11	3	1	1	32
TB-6Lb	10	9	2	0	0	21
TB-9Lc	8	4	0	0	0	12
TB-9Sd	84	12	2	1	0	99
TB-9Sb	7	1	0	0	0	8
TB-10Lb	39	34	8	2	0	83
Normal stocks						
L289	44	9	1	0	0	54
ACR-njW23	67	8	0	0	0	75
Other Combinations						
TB-5La + extra B	13	3	1	2	0	19
TB-6Ld + extra B	4	3	2	0	0	9

The number of bridges per cell (0, 1, 2, 3, 4, etc.) follows a Poisson distribution. Consequently, their distribution appears to be random, but their frequency is significantly greater in the hyperploid stocks compared to normal stocks. The maximum number of these bridge-like structures was four.

Although much has been observed and reported about the behavior of B chromosomes and their effects, most of it has dealt with the mitotic microspore divisions. It is suggested here that B chromosome material in B-A translocation stocks promotes other effects during meiosis. Further tests are being made.

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Induction of resistance to Helminthosporium maydis, race T in Texas maize

In order to obtain resistant plants, two kinds of mutagenesis were carried out on seeds of the French line F7-T: (1) exposure to gamma rays (15,000 R), and (2) soaking in a 2.5 g/l ethyl methyl sulfonate solution (EMS).

The plants from the treated seeds are called M1 generation; crosses with a restorer line (F71) produce a male fertile progeny called M2 giving M3 by selfing. In order to screen for resistance to HmT, M3 seedlings are checked either with the cultured filtrate medium or by direct inoculation with conidia. Tests revealed resistant plants from 42 M2 progenies (6.7%) after treatment and from only one M2 progeny after gamma ray irradiation (see for details Cassini et al., Ann. Amélior. Plantes, 1977, 27:753-766).

In all cases one M2 plant carrying the resistant trait appeared to segregate resistant and susceptible plants in its M3 progeny. This resistant trait appeared to be transmitted to M4 progenies for only 15 families:

Mutagenic Treatments	No. Families from M1 Plants	M2 Selfed Plants	Families Producing Nonsusceptible Plants in M3 or M4	Families Entirely Nonsusceptible in Field in M5
gamma rays	670	2,330	1	1
EMS	692	2,167	14	6
Total	1,362	4,497	15	7

M5 plants were grown in fields with climatic conditions favorable to the fungus; this test revealed homogeneous resistant lines in seven distinct families which were named A type families. Other families, with less striking resistance characteristics, kept segregating in M5 and constituted B-type families.

A-type families have the following characteristics (fig. 1): (1) A majority of nonsusceptible plants appear in M3, (2) No male-sterile individuals in some of the M3 offspring, (3) M2 plants, grown from spare seeds, appear as nonsensitive to leaf scarification tests, (4) from the M4 on, it is possible to obtain lines that are both resistant and male-fertile and which do not segregate for these characters; resistance and male-fertility can be maintained either by selfing or by crossing with a Texas maintainer inbred, (5) by crossing with Texas male-sterile inbred, as female, susceptible offspring are obtained, either all male fertile, or all male sterile, or segregating fertile/sterile.

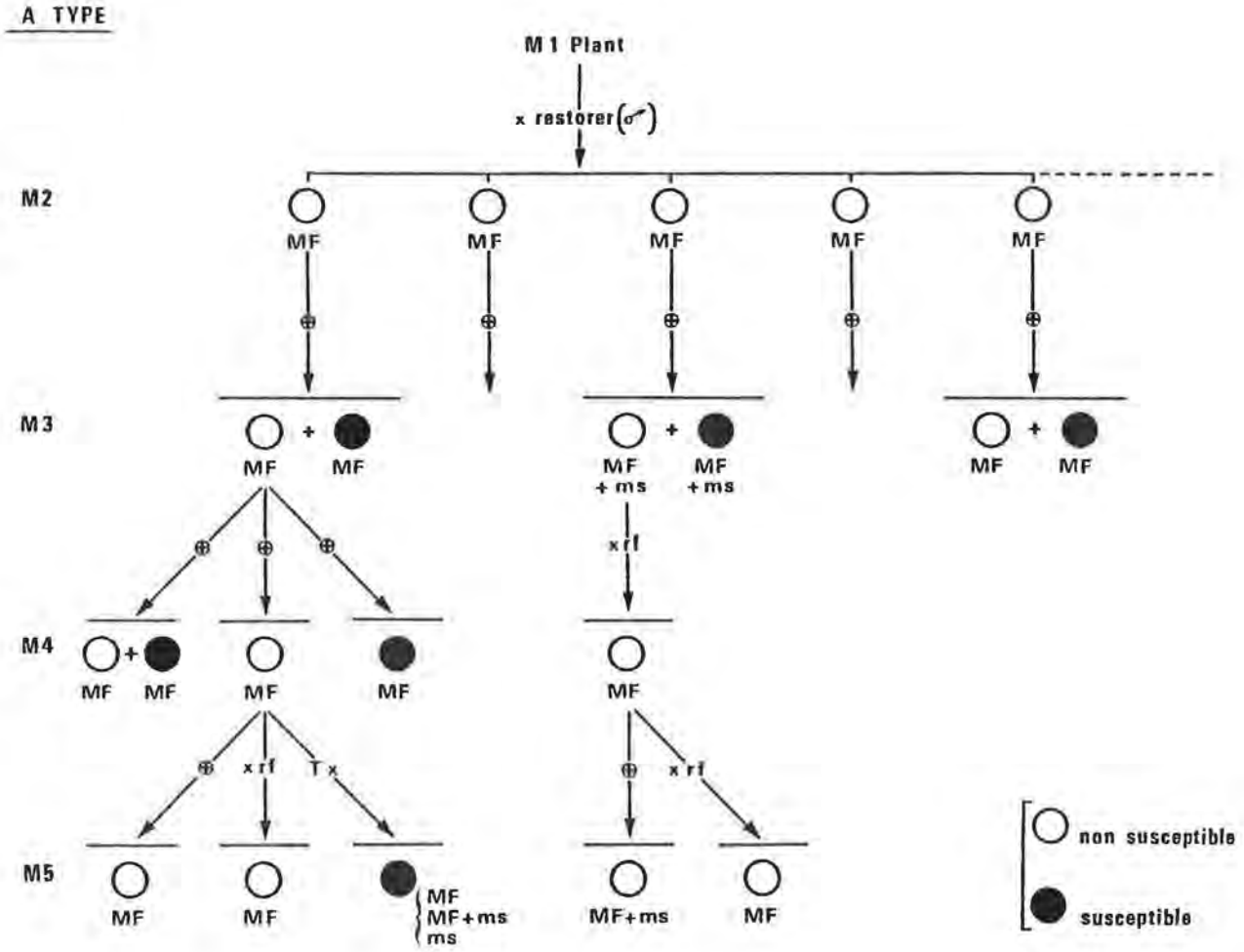

Figure 1

From these results, it can be concluded that: (i) induced HmT resistance and male fertility are not pollen transmissible, (ii) in these families, there are male fertile plants recessive for restorer genes; (iii) as a consequence, male fertility and resistance to HmT, simultaneously reverted by a mutagenic treatment, are due to cytoplasmic modification(s) in the Texas material.

"Male-sterile" (ms) plants, appearing in M3 or later on, are of various types: aborted tassel, non-opened anthers, tassel seed types, etc. These types of male sterility are not maintained in crosses with Texas maintainers. However, one can find in subsequent generations, after selfing, these male sterile types again (fig. 1). These phenomena are strongly analogous to these described by Gengenbach et al. (P.N.A.S., 1977, 74:5113-5117).

B-type families are characterized as follows (fig. 2): (1) the M3 fertile/sterile segregation is apparently normal, (2) individuals with intermediate susceptibility appear in M3; this character can be detected by tests on germinating seeds, on leaves (scarification test) and on isolated mitochondria (A. Berville, 1978, in Plant Mitochondria, ed. by G. Ducet and C. Lance, 427-434), (3) M2 plants were generally susceptible to HmT, (4) after the M3 generation, intermediate susceptibilities and sometimes intermediate male fertility are found, but no strict correlation seems to exist at this level, between such types of resistance and

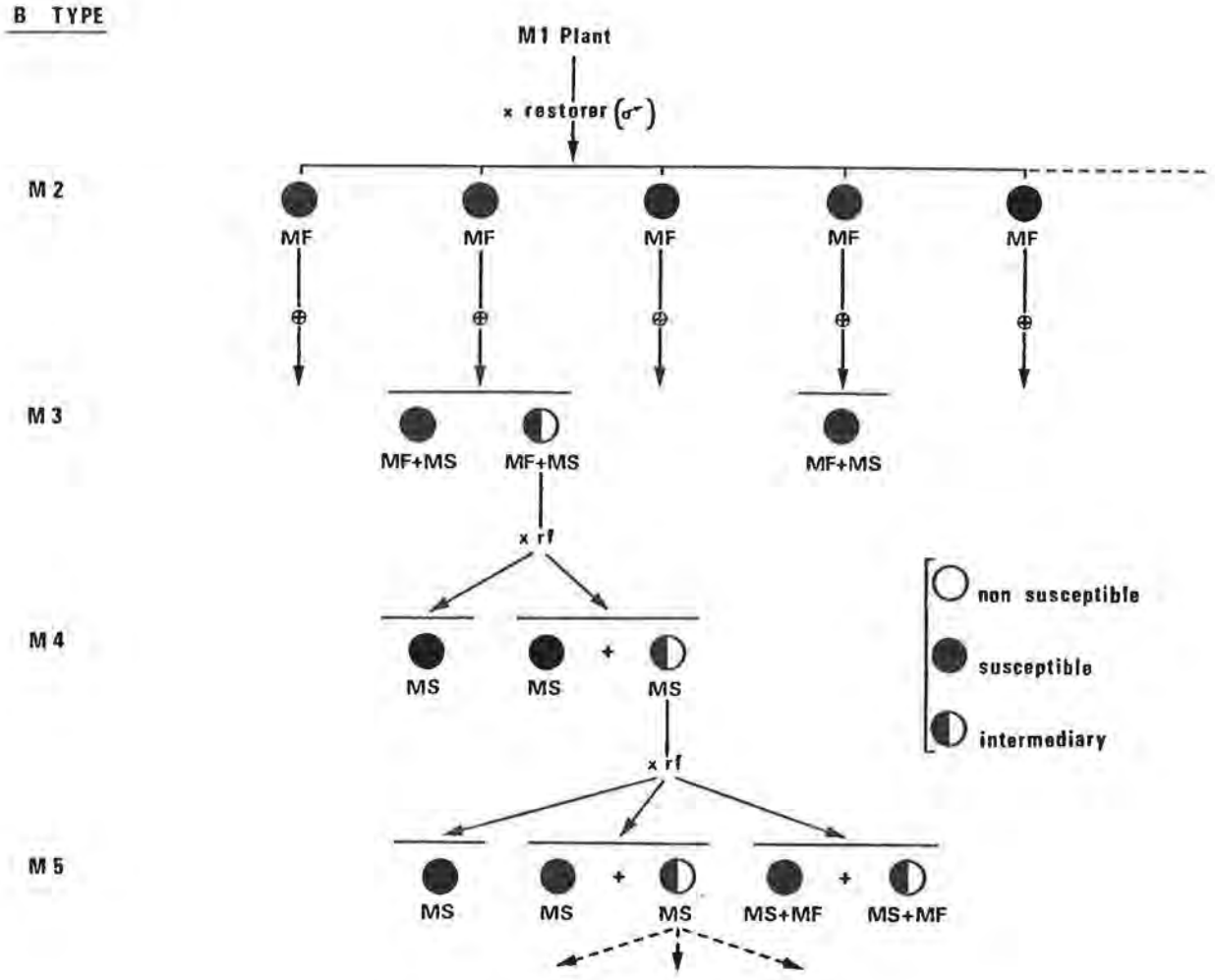

Figure 2

fertility. It is possible that minor modifications of nucleus-cytoplasm interactions are involved. These modifications could set up an intermediate balance which seems to be hard to stabilize.

In conclusion, these results, together with those obtained by Gengenbach et al. (1977), after in vitro culture of maize calluses, prove that Texas cytoplasmic hereditary characteristics can be modified. If this can be done for the Texas system, then there is no reason to believe that it cannot be performed for other cytoplasmic systems.

A. Cornu, R. Cassini and A. Berville

DONIPHAN, NEBRASKA
Pfizer Genetics, Inc.

Results of a comprehensive genic male sterility conversion program

A large program of conversion to genic male sterility was initiated in 1972 using 26 widely used public corn inbreds. By 1977, only three of the original inbreds had been successfully converted: W64A, W117 and A619. Difficulties were encountered with the duplicate-deficient maintainer versions of the remaining 23

inbreds. Maintainer plants were all extremely late, short and extremely poor pollen shedders. Sterile plants obtained showed less than 0.1% fertility, but increase of the steriles was virtually impossible due to the poor pollen shed of the maintainer plants. The T9-10a translocation, coupled with the ms2 gene, was successfully used in the conversion of W64A, W117 and A619.

Miniature seed fields were grown in 1977 to determine the economic feasibility of using the system. One isolation field grown near Eldora, Iowa, consisted of W64A sterile and maintainer rows in a four to two ratio. Another isolation in the area contained A619 sterile and maintainer rows in a similar ratio. Under drought stress conditions, both fields produced female yields of less than one bushel per acre. Conventional detasseled seed fields in the immediate area yielded 15-20 bushels per acre.

Similar seed fields of W64A and W117 were grown under more optimum moisture conditions near Olivia, Minnesota in 1977. Yield data are shown below:

Genotype	Range, % water	Range, Yield, Bu/A
W64A ms2	29.2-36.7	1.20-8.23
W64A dp-df	22.5-28.1	1.24-5.32

The W117 field produced only scattered kernels and was abandoned. Seed fields of W64A in normal cytoplasm produced yields ranging from 30 to 55 bushels per acre in the immediate area in 1977.

This project was discontinued for the following reasons:

1. Yields of female and male plantings were extremely low in 1977 despite optimum growing conditions and an excellent pollination period.
2. Extremely high foundation seed production costs would more than offset the amount of detasseling costs in this system.
3. Increasing and maintaining male seed is extremely time consuming.
4. Due to the length of time involved in conversion, inbred lines can become outdated before conversion is completed.
5. Personal communication with other plant breeders indicates much difficulty with the conversion programs.

Delmer Gross

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Friable maize callus and suspension cultures using IAA-amino acid conjugates

2,4-D is the traditionally used hormone in maize tissue culture; however, with many lines the callus obtained on 2,4-D media is less than ideal. A recent paper (Hangarter, R. P., Peterson, M. D., and Good, N. E., Plant Phys., in press) demonstrates that certain IAA-conjugates can be used as hormone sources for tobacco and tomato tissue cultures. IAA-L-alanine and IAA-L-glycine suppress organogenesis and promote rapid callus growth, whereas other conjugates (e.g., IAA-L-phenylalanine) allow shoot formation but suppress root formation.

Using the more active of the IAA-conjugates it has been possible to establish friable callus cultures from various anthocyanin genetic stocks in either W23 background or F2 progeny of a W23 x K55 cross. Mesocotyl sections of 14-day-old seedlings were plated on Green's media with 50 μM IAA-conjugate substituted for the 2,4-D. The resulting calli were maintained on the same media and sub-cultured at 3-week intervals. IAA-L-alanine, IAA-L-glycine and IAA-myoinositol all gave

similar results in early tests; IAA-L-alanine is routinely used. Some of these lines are now more than one year old and are still friable and growing rapidly, although they are somewhat rooty in appearance.

Suspension cultures are easily obtained from these calli in liquid media of the same composition. The suspensions are very finely divided (1-20 cell clusters) and have a doubling time of about 7 days. These suspensions are not long-lived, however, the maximum thus far being 3 months. Experiments in progress are aimed at plating out cells from these suspensions and regenerating roots.

Some of the callus lines initially produced anthocyanin pigment; this expression was greatly reduced or lost upon further subculture. Transfer of callus to 50 μM IAA-L-phenylalanine media greatly enhances anthocyanin pigmentation. IAA-L-phenylalanine also allows the formation of normal roots from the callus.

In summary, IAA-conjugates may be useful in initiating callus from recalcitrant maize stocks, and combinations of different conjugates may be useful in controlling morphogenesis in maize tissue cultures. Procedures for the synthesis of the conjugates are outlined in Hangarter et al. (This study supported by NSF grant SP178-15616.)

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Mitochondrial DNA transposition associated with reversion to fertility in cms-Vg maize

Two plasmid-like DNAs, S-1 and S-2 (formerly designated S-S and S-F respectively) of molecular weights 4×10^6 and 3.5×10^6, respectively are present in the mitochondria of members of the S group of cms in maize (PNAS 74:2904, 1977). Unlike cms-T and cms-C, the cms-S exhibits instability in the expression of sterility. An episomal mechanism was hypothesized to explain the high reversion rates of sterile to fertile plants (J. R. Laughnan and S. J. Gabay, 1975, Genetics and Biogenesis of Mitochondria and Chloroplasts, C. W. Birky, Jr., P. S. Perlman and T. J. Byers, ed.). Subsequently, the concomitant disappearance of S-1 and S-2 from mitochondria of spontaneous fertile revertants (Vg-revertants) was observed (MNL 53:83, 1979). Here, we report evidence that the plasmid-like DNAs or segments of them are integrated into mitochondrial chromosomal DNA (mtDNA) of Vg-revertants.

MtDNAs were isolated from each of several different cms-Vg and from Vg-revertants of them. The purified DNAs were digested with each of several restriction endonucleases and the resultant fragments electrophoretically resolved on agarose gels. Patterns (visualized by ethidium binding under UV) were compared between sterile parent and Vg-revertant progeny as well as among all sterile and fertile plants. While the restriction patterns of the several sterile cms-Vg were indistinguishable, the patterns of the revertant DNAs differed from those of the sterile cms-S and from one another. New restriction fragments, not present in mtDNA from sterile plants, were evident in the revertants and some of the new fragments were unique to a particular revertant. Analogous to prokaryotic genetic transpositions, the concomitant disappearance of the plasmid-like DNAs together

with the appearance of new endonuclease restriction fragments in the Vg-revertants suggests the integration of the S-1 and S-2 DNAs upon the plant's reversion to fertility. To test this hypothesis we isolated and resolved the S-1 and S-2 DNAs and labeled them with (α-^{32}P) by nick-translation for use as hybridization probes. Restriction digests of mtDNAs from the several cms-Vg and Vg-revertant plants were Southern blotted onto membranes and then hybridized with labeled fragments of either S-1 or S-2 DNAs.

Results obtained with one pair, i.e. a parental cms-Vg and a progeny fertile-revertant (296) are shown (diagrammatically) in Fig. 1. The electropherogram (compare lanes C and D) of Xho I digested mtDNAs shows that both cms-Vg and Vg-revertant DNAs yield almost identical restriction patterns. However, at least

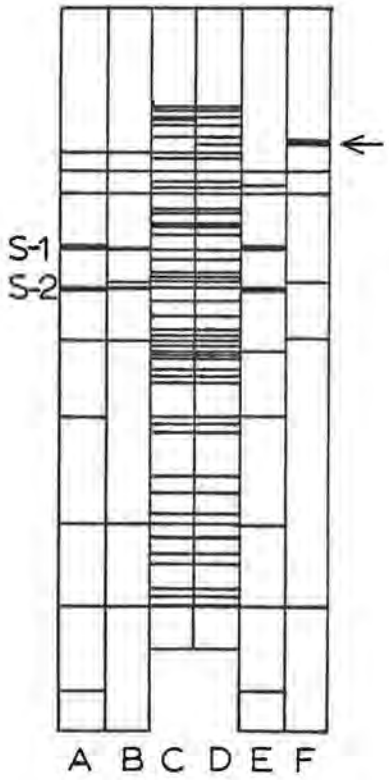

Fig. 1. Electropherograms (C and D) and autoradiographs (A, B, E and F) of Xho I restriction digests of mtDNA from a male-sterile (A, C and E) and a male fertile-revertant (B, D and F) of Vg cytoplasm. A and B are hybridizations with S-1 DNA probe and E and F are hybridizations with S-2 DNA probe. Positions of S-1 and S-2 are marked and the arrow indicates the position of a unique Xho I restriction fragment and its extensive hybridization with S-2 DNA.

one "new" fragment (at arrow) is present in this Vg-revertant. The autoradiogram developed with S-2DNA as the hybridization probe (compare lanes E and F) shows: (1) this "new" fragment shares homologous sequences with S-2; (2) additional fragments of the Vg-revertant DNA share homology but differ in size from the Xho I digestion products of S-1 and S-2 detected in cms-Vg DNA. On the other hand, the autoradiogram developed with S-1 DNA as the hybridization probe (compare lanes A and B) yielded homologous patterns between cms-Vg and Vg-revertant DNAs except for the absence of the terminal Xho I fragments of both plasmid-like DNAs in the Vg-revertant pattern. The data from this and other cms-Vg and Vg-revertant analyses indicate that the mtDNA sequences have undergone rearrangement upon the apparent integration of portions of the plasmid-like DNAs.

We conclude that the S-1 and S-2 DNAs may be physical manifestations of the episomal fertility elements postulated by Laughnan and Gabay-Laughnan to account for high frequency cytoplasmic reversions to fertility. In any case, these observations provide a molecular approach to the mode of integration as well as the

specific genetic information encoded in the integrated sequences and their relationship to cytoplasmic male sterility in maize.

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The continued search for maize auxotrophs

In updating our previous report (Sheridan, Neuffer and Bendbow, MNL 52:88-90) on the search for auxotrophs by culturing immature embryos of lethal, defective kernel mutants we have two points of interest.

First, we have determined that mutant E1121 and Coe's A342 mutant are allelic to the pro-1 mutant of Gavazzi et al. (Theor. Appl. Genet. 46:339-346, 1975). Furthermore, pro-E1121 and pro-A342 respond identically to immature embryo culturing. They die on basal medium, are rescued on basal medium plus amino acids and basal medium plus proline, but are not rescued by basal medium plus ornithine.

In a recent report from Gavazzi's laboratory, it was suggested that the genetic block in proline synthesis in the pro-1 mutant occurs between Δ' pyrroline-5-carboxylic acid (P5C) and proline (Racchi, Gavazzi, et al., Pl. Sci. Lett. 13:357 364, 1978). This conclusion is based on the assumption that proline biosynthesis proceeds from glutamate via glutamic δ-semialdehyde and Δ'-pyrroline-5-carboxylic acid and that ornithine is connected to this pathway by conversion to glutamic δ-semialdehyde. It has been recently reported, however, that the actual route of proline synthesis in plants may be by conversion of ornithine to proline via α-keto-δ-aminovaleric acid and Δ'-pyrroline-2-carboxylic acid (P2C) (Mestichelli et al., J. Biol. Chem. 254:640-647, 1979).

The lack of rescue of the pro-1 mutant by including P5C in the culture medium (Racchi, Gavazzi et al., 1978) is in agreement with the suggested pathway of Mestichelli et al. (1979); however, since Gavazzi and coworkers also observed that α-amino-δ-hydroxyvaleric acid would not rescue the mutant, then the block must occur either between this compound and P2C, or between P2C and proline if, indeed, Mestichelli et al. are correct. It is apparent, therefore, that the critical test will be to attempt to rescue the pro-1 mutant with P2C.

We will be grateful for assistance in locating a source of P2C since it is not commercially available.

Second, among the 102 EMS induced mutants tested to date by embryo culturing, 19 mutants have displayed a superior shoot growth on enriched medium compared to that on basal medium. These mutants are listed in the accompanying table. Among these mutants, there were 11 mutants with a mean shoot growth value on enriched medium of greater than 100 mg. and two mutants displayed that amount of growth on ammonium-free enriched medium. The table also includes the data for the pro-1 mutant and similar results have been obtained for the pro-A342 mutant (not shown). Among these mutants the E1121 mutant has been shown to be proline requiring (see above) and the other mutants are promising mutants for future study.

Promising mutants with greater than 150% growth on enriched medium compared to basal medium*

Enriched 1977				Enriched 1978				NH4-free enriched 1978			
E#	Wt. E/B %	Mean Wt.-mg E/B	Number Shoots E/B	E#	Wt. E/B %	Mean Wt.-mg E/B	Number Shoots E/B	E#	Wt. E/B %	Mean Wt.-mg E/B	Number Shoots E/B
744	317	073/023	05/05	873	850	051/006	10/10	931A	166	073/044	05/09
873	936	206/022	08/06	948A	197	059/030	08/11	1319A	189	278/147	18/09
1121	520	608/117	05/10	1024A	214	047/022	10/12	1404	198	315/159	07/08
1202A	227	148/065	07/07	1054	191	126/066	14/15				
1255B	1080	2.7/.25	08/06	1121	223	172/077	09/10				
1411	311	112/036	07/08	1255B	264	029/011	06/06				
1417	267	131/049	07/07	1308A	671	047/007	15/14				
				1373A	171	906/530	15/15				
				1392A	235	254/108	10/10				
				1405A	219	1166/533	10/10				
				1430	291	131/045	14/07				
				1431	182	178/098	15/15				
				pro-1	237	322/136	10/09				

*The mean fresh weights of the shoots is shown with the value to the right of the diagonal line indicating the weight for shoots grown on basal (B) medium and the value to the left of the diagonal line indicating the weight for shoots grown on enriched (E) medium. The ratio of these weights is presented in the percent columns.

The number of plants harvested and used to determine the fresh weight of shoots is shown in the column labeled "E/B" with the number to the right of the diagonal line indicating the number for basal (B) medium and the number to the left of the diagonal line indicating the number from the enriched (E) medium tested (enriched or NH4-free enriched).

All of the above mutants are lethal and fail to germinate when tested as mature kernels except for 948A, which is uncertain, and E1431 which remains to be tested. The chromosome arm locations are E744, 9L; E873, 9S; E948A, 1L; E1024A, 2L; E1121a, 8; E1308A, 1S; E1417, 10L and pro-1, 8; while the other mutants, although tested, were not uncovered by the 18 B-A translocation stocks used in the test cross.

William F. Sheridan and M. G. Neuffer

GRINNELL, IOWA
Cargill, Incorporated

Non-Corn Belt Dent populations

The Maize Research and Development Section of Cargill, Inc. announces the release of five non-Corn Belt Dent populations derived separately and in major proportion from the Latin American racial complexes Tuxpeno, Coastal Tropical Flint-Dent, Southern Cateto, Cuzco and Coroico. Developmental procedures were appropriate

that a reasonably representative sample of each race was recovered adapted to the Central Corn Belt of the USA. The principal developmental feature, the alteration from a short to a long day adaptation, has offered both an added form of preservation for such germplasm and the opportunity for its further evaluation and study under new environments.

Cargill North Temperate Zone Mexican Dent--An unimproved population having the proportionate composition:

Tuxpeno Inbreds	
T2	7.3%
T10	7.3%
T11	7.3%
T12	7.3%
BR10	3.8%
BR15	3.8%
BR20	3.8%

Tuxpan Inbreds	
BR25	7.3%
BR30	3.8%
BR35	3.8%

Celaya Inbred	
Lote 829	7.3%

Venezuelan Inbred	
Llera III	3.8%

Tuxpeno Populations	
Maya	3.8%
Azteca	3.8%
Oaxaca 84	3.8%
Vera Cruz 149	3.8%
Vera Cruz 208	3.8%

Tuxpeno x Cateto Hybrid	
Phoenix 1211	3.8%

Early USA Inbreds	
WD	0.5%
R181B	0.5%
W182D	1.0%
MS206	0.5%
A257	0.5%
A375	0.5%
A427	0.5%
A509	0.5%
A554	0.5%
A629	0.5%
MS1334	0.5%

Canadian Inbred	
CMD5	1.0%

This population has the equivalent of a 94% recovery of tropical germplasm. Six of the tropical inbreds were initially adapted to the Central Corn Belt through a backcross approach incorporating two backcrosses to tropical. The early USA and Canadian inbreds were the sources of earliness. A composite of these six adapted tropical inbreds was in turn crossed with each of the other tropical entities and a new population aggregate formed through intercrossing. Adaptation to the Central Corn Belt was regained through phenotypic recurrent selection. Kernel color is predominantly white with some light yellow. Cob color is white. As could be expected, there is a strong resemblance to Corn Belt Dent and the material can be handled in like manner.

Cargill North Temperate Zone Caribbean Flint-Dent--An unimproved population having the proportionate composition:

Caribbean Inbreds	
Cuba 312-206-X	7.3%
Cuba 312-219-X	7.3%
Cuba 325-223-X	7.3%
BR40	7.3%
ETO-5C	7.3%
PTR-20A	7.3%

Caribbean Populations	
College Yellow Flint	8.3%
Cuba	8.3%
Syn. Cuba Type	8.3%
Compuesto de Cuba	8.3%
Comp. Yellow Var.	8.3%
Costeno Blanco	8.3%

Canadian Inbred	
CMD5	0.5%

Early USA Inbreds	
Wf1	0.5%
B8	0.5%
B9	0.5%
Mt42	1.0%
Oh56	0.5%
W59E	0.5%
W59M	0.5%
MS206	0.5%
A251	0.5%
A509	0.5%

This population has the equivalent of a 94% recovery of tropical germplasm. Each of the six tropical inbreds was initially adapted to the Central Corn Belt through a backcross approach incorporating two backcrosses to tropical. The early USA and Canadian inbreds were the sources of earliness. A composite of the six adapted tropical inbreds was in turn crossed with each of the six tropical populations and

a new population aggregate formed through intercrossing. Adaptation to the Central Corn Belt was regained through phenotypic recurrent selection. Kernel hardness varies from hard dent to near-flint. Kernel color is predominantly white with some light yellow. Cob color is white. Husk coverage is heavy and often tight. There is a general resemblance to Corn Belt Dent and the material can be handled in like manner.

Cargill North Temperate Zone Cateto--An unimproved population having the proportionate composition:

Argentine Flint Inbreds	
Arg-1	4.70%
Arg-2	4.70%
Arg-3	4.70%
Arg-4	4.70%
Arg-5	6.25%
Arg-6	6.25%
Arg-7	6.25%
Arg-8	6.25%

Brazilian Cateto Populations	
Cateto S. Sirao	6.25%
Minas Gerais II	6.25%
Cateto Composto	6.25%
Rio G. S. XIV	6.25%

Argentine Cuarentin Population	
Cuarentin Rossi	25.00%

Early USA Inbreds	
WD	0.8%
W37A	0.8%
MS206	0.8%
A509	0.8%

Canadian Inbreds	
CMV3	0.8%
CMD5	1.0%
CK27	0.8%
CM37	0.8%
KD54	0.8%

This population has the equivalent of 94% Cateto flint germplasm. All of the Argentine flint inbreds trace back to longtime open-pollinated varieties and are unadulterated by introduced germplasm. Four of these inbreds had previously been converted to earlier forms by a backcross approach where the early USA and Canadian inbreds served as sources of earliness. The other Argentine inbreds and the Cuarentin population have a late temperate zone maturity. The Brazilian populations are fully tropical. Temperate and tropic zone material were joined in a single population and this adapted to the Central Corn Belt through phenotypic recurrent selection. This fully flint material ranges in color from deep yellow to orange. Cob color is white. Husk coverage tends to be heavy. Plant type generally resembles higher-eared Corn Belt Dent and the material can be handled in like manner.

Cargill North Temperate Zone Cuzco--An unimproved population having the proportionate composition:

Cuzco Populations	
C. Cristalino Amarillo	29.00%
C. Gigante Shaver	29.00%
Cuzco 66	12.50%
Cuzco Manuel	11.00%
C. Gigante 13605	4.00%
Cuzco 13623	4.00%
Cuzco 13634	4.00%

Early Dent Population	
Minnesota A	6.25%

This population has the equivalent of a 94% recovery of tropical germplasm. Initially Cuzco Manuel was crossed with the source of earliness, Minnesota A. Through a series of three backcrosses to tropical, various of the seven different Cuzco populations were used at each generation to give the resulting proportions. Interpollination among the different basic sources was practiced following each backcross. An adapted population was formed through phenotypic recurrent selection out

of the third backcross generation. This population differs considerably in appearance from typical Corn Belt Dent, giving an overall impression of heaviness or coarseness for many plant traits. Ears are short and blocky. Kernel row number is low, and kernels themselves range in size from typical Corn Belt Dent to 70% that of gigante. Texture ranges from dented flour to near-flint. Kernel color varies from white through medium yellow. Cob color is white and varying shades of red. Husk coverage is extremely heavy and tight. This together with a stiffly upright ear leads to extensive ear rot and lowered germination unless pollinating bags are removed early and harvest is timely. There is a strong tendency for barrenness unless plant densities are kept below 40,000 plants per hectare.

Cargill North Temperate Zone Coroico--An unimproved population having the proportionate composition:

Coroico Populations		Early Flint Population	
Red Chavantes	27.50%	Early Russian	6.25%
Entrelacado	15.00%		
Xingu	15.00%		
Amazonas	15.00%		
White Chavantes	15.00%		
Black Chavantes	6.25%		

This population has the equivalent of a 94% recovery of tropical germplasm. Although the three Chavantes populations were presumably collected from the same Indian tribe, Chavantes, they differ considerably in maturity and gross appearance under Hawaiian growing conditions. Initially Red Chavantes was crossed with the source of earliness, Early Russian. During a series of three backcrosses to tropical, Red Chavantes was always involved and four additional representatives of this race were added at the second backcross. Black Chavantes was involved at the first backcross only. Interpollination among the different sources was practiced following each backcross. An adapted population was formed through phenotypic recurrent selection out of the third backcross generation. Appearance of this material is profoundly different from that of Corn Belt Dent. Ears are very slender with a tendency for low kernel row number towards the tip and a compounding of row numbers on enlarged butts. Ear placement is high with occasional prolificacy. Kernel texture ranges from floury to flinted-flour. Kernel color ranges from white through varying shades of yellow to occasional red. Leaves are long and slender. Tassels are very large and thin, but with profuse pollen shed. Stalks are brittle. There is a lower than average tolerance to heat, drought and high plant density. Best results are obtained where plant densities are kept below 40,000 plants per hectare.

Barring a failure in the 1979-80 and 1980 crop seasons, seed of these five adapted exotic races should be available late in 1980 from the North Central Regional Plant Introduction Station, Iowa State University, Ames, Iowa. Plant accession numbers have not yet been assigned.

E. E. Gerrish

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Pfizer, Inc.

Initiation of totipotent tissue cultures from undeveloped axillary and secondary ears

Tissue cultures competent to regenerate plants have been isolated previously in this laboratory from three cv A188 tissue sources; the scutellum of immature embryos, the nodal stem sections of 14-day-old seedlings, and immature tassel

flowers. An experimental approach combining a standard culture medium and routine incubation conditions with a specific visual selection process was successful in each case (Gordon, Robarts and Rice, MGNL 51:79-80, 1977; Rice, Reid and Gordon, Progagation of Higher Plants Through Tissue Culture, Univ. of Tenn. Symposium Proc., p. 262, 1979). The same approach has now been employed to establish competent, totipotent cultures from undeveloped axillary and secondary ears. The strategy for using our tissue culture methods to initiate totipotent cultures from a new meristematic tissue source was to focus on the characteristics of the explant. The variables involved included the age and physiological characteristics of the source plant, the developmental characteristics of the axillary and secondary ears, the nature of the explant itself and the orientation of the explant on the medium.

Greenhouse grown plants of cv A188 were used for this study. Axillary ears were taken from the lower nodes and secondary ears were removed from the shank of the primary ear. Axenic explants were successfully established from 49 ears. Totipotent cultures were established in 3 separate experiments from a total of 4 ears, 2 axillary ears and 2 secondary ears. These four ears were all less than 1 cm in length, and appeared morphologically normal, healthy and fully formed. They were removed from three plants which were 126, 135, and 137 days old respectively. In the successful experiments, the ears were sliced transversely, or sectored longitudinally and later sliced transversely, into thin tissue slices ($\leq$ 0.1 cm); transverse slices were placed with basal side in contact with the culture medium. Within 3-4 weeks, some explants generated complex tissue/organ cultures containing totipotent tissues which were selectively excised and subcultured. The cultures have been maintained for five months and are morphologically indistinguishable from cultures derived from other tissue sources. Numerous plants have been regenerated and grown to maturity.

It is not clear based on these preliminary experiments whether positive results depend on using ears at a particular developmental stage, and the specific tissue from which cultures are initiated is not yet known. However, these results demonstrate the presence in mature plants of tissues which remain competent to establish totipotent cultures. (Supported in part by NSF Grant #75 20882 administered through Michigan State University).

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Biochemical studies on the iojap mutant of maize

The plastids in the white tissue of green-white striped or entirely white leaves of the nuclear gene induced iojap mutant are much smaller than the normal chloroplasts of green mesophyll or bundle sheath cells. Their matrix contains membranous structures and DNA fibrils whereas no grana thylakoids and no ribosomes could be found by electron microscopy (L. K. Shumway and T. E. Weier, 1967). This mutant may serve as an appropriate tool for the study of the function of plastid DNA and ribosomes and of the interaction between the genetic systems of the plastid and the nucleo-cytoplasm during biogenesis of the chloroplasts.

We checked green and white leaf tissue of iojap maize for the presence of fraction I protein and plastid coupling factor CF1 in order to test the function of the protein-synthesizing system of the plastids (subunits of both proteins are synthesized on chloroplast ribosomes). Fraction I protein was shown to be present in green tissue by reaction with antibodies against fraction I protein from barley by means of crossed immunoelectrophoresis. However, no precipitation peak could be

observed in the case of white tissue. The plastid coupling factor CF1 was solubilized by EDTA treatment of washed plastid membranes. After polyacrylamide gel electrophoresis of the ten-fold concentrated extract the gels were stained for ATPase activity (T. Börner, R. Manteuffel, A. R. Wellburn, Protoplasma 98:153-161). In extracts of plastids from white tissue no activity could be detected whereas EDTA extracts from green tissue yielded an intense white ATPase band in the gels. The identity of this ATPase with plastid coupling factor was shown by reaction with antiserum against the plastid coupling factor CF1. These results indicating a plastid ribosome deficiency support the observations of V. Walbot and E. H. Coe Jr. (PNAS 76:2760-2764) that plastids of white iojap tissue contain no rRNA and are unable to incorporate amino acids.

In contrast the activity of PEP carboxylase could easily be found in white leaf tissue. Extracts of white leaves (ij/ij) show about 40% of the activity (fresh weight basis) observed in green leaves:

	Mutant	Control
Activity in µmol/min ml	0.57 ± 0.1	1.45 ± 0.16
Activity in %	39.3	100

Since the plastid ribosomes are obviously missing in the white tissue, this enzyme should be synthesized on cytoplasmic ribosomes. The absorption spectrum of white leaves exhibits a very reduced content of carotenoids and chlorophyll as compared with green leaves. The height of the peaks at 482 nm and 670 nm corresponds to 1% to 2% of carotenoid content and to less than 0.1% of chlorophyll a content of green leaves. In agreement with the reduced content of photosynthetic pigments the white iojap tissue shows no trace of photosynthetic activity as examined by delayed light emission. In order to check the influence of the iojap mutation on mitochondria we measured the oxygen consumption (nmol per min per 50 mg) of small pieces of tissue by a Clark type electrode. Mitochondria of white tissue are much less active than those of green tissue:

	Mutant	Control
Dark	3.3 ± 0.2	8.7 ± 0.4
Light	3.3 ± 0.2	5.1 ± 0.02

This might be caused by a further effect of the mutation or by a shortage of substrate, respectively. (We thank E. H. Coe for kindly supplied gifts of seeds of iojap maize.)

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Antigen and isozyme spectra of maize and teosinte

Recently we have compared isozyme patterns of several enzymes and antigen spectra of reserve globulins in maize and annual teosinte [Z. mays ssp. mexicana (Schrad.) Iltis]. While isozyme spectra were identical in maize and teosinte (MNL 51:83, 1977), Guatemalan teosinte race Huixta had apparently lower content of the slow-migrating globulin component than maize and the Mexican race of teosinte, Chalco (MNL 53:44, 1979).

Here we present protein patterns comparing maize, teosinte Chalco (which is the most maizoid by its morphological features), and four more distant forms of teosinte, namely Z. mays ssp. mexicana, race Huehuetenango, Z. mays ssp. luxurians (Durieu) Iltis, Z. perennis (Hitchcock) Reeves and Mangelsdorf, and Z. diploperennis Iltis, Doebly & Guzman. Seed samples of teosinte were kindly provided by Dr. H. H. Iltis (University of Wisconsin, Madison). Several samples of two indigenous races of maize, namely Palomero Toluqueno and Nal-Tel, were obtained from Krasnodar and Raleigh collections by courtesy of Dr. V. S. Shcherbak (Krasnodar Agricultural Research Institute) and Dr. M. M. Goodman (North Carolina State University).

Maize (hybrid Krasnodarsky 303 TV) and teosinte differed quantitatively in their antigen spectra, the content of the slowest globulin component decreasing in the following order: maize > Chalco > Huehuetenango = luxurians > perennis = diploperennis (Fig. 1). The difference was especially pronounced when antiserum raised

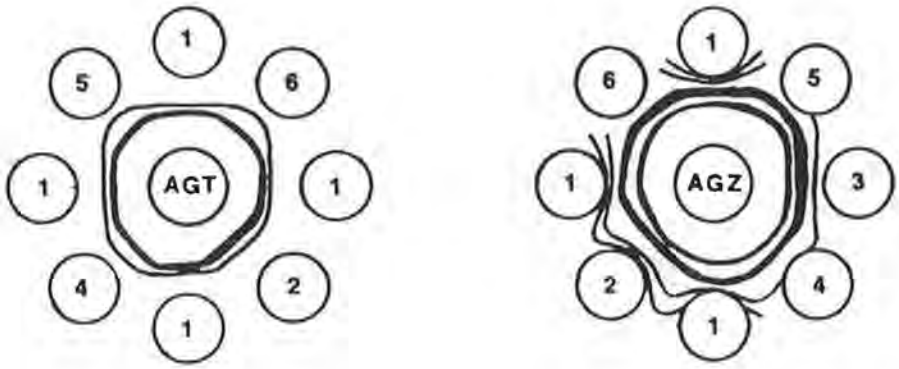

Fig. 1. Comparison of reserve globulins from ungerminated caryopses of maize and teosinte by double immunodiffusion test. AGZ, AGT, antisera against maize and wheat globulins. Antigens: (1) maize, hybrid Krasnodarsky 303 TV; teosinte (2) Chalco, (3) Huehuetenango, (4) luxurians, (5) perennis, (6) diploperennis.

against wheat globulins was used instead of that of maize. However, it should be mentioned that this difference may partly depend on the relative size of the embryo where globulins are preferentially localized (Khavkin et al., Planta 143:11, 1978).

