Mc Clintock

MAIZE GENETICS COOPERATION

NEWS LETTER

55

March 15, 1981

The data presented here are not to be used in publications without the consent of the authors.

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and
U.S. Department of Agriculture
University of Missouri
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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, single-spaced, and ready for the camera.

References should be used sparingly; when needed, they should be identified in abbreviated form in the text (parenthetically), including author's initials to facilitate indexing.

Deadline for contributions for the next issue (number 56, 1982) is January 1, 1982.

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. IX. C. B. Henderson, Illinois Foundation Seeds, Inc., Box 722, Champaign, Illinois 61820, 1980.

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

About 850 copies of this issue will be sent to research workers, laboratories and libraries around the world. The costs of preparation, reproduction and mailing as well as office support are borne by the U. S. Department of Agriculture in the facilities of the University of Missouri. This support and encouragement is of course indispensable, and we are all grateful for it.

50 years ago, during 1931, no cooperation materials appear to have been promulgated (see chronologies in MNL 50:2-4 and 52:146).

The questionnaire of November 5, 1980, about the News Letter, the Stock Center, and cooperation has been summarized (by unanticipated effort and in undue haste) for this issue.

Zealand 1981 summarizes new factors and linkage data for the current year.

The Stock Center is again supported and functioning through interim funding from the U.S.D.A. by Cooperative Agreement with the University of Illinois. Dr. Lambert will serve as interim Director of the Stock Center while arrangements are being made to relieve him of these responsibilities as he has requested.

A limited supply of wall-size reproductions of the linkage map, with locus names, has been made available through the efforts and generosity of W. F. Sheridan. Copies will be sent upon request to Coe at the University of Missouri.

Back issues of No. 30 (1956) to date will be sent upon 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.

The deadline for the next issue is January 1, 1982; see inside front cover.

The encouragement and support of my colleagues continues and is most appreciated. The work has also been aided by the efforts of willing and enthusiastic participants: Stephen Modena, Kathryn Kind and Christopher Browne in various tasks; Manjit Kang in programming and other computer developments. Shirley Kowalewski, in addition to handling the year's office load (correspondence, publications, mailing list and such) with enthusiasm, has invented some pictorials for our edification. Mary Nelson once again has been composition specialist, guardian of accuracy, efficiency and clarity, and producer of final copy, with her accustomed tenacity and spirit.

E. H. Coe, Geneticist, USDA-SEA-AR; Professor of Agronomy
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II. REPORTS FROM COOPERATORS

AMES, IOWA
Iowa State University

The striping phenotype in mutator stocks: A viral etiology?

Several years ago I gave Dr. Michael Freeling a couple of stocks of Mu to use in his research project. He later reported that plants of the Mu stocks I furnished him, when grown at Berkeley, frequently showed yellow or white striping. These original stocks were outcrosses of Mu to a standard line. The progeny of selfs of striped plants segregated for a high proportion of striped plants as well as other pigment mutants, runts, etc. Outcrosses of striped plants to normals frequently would have striped plants in the progeny, in seedlings as well as mature plants. Because striping was only very rarely observed in my nursery, I asked Dr. Freeling to furnish me with some samples of his striped stocks to grow in Iowa. These were grown in 1978. I did not observe striping in any of his material in the field that year but the plants were self-pollinated and outcrossed to one of my standard lines. The progenies of the selfs and outcrosses were seedling tested but no striped seedlings were observed.

Dr. John Mottinger was on leave last school year in Dr. Freeling's laboratory and had opportunity to observe the striped plants. Some had a phenotype that suggested they might have a viral infection so he tried to transmit the striping phenotype to normal (non-Mu) plants by infection. He reported at the 1980 Maize Genetics Meeting that an occasional stripe was observed in some of the infected plants.

This past summer (1980) I was on leave at the University of California, Davis, where I grew part of my nursery. I also sent material to Dr. Freeling at Berkeley to grow for me. The Berkeley material included Dr. Freeling's original striped stocks (made at Ames) and outcrosses of them. Also included were several of my mutator stocks and lines that had lost Mu activity. At Davis I also grew some of Dr. Freeling's striped stocks.