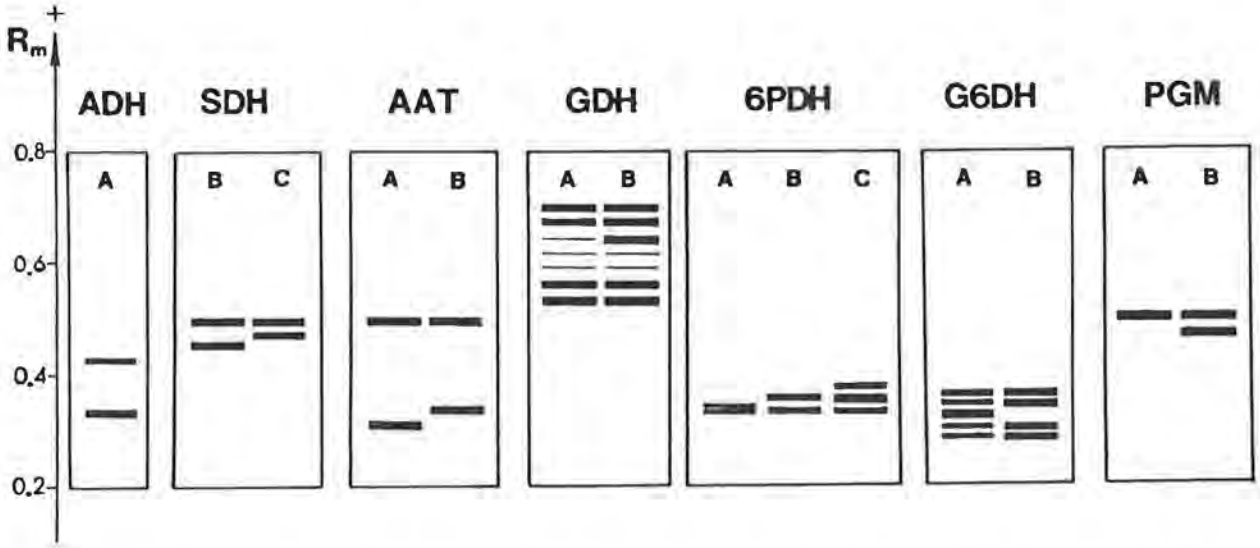

Fig. 2. Phenotypic classes of isozyme spectra of alcohol (ADH), succinate (SDH), glutamate (GDH), 6-phosphogluconate (6PDH) and glucose 6-phosphate (G6DH) dehydrogenases, aspartate aminotransferase (AAT), and phosphoglucomutase (PGM) in the scutella of the 3- to 5-day-old seedlings of maize and teosinte.

Seven isozyme patterns (Fig. 2) were employed to evaluate genetic polymorphism in maize races and teosinte. Monomorphic spectra were characteristic of both Krasnodar samples while in the Raleigh collections several samples were polymorphic for two or three enzymes (Table 1). The data for two collections usually agreed, however, there were some discrepancies concerning the patterns of glutamate,

Table 1. Phenotypic classes of isozyme spectra (for details see Fig. 2; AB - hybrid phenotypes)

		ADH	SDH	AAT	GDH	6PDH	G6DH	PGM
Maize	Palomero Raleigh MEX 5	A	B	A,AB	A	A,AB	A	A
	Toluqueno " MEX 6	A	B	A	A	AB,C	A	A
	Krasnodar	A	B	A	A	A	A	A
	Nal-Tel Amarillo Tierra Baja,Raleigh GUA 110	A	B	A	B	A	A	A
	Nal-Tel B.T.B.,Raleigh GUA 280	A	B,C	A	B	A	A	A
	GUA 765	A	B	A,AB	A	B	B	A
	Nal-Tel B.T.A., Raleigh GUA 20	A	B,C	A,AB	B	AB	A	B
	GUA 161	A	B	A,AB	A	A	A	A
	Nal-Tel Ocho, Raleigh GUA 458	A	B,C	A,AB	A	AB	A	B
	Nal-Tel,Raleigh YUC 7	A	B,C	A,AB	B	A	A	A
	Nal-Tel Krasnodar	A	B	A	B	A	A	A
Teosinte	Chalco	A	B	A	A	A	A	A
	Huehuetenango	A	B	A,B	A	C	A	A,B
	luxurians	A	B	A	A	C	A	A
	diploperennis	A	B	A,AB	A	C	A	A,B

6-phosphogluconate and glucose 6-phosphate dehydrogenases, and phosphoglucomutase (especially samples GUA 458 and 765).

While teosinte Chalco bore the most typical "maizoid" isozyme spectra identical to that of Palomero Toluqueno maize, race Huehuetenango and two more distant forms of teosinte, luxurians and diploperennis, were wide apart from Chalco by their pattern of 6-phosphogluconate dehydrogenase.

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A mutant for condensed plant type in the inbred NY544

A mutant gene with a distinctive phenotype has been found in the inbred NY544. Mapping procedures are currently underway to determine linkage and allelism.

While not dwarf or brachytic, the plants are short, approximately 5 feet, and compact, with short upright leaves. The tassel is highly condensed with many short branches; the ears are small and roundish with a high row number (18-20) and small kernels giving them a high condensation index.

In crosses to 11 different inbreds the distinctive phenotype appeared in the F2 in a ratio of 179 normal to 58 mutants, a good fit to a 3:1 ratio, $\chi^2 = 0.3516$, n.s. The χ^2 values for the 11 crosses ranged from 0 to .71, n.s. All the F2 plants having the recessive gene are quite similar in appearance. However, the progeny of one cross may be slightly taller than that of another, apparently due to modifiers for tallness in the outcross parents.

W. F. Tracy and H. L. Everett

Genetics of cms-C fertility restoration

Some preliminary results of studies of fertility restoration of several C type cytoplasms were reported last year (Kheyr-Pour et al., MNL 53:48-51). Additional data from a systematic series of crosses, backcrosses and selfs this year substantiate our contention that fertility restoration of the C, Bb, ES, PR and RB cytoplasms is controlled by no more than 2 co-dominant genes in the lines that we have studied. We did not find any evidence for the involvement of 3 or more restorer factors in C restoration as has been reported previously by Josephson et al. (Proc. 33rd Ann. Corn & Sorghum Res. Conf.:48-59, 1978) for a somewhat different group of inbred lines. In fact, in most lines we studied, only one restorer gene is apparent, but some data suggest that, at least for a few lines, a second gene may be involved.

In our studies, most inbreds segregated for a single restorer gene (Table 1). Progeny of single crosses between lines that were presumably of $\frac{rf*}{rf*}$ and $\frac{Rf*}{rf*}$ genotypes gave approximately 1:1 segregation ratios in Aurora, N.Y. (1979) and in Homestead, Fla. (1978-79 and 1979-80 winter nurseries). Numerous self progenies of theoretically heterozygous plants, produced by crossing NY821LERf onto several C sterile plants, when crossed onto a C sterile tester gave a segregation ratio of 3 fertile to 1 sterile. This, again, indicated that a single restorer gene was segregating in the lines tested.

Table 1. Fertility restoration reaction of C group cytoplasms in crosses involving C rfrf X C Rfrf genotypes.

	Heterozygous restorer lines (C Rfrf)														
	(W182BN x A619)			(W182BN x NY821 LERf)			(W64A x W182:N)			(R181B x A619)			(NYD410 x NY821 LERf)		
Sterile versions (C rfrf)	S	:Pf	:F	S	:PF	:F	S	:PF	:F	S	:PF	:F	S	:PF	:F
C x W182BN	26	: 4	:43	102	: 6	:99	62	: 5	:57	34	:14	:54	83	:15	:114
Bb x "	40	: 5	:48	14	: 2	: 8	27	: 1	:36	-			-		
ES x "	68	: 5	:61	80	: 5	:83	35	: 2	:53	-			-		
PR x "	40	: 4	:36	78	: 7	:59	52	: 5	:33	-			-		
RB x "	47	: 8	:45	41	: 8	:38	57	:20	:38	-			-		
C x Col07	61	: 4	:62	55	: 9	:67	365	:17	:327	59	: 6	:53	5	: 0	: 4
Bb x "	62	: 7	:70	113	: 1	:87	100	: 4	: 87	-			-		
ES x "	65	: 2	:65	70	: 0	:63	394	: 7	:249	-			-		
PR x "	66	: 4	:72	62	: 1	:57	295	: 9	:261	-			-		

[a]All progenies were rated on 1-5 scale (1=sterile, 5=fully fertile) in Florida winter 1978-79, 1979-80, and Aurora, summer 1979 nurseries.

[b]Most of the partially fertile plants (PF=ratings of 3 and 4) exhibit a "late breaking"of sterility.

A preliminary series of crosses between several different lines that were C sterile and had shown single gene segregation when crossed with restorer lines failed to give any fully fertile progeny suggesting that these 7 inbreds tested do not possess complementary restorer genes (Table 2). There were some partially fertile progeny which typically exhibited a delayed breaking of pollen which occurred about 5-10 days post-silking. However, an additional series of crosses involving dent inbreds A498, NYD410, NY254, NY306, NY317, NY453, Oh480 and W37A crossed onto sterile PR or C cytoplasm versions of sweet corn lines Pf41 and Me2Rt did suggest the presence of an additional restorer gene. Several of these lines restored the Me2Rt cytoplasms but did not restore the Pf41 cytoplasms. The ability

Table 2. Fertility restoration reactions of C group cytoplasms in crosses involving C rfrf x C rfrf genotypes.

Sterile inbreds	(NYD410 x Oh51A)			W182BN		
	S	:PF	:F	S	:PF	:F
W182BN-C	99	: 5	: 0	90	: 0	: 0
Col07-C	136	: 7	: 0	92	: 0	: 0
NYD410-C				92	: 0	: 0
Oh51A-C				90	: 0	: 0
R181B-C				93	: 0	: 0
A636-RF				88	: 0	: 0
SD10-RB				62	:23	: 0

[a]All progenies were rated on 1-5 scale (1=sterile, 5=fully fertile) in Florida winter 1978-79, 1979-80, and Aurora, summer 1979 nurseries.

[b]Most of the partially fertile plants (PF=ratings of 3 and 4) exhibit a "late breaking" of sterility.

of these dent inbreds to restore the C cytoplasms in the Me2Rt background only suggests that they possess a restorer gene that complements with another gene present in the Me2Rt background but lacking in the Pf41 background. Additional tests are underway to determine whether or not two complementary genes are involved in C fertility restoration for these and certain other lines.

The selection of A632-PR cytoplasm types that do not exhibit a late break of pollen fertility was continued. Last summer at Aurora, N.Y. ears selected for low levels of late breaking in the 1978-79 Florida generation produced rows with from 0-14 plants (out of 24) showing late breaking while non-selected ears produced rows with from 18-20 plants that showed late breaking of pollen. In the 1979-80 Florida generation, all of the progeny of non-late breaking plants from the 1979 summer nursery were completely sterile. None of the plants exhibited a late break. Whether this complete sterility will continue to hold in other environmental regimes is not known, but the results are promising. The data suggest that the late breaking of fertility in lines such as A632 which lack a major restorer gene may be influenced by several modifier genes as well as environmental conditions.

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Chromosome knob patterns in maize and annual teosinte

The work of Kato, Longley, Blumenschein, McClintock and Brown has provided us with abundant data on chromosome knob frequencies for most regions and subdivisions of maize and teosinte. A reanalysis of these data has been part of a 15-year survey of variation patterns in the genus Zea, based on iterative analysis of the many data tables. It has been possible to describe groupings of taxa (collections and races, Table 1) and of variables (knob presence or frequency, Table 2).

Table 1. The population samples used to calculate the averages in Table 3. Generally prior classifications can be used, but Balsas is divided because of significant differences between the northwest and southeast ends of its range. There is remarkably little difference between the Guanajuato and Michoacán populations of Central Plateau teosinte.

Taxonomic unit	Samples used for averages
Zea luxurians	Cutler 202 A; Wilkes 51764, 51839, 51850
Zea mexicana	
Huehuetenango	Wilkes San Antonio Huixta, Tzibaj, Monajil
Balsas, SE	Kato K-69-13; Beadle 1972 El Salado (3 collections); Wilkes 47935
Balsas, NW	Kato K-67-13, -14; Wilkes 47890, 47942
Central Plateau	from Guanajuato: Kato K-69-1, -2, -7, -10, -11; from NE Michoacán: Kato K-69-3, -4, -5, -6, -8, -9; Wilkes 45470
Chalco	Kato K-65-2, K-66-1, K-67-1, -2, -3, K-68-1, -2, -4, -6, K-69-12; 1970 T-1, T-2, T-3, T-4
Nobogame	Wilkes Nobogame (2 collections)
Zea mays	
Olotillo	Yucatan 37; Guatemala 108, 130, 131, 134, 314, 322, 600, 744, 769, 875
Nal-tel	Campeche 18, 29, 37, 102; Yucatan 7, 102, 129, 146; Guatemala 52, 115, 145, 250
Pollo	Cundinamarca 401; Pollo Segregaciones
Cónico	Guanajuato 2; Hidalgo 22; Mexico 3, 182, 207; Tlaxcala 1
Coroico	Bolivia 992, 1035, 1063, 1071
Chulpi	Chile 435, 438; Ecuador 387, 434, 598, 697

Table 2. Knobs arranged into sets according to their intercorrelations and listed in the order of their average frequency. A is the Andean set and is the only one present in dozens of high altitude races. C1 and C2 contain the most frequent knobs in the Caribbean and Middle American lowland races. One or two more sets of internal knobs could be defined for the latter region, usually found in low frequency.

Set	Knobs
Terminal knobs	
T1	2S3, 1S3, 6L5, 4L3, 10L3, 2L2, 7L3, 5L2, 9L3, 8L3
T2	4S2, 3S2, 5S2
T3	9S, 7S, 8S
Internal knobs	
C1	5L1, 8L1, 4L1, 3L1, 2L1, 6L2
C2	1S2, 8L2, 9L2
A	7L1, 6L3

In maize there is great contrast between Andean-Amazonian races with high frequencies of knobs at the 7L1 and 6L3 positions (Knob set A) and Caribbean-Middle American races with four sets of knobs in varying frequencies (Sets A, C1, C2 and T3). Within each of these regional subdivisions, frequencies vary greatly.

In annual teosinte the major variation is between the Guatemalan teosintes with many knobs terminal on long and short chromosome arms and Mexican races with few terminal knobs and many internal knobs. However, tassels and spikelets of Zea luxurians of southeast Guatemala differ greatly from those of race Huehuetenango of northwest Guatemala which has the Z. mexicana form (Table 3). Mexican annual teosintes differ more subtly; all are fairly similar in knob patterns to Caribbean-Middle American maizes, with Nobogame the least so. Chalco seems to be the most like maize in knob pattern,

Table 3. Chromosome knob frequencies, by sets of knobs, using data from Kato (1976, Mass. Agr. Exp. Sta. Bull. 635), Longley and Kato (1965, CIMMYT Res. Bull. 1) and McClintock (in Ramírez E. et al., 1960, Races of Maize in Bolivia; in Timothy et al., 1961, Races of Maize in Chile; in Timothy et al., 1963, Races of Maize in Ecuador). Few knob positions are occupied in all members of a race. The population samples used and the knob set compositions are listed in Tables 1 and 2. N' is the number of population samples used per race, and N" is the number of plants used for the knob counts.

		Percent of knob positions filled					
		Terminal sets			Internal sets		
Taxonomic unit	N':N"	T1	T2	T3	C1	C2	A
Zea luxurians	4:18	73	69	0	0	0	0
Zea mexicana							
Northwest Guatemala							
Huehuetenango	3:26	53	76	75	0	0	0
Central Mexico							
Balsas, SE	5:26	0	20	27	44	18	86
Balsas, NW	4:25	0	20	63	67	40	60
Central Plateau	12:59	0	2	13	60	42	42
Chalco	14:33	0	8	36	75	27	52
Northwest Mexico							
Nobogame	2:16	0	0	3	20	4	3
Zea mays							
Caribbean pattern							
Olotillo	11:35	0	0	39	94	79	97
Nal-tel	12:64	0	1	37	89	61	98
Pollo	2:15	0	0	27	74	20	63
Cónico	5:49	0	0	16	39	10	41
Andean pattern							
Coroico	4: 6	0	0	0	7	0	100
Chulpi	6: 9	0	0	0	0	0	67

as well as plant form. Central Plateau, including several geographic populations with somewhat different knob frequencies, is much like Chalco in several ways. There is considerable variation in the Balsas race, resolvable into a northwest group of populations, in southern Michoacan, with levels of knobs 7S, 8S, 4L1, 2L1, 1S2, 3L2, 7L2 and 3S1 higher than in a southeast group near Chilpancingo, Gro. (El Salado, Mazatlán, etc.). The latter group has shorter plants with more tillers and

narrower leaves than the Michoacan group. Nobogame of Chihuahua in northwest Mexico has low knob frequencies and several traits indicative of introgression with local maize. Several teosinte populations are not on Table 3. A Central Balsas group (Kato's no. 8-11 and 16), a western state of Mexico group (no. 32-37), and collections from eastern Michoacan (no. 49-54) are intermediate between two or more of the other groups.

There is considerable correlation between many of the knobs--7S correlates with 9S, 8L2 with 9L2, etc. The "sets" of Tables 2 and 3 are groups of knobs demonstrating similar trends for at least the major types of maize and teosinte. The correlations between knobs are important in two ways--a reduced set of factors seems to be responsible for their frequencies and many fewer measurements are needed to derive the same patterns. Knobs have varying degrees of independent control, so they have varying importance in taxonomic and evolutionary models. In low frequencies there are 19 other knobs, all with some geographical-racial relationships--two terminal knobs are limited to northwest Guatemala teosinte (average frequency of 13%), seven internal knobs are shared by Mexican teosinte and Caribbean-Middle American maize (averages, 26% and 7%, respectively), and ten internal knobs are restricted to Mexican teosinte (average, 4%).

Robert McK. Bird

What is the age of the oldest Bat Cave maize?

I am prompted to write this note because maize evolutionists continue to use 3000 B.C. as the date of introduction of maize to Bat Cave in southwest New Mexico. H. W. Dick (1965, Bat Cave, Santa Fe) reports much maize from six artificial 1-foot levels at various places in the midden, uncovered during three seasons of excavation (1947, 1948, 1950). Whole and broken cobs reported from the lowest level, VI, number 25, and 68 came from level V (Mangelsdorf and Smith, 1949, Leafl., Bot. Mus., Harvard U., 13:213; Mangelsdorf, Dick and Cámara-Hernández, 1967, loc. cit., 22:1). The earliest reasonably acceptable date for material found near the lowest maize is 912 B.C. ± 250 (Yarnell, 1976, in Cleland, Cultural Change and Continuity, p. 266), but this may not date the maize. There are several reasons for this uncertainty.

1) The radiocarbon dates are erratic. Material from level V produced three radiocarbon dates, 912 B.C. ± 250, 3049-5549 B.C. (a "poor counting run," Dick, 1965, p. 95), and 3655 B.C. ± 290. The last was charcoal "in association with the most primitive corn found in Bat Cave to date" (ibid., p. 19). However, Mangelsdorf et al. (1967) state that the 3655 B.C. date is probably not valid for dating the maize, for unexplained reasons. There are a number of possibilities--level V cut through several irregular sloping strata (Dick, 1965, fig. 16-19) and remained 48-60" below a level line at floor surface, no matter what depth or slope the deposit had; most of the dated material came from midden outside the shelter so when refuse was ejected from inside, older material could have mixed with younger cobs; and/or the wood burned by early occupiers of the cave could have been grown many centuries earlier. One must realize that Mangelsdorf and Smith label the bottom level"I" while the two later reports label it "VI"!

2) Although Mangelsdorf and Smith (1949) describe level VI maize, Mangelsdorf et al. (1967) do not discuss any maize from this level. One might assume this set has dubious association or statistical value.

3) The estimate of 2300 B.C. as the earliest possible starting date of maize at Bat Cave (ibid.) is based on morphological comparison of the early cobs (without presenting comparative data) to cobs from Puebla and Tamaulipas, Mexico, 2012 km and 1440 km away, too far for such comparisons. Moreover, they give the impression that the radiocarbon dates correspond to this estimate by reporting radiocarbon ages as "dates" in Table 1.

4) Antevs (fide Dick) estimated that the underlying buff sand might have been deposited through the 5000-2000 B.C. period.

5) Projectile points of the San Pedro Stage (at Bat Cave dating 900-100 B.C.) are distributed through levels I to V, like most (?) of the maize (all of the maize discussed in 1967).

Because of messy associations, possible intrusions, and variable radiocarbon dates, the earliest Bat Cave maize cannot be reported as predating 662-1162 B.C.; maize there could prove to be much older or much younger. A sample from level III dates 666-1066 B.C.

Robert McK. Bird

Notes on Zea luxurians (Durieu) Bird and some requests

Since the teosinte race often called Guatemala was renamed as a third species of Zea (Taxon 27:363, 1978), further evidence has become available which affects the delineation of that species. Z. luxurians differs from maize and Mexican annual teosinte in many more ways than at first understood, but the Honduras population which was tentatively included in the species must be excluded, as must the cytologically similar Huehuetenango race of northwest Guatemala.

A recent paper by Timothy, Levings, Pring, Conde and Kermicle (PNAS 76:4220, 1979) describes the agarose gel electrophoretic patterns obtained from restriction endonuclease digests of chloroplast DNA and mitochondrial DNA. Three endonucleases were used on ctDNA and four on mtDNA. Z. luxurians differed in all seven cases from Z. mays and Z. mexicana, including Huehuetenango, sometimes by many bands. It was identical to Z. perennis in three digests of ctDNA, none of the mtDNA. Huehuetenango was identical to a northwest Balsas sample from Michoacan in all seven cases. These were identical to either maize or Mexican annual teosinte in each case. However, the sampling per race was very narrow.

Over the past year, we have grown small samples of a wide range of teosinte materials, partly to obtain morphological specimens, partly for genetic purposes. The tassels from these have been examined with particular attention being paid to the spikelets. Iltis (26th Annual Systematics Symposium of the Missouri Botanical Garden, abstracts, 1979) states that Z. luxurians, Z. perennis and Z. diploperennis differ greatly from maize and Mexican annual teosinte, and using male spikelet morphology, he and Doebley (in press) are splitting the genus into Sect. Luxuriantes, with the first three species, and Sect. Zea with the last two taxa condensed into Zea mays. We lack specimens of Z. perennis and Z. diploperennis, but Z. luxurians is certainly very different.

The lower or outer glumes of the Z. luxurians tassel spikelets have two prominent angles or ridges with one or more veins bearing hairs, between which there are about 15 veins spread across the flattened surface. Those of maize and the Nobogame, Chalco, Balsas (Mazatlán) and Huehuetenango teosinte races, at least, have 1-6 veins on a more rounded surface between obtuse angles bearing shorter hairs. In Z. luxurians the pedicels of the pedicellate spikelet are fused to the branch rachis for about 1 mm; the branch rachises are usually 1.0 mm or more broad with prominent abscission creases below the nodes; and the nearly unbranched primary branches form very narrow angles with the main rachis. In the maize and Mexican annual teosinte which we examined, the pedicellate spikelets are free of the branch rachis; these rachises are usually less than 1 mm broad; abscission creases are absent, not visible or not prominent; and the primary branches usually form wide angles with the main rachis. Nearly always there are many 2º and 3º branches. Further differences have been noted, but these are sufficient to allow characterization of specimens. Four samples from southeast Guatemala (PI 306615, 306616, 306617 and 343231) can be identified as Z. luxurians; the first may be the most free of maize introgression. Our one sample of Florida teosinte also has the

Z. luxurians form, but the one sample of Honduras teosinte which we grew definitely has the other form.

The morphology of the teosinte fruit-case or alicole, including the cupule and spikelets, has been noted by several investigators to indicate not only some major divisions between races, but also introgression from maize. The Honduras teosinte sample we have has very maizoid alicoles--many have two spikelets indicating that maize or a maizoid teosinte has had a great influence on it.

A further correction--all Z. luxurians examined has a recognizable central spike in the tassel, sometimes a little thicker than the primary branches with three ranks of spikelet pairs. Usually primary tassel branches are decussately arranged on the main rachis giving four ranks; five ranks of solitary branches have been seen.

We would like very much to have specimens of other collections of Z. luxurians and its seeming nearest relatives, the Huehuetenango and Honduras populations, Z. perennis and Z. diploperennis, for comparison. Of special interest would be specimens of Florida teosinte so that we can check whether that material, which so often has represented Z. luxurians in genetic experiments, is a good representative. Plants which seem to be the product of hybridization with maize are reported in the populations in Guatemala, and some of our Z. luxurians plants have varied in the direction of Z. mays or Z. mexicana. Perhaps a measure of such a tendency could be used as a factor in interpreting genetic experiments. Tassels and ear branches (especially from the 7th node from the tassel) would be appreciated, picked when flowering, if possible (please send them to the first author, P.O. Box 9983, Kirkwood, MO).

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Two-tassel mutant of maize

Dichotomously branched and two-tassel plants were found as spontaneous mutants in three stocks of maize: K-851, local from Bulgaria; K-2847, Brazilian blue; K-2858, local from Afghanistan, and in two hybrids. For the short designation of this mutant the symbol "dib" is proposed. The attempt to maintain this character was successful only in K-2858 and the description below is concerned with this stock.

The expression of the mutant varies. Usually the stalks are divided into two branches at the 4-8th node above the ground, more rarely at the very base or near the tassel. Therefore the mutant character may easier be observed after the tasseling. As a rule both branches develop similarly. The leaves and the ears are formed both on the common stalk and on each of the branches. The plants branching lower as a rule have more leaves and ears. The mutants differ insignificantly from the normal individuals in plant height and size of the elements of the plant structure (leaves, ears, tassels), but they develop two times more male spikelets (in two tassels) and about one and a half times more leaves and ears than normal plants.

In order to determine the hereditary basis of this mutant the dichotomously branched plants were selfed, sib pollinated and outcrossed to normal lines and stocks. From 403 selfed progenies which were studied 80 consisted only of normal individuals. In 230 segregating progenies mutant plants made up under 20%, in another 83 about 25%, and in 9 about 50%. Only in one progeny all 19 mature plants were branched, but in the next selfed generation the usual segregation was

observed. It should be noted that in the above-mentioned progeny 18 seedlings (from 40 planted seeds) were lethal (white and yellow-white). Most probably the lethal genotypes may have normal phenotypes.

In the sibbed progenies as well as in the F1 outcrosses, both when the mutants were used as female and as male components, segregation was the same. But in this material the number of branching plants was significantly less than in the progenies of selfing of mutants. The normal plants from the sibbed progenies and from F1 were selfed too. The majority of these progenies consisted entirely of normal plants and only about 20% of them contained rare mutants.

It is important to note that in the whole material besides two-tassel plants there were many other mutants such as: tasselless plants, defective seeds, and lethal seedlings, which complicated genetical analysis.

Cytological analysis of the two-tassel mutant had been undertaken and the results were published (Micu, V. E., and S. G. Kaptari, 1973. Dichotomous branching of stalk and the absence of tassel in maize caused by aneuploidy. Genetika 9 (4):5-11). Chromosome numbers in the root tips of normal and two-tassel plants were determined. It was found that the chromosome number in the somatic tissue cells varied from 20 to 22 and in addition fragments were observed. Thus preliminary genetical and cytological study showed that the two-tassel mutant is due to aneuploidy.

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Inheritance of induced molecular variation

The inheritance between the gene C*-IE7002 and the exceptional cytoplasm of Euchlaena (M.N.L. 52:35-36) has resulted in induced inheritable molecular variation, consisting of DNA increase of the knobs. The relative, and only for comparative purpose, DNA content of knobs was measured in an area of 0.1963 square micra in the central region of maximum absorption at 560 nm (Feulgen) of each knob, multiplied by their geometric area, as shown in the following table:

	Number of knobs	Relative DNA content	t
Zea cytoplasm	72	0.222	6.7***
Euchlaena cytoplasm	75	0.313	8.7***
			1.7
In Zea cytoplasm, but transferred from Euchlaena cytoplasm	69	0.341	

***P < 0.001

The DNA increase is possibly from greater spiralization, duplex position aggregation (‾‾‾‾‾‾‾‾) or axial aggregation (————·····).

My hypothesis is that axial aggregation of free replicates of C*-IE7002 gene in inert position chromosomic, increases DNA in the knobs region; the hypothesis would also indicate a possible evolutionary mechanism for the origin of repetitive DNA segments of chromosomes A, B and abnormal 10 chromosome.

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Pollen studies

Corn pollen has been the subject of several investigations in our laboratory. All the studies have been designed to test--or emerge from--the thesis that there is a large number of genes in the maize genome responsible for the development, maturation and function of the male gametophyte. How many--and which--genes are 'sex-limited' and how many express in both the sporophyte and the gametophyte remains an unanswered question.

I have attempted to separate into discrete classes the pollen from various heterozygotes on the basis of physical parameters: size, density and electrostatic charge. The most useful technique appears to be separation through a series of graded sieves. A nest of Standard sieves with mesh of 125 μ, 105 μ, 88 μ, 76 μ, 63 μ and 52 μ has been used extensively. Pollen, for instance from a translocation heteromorph, will collect on all sieves, albeit very little on the latter two. Sparse pollinations (less than 100 pollen grains, made with a #2 camel's hair brush) demonstrate that pollen grains carrying an adjacent segregation will function for many translocations. As high as 75% of several hundred kernels from pollen on the 63 μ sieve have been shown to be adjacent segregants in some translocations. In conjunction with E. B. Patterson (Urbana) we have now screened for functional adjacent-segregate pollen grains from translocations occurring in the distal regions of several arms. Separation of pollen grains on size differences affords workers an easy-to-use tool for any situation in which linkage of a desired trait can be obtained with the size difference factor.

Pollen storage is routine for 10-14 day periods. Reasonably dry (air) pollen can be kept in a variety of containers at temperatures +5° C to -5° C. For extending pollen (sparse pollinations, etc.) one of the best diluents is killed corn pollen. Pollen germination (in vitro and in situ) is usually enhanced following 6-24 h refrigeration.

Germination of pollen in vitro has received somewhat cyclic interest. Our data and that of Gabay (MGCNL 48:43) indicate that most stocks have specific requirements for the composition of the medium; the medium of maximal germination is apparently genotypically dependent. Germination can be attained in a liquid medium as well as on the surface of supplemental agar and other support matrices.

Recently, I have initiated a series of studies utilizing germinating pollen grains and pollen tube growth as a bioassay. Our work follows from the demonstration by Laughnan and Gabay (Crop Science 13:681, 1973) that T Rf pollen grains were more sensitive to the pathotoxin from H. maydis (T) than to pathotoxin of other races or than N Rf pollen grains were to the pathotoxin from H. maydis (T). Our tests (preliminary results reported below) are designed to ascertain if: 1) there is a differential cultivar response (as measured by pollen germination and tube growth) to various herbicides, pesticides, pathotoxins, and various gametocidal compounds; 2) there is within cultivar differential response to agrichemicals, etc.

If there are genes for sensitivity or resistance to the agrichemicals, gametocidal compounds, etc. and if the gene expresses in both the gametophyte and the sporophyte, this bioassay will provide breeders with an easy, non-destructive tool

for gamete selection. Such a bioassay may also be useful for pre-release testing of next generation agrichemicals. The usefulness of the pollen germination/tube growth assay for screening extracts from plant pathogens also looks promising at this time.

Several workers have studied methods for discrete gamete selection. For instance, Coe and Neuffer have suspended pollen in EMS-paraffin oil mixture and recovered mutants from individual pollen grains. Schwartz, Osterman and Freeling have employed the vapors of allyl alcohol as a selection agent acting on the Adh1-allele. It appears as though a variety of agents may be employed for gamete selection. If the selection is to be done in or on a medium such that one is selecting for/against the processes of germination and/or tube growth, rather than for/against components of the pollen grain, one problem remains--how does one obtain syngamy utilizing that already growing male gametophyte? We report below (3d article) success with a totally in vitro system and presumed success with field methods.

Corn pollen is very rich in protein (22-24% on a dry weight basis). Clearly microspore transcription and translation processes have a short time-frame within which to operate. If a large number of genes are transcribed in the male gametophyte, protein separation techniques may reveal such phenotypes. Ideally, one would like to work with microtechniques that would employ one pollen grain. We have not accomplished this level of miniaturization; we report methods and technology below (in the 4th, 5th, and 6th articles) which permit detection of several dozen discrete proteins/peptides from approximately 100 pollen grains.

D. B. Walden

A pollen bio-assay for agrichemicals

We report below the development of a bioassay employing pollen germination and pollen tube elongation. Five insecticides and five herbicides were tested against 14 inbreds in all possible combinations (Table 1). An additional six inbreds and 12 F1's were also tested against a selection of these agrichemicals. All chemicals were tested at 3 concentrations: the manufacturer's recommended field dose, a tenfold dilution and a one hundredfold dilution of the field dose. 0.1 ml of each concentration was overlaid onto petri plates containing our basal medium which was prepared daily. Control plates received no overlay. All treatments were performed in triplicate. Pollen of known genotype was collected and sieved just prior to application and was delivered to the medium using a No. 2 Camel's hair brush 30 minutes after chemical overlay. Pollen was allowed to germinate for 15 minutes. Five random sample areas from each plate were photographed (Plus X) for a total of 15 samples (approximately 1,000 pollen grains) per treatment. The data are stored on approximately 600 rolls of 35 mm film.

Table 1. List of materials employed.

AGRICHEMICALS	
Herbicides	Insecticides
Atrazine	Basudin (diazinon)
Banvel (dicamba)	Lannate
2,4-D	Lindane
Killex	Malathion
Roundup	Sevin
POLLEN SOURCES	
A 158	Mo 17
A 619	N 28
A 632	Oh 43
B 14A	Oh 51A
B 73	Va 26
H 95	W 22
M 14	W 23

Some preliminary data are presented in Table 2. These results are indicative of the differential responses that we are seeing as we work through the large data

Table 2. Index of pollen (germination) performance (multiples of 15 observations per entry).

Inbred	BASUDIN (F.D.)* control	.01	0.1	1.0
A 158	1.0	1.09	1.04	0.66
M 14	1.0	0.92	0.96	0.56
Oh 43	1.0	2.60	2.86	1.61
W 23	1.0	1.50	1.78	0.57
W 64A	1.0	0	0	0
	ATRAZINE (F.D.)* control	.01	0.1	1.0
A 158	1.0	0.77	0.65	0.54
M 14	1.0	0.41	0.35	0
Oh 43	1.0	1.70	0.81	0.04
W 23	1.0	0.67	0.36	0
W 64A	1.0	0.80	0.46	0

* F.D. = manufacturer's recommended field dose;
Basudin: 1 ml/l
Atrazine: 10 gm/l

pool. Most obvious is the apparent enhancement response of the three inbreds (A158, Oh43, W23) to the insecticide basudin at low concentration and the inhibitory effect of the higher dose.

In contrast, M14 germinability is not altered by low concentrations of basudin but does show the expected decrease at the higher dose. Germination of W64A pollen was prevented at the concentrations tested. This apparent super-sensivity will be studied further including the possibility that selective male gametocides could be identified initially with this bioassay.

Response to atrazine shows a definite dosage dependency although the inbreds clearly differ in the magnitude of response. The relative insensitivity of A158 appears unique among the inbreds tested.

We will be introducing several innovations in 1980 now that we have identified the range of response that can be anticipated in the system. The active ingredient(s) of these and other chemicals remain to be tested. In addition, we shall attempt pre-treatment of pollen prior to dehiscence. Breeding and selection studies have been initiated to identify the genetic factors in the pollen. Identification of individual plants whose pollen is sensitive or tolerant to an array of chemicals is now possible. Coupled with gamete selection techniques, breeders may be able to incorporate determinable levels of sensitivity into future hybrids.

K. A. Startek and D. B. Walden

Syngamy from in vitro germinated pollen grains

As outlined in the first article, we have attempted to recover zygotes from male gametophytes that were first germinated on a suitable medium and then transferred to the female gametophyte, suitably juxtapositioned to maximize micropyle penetration by the tube and hopefully fertilization. We have been successful in employing the method outlined below:

(1) Explant mature, unpollinated ovaries (following a modified protocol of Gengenbach, Planta 134:91-93, 1977).
(2) Germinate pollen on medium (Can. J. Bot. 43:779, 1965) for 15-30 min or until pollen tube is desired length.
(3) Prepare ovary by cutting silk back to within 1 mm.
(4) Carefully cut a block of agar (from step 2) such that a gametophyte remains intact, shaving the edge nearest the tube tip so that contact with the cut end of the silk can be made.
(5) Juxtaposition male gametophyte to female. Incubate at 25^{o}-30^{o} C for period of growth of caryopsis.
(6) Storage of caryopsis; normal planting of seed. Or, embryo explant to medium followed by transplant to soil.

Since most of our evidence is photographic, it will be recorded elsewhere. Our success rate is now 25 mature, fertile plants from 212 attempted juxtapositions. Undoubtedly experience and technical modification will improve this ratio. It

appears that it is now feasible to employ any selection agent on pollen such that survival rates of $1x10^{-6}$ and lower are useful (and desirable). We attempted to extend this technology to field scale in 1979. Fresh pollen (or pollen stored at +5° C) from a variety of genetically marked cultivars was employed. Germination (approximately 30 min) was accomplished on the supplemented agar medium or on the surface of the same medium without agar.

Various preparative methods of the female tissue were attempted. 'Windows' were cut in the sides of bagged ears to reveal silks. Ultimately we opted for the simplest method--the normal preparation of a brush of silks. Contamination was a critical problem. Precautions were taken and we expect that contaminants can be genetically identified. A 2 m x 1 m x 1 m plastic covered, portable enclosure was built and deployed to several cultivars in the field during the pollinating season. Pollination attempts that were undertaken outside the enclosure were conducted during hours of least contamination (evening and night).

Delivery of the pollen plus tube was by Pasteur pipette or by spatula. Insofar as was possible, with the aid of a field microscope, only germinated pollen grains with tubes longer than one diameter were applied to the brush of silks. A variety of 'controls' were attempted. The most informative control, listed in Table 1, utilized the application of burst and non-germinated pollen grains from the same plates as were taken the germinated ones.

Table 1. 'Phenotypic success' from germinated pollen grains

	Number		
Treatment*	Ears attempted	Ears with kernels	Kernels (range)
A	13	9	1-11
B	12	11	1-43
C	63	55	1-61
D	9	9	1-47
Control	10	0	-

*A = pollen germinated on agar, delivered by spatula; female in enclosure
B = pollen germinated on liquid, delivered by pipette; female in enclosure
C = treatment B except female not in enclosure
D = treatment A except female not in enclosure
control = treatments A, B, C or D but only burst or non-germinated pollen grains used

Each female ear in the study was 'pollinated' on at least four different days, each time with a genotypically different pollen source. The data in Table 1 must be viewed with reservation. Plants from kernels from various ears are growing in the 1980 winter nursery and will be testcrossed for confirmation of genotypic identity.

From these two studies--in vitro and in situ--it appears that manipulation of the male gametophyte to permit the challenge of a selection pressure (physical, chemical or biological) followed by recovery of a surviving gametophyte is now feasible.

D. B. Walden and K. Raman

Two-dimensional electrophoresis of maize proteins: methodology

One of the most powerful techniques for the separation of protein involves two dimensional resolution on polyacrylamide gel by molecular weight and charge. In situations where sample quantities are limited or speed of analysis is required, such separation methods are constrained. For these reasons, a variety of microgel systems have been developed (Ruchel, J. Histochem. Cytochem. 24:773-791, 1976; Condeelis, Anal. Biochem. 77:195-207, 1977) for the rapid reproducible analysis of nanogram quantities of protein. These micro-methods are almost exclusively used in the field of neurophysiology where the analysis of single large cells is desired.

It has long been observed that differences in Zea mays L. genotypes are expressed to varying degrees in the sporophytic generation. However, very few genotypic-phenotypic relationships are available in the gametophytic phase. Indeed, in the case of corn pollen, very few methods are capable of describing phenotypic variation among the grains from sporophytes of known backgrounds. Thus, new probes which can detect some components of genetic diversity in the gametophyte generation are needed urgently. A review of the biochemical literature revealed that approximately 100 enzymes have been identified in the tissues of the corn plant; fewer than 40 of these have been identified in the male and female gametophytes.

The electrophoretic separation of protein from plant tissue extracts is fundamentally the same as that employed in the resolution of animal tissue extracts. However, one primary difference resides in the method of protein extraction (see 6th contribution). The implementation and modification of a two dimensional microelectrophoretic technique originally reported by Ruchel (J. Chromat. 132:451-468, 1977) is described.

Hardware: A high voltage-low current power supply was built from a modified circuit outlined by Wurtzburg (Power Supply Handbook, Motorola Semiconductor Inc., Tucson Arizona, 1976). The power supply will function in either constant voltage (0-300 V) or constant current mode (0-100 μA) with less than .01% fluctuation in the electric field generated. As gel chambers, Drummond (Broomall, PA) 5 μl capillary tubes are employed in the first dimension and double diamond glass plates, separated by teflon spacers, in the second. One of the glass plates is constructed with a rectangular notch (1 cm x 4 cm). The glass plates are fixed to the teflon spacers by a light coating of vacuum grease. The volume of the second dimension chamber is approximately 1000 μl (.08 x 4 x 3.5 cm) and has sufficient length to accommodate one cylindrical microgel (.07 x 3.3 cm). The first dimension buffer chamber is constructed by boring holes (1 to 6 usually) in the bottom of a 50 ml disposable plastic beaker. The rubber grommets supplied with the microcapillary tubes are inserted into the holes. Capillary gel tube chambers are inserted through the grommets thus forming the upper buffer reservoir. The lower reservoir is served by a 100 ml glass beaker on which the upper reservoir is seated. Platinum wire electrodes are fixed to both reservoirs. The second dimension buffer chamber is constructed of plexiglass to form a five-sided rectangular box. The long sides of the box are notched to match the notch on the second dimension slab gel chamber. Two gel chambers are clamped (with notches adjacent to each other) on opposite sides of the buffer chamber. A light coating of vacuum grease ensures a leakproof seal. This subassembly becomes the upper buffer chamber of the slab gel apparatus. The lower chamber, a large Coplin jar, allows sufficient area to insert the upper chamber. Platinum wire electrodes are fixed to both reservoirs.

Preparation of isoelectric focussing (IEF) gels: The gel mixture has been modified from Ruchel (1976). The mixture is composed of stock solutions prepared fresh each week and stored in dark containers at 4° C. All solutions are prepared in double distilled water.

Solution (1) 50 mg/ml Acrylamide + 5 mg/ml N,N^1-methylene bisacrylamide

Solution (2) .03% N,N,N^1,N^1-etramethylene diamine (v/v)

Solution (3) 10 mg/ml ammonium persulphate

Solution (4) 40% commercial preparation of aliphatic amino carboxylic acids, pH range 3.0-10.

Solution (5) 9.0 M UREA

2% NP-40 (v/v)

The following flow chart describes the remainder of the method.

Stock solutions are dispensed into a ØØ BEEM capsule according to the following schedule

1) Solution 5 - 140 µl
2) Solution 1 - 20 µl
3) Solution 3 - 15 µl
4) Solution 2 - 5 µl
5) Solution 4 - 20 µl

} yields 40, 4 µl gels of 5% acrylamide .5% bisacrylamide 6.3 M UREA 1.4 % NP-40 and 4% ampholyte concentration

↓

degass under vacuum for 1 minute

↓

with forceps, dip a clean 5 µl capillary into the mixture and allow to fill 4/5 of the capillary length

↓ ← place enough 60% sucrose to cover 5 ml beaker bottom to a depth of 1 mm

place the filled capillary, in an upright position, into the 5 ml beaker

↓

repeat filling procedure until 40 gels are produced or 10 minutes has elapsed

↓ Gels will polymerize in 15 to 30 minutes

place the 5 ml beaker into a high humidity environment

↓

Allow the gels to age overnight at room temperature

↓ 12-20 hours

Store the gels at 4°C until required

↓

Discard unused gels after 72 hours has elapsed

Preparation of sodium dodecyl sulphate (SDS) slab gels: The gel mixture employed in the second dimension has been modified from a method of Atkinson (Personal communication). The mixture is prepared by combining stock solutions prepared fresh each fortnight. All stock solutions are prepared in double distilled water and stored in dark containers at 4° C.

Solution 1 40 mg/ml Acrylamide + 4 mg/ml N,N^1-methylene bisacrylamide

Solution 2 3 M TRIS pH 8.9

.8% SDS (w/v)

Solution 3 1 M TRIS pH 6.8

.8% SDS (w/v)

Solution 4 99% commercial preparation of N,N,N^1,N^1-tetramethylene diamine

Solution 5 10 mg/ml ammonium persulphate

Solution 6 30 mg/ml Acrylamide + .8 mg/ml N,N^1-methylene bisacrylamide

The following chart describes the remainder of the procedures:

Loading and running IEF gels: Protein mixtures, stored on ice, are drawn up through a tuberculin syringe with a 30 gauge needle, then inserted into the upper end of the gel chamber by gentle pressure to the syringe. Failure to remove air bubbles in this procedure results in erratic conductivity during electrophoresis.

Microgels loaded with sample are inserted into the upper buffer chamber of the electrophoretic apparatus. The upper chamber is overlaid with anolyte (.5 N NaOH), the lower chamber with catholyte (.5 N H_3PO_4). The voltage is set to a constant field strength of 30 V/cm. Chromatophoric tracking dyes in the protein samples allow the monitoring of protein migration. Proteins are thought to be focused in the gel when the dye Xylene cyanole FF reaches the brownish precipitate of the faster migrating bromophenol blue (pI = 3.2).

Loading and running second dimension gels: The electrophoresed IEF gel is easily removed from the capillary by hydrostatic pressure delivered through a syringe fitted with 1/32" Tygon tubing. The gel is extruded into the notch of the second dimension gel chamber (previously attached to the upper buffer chamber), and pushed down onto the slab gel with a piece of filter paper. Immediately, running buffer (.1% SDS, .025 M TRIS pH 8.3, .2 M glycine, .001% Bromophenol Blue, .001% Xylene cyanole FF) is added to the upper buffer chamber. The lower buffer chamber is filled with running buffer (lacking tracking dye), and air bells are dispersed from the bottom and top of the gel chamber. A constant field strength of 100 µA/cm is allowed to flow from the top of the separation apparatus. The run is completed in approximately 30 minutes or when the marker dye just leaves the bottom of the gel.

Staining: The method outlined is employed as a general purpose staining procedure. All steps are performed at room temperature and with agitation of solutions: Remove gel from chamber; immerse in 10 volumes of fixer (10% glacial acetic acid + 50% methanol), prefix 15 minutes; transfer to staining solution (10 volumes of .1% Coomassie brilliant blue R-250 in 7% acetic acid + 30% methanol), stain 10 minutes; transfer to destain solution (10 volumes of 7% acetic acid + 10% methanol), destain 1 to 2 hours; transfer to fixer solution (10 volumes of 7% acetic acid + 5% methanol + 2% glycerol), postfix 15 minutes; photography; dehydration/storage.

The method will resolve nanogram quantities of protein. However, the differential dye binding capacity of some proteins will not allow this method to be employed in absolute protein quantitation. Alternate protein visualization methods are presently being tested.

Either dimension may be used separately. For separation on the basis of isoelectric point, cylindrical gels are immediately stained. Separation on the basis of molecular weight is accomplished by a slight modification to the slab gel apparatus. A template comb (cut from .8 mm teflon material) is inserted into solution 3 before polymerization takes place. Removal of the comb after polymerization leaves 8 wells (1 cm long x 3 mm wide) in the stacking gel of the slab. Gels produced in this way are attached to the buffer chamber apparatus as previously described. The assembled buffer chamber is then filled with running buffer and 1 to 5 µl of protein sample solutions are applied to each well. Electrophoresis and staining are carried out as before.

Employing the above microelectrophoretic procedures we have analyzed a number of tissues of the maize plant (e.g. pollen, primary root tips and leaf mesocotyl protoplasts). The results obtained with the micromethod are consistent with those yielded by the analysis of replicate samples employing a modified O'Farrel (J. Biol. Chem. 10:4007-4021, 1975) technique. However, the micromethod does allow a 100-fold increase in protein detection sensitivity by Coomassie brilliant blue R-250 staining, decreased preparation time, and smaller protein sample volumes for analysis.

W. G. Hughes

Two-dimensional electrophoresis of maize proteins: computerized densitometry

Utilizing the above procedures, it is possible to visualize proteins as stained spots on the electropherogram surface. Due to the small size of the gels produced, stained proteins are not easily resolved with the unaided eye or conventional densitometry. A high resolution densitometer is required before maximum information can be obtained. Some two-dimensional densitometry equipment can discern variation in optical density of photographic films in 1 square micron areas. Due to the nature of the scanning method engineered into the Optronix-100, direct densitometry of gels was impossible. The machine requires a flexible photographic image for scanning. The image is mounted on a rotating drum. An output of discrete intensity value is achieved by focusing a beam of light through the image onto a photodetector, at a position in the image defined by translation of the beam (x) and rotation of the drum (y). The output is in the form of a binary coded magnetic tape. Computer analysis facilitates the graphic and enumerative representation of the number of protein species, relative quantity, charge and molecular weight into patterns or protein "landscapes." Such landscapes with the activity of specific genes (i.e. the "landmarks") allow the production of a genetic/biochemical "map," to "chart" the "latitude" and "longitude" of growth, development and determination of any biological tissue.

Photography of gels: The stained gel is photographed with fluorescent back light, 12 hours after fixation, with a 35 mm Pentax Camera, 35 mm wide angle lens, and a focal distance of 3 inches, and the image is produced on Kodak High Contrast Copy Film (ASA 50). The film is developed for 7 minutes at 20° C in Kodak Microdol X (diluted 1:1 with distilled water), fixed for 10 minutes in Kodak Fixer and treated for 1 minute with a 1:1000 dilution of Kodak Photoflow surfactant. A 16 x 20 cm positive enlargement of the negative image is produced on Kodak Professional Fine Grain film. The film is developed for 2 minutes at 20° C in Kodak Dektol (diluted 1:3 with distilled water) and fixed as before.

Densitometry of gels: The enlargement is scanned with the Optronix 100 at the sequential x and y increments of 200 microns. Each 3 micron square gel area is interpreted as a 2 mm square photographic representation. The digitized density, ranging from 0 (lightest) to 255 (darkest), and coordinated values are output to a nine track magnetic tape. The format of the output file is 700 records (each representing one 200 micron step in the x direction) containing 800 (successive 200 μ steps in the y direction) eight-bit octal numbers. Each number (ranging from 0 to 255) represents the intensity of one 200 micron square of the gel. These raw data are then translated by suitable FORTRAN language programs with a Control Data Corporation CYBER 73 computer to a disk device output file. The output file is represented in the computer as a two-dimensional matrix (x and y) such that each cell in the matrix contains a single intensity value. The matrix usually consists of some 560,000 elements. The data may now be discretized by applying the function f(x,y) as a descriptor of intensity. Such a function is integratable and may be ascribed integer limits ($0 \leq f(x,y) \leq 255$).

Having established the means to enumerate and represent the electrophoretic gel as a digital density surface, the aim of subsequent metrification is to reveal some form of identification pattern within the surface. This first step in image segmentation is based on analysis of each matrix cell. Summing the number of occurrences of each density level in the image matrix and dividing by the total number of matrix elements allows the construction of a frequency-gray level histogram.

The data for the histogram are obtained by applying the following equation:

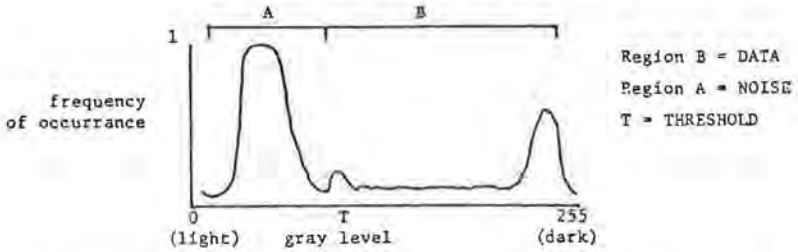
$$H(I) = \frac{1}{MN} \sum_{N=0}^{x} \sum_{M=0}^{y} f(N,M)$$

where I = (0,1,2...255) or the number of discrete gray levels

N = the maximum extent of the x vector direction

M = the maximum extent of the y vector direction

A typical result is shown in the figure below



This type of intensity distribution is typical of a positive gel image (i.e. dark spots on a light background). Within the distribution, a single density value (T) may be selected as a threshold value. The selection of a threshold allows the reduction of the amount of information required to describe the edges of resolved protein spots in the electrophoretic gel. The raw data matrix may be

subdivided into two major components: values above T (region B), considered valid protein data descriptors; and values below T (region A), considered as experimental and machine noise/artifacts. The value of T is arrived at by operator intervention. Having achieved a T value, the density matrix within the computer is subdivided into 40 or more 100 x 100 point sequential matrices which we have termed R matrices. A corresponding set of 40 matrices (termed T matrices) are also constructed where those intensity values below the value of T are scored as zeroes, those above T are unaltered. Therefore, the edges of protein spots within a gel image can be discretely bound mathematically.

The edges of the figures described within such T matrices are then plotted with the aid of a drum plotter (Calcomp, Anaheim, CA) or displayed on a graphics monitor device (Tektronix, Beaverton, OR). This output result (a contour map) can then be compared visually to the original gel image. Having obtained contours which reasonably describe the original proteins resolved in the gel, a maxima-minima algorithm is applied to the data enclosed by each contour. In this way, single co-ordinated pairs may be used to describe protein-spot-overlaps. The co-ordinates define the isoelectric point and the molecular weight for each protein. The above results are plotted as a three-dimensional graph of the electropherogram surface (x = pH, y = molecular weight and z = relative intensity).

The raw data, T matrices, contour plot data and three dimension graphic coordinates are then stored on magnetic tape for future reference. Employing such methods of analyses, we have been able to detect some 190 different proteins in a single electrophoretic gel where conventional densitometry or the human eye showed less than 75 species.

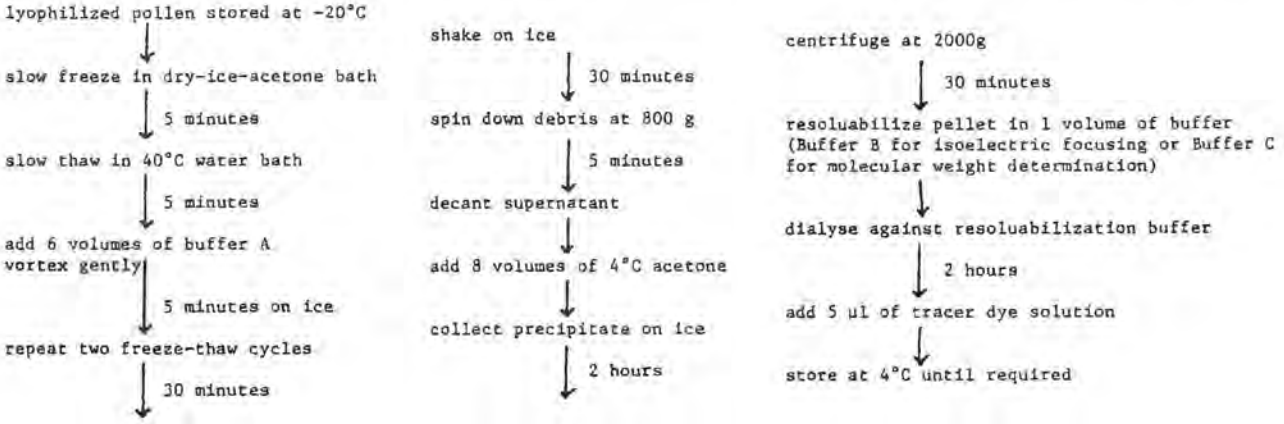
The technique is useful in situations which require the transformation of a complex visual image into a simple enumerative data base.

W. G. Hughes

Two-dimensional electrophoresis of maize proteins: pollen

Our interest in corn pollen is outlined above. Employing microelectrophoretic protein resolution and computerized digital densitometry (contributions 4 and 5), it is possible to analyze extractable protein of anthetic corn pollen. Pollen from a number of cultivars (grown under identical field conditions), was collected according to the schedule: Freshly dehiscent tassel bagged (6 hr maximum); bag carefully removed (1 hr); sieve pollen free of debris through 125 μ mesh (30 min); transfer 10 mg of protein to 5 ml glass test tube; freeze pollen in dry-ice-acetone bath (5 min); lyophilize (24 hr); test tube stoppered, coded and stored at -20° C.

The electrophoretic separation of protein from plant tissue extracts is complicated by other macro-ions indigenous to the plant. Our method of extraction attempts to minimize the presence of such compounds (e.g. aromatic hydrocarbons, starch, fatty acids):



Buffer A consists of: 9 M urea, 3% NP-40 (v/v), 5% 2-mercaptoethanol (v/v), 2.5% carrier ampholytes (pH 3-10, v/v), 3% glycerol (v/v), 1% sodium dodecyl sulphate (w/v), and 1% polyvinyl pyrolidone (w/v). Buffer B is formulated of: 9.0 M urea, 1% NP-40 (v/v), 5% 2-mercaptoethanol (v/v), 2% carrier ampholytes (pH 3-10, v/v), and 3% glycerol (v/v). Buffer C is made by combining: 8 M urea, 20 mM TRIS pH 7.0, 2.5% 2-mercaptoethanol (v/v), 10 mM EDTA, 2% sodium dodecyl sulphate (w/v), and 3% glycerol. The tracer dye solution is .01% Bromophenol blue (w/v), .01% xylene cyanole FF (w/v), in 15% glycerol.

Extracts of two inbred lines (A and B) were selected for electrophoretic protein comparison. Two replicate sets of four gels were used to obtain electrophoretic patterns by isoelectric focusing, molecular weight and two-dimensional separation methods (see contribution 4).

The patterns observed by isoelectric precipitation of lines A and B are nearly identical. Protein is resolved throughout the pH range of 3-10. The largest proportion of protein precipitation is localized in three pH ranges (3-4, 7-8 and 9.5-10). Three variations were identified in the patterns of A and B: two protein bands (pI 3.4 and 4.7) were present in A but not B; one protein band (pI 8.4) was absent in A but not B; line A was resolved into 33 bands, line B into 32 bands.

Molecular weight resolution of lines A and B is carried out over a range of 14 K to 200 K daltons. Most of the proteins are resolved above 60 K daltons. The comparison of line A and B protein band patterns showed that: three protein bands (65 K, 78 K and 130 K daltons molecular weight) are detectable in line A but not B; line B possesses two protein bands (43 K and 200 K daltons molecular weight) which are not found in the pattern of line A; and lines A and B could be resolved into 19 and 17 bands respectively.

Two-dimensional electropherograms of lines A and B showed greater complexity in the patterns and number of protein spots resolved (136 and 135 respectively). In general the resolved patterns of A and B are similar with the following exceptions: three protein species (pI and molecular weight coordinate pairs of 3.3, 130 K daltons, 3.2 and 200 K daltons, 7.0 and 81 K daltons respectively) are present in A but not B; and three protein species (pI and molecular weight coordinate pairs of 8.1 and 40 K daltons, 8.1 and 43 K daltons, 7.9 and 65 K daltons respectively) are present in B but not A.

These results demonstrate the feasibility of characterizing proteins extracted from pollen. We have as yet an incomplete library of such protein landscapes; nevertheless, we have observed differences in the numbers and coordinates of several bands among several stocks. Since these methods can be used with small amounts of tissue, it is possible to study 'landscapes' as a function of growth and differentiation in the sporophyte.

We have found that the pollen from most of the inbreds we have studied: (1) yields repeatable landscapes; and (2) differs at one or more coordinates. Such methods as we report above may provide high resolution identification of stocks, hybrids, seed purity and may be useful in large scale breeding programs.

W. G. Hughes and D. B. Walden

Alterations of several nuclear processes in maize by cycloheximide

Cycloheximide was used to study various aspects of cellular metabolism in root meristem cells of a single-cross hybrid, Seneca-60. Changes in the mitotic index (M.I.) were monitored for up to 8 hours at 30-minute intervals under three different conditions which varied in time or concentration of cycloheximide treatment. In all cases, a peak in mitotic activity occurred early in the treatment which was apparently due to an increase in the number of cells at metaphase. Root tips subjected to 7.5 µg/ml of cycloheximide for either 60 or 120 minutes demonstrated this peak at 60 minutes. Following the peak, the M.I. dropped rapidly to a value

well below the control before recovering to the control value. The time of recovery was much longer for the 120-minute than for the 60-minute treatment. Using a cycloheximide concentration of 75.0 µg/ml for 60 minutes, the M.I. peak occurred at 15 minutes followed by a rapid drop and eventual recovery similar to the 120-minute treatment at the lower cycloheximide concentration.

The very low frequency of anaphases and high frequency of metaphases relative to the control (Table 1) at the peak of mitotic activity was attributed to a block in metaphase which either prevented or decreased the number of cells leaving metaphase. The recovery of anaphases following removal of the chemical further supports this suggestion. The drop in mitotic activity after 60 minutes in the cycloheximide-treated root tips is attributed to a transition point in G2 since the decrease in M.I. was due to a decline in the number of cells entering prophase. The duration of treatment, the length of time before the prophase frequency began to decrease, and the length of time until it reached the minimum value are all very similar between treatments (Table 1) and suggest that in maize, at least one cycloheximide-inducible, G2 transition point is about 1-1.5 hours before the onset of mitosis.

Table 1. Data for mitotic index study of cycloheximide treated maize root tips.

Parameters	CYCLOHEXIMIDE TREATMENT			
	Control	60 min. @ 7.5 µg/ml	120 min. @ 7.5 µg/ml	60 min. @ 75.0 µg/ml
Maximum mitotic index:				
Time (min) from treatment start	60	60	60	15
Mitotic index ± S.E.	7.02 ± 0.14	8.73 ± 0.62	8.73 ± 0.62	8.82 ± 0.21
% Prophase	4.44	5.66	5.66	4.89
% Metaphase	1.06	2.99	2.99	2.16 (2.75 @ 60')
% Anaphase + Telophase	1.52	0.07	0.07	1.72 (0.05 @ 60')
Minimum mitotic index:				
Time (min) from treatment start	30	150	270	180
Mitotic index ± S.E.	6.86 ± 0.20,	5.17 ± 0.77	3.39 ± 0.33	3.35 ± 0.14
% Prophase	3.01	2.73	2.18	1.82
% Metaphase	1.84	1.85	1.05	1.25
% Anaphase + Telophase	2.01	0.61	0.16	0.28
Total recovery time (min)	-	210-240	540-570	540-600
Length of time before prophase frequency begins to decrease (min)	-	90	60-90	60-90
Length of time before prophase frequency reaches minimum (min)	-	60-90	90	60-90

The difference in total recovery time may be due to the disruption of other metabolic processes such as respiration or protein synthesis.

The effects of a 60-minute cycloheximide treatment on ^{14}C-leucine incorporation into proteins were studied at various concentrations of cycloheximide and the percent inhibition is shown in Table 2 for both total and nuclear proteins. Labelling for the last 30 minutes of the cycloheximide treatments with 5.0 µCi/ml of ^{14}C-leucine was found to be suitable. The results indicate a dose-dependent inhibition of label incorporation into proteins. The apparent selective

Table 2. Inhibition of ^{14}C-leucine incorporation into proteins as a function of cycloheximide concentration.

Cycloheximide Concentration (µg/ml)	% Inhibition	
	Total Proteins	Nuclear Proteins
0	0	0
0.75	1.4	5.7
7.5	15.1	55.9
75.0	81.2	61.7
750.0	95.9	76.3

decrease of label incorporation into nuclear proteins at 7.5 µg/ml of cycloheximide suggests that this chemical either selectively inhibits the synthesis of these nuclear proteins or their accumulation in the nucleus following synthesis.

When label incorporation into proteins was monitored under the conditions used in the M.I. studies, it was found that for 75.0 µg/ml of cycloheximide, there was a rapid drop in the incorporation rate in the first 30-60 minutes. Following removal of cycloheximide, recovery of 60-70% of the activity occurred rapidly (about 1 hr), with the remaining recovery taking considerably longer (6-8 hr). Since cycloheximide can inhibit amino acid biosynthesis as well as RNA synthesis, the long recovery period probably represents the time required for the production of these precursors and the re-establishment of normal protein synthetic rates.

An interesting feature noted at a cycloheximide concentration of 75.0 µg/ml, was an elevation in the frequency of variants associated with chromosome structure and organization. At least nine classes were observed in this study and these could be arranged into two groups as shown in Table 3. The frequencies of the variants are shown in Table 4 in which the values represent the mean percent of variants in all metaphases, anaphases and telophases for 3 root tips in each treatment (about 2500 nuclei per root tip). In all cases, the treatment values were significantly higher than the controls and appeared to increase with time of treatment.

Table 3. Classes of cytogenetic variants.

I. Variants of chromosome organization
   1. Metaphase with distinct chromatid separation
   2. Anaphase with visible chromatid separation
   3. Metaphase with random despiralization
   4. Chromosomes with apparent banding

II. Variants of nuclear organization
   1. Anaphase with bridges
   2. Anaphase with laggards
   3. Micronuclei and multiple daughter nuclei
   4. Circular metaphases
   5. Polar metaphases

Table 4. Frequencies of cytogenetic variants (mean % ± S.E.)

I. Variants of chromosome organization

Time (min.)	Control	Treatment
15	2.23 ± 0.41	12.09 ± 0.33
30	2.24 ± 0.47	19.58 ± 1.52
60	1.63 ± 0.29	23.64 ± 0.92

II. Variants of nuclear organization

Time (min.)	Control	Treatment
15	0.90 ± 0.45	5.78 ± 0.87
30	0	11.87 ± 0.52
60	1.14 ± 0.64	13.41 ± 0.59

It is evident from these studies that, shortly after cycloheximide treatment, the frequency of cytogenetic variants increases. Since proteins are involved in the processes of chromosome condensation, movement and organization within the nucleus, the apparent decrease in proteins in the nuclear fraction following cycloheximide treatment may be responsible for the increased variants. An attempt to demonstrate an involvement of decreased nuclear protein levels with enhanced cytogenetic anomalies is presently underway.

C. L. Baszczynski, D. B. Walden and B. G. Atkinson

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A cytoplasmic influence on tassel seed gene

At the University of Georgia, seeds of the long-time maize inbred CI21(Athens) were prepared with the genotype of CI21(A) and the normal cytoplasms of inbreds GA199, GT112 and CI21(A) separately in backcross programs. Similarly, GT112 inbred seeds were also prepared in simultaneous backcross programs. At the end of the backcross programs, each inbred was selfed for several generations. Thus, each lot of seed had either the CI21(A) or the GT112 nuclear genotype in a homozygous condition with a different cytoplasm. A pedigree analysis of each of these long-time inbreds clearly shows that these inbreds are unrelated either nuclearly or cytoplasmically.

Seeds from several selfed plants within each cytoplasmic source were harvested in 1978 at the University of Georgia and were planted on Texas Tech University research farm for seed increase. During the month of August, tassels with silks were observed for the first time in these cytoplasmic stocks. The tassel silks were terminal in position and present only on the tillers. The percentages of plants with tassel silks were as follows:

Cytoplasmic Source	%
GT112 x CI21(A)^8	54
GA199 x CI21(A)^8	61
CI21(A) selfed	29.6

The data indicate that the CI21(A) nuclear genotype in its own cytoplasm produced fewer tassel silks than in GA199 or GT112 cytoplasms. The latter cytoplasms provided more favorable environment for 'ts' gene to express most. Apparently, the 'ts' gene is under the control of CI21(A) nuclear genotype and environment in these inbreds. Presumably, differences in auxin concentration levels, particularly during the later part of growth period, might be the basis for production of tassel seeds on the tillers alone but not on the main stalks. Other cytoplasmic sources with GT112 nuclear genotype did not produce any tassel silks.

Arelli P. Rao, John C. Bickel and A. A. Fleming

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Punjab Agricultural University

Genetic variation for protein concentration in a random mating opaque-2 variety of maize

The variability for protein concentration in a composite cultivar named "Rattan" was studied using half sib and full sib progenies developed by following nested mating design (Design-1 of Comstock and Robinson, Biometrics 4:254-266, 1948). Sixty-four plants were selected at random and each as a male was crossed to four randomly taken plants used as females, making 64 half sibs and 256 full sibs. These were grown in two agro-climatically different locations in an incomplete block design with two replications.

Table 1. The estimates of various variance components along with standard errors

Variance components	Pooled	Location I	Location II
Additive genetic	0.01 ± 0.12	-0.19 ± 0.17	-0.71 ± 0.32
Dominance	-0.03 ± 0.33	1.86 ± 0.44**	4.53 ± 0.94**
Additive x environment	-0.40 ± 2.40	-	-
Dominance x environment	3.80 ± 0.96**	-	-

**Significant at 1 percent probability level

Perusal of Table 1 indicates that only dominance variance component was significant in the individual locations analysis. However, in the pooled analysis the only component that was significant was due to dominance x environment interaction. Negative estimates were also obtained contrary to the theoretical expectations. The results indicated that the population is not suited for protein improvement through intra-population selection. It may be added that remarkable progress has been made in the manipulation of protein concentration in "Burr White" in a classical long-term selection experiment at Illinois (Dudley, pp. 459-473, in Proc. Internat. Conf. Quant. Genetics, Pollak et al., eds., Iowa State Univ. Press, Ames, 1977).

S. S. Pal, A. S. Khehra, B. S. Dhillon and K. S. Sekhon

Correlated response for maydis leaf blight incidence in a maize population improved for brown stripe downy mildew resistance

An open-pollinated maize population 'Makki Safed 1' was subjected to two cycles of mass (both sexes) and one cycle of full-sib selection. The selection was primarily carried out for the resistance to brown stripe downy mildew, caused by Sclerophthora rayssiae var. zeae, the other traits kept in view being grain yield, height and standability. The improved population showed a remarkable improvement over the original for the reaction to brown stripe downy mildew, 1.5 against 4.5 on a 1 (good) to 5 (poor) scale. A correlated response for maydis leaf blight, caused by Helminthosporium maydis, was also observed. The ratings were 2.2 of the improved version against 3.2 of the original population (1-5 scale), under artificial inoculation, based on replicated trials conducted over two years.

A. S. Khehra, V. K. Saxena, S. C. Sharma, N. S. Malhi and S. S. Pal

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University of Wisconsin

gay, a new mutant in chromosome 1

Recessive mutations conditioning a germless, anthocyaninless and carotenoidless kernel phenotype have arisen in our colored aleurone stocks three different times since 1974. All three mutations proved to be allelic. Kernels carrying the new mutation, termed gay (g = germless; a = anthocyaninless; y = non-yellow), lack a discernible embryo but possess a variably developed, chalky white endosperm. The endosperm in these kernels does develop sufficiently to allow expression of characters like sh and wx.

The first instance of gay arose in a stock which was segregating coincidentally for variants at the P locus. A very strong linkage between P and gay immediately became evident. Subsequent crosses of gay/+ heterozygotes to TB-1Sb revealed that gay was uncovered by this translocation. Since Neuffer had described (personal communication and MNL 52:87, 89) mutants with similar phenotype mapping to 1S, allelism tests were conducted between gay and Neuffer's mutants E628A, E792, E1348, E1394 and E1401. (Ed. note: The symbol clf was assigned to the 1S factor in Neuffer, 1978, pp. 579-600 in D. B. Walden, ed., Maize Breeding and Genetics.) These tests established allelism between gay and Neuffer's mutants E792, E1348, E1394 and E1401, but not E628A.

Subsequently, the following 3-point cross was performed: (P-WR gay) + / (P-WW +) zb4 x (P-WW +) zb4. Normal (i.e., non-gay) kernels from the above backcross were planted and the resulting plants were scored for zb4 and for gay segregation and P after selfing. The 3-point data and the map constructed from them are given below.

P-WR gay +	P-WW + zb4	P-WR gay zb4	P-WW + +	P-WW gay zb4
51	50	3	5	1

Genetic map: 1 S (centromere) -- gay 0.8 P 7 zb4

The estimated distance between P and zb4 is in excellent agreement with that published in "The Mutants of Maize" (Neuffer, Jones and Zuber). Further 2-point data can be used to obtain a better estimate of the gay-P distance. The following F2 progeny from gay P-WR/+ P-WW plants has been fully classified: 104 P-WW +/ P-WW +; 22 P-WR gay/P-WW + (resolved by F3 testing), and 2 P-WR +/P-WW + (by F3 testing). The fraction of strands recombinant between P and gay is 2/256 or 0.78%. If the backcross and F2 data are pooled this fraction is 3/366 or 0.82%. Therefore, the best estimate of the distance between P and gay is 0.8 map units.

Hugo K. Dooner

Translocation of ^{14}C-compounds from maternal tissue into maize seeds grown in vitro: A test of a hypothesis concerning the absence of auxotrophs in higher plants

Translocation of various ^{14}C-compounds from maternal tissue into developing maize seeds was examined by using caryopsis cultures (Gengenbach, 1977, Planta 134:191) in order to test a hypothesis that the absence of auxotrophs in higher plants is due to inadequate translocation of essential compounds from maternal tissue to developing seeds. Fertilized zygotes homozygous for a mutant in a locus coding for a step in the synthesis of an essential compound have to receive the missing metabolite from the maternal tissue to survive to a dormant stage. Therefore, a lack of adequate translocation of the metabolites from the maternal tissue to developing seeds would lead to the death of mutant zygotes.

Ears of inbred W22 (5DAP) were cut into cob blocks containing four caryopses, grown on the standard medium for 10 days, transferred onto ^{14}C-containing medium, and incubated for 7 days. Five cob blocks were placed on the medium (50 ml) in a 125 ml Erlenmeyer flask, and duplicate flasks were used for each compound. At harvest, the five cob blocks within each flask were bottled for processing. The material was divided into four tissue groups; embryo, endosperm, pericarp and pedicel, and cob were dried, ground to powder, and radioactivities counted by using a liquid scintillation counter.

Table 1 shows total uptake of ^{14}C-compounds by cultured cob blocks. The tested compounds can be grouped into three distinct classes according to their relative efficiencies of uptake into the cultured cob blocks. The first class of compounds which was most efficiently taken up into the cultured tissue includes the three

Table 1

Total ^{14}C Uptake by Cultured Cob Blocks

^{14}C Compound	Total ^{14}C Added ($\frac{cpm \times 10^{-6}}{flask}$)	Total Amounts ($\frac{nmole}{flask}$)	Specific Activity ($\frac{cpm}{nmole}$)	Total ^{14}C Taken Up ($cpm \times 10^{-4}$)		Total Uptake (nmole /flask)		Total Uptake (nmole/g D.W.)		% Total ^{14}C Taken Up/g D.W.	
				Fl. 1	Fl. 2	Fl. 1	Fl. 2	Fl. 1	Fl. 2	Fl. 1	Fl. 2
Sucrose	27.8	7.3×10^6	3.8×10^6	18.0	17.3	4.7×10^4	4.5×10^4	1.1×10^5	1.0×10^5	1.5	1.4
Fructose	23.1	62	3.7×10^{11}	51.2	ND	1.38	ND	2.7	ND	4.4	ND
Leucine	16.5	152	1.0×10^{11}	163.9	161.7	14.90	14.70	41.0	29.4	27.3	19.3
Phenylalanine	28.7	30	9.6×10^{11}	383.4	454.4	4.00	4.73	7.8	9.0	26.0	30.0
Proline	10.8	19	5.7×10^{11}	103.9	126.6	1.82	2.22	4.2	5.7	22.1	30.0
Adenine	11.9	107	1.1×10^{11}	190.2	185.2	17.29	16.83	31.9	31.0	29.8	29.0
Thymine	13.5	128	1.1×10^{11}	3.9	3.9	0.35	0.35	0.7	0.8	0.5	0.6
Thiamine HCl	11.2	289	3.9×10^{10}	29.2	41.6	7.49	10.67	17.5	20.7	6.1	7.2
Nicotinic acid	9.1	75	1.2×10^{11}	105.6	110.5	8.80	9.21	20.1	18.8	26.8	25.1

amino acids tested, adenine, and nicotinic acid. The second group having the intermediate degree of uptake consists of fructose and thiamine HCl. Thymine, characterized by its extremely low efficiency of uptake, can be included in the third class. Because the amount of sucrose in the medium was approximately five orders of magnitude higher than other compounds, this compound was not grouped into the three classes mentioned above.

Table 2 shows the distribution of ^{14}C in various tissues of cultured cob blocks. Each compound had a characteristic pattern of ^{14}C distribution between different tissues. For instance, sucrose and fructose had a gradient of increasing ^{14}C concentration in the order of cob-pericarp and pedicel-endosperm-embryo. However, for leucine and phenylalanine, this order was completely reversed. The rest of the compounds tested had an order, endosperm-embryo-pericarp and pedicel-cob from low to high. Nonetheless, the considerable enrichment of ^{14}C in the cob and the pericarp and pedicel was also found for these compounds. To obtain an idea of relative concentration of ^{14}C in various tissues, ratios of ^{14}C concentrations between different tissues are shown in the right half of Table 2. For example, the endosperm had approximately five times more counts than the cob when ^{14}C-sucrose or ^{14}C-fructose was supplied. Conversely, the cob accumulated 10-50 times greater amounts of ^{14}C than the endosperm did when amino acids, adenine, or vitamins were supplied. When the ratios of ^{14}C concentrations between the endosperm and the embryo were examined, the unique aspect of thiamine HCl became apparent. This compound was almost ten times higher in the embryo than in the endosperm.

Table 2

Distribution of ^{14}C in Various Tissues

^{14}C compound	Flask	Total ^{14}C Uptake (cpm/mg DW) Cob	Per & Ped	Endo	Emb	Ratio of ^{14}C Concentration Between Tissues Per & Ped/Cob	Endo/Cob	Emb/Endo	Emb & Endo/Cob
Sucrose	1	174	276	818	2624	1.59	4.70	2.47	5.05
	2	169	246	845	2854	1.46	5.00	3.38	5.46
Mean		172	261	832	2439	1.52	4.84	2.92	5.26
Fructose	1	378	497	1804	3423	1.31	4.77	1.90	5.03
Leucine	1	11927	2602	1085	660	0.22	0.09	0.61	0.09
	2	9875	1860	828	631	0.19	0.08	0.76	0.09
Mean		10901	4462	957	646	0.20	0.09	0.69	0.09
Phenylalanine	1	19526	3964	1476	1061	0.20	0.08	0.72	0.07
	2	19812	5487	2501	1890	0.28	0.13	0.76	0.12
Mean		19669	4726	1989	1476	0.24	0.10	0.74	0.10
Proline	1	6860	1860	363	437	0.27	0.05	1.20	0.05
	2	7504	2355	342	405	0.31	0.05	1.18	0.05
Mean		7182	2108	353	421	0.29	0.05	1.19	0.05
Adenine	1	8209	3626	183	210	0.44	0.02	1.15	0.02
	2	7504	2762	161	203	0.37	0.02	1.26	0.02
Mean		7857	3144	172	207	0.41	0.02	1.21	0.02
Thymine	1	104	83	53	121	0.80	0.51	2.28	0.57
	2	124	70	49	144	0.56	0.40	2.94	0.48
Mean		114	77	51	133	0.78	0.45	2.61	0.53
Thiamine HCl	1	1310	553	74	683	0.42	0.06	9.23	0.09
	2	1634	952	95	954	0.58	0.06	9.95	0.10
Mean		1472	753	85	814	0.50	0.06	9.59	0.10
Nicotinic Acid	1	3642	2969	518	876	0.81	0.14	1.69	0.15
	2	3990	2833	506	1061	0.71	0.13	2.07	0.14
Mean		3817	2901	512	969	0.76	0.13	1.88	0.14

Distribution of ^{14}C among various compounds in water or 5% TCA extracts from cultured tissues was analyzed by paper chromatography, and the results are shown in Tables 3-5. After the entry into the cob tissue, vitamins appeared to experience little conversion (Table 3). For instance, the counts supplied as nicotinic acid remained in nicotinic acid in the cob tissue. Similarly, approximately 80% of total ^{14}C in cob extracts was recovered as thiamine HCl. This was also true in the endosperm and embryo extracts. A limited amount of conversion of adenine and thymine in the cob was

Table 3

Distribution of ^{14}C Among Various Compounds in Tissue Extracts: Nucleic Acid Bases and Vitamins

^{14}C Compound Added in the Medium	Tissue	% Total ^{14}C in Extracts: Original Form	Phosphory. Nucleosides	Total
Adenine	Cob	31.0	55.2	86.2
	Endo	43.9	56.1	100.0
Thymine	Cob	52.6	15.5	68.1
	Endo	34.3	27.3	61.6
Thiamine HCl	Cob	70.9		
	Endo	85.1		
	Emb	81.0		
Nicotinic Acid	Cob	100.0		

Table 4

Distribution of ^{14}C Among Various Compounds in Tissue Extracts: Amino Acids

^{14}C Compound Added In the Medium	Tissue	% Total ^{14}C in Extracts								
		Original Form	Amino* Acids	Amino** Acids	Sub-Total	Sucrose	Glucose	Fructose	Sub-Total	Total
Leucine	Cob	29.5	6.1	9.2	44.8	3.1	2.2	3.9	9.2	54.0
	Endo	31.4	3.8	6.1	41.3	4.9	3.8	6.1	14.8	56.1
Phenylalanine	Cob	23.9	6.6	8.8	39.3	3.9	3.3	13.9	21.1	60.4
	Endo	23.2	6.8	6.8	36.3	5.7	4.0	5.3	15.0	51.8
Proline	Cob	18.7	18.5	11.0	48.2	10.9	10.9	6.5	28.3	76.5
	Endo	31.4	21.5	13.0	65.9	6.6	7.6	5.9	20.1	86.0

*Aspartic acid and some others.

**Glutamic acid and some others.

Table 5

Distribution of ^{14}C Among Various Compounds in Tissue Extracts: Sugars

^{14}C Compound Added in the Medium	Tissue	% Total ^{14}C in Extracts							
		Sucrose	Glucose	Fructose	Sub-Total	Amino* Acids	Amino** Acids	Sub-Total	Sum Total
Sucrose	Cob	4.7	2.3	9.4	16.4	9.2	14.9	24.1	40.5
	Endo	10.0	12.7	15.8	38.5	15.1	27.2	42.3	80.8
Fructose	Cob	6.0	2.9	17.9	26.8	7.1	20.6	27.7	54.5
	Endo	8.0	11.3	13.2	32.5	13.7	22.3	36.0	68.5

*Aspartic acid and some others.

**Glutamic acid and some others.

observed (Table 3). Corresponding phosphorylated nucleosides were the only compounds which had appreciable ^{14}C other than the original compounds. In contrast, amino acids were often converted to other compounds within the cob tissue (Table 4). Approximately 20% of total ^{14}C activity in the cob and endosperm extracts was recovered as the amino acids supplied. In addition, the ^{14}C label was also found in other amino acids and simple sugars. Among the amino acids derived from originally supplied ones, aspartic acid (also possibly glycine and alanine) and glutamic acid (also possibly arginine) were found in greatest amounts. They were tentatively identified based on their color reactions and Rf values. As expected,

sucrose and fructose were converted to a variety of compounds in the cob tissue although 16 and 27% of ^{14}C was still found in simple sugars where ^{14}C-sucrose and ^{14}C-fructose, respectively, were fed (Table 5).