I have never consistently observed striping in my mutator stocks at Ames. An occasional plant is observed that has a single stripe typical of a sector due to the mitotic loss of a gene or mitotic mutation but certainly nothing that would resemble a viral infection.

The material grown at Davis did not differ from what I had observed in my stocks at Ames. Even the Freeling striped stocks did not have an obvious striping phenotype.

The material grown at Berkeley, however, did have a high proportion of striped plants. Most of the striping was of the mitotic sector type, frequently with numerous sectors per plant. Some plants had a "striate-like" phenotype that might be expected of a viral infection. The sector type of striping was found in all of the Mu stocks planted (i.e., Dr. Freeling's and mine). The non-Mu lines and standard lines did not show the striped phenotype. Also some plants had a blotched phenotype in which there were numerous large irregular areas of pale green tissue on the leaves. This phenotype was observed in some Mu stocks but was also common in families of my Q60 standard. The Mu stocks with blotches were those that had been crossed to the Q60 standard.

It is obvious that Mu stocks are susceptible to striping when grown at Berkeley but not at Ames or Davis (or Hawaii where I have my winter nursery). The one obvious difference in growing conditions found at Berkeley and not at the other locations where Mu stocks have been grown is the temperature over the growing season. Berkeley's growing conditions are considerably cooler. Many cool, foggy and/or cloudy mornings (or complete days) are observed. Temperatures rarely get

into the eighties for any extended period of time. These conditions must be favorable for the expression of the striping phenotype. Plant pathologists have told me that cool temperatures frequently enhance the expression of viral symptoms in plants. These observations along with Dr. Mottinger's infection experiments suggest the presence of a virus in mutator stocks.

Electron microscopic studies of Mu stocks from Ames, and striped stocks from Berkeley have revealed rare rod-like bodies of dimensions similar to those of other plant viruses. However, plant virologists are not certain these bodies are indeed viruses. One was of the opinion that they were microtubules. Thus, additional tests must be made to confirm the presence of a virus.

Outcrosses were made of the striped and non-striped plants at Berkeley. The plants were evaluated for the degree of striping and classified into five classes from non-striped to heavily striped (i.e., non-striped, +, ++, +++ and ++++). Outcrosses of plants from each of these classes will be grown next summer to determine if there is any relationship between the degree of striping and the mutation frequency. If the striping is caused by a virus, and if there is a relationship between the severity of the infection and the amount of striping, and if (a big if) the virus is responsible for the mutator activity, then there may be a direct relationship between the mutation frequency in an outcross and the amount of striping observed in the tested parent.

One additional experiment is underway which is designed to test for viral involvement in Mu. Extracts of mutator plants were rubbed on leaves, dusted with silicon carbide powder. If a virus is involved, the standards might be infected and become mutator plants which would transmit mutations to their outcross progeny. Outcrosses of these "infected" plants are being grown this winter in Hawaii.

Donald S. Robertson

Forward mutation frequency of Bt in the presence of Mu

To date, the effect of Mu on the forward mutation rate of a specific locus has not been measured. In 1979 two isolation plots were set up. In one the female rows were a2 bt and the pollen rows were a purple aleurone Bt Mu stock. In the second plot the female rows also were a2 bt but the male rows were a purple aleurone Bt non-Mu stock. The frequency of bt seeds with colored aleurone in both of these plots was:

	bt	Total	Freq. of bt
Mu	37	255,347	14.5×10^{-5}
non-Mu	7	205,242	3.4×10^{-5}

contingency $\chi^2 = 16.4109$ (P .01 = 6.635)

There is about a fourfold higher mutation frequency in the Mu line. This difference is significant as determined by a 2 x 2 contingency χ^2 test. Although Mu seems to increase the forward mutation frequency of Bt the increase for this one locus is much less than the increase in the overall forward mutation frequency for seedling mutants, which is about 50-fold. This suggests that not all loci are equally sensitive to Mu.

Donald S. Robertson

Mutator activity in Mu x Mu Plants

F1 plants from the cross of two Mu lines (Mu x Mu) were tested for Mu activity