Based on relative ^{14}C concentrations in the cob and the endosperm, it is concluded that the translocation of the vitamins, thiamine HCl and nicotinic acid, from the cob to the endosperm is strongly inhibited in in vitro conditions. Nucleic acid bases and their phosphorylated nucleosides appeared also poorly translocated into the endosperm through the cob tissue.

Due to extensive metabolic conversions observed in the cob during the culture period, the observations of the translocation of amino acids should be evaluated with caution. With regard to compounds converted from an amino acid taken up into the cob, they would be grouped into two classes according to their properties of translocation. The first class includes those compounds which have similar or lower relative efficiencies of translocation from the cob to the endosperm. Presumably, amino acids derived from the originally labeled one would be in this class. Also, intermediates in catabolic processes could possibly be included in this class. This class of compounds would be a major class of converted labeled compounds and would not considerably affect the endo/cob ^{14}C ratio. The second class of compounds derived from a labeled amino acid would be those that are more easily transported into the endosperm through the cob than the originally labeled amino acid. Simple sugars would be included in this category. This class of labeled compounds is a minor group of derivatives but increases the endo/cob ^{14}C ratio of an originally labeled amino acid. Based on above discussions, the efficiency of translocation for amino acids deduced from the relative enrichment of ^{14}C labels in the endosperm and the cob could possibly be overestimates. Therefore, it is not unreasonable to conclude that there is also a strong translocation barrier between the cob and the endosperm for amino acids in in vitro conditions.

Supposing that a similar restriction of translocation operates in vivo, the results suggest the following: 1) Most (or all) of nutritionally essential compounds other than simple sugars are subjected to a strong inhibition of translocation from maternal tissue to the seeds. This inhibition may be strong enough to prevent the development of mutant zygotes lacking the capacity to synthesize a vital metabolite to a mature dormant seed. 2) That thiamine auxotrophs are the only obligate auxotrophs known in higher plants may be partly explained by the concentration of thiamine HCl in the embryo. Although the translocation of this compound from the cob to the endosperm is no better than that of other compounds, this vitamin is accumulated in the embryo almost ten times more efficiently than in the endosperm. In addition, the small requirement for vitamins for normal growth compared with amino acids or nucleic acid precursors may possibly be an additional factor explaining the presence of thiamine auxotrophs in higher plants.

Ko Shimamoto and Oliver E. Nelson

Location of indeterminate gametophyte (ig) on chromosome 3

A set of chromosome-9, waxy translocations furnished by the Maize Cooperation Stock Center was used to place ig to a chromosome arm. To score ig, advantage was taken of the fact that many female gametophytes carrying it yield kernels of reduced size (miniature kernel class). Because this trait is incompletely penetrant, full-sized kernels present in the backcross populations could have inherited ig or Ig. Kernels of the miniature class, however, can reasonably be assumed to carry ig. Linkage would cause a deficit below 50% of waxy kernels within the miniature class. All of the translocations tested gave an acceptable fit to 1 Wx:1 wx except for a moderate deficit in the waxy class for two chromosome 6 translocations and a marked deficit for two 3L stocks. The following data for

these four translocations were obtained from crosses of the type (T wx Ig/(N Wx ig) x wx wx Ig Ig:

Translocation	Breakpoints	Waxy among miniature	
		Proportion	%
T6-9a	6S.79; 9L.40	89/223	39.9
T6-9b	6L.10; 9S.37	95/255	37.3
T3-9c	3L.09; 9L.12	19/153	12.4
T3-9(8562)	3L.65; 9L.22	42/148	28.4

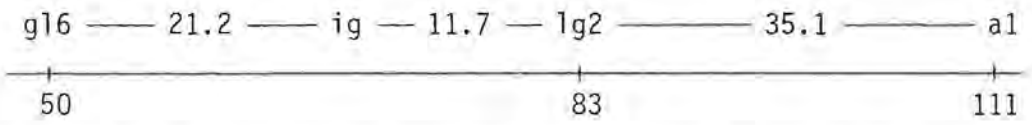
Further tests focused on chromosome 3 because a moderate deficit of waxy kernels involving the chromosome 6 backcrosses could be explained by functioning of aneuploid gametes.

A two-point test of linkage involving lg2 in repulsion with ig yielded 226 miniature kernels. Of these, 24 or 10.6% gave liguleless seedlings, indicating linkage.

Four-point linkage data were obtained utilizing the Coop's gl6 lg2 a1 tester. Because size was highly variable in the backcross kernel population produced by pollinating heterozygotes with the tester, it was not possible in this case to identify an ig carrying class on the basis of this trait. Alternatively, the induction of multiple seedlings by ig was utilized. Among 4699 kernels sprouted, 365 yielded multiple seedlings of which 359 sets could be scored for both gl6 and lg2. Because multiple seedlings induced by ig derive from a single embryo sac, members of one set are expected to be identical with respect to the heterozygous markers. Each set therefore tests only one gamete. The 359 sets gave the following distribution:

	Gl Lg	Gl lg	gl Lg	gl lg
A	144	7	57	3
a	103	29	13	3

The critical recombination values are given below in conjunction with the standard map locations of gl6 lg2 and a1.



Placing ig proximal to lg2 gives good linear additivity, with only six cases classified as double crossovers in the gl6 - ig - lg2 interval. Combining the available two and four-point data gives 66/585 or 11.3% recombination between ig and lg2.

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Gametophyte competitive ability in maize: haploid determination and effects on the sporophytic progeny

Gametophytic expression of many genes has been shown in higher plants (E. Ottaviano and M. Sari Gorla, Israeli-Italian Joint Meeting on Genetics and Breeding in Crop Plants, Rome, pp. 89-106, 1979). Direct proof of this phenomenon is obtained when genetical variability is expressed within the pollen population produced by a single heterozygous plant. In maize this has been observed with regard to genes controlling either the reproductive system or sporophytic traits. Some components of the male gametophyte competitive ability are affected by haploid genetic effects. Gametophyte variability resulting from haploid gene expression may play an important role in natural selection, particularly if the phenomenon is related to genes expressed both in sporophytic and gametophytic phase. In maize a positive correlation between pollen competitive ability and values of sporophytic metrical traits has been shown (D. L. Mulcahy, Science 171:1155-1156, 1971 and Nature 249:491-492, 1974). However, in order to evaluate the relative importance of the sporophytic and gametophytic determination of this association, a selection for gametophyte competitive ability experiment was performed, and the correlations between gametophytic and sporophytic traits were evaluated.

The selection for gametophyte competitive ability is based on the different length of the silks from the apex to the ovaries, according to the position of the flower on the ear: the distance decreases from the base flowers upwards. Thus, the probability of fertilization of the most competitive gametophyte, especially if this is due to the pollen tube growth rate, increases from the apex downwards. The Long Ear Synthetic population was used as basic material. From full fertilized ears, two samples of 40 kernels were taken: one from the top and the other from the base. The remaining kernels were discarded. The lines of the first group were reproduced using top kernels, for three selfing generations, while those of the second group were developed using base kernels. The choice of plants for reproduction was random: selection for plant traits was carefully avoided.

The evaluation of pollen competitive ability was carried out using pollen produced by S3 plants and by means of the pollen mixture technique. Pollen of each line (5 of the first group and 7 of the second) was mixed with an equal volume of pollen of an inbred (W22) with colored aleurone, which was taken as a standard. The mixture was used to pollinate plants of an unrelated F1 (A632 x Mo17) with uncolored aleurone. Ten fully fertilized ears of each line were considered. Each of these was divided into five segments of equal length and scored for aleurone color. The competitive ability, in relation to that of W22, of each selected line was evaluated as variation of the frequency of uncolored kernels from apex to base of the ear. Accordingly, it was estimated as linear regression coefficient of P (proportion of uncolored kernels) on ear segments: a positive value indicates a competitive ability greater than that of the standard. Because the dependent variable is a proportion, referred to binomial data, the method of Armitage was adopted.

Kernel weight and seedling dry weight were considered as sporophytic traits. Kernels from the medium segment of each ear were weighed and sown in the greenhouse for evaluation of seedling weight at two weeks from emergence. For this trial three complete randomized blocks, with plots of ten seedlings, were used.

Table 1 shows the values of the selected S3 lines with regard to gametophyte competitive ability and sporophytic traits in hybrid combination. Positive values of the regression coefficient indicate a gametophyte competitive ability of the selected lines greater than that of the standard (W22). Six of the seven S3 lines

Table 1. GAMETOPHYTIC COMPETITIVE ABILITY AND SPOROPHYTIC VALUE OF S_3 LINES

	LINES	GAMETOPHYTIC TRAITS		SPOROPHYTIC TRAITS IN HYBRID COMBINATION	
		b x 100	r	10-seedlings dry wt. (g)	kernel wt. (g)
Ear base progeny	1	5.39	.99	1.11	.336
	2	3.86	.97	1.18	.370
	3	3.63	.95	1.04	.358
	4	2.39	.97	.91	.308
	5	-3.95	-.93	.93	.297
	6	2.43	.93	.78	.318
	7	2.40	.75	.91	.355
	m	2.31		.98	.335
Ear top progeny	1	-3.47	-.97	.68	.298
	2	-3.28	-.89	.98	.297
	3	.54	.37	.96	.353
	4	1.65	.91	1.03	.344
	5	- .20	.10	.93	.310
	m	-0.95		.91	.320
	d			.07*	.015*
	d%			7.6	4.7

m : means
d : differences
* : significant difference ($P < .05$)
r is reported as an index of the amount of the variability of P (proportion of uncolored kernels) linearly related with sector.

obtained from the base of the ear proved to be more competitive than the standard, and one less competitive. A different situation is observed with regard to the lines obtained from apical kernels: competitive ability of S3 lines was less than that of the standard in two cases, in another two about the same, while in the case of only one line was slightly greater. Clearly the choice of kernels from the base or from the apex of the ear led to the formation of two groups of lines differing in male gametophyte competitive value: the long styles of the basal flowers enable the gametophyte with the higher tube growth rate to be selected. The breeding method used operates essentially on within-plant variability, therefore the observed response to selection is a direct proof that haploid expression of genes is an important factor controlling pollen tube growth.

The hybrid progeny of the first S3-line groups (from ear base kernels) proved to have greater kernel and dry seedling mean weights: there was a positive association between differences in gametophyte competitive ability and differences between sporophytic traits. Because gametophyte competitive ability and sporophytic traits were evaluated in separate experiments, the association has to be interpreted as due to genetical causes, arising from linkage and/or pleiotropy. Since the basic material consisted in an open pollinated population, where linkage between sporophytic and gametophytic factors should tend to the equilibrium, it can be concluded that one of the most important factors giving rise to the observed association is the effect of genes expressed both in the haploid and the diploid phase.

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Isolation of the individual constituent genes of the anthocyanin gene cluster at the R locus in R-ch

It was earlier reported (MGCNL 49:43-46, 1975) that the R region in R-ch alleles, controlling anthocyanin pigmentation in various seed and plant tissues, consists of a battery of duplicate genes each producing anthocyanin pigmentation but differing in tissue specificities which coincide with various developmental stages of the plant. Topographical maps of this region in two R-ch isolates were prepared from recombinational analysis from test cross data.

Attempts were made subsequently to isolate from the Ecuador R-ch stock, individual recombinants carrying one or more of the constituent duplicate genes of the R-ch region in each. We have been able to identify and multiply such isolates from colorless seeds from selfed ears of the G R-ch/g r-g heterozygote. These results finally confirm and establish the para-allelic nature of the constituent genes. The gene sequence and map distances for nine members, Au, Ch, Si, Nr, Lc, P, Lm, Glm and S, are as follows:

G....S....P 0.42 Glm 0.42 Lm 0.78 Lc 0.71 Nr 1.01 Si 0.89 Ch 1.20 Au

This sequence and map distances generally correspond to the earlier one worked out from test cross data excepting for the relative positions of Au and Si.

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Visualization of sister-chromatid exchanges in maize mitotic chromosomes utilizing 5-bromodeoxyuridine

We have recently applied the fluorescence plus Giemsa technique to maize root-tip somatic chromosomes to visualize sister-chromatid exchanges (SCE's). Several different lines of corn have been used successfully with the protocol given below.

Kernels were germinated in the dark at 27° C. Primary roots about 2-3 cm long still attached to the kernel were immersed in an aqueous solution containing 300 μM 5-bromodeoxyuridine, 0.1 μM 5-fluorodeoxyuridine, and 5 μM uridine for one cell cycle (8.8 hr). They were then transferred to an aqueous solution containing 300 μM thymidine and 5 μM uridine for a second cell cycle. After the above treatment, roots were excised and treated with a 0.002 M 8-hydroxyquinoline solution for 3 hr, and then fixed in an ethanol-acetic acid (3:1 v/v) solution. Root-tips were stored in the fixative at -22° C. All treatments were carried out in the dark or under a safelight equipped with a Kodak OC filter at 27° C. After fixation, the roots were washed in a citric acid buffer (0.01 M, pH 4.7) and incubated for 60 min at 27° C with 0.5% pectinase (Sigma Chemical Co.) dissolved in the same buffer. Meristematic regions of root-tips were placed on a glass slide and macerated in 45% acetic acid. The coverslips were removed using dry ice and the preparations were passed through a 100, 95, 85, 70, 50, and 30% ethanol (v/v) series to distilled water. The slides were incubated for 60 min at 27° C in a RNase solution made up of 10 ml of 0.5xSSC (sodium saline citrate) containing 1 mg ribonuclease A type 1-A from bovine pancreas (Sigma Chemical Co.). The slides were then rinsed with 0.5xSSC and treated with a Hoechst 33258 solution in 0.5xSSC for 25 minutes at the same temperature. The Hoechst 33258 solution was prepared by dissolving 1 mg of the fluorochrome in 1 ml of absolute ethanol and 0.1 ml of this solution was added to 200 ml of 0.5xSSC. A drop of 0.5 SSC was placed on the slide, a cover glass was placed over the cells, and the cover glass was sealed with rubber cement. The slides were then placed 10 cm from a fluorescent sun lamp (Westinghouse FS 20) for 13 hr. After exposure, slides were incubated at 55° C in 0.5xSSC for 1.5 hr, stained with 3% Giemsa stain in phosphate buffer at pH 6.8 for 8 minutes, and washed in the same buffer, air dried, and mounted in Permount (Fisher).

After this treatment, the unifiliary substituted chromatid can clearly be distinguished from the unsubstituted chromatid of each chromosome and sister-chromatid exchanges are easily identified.

Black Mexican sweet corn without B chromosomes has been examined. of 390 chromosomes, 59 had one, 13 had two, and one had three sister chromatid exchanges. Thus, 88 SCE's were present in 390 chromosomes scored giving a frequency of 0.22 SCE's per chromosome.

Tau-San Chou and David Weber

Using compound B-A translocations in maize to segment chromosomes

The synthesis and use of compound B-A translocations has been described by Rahka and Robertson (Genetics 65:223-240, 1970). To date, they have been utilized almost exclusively to uncover regions in specific chromosome arms for which no simple B-A translocation was previously available. Both simple and compound B-A translocations have been extremely valuable in mapping genes to chromosome arms and for altering gene dosage in specific chromosomal segments.

The construction of a series of compound B-A translocations for a specific chromosome arm using a single precursor B-A translocation could provide a powerful tool for mapping genes within a specific chromosome arm and in testing for dosage effects for specific segments of that chromosome arm. Such a series can be generated by crossing plants containing a simple B-A translocation with plants containing reciprocal A-A translocations which have one of their breakpoints distal to the breakpoint in the A chromosome of the B-A translocation. For instance, one could cross a TB-5La plant (breakpoint in chromosome 5 is at 0.1 in the long arm) with T3-5(8528) which has its breakpoint in 5L at .72. When recombination occurs in 5L between the breakpoints, a chromosome is generated which contains a B centromere, proximal B chromatin, chromosome 5L between the two breakpoints in chromosome 5 (0.1L to 0.72L) and a segment of chromosome 3. When this plant is crossed as a male and the B centromere undergoes nondisjunction during the second microspore division, the number of copies of the segment of chromosome 5 between .1L and .72L is altered. When TB-5La chromosome undergoes nondisjunction, the entire segment distal to 0.1 is altered in gene dosage. The segment distal to 0.72 is unaltered in gene dosage in the former case while it is altered in the latter. By comparing these two, one can determine if a given gene is located proximal or distal to 0.72 in 5L. These can also be used for gene dosage comparisons.

Given a series of such translocations involving a common A chromosome, it would be possible to assign genes to specific segments of a given chromosome arm. This would be an extremely efficient method to place genes previously located to a specific chromosome arm with simple B-A translocations.

We have undertaken the production of a series of compound translocations for the long arm of chromosome 5. Presumptive compound translocation-containing kernels with segments of 5L between breakpoints 0.1 and 0.21, 0.48, 0.57, 0.60, 0.61, 0.72, and 0.87 have been recovered. We are in the process of further genetic and cytological verification of these as well as increasing them. We hope to illustrate the usefulness of this series of compound translocations in the manner discussed above.

We have determined that there is a dosage-dependent factor distal to the breakpoint of TB-5La which significantly alters the amounts of oleic and linoleic acid in maize embryos (Shadley and Weber, Can. J. Genet. Cytol. 22:11-19, 1980). The compound translocations we are generating are being utilized to further define the location of the factor(s) responsible for this alteration.

Several new mutations have been induced with ethyl methane sulfonate by Neuffer which are uncovered by TB-5La. We will be assigning these mutants to specific chromosomal segments utilizing this new series of compound translocations. If any additional unplaced mutants are available which are uncovered by TB-5La, we would

appreciate it if they could be forwarded to us. Hopefully, the results will bear witness to the usefulness of such translocation stocks and lead to the generation of further series of compound translocations for other chromosome arms.

Jeff Shadley and David Weber

Proof that univalent chromosomes undergoing equational division at anaphase I are not lost during the second meiotic division

Monosomics in a diploid organism are ideal for characterizing the behavior of univalent chromosomes because each meiotic cell contains a univalent chromosome. We have isolated microsporocyte samples from all monosomic types except monosomics 3 and 5 and have carried out extensive analyses of the meiotic behavior in each of the different available monosomic types.

From these studies, it is clear that univalent chromosomes can undergo equational division at the first anaphase and the resultant monads are not lost during the remainder of meiosis.

Prophase II cells were analyzed to determine the frequency of cells containing 9 dyads and 1 monad in each of the resultant prophase II cells from a single microspore mother cell. Four-hundred-fifty-three prophase II cell pairs were analyzed from six different monosomic-seven plants and 53.1 ± 5.4% of the cell pairs contained 9 dyads in one cell and 10 in the other (9-10 cell pairs). Nine dyads and 1 monad were found in each of the two sister prophase II cells in 19.1 ± 1.7% of the pairs (9+U-9+U cell pairs), and nine dyads were found in each of the two sister prophase II cells in 27.8 ± 5.9% of the prophase II cell pairs (9-9). The first class is produced when the univalent passes undivided to one of the poles at anaphase I, the second when the univalent divides equationally and a half-univalent (monad) passes to each pole, and the third when the univalent is not incorporated into either cell.

If the monads were lost before the quartet matured, only the 9-10 prophase II cell pairs could produce viable mature pollen. Because the single chromosome 7 would be incorporated into only two of the four members of a quartet, the pollen fertility of such a plant would be predicted to be no higher than 53.1%/2 or 26.6%.

If, on the other hand, monads were not lost but were incorporated before the quartet matured, both the 9-10 prophase II cell pairs and the 9+U-9+U types would produce viable pollen. In this case, the predicted pollen viability would be no higher than (53.1% + 19.1%)/2 or 36.1%.

The actual pollen fertility determined for four monosomic 7 plants (14,295 pollen grains scored) is 36.9%. This value is remarkably close to the estimated value of 36.1% if the equationally divided univalents were not lost. Clearly, the univalents which underwent equational division at anaphase I were not lost during later stages of meiosis. Similar results were obtained for other monosomic types.

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An electron microscopic study of two meiotic mutants

Meiosis was studied in more detail in the maize mutant afd. It was found that the first division of meiosis resembles mitosis proceeding abnormally with pulverization and fragmentation of chromosomes at the stage of anaphase I. This indicates that afd affects the intimate mechanisms of meiotic recombination (Table 1).

Table 1. The pattern of meiotic irregularities in homozygous afd plants

Meiotic stage	Normal cells		Abnormal cells: Chromosome pulverization and micronuclei formation		Abnormal cells: Chromosome fragmentation and microfragment formation		Total number of cells examined
	Number	%	Number	%	Number	%	
Anaphase I	42	26.6	104	67.0	10	6.4	156
Interkinesis	170	61.7	100	36.6	10	1.8	275
Tetrads	17	1.7	1227	98.3	-	-	1244

Cytogenetic investigation of afd plants disclosed a discrepant situation: no visible homologous chromosome pairing (Int. Rev. Cytol. 58, 1979) on the one hand, and meiotic recombination, although impaired, on the other. At present, the relation between homologous pairing and meiotic recombination is established (Ann. Rev. Plant Physiol., 28, 1978); for this reason, only an electron microscopic study of prophase I of meiosis could explain this discrepancy.

As a result of electron microscopic observations, it was found that the ultrastructure of the prophase I of afd plants differs very much from that of normal maize plants. At the early prophase I, only short pieces of the synaptonemal complex (SC), randomly lying in the nucleus, are seen in the electron microscope; at the subsequent stages of prophase I, these short pieces disappear. These observations suggest that homologous chromosome pairing is initiated in mutant afd, as evidenced by the short SC pieces (however, nonhomologous chromosome pairing cannot be entirely excluded). This initiation seems to be sufficient to activate enzyme systems involved in meiotic recombination. The normal course of both homologous pairing and meiotic recombination most probably requires another important, genetically regulated step. It is this step that is perhaps blocked by afd. As a result, the pieces of the SC are destroyed and the chromatin fragments are not repaired, as judged by chromosome fragmentation at the stage of anaphase I.

Mutation dsy causes desynapsis of homologues. Under the light microscope, asynaptic regions are seen in distinct bivalents during pachytene; the chromosomes are represented by univalents at the beginning of diakinesis-metaphase I (MNL 53, 1979).

An ultrastructural study of prophase I in dsy plants showed that the SC develops regularly during zygotene-pachytene; the appearance of the SC does not differ from that of the normal meiotic cells. Novel features appear approximately in the middle of pachytene: namely shortening of the SC and structurally altered central and lateral elements. The observations made indicate that dsy does not affect the structure of the SC, but accelerates its destruction, as compared with normal.

Comparisons of the electron microscopic patterns at prophase I of meiosis in the two meiotic mutants justify the assumption that they both interfere with the same chain of meiotic events, with afd acting earlier than dsy. The segregation pattern of the meiotic characters in progenies of self-pollinated double heterozygotes afd +/+ dsy (MNL 53, 1979) supports this assumption.

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Mitochondria studies of the mutagenesis progenies

The mitochondrial test allows us to discern the resistant mitochondria from the susceptible ones after the mutagenesis experience (R. Cassini et al., 1977). This test is performed by the help of the three following parameters: (1) the respiratory control ratio (RCR), (2) the ADP/O ratio which estimates the energy production, and (3) the stimulating coefficient (SC) determined by the ratio of the oxygen uptake in the presence of NADH after adding toxin to that before adding toxin, or (state 2 + toxin)/state 2.

We examined a lot of progenies (about 150). The test is accurate and rapid. The mitochondria by their quantitative response to the toxins of Helminthosporium maydis and Phyllosticta maydis and to the insecticide methomyl allow us to point out some differences between progenies which we might have disregarded. Moreover, the mitochondrial test is applied as soon as the maize seed germinates. This screening among the mutagenesis progenies led us to notice an intermediary resistance level. So, we can now distinguish between: (1) fully resistant progenies which behave like the resistant control with the normal "N" cytoplasm (the RCR is untouched and there is no stimulation of the NADH oxidation, SC = 1); (2) fully susceptible progenies which behave like the susceptible control with the Texas "T" cytoplasm [there is no coupling, RCR = 1 and the SC is maximum (Fig. 1)]; (3) intermediary resistant progenies (RI) according to SC and RCR. Combinations between these two values are possible from RCR = 1 to RCR maximum whereas SC maximum runs to SC = 1.

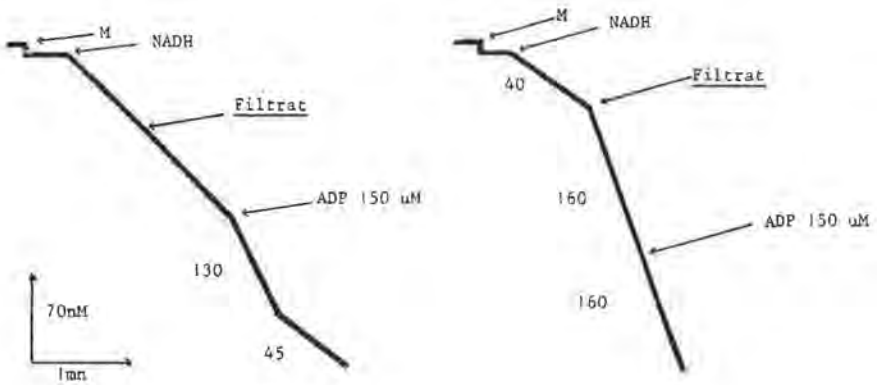

Fig. 1 - Resistance control (F_7N) and susceptibility control (F_7T) comparison

For attempting to understand what this intermediary resistance level means, we compared the intermediary progenies with mixed mitochondria extracted from seedlings carrying the N cytoplasm or the T cytoplasm. The mixture was made in large proportions. For each proportion (from 0% N:100% T to 100% N:0% T), we measured the RCR, the ADP/O and the SC ratios.

We have seen clearly that the mutagenesis progenies do not behave like the experimental mixtures of resistant and susceptible mitochondria. The progenies cannot be classed in front of the same mixture proportion for the three mitochondrial parameters (RCR, ADP/O and SC) (Fig. 2). Two hypotheses can answer to this observation: either there are interactions between the resistant and the susceptible mitochondria within the intermediary progenies, or we are in the presence of a new kind of mitochondria.

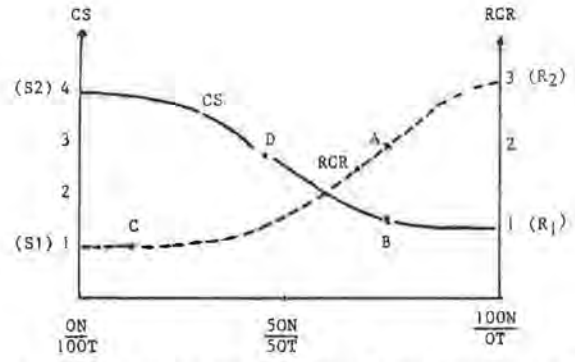

Fig. 2 - Comparison between RI "mutants" and the normal + Texas mitochondria mixtures.

The progenies of the mutagenesis treatment we called RI are for example in A and B (RCR decreasing, no stimulation) or in C and D (RCR = 1, a small stimulation). A fully resistant progeny (like F_7N) is in R_1 and R_2 whereas a fully susceptible one (like F_7T) is in S_1 and S_2.

Till now, the resistance acquisition at the plant level was always associated with a fertility return. We made an extended study of the mitochondria in a family which kept the Texas male sterility after mutagenesis. This study was performed over several generations. We showed that some resistance level was present by the M6 generation (Table 1).

Table 1. Resistance level acquisition within family 80

	Toxin					
	Hm			Pm		
Generation	R	RI	S	R	RI	S
M4			100%			100%
M5		4%	96%		4%	96%
M6		35%	65%		23%	77%

The mutagenesis experience has proved that it is possible to break the phenotypic binding group between Texas male sterility and susceptibility. Moreover, there is no correlation between the different susceptibility levels to the three toxic substances. This is providing a lot of applications since we can now expect to find a propitious association between resistance and male sterility at the plant level.

Michèle Paillard and A. Bervillé

Genotypic effects on mitochondrial activities

It is verified that inbreeding in cross-pollinated plants is leading to a decrease of vigor of the progeny. Hybrid organisms show inverse effects of an unusual vigor--hybrid vigor or heterosis. Several authors described ways to explain hybrid vigor by genetic mechanisms. But physiological explanations of hybrid vigor remain unclear. The nucleo-cytoplasmic interactions might be involved --above all the mitochondrial-nuclear interactions.

Mitochondria were isolated from the same corn hybrid genotype (F7 x F2) on various cytoplasms (N, T, C) and from the parental lines (F7N, F7T, F7C, F2). Mitochondria exhibited a large variability as judged by the following parameters: Respiratory Control Ratio (RCR), ADP/O Ratio and oxygen uptake. We have studied the mitochondrial activities after 2, 3, 4, 5, 6, 7 or 8 days of germination with NADH or malate as substrate.

The hybrids exhibit the highest activity for 3-day-old seedling with NADH and for 4- or 5-day-old seedling with malate. The lines exhibit the highest activity for 5- or 6-day-old seedling with NADH and for 4- or 5-day-old seedling with malate. In all the genotypes the highest protein quantity is shown from 2 to 4 days. At the 5-day stage the protein quantity decreases suddenly and from 6 or 8 days the quantity increases but never as high as it is at the first 4-day stage. We think that during the first 4 days the shoot growth is owed to the lipid storage of kernels. After 5 days the plants are built from the catabolism of glucose.

For explaining the variation of the protein quantities in the preps we think that once the lipids are used up the protein composition is changed; the lipolysis enzymes disappear. The glycolytic enzyme pathway takes place at the 6-day stage; this corresponds to an increasing of the protein quantity.

The same hybrids on N or T cytoplasm show similar mitochondrial activity variations, while the variations for F7C x F2 are different. The F7 lines on C and T cytoplasm show similar mitochondrial activity variations while the variations for F7N are different.

The mitochondrial activities depend both on the kind of cytoplasm and on the nuclear genotype, so that we cannot measure the mitochondrial activity from the N, T or C cytoplasm but always an interaction of N, T or C cytoplasm and a nuclear genotype. If we compare the activities of a hybrid and its parental lines we state that the hybrid follows always the same variation as the female line but it may be different. The male line follows a different scheme of variation.

Maryse Charbonnier and A. Bervillé

Effect of toxins on T corn mitochondria: permeabilization

Since 1974 we have carried out experiments in order to point out the mechanism of the H. maydis, P. maydis toxins and methomyl in T corn mitochondria. These toxins are extracted from liquid cultures by G. Aranda et al. (Ann. Phytopathol. 10: 315, 1978). The methomyl from du Pont de Nemours is purified after recrystallization by Aranda. Since the rate of NADH oxidation is enhanced by H. maydis toxin, P. maydis toxin and methomyl, we look for which pathway the electron flow might follow: either the NADH external dehydrogenase or the NADH internal dehydrogenase. In the first case the stimulated rate of NADH oxidation must be inhibited by Antimycin A. In the second case the stimulated rate must be inhibited by both rotenon and Antimycin A.

Several facts conform to the second hypothesis: in the presence of rotenon the stimulated rate of NADH oxidation is not induced by the toxins or methomyl and the stimulated rate is inhibited by Antimycin A. Moreover the transport ability through the inner dehydrogenase complex is higher than through the outer membrane. The toxins or methomyl are able to induce a stimulating coefficient as high as 6 or 9 although the ADP cannot induce more than 3. Furthermore the toxins inhibit malate oxidation. We observed that malate oxidation can be restored by adding NAD. Nevertheless the phosphorylating ability is not restored by NAD.

In order to explain the toxin effect on T mitochondria both on the pathway of exogenous NADH oxidation and on malate oxidation we assume that the first effect of the inhibition is at the membrane level. Under the toxin action the membrane

should be permeabilized so that the exogenous NADH could penetrate into the internal NADH dehydrogenase complex; on the other hand, the inner pool of the NAD should be diluted in the medium, consequently the malate dehydrogenase should be inhibited. In this way the first effect of the toxin should be to permeabilize the mitochondrial membranes. The leakage of NAD explains also the inhibition of the oxoglutarate. Further investigations may reveal a component involved in the loss of the ability to produce energy.

Michèle Paillard, Maryse Charbonnier and André Bervillé

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A fluorescence technique for the detection of chromosome knobs in maize

Vosa and de Aguiar (MGN 46:165-7, 1972) described a Giemsa staining technique by means of which the positions of chromosome knobs may be located in mitotic chromosomes. The present work describes a fluorescence technique which indicates their positions with even greater clarity. Like the Giemsa method, it is a heterochromatin staining technique based on denaturation-reannealing, but this is followed in the present case not by Giemsa staining but by treatment with the AT-binding fluorochrome "Hoechst 33258."

Actively growing root tips are pretreated by immersion in saturated, aqueous α-monobromonaphthalene for 4-5 hours, and fixed in 3:1 ethanol:glacial acetic acid for 8-24 hours. They are then hydrolyzed in 0.2 N HCl at 60° C for 2.5 minutes, and squashed in 45% acetic acid under an albumenized coverslip, which is floated off in absolute ethanol and air-dried. The coverslips are then immersed for 6 minutes in a saturated aqueous solution of barium hydroxide at room temperature, rinsed in running deionized water, incubated in 2X saline sodium citrate buffer at 60° C for one hour, rinsed again in deionized water, and air-dried. Following this the preparations are stained for 5 minutes in a 0.02% ethanolic solution of Hoechst 33258, rinsed in ethanol, air-dried, mounted in 50% glycerol, and viewed using a Zeiss fluorescence microscope with exciter filter BG12 and barrier filters 50 plus 53. If desired, the preparations may then be made permanent by Giemsa staining according to the method of Vosa and de Aguiar.

The knob regions are revealed by the fluorescence technique as regions of intense fluorescence, and by the Giemsa technique as regions of heavy staining. Both methods yield good results, though for the most part the fluorescence technique is the more consistent, being less sensitive to minor variations in the temperature of denaturation and the duration of staining. Compared to conventional techniques, both methods possess the important advantage of employing mitotic material, hence eliminating the necessity of procuring meiotic material of the plants to be examined.

C. G. Vosa (Oxford) and D. J. Mogford (Grahamstown)

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Inverted repeats in chloroplast DNA from the genus Zea

Chloroplast DNAs (ctDNAs) of corn and among teosintes differ by restriction endonuclease fragment pattern analyses (D. H. Timothy, C. S. Levings III, D. R. Pring, M. F. Conde, and J. L. Kermicle, Proc. Nat. Acad. Sci. USA 76:4220-4224, 1979). Additionally, the patterns of the differences formed a hierarchical structure of taxonomic validity when compared to the conventional biosystematic classifications of the taxa. Those groupings were a reflection of the differences in the number and position of hexanucleotide sequences in the ctDNA molecules of each taxa. Electron microscopy of ctDNA from corn, lettuce, and spinach has shown that each contains a large sequence repeated one time in reverse polarity, and that the structure of the inverted sequence is highly conserved in the plants (R. Kolodner and K. K. Tewari, Proc. Nat. Acad. Sci. USA 76:41-45, 1979). In that study, the inverted segment was approximately 16% of the native length of the three ctDNAs. The repeated sequence in corn is about 22,500 base pairs long (R. Kolodner and K. K. Tewari, Biochim. Biophys. Acta 402:372-390, 1975). The structure of the corn ctDNA (J. R. Bedbrook, R. Kolodner and L. Bogorad, Cell 11:739-750, 1977) is such that one copy of the two sets of chloroplast specific rRNA genes (J. R. Thomas and K. K. Tewari, Proc. Nat. Acad. Sci. USA 71:3147-3151, 1974) is found in each of the inverted sequences of the ctDNA. This preliminary report deals with additional characterization of ctDNA in the genus Zea.

Preparations of corn and teosinte ctDNAs were denatured, neutralized, allowed to self-renature, and examined by electron microscopy. Molecular conformation was that of a small single-stranded DNA loop, separated from a large single-stranded loop by a large duplex region (Figure 1). The lengths of these portions of the

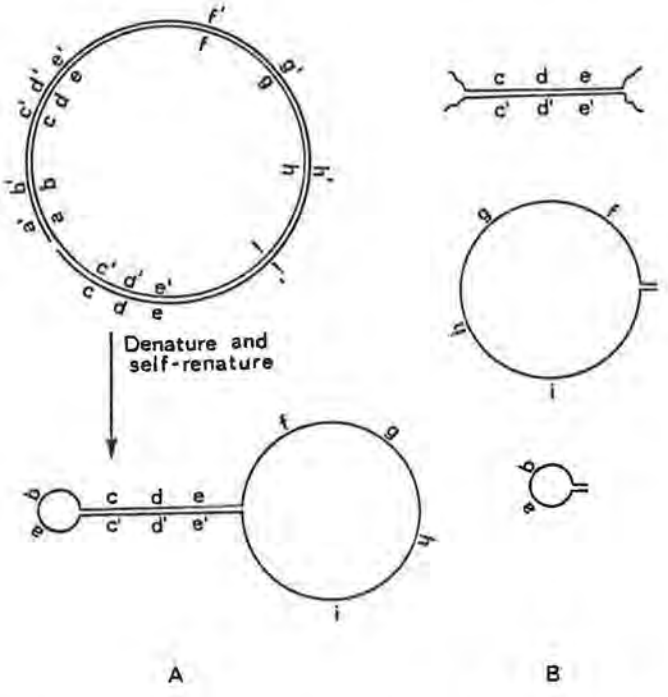


Fig. 1. (A) Illustration of a self-renatured molecule from a nicked circular ctDNA molecule containing an inverted repeat. (B) Duplex region (top), and small and large single-stranded loops (bottom) from broken molecules in (A).

partially duplexed ctDNA molecules are summarized in Table 1. Included in these data are measurements of single-stranded loops and duplex segments resulting from broken molecules as illustrated in Fig. 1B and of either single-stranded loop with the duplex segment. Only the measurements from complete and unbroken loops and duplex segments are reported.

Table 1. Length measurements on self-renatured ctDNA molecules in Zea.

Taxa	Small loop, ϕ X units*	Double segment, ϕ X units	Large loop ϕ X units	Duplex segment in % of total molecule length
Corn	2.32 ± 0.04 (7)	3.90 ± 0.05 (10)	15.24 ± 0.32 (6)	15.4
Central Plateau	2.35 ± 0.07 (19)	4.10 ± 0.06 (15)	14.75 ± 0.74 (2)	16.2
Huehuetenango	2.23 ± 0.04 (9)	3.93 ± 0.07 (9)	14.03 ± 0.20 (3)	16.3
Guatemala	2.35 ± 0.07 (12)	4.05 ± 0.05 (12)	15.51 ± 0.31 (7)	15.5
Perennial (4N)	2.26 ± 0.14 (10)	4.08 ± 0.07 (10)	15.55 ± 0.60 (6)	15.7

*Lengths are reported as a ratio in ϕ X units, using the double-stranded or single-stranded forms of the bacteriophage ϕ X 174 as an internal standard against the respective double- or single-stranded portions of the ctDNA molecules. Numbers of molecule portions measured are enclosed in ( ).

Although previous work using restriction endonucleases has distinguished evolutionary differences among ctDNAs of teosinte and corn, the number of molecules reported here with self-renaturation are insufficient to make those distinctions. Additionally, the specificity and resolution of the two techniques is somewhat different. However, it is now apparent that both corn and teosinte ctDNA genomes contain a sequence repeated once in reverse polarity, that each sequence is approximately 16% of the native length of the ctDNA, and that the sequence is highly conserved. Although we have no evidence that the inverted ctDNA sequence in teosinte codes for the chloroplast rRNA genes, as in corn, the similarity in the conformation of the corn and teosinte ctDNAs allows the speculation that the teosinte inverted repeat has a similar function to that of corn.

D. H. Timothy, W. W. L. Hu, and C. S. Levings, III

A comparison of maize mtDNA from normal and male sterile cytoplasms

In maize there are several basic types of cytoplasmic male sterility which can be distinguished on the basis of nuclear genes that restore fertility. Restriction endonuclease fragment analysis also separates the various cytoplasms by distinctions in the banding patterns of their mtDNA. By the hybridization experiments described below, differences have been demonstrated among the mtDNAs from normal (fertile) and the T and S male-sterile cytoplasms. Sequence similarities, duplications, possible rearrangements and deletions of portions of the mitochondrial genome were evident.

MtDNA isolated from the male-fertile hybrid, NC7 x T204, was digested with Bam H1 and the resulting fragments cloned with the plasmid PBR 322 in E. coli, strain LE 392. Fragments which had been taken up by the plasmid and replicated were screened to insure that each insert contained only one restriction fragment.

Cloned inserts were isolated and ^{32}P-labelled by nick translation for use as hybridization probes.

MtDNAs from the normal and cms-T strains were restricted with Bam H1 and the resulting fragments fractionated by gel electrophoresis on a .8% agarose gel. Unrestricted cms-S mtDNA and the insert, which would later be used as the probe in the hybridization experiments, were also loaded in adjacent slots on the gel. In this case, the insert served as a marker while homology with S-1 and S-2 DNA species could be assayed on the slot containing the unrestricted cms-S mtDNA.

DNA digests were transferred from the electrophoretic gels to nitrocellulose membranes according to the Southern blot technique. Labelled probes were heat denatured and incubated with the nitrocellulose membranes for 20-40 hours at 65° C. Autoradiography was used to detect hybridization.

At the present time, fourteen different cloned fragments have been studied by the hybridization techniques. Of these, eight demonstrated homology with bands of the same electrophoretic mobility in the normal and T restriction patterns (Fig. 1a). Earlier restriction enzyme analysis showed that when mtDNA from normal and male-sterile cytoplasms were digested with a common enzyme, 75-80% of all the fragments appeared to be of the same molecular weight. Therefore, it was expected that most of the autoradiographs would show identical hybridization patterns between N and T. It can now be added that not only are the majority of the fragments similar in size but they contain sequence homologies as evidenced by hybridization with the labelled probes.

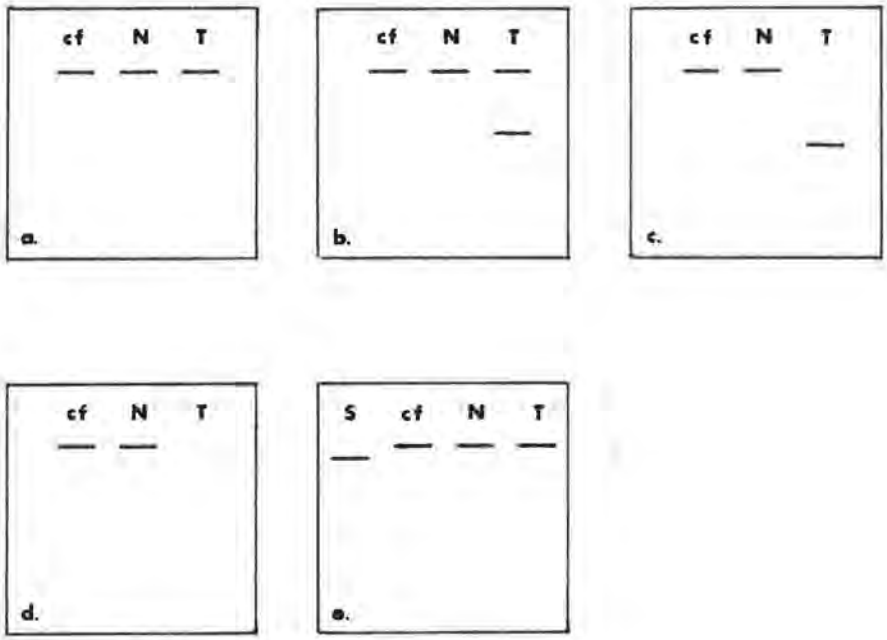


Figure 1. Autoradiographic patterns produced by hybridizations of specific cloned fragments (cf) with Southern blots of digested normal (N) and cms-T (T) mtDNA and undigested cms-S (S) mtDNA. For details see text.

The next most frequent type of autoradiographic pattern (four of the fourteen) showed an "extra" band present in T that was not detected in N (Fig. 1b). One of the two bands in T was analogous to the band in N while the additional band appeared smaller in molecular weight. This suggests that recombinational events

which either duplicated or rearranged DNA sequences may have occurred in T. Interestingly, none of the labelled clones has displayed homology with more than one band in the normal pattern.

One autoradiograph exhibited a pattern where the band in T was displaced or did not line up exactly with the band in N (Fig. 1c). This result could have arisen by sequence rearrangements in the mtDNA or perhaps even a deletion event.

Evidence has been obtained for additional sequences present in normal mtDNA that is missing in male sterile mtDNA. One of the cloned fragments of normal mtDNA showed no homology with any of the T restriction bands (Fig. 1d).

Another cloned fragment is particularly noteworthy. The autoradiographic pattern indicated homology with corresponding bands in N and T and also with S-1, one of the plasmid-like DNAs found associated with the mtDNA in cms-S (Fig. 1e). This demonstrates that sequences in common with the plasmid-like DNA, S-1,are also found in the mitochondrial chromosomal DNA.

In summary, hybridization with cloned fragments has revealed: sequence homology between a majority of the restriction fragments from normal and cms-T mtDNA, a single case of sequence differences between normal and cms-T mtDNA, evidence for recombinational and/or deletional events among the mtDNAs, and evidence that DNA sequences in common with the plasmid-like DNAs are found in the mitochondrial chromosomal DNA.

W. M. Spruill Jr., R. R. Sederoff and C. S. Levings III

Genetics of 6-PGD isozymes in corn

We are using two starch gel buffer systems (L-histidine, citric acid at pH 5.7 and pH 6.5) for the separation of 6-PGD isozyme bands. Genetic studies of the variants indicate that two loci are involved in the expression of the 6-PGD banding patterns. We have identified nine alleles at the Pgd1 locus and three alleles at the Pgd2 locus. Heterodimers are formed between allelic isozymes at each locus and between nonallelic isozymes for the two loci.

Analyses of data from F2 populations suggest that the two loci segregate independently:

	Pgd1											
Pgd2	A2/A2			A2/A3.8			A3.8/A3.8			Total		
B2.8/B2.8	(2.4)[a]	1	[2.6][b]	(5.6)	6	[5.1]	(2.0)	3	[2.6]	10	[10.3]
B2.8/B5	(4.6)	4	[5.1]	(10.7)	13	[10.3]	(3.7)	2	[5.1]	19	[20.5]
B5/B5	(2.9)	5	[2.6]	(6.7)	4	[5.1]	(2.3)	3	[2.6]	12	[10.3]
Total		10	[10.3]		23	[20.5]		8	[10.3]	41	

χ^2_4 (independence) = 5.589 $\quad 0.10 < P < 0.25$

χ^2_8 (4:2:2:2:2:1:1:1:1) = 6.707 $\quad 0.50 < P < 0.75$

[a]Expected values, based upon independence, shown in parentheses.

[b]Expected values, based upon 4:2:2:2:2:1:1:1:1 segregation, shown in brackets.

Using linkage and trisomic analyses, Pgd1 has been located on chromosome 6 about five map units from the Ep locus. Pgd2 has not yet been assigned to a specific chromosome.

C. W. Stuber and M. M. Goodman

Genetics of IDH isozymes in corn

We are separating IDH isozymes with starch gel electrophoresis using a pH 6.5 L-histidine, citric acid buffer system. Genetic analyses of the variants observed indicate that two loci are involved in the expression of the IDH bands. We have identified four alleles at each locus. Heterodimers are formed between allelic isozymes at each locus and between nonallelic isozymes for the two loci.

Analyses of data from F2 populations suggest that the two loci segregate independently:

	Idh1											
Idh2	A4/A4			A4/A6			A6/A6			Total		
B4/B4	(4.3)[a]	3	[3.5][b]	(7.5)	8	[7.0]	(3.2)	4	[3.5]	15	[14]	
B4/B6	(7.4)	10	[7.0]	(13.0)	12	[14.0]	(5.6)	4	[7.0]	26	[28]	
B6/B6	(4.3)	3	[3.5]	(7.5)	8	[7.0]	(3.2)	4	[3.5]	15	[14]	
Total		16	[14]		28	[28]		12	[14]	56		

χ^2_4 (independence) = 2.633 $\quad 0.50 < P < 0.75$

χ^2_8 (4:2:2:2:2:1:1:1:1) = 3.429 $\quad 0.90 < P < 0.95$

[a]Expected values, based upon independence, shown in parentheses.

[b]Expected values, based upon 4:2:2:2:2:1:1:1:1 segregation, shown in brackets.

Linkage data indicate that Idh2 is tightly linked (less than 5% recombination) to Mdh2 on chromosome 6. Preliminary data suggest that Idh1 is about 20 map units from Mdh1 which has been located on chromosome 8 (see K. Newton elsewhere in the Newsletter).

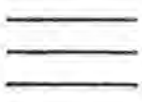
C. W. Stuber and M. M. Goodman

Further genetics of MDH

Earlier we (MGCNL 53:72-73) and Newton (MGCNL 53:16-21) reported independent discoveries (from different materials) of an electrophoretic "activity null" for Mdh2 on chromosome 6. This allele produces no apparent homodimer but does produce interallelic heterodimers with products of the nonnull alleles of Mdh2 as well as intergenic heterodimers with the nonnull alleles of Mdh1 (on chromosome 8--see Newton in this volume) and Mdh3 (on chromosome 3 near sh2). More recently we have discovered a similar allele for Mdh1 among several collections from Peru and Bolivia.

One of the most striking variants we have encountered in our isozyme survey of Latin American collections has been the D8.5 allele of Mdh4 (on chromosome 1). This variant, isolated from a Venezuelan collection, results in heterodimers which do not show the usual migration pattern of lying approximately half the distance between the corresponding homodimers. The interallelic heterodimer of D8.5 with D12 (the common variant) migrates only slightly beyond the homodimer of D8.5 itself, while the homodimer corresponding to D12 migrates substantially further on both our pH 5.0 and pH 5.7 histidine-citrate gels:

The interallelic heterodimer of D8 (another rare variant of Mdh4) and D8.5 is even more striking as it fails to migrate as far as either corresponding homodimer:



That this phenomenon is not unique to the D8 and D8.5 alleles at the Mdh4 locus is demonstrated by the fact that it also occurs for the interallelic heterodimer of D8.5 and D10.5 (another rare Mdh4 allele).

Recently we have shown that the same relative migration pattern (with the heterodimer lying outside the range of the corresponding homodimers) holds for the intergenic heterodimer of D8.5 and a rare allele at the Mdh5 locus (on chromosome 5).

M. M. Goodman and C. W. Stuber

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Five sets of enzyme genes encompassing 13 loci on 4 chromosomes--some possible implications for chromosome segment duplications

Linkage studies with isozymes revealed four genes linked to Adh1 on the long arm of chromosome 1. The arrangement of the loci is based on a 358-plant, five-point testcross. The standard errors for the map distances vary from 1% for Mdh4 - mmm and 2% for mmm - Pgm1 to less than 3% for the entire span, Mdh4 to Phi:

Mdh4 4.4% mmm 19.0% Pgm1 5.8% Adh1 13.7% Phi
/----------42.9%----------/

(Recombinant chromosomes = 41.9%, including double crossover types)

Segregation data for Mdh5, Pgm2 and a2 on chromosome 5 indicate about 16% (± 4%) recombination between Mdh5 and Pgm2 and about 32% (± 7%) recombination between a2 and Pgm2.

On chromosome 6 we have previously reported about 5% recombination between Ep and Pgd1 near Y; now we can report that, in the distal region of the long arm of chromosome 6, Idh2 and Mdh2 show less than 5% recombination.

Our preliminary data show about 19% (± 5%) recombination between Idh1 and Mdh1; the localization of the latter to chromosome 8 is reported elsewhere in this volume by Newton.

We thus have two parallel cases of linkage:

A { Mdh4 - Pgm1 on chromosome 1 with 23% (± 2%) recombination;
Mdh5 - Pgm2 on chromosome 5 with 16% (± 4%) recombination;

B { Idh1 - Mdh1 on chromosome 8 with 19% (± 5%) recombination;
Idh2 - Mdh2 on chromosome 6 with less than 5% recombination.

These data suggest that duplication of chromosome segments involving isozyme loci may not be as uncommon as the cytological evidence would imply.

M. M. Goodman, C. W. Stuber, K. J. Newton and H. H. Weissinger

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Map position of male sterile-10

Male sterile-10 (ms10) was mapped using the marker uncovering analysis outlined by H. Roman and A. J. Ullstrup (Agron. J. 43:450). The mutant was crossed as pistillate plants with a set of B-10 translocations isolated by the writer (MGNL 46:193). Only 34 of the 37 translocations whose B^{10} elements carried g and r were used. Fifteen of these uncovered ms10 and 19 did not. Two of the former also uncovered zn, du, bf2 and li, one du as well as bf2 and li, and one only bf2 and li (MGNL 48:182). The data place ms10 distal to bf2 (and li) but proximal to g with 11 translocations located in the first region and 19 in the second. The translocations of the first group include TB-10L(1), TB-10L(3), TB-10L(4), TB-10L(7), TB-10L(8), TB-10L(10), TB-10L(20), TB-10L(25), TB-10L(28), TB-10L(31) and TB-10L(36). The previously established translocation TB-10La belongs to the second group, according to J. B. Beckett's data (MGNL 47:145).

Bor-yaw Lin

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Relationships among several characteristics in maize related to the kernel moisture content at harvest

Simple correlations among 13 characteristics of 53 maize single cross hybrids, grown in a performance trial planted April 20 and harvested October 10, 1979, are estimated (Table 1).

The kernel moisture content at harvest correlates highly significant negatively to the amount of active temperature for maize (over 10° C and below 30° C) between the date of "black layer" formation and the date of harvest ($r = -0.72^{***}$), to the kernel percentage in the ear (shelling percent) ($r = -0.60^{***}$), and highly significant positively to the ear length ($r = 0.61^{***}$). Lower but significant positive correlations are observed between kernel moisture at harvest and ear height ($r = 0.48^{**}$), pericarp thickness ($r = 0.43^{**}$), grain yield per hectare ($r = 0.43^{**}$), kernel size ($r = 0.38^{**}$), and ear diameter ($r = 0.37^{**}$). The length of ear shank, the ear husk number, and the kernel row number do not correlate significantly to the kernel moisture content in this experiment.

Table 1. Simple correlation coefficients among 13 characteristics in 53 maize hybrids

Characteristics	Mean value	Variation	Characteristics 2	3	4	5	6	7	8	9	10	11	12	13
1.Kernel moisture, %	20	13-28	-.72+++	.43++	.48++	.15	.11	.61+++	.37++	.03	-.60+++	.38++	.23	.43++
2.Active temperature, C°	160	30-465	-	-.70+++	-.73+++	-.16	-.02	-.62+++	-.43++	.00	.35++	-.62+++	-.49++	-.46++
3.Grain yield, kg/ha	7480	4560-10060	-	-	.69+++	.21	-.05	.56+++	.45++	.07	-.09	.46++	.34+	.33+
4.Ear height, cm	88	43-120	-	-	-	.08	-.23	.53+++	.40++	.11	-.32+	.47++	.33+	.40++
5.Ear shank, cm	14	8-22	-	-	-	-	-.07	.29+	-.04	-.34+	.10	.45++	.52+++	.51+++
6.Husk number	11	8-14	-	-	-	-	-	-.13	.38++	.27+	-.01	-.12	-.12	-.21
7.Ear lenght, cm	22	18-26	-	-	-	-	-	-	.20	-.12	-.47++	;56+++	.41++	.54+++
8.Ear diameter, mm	51	43-60	-	-	-	-	-	-	-	.58+++	-.34+	.13	.00	-.10
9.Kernel row number	17	14-24	-	-	-	-	-	-	-	-	.29+	-.53+++	-.62+++	-.47++
10.Shelling percent	81	76-87	-	-	-	-	-	-	-	-	-	-.10	.04	-.24
11.Volume of 1kernel, mm^3	282	192-368	-	-	-	-	-	-	-	-	-	-	.91+++	.83+++
12.1000 kernels weight, g	281	188-358	-	-	-	-	-	-	-	-	-	-	-	.67+++
13.Pericarp thickness, microns	73	48-102	-	-	-	-	-	-	-	-	-	-	-	-

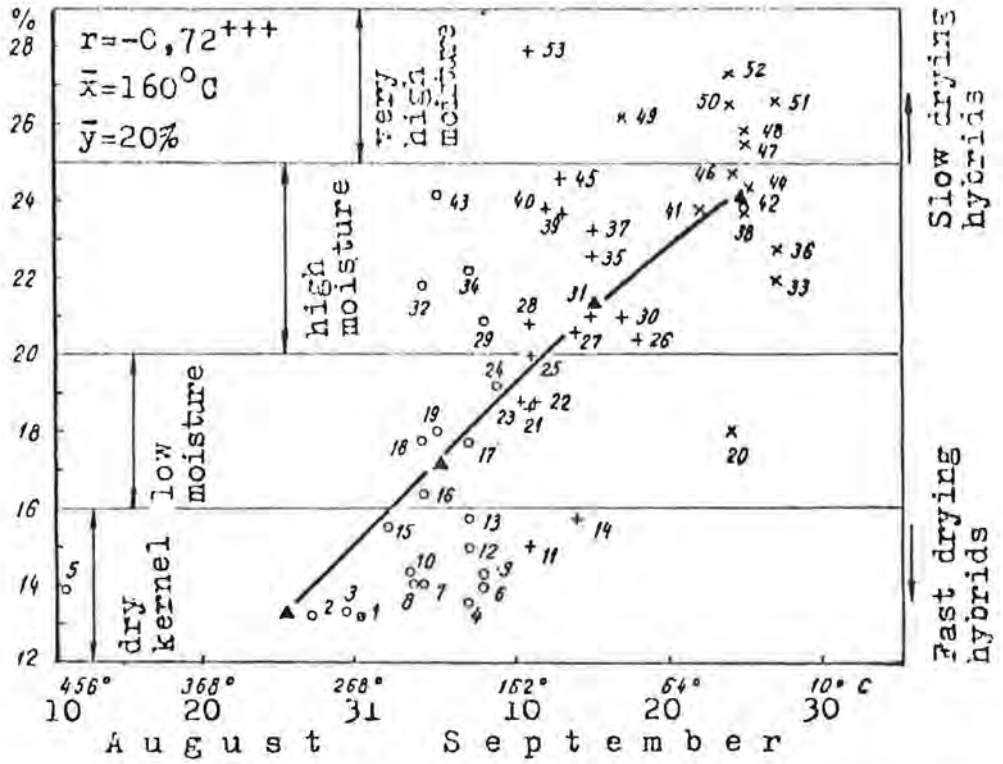

Fig. 1. Relationship between the amount of active temperature for maize (C°) since "black layer" formation date up to harvest date, and kernel moisture content at harvest in 53 single crosses. Black layer formation in different hybrids: 0--before Sept. 10; +--Sept. 11-20; x--after Sept. 20.

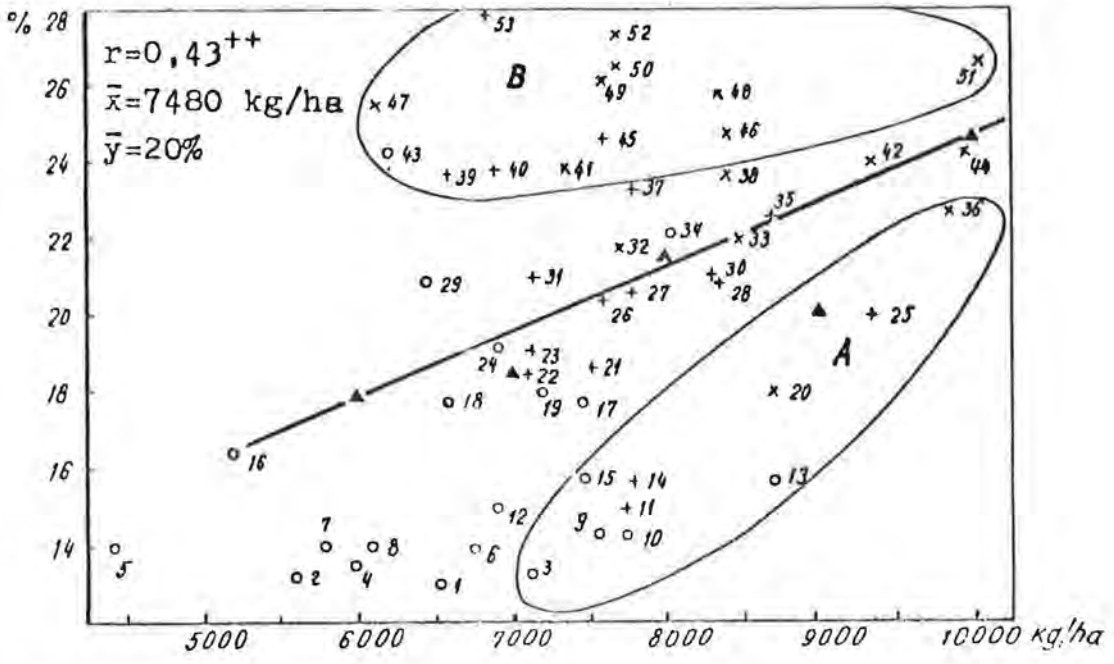

Fig. 2. Relationship between grain yield (kg/ha) and kernel moisture content (%) at harvest in 53 single crosses. A--high yielding fast drying hybrids; B--slow drying hybrids.

Large difference in kernel moisture content among hybrids of the same maturity (black layer formation stage) is observed (Fig. 1), due to the differences in kernel size, shelling percent, pericarp thickness and other characteristics. Hybrids of the same yield per hectare differ in kernel moisture content at harvest (Fig. 2) because of the differences in characteristics related to the kernel drying rate.

The low moisture content at harvest of some hybrids is due to the early physiological maturity (black layer formation) date, short ear, small ear diameter, while the low moisture content in other hybrids, more productive and later in "black layer" formation date, is due to the thinner pericarp, larger kernel row number, smaller kernel size, and smaller husk number.

The relationships among the characteristics studied show the possibility for improvement of drying rate in maize by breeding work without reduction of yield.

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A maize trisome which produces hypertriploid (3n + 2) plants

A trisomic maize plant (GH 42-3), obtained from a commercial hybrid seed population, was crossed as female parent to the inbred line W22 and chromosome counts were made on squashed root tips of a sample of 90 progeny plants. The progeny consisted of diploid, trisomic or hypertriploid plants with 32 chromosomes (3n + 2):

	Chromosome number			Total
	20	21	32	
No. of plants (and %)	56 (62.2)	26 (28.9)	8 (8.9)	90

Cytological examination revealed that the chromosome involved in the aneuploid condition could be chromosome 3 or 4, as valued by relative chromosome length and arm ratio.

The morphology of the plants made for easy identification of both hypertriploid and trisomic individuals. When examined 30 days after planting, hypertriploids showed only 4 to 5 leaves:

Chromosome Number	No. of Plants	No. of Leaves*	Leaf Width (cm)	Plant Height (cm)	Days to Anthesis
20	56	7-8	12.78 (s.e.=0.2)	262.1 (s.e.=5.4)	73-76
21	26	5-6	14.32 (s.e.=0.4)	204 (s.e.=6.9)	83-87
32	8	4-5	9.65 (s.e.=1.8)	126 (s.e.=20.1)	92-99

*On the 30th day from planting.

At maturity they were considerably shorter than their diploid or trisomic sibs; moreover, hyperpolyploidy had a negative effect on leaf blade width (as measured on the 6th leaf from the base) and on the number of days to anthesis. The trisomic plants had a slower growing habit than their diploid sibs; at maturity the leaf blade width was greater in trisomic individuals which were, however, shorter than the diploid plants.

When the pollen grains were observed under the microscope after staining by Lugol's solution, striking differences were revealed among the progeny plants:

Chromosome Number	No. of Plants	Frequency (%) of Unstained Pollen Grains
20	24	0.4 - 5.7
21	8	5.7 - 7.7
	16	13.4 - 21.4
32	6	61.5 - 86.8

While 2n plants and one-third of 2n + 1 individuals showed a low frequency of unstained pollen grains, the remaining trisomic plants and the hypertriploid plants showed much higher values.

The seeds freely developed in both diploid and trisomic plants. In those hypertriploid plants which reached maturity, however, despite an apparently regular seed set, the majority of the seeds showed an irregular development.

The inheritance of hypertriploid induction was studied by cytological examination of root tips of a sample of 165 progeny plants obtained by crossing the trisomic plant no. 3604-12 (belonging to progeny of plant GH 42-3) as the female parent to the W.M.T. The hypertriploid-inducing capacity can be transmitted through the female at least, as shown in the following:

	Chromosome number			Total
	20	21	32	
No. of plants (and %)	126 (76.4)	37 (22.4)	2 (1.2)	165

In the progeny of this cross two classes of kernels with dark or pale aleurone were observed. Chromosome counts within these classes (see Table 5) indicate that an unidentified aleurone pigment factor is associated to this trisomic condition and may help selecting trisomic individuals through a dosage effect:

		Chromosome No.		
		20	21	Total
Aleurone color	dark	3	12	15
	pale	65	9	74

Moreover, after germination of kernels, two distinct classes were observed for the phenotype of the primary root. The thick phenotype seems to have some association with the aneuploid condition:

		Chromosome No.			
		20	21	32	Total
Primary root	thick	9	23	2	34
	thin	117	14	-	131

Hypertriploid plants could be produced if during fertilization a 2n + 2 egg fuses with an n male gamete. Such a female gamete could possibly originate by a post-meiotic event involving the fusion of two n + 1 nuclei. The fact that eutriploid individuals were not observed in the progeny of hypertriploid-inducing trisomic plants would indicate that this phenomenon affects only the n + 1 nuclei.

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DNA/DNA hybridization of maize to related grasses

Maize DNA, W64A, was hybridized to DNA of Tripsacum laxus; teosinte, race Chalco; teosinte, race Guatemala; and popcorn, to assess the extent of sequence homology. The divergence between homologous sequences is determined by the thermal stability of hybrid DNA molecules: the difference in T_m, ΔT_m, is approximately equal to the percent mismatch. Maize DNA was reassociated to DNA, ^3H-labeled by nick-translation, at a ratio greater than 2000:1; thus, labeled DNA only reassociates with unlabeled driver. The DNA samples were allowed to reassociate to Cot 100 or Cot 10,000, loaded onto hydroxyapatite and thermally eluted in 4-degree increments. The T_m of the homologous duplex, maize-maize, was determined by its A_{260nm}. The T_m of the heterologous duplex was determined by TCA precipitation of chromatographed DNA onto glass fiber filters and counting in scintillation fluid. The data are presented in Table 1. Fig. 1 is a graph of the thermal stability of a Cot 10,000 Guatemala teosinte-maize duplex.

At Cot 100 the reassociated duplexes include most of the repetitive sequences but very few of the unique sequences. The ΔT_ms for popcorn, teosintes Chalco and Guatemala are, respectively, 1.7, 2.1, and 1.9 degrees. Maize DNA was also reassociated with labeled self DNA; the ΔT_m was 0.4 degrees. Given the standard deviations, it is difficult to say if one sample is significantly more divergent than another. The extent of reassociation was approximately the same as the homologous duplex in each case. The ΔT_m for Tripsacum is significantly larger, 7.0 degrees, and the extent of reassociation is 56% of the maize-maize duplex.

At Cot 10,000 all repetitive and most unique sequences have reassociated (the $Cot_{\frac{1}{2}}$ pure for unique sequences is 2100). The difference in ΔT_m from the Cot 100 results can be attributed to the reassociation of unique sequences. The ΔT_ms for popcorn, teosintes Chalco and Guatemala, and Tripsacum are respectively, 2.3, 4.2 3.2 and 8.2 degrees. The percent of shared sequences is approximately equal to the homoduplex in all cases except for Tripsacum which hybridizes to 51% of the extent

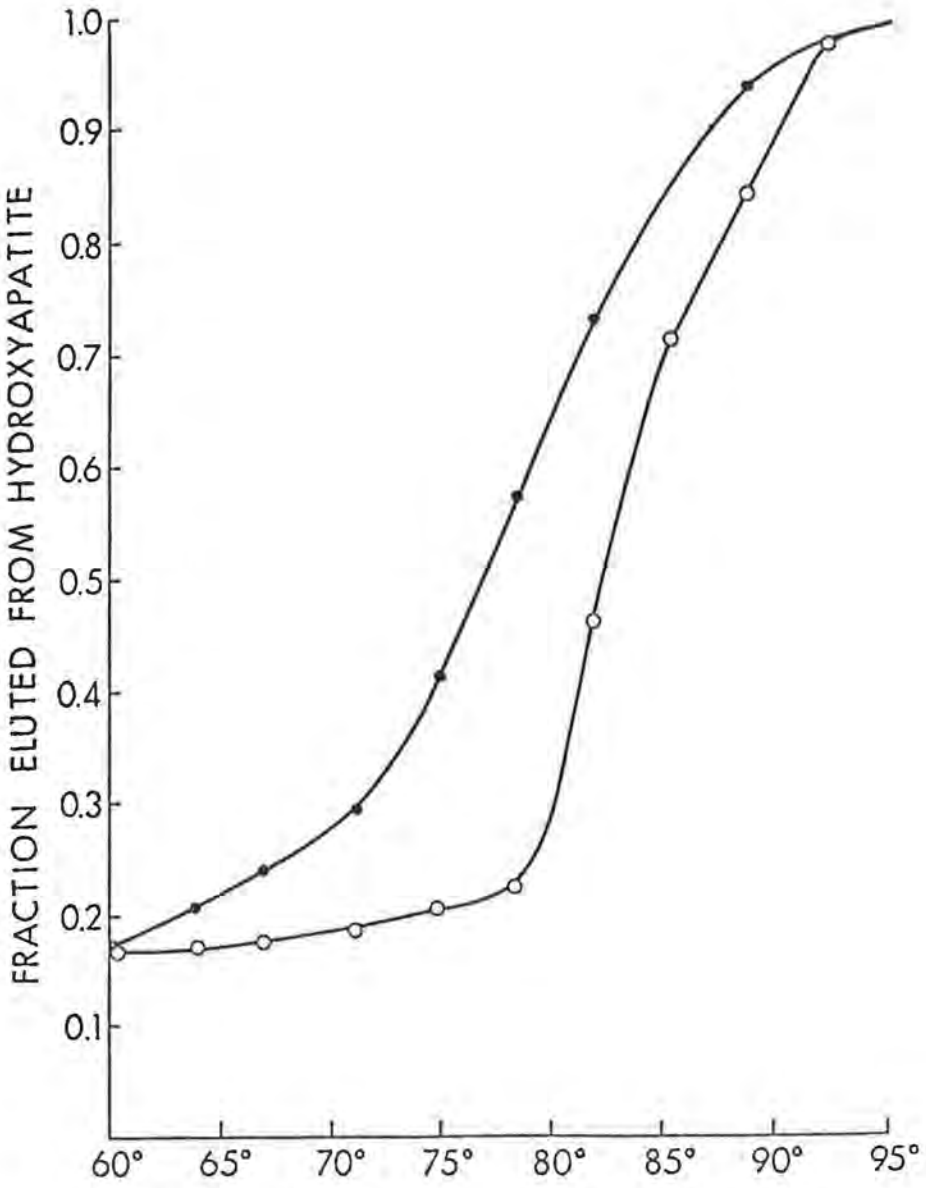

Fig. 1. Hydroxyapatite thermal chromatography of Zea mays W64A DNA duplex formed with tracer teosinte Guatemala DNA to equivalent Cot 10,000. O homologous duplex as monitored by $A_{260\ nm}$; ● heterologous duplex.

Table 1. DNA/DNA hybridization of Zea mays to related grasses

Cot	Tracer[a]	ΔT_m°C[b]	Percent Reassociation of tracer to driver	Number of hybridizations
100	Zea mays W64A	0.4	100	1
100	Zea mays Mol7	0.95 ± 1.06	100	2
100	teosinte Chalco	2.1 ± 0.53	100	2
100	teosinte Guatemala	1.9 ± 1.70	100	2
100	Ladyfinger Pop	1.7 ± 0.6	100	2
100	Tripsacum	7.0	56	1
100	wheat	>20	10	1
10^4	Zea mays Mol7	0.2	100	2
10^4	teosinte Chalco	2.3 ± 1.0	100	3
10^4	teosinte Guatemala	4.2	100	2
10^4	Ladyfinger Pop	3.2 ± 0.45	100	3
10^4	Tripsacum	8.2 ± 0.64	51	2
10^4	wheat	>20	10	1

a Driver in all cases is W64A maize DNA. Teosinte (Z. mexicana) races are identified by region of origin.

b The ΔT_m is the difference in T_m between driver, monitored by $A_{260\ nm}$, and tracer, monitored by cpm.

of the homoduplex. It appears that the unique sequences are all more divergent than the repetitive sequences except for Chalco teosinte. Guatemala teosinte unique sequences appear to be more divergent than Chalco. This difference at the DNA level parallels their morphological characteristics and organellar DNA organization (D. H. Timothy et al., P.N.A.S. 76:4220-4224, 1979). Tripsacum is twice as divergent as teosinte or popcorn from dent corn, but not much more divergent in unique than repetitive sequences.

Clearly, popcorn and both Guatemala and Chalco teosintes have contributed to the present day maize genome, either ancestrally or due to introgression. Tripsacum is less related in both sequence homology and extent of shared sequences, though there are definite sequences in common. If the changes in the genome occur purely randomly at a clock-like rate of 1% mismatch per 5 million years, we calculate that maize diverged from teosinte 10-20 million years ago and from Tripsacum 40 million years ago. These calculated divergences are unlikely in view of the fact that the grasses are only 70 million years old and individual genera 20-40 million years old. Presumably the intense impact of human selection has contributed to the apparent distance of maize from close relatives.

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University of Minnesota

Chromosome 6 satellite location of a high chlorophyll fluorescence mutation (hcf*-26)

Last year we reported (MGCNL 53) that a mutant (hcf*-26) blocked in light reaction photosynthesis was beyond the middle chromomere of the satellite and could be located in the distal chromomere. The mutant hcf*-26 possesses a yellow-green phenotype and had been reported to be uncovered by TB-6Sa (Leto and Miles, MGCNL 51:57-59). In order to more precisely cytogenetically locate hcf*-26, we crossed heterozygous satellite-interchanges as the female parent with heterozygous hcf*-26 plants as male parent. Under our greenhouse sandbench conditions, seed from self-pollinations of the heterozygous hcf*-26 plants resulted in green and near-luteus seedlings. None of the crosses (Table 1) between the heterozygous interchanges as female and heterozygous hcf*-26 as male yielded near-luteus seedlings when the

Table 1. Tests to cytogenetically locate hcf-26. Smaller seed and a portion of remaining seed from crosses of heterozygous interchanges as female parent with heterozygous hcf-26 plants were planted. Data were collected from seed produced during the summers of 1978 and 1979.

			Smaller seed[2]		Remnant seed	
	Satellite[1]	Number		Chlorophyll		Chlorophyll
Interchange	break pt.	of crosses	Green	deficient	Green	deficient
3-6b	proximal end of distal chromomere	4	144	0	259	0
2-6(001-15)	distal end of distal chromomere	3	162	0	273	0
6-7(7036)	distal end of distal chromomere	6	115	0	325	0
5-6(8219)	"satellite"	2	34	0	70	0

[1]The satellite is comprised of 3 chromomeres in these strains.
[2]Smaller seeds are expected to include Dp-Df heterozygotes.

satellite breakpoint was distal to the breakpoint of interchange T4-6(5227), which is located between the middle and distal chromomeres. Our results indicate that hcf*-26 is located between the breakpoint of T4-6(5227) and the proximal end of the distal chromomere marked by T3-6b. Thus, hcf*-26 is either between the middle and distal chromomeres or in the proximal portion of the distal chromomere. The breakpoint of T5-6(8219) has not been localized cytologically within the satellite; the lack of near-luteus seedlings in testcrosses of heterozygous T5-6(8219) and heterozygous hcf*-26 plants suggests that the breakpoint is in the distal chromomere.

R. L. Phillips and S. A. Thompson

Ethidium bromide ineffectiveness and production of all male-sterile progeny by combining tillering and genetic male sterility

Research initiated in 1977 was to study the mutagenic induction of cytoplasmic fertility restoration of genetic male sterility in maize. Mutagenesis was attempted using ethidium bromide, an acridine dye used extensively to induce

cytoplasmic mutations in yeast and reported to induce cytoplasmic male sterility in plants. To facilitate selection and recovery of any altered cytoplasm, genetic male steriles were incorporated into high tillering lines. In this way high tillering plants that also were male sterile could be examined for differences in sterility between the main tassel and the tiller tassel(s). Any sterility/fertility differences between the tassels could suggest a cytoplasmic change restoring fertility to the genetic male sterile. Recovery of the altered cytoplasm would be possible in these high-tillering lines because the entire tiller is represented by approximately two cells in the mature kernel; cells for the ear and tassel primordia have not been differentiated for the tiller. Therefore, a cytoplasmic change induced in one of these cells should be expressed in at least a sector throughout the tiller. Any cytoplasmic change noted in the tiller tassel also would be expected to be present in the ear of that tiller. This can be compared with the tassel and ear of the main stalk where the tassel is represented by two to eight cells in the mature kernel, and the ear is represented by a different two to four cells. A cytoplasmic change induced in a cell destined to become part of the main stalk tassel will not necessarily occur in a cell destined to become part of the main stalk ear.

Lines established for mutagenesis included nine different genetic male-sterile loci in two inbred backgrounds (A632 and Oh43) used individually in crosses with three high-tillering lines. Genetic male-sterile loci included ms1, ms2, ms5 ms8, ms9, ms10, ms14, ms17, and po. The high tillering lines included 'Butter and Sugar' sweetcorn, WAICO, and a multihybrid for plant color (from Dr. E. H. Coe, Univ. of Missouri). Sufficient quantities of segregating lines were obtained by backcrossing the ms/high-tillering F1 with the appropriate male-sterile plant. Approximately 27,000 kernels from these lines were subjected to various ethidium bromide treatments (Table 1). Although long ethidium bromide treatments would completely inhibit kernel germination, there was no decrease in plant height and no increase in frequencies of seedling mutants, chlorophyll mutants, kernel mutants, etc. in any of the treatments.

Table 1. Ethidium bromide (EB) treatment variables.†

EB Conc.(M): 0.005, 0.05, 0.1
Treatment Length (h): 12, 18, 24, 36, 40, 42, 48, 58
Temp.(°C): 4, 24, 35
Solvent: H_2O, 5% DMSO, pH 3 phosphate buffer

†31 different treatments conducted from these variables.

Several instances of extruded anthers were noted on tiller tassels of otherwise male-sterile plants in one ms/high tillering combination. In most cases, pollen was not observed from these extruded anthers. There were three instances, however, where tiller tassels from plants in two consecutive cultures had extruded anthers that were shedding pollen. These plants were BC1 progeny from an A632 ms14 x Coe's multihybrid cross. Self pollinations were made on the tillers with extruded anthers, and an ear was formed from each of the three tillers with kernel numbers ranging from approximately 50 to 300 kernels per ear. One cross with a fertile sib (heterozygous for ms14) was made onto the main stalk ear of one of the three plants.

We planted kernels from each of the three self pollinations in our Hawaiian nursery but were limited to kernels from two of the three selfs in St. Paul. An average of 13 kernels per self germinated in Hawaii and produced all male-sterile plants. Observations from St. Paul corroborated that all progeny were male-sterile (Table 2). A total of 337 kernels from two of the three self pollinations germinated and produced male-sterile plants. Of these plants, 20% had extruded anthers either on the main stalk tassel or tiller

Table 2 S_1 progeny from self pollinations of tillers with extruded anthers on otherwise male-sterile plants.

Culture	% male steriles(no.)	% plants with anther extrusion(no.)
311-1	100(115)	25(29)
312-1	100(222)	18(39)
Total	100(337)	20(68)

tassel or both. Progeny from the sib cross to Ms14 ms14 resulted in a 1:1 segregation of male fertiles to male steriles. This segregation ratio was expected if the plant was sterile from being homozygous recessive for the ms14 locus. The 1:1 ratio also suggested that a cytoplasmic male sterile had not been induced by ethidium bromide as all progeny would have been expected to be male sterile if such a mutation had occurred.

The occurrence of all male-sterile progeny from a self pollination made on the tiller of a genetic male-sterile plant seems to be another example of how a gene can be expressed differently in the maize main stalk compared with the tiller. We do not believe that ethidium bromide had a significant role in the extruded anther observations as other types of mutations were not increased. Anther extrusion may be more the result of the tiller physiology and represent an interaction of ms14, A632, and Coe's tillering multihybrid.

M. C. Albertsen and R. L. Phillips

Localization, multiplicity, and repeat size of the 5S rRNA genes

In 1974 Wimber et al. (Chromosoma 47:353-359) reported that the maize 5S rRNA genes probably are located in 2L. In 1979 (Genetics 91:S76) we confirmed the 5S rRNA gene location. With two homozygous interchange lines, T2-6(8786) (6SNOR, 2S.97) and T3-6(030-8) (6SNOR, 3S.05) the 5S rRNA sequences hybridized to a site in 2L. Steffensen and Patterson (Genetics 91:S123, 1979) used the same approach to confirm the location of the 5S genes. Using a heterozygous interchange stock T2-6(5419) (6SNOR, 2L.82), they showed that the 5S genes are beyond 0.82 in 2L. Independently we performed in situ hybridization with T2-6(5419) but in homozygous condition. Our results place the genes at 2L.88. Only one site of silver grain localization has been observed in the various strains.

Using filter DNA/5S rRNA saturation hybridization we estimate 12,000 5S rRNA genes/2c nucleus in the inbred A188. For comparison, A188 possesses 7000 18 and 28S rRNA genes/2c nucleus.

We have begun to characterize the 5S rDNA repeat unit using restriction endonucleases. When maize DNA is digested to completion with the enzyme Bam H1 a basic unit occurs of 310 nucleotides. Dimers and multimers up to 10 times the size of the basic repeat unit are also clearly seen in these digests. This suggests that either the 5S genes have undergone considerable divergence or that the bases are modified rendering them unrecognizable by the enzyme. A more detailed report on this system is in preparation.

P. N. Mascia, R. L. Phillips, A. S. Wang and I. Rubenstein

Field tests of toxin-resistant plants derived from tissue cultures of T-cytoplasm maize

This investigation was performed to further characterize the effect of selected Helminthosporium maydis (race T) pathotoxin resistance in maize plants regenerated from cell culture (Gengenbach and Green, 1975, Crop Sci. 15:645-649; Gengenbach et al., 1977, PNAS 74:5113-5117).

Bulked seeds were obtained for the following lines: A188(N), a non-sterile cytoplasm resistant to pathotoxin; A188(T) obtained from the cross Wf9(T) x W22 and backcrossed to A188(N) seven times. A188(T) is a Texas male-sterile cytoplasm (T-cms) susceptible to pathotoxin; A188(T-R2) traces to a toxin-resistant cell line-2 plant selected in tissue culture during the second backcross generation of A188(T) and has subsequently been backcrossed four more times by A188(N).

Experimental design was a randomized complete block with four replications at each of two locations. Field plot measurements included emergence, silking and pollen shedding dates, and percent germination. Five randomly selected plants/plot

were either inoculated with H. maydis inoculum and pathotoxin or used to measure several morphological characters.

Nonsignificant differences were found for field plot measurements on emergence and silking dates (Table 1). A188(N) and A188(T-R2) responded similarly with

Table 1. Field plot measurements and H. maydis pathotoxin/inoculum reactions.

Genotype	Days to[1] Emergence	Days to[1] Pollen shed	Days to[1] Silking	% Germination	Pathotoxin/inoculum reactions[2]
A188(N)	7.0	66.5	68.0	86.0	-
A188(T)[3]	7.5	-	67.5	84.5	+
A188(T-R2)	7.0	65.5	67.5	91.5	-

[1] Based on 50% of the total number of plants.
[2] As indicated by the presence or absence of chlorotic lesions.
[3] T-cms.

respect to pollen shedding date and reaction to H. maydis pathotoxin and inoculum. The male-fertility and disease resistance traits associated with A188(T-R2) have been previously shown to be inherited only through the female (Gengenbach et al., 1977). Percent germination for A188(T-R2) was, on the average, higher than both A188(N) and A188(T).

Table 2. Total plant height, tassel culm length, and plant height above and below the ear (in centimeters).

Genotype	Total hgt	Tassel culm	Hgt below ear[2]	Hgt above ear
A188(N)	159.1a[1]	54.1	47.1a	57.9a
A188(T)	147.2b	51.2	44.7b	51.3b
A188(T-R2)	153.8a	51.6	44.3b	57.9a

[1] Change in lower case letter indicates significance at the .05 level.
[2] Significant T-cms by environment interaction.

Tassel culm lengths for A188(N), A188(T), and A188(T-R2) did not significantly differ (Table 2). Environmental interactions were observed for plant height below the ear but A188(T-R2) was significantly shorter than A188(N). This result may be correlated with the significantly fewer number of nodes below the ear (Table 4). Total plant height and plant height above the ear for A188(T) was found to be significantly less than A188(N) and A188(T-R2). Because of nonsignificant node number above the ear (Table 4), height differences were primarily due to shorter internodes in A188(T) (Table 3). Significantly shorter internode lengths were

Table 3. Average internode lengths for plants with ears at the 5th node (in centimeters).

Genotype	Internode number 1	2	3	4	5	6	7	8	9	10	11	12
A188(N)	12.0	12.4	12.2a[1]	11.1a	9.5a	11.2a	10.9	9.1	7.1	4.6	2.6	1.7
A188(T)	12.7	12.1	11.4b	9.8b	8.6b	10.3bc	10.4	8.7	6.6	4.6	2.4	1.2
A188(T-R2)	13.2	12.7	12.6a	11.2a	9.5a	11.1ac	10.1	8.9	6.7	4.2	2.8	1.8

[1] Change in lower case letter indicates significance at the .05 level.

observed for the three internodes directly above the ear and the internode immediately below the ear. Duvick (1965, Adv. Genetics 13:1-56) and others (Grogan and Sarvella, 1964, Crop Sci. 4:567-570; Josephson and Kincer, 1962, Crop Sci. 2:41-43) have indicated similar results with T-cms. Duvick also reported that plant shortening is enhanced by pollen sterility which in this case is caused by T-cms. The loss of pollen sterility observed in A188(T-R2) may partially explain the increase in plant height. Similar effects have been seen when T-cms was restored to fertility (Duvick, 1965; Sarvella and Grogan, 1965, Crop Sci. 5:235-238).

Table 4. Average total number of tassel branches, leaves/plant, nodes below and above the ear, and total number of nodes.

Genotype	Tassel branches	Leaves/plant[1]	Nodes below ear[2]	Nodes above ear	Total
A188(N)	19.5	10.8a	6.6a	5.3	11.8a
A188(T)	19.0	10.3b	6.2ab	5.0	11.2b
A188(T-R2)	19.5	10.1b	6.0b	5.1	11.1b

[1] Change in lower case letter indicates significance at the .05 level.
[2] Significant T-cms by environment interaction.

Number of leaves/plant was based on the visible number of nodes/plant. A188(T) and A188(T-R2) gave similar responses but had significantly fewer leaves/plant than A188(N) (Table 4). Duvick (1965) reported a parallel situation based on the number of visible leaves in T-cms restored, nonrestored and normal cytoplasm.

Nonsignificant differences were observed for the number of tassel branches and number of nodes above the ear (Table 4). A significant environmental interaction was found for the number of nodes below the ear but A188(T-R2) had significantly fewer nodes than A188(N). Grogan and Sarvella (1964) found that differences in these characters depended on genotype and environment.

The effects of T-cms appear to be consistent with results previously cited in the literature. The response of A188(T-R2) was similar to A188(N) except for the number of nodes and internode length below the ear, total number of nodes, and number of leaves/plant.

P. F. Umbeck and B. G. Gengenbach

Notes on golden and brown midrib mutants

Golden: The golden segregating in F2 from one of three F1 plants from A344 x A659 (MGCNL 53:89) is allelic to golden-1.

Brown midrib-3: Seed obtained from A. N. Hume, Brookings, South Dakota and grown by me at Madison, Wisconsin in 1928 was homozygous brown midrib. One lot of seed was Hume's 35-69-24#86F4, the other was his 34-69-24#86F4. My cross with brown midrib-1 obtained from Wm. H. Eyster and with the Wisconsin brown midrib-2 (J. Amer. Soc. Agron. 24:960-963, 1932) showed it to be genetically different from both. None of the previous Maize News Letters has this information.

Other brown midrib stocks: One that was segregating in Coop 60-M14/236-2, labeled M14 gl9 + bm is allelic to bm2. Another that traces back to a cross of A188 x su la is allelic to bm1.

C. R. Burnham

Tests for cytoplasmic restoration of genetic male sterility

F2's from all reciprocal crosses between the seven inbreds in one group, six inbreds in another group and six inbreds in another failed to segregate for male sterility (see Maize News Letter 53:88-89 for the list of inbreds).

All except inbred A659 have been tested as female parents against male sterile-1. The yellow inbreds were crossed with y +/y ms and only F2's from ears segregating Y vs. y were grown. For Oh43 and A73, one of the two ears segregating Y vs. y and for A638 both ears segregating Y vs. y did not segregate for male sterility. These are probably from y + crossovers, rather than the result of cytoplasmic restoration, but will be tested further. For the white endosperm inbreds, only Y ms/Y + plants were available. For K55 three F2's segregated male-sterility and three did not. For CI66, the six F2's did not segregate male sterility. The crosses with inbred CI66 will be tested further.

White endosperm lines from several exotic bulks are being tested also against ms1. Plants that are Y ms/y + are now available for those tests.

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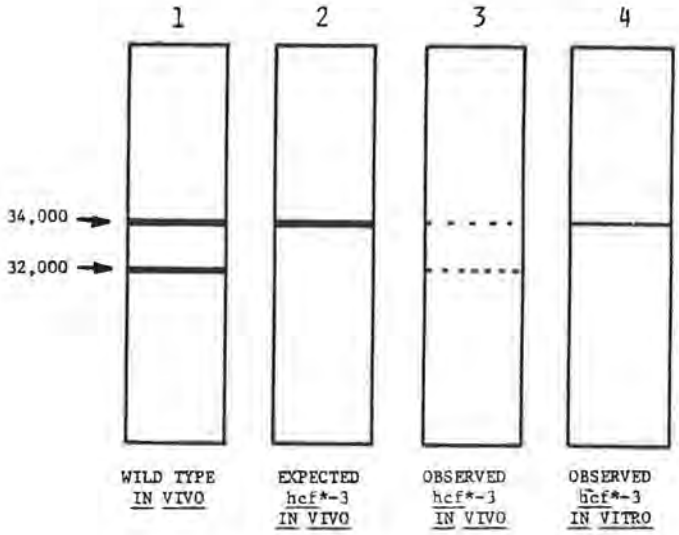
Does the nucleus control certain chloroplast transcriptional translational events?

Several laboratories are currently investigating the processing (i.e. post-translational modification) of chloroplast membrane proteins. One such protein which undergoes processing in maize plastids is the 32,000 dalton lamellar polypeptide. Extensive work in the laboratory of Dr. Lawrence Bogorad suggests the following with respect to the 32,000 dalton lamellar polypeptide in maize: 1) the structural gene for this polypeptide resides on chloroplast DNA; 2) the polypeptide is first synthesized, both in vivo and in vitro, as a precursor with an apparent molecular weight of 34,500 daltons; 3) translation of the precursor takes place on 70S ribosomes; 4) processing of the precursor polypeptide involves a reduction in apparent molecular weight from 34,500 daltons to 32,000 daltons; 5) nuclear information may be necessary for the processing step to occur; and 6) the production of the 34,500 dalton precursor polypeptide is primarily under transcriptional control during photoregulated development (i.e. greening) (for further details see Bedbrook et al. PNAS 75:3060; Grebanier et al. JCB 78:734). Thylakoids purified from the photosynthetic mutant hcf*-3 are missing the 32,000 dalton polypeptide (MGNL 53:38-

40); in accordance with (5) above, we expected that this lesion might affect the processing of the precursor polypeptide, possibly resulting in the accumulation of the 34,500 dalton polypeptide and an accompanying loss of the 32,000 dalton species.



In the accompanying figure we present autoradiograms of thylakoid membrane proteins which were labeled with ^{35}S-methionine. Coomassie stained polypeptide profiles are not presented for two reasons: 1) the homology between Coomassie stained bands and radiolabeled polypeptides comigrating with stained bands in the 32,000 to 35,000 dalton region of the gel is uncertain, and 2) the product-precursor relationship described above, as well as the physical mapping data locating the structural gene to chloroplast DNA, have both been elucidated using radiolabeled, rather than stained, polypeptides. For simplicity, the complex pattern of radiolabeled thylakoid membrane proteins obtained upon in vivo or in vitro labeling is not shown in order to focus attention on changes in the 32,000 to 35,000 dalton region of the gel. In control experiments chloroplasts from both hcf*-3 and sib controls were able to incorporate radiolabeled methionine into thylakoid proteins either in vivo or in vitro; the similarity of the patterns obtained from hcf*-3 and sib controls in regions other than the 32,000 to 35,000 dalton region suggests that photosynthetically inactive chloroplasts from hcf*-3 are capable of protein synthesis.

The labeling patterns reported here are in general agreement with the patterns obtained by Grebanier et al.; as shown in lane 1, lamellar polypeptides with apparent molecular weights of 34,000 and 32,000 daltons become heavily labeled when whole leaves are fed ^{35}S-methionine. The small discrepancy between the molecular weight assignments for the larger polypeptide reported by Grebanier (34,500 daltons) and that reported here (34,000 daltons) is probably due to differences in electrophoretic technique and/or gel calibration. According to the data discussed in (5) above, nuclear mutation at the hcf*-3 locus might be expected to block the processing of the radiolabeled 34,000 dalton polypeptide; the anticipated pattern would be as diagrammed in lane 2. In contrast, when whole leaves from hcf*-3 were fed ^{35}S-methionine, very little label was seen at either 34,000 or 32,000 daltons (lane 3), suggesting that the synthesis of the precursor is largely blocked. The small amount of the 34,000 dalton polypeptide labeled in the mutant was accompanied by a similarly small amount of the "processed" 32,000 dalton species.

A further surprising result was found upon in vitro labeling of chloroplasts isolated from hcf*-3; as shown in lane 4, there are indications that these chloroplasts are able to synthesize the 34,000 dalton polypeptide! This would be consistent with the production of a diffusible inhibitor as a consequence of the hcf*-3 mutation; removal of this inhibitor during chloroplast isolation would permit the synthesis of the 34,000 dalton species. Grebanier has reported that isolated plastids are able to synthesize, but not to process, the 34,000 dalton polypeptide; our autoradiograms show little, if any, processing.

These data suggest that the nuclear lesion hcf*-3 may affect transcriptional or translational events in the chloroplast which normally lead to the synthesis of the 34,000 dalton polypeptide; the small amount of this polypeptide present in the mutant is apparently processed normally. The fact that the radiolabeled 32,000 and 34,000 dalton polypeptides are the only polypeptides affected by the mutation suggests that such nuclear control over chloroplast transcription/translation is specific. We cannot as yet rule out (by transmission genetics) the possibility that the chloroplast DNA is specifically altered in plants homozygous recessive for hcf*-3; the absolute lack of photosytem II activity leads to seedling lethality. The in vitro labeling study, however, suggests that the chloroplast DNA is unaltered; production of a labeled 34,000 dalton polypeptide apparently occurs under these conditions. Further experimentation is planned to firmly establish the structural identity of the 32,000 dalton polypeptide produced in vivo with the 34,000 dalton polypeptide produced both in vivo and in vitro; collaborative experiments are planned to distinguish between possibilities of transcriptional vs. translational control.

Kenneth Leto and Charles Arntzen

Chloroplast membrane structure in a green photosynthesis mutant

As previously described in the Newsletter, nuclear mutations affecting light reaction photosynthesis can be selected by screening seedlings for elevated levels of chlorophyll fluorescence. One of these mutants, hcf*-3, is specifically blocked in photosystem II; this loss appears to be strongly correlated with the loss of a major lamellar polypeptide with an apparent molecular weight of 32,000 daltons (MGNL 53:38-40). In contrast to most photosynthetic mutants described in flowering plants, hcf*-3 is nearly fully green. As part of a larger project, we have investigated the ultrastructure of plastids from hcf*-3 to determine whether the mutational loss of activity is accompanied by alterations in plastid structure.

Our examination of thin sectioned leaf material extends a previous study by Miles (Plant Physiol. 53:589). Mesophyll chloroplasts from hcf*-3 show extensive areas of membrane appression (grana stacking), although the number of thylakoids per granum is reduced and the length of the grana stacks is increased as compared to chloroplasts from control sib seedlings. Bundle sheath chloroplasts from both hcf*-3 and control sibs are typically agranal; ultrastructural differences between the two were minimal. Numerous ribosomes were seen in both mesophyll and bundle sheath plastids from mutant and control sibs. These observations suggest that 1) although photosystem II activity is preferentially localized in grana (Armond and Arntzen, Plant Physiol. 59:398), the loss of photosystem II function in hcf*-3 does not prohibit grana stacking, and 2) plastids from hcf*-3 should be capable of 70S ribosome-dependent protein synthesis.

The internal organization of the thylakoid membrane was examined by freeze-fracturing chloroplasts obtained from both hcf*-3 and wild type sibs; this technique splits the membrane along its hydrophobic interior and allows the visualization of protein complexes which appear as particles of characteristic sizes and densities on the fracture faces. We were particularly interested in determining whether chloroplasts from hcf*-3 contained particles on the exoplasmic (EF) faces; large particles on these faces, particularly in stacked regions (EFs), have been correlated with photosystem II activity. These large particles consist of a "core" which probably contains the reaction center for photosystem II. The core is in turn surrounded by subunits of the light harvesting chlorophyll a/b pigment protein complex (LHC), which serves a role both in capturing incoming quanta and in the maintenance of grana stacking (Arntzen, in Current Topics in Bioenergetics, Vol. 8, p. 112). Examination of freeze fracture replicas of mesophyll and bundle sheath

chloroplasts from hcf*-3 revealed a marked decrease in both the size and the density of the EFs particles, and a marked reduction in the size of particles found on this face in unstacked regions (EFu). Examination of the complementary protoplasmic (PF) face showed an increase in particle density on both the stacked (PFs) and unstacked (PFu) faces.

We interpret these data as follows: the nuclear lesion hcf*-3 causes the loss of a 32,000 dalton lamellar polypeptide. This polypeptide functions in organizing the photosystem II reaction center core complex; in the absence of the 32,000 dalton polypeptide the cores of the large EFs particles are not formed, and photosystem II activity is lost. Without an organized photosystem II core the large EFs particles (consisting of the photosystem II core plus peripheral LHC) cannot organize, leading to the loss of the large particles on the EFs face. We know from electrophoretic analysis that the LHC is nonetheless present in thylakoids isolated from hcf*-3; the presence of the LHC, which is necessary for grana stacking, facilitates the formation of grana even in the absence of the large EFs particles. The "defective" EFu particles, as well as some of the "extra" particles seen on the PF faces, may represent "free" LHC subunits which are not associated with photosystem II cores.

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Isolation and characterization of maize flavonoids

Efforts to identify the flavonoids in maize started in the early twenties when C. E. Sando and H. H. Bartlett (J. Biol. Chem. 54:629-654, 1922) reported the presence of isoquercitrin in extracts of brown husked (a B Pl) maize. Later, C. E. Sando, R. T. Milner and M. S. Sherman (J. Biol. Chem. 109:203-211, 1953) identified chrysanthemin from purple husked (A B Pl) maize. Since that time, interest has been concerned mainly with the anthocyanins, and in many cases reports have indicated only the aglycone base. Recently, characterizations of flavonoids in silks were made by C. S. Levings and C. W. Stuber (Genetics 69:491-498, 1971), and J. Trautman and B. C. Mikula (MGCNL 49:29-32, 1975) reported spectral data for a number of compounds in different tissues, although some of their tentative identifications did not agree totally with their spectral data.

To understand fully the factors controlling maize flavonoid synthesis, all of the flavonoids in maize should be completely characterized. Ideally this requires isolation and purification of enough of each compound to allow characterization by UV and NMR spectra. This task is made simpler if the genotype and tissue of the plant is chosen to maximize the yield of the desired compounds and minimize the yield of other flavonoids that might interfere with their purification.

We have so far identified two compounds by the following procedure: Dried husks from a B Pl P-WW plants (which accumulate mostly flavonol glycosides because the flavone pathway is blocked by the P-WW allele) were extracted in 80% MeOH. The extract was concentrated under reduced pressure; taken up in boiling water for treatment with Celite Analytical Filter Aid; filtered under vacuum and then extracted with ethyl acetate (F. W. Collins and B. A. Bohm, Can. J. Botany 52:307-312, 1974). An additional extraction of the aqueous extract by BuOH improved the yield of the polar flavonoids (G. A. Guppy and B. A. Bohm, Biochem. Syst. Ecol. 4: 231-234, 1976). Initial separation was made on a Sephadex LH-20 column using a linear elution gradient of increasing concentration of methanol in water. Each

fraction taken from the Sephadex column was subjected to a further separation on a Polyamid SC-6 column using a linear elution gradient consisting of ethyl acetate: butanone:90% MeOH operated from 50:50:10 to 50:50:100. Final purifications of the compounds were achieved by repeated TLC on Polyamid DC-6.6, using dichlorethane: butanone:H_2O:MeOH:HOAc (50:20:5:20:5), on Avicel microcrystalline cellulose, using 15% acetic acid in water or ethyl acetate:formic acid:H_2O (10:2:3). Hydroxylation and glycosylation patterns were determined by inspection of Rf, analysis of UV spectra (T. J. Mabry et al., The Systematic Identification of Flavonoids, Springer, New York, 1970) and identification of acid hydrolysis products. Acid hydrolysis was performed using 0.1 N HCl at 100° C for 1 hr. Aglycones were identified by Rf on Polyamid DC-6.6 TLC using chloroform:butanone:MeOH (70:15:15) and by color in UV light after spraying with 0.1% diphenylboric acid aminoethyl ester in MeOH:H_2O (1:1). Sugars were chromatographed on Avicel microcrystalline cellulose TLC in ethyl acetate:pyridine:water (10:3:2) and were detected by spraying with reagent according to T. J. Mabry et al. (The Systematic Identification of Flavonoids, Springer, New York, 1970). NMR spectra were determined using TMS as internal standard.

Chromatographic and spectral data of two flavonols in maize

*Compound	R_f x 100			λ max					***Colour			Aglycone
	**I	II	III	MeOH	NaOAc	NaOAc + H_3BO_3	$AlCl_3$	$AlCl_3$+ HCl	UV	NH_3	Na_2CO_3	
A Quercetin 3-glucoside	29	54	34	255,290sh 355	267,308sh 385	260,377	275,336 430	264,342 393	D	Y	Y	Quercetin
B Isorhamnetin 3-glucoside	42	70	33	226,257 268sh 308sh,356	273,325 368	256,310sh 353	266,304 363,396	265,305 357,393	D	Y	YG	Isorhamnetin

*Compound A = Quercetin-3-O-β-D-glucopyranoside
Compound B = Isorhamnetin-3-O-β-D-glucopyranoside

**I - dichlorethane:butanone:H_2O:MeOH:HOAc (50:20:5:20:5). Polyamid DC 6.6
II - ethyl acetate:formic acid:H_2O (10:2:3). Avicel microcrystalline cellulose
III - 15% HOAc. Avicel microcrystalline cellulose

***Colour in UV light alone, in presence of ammonia and in UV after Na_2CO_3 (3% in MeOH) spray
D - dark
Y - yellow
YG - yellow green

The two compounds so far identified by this process are quercetin-3-glucoside (isoquercitrin) and isorhamnetin-3-glucoside. The latter compound is reported for the first time in maize. It is usually overlapped by quercetin-3-glucoside on a chromatogram of a crude extract and is easily overlooked. These two compounds correspond to the spots Qu1 and Qu11 on the TLC figure shown in last year's News Letter. There are several other flavonols present in this tissue but in smaller quantities and we have not yet enough material for the NMR spectra.

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Diploperennis, a premaize teosinte of value in corn breeding

Zea diploperennis is a perennial diploid teosinte that was only recently discovered by Iltis in Mexico. It is ancestral to the tetraploid perennial known for over two-thirds of a century earlier from the same general area (southern Jalisco).

The detailed morphology and identification of the individual chromosomes of two collections (H. Iltis and T. A. Kato) of the material is underway. The chromosomes although essentially knobless show strikingly prominent chromomeres terminating one or both the arms. In a few cases where these fuse they give the appearance of very small knobs described by Longley as dimunitive knobs in the 4n perennial.

From the analyzable pachytene preparations, chromosomes six, seven, eight and ten have been identified. In essence the chromosomes of maize and diploperennis are similar, if not identical.

Meiosis is regular. Ten bivalents are formed. In a few instances nine bivalents and two univalents are noticed. Chromosome distribution at anaphase is normal with sporadic occurrence of laggards.

Contrary to expectations the diploid has larger pollen than the tetraploid. The pollen of the 2n is similar in size to the pollen of Guatemalan teosinte and that of primitive corn (Chapalote).

The 2n is more primitive than the 4n in being a stronger perennial. The 2n develops enlarged underground buds (tuber-like) that may remain dormant for a month or more while the 4n is in a state of continuous growth. Even the F1 hybrid with corn has a month to six-week dormancy period between the maturation of the plant and appearance of a basal flush of tillers. At first the F1 hybrid may appear to be annual like its corn parent but patience by the observer shows this not to be the case. Studies on the inheritance of perennialism will be complicated by this dormant behavior.

In contrast to the paired female spikes of the annual teosintes, the 2n perennial usually has solitary spikes like most corn. In the 2n hybrid of diploperennis with corn, both the spikes and spikelets tend to be paired.

Diploperennis has potential for the development of new types of corn. Like corn, it is not winter hardy in northern United States, despite its adaptation to high elevations in Mexico. The dormancy factor might help it to overwinter in southern United States.

Walton C. Galinat and Chandra V. Pasupuleti

Preliminary studies of maize vs. teosinte pollen-tube competition in short styles

The feasibility of techniques designed to determine why the pollen of modern teosinte is significantly smaller than that of its sympatric maize was tested in a pilot experiment. The following conclusions now stand: (1) Purple aleurone works satisfactorily as a marker for the fertilizing success of maize pollen in mixture with teosinte pollen. (2) Maize styles may be sheared to about a length of one inch for applications of maize-teosinte pollen mixtures. (3) In Massachusetts, at least, about 3 days after pollination of the sheared silks an insecticide dust such as Chlordane should be applied to control damage from earwigs. These insects prefer the maize-teosinte hybrid kernels. (4) Small piles of maize and teosinte pollen placed in the crease of a folded piece of paper may be rocked into a mixture. Because the maize pollen is larger in diameter than that of teosinte, the

apparent size of the pile of maize pollen going into the mixture should slightly exceed that of teosinte in order to approximate a 50-50 mixture. (5) Because the actual frequency of the two types of pollen going into the mixture is only an approximation or guess, about half of the mixed pollen from a single batch used in each pollination on a sheared ear should also be used on the silks of a normal (not-sheared) control ear shoot.

In the preliminary tests so far, pollen of Hopi Blue Flour was mixed with that of Northern teosinte and then placed on the shortened styles of the dent corn hybrid B73 x Mo17. The results for five such pollinations totaled 441 blue kernels and 768 yellow kernels. Thus it would appear at first that the teosinte pollen had a greater frequency of fertilizing success in competition with corn pollen within short styles. But in mixing the pollen, adjustment in the volume was not made to account for the smaller size of teosinte pollen. Controls on long style ears should also have been made for each batch of mixed pollen. The experiment will be repeated next year taking these factors into account.

The pollen-size problem is involved in the origin of corn. Because 5 out of 14 fossil pollen grains from a drill core dated at 80,000 years are too large to be that of modern teosinte and are more similar in size to that of modern corn, it was concluded that the ancestor of corn is corn and not teosinte.

Walton C. Galinat

Indeterminate vs. determinate ears

Field corn breeders have generally appreciated the value of selection for ears with slightly barren or unfilled tips which have one or more non-functional spikelets near or at the growing point. Such indeterminate ears have a potential to elongate or continue growth under unusually favorable growing conditions. This capacity for continued elongation occurs in various grasses with indeterminate inflorescences such as the relatives of corn.

In contrast, the trait for determinate ears occurs in certain strains of corn, especially in sweet corn where consideration for "complete tip fill" with deep kernels tends to conflict with selection for increased ear length and increased yields. In the determinate ear type, continued differentiation is abruptly terminated resulting in a terminal functional spikelet. Sometimes the expression is semi-determinate in that the uppermost spikelet is male with a capacity to continue male differentiation. When the determinate or semi-determinate ear encounters unusually favorable growing conditions, it can't respond with growth in ear-length. Rather it has to take other options. The extra energy may be channeled toward the development of deeper kernels which is highly desirable. But it may also be wasted on the development of non-functional tassel tips on the ear or sometimes in the form of secondary and lower non-usable ears. Since the tip of the ear in sweet corn is frequently snapped off by man or destroyed by earworms anyway, it would seem more practical to select for the indeterminate type of ear. Then a potential for increased ear length could be realized in favorable years. Increased kernel depth is independent of ear type although it is common in high kernel-row number ears. It must be borne in mind that only a given amount of energy is available, regardless of what ear type or kernel size and shape it is packaged in.

The indeterminate ear is largely dominant in expression. Such a factor occurs on chromosome 9 in teosinte and apparently in the same position in corn.

Walton C. Galinat

Priorities in sweet corn trials

Most sweet corn breeders have in the past regarded sweet corn trials to mean simple yield trials. If sweetness and tenderness is evaluated, it is on one's own hybrids, seldom for the hybrids of someone else that are included in the trial.

Yet the consumer, the customer is much more interested in the sugar content and tenderness than he is in yield. The customer has demonstrated that he is more than willing to pay a much higher price for a higher quality sweet corn and the farmer a higher price for the seed. In the future corn breeders will be forced by competition to pay more attention to endosperm quality as measured by the use of hand-refractometers in their breeding nursery and hybrid trials. The hand-refractometer measures a combination of sucrose and WSP (water soluble polysaccharide or phytoglycogen) often giving readings up to 30% in su su se se combinations. In contrast the so-called super sweets based on sh2 without WSP may give readings of only 5 to 9% sucrose.

There are conflicts and contradictions in present breeding practices. While on the one hand the breeder is selecting for high yielding capacity in his trials, on the other he selects for completely-filled determinate ears that have a restricted potential to produce long ears and high yields. In the area of high eating quality, the seed producer wants a smooth pseudo-starchy type of kernel that can be roughly treated in harvesting and shelling. In other words, high eating quality is the opposite from high seed quality.

Walton C. Galinat

Measurement of heterosis by both electrophoresis and yield in hybrids containing teosinte and Tripsacum germplasm

An investigation is underway to examine the combining ability of maize inbreds containing various teosinte segments that have been crossed with a Tripsacum addition stock and the normal control. Heterosis is being tested in the field by a three-way yield trial. The first block consists of seven different hybrid combinations of introgressed segments from teosinte within an isogenic background of A158. The second block results from the crossing of seven A158 teosinte derivative lines with a Havels-A158 line carrying a Tripsacum addition disome (Tr7). The third block operates as a control in that it is a cross between the seven teosinte derivative lines and the Havels-A158 line without the Tripsacum chromosome.

The yield of each line is recorded. Then, comparisons between and within the three blocks allow an estimation of hybrid vigor and of general combining ability.

A cytological examination of the hybrids involving the Tripsacum chromosome is made to verify its presence. It was observed in each line in only 50 to 75% of the plants examined, showing reduced transmission in this material.

A further measure of genetic interaction within the hybrids will involve their examination via gel electrophoresis. Kernel proteins as well as isozymes will be investigated. Preliminary results indicate that certain combinations of teosinte and Tripsacum germplasm give a significant increase in yield. The associated electrophoretic study will hopefully quantify this interaction. The lines will also be evaluated in terms of the hybrid dysgenesis syndrome to determine if this process occurs in these hybrids.

This investigation is being undertaken as part of my doctoral research requirements for the Ph.D. degree under supervision of Dr. Walton C. Galinat.

Joel I. Cohen

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Anthranilic acid accumulation and pistil proliferation: a second instance?

Pt (Polytypic ear) is a dominant gene on chromosome 6 in maize which causes a variety of disturbances in floral development (see Nelson and Postlethwait, Amer.

J. Bot. 41:734-748, 1954, and 51:238-243, 1964). Among biochemical correlates of Pt expression is elevation of anthranilic acid level in developing florets (Williams, Dissertation Abstracts 27:3801B, 1967).

Homozygous Bf (Blue fluorescent) maize seedlings and heterozygous/homozygous Bf anthers accumulate sufficient amounts of anthranilic acid to alter the color of U-V fluorescence (see Teas and Anderson, PNAS 37:645-649, 1951). Apparently, no morphological modification of vegetative or reproductive structures has been associated with Bf.

In 1975, I requested seeds of the Coop's wx Bf stock from Dr. Lambert with the intention of eventually looking at interaction of Pt and Bf. On several of the plants from those seeds, no silks emerged from the ears because--as I discovered too late to use the pollen, and much to my surprise--of Pt-like (sterile) pistil proliferation from both upper and lower ear florets. These plants and all their sibs had been detasseled (to protect a nearby isolation plot) and no sibs were selfed. However, several sibs were used as females in specific crosses.

I found no such Pt-like symptoms on ears from any sibs, nor on any ears on F1's from the sibs. Of 216 F2 plants (a sample aggregate from 21 F1's), all were female fertile, but ears from seven did show lower floret and occasional upper floret pistil proliferation. Though pollination of the F2 ears was not controlled, kernels from the seven ears showing Pt-like symptoms produced blue fluorescent seedlings in high enough proportion to indicate all were homozygous Bf. Only two of the seven apparently were homozygous wx.

A second supply of wx Bf seeds was obtained from Dr. Lambert in 1979. Six-week-old plants from these seeds were partially defoliated (a practice which considerably attenuates Pt expression--perhaps by slowing metabolic rate in developing florets?). All ears "silked" normally, and I was able to self all but two plants. Ears from three of eighteen plants (including an unpollinated one) showed pistil proliferation from lower florets.

Dr. Lambert has indicated that contamination of the wx Bf stock with Pt cannot account for the Pt-like symptoms I am observing. My limited data are consistent with the hypothesis that these symptoms are due rather to a recessive gene which may depend on homozygous Bf for expression. However, other explanations involving variable penetrance (a characteristic of Pt!) cannot yet be ruled out.
Dr. Lambert's stock number for the 1979 seed sample is 74-853-6. Over the next couple of years, I will be trying to establish a strain (homozygous??, Bf??) from the above-mentioned selfed pistil-proliferating ears which expresses this phenotype at or near the 100% level.

If anyone is aware of published or unpublished examples of similar morphological correlates of Bf, bf2, or any gene other than Pt, please let me know.

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Notes on the selection of point mutations in inbred lines

The procedure used to select point mutations in inbred lines involves the treatment of plants before meiosis with a mutagen and using the pollen as a screen to screen out undesirable mutations. Most of the mutations due to chromosome breakage events will be screened out due to pollen abortion. A few very small deficiencies may pass through the pollen, however many of these will produce smaller size pollen. Cytoplasmic mutations will be screened out since little or no cytoplasm passes through the pollen. This procedure permits the use of high dosages of the mutagen. Point mutations should occur more frequently at high

dosages (however, unless the undesirable mutations are screened out the load of chromosome breakage events may be so high that it may be impossible to select the point mutations, in which case lower dosages of the mutagen should be used.) The procedure used most frequently involves treating the seed of an inbred line with a dosage of a mutagen which results in about 10 to 20 percent of the plants producing a tassel. Pollen is collected from these plants and crossed to the normal inbred line plants. Plant progeny from such crosses appear similar to the normal inbred line plants except for an occasional plant. Usually, we grow 50 plants from an individual cross involving a mutagen and self 10 to 15 plants. Inbred line Oh43 is being used in our studies. One type of mutation being sought are those which increase the vigor of the plant. One plant considerably larger than the others was selfed and found to be heterozygous for a recessive allele (a deficient type endosperm in this case). Plants homozygous for the mutant allele appeared to be the same size as the normal inbred line plants; the heterozygotes are larger. Several other plants (not all) classified as slightly taller were also found to be heterozygous for various visible recessive alleles. A series of various visible recessive alleles have been produced and a study is in progress to determine the vigor characteristics associated with these alleles in the relatively homozygous background of the inbred line. The data are not complete nor an analysis made at this time, however observation suggests that the most frequent characteristic associated with heterozygotes involving visible recessive alleles is early silking and early pollen shed.

E. J. Dollinger

Vigor effects of visible recessive alleles in hybrids

Since a number of the visible recessive alleles (point mutants) appear to affect vigor characteristics as heterozygotes in the inbred line a study is in progress to study the vigor characteristics associated with these alleles as heterozygotes in hybrid combination. At this time the data have been analyzed for one such allele in hybrid combination. The allele involved is case 14, ora3 (orange endosperm). The control hybrid is Oh43 x Oh551 which is compared with Oh43-ora3 x Oh551. The results are presented below:

	+/+	+/-
Days to silk	78.69	77.71**
Plant height (cm)	235.94	244.84**
Grain wt. per 100K (gm)	36.06	38.61**
Grain wt. per plant (gm)	229.68	221.83*
Ear length (cm)	18.25	17.80**
Ear diameter (cm)	4.83	4.76**
Kernel row no.	15.23	14.81*
Ears per plant	1.30	1.28

*, ** significant at P = 0.05 and 0.01 levels, respectively.

Thus, this allele as a heterozygote in hybrid combination decreases the time to silking, increases plant height, increases kernel weight and decreases yield expressed as grain weight per plant due to smaller ears. The number of kernels of the heterozygote must be less. The data have not been analyzed on the vigor effects of this allele in the inbred line, however observation indicates that the heterozygous plants are taller than those of the normal inbred line plants.

E. J. Dollinger

ADDENDUM

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Effect of Sup-W70 o2/o2 gene on fractional composition of endosperm proteins

In our earlier paper (MGC, 1979, 53:108-111) we reported about the dominant mutation converting loose outer portions of opaque-2 endosperm into dense flint-like ones. Due to this flint shell high lysine corn improves its resistance to Fusarium diseases and low temperatures in soil at emergence (Doklady, WASHNIL, 1979, 5:3-5).

Table 1. Protein and lysine content in the endosperms of W70 line mutants

Genotype	Endosperm type	Share of dense tissue of endosperm	Protein content (%)		Lysine content in protein (%)	
			Integral endosperm	dense part of endosperm	Integral endosperm	dense part of endosperm
o_2o_2 sup sup	floury	0.0	9.8 ± 0.52	---	3.68 ± 0.046	---
o_2o_2 Sup Sup	modified	0.4	10.5 ± 0.44	10.9 ±0.71	3.28 ± 0.069	2.93 ± 0.051
$o_2^+o_2^+$ sup sup	flint-floury	0.7	11.0 ± 0.52	11.2 ±0.68	2.50 ± 0.042	2.28 ± 0.078

The data on lysine and protein fractions distribution in different parts of a modified endosperm (Tables 1, 2) show a local specific effect of a suppressor. The major effect of the suppressor and a dominant allele of o2 gene results in intensification of zein synthesis. However, while the o2+ allele intensifies zein synthesis in an integral endosperm by 3.9 times, the suppressor in 3 doses increases it only by 2.2 times. Practically, the suppressor does not influence the total content of water-soluble proteins. The additional synthesis of zein mainly takes place in a dense portion of an endosperm for account of glutelin-3 fraction.

Table 2. Content of non-protein and protein nitrogen in endosperm of W70 mutants

Endosperm	Nitrogen content (%)						
	albumins & globulins	zeins	glutelins G_1	glutelins G_2	glutelins G_3	extractive	non-extractive residue
floury, integral	11.51	12.14	7.05	9.47	38.85	11.66	9.32
modified, integral	10.73	26.58	7.19	9.35	29.81	8.30	8.06
dense part of modified endosperm	10.76	40.21	6.61	9.04	21.57	6.80	6.08
flint, integral	5.72	47.04	5.51	9.18	22.30	6.65	6.20

At the same time considering the equal concentration of lysine in protein of floury and flinty parts of an endosperm (Table 1) the dominant allele of the o2 gene manifests in a similar way in all parts of an endosperm. In contrast to the suppressor the o2+ allele hampers synthesis of albumins and globulins greatly (Table 2).

A. S. Mashnenkov

Use of ig mutation for cms counterparts of corn lines

In 1972 the ig mutation stimulating the occurrence of androgenic haploids was obtained from Maize Genetics Cooperation. We tried to find out possible ways of use of this mutation in corn breeding. Dr. J. L. Kermicle (Science, 1969, 166: 1422-1424), who discovered it, reported that its presence in a female parent results in the occurrence of androgenic haploids up to 3% frequency. In our six-year experiments the average frequency of androgenesis due to ig mutation was about 0.03%. However, in some ears it reached 1.5%. Such pleiotropic effects of the ig gene as a lack of some kernels in ear and small size kernels, somewhat hamper the isolation of haploids through the A C R-nj marker system. Therefore, it proves expedient to use matroclinical haploids for the development of homozygous lines.

Mutation ig may successfully be used for the transfer of lines to cms by androgenesis. To realize this use ig and A C R-nj genes were incorporated into individuals with C, S and T types of cms. Some androgenic haploids were obtained from more than 20 lines carrying cytoplasms of N, C, S and T types. The sterile counterparts of V35, B59, N8, WF9 and other lines were developed by this method.

Table. Spontaneous female fertility of androgenic haploids pollinated with the pollen of the original lines

Source of androgenic haploids	Number of pollinated haploid plants	Number of kernels set per ear $\bar{X} \pm S\bar{X}$
V35	6	31 ± 7.2
N8	8	27 ± 8.3
B59	6	18 ± 6.5
WF9	37	42 ± 10.1
64	17	33 ± 4.1
155	8	8 ± 2.7

As natural female fertility in haploids is high (Table) the artificial diploidization of androgenic haploids with colchicine for the transfer of the lines to a sterile base is not needed. From more than 200 pollinated androgenic plants only nine plants did not set kernels. It should be noted that the best seed set in haploids is obtained when pollination is 5-10 days later.

Thus, the ig mutation may be used for the development of sterile counterparts of lines and for various genetic studies dealing with determination of the importance of the cytoplasm.

M. V. Chumak

III. ZEALAND 1980

		Reference (Publ. or MNL #)
Chromosome 1		
alh	(*H1a); near bm2; located by monosomic 1 and TB-1La; high recombination with TB-1La (1L.2) but low with gs and none with bm2	Stout & 1979
protein	(*Pro-L, -I, -S); Bz2 15.5 Pro 13.1 Adh1	Schwartz 1979
Mdh4	TB-1La and TB-1La-5S8041 locate	Newton 54
bz2	between T1-3e (1L.58) and T1-3(5267) (1L.72) per compounds with TB-1La	Newton & 54
D8	bz2 13.8 D8 2.5 gs	Coe 54
Les2	association with wx T1-9a	Neuffer & 54
Les*-1449	association with wx T1-9(4997)	"
Les*-1461	association with wx T1-9(8389)	"
clf	(*gay) clf 0.8 P 7 zb4	Dooner 54
Mdh4	4.4 mmm 19.0 Pgm1 5.8 Adh1 13.7 Phi	Goodman & 54
ag	1-(14); apparently lost; exclude from working maps	Cooperators
ga6	1-15; " " "	"
pa	1-58; " " "	"
Ts3	1-119; " " "	"
v19	1-; " " "	"
zl	1-28; " " "	"
Chromosome 2		
Inv2e	breakpoints 2S.84, 2S.44 (Doyle)	McKinley & 1979
5SrRNA	hybridizes in situ beyond T2-6(5419) (2L.82), at 2L.88	Mascia & 54
rp7	2-11+; apparently lost; exclude from working maps	Cooperators
Chromosome 3		
Histone 1b	(*H1b); not located by monosomics 1, 2, 4, 5, 6, 7, 8, 9, 10 or by TB-3La	Stout & 1979
Inv3c	breakpoints 3L.05, 3L.95 (Doyle)	McKinley & 1979
a3	left of a1 4 to 16 units	Coe 54
Les*-1376	association with wx T3-9c	Neuffer & 54
ig	association with wx T3-9c; gl6 21.2 ig 11.3 lg2	Kermicle 54
Mdh3	2.6 sh2	Newton 54
pg2	3-; apparently lost; exclude from working maps	Cooperators
Chromosome 4		
zein	IEF band 12 located by TB-4L-9S(?) IEF band 13 located by TB-4Sa	Valentini & 1979
Mal2	46.2 Su1	de Miranda 54
Asr1	43 Su1	"
Les*-1375	association with wx T4-9g	Neuffer & 54
del	4-1; apparently lost; exclude from working maps	Cooperators
del6	4-74: " " "	"
lol	4-73; " " "	"
spl	4-66; " " "	"
Chromosome 5		
bm1	distal to 5S.19: not uncovered by Df-Dp from T1-5(6197) (1L.02, 5S.02) /T1-5(6401) (1L.16, 5S.19)	Kasha 1979
bt1	between 5L.05 and 5L.06: uncovered by Df-Dp from T1-5b (1S.09, 5L.05) /T1-5(6197) and T5-9c (5S.07, 9L.10)/T5-9(4817) (5L.06, 9S.07)	"
mep	(modifier embryo protein); uncovered by TB-5La; Mep 12.6 pr	Schwartz 1979
Inv5b	breakpoints 5S.80, 5L.91 (Doyle)	McKinley & 1979
Mdh5	located by TB-1La-5S8041 but not by TB-1La; "approximately 20% recombination between Mdh5 and a2"	Newton 54

(Chromosome 5, continued)		
Les*-1451	association with wx T5-9a	Neuffer & 54
Mdh5	16±4 Pgm2; Pgm2 32±7 a2	Goodman & 54
tn1	5-; apparently lost; exclude from working maps	Cooperators
Chromosome 6		
*Mdh1	mMDH1,2; trisomic 6 and TB-6La locate; su2 24.4 Mdh1; py 12 Mdh1	McMillin & 1979
*Mdh2	mMDH3,5; " " " ; " Mdh2: " Mdh2	"
Ep	(*Enp); "Mdh1, Mdh2 were not linked to Enp-1"	"
NOR	T6-7(4964) (6SNORHet.32, 7L.67) has 24% of rDNA proximal to break T6-9a (6SNORHet.67, 9L.32) has 60% of rDNA proximal T6-7(5181) (6SNORHet.71, 7L.85) has 62% of rDNA proximal T2-6(027-4) (6SNORsec.constr.prox., 2L.04) has 71% of rDNA proximal T3-6(032-3) (6SNORsec. constr.mid., 3S.34) has 79% of rDNA proximal T5-6(8696) (6SNORsec.constr.mid., 5L.79) has 99% of rDNA proximal T5-6d (6Ssat.prox.half, 5S.58) has 100% of rDNA proximal	Phillips & 1979 " " " " " "
Inv6b	breakpoints 6S.38, 6L.92 (Doyle)	McKinley & 1979
Pgd1	"trisomic analyses...on chromosome 6 about five map units from the Ep locus"	Stuber & 54
Idh2	"tightly linked (less than 5% recombination) to Mdh2"	"
*Mdh2	TB-6La and TB-6Lb locate distal to Pt	Newton 54
hcf*-26	proximal to T3-6b (6Ssat.dist.quarter): not uncovered by Df-Dp for translocations with breakpoints in or beyond the proximal end of the distal chromomere of the satellite	Phillips & 54
Chromosome 8		
Clm	27.8 T8-9(6673)(8L.35, 9S.31); association with wx T8-9(6673) and wx T8-9d(8L.09, 9S.16)	Robertson 1979
*Mdh1	association with wx T8-9d and wx T8-9(6673)	Newton 54
Idh1	19±5 Mdh1	Goodman & 54
Chromosome 9		
Inv9c	breakpoints 9S.10, 9L.67 (Doyle)	McKinley & 1979
zein	IEF band 12 located by TB-4L-9S(?)	Valentini & 1979
mal1	14.6 Wx	de Miranda 54
bp	9-44; apparently lost; exclude from working maps	Cooperators
Chromosome 10		
TB-10L(18)	breakpoints BS, 10Lnear ctr.; uncovers zn, du, bf2, li, ms10	Lin 1979
TB-10L(19)	breakpoints BL, 10Lnear ctr.; uncovers zn, du, bf2, li, ms10	"
TB-10L(1), (3), (7), (8), (10), (20), (25), (28), (31), (36)	uncover ms10, g, r, but not zn, du, bf2, li, placing ms10 distal to bf2 and li	Lin 54
zein	IEF band 2 located by trisomic 10; near R	Valentini & 1979
K10	differential segment (relative to N10) is inserted in order: R diff. seg. o7? w2 sr2 K10 (deletions of K10 uncover sr2 in each instance and w2 usually)	Rhoades & 54
DfK10(A) through (K),	homozygous deficiencies for w2 sr2 K10 have spotted aleurone color and variably defective endosperm (deficiencies for sr2 K10 alone do not); original w2 of Lindstrom also had defective character	"
Les*-1438	association with wx T9-10b	Neuffer & 54
R-ch:Ecuador	components g S P 0.42 Glm 0.42 Lm 0.78 Lc 0.71 Nr 1.01 Si 0.89 Ch 1.20 Au	Sarkar & 54
12	10-(99); apparently lost; exclude from working maps	Cooperators
18	10-near du; apparently lost; exclude from working maps	"
sp2	10-near du: apparently lost; exclude from working maps	"
Unplaced		
E8-S, -N	not uncovered by TB-1La	Birchler 1979
se	independent of su	Ferguson & 1978
cfl2	complementary to fl2	Paliy & 1979
*Ub	ubiquitous controlling element for receptor Rub	Peterson 54

(Unplaced, continued)

Rub	receptor of controlling element Ub	Peterson 54
Rf*-Kheyr-Pour	restoration for cms-C; one factor for most sources; some data suggest a second factor in some sources	Kheyr-Pour & 54
dib	dichotomously branched; variable expression	Micu 54
ct*-Tracy	condensed plant	Tracy & 54
Pgd2	6-PGD isozymes	Stuber & 54
ora3	orange endosperm	Dollinger 54
bl	apparently lost; drop from working lists	Cooperators
de17	" " "	"
gm	" " "	"
lu2	" " "	"
Pu1, Pu2	" " "	"
S1, S2, S3, S4, S5	" " "	"
so1, so2	" " "	"
sy	" " "	"
wl	" " "	"

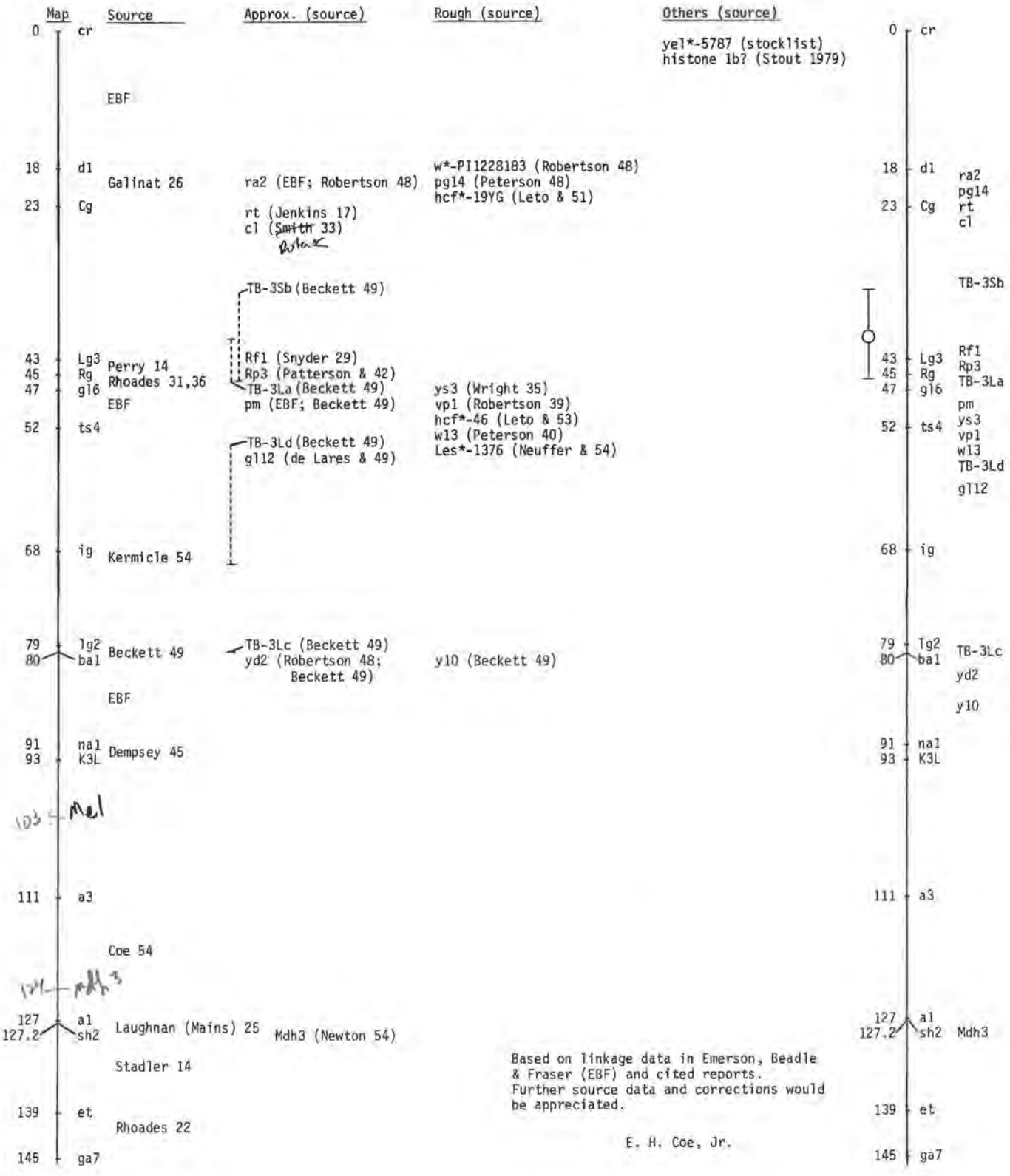
*Symbols preceded by asterisk need to be resolved to be in conformity with nomenclatural standards, prior assignments, or consensus of interpretation.

Requests

Offtypes (e.g., small, runty plants or other deteriorations) segregating in established inbred lines.	D. S. Robertson (Ames)
Specimens of Z. luxurians, Z. perennis, Z. diploperennis	R. M. Bird (Kirkwood)
Unplaced mutants uncovered by TB-5La	D. Weber (Normal)

Compiled by E. H. Coe, Jr.

A revision of the working linkage map for chromosome 3



IV. REPORT OF MAIZE GENETICS COOPERATION STOCK CENTER

During 1979, the Maize Genetic Stock Center received 105 seed requests. The number of seed requests decreased by 12 percent compared to 1978. Seventy-seven percent of the requests were domestic and twenty-three percent foreign. The categories of seed requests were as follows: maize geneticists 52%, maize breeders 19%, plant physiologists 23%, and educational 13%. A total of 950 seed packets were sent to fill these requests.

Each year a number of allele tests are made with genetic stocks carrying unknown loci. These cultures occur in the stock collection or are sent in by maize geneticists or breeders. The unknown culture is tested and if allelic to an already known loci the culture is usually added to the collection. The following is a list of some of the allele tests conducted over the past several years:

Chromosome 1

ad*-3047 (Funk) = ad1
ts*-8135 (Funk) = ts2
gs*-PI262495 = gs
bm*-PI267186 = bm2

Chromosome 2

g1*-61-554 = g13
wt*-A188 = wt

Chromosome 4

bm*-73-2832 = bm3
1a*-1087 (Funk) = 1a
1a*-1081 (Funk) = 1a
1a*-2482 (Funk) = 1a
1a*-PI239110 = 1a
O*-RYDALex = f12
su-am*-68M85-1 = su-am

Chromosome 5

bm*-68M62 = bm
bm*-68M139 = bm
bm*-68M62-12 = bm

Chromosome 5 (Cont.)

bm*-PI251009 = bm
bm*-PI251942 = bm
bm*-PI267186 = bm
ys*74-1924 = ys
ys*-Bell = ys
nec*-69-840-3 = nec3

Chromosome 6

y*-73-2262 (Funk) = y

Chromosome 10

g*-PI251942 = g
g*-PI262473 = g
sr*65-2239 = sr2
w*-Burnham = w2

Unplaced

zn*68M168 = zn2
gs*PI262485 ≠ gs; ≠ gs2

Requests for stocks and correspondence relative to the stock center should be addressed to:

Dr. R. J. Lambert
Department of Agronomy
S-118 Turner Hall
University of Illinois
Urbana, IL 61801

Catalogue of Stocks

Chromosome 1

sr zb4 P-WW
sr P-WR
sr P-WW
sr P-WR an gs bm2
sr P-WR an bm2
sr P-RR an bm2
sr P-RR gs bm2
sr P-WR bm2
vp5
zb4 ms17 P-WW
zb4 ms17 P-WW rs2
zb4 ts2 P-WW br f bm2
zb4 ts2 P-WW bm2
zb4 P-WW
zb4 P-WR
zb4 P-WW br
zb4 P-WW br f bm2
zb4 P-WW bm2
ms17
ts2 P-RR
ts2 P-WW bm2
ts2 P-WW br bm2
ts2 br f bm2
P-CR
P-RR
P-RW
P-CW
P-MO
P-VV
P-RR as br f an gs bm2
P-RR br f an gs bm2
P-RR br f an gs bm2 rd
P-RR br f an gs bm2 id
P-RR br f an gs bm2 v*-8983
P-RR br f an gs bm2 v*-8943
P-RR an ad bm2
P-RR an gs bm2
P-RR ad bm2
P-WR an Kn bm2
P-WR an ad bm2
P-WR an bm2
P-WR an br bm2
P-WT = WR an bm2
P-WR br Vg
P-WR br f gs bm2
P-WR br f an lw gs bm2
P-WR br f bm2 id
P-WW rs2
P-WW rs2 br f
P-WW as br f bm2
P-WW hm br f
P-WW br f ad bm2
P-WW br f bm2
P-WW br f an gs bm2
P-WW br Vg
as
as br2
as rs2
rd Hy
br f
br f bm2 v*-5568
br f Kn
br f Kn Ts6
br f Kn bm2
br bm2
Vg
Vg an bm2
Vg br2 bm2
v22
bz2 m ; A A2 C Pr
bz2 M ; A A2 C R Pr
bz2 ad bm2 ACR
an bm2
an-bz2-6923 (apparent deficiency including an and bz2)
br2
br2 bm2
br2 an bm2
tb-8963
Kn
Kn Ts6
Kn bm2
lw
Adh1-S
vp8

Chromosome 1 (continued)

gs
gs bm2
Ts6
bm2
id
nec2
ms9
ms12
ms14
mi
D8
Lls
TB-1La (1L.20)
TB-1Sb (1S.05)

Chromosome 2

ws3 lg gl2 B
ws3 lg gl2 B sk
ws3 lg gl2 B sk v4
ws3 lg gl2 B sk fl v4
ws3 lg gl2 B gs2 v4
ws3 lg gl2 B ts
ws3 lg gl2 b
ws3 lg gl2 b sk
ws3 lg gl2 b sk v4
ws3 lg gl2 b gs2 v4
ws3 lg gl2 b fl v4
ws3 lg gl2 b sk fl v4
ws3 lg gl2 fl v4
ws3 lg gl2 b v4
al
al lg
al lg gl2 B sk v4
al lg gl2 b
al lg gl2 b sk v4
al lg gl2 b sk fl v4
lg
lg gl2
lg gl2 B
lg gl2 B gl11
lg gl2 B gs
lg gl2 B gs2 v4
lg gl2 B gs2 Ch
lg gl2 B gs2 sk Ch
lg gl2 B gs2 sk v4
lg gl2 B sk
lg gl2 B sk v4
lg gl2 B v4
lg gl2 b
lg gl2 b gs2
lg gl2 b gs2 Ch
lg gl2 b gs2 sk Ch
lg gl2 b gs2 v4
lg gl2 b gs2 v4 Ch
lg gl2 b gs2 sk v4 Ch
lg gl2 b sk
lg gl2 b sk fl
lg gl2 b sk fl v4
lg gl2 b sk v4
lg gl2 b wt v4
lg gl2 b fl
lg gl2 b fl v4
lg gl2 b fl v4 Ch
lg gl2 b v4
lg gl2 b v4 Ch
lg gl2 mn v4
lg gl2 wt
lg gl2 b gs2 wt
lg gl2 w3
lg gl2 w3 Ch
lg gl2 Ch
lg b gs2 v4
lg Ch
gl2
d5 = d*-037-9
B gl11
B ts
gl14
gl11
wt
mn
fl
fl v4 Ch

Chromosome 2 (continued)

fl Ht v4
fl Ht v4 Ch
fl w3
fl v4 w3
fl w3 Ch
fl v4 w3 Ch
ts
v4
v4 w3 Ht
v4 w3 Ht Ch
v4 Ht Ch
w3
w3 Ht
w3 Ht Ch
w3 Ch
Ht (A & B source)
ba2
R2 ; r A A2 C
r2 r-g A A2 C
Ch
gs2
Les
TB-1Sb-2L4464
TB-3La-2S6270
Primary Trisomic 2

Chromosome 3

cr
cr d
cr d Lg3
cr pm ts4 lg2
cr ts4 na
d-Tail = d*-6016 (short)
d rt Lg3
d Rf lg2
d ys3
d ys3 Rg
d ys3 Rg lg2
d Lg3
d Lg3 gl6
d Lg3 ts4 lg2
d Rg
d Rg ts4 lg2
d pm
d yg*-(W23)
d ts4 lg2
d ts4 lg2 a-m ; A2 C R Dt
d ts4
d gl6
d lg2 a-m A2 C R Dt
d a-m A2 C R Dt
ra2
ra2 Rg
ra2 Rg ts4 lg2
ra2 Rg gl6
ra2 ys3 Lg3 Rg
ra2 ys3 Rg
ra2 Rg lg2
ra2 pm lg2
ra2 ts4
ra2 ts4 lg2
ra2 lg2
Cg
cl
cl ; Clm-2
cl ; Clm-3
cl-p ; Clm-4
rt
ys3
ys3 Lg3
ys3 Lg3 gl6
ys3 gl6 lg2 a-m et ; A2 C R Dt
ys3 ts4
ys3 ts4 lg2
Lg3
Lg3 Rg pm
gl6
gl6 lg2 A ; A2 C R
gl6 lg2 A-b et ; A2 C R Dt
gl6 lg2 a-m et ; A2 C R Dt
gl6 lg2 a-m et ; A2 C R Dt

Chromosome 3 (continued)

pm lg2
ts4
ts4 na
ts4 na pm
ts4 ba na
ts4 lg2 a-m ; A2 C R Dt
ts4 na a-m ; A2 C R Dt
ba
y10
lg2
lg2 A-b et ; A2 C R Dt
lg2 a-m sh2 et ; A2 C R Dt
lg2 a-m et ; A2 C R dt
lg2 a-m et ; A2 C R Dt
lg2 a-st sh2 et ; A2 C R Dt
lg2 a-st et ; A2 C R Dt
na
na lg2
A sh2 ; A2 C R B Pl dt
A-d31 ; A2 C R
A-d31 ; A2 C R pr dt
A-d31 ; A2 C R B Pl dt
A-d31 ; A2 C R Dt
A-d31 ; A2 C R pr Dt
A-d31 sh2 ; A2 C R B Pl dt
A-d31 sh2 ; A2 C R Dt
A-d31 sh2 ; A2 C R B Pl Dt
A-d31 et ; A2 C R Dt
a-m ; A2 C R B Pl dt
a-m ; A2 C R Dt
a-m ; A2 C R B Pl Dt
a-m sh2 ; A2 C R B Pl dt
a-m sh2 ; A2 C R B Pl Dt
a-m et ; A2 C R Dt
a-st ; A2 C R Dt
a-st sh2 ; A2 C R Dt
a-st sh2 A2 C R B Pl Dt
a-st sh2 et ; A2 C R Dt
a-st et ; A2 C R Dt
a-p sh2 et ; A2 C R B Pl Dt
a-p et ; A2 C R dt
a-p et ; A2 C R B Pl Dt
a-xl
a-x3
a Ga7 ; A2 C R
sh2
vp
Rp3
pg14
a3
g5
te
h
yel*-5787
TB-3La (3L.10)
TB-3Sb (3S.50)
TB-3Lc (distal to 3La (3L.10)
Primary Trisomic 3

Chromosome 4

Rp4
Ga
Ga su
Ga-S
Ga-S ; y
Ga-S ; A A2 C R
at
at Ts5
at f12
Ts5
Ts5 f12
Ts5 su
Ts5 la su gl3
Ts5 su zb6
Ts5 su zb6 o
Ts5 su gl3 o
Ts5 Tu
la
la su Tu gl3
la su gl3

Chromosome 4 (continued)

la su gl3 c2 ; A A2 C R
la su gl3 o
la su bt2 gl3
f12
f12 su
f12 bt2
f12 su bm3
f12 su gl4 Tu
su
su-am
su bt2 gl4
su bm3
su zb6
su zb6 bt2
su zb6 Tu
su zb6 gl3 dp
su gl4 j2
su gl4 o
su gl4 o Tu
su j2
su gl3
su gl3 o
su o
su gl4
bt2
bm3
gl4
gl4 o
Tu
Tu-1 1st
Tu-1 2nd
Tu-d
Tu-md
Tu gl3
j2
j2 c2 ; A A2 C R
j2 C2 ; A A2 C R
j2 gl3
v8
gl3
gl3 o
gl3 dp
c2 ; A A2 C R
C2 ; A A2 C R
C2-Idf (Active-1) ; A A2 C R
dp
o
v17
v23
ra3
Dt4 su ; a-m A2 C R
TB-4Sa (4S.20)
TB-1La-4L4692
TB9Sb-4L6504 (9S.40-.83; 4L.09)
TB7Lb-4L4698 (7L.30-.74; 4L.08)
Primary Trisomic 4

Chromosome 5

am a2 ; A A2 C R
lu
lu sh4
msl3
gl17
gl17 A2 pr ; A C R
gl17 a2 ; A C R
gl17 a2 bt ; A C R
gl17 a2 bt v2 ; A C R
A2 vp7 pr : A C R
A2 bm bt pr ys ; A C R
A2 bm pr ; A C R
A2 bm pr ys ; A C R
A2 bm pr ys eg ; A C R
A2 bm pr v2 ; A C R
A2 bt v3 pr ; A C R
A2 bt pr ; A C R
A2 bt pr ys ; lu A C R
A2 v3 pr ; A C R
A2 pr ; A C R
A2 pr v2 ; A C R
A2 pr na2 ; A C R
A2 pr ys ; A C R
A2 pr zb3 ; A C R

Chromosome 5 (continued)

A2 pr v12 ; A C R
a2 ; A C R
a2 bm bt bv pr ; A C R
a2 bm bt pr ; A C R
a2 bm bt pr ys ; A C R
a2 bm pr v2 ; A C R
A2 v3 pr ; A C R
a2 bt v3 pr ; A C R
a2 bt v3 PR ; A C R
a2 bt pr ; A C R
a2 bt v2 ; A C R
a2 v3 pr ; A C R
a2 pr ; A C R
a2 pr ; A C R B Pl
a2 pr v2 ; A C R
vp2
vp2 pr
vp2 gl8
vp7
bm
bm yg
bt
ms5
v3
td ae
ae
sh4
gl8
na2
lw2
ys
eg
v2
yg
msl3
v12
br3
nec3
TB-5La
TB-5Lb
Primary Trisomic 5

Chromosome 6

rgd po y
rgd po Y
rgd y
rgd Y
po = ms6
po y pl
po y Pl
po y wi
po Y pl
y = pb = w-m
y rhm
y 110
y 111
y 112
y W15
y pb4
y pb4 pl
y pb4 Pl
y si
y wi Pl
Y Dt2 ; a-m A2 C R
y pg11 ; Wx pg12
y pg11 wi ; wx pg12
Y pg11 ; Wx pg12
y pg11 ; wx pg12
Y pg11 ; wx pg12
y pg11 su2 ; wx pg12
y pl
y Pl
y Pl Bh ; c sh wx A A2 R
y pl Bh ; c sh wx A A2 R
y su2
Y 110
Y 112
Y pb4
Y wi pl
Y wi Pl
Y su2
wi

Chromosome 6 (continued)

Pl Dt2 ; a-m A2 C R
pl sm ; P-RR
Pl sm ; P-RR
Pl sm py ; P-RR
Pl sm Pt py ; P-RR
Pt
w
wl4
ms6
2NOR ; a2 bm pr v2
TB-6Lb
Primary Trisomic 6

Chromosome 7

Hs o2 v5 ra gl
In-D
In-D gl
o2
o2 v5
o2 v5 ra gl
o2 v5 ra gl sl
o2 v5 ra gl Tp
o2 v5 ra gl ij
o2 v5 gl
o2 v5 ms7
o2 ra gl ij
o2 ra gl sl
o2 gl
o2 gl sl
o2 ij
o2 bd
in ; A2 pr A C R
in gl ; A2 pr A C R
v5
vp9
vp9 gl
ra
ra gl ij bd
gl
gl-M
gl Tp
gl o5
gl mn2
Tp
ij
ms7
ms7 gl Tp
Bn
bd
Pn
o5
o5 mn2 gl
va
Dt3 ; a-m A2 C R
V*-8647
yel*-7748
TB-7Lb (7L.30)
Primary Trisomic 7

Chromosome 8

gl18
v16
v16 j
v16 ms8 j
v16 ms8 j nec
v16 ms8 j gl18
ms8
nec
v21
fl3
fl3 j
TB-8La (8L.70)
Primary Trisomic 8

Chromosome 9

yg2 C Bz Wx ; A A2 R
yg2 C sh bz ; A A2 R
yg2 C sh bz wx ; A A2 R
yg2 C-I sh bz wx ; A A2 R
yg2 c sh bz wx ; A A2 R
yg2 c sh bz wx gl15 ; A A2 R
yg2 c sh bz wx gl15 K-L9 ; A A2 R-g
yg2 c bz wx ; A A2 R
wd-Ring C-I ; A A2 R
C sh bz ; A A2 R
C sh bz wx ; A A2 R
C sh bz wx bm4 ; A A2 R
C-I sh bz wx ; A A2 R
C sh bz wx gl15 bm4 ; A A2 R
C sh ; A A2 R
C sh wx ; A A2 R
C wx ar ; A A2 R
C sh wx K-L9 ; A A2 R
C sh ms2 ; A A2 R
C bz Wx ; A A2 R
C Ds wx ; A A2 R PR y
C Ds wx ; A A2 R pr y
C-I Ds wx ; A A2 R
C-I ; A A2 R
C ; A A2 R
C ; A A2 R B Pl
C wx ; A A2 R
C wx ; A A2 R B Pl
C wx ; A A2 R b Pl
C wx ; A A2 R B pl
C-I wx ; A A2 R y
C-I wx ; A A2 R y B pl
C wx ar da ; A A2 R
C wx v ; A A2 R
C wx v ; A A2 R Pl
C wx gl15 ; A A2 R
C wx gl15 ; A A2 R pr
C wx Bf ; A A2 R
c bz wx ; A A2 R
c sh bz wx ; A A2 R y
c sh wx ; A A2 R
c sh wx v ; A A2 R
c sh wx gl15 ; A A2 R
c sh wx gl15 bk2 ; A A2 R
c sh wx gl15 Bf ; A A2 R
c sh wx bk2 ; A A2 R
c ; A A2 R
c wx ; A A2 R y
c wx v ; A A2 R
c wx gl15 ; A A2 R
c wx Bf ; A A2 R
sh
sh wx v
sh wx d3
sh wx pg12 gl15 ; y pg11
lo2
wx*
wx-a
wl1
wx d3
wx d3 wl1
wx d3 v gl15
wx d3 gl15
Wx pg12 ; y pg11
wx pg12 ; y pg11
Wx pg12 ; Y pg11
wx pg12 ; Y pg11
wx pg12 bm4 ; y pg11
wx v
wx bk2
wx bk2 bm4
wx Bf
wx Bf bm4
v
ms2
gl15
gl15 Bf
gl15 bm4
bk2 Wx
Wc
bm4
bm4 Bf
16

Chromosome 9 (continued)

17
yel*-034-16
w*-4889
w*-8889
w*-8951
w*-8950
w*-9000
TB-9La (9L.40)
TB-9Sb (9S.40)
TB-9LC
Primary Trisomic 9

* Additional waxy alleles available from collection of O. E. Nelson.

Chromosome 10

oy
oy R ; A A2 C
oy bf2
oy msl1
oy bf2 R ; A A2 C
oy bf2 msl0
oy zn R ; A A2 C
oy du R ; A A2 C
oy du r ; A A2 C
oy sr2
oy zn
Og
Og B Pl
Og du R ; A A2 C
msl1
msl1 bf2
bf2
bf2 zn
bf2 li g r ; A A2 C
bf2 g R sr2 ; A A2 C
bf2 g r sr2 ; A A2 C
bf2 r sr2 ; A A2 C
nl zn g R ; A A2 C
nl g R ; A A2 C
nl g r ; A A2 C
nl g R sr2 ; A A2 C
y9
y9 v18
nl
li zn g r ; A A2 C
li g R ; A A2 C
li g r ; A A2 C
li g r v18 ; A A2 C
li g r v18 ; A A2 C
msl0
du
du v18
du o7
du g r ; A A2 C
du sr2
zn
zn g
zn g R sr2 ; A A2 C
zn g r ; A A2 C
Tp2 g r ; A A2 C
g R sr2 ; A A2 C
g r ; A A2 C
g r sr2 ; A A2 C
g r sr2 l ; A A2 C
g R-g sr2 ; A A2 C
g R-g sr2 v18 ; A A2 C
g R-g K10 ; A A2 C
g R-g sr2 ; A A2 C
g R-r K10 ; A A2 C
g r-r sr2 ; A A2 C
Ej r-r ; A A2 C
Ej r-r sr2 ; A A2 C
r sr2 l ; A A2 C
R-g ; A A2 C
r-g sr2 ; A A2 C
r K10 ; A A2 C
r-g ; A A2 C
r-r ; A A2 C
r-ch Pl ; A A2 C
R-mb ; A A2 C
R-nj ; A A2 C

Chromosome 10 (continued)

R-r ; A A2 C
R-ch B Pl ; A A2 C
R-lsk ; A A2 C
R-sk-mc.2 ; A A2 C
R-sk ; A A2 C
R-st : A A2 C
R-st Mst
R-st Mst o7
Lc
w2
w2 l
o7
o7 ; o2
l
vl8
mst
l yel*-5344
yel*-8721
yel*-8454
yel*-8793
TB-10La (10L.35)
TB-10Sc
TB-10L19
Primary Trisomic 10

Unplaced Genes

dv
dy
el
l4
Les2
Rs
vl3
ws ws2
ub
zb
zb2
zn2
l*-4923
nec*-8376

Multiple Gene Stocks

A A2 C R-g Pr B Pl
A a2 C R-g Pr B pl
A A2 C C2 R-g b Pl
A A2 C r-g Pr B Pl
A A2 C r-g Pr B pl
A A2 c R-g Pr B pl
A A2 C R-r Pr B Pl
A A2 C R-r Pr B pl
A A2 C R-r Pr b Pl
A A2 c R-r Pr B Pl
A A2 C r-r Pr B Pl
A A2 c r-r Pr B Pl
A A2 C R Pr
A A2 C R Pr wx
A A2 C R Pr wx gl
A A2 C R Pr wx y
A A2 C R pr
A A2 C R pr y gl
A A2 C R pr y wx
A A2 C R pr y wx gl
A A2 c R Pr y wx
A A2 C r Pr y wx
bz2 a c2 a2 y c r
bz2 a a2 c c2 pr Y/y bz wx
a su A2 C R
bm2 lg a su pr y gl j wx g
colored scutellum
lg gl2 wt ; a Dt A2 C R
lg su bm2 y gl j
su y wx a A2 C R-g pr
a su pr y gl wx A A2 C R
y wx gl
hm hm2
ts2 ; sk

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
Gaspe Flint
Gourdseed
Maiz Chapolote
Papago Flour Corn
Parker's Flint
Tama Flint
Zapaluta Chica

Tetraploid Stocks

P-RR
P-VV
Ch
B Pl
a A2 C R Dt
su
pr ; A A2 C R
y
gl
ij
Y sh wx
sh bz wx
wx
g A A2 C R
A A2 C R B Pl

Cytoplasmic Steriles and Restorers

WF9-(T)	rf rf2
N6 (S)	
WF9	rf rf2
N6	rf Rf2
RZ13	Rf rf2
Ky 21	Rf Rf2

Waxy Reciprocal Translocations

wx 1-9c (1S.48; 9L.22) * Sx
wx 1-94995 (1L.19; 9S.20) * Sx
wx 1-98389 (1L.74; 9L.13) W23 only
wx 2-9b (2S.18; 9L.22) * Sx
wx 3-9c (3L.09; 9L.12) * Sx
wx 4-9b (4L.90; 9L.20) * Sx
wx 4-95657 (4L.33; 9S.25) * Sx
wx 4-9g (4S.27; 9L.27) W23 only
wx 5-9a (5L.69; 9S.17) * Sx
wx 5-9c (5S.07; 9L.10) W23 only
wx 6-9a (6S.79; 9L.40) * Sx
wx y 6-9b (6L.10; 9S.37) * Sx
wx 7-9a (7L.63; 9S.07) * Sx
wx 7-94363 (7 cent; 9 cent) * Sx
wx 8-9d (8L.09; 9L.16) * Sx
wx 8-96673 (8L.35; 9S.31) * Sx
wx 9-10b (9S.13; 10S.40) * Sx

Non-waxy Reciprocal Translocations

Wx 1-9c (1S.48; 9:.24) * Sx
Wx 1-94995 (1L.19; 9S.20) * Sx
Wx 1-98389 (1L.74; 9L.13) * Sx
Wx 2-9c (2L.49; 9S.33) W23 only
Wx 2-9b (2S.18; 9L.22) * Sx
Wx 3-98447 (3S.44; 9L.14) *
Wx 3-98562 (3L.65; 9L.22) * Sx
Wx 4-9c (4S.53; 9L.26) * Sx
Wx 4-95657 (4L.33; 9S.25) * Sx
Wx 5-9c (5S.07; 9L.10) * Sx
Wx 5-94817 (5L.69; 9S.17) M14 only
Wx 5-98386 (5L.87; 9S.13) * Sx
Wx 6-94778 (6S.80; 9L.30) * Sx
Wx 6-98768 (6L.89; 9S.61) *
Wx 7-94363 (7 cent.; 9 cent.) *
Wx 7-9a (7L.63; 9S.07) W23 only
Wx 8-9d (8L.09; 9L.16) * Sx
Wx 8-96673 (8L.35; 9S.31) * Sx
Wx 9-108630 (9S.28; 10L.27) M14 only
Wx 9-10b (9S.13; 10S.40) * Sx

* = Homozygotes available in both
M14 & W23 backgrounds

Sx = Single cross of homozygotes between
M14 & W23 versions available

Inversions

Inv.1a (1S.30-L.50)
Inv.1c (1S.35-L.01)
Inv.1d (1L.55-L.92)
Inv.1L-5131-10 (1L.46-L.82)
Inv.2a (2S.70-L.80)
Inv.2-3713 (2S.93-L.65)
Inv.2-3778 (2S.44-L.84)
Inv.2S-L8865 (2S.06-L.05)
Inv.2L-5392-4 (2L.13-L.51)
Inv.3a (3L.38-L.95)
Inv.3L (3L.19-L.72)
Inv.3L-3716 (3L.09-L.81)
Inv.4b (4L.40-L.96)
Inv.4c (4S.86-L.62)
Inv.4e (4L.16-L.81)
Inv.5-8623 (5S.67-L69)
Inv.6-8452 (6S.77-L.33)
Inv.6-8604 (6S.85-L.32)
Inv.6-3712 (6S.76-L.63)
Inv.7b (6S.32-L.30)
Inv.7L-5803 (7L.17-L.61)
Inv.7-8540 (7L.12-L.92)
Inv.7-3717 (7S.32-L.30)
Inv.8a (8S.38-S.15)
Inv.9a (9S.70-L.90)
Inv.9b (9S.05-L.87)
Inv.9c (9S.10-L.67)

NEW YORK STATE COLLEGE OF AGRICULTURE AT CORNELL UNIVERSITY
CORNELL UNIVERSITY AGRICULTURAL EXPERIMENT STATION
ITHACA, N. Y.
DEPARTMENT OF PLANT BREEDING

Dec. 19, 1929

Dear Sir:

In the form letter sent out under date of November 23rd, regarding data for the summary of linkage in maize it was not specifically stated whether or not we were planning to assemble the data showing independent inheritance between unlinked factors and factors the linkage relations of which are known. We do plan to summarize such data as we feel that it will be of advantage to know what tests have been made with a given unlinked factor. For example, the linkage relations of japonica are not known but it has been tested with factors in several of the linkage groups. The advantages of having available a summary of such data are apparent. We are therefore asking that you include such data.

Sincerely,

G W Beadle

G. W. Beadle

GWB:C

NEW YORK STATE COLLEGE OF AGRICULTURE AT CORNELL UNIVERSITY
CORNELL UNIVERSITY AGRICULTURAL EXPERIMENT STATION
712 ITHACA, N. Y.
DEPARTMENT OF PLANT BREEDING

February 5, 1930

Dr. E. G. Anderson
Institute of Technology
Pasadena, Calif.

Dear Sir:

We are planning to start work on the revision of the summary of linkage data on maize as soon as possible. However, we have not yet completed the work of collecting data from various sources. We are wondering whether you have available data which you are planning to send for inclusion in the summary. If you have, we should very much appreciate receiving it as soon as possible so that we may get the summary revised before the rush of spring work comes on.

Sincerely yours,

G W Beadle

GWB:G

G. W. Beadle

1395
NEW YORK STATE COLLEGE OF AGRICULTURE AT CORNELL UNIVERSITY
CORNELL UNIVERSITY AGRICULTURAL EXPERIMENT STATION
ITHACA, N. Y.
DEPARTMENT OF PLANT BREEDING

April 17, 1930

To Students of Maize Genetics :-

I had hoped to send you before now a complete revision of the Summary of Linkage in Maize. Dr. Beadle has tabulated the data which you have been good enough to send him, but unforeseen circumstances have made it impossible to have all the stencils cut in time to be of service to you in planning your summer's work. We have thought best, therefore, to have the revised maps sent out at once without the detailed data such as was furnished last year. The latter will be prepared as soon as possible. Any of you who desire the data for particular combinations of genes can obtain them at once by writing Dr. G. W. Beadle at this address.

You will note that the linkage maps are much better than last year -- thanks to your willingness to send us your data. We trust that you will get the present season's data to us promptly and hope to be able to prepare the material for publication next winter. This will include lists of known genes and a discussion of their interactions. Since it will presumably take a year to get the publication out, we shall probably have to send out mimeograph sheets again next spring.

Sincerely,

R A Emerson

R. A. Emerson

RAE:E

LIST OF LINKED FACTORS IN MAIZE

CLASSIFIED BY LINKAGE GROUPS

C-WX GROUP — no 9

ar	Argentia - finely striped leaf	Eyster 1929
au_1	Aurea chlorophyll-yellow plant	Eyster 1929
au_2	Aurea chlorophyll-yellow seedling	Eyster 1929
bp	Brown pericarp with a	Meyers 1927
C	Colored aleurone with A and R	East and Hayes 1911
d_3	Dwarf plant	Suttle
de_{15}	Defective endosperm	Brink 1927
gm_8	Germless ("gm_1" of Eyster)	Eyster 1929
I	Inhibitor for aleurone color	East and Hayes 1911
pk	Polkadot leaf	Eyster 1924
sh	Shrunken endosperm	Hutchison 1921
v_1	Virescent seedling	Demerec 1924
v_{14}	Virescent seedling	Phipps 1929
v_{15}	Virescent seedling	Phipps 1929
w_{11}	White seedling	Demerec 1926
wx	Waxy endosperm	Collins 1909
yg	Yellow-green plant	Jenkins 1927

R-G_1 GROUP — no 10

df	Flint defective	Lindstrom 1925
G_1	Golden plant	Emerson 1912
gm_2	Germless	Demerec 1926
l_1	Luteus seedling	Lindstrom 1917
l_2	Luteus seedling	Lindstrom 1925
l_4	Luteus seedling	Jenkins and Bell
li	Lineata leaves	Kempton 1920
Lt	Mottled aleurone ("S" of Kempton)	Kempton 1919
nl	Narrow leaf	Emerson
pg_1	Pale green seedling	Brunson 1924
R	Aleurone color	East and Hayes 1911
v_{18}	Virescent seedling	Phipps 1929
v_{20}	Virescent seedling	Phipps 1929
w_2	White seedling	Carver 1924

SU-TU GROUP — no 1

de_1	Defective endosperm	Mangelsdorf & Jones 1925
de_{16}	Defective endosperm	Wentz 1925
Ga	Gamete - pollen tube growth	Mangelsdorf & Jones 1925
gl_3	Glossy seedling	Hayes & Brewbaker 1928
S_1	Colored scutellum	Sprague
su	Sugary endosperm	East and Hayes 1911
Ts_5	Tassel-seed	Emerson
Tu	Tunicate ear	Collins 1917
v_8	Virescent-seedling	Demerec 1926
wl	White-base leaf	Stroman 1925

B-LG GROUP — no 7

B	Intensifier of plant color	Emerson 1918
fl	Floury endosperm	Hayes and East 1915
gl_2	Glossy seedling	Hayes and Brewbaker 1928
lg	Liguleless	Emerson 1912
sk	Silkless	Jones 1925
ts_1	Tassel-seed	Emerson 1920
v_4	Virescent seedling	Demerec 1924

Y-PL GROUP

al	Albescent	Phipps
Bh	Bleached aleurone with A c R g	Emerson
fi	Fine striped leaves	Anderson 1928
mo_1	Male sterile	Singleton & Jones
$P1$	Purple plant color	Emerson 1918
sb	Slit blade	Beadle 1930
sm	Salmon silks	Anderson 1921
v_6	Virescent seedling	Carver 1927
v_7	Virescent seedling	Carver 1927
w_1	White seedling	Stroman 1924
w_5	White seedling with w_6	Demerec 1924
w_6	White seedling with w_5	Demerec 1924
Y	Yellow endosperm	Correns 1901

P-BR GROUP

ad	Adherent	Kempton 1921
an	Anther ear	Emerson and Emerson 1922
br	Brachytic	Kempton 1920
f_1	Fine striped	Lindstrom 1918
gs	Green striped	Emerson 1912
P	Pericarp and cob color	Lock 1906
ta_2	Tassel-seed	Emerson 1920

RA-GL_1 GROUP

Bn	Brown aleurone	Kvakan 1924
fr_1	Frayed-1	Jenkins and Pope
fr_2	Frayed-2	Jenkins and Pope
gl_1	Glossy seedling	Kvakan 1924
Ij	Iojap	Jenkins 1924
In	Intensifier of aleurone	Frazer 1924
pG_3	Pale-green seedling	Demerec 1925
ra	Ramosa	Gernert 1912
sl	Slashed seedling	Brewbaker 1929
sr_2	Striate (Same as iojap)	Brunson
v_5	Virescent seedling	Demerec 1924

D_1-PG_2 GROUP

cr	Crinkly leaves	Emerson 1921
d_1	Dwarf plant	Emerson 1912
pG_2	Pale-green seedling	Demerec 1924

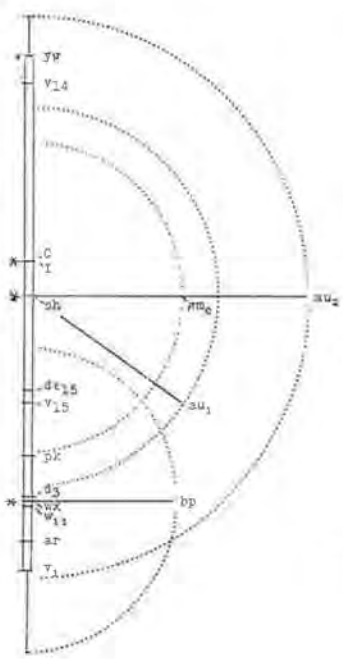
PR-V_2 GROUP

bm_1	Brown midrib	Eyster 1926
bt	Brittle endosperm	Mangelsdorf 1926
bv	Brevic - semi-dwarf plant	Suttle (Unpub.)
f_2	Fine striped leaves	Eyster 1926
Pr	Purple aleurone	East and Hayes 1911
sc_1	Scarred endosperm	Eyster 1926
tn	Tiny plant	Eyster 1926
v_2	Virescent seedling	Demerec 1924
v_3	Virescent seedling	Demerec 1924
v_{12}	Virescent seedling	Phipps 1929
yG	Yellow green	Eyster 1926
ys	Yellow-stripe	Beadle 1929

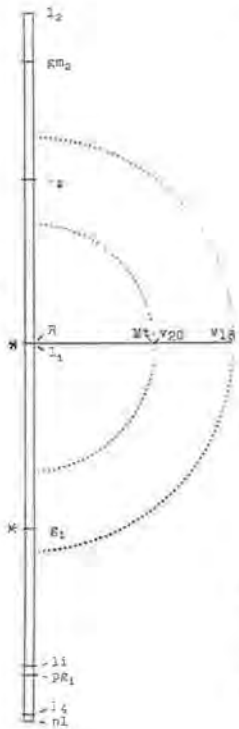
A-TS_4 GROUP

a	Anthocyanin pigment	Emerson 1918
na	Nana - dwarf plant	Suttle
ts_4	Tassel-seed	Phipps 1928

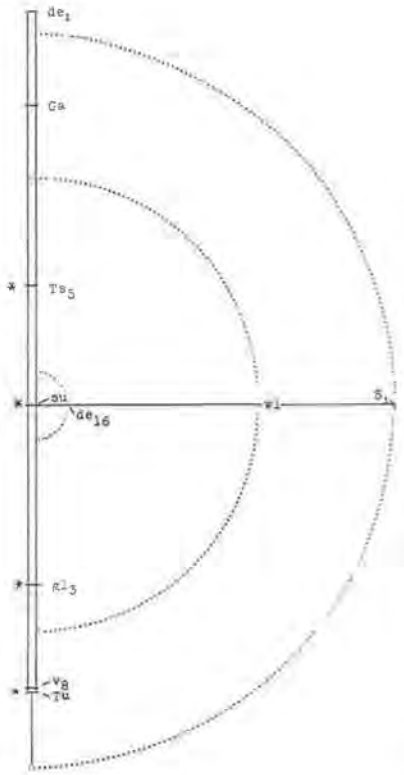
C WX GROUP



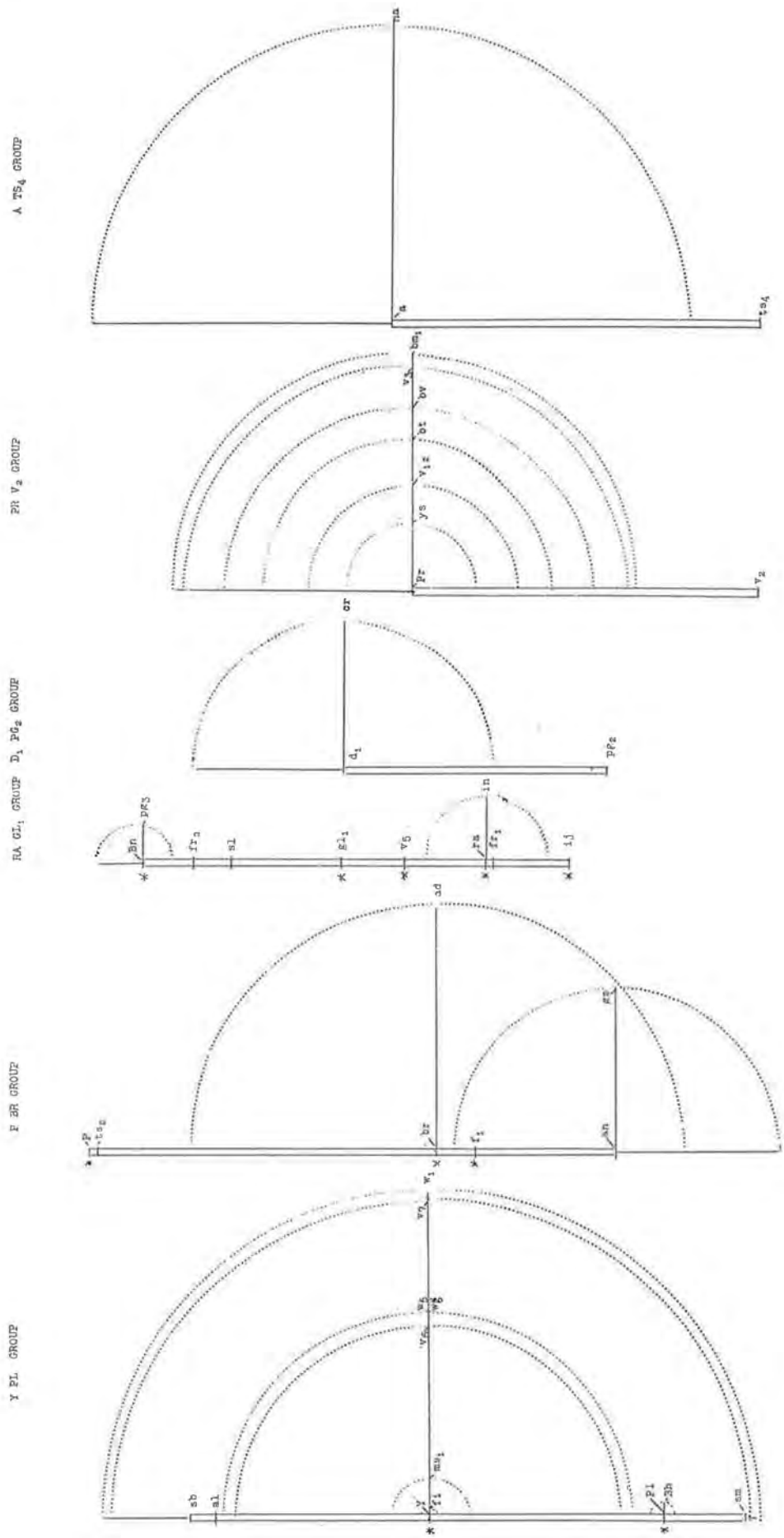
R G GROUP



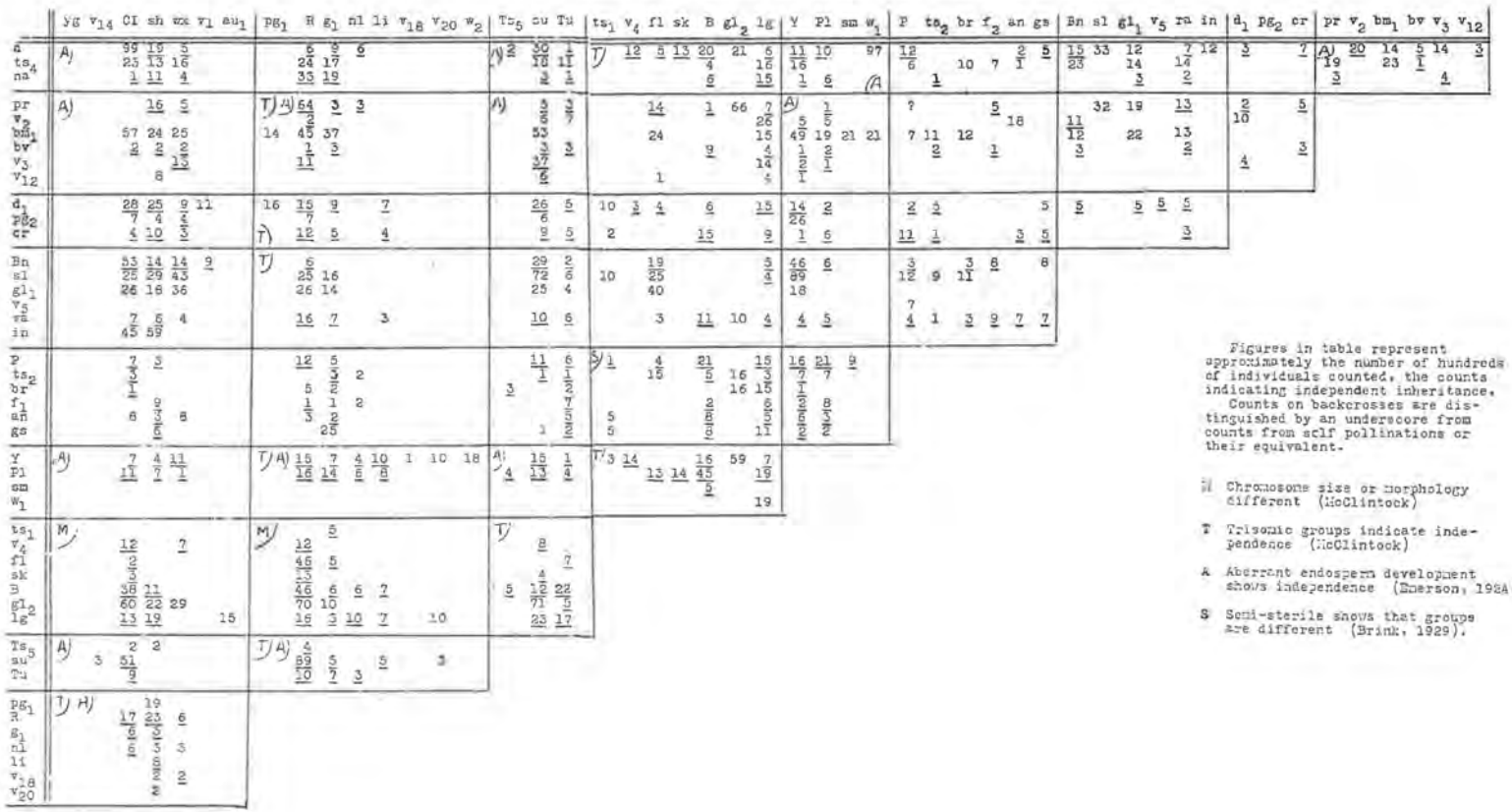
SU TU GROUP



B LG GROUP


A TS4 GROUP
PH V2 GROUP
RA GL1 GROUP D1 PG2 GROUP
F ZR GROUP
Y PL GROUP

Summary of Data on the Independence of the Linkage Groups in Maize



Figures in table represent approximately the number of hundreds of individuals counted, the counts indicating independent inheritance.

Counts on backcrosses are distinguished by an underscore from counts from self pollinations or their equivalent.

M Chromosome size or morphology different (McClintock)

T Trisomic groups indicate independence (McClintock)

A Aberrant endosperm development shows independence (Emerson, 1928A)

S Semi-sterile shows that groups are different (Brink, 1929).

NEW YORK STATE COLLEGE OF AGRICULTURE
CORNELL UNIVERSITY
ITHACA, N. Y.

DEPARTMENT OF PLANT BREEDING

July 26, 1930

To Maize Geneticists :-

Earlier this year there were sent you chromosome maps based on a summary of linkage data in maize, but the summarized data could not be mimeographed in time to be of use to you before the planting season. Dr. Beadle now has these data ready and they are sent you with this to be added to the material sent earlier.

Sincerely,

R. A. Emerson

RAE:B

R. A. Emerson

ENCLOSURES

LINKAGE DATA ON MAIZE

Note on Maps of Linkage Groups

On the map of the Sa Gl_1 linkage group, fr_2 is placed too far from gl_1. This distance should be about 10 units. A more probable location of the fr_1 gene is to the right of it.

C - WX GROUP

ar	Argentia-finely striped leaf	Eyster 1929
au_1	Aureau chlorophyll-yellow plant	Eyster 1925
au_2	Aureau chlorophyll-yellow seedling	Eyster 1929
bp	Brown pericarp with a	Meyers 1927
C	Colored aleurone with A and R	East and Hayes 1911
d_3	Dwarf plant	Suttle
de_{15}	Defective endosperm	Brink 1927
gm_2	Gamless ("gm_1" of Eyster)	Eyster 1929
I	Inhibitor for aleurone color	East & Hayes 1911
pk	Pallida leaf	Eyster 1924
sh	Shrunken endosperm	Hutchison 1921
v_1	Virescent seedling	Demerec 1924
v_{14}	Virescent seedling	Phipps 1929
v_{15}	Virescent seedling	Phipps 1929
w_{11}	White seedling	Demerec 1926
wx	Waxy endosperm	Collins 1909
yg	Yellow-green plant	Jenkins 1927

Notes

pk — The 1929 data of Eyster on pk are not consistent with his earlier data. He makes the statement in his 1929 paper that pk and ar show relatively close linkage— hence pk probably lies on the wx side of C.

ar_1 — The location of au_1 to the right of sh is somewhat doubtful. Recombination values with C and sh are based on separate progenies. Neither au_1 or au_2 have been tested with yg for allelomorphism.

v_{14} — Virescent-14 was shown by Phipps (1929) to be located in the C-wx group but his data was of such a nature that the location of the factor could not be determined.

Linkage Data

Genes	Link. phase	Number of individuals					Recombinations		Authority
X Y		X Y	X y	x Y	x y	Total	No.	%	
C Wx	R B	115	340	296	92	845	207	24.5	Bregger '16
	C B	856	310	311	781	2260	621	27.5	Bregger '16
	C B	371	115	125	397	1008	240	23.8	Kempton '19
	C B	2542	717	739	2710	6708	1456	21.7	Hutchison'22
						42511	9388	22.1	Stadler '25
						249663	67402	27.0	Collins &
						302995	79314	26.2	(Kempton '27
C Sh	C S	4032	149	152	4035	8368	301	3.6	Hutchison'22
	C S	10077	368	397	9866	20706	763	3.7	Eyster '29
	P S	638	21379	21096	672	43785	1310	3.0	Hutchison'22
						72849	2374	3.3	
Sh Wx	R S	1531	5991	5885	1488	14895	3019	20.3	Hutchison'22
I Sh	C S	9452	364	402	9377	19615	766	4.0	Hutchison'22
I Wx	C S	1467	584	547	1620	4138	1131	27.3	Hutchison'22
	R S	790	2217	2283	792	6082	1582	26.0	Hutchison'22
						10220	2713	26.6	
C V_1	R S	300	676	711	294	1981	594	30.0	Demerec '24
Wx V_1	R	70	84	40	3	197		7±	Demerec '24
C Pk	C S^1	128	6	54	56	244		2	Eyster '24
	C S^2	148	5	128	92	373		2	Eyster '24
Sh Pk	R S^3	140	61	60	8	263		10	Eyster '24
	R S^3	382	173	173	11	739		24.5	Eyster '29
	R S^3	73	163	366	70	672	143	16.4	Eyster '29
Sh D_3	R S	329	162	138	8	637		22.8	Demerec '26
	R S	258	112	148	20	544		31.2	Burnham
Wx D_3	R S	265	132	147	0	544			Burnham
Sh W_{11}	R S	457	193	161	16	857		31.2	Demerec '26
	C S	320	26	25	67	438		13.4	Demerec '26
Wx W_{11}	R S	496	256	315	1	1060		5	Burnham
C Yg	C S					30817		20.5	Jenkins '27
	R S					3885		23.0	Jenkins '27
	R S	10	57	52	7	126	17	13.5	Jenkins '27
Sh Yg	R S	193	646	429	99	1267	292	23.0	Jenkins '27
	R S	2683	1212	1057	69	4941		28.6	Jenkins '27
Wx Yg	C S	397	269	297	412	1395	586	42.0	Jenkins '27
	R S	76	120	136	80	414	158	38.2	Jenkins '27
						1809	744	41.1	Jenkins '27
De_{15} Pk	C S	4075	461	1609		6145		19.4	Brink '27
De_{15} Sh	R S	2409	1146	1237		4832		16.5	Brink '27
Wx Bp	R S	9	56	49	9	123	18	14.6	Meyers '27
C Ar	R S^4	3178	4692	4166	1307	12543	3685	29.4	Eyster '29
Sh Ar	R S^4	1935	4763	4177	1221	12086	3146	26.0	Eyster '29
Sh Au_1	C S	2108	311	310	492	3221		21.6	Eyster '29
C Au_1	C S^1	546	79	638	305	1568		26.5	Eyster '29
Sh Au_2	R S^3	340	133	146	10	629		28.0[5]	Eyster '29
Sh Gl_1	C S	2693	301	256	702	3954		15.3	Eyster '29
Wx V_{15}	R S^3	297	128	139	2	566		19	Phipps '29
Sa V_{15}	R S^3	365	171	172	5	714		20	Phipps '29
Sh V_{14}	R S	766	367	307	16	1478		21.4	Beadle
Wx V_{14}	R S	812	352	263	51	1478		39	Beadle

[1] C and R segregating - 9:7 ratio

[2] A, C and R segregating - 27:37 ratio

[3] Ratio corrected for germination by author

[4] See Three-point test data

[5] Recombination value recalculated - author's calculation given as 39.7.

R-G_1 GROUP

List of Genes

df	Flint defective	Lindstrom 1925
G_1	Golden plant	Emerson 1912
gm_2	Germless	Demerec 1926
l_1	Luteus seedling	Lindstrom 1917
l_2	Luteus seedling	Lindstrom 1925
l_4	Luteus seedling	Jenkins & Bell
li	Lineate leaves	Kempton 1920
Mt	Mottled aleurone(*S* of Kempton)	Kempton 1919
nl	Narrow leaf	Emerson
Pg_1	Pale green seedling	Brunson 1924
R	Aleurone color	East & Hayes 1911
v_{18}	Virescent seedling	Phipps 1929
v_{20}	Virescent seedling	Phipps 1929
w_2	White seedling	Carver 1924

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals: X Y	X y	x Y	x y	Total	Recombinations: No.	%	Authority
R	G_1	C S	200	55	58	174	487	113	23.2	Lindstrom'17&'18
		C B	121	25	50	117	313	75	24.0	Lindstrom
		C B	644	60	90	550	1344	150	11.2	Emerson
		R B	29	81	86	18	214	47	22.0	Lindstrom '18
		R B	114	612	635	120	1481	234	15.8	Emerson
R	L_1	C S	303	2	5	121	431		1.6	Lindstrom '21
G_1	L_1	R B	8	35	21	5	69	13	18.8	Lindstrom '18
R	Pg_1	C S[2]	1907	300	1053	686	3946		23.3	Brunson '24
		R S	1199	506	445	32	2182		27.2	Brunson '24
G_1	Pg_1	C S	628	59	57	146	890		14.6	Tentz
L_{4_1}	Pg_1	R S	194	71			265		45	Brunson '24
R	w_2	C S	1329	171	202	402	2104		18.5	Carver '24
		C S	648	74	81	157	960		17.8	Lindstrom '24
		C S	2095	197	228	437	2957		16.6	Lindstrom
		R S	43	16	22	2	83		30.8	Carver '24
w_2	L_1	R S		815	210	10	1035			Lindstrom '25
		R S[3]		585	348	84	1017			Lindstrom '25
		R S[4]		560	318	70	948			Lindstrom '25
		R S[5]		380	402	115	897		22.0	Lindstrom '25
w_2	G_1	R S	1424	651		605	2680		25.0	Lindstrom
R	L_2	C S[2]	837	197	582	277	1893		35.4	Lindstrom '25
		C S	1277	270	323	247	2117		33.0	Lindstrom
		R S	986	405	433	69	1893		33.9	Lindstrom '25
		R S	1254	553	595	75	2478		33.0	Lindstrom
L_2	G_1	R S	1904	673		866	3443		41.0	Lindstrom
w_2	L_2	R S	935	420		328	1683		25.0	Lindstrom
R	Gm_2	R S	2239	784	976	84	4083		31	Demerec '26
		R S	6675	2947	1162	90	11095		27	Wentz
Gm_2	G_1	R S	2810	873			3683		50 ±	Wentz
Gm_2	Pg_1	R S	635	255			1090		50 ±	Wentz
R	V_{18}	C S[6]	51	15	43	93	202		20	Phipps '29
R	V_{20}	C S[6]	77	10	80	152	319		12.5	Phipps '29
G_1	Li_1	R B	148	617	924	111	2000	259	13.0	Hutchison
		C B	222	45	50	211	528	95	18.0	Lindstrom
							2528	354	14.0	
R	Li_1	C B	208	74	86	138	506	160	31.6	Hutchison
		C B[6]	460	191	282	374	651[7]	191	29.3	Hutchison
G_1	Nl	C B	262	100	74	281	717	174	24.3	Emerson
		R B	196	761	831	129	1917	325	17.0	Emerson
							2634	499	18.9	
R	Nl	C B	385	164	199	316	1064	365	34.2	Emerson
		R B	142	348	356	163	1009	305	30.2	Emerson
							2073	670	32.3	
R	L_4	C S	471	114	101	68			36	Jenkins & Bell
		S S	612	239	247	39			17	" "
w_2	L_4	C S	3217	772	1196				35	" "
		R S	2926	536	1606				20	" "
L_2	L_8	R S	1156	963					43	" "

Notes

1 1918 data indicate complete linkage

2 C and R segregating - 9:7 aleurone ratio

3 w_1 and w_2 segregating

4 w_2 and w_3 segregating

5 w_1, w_2 and w_3 segregating

6 C and R segregating

7 First two classes only.

df Lindstrom states that df and w_2 are very closely linked but presents no data.

S Kempton (1918) postulated this spotting factor, located so as to give about 12.5% recombinations with R. Emerson (Unpub.) has additional evidence in support of this assumption.

SU - TU GROUP

List of Genes

de_1	Defective endosperm	Mangelsdorf & Jones 1925
de_{16}	Defective endosperm	Wentz 1925
Ga	Gamete - pollen tube growth	Mangelsdorf & Jones 1925
gl_3	Glossy seedling	Hayes & Brewbaker 1926
S_1	Colored scutellum	Sprague
su	Sugary endosperm	East & Hayes 1911
Ts_5	Tassel-seed	Emerson
Tu	Tunicate ear	Collins 1917
V_5	Virescent-seedling	Demerec 1926
wl	White-base leaf	Stroman 1925

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals: X Y	X y	x Y	x y	Total	Recombinations: No.	%	Authority
Su	Tu	C S	113	4	7	25	149		8.3	Jones & Gallastegui '19
		C B	430	175	169	406	1180	344	29.1	Eyster '21
		C S	749	341	264	664	1958	555	28.4	Emerson
		R B	1031	2495	2093	807	6429	1838	28.6	Eyster '22
		R B	63	215	164	57	499	120	24.0	Emerson
							10105	2887	28.6	
Su	Nl	R S	44	19	11	1	75		25.0	Stroman '24
		R S	4492	2018	1961	93	8564		22.0	Carver '27
De_{16}	Su	C S	20622	453	7201		28276		3.2	Wentz '25
Su	V_5	C S	940	214	179	146	1481		32.4	Demerec '26
V_5	Tu	C S	450	1	Lethal		451		<1	Phipps
De_1	Su	R S	601	238	247	64	1150		39	Mangelsdorf & Jones '25
Su	Ts_5	C B	657	102	51	522	1331	153	11.5	Emerson
		R B	16	344	173	60	600	78	13.0	Emerson
							1931	229	11.9	
Ts_5	Tu	C B	147	62	69	136	416	131	31.5	Emerson
		R B	49	166	115	48	378	97	25.7	Emerson
							794	228	28.7	
Su	Gl_3	R B	78	271	255	82	686	160	23.3	Thomas
Tu	Gl_3	C S	1093	107	166	1195	2563	275	10.7	Thomas
Su	S_1	R B	141	221	229	130			37.6	Sprague

Notes

de_{16} is used instead of de_{su} for sugary defective of Wentz.

V_5 is very near Tu but whether to the left or right is unknown.

Ga is to the left of su because it disturbs the Tu-tu ratio very little if at all in pedigrees in which it disturbs the Su-su ratio materially (Emerson Unpub.)

de_1 is presumably to the left of Ga, because Ga is between de and su (Mangelsdorf and Jones 1925).

B-LG GROUP

List of Genes

B	Intensifier of plant color	Emerson 1915
fl	Floury endosperm	Hayes & East 1915
gl_2	Glossy seedling	Hayes&Brewbaker '28
lg	Liguleless	Emerson 1912
sk	Silkless	Jones 1925
ts_1	Tassel-seed	Emerson 1920
v_4	Virescent seedling	Demerec 1924

Linkage Data

Genes X Y	Link. phase	Number of individuals: X Y	X y	x Y	x y	Total	Recombinations: No.	%	Authority
B Lg	C B	240	134	102	243	719	236	32.8	Emerson '18
	C B	642	291	282	620	1835	573	31.2	Emerson
	C B	2487	1469	1557	2609	8122	3026	37.2	Emerson & Hutchison'21
	R B	498	1085	1037	504	3124	1002	32.1	Emerson
						13800	4837	35.0	
B Ts_1	C B	259	78	91	205	633	169	26.7	Emerson
	R B	30	106	159	20	315	50	15.9	Emerson
						948	219	23.1	
Lg Ts_1	C B	117	52	72	74	315	124	39.4	Emerson
	R B	51	65	64	42	222	93	41.9	Emerson
						537	217	40.4	
B V_4	C B	113	24	21	110	268	45	16.8	Demerec '24
V_4 Lg	R B	412	501	521	366	1800	778	43.2	Demerec '24
	C B	292	216	203	299	1010	429	42.5	Beadle
						2810	1207	42.9	
B Sk	C B	993	78	50	928	2079	156	7.6	Anderson '29
		339	19	26	298	682	45	6.6	Anderson
	R B	2	82	66	6	156	8	5.1	Anderson
						2917	211	7.2	
Lg Sk	F B_4	187	288	315	167	957	364	37.0	Anderson '29
	C B	148	60	67	133	408	127	31.1	Anderson
						1365	491	36.2	
Lg Gl_2	R B	163	678	697	175	1713	338	19.7	Hayes & Brewbaker '29
Ts_1 Gl_2	R S	1191	450	435	48	2124		33.2	Hayes & Brewbaker
Gl_2 Fl	R B	175	426	388	139	1128	314	27.8	Hayes & Brewbaker '29
B Fl	C B	607	109	142	593	1451	251	17.3	Beadle
		135	41	33	136	345	74	21.4	Burnham
						1796	325	18.1	
Lg Fl	R B	376	417	453	339	1585	715	45.1	Hayes & Brewbaker
		210	285	320	195	1010	405	40.1	Beadle
						2595	1120	43.2	
Ts_1 Fl	R B	232	404	159	10	805		6.2	Hayes & Brewbaker
V_4 Fl	R B	76	430	452	50	1010		12.7	Beadle

Y - PL GROUP

List of Genes

al	Albescent with	Phippe
Bh	Blotched aleurone/ A c R i	Emerson
fi	Fine streaked leaves	Anderson 1922
ms_1	Male sterile	Singleton & Jones
Pl	Purple plant color	Emerson 1918
sb	Slit Blade	Beadle 1930
sm	Salmon silks	Anderson 1921
v_6	Virescent seedling	Carver 1927
v_7	Virescent seedling	Carver 1927
w_1	White seedling	Stroman 1924
w_5	White seedling with w_6	Demerec 1924
w_6	White seedling with w_5	Demerec 1924
y	Yellow endosperm	Correns 1901

Linkage Data

Genes X Y	Link. phase	Number of individuals: X Y	X y	x Y	x y	Total	Recombinations: No.	%	Authority
Y Pl	C B	79	22	28	71	200	50	25.0	Emerson '18
		545	221	234	506	1506	455	30.2	Anderson'21
		80	51	30	55	216	81	37.5	Anderson
		173	46	59	176	454	105	23.1	Hutchison
	R B	367	880	897	372	2516	739	29.4	Anderson'21
		135	398	374	118	1025	253	24.7	Anderson
						5901	1683	28.5	
Fl Sm	C B	1076	145	146	964	2361	291	12.3	Anderson'21
		84	1014	971	76	2145	160	7.5	Anderson'21
						4506	451	10.0	
Y Fi	C B	353	0		many				Anderson'22
Y w_5	C S	250	37	35	54	376		24.3	Demerec '23
Y (w_5 / w_6)	S[1]	349	12	60	33	454		(24.3 / 24.5)	Demerec '23
Y W_1	C S	1020	237	259	191	1707		35	Lindstrom'24
	C S	1132	321	347	175	1975		48	Stroman '24
	S S	466	161	186	41	854		48	Stroman '24
Y V_6	R S	467	225	209	12	913		23	Carver '27
Y V_7	C S_2	592	149	178	79	998		42	Carver '27
	C S^2	445	277	106	116	944		36	Carver '27
V_6 V_7	R S	497	179	237		913		42	Carver '27
Bh Y	C B	141	51	118	210[3]	523	169	32.3	Anderson
Bh Fl	C B	58	1	26	47[3]	132		1.7[4]	Anderson
Y al[5]	C S	809	175	144	202	1330		26.5	Phippe
Fl al	C S	166	25	125	31				Phippe
Y ms_1	C B					308	13	4.2	Singleton & Jones
	R B					118	6	5.1	
						426	19	4.5	
Fl ms_1	C S	73	15	14	18	120		27	Singleton & Jones
ms_1 Sb	C S	630	21	54	136	741		10	Beadle '30
Y w_1	R S	323	137	120	4	584		19	Beadle '30
Y Sb	R S	347	99	114	14	574		36	Beadle '30
Fl Sb	C S	91	76	76	65	308	152	49.4	Beadle '30
Y Sl	S S	463	228	205	4	894		13.8	Fraser
Fl Sl	C S	155	16	33	29	233		24.0	Fraser

[1] w_5 and w_6 duplicate genes

[2] Segregating for another Y - not linked

[3] Probably part of this class actually Bh

[4] From Bh class

[5] F_2 data in coupling

m_1) Stroman presents data which he interprets as showing
m_2) linkage between m_1 and m_2 and also between B_1 and Y. His data are sufficiently extensive only to suggest that these factors may belong to this linkage group.

P - BR GROUP

List of Genes

ad	Adherent	Kempton 1921
an	Anther ear	Emerson & Emerson 1922
br	Brachytic	Kempton 1920
f_1	Fine striped	Lindstrom 1918
gs	Green striped	Emerson 1912
P	Pericarp and cob color	Lock 1906
ts_2	Tassel-seed	Emerson 1920

Linkage Data

Genes X Y	Link. phase	Number of individuals: X Y	X y	x Y	x y	Total	Recombinations: No.	%	Authority
		81	0	0	77	158	0	0.0	Emerson '20
P Ts_2	C B	1219	15	14	1174	2422	29	1.2	Emerson
		258	4	7	259	528	11	2.1	Brunson
	R B	0	94	92	2	188	2	1.0	Emerson
						3296	42	1.3	
P Br	C B	204	153	154	165	676	307	45.4	Emerson
		508	397	432	518	1855	829	44.7	Brunson
	R B	70	71	76	44	271	124	45.8	Emerson
						2802	1260	45.0	
Ad Sr	R S	217	91	85	4	397		22.2	Kempton '22
	R B	86	188	178	71	523	157	30.0	Kempton '22
P F_1	C B	318	107	175	248	848	282	33.3	Emerson
	C B	359	284	325	359	1327	609	45.9	Brunson
	C B	125	77	111	89	402	188	46.8	Lindstrom
	R B	65	132	163	77	457	162	35.5	Emerson
						3024	1241	41.0	
Br F	C B	197	10	9	210	426	19	4.5	Emerson
		636	33	48	610	1327	81	6.1	Brunson
	R B	18	325	320	13	677	32	4.7	Emerson
						3430	132	5.4	
Br Ts_2	C B	146	125	119	136	528	244	46.2	Brunson
F_1 Ts_2	C B	331	177	123	266	897	300	33.4	Emerson
	R B	136	247	199	110	692	246	35.5	Emerson
						1589	546	34.4	
Br An	F S	526	255	273	18	1042		25	Collins & Kempton
		300	91	134	1	426		11	Emerson
An F	R B	76	92	72	57	299	135	45.2	Emerson
An Co	R B	5	14	15	2	36	7	19.4	Anderson
	R S	916	312	271	16	1514		27	Emerson
	R S	458	147	163	9				
	C S	24	2	8	6[1]	40		23	Emerson
		151	2	22	18	193		9	Emerson
Br Co	R S	116	41	56	3	216		26	Emerson

[1] 21 ms plants not classified for anther ear.

RA-GL_1 GROUP

List of Genes

Bm	Brown aleurone	Kvakan 1924
fr_1	Frayed-1	Jenkins & Pope
fr_2	Frayed-2	Jenkins & Pope
gl_1	Glossy seedling	Kvakan 1924
ij	Iojap	Jenkins 1924
in	Intensifier of aleurone	Fraser 1924
ps_3	Pale-green seedling	Demerec 1925
ra	Ramosa	Gernert 1912
sl	Slashed seedling	Brewbaker 1929
sr_2	Striate (Same as iojap)	Brunson
v_5	Virescent seedling	Demerec 1924

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals X Y	X y	x Y	x y	Total	Recombinations No.	Recombinations %	Authority
Bm	Gl_1	C	S 177	63	54	192	486	117	24.1	Kvakan '24
		C	B 81	39	32	81	226	64	28.3	Beadle
							712	181	25.4	
Gl_1	V_5	C	B 106	9	6	120	241	15	6.2	Kvakan '24
		C	B 235	22	24	259	540	46	8.5	Beadle
							781	61	7.8	
Bm	V_5	C	B 83	31	29	98	241	60	24.9	Kvakan '24
		C	B 74	35	35	78	226	70	31.0	Beadle
							467	130	27.8	
Bm	Ps_3	C	B 169	104	100	161	534	204	38.2	Kvakan '24
Bm	Ps_3	C	S 203	8	5	65	281		4.5	Demerec '25
Y_2	Gl_1	C	S 554	143	183	100	984		36.5	Hayes&Brewbaker '26
Yp	Gl_1	C	S 1351	186	225	375	2135		20.5	Hayes&Brewbaker '26
Gl_1	Sl	R	B 513	858	1014	220	2607		22.1	Brewbaker
Bm	Sl	C	B 1417	243	266	1403	3339	599	17.9	Brewbaker
Tr	Sl	R	B 445	1157	1312	289	3203		29.7	Brewbaker
Gl_1	ij	R	S 97	269	342	63	791	160	20.2	Brunson
		R	B 11	63	63	12	149	23	15.4	Jenkins & Pope
							940	183	19.5	
		C	S 334	30	55	71	490		15.2	Jenkins & Pope
Ra	Ij	R	B 251	1792	2004	180	4227	431	10.2	Jenkins & Pope
Gl	Fr_1	C	SS 454	62	271	196	693		17.6	Jenkins & Pope
		C	S 964	115	162	230	1471		20.6	
Fr_1	Ij	R	S 375	175	192	2	744		10.0	Jenkins & Pope
Gl_1	Fr_2	C	B 67	4	12	96	199	16	8.0	Jenkins & Pope
		C	SS 137	11	74	71	293		8.0	
		C	S 3274	306	375	936	4891		15.1	
Fr_2	Ij	RS	B 256	287	101	35	679		35.7	Jenkins & Pope
		RS	2886	1196	1170	109	5361		30.	
Fr_1	Fr_2	CS	5311			666	6977		38	Jenkins & Pope
		RS	1242			164	3306		44	
Ra	In	RS	223	100	131	1	455		9.2	Fraser

Notes

sl, fr_1 — These two genes are located at about the same place in the chromosome and result in somewhat the same type of character. They may be identical or allelomorphic.

D_1 – PG_2 GROUP

List of Genes

cr	Crinkly leaves	Emerson 1921
d_1	Dwarf plant	Emerson 1912
PG_2	Pale-green seedling	Demerec 1924

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals X Y	X y	x Y	x y	Total	Recombinations No.	Recombinations %	Authority
D_1	Pg_2	R	S 1364	584	580	65	2593		32	Demerec '24
		R	S 402	165	167	16	750		30.	Brunson
		R	S 565	280	269	20	1134		35.	Suttle
D_1	Cr	R	B 15	53	48	15	131	30	22.9	Emerson
		C	B 516	102	107	482	1209	209	17.3	Emerson
							1340	239	17.8	

PR – V_2 GROUP

List of Genes

bm_2	Brown midrib	Eyster 1926
bt	Brittle endosperm	Mangelsdorf 1926
bv	Brevis-semi-dwarf plant	Suttle (Unpub.)
f_2	Fine-striped leaves	Eyster 1926
pf	Purple aleurone	East and Hayes 1911
sc_1	Scarred endosperm	Eyster 1926
tn	Tiny plant	Eyster 1926
v_2	Virescent seedling	Demerec 1924
v_3	Virescent seedling	Demerec 1924
v_{12}	Virescent seedling	Phipps 1929
yg	Yellow green	Eyster 1926
ys	Yellow stripe	Beadle 1929

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals X Y	X y	x Y	x y	Total	Recombinations No.	Recombinations %	Authority
Pr	V_2	R	B 377	532	499	366	1774	743	41.9	Phipps '29
		C	B 67	46	41	51	205	67	42.4	
							1979	830	42.0	
Pr	V_3	R	S 183	296	320	102	241	225	25.8	Phipps '29
Pr	V_{12}	C	S 492	37	39	137	705	19	12.4	Phipps '29
Pr	Ys	R	219	323	209	19	770		8.3	Beadle '29
Pr	Bm_2	R	S 2288	966	939	77	4270		28.2	Jorgenson
Pr	Bt	R	S 343	832	987	163	2325		21.8	Li
Bv	V_3	R	S 396	88	183	5	672		22.6	Li
Pr	Bt	R	S 792	394	352	13	1551		18.4	Burnham

Notes

bm — Eyster (1926) states that bm shows about 20 per cent recombinations with Pr but presents no data.

f_2, sc_1, tn, yg — Eyster states that these genes belong to the Pr linkage group but presents no data.

A-TS_4 GROUP

List of Genes

a	Anthocyanin pigment	Emerson 1918
na	Nana – dwarf plant	Suttle
ts_4	Tassel-seed	Phipps 1928

Linkage Data

Genes X	Genes Y	Link. phase	Number of individuals X Y	X y	x Y	x y	Total	Recombinations No.	Recombinations %	Authority
A	Ts_4	C	B 90	63	70	85	308	133	43.2	Phipps '28
		R	B 282	351	372	333	1318	595	45.1	Phipps '28
							1626	728	44.8	
A	Na	R	BS 196	363	355	199	1113	395	35.5	Li

SUMMARY OF THREE-POINT LINKAGE TESTS IN MAIZE

Parent No. 1			Parental combinations No. 1	No. 2	Recombinations Region 1	Region 2	Regions 1 & 2	Total	Coincidence	Authority
C	sh	Tx	2538	2708	116 113 229 3.4%	501 626 1227 18.3%	4 2 6 0.12%	6708	0.14	Hutchison '22
			5246							
I	Sh	wx	2215	2280	121 139 260 4.3%	669 553 1322 21.7%	2 3 5 0.08%	6082	0.09	Hutchison '22
			4495							
yg	C	Sh	54	51	7 9 16 12.7%	3 1 4 3.2%	1 0 1 0.8%	126		Jenkins '27
			105							
C	sh	dr	4678	4136	259 192 451 3.6%	1240 1986 3234 25.8%	14 28 42 0.44%	12543	0.33	Eyster '29
			8816							
R	G	nl	96	117	5 16	35 16	2 7	292		Emerson
R	g	l.	159	121	34 32	37 51	7 4			Emerson
R	g	nl	238	219	43 43	61 88	12 13			Emerson
			950		171 11.8%	288 19.8%	45 3.1%	1454	0.91	
Ts_5	Sh	Tu	122	93	9 15	35 31	5 16	326		Emerson
Ts_5	Su	tu	163	113	9 12	37 39	2 3	378		Emerson
			491		45 5.4%	142 20.2%	26 3.7%	704	1.53	
Ts_5	Su	tu	163	113	9 12	37 39	2 3	378	0.88	Emerson
			276		21 5.6%	76 20.1%	5 1.3%			
Ts_1	b	Lg	111	71	24 17	48 35	6 3	315		Emerson
Ts_1	B	lg	57	57	20 21	31 21	7 8	282		
			296		82 15.3%	135 25.1%	24 4.5%	537	0.77	
Sk	B	Lg	148	131	13 8	56 52	0 2	410	0.36	Anderson
			279		21 5.1%	108 26.3%	2 0.5%			
Y	Pl	Sm	191	160	109 104	21 31	5 5			Anderson '21
Y	pl	Sm	436	377	165 206	45 50	5 1			
Y	Pl	sm	305	265	107 124	28 30	0 1			
Y	pl	sm	333	411	183 152	66 59	16 12			
			2496		1150 28.6%	330 8.2%	45 1.12%	4023	0.40	
P	Br	P_1	346	346	264 290 554 41.7%	20 35 55 4.1%	13 13 26 2.0%	1327	0.75	Brunson
			692							
P	Ts_2	Pr	141	135	3 5	117 124	1 2			Brunson
			276		8 1.5%	241 45.6%	3 0.6%	528	0.67	
Ts_2	br	P_1	12	8	3 9	0 3	0 0			Emerson
			20		12 34.3%	3 8.6%	0 0.0%	35		
Bm	Gl_1	V_5	83	98	22 23	9 6	0 0	241		Kvakan '24
Bm	Gl_1	V_5	77	77	31 31	4 4	1 1	226		Beadle
			335		107 22.9%	23 4.9%	2 0.4%	467	0.32	

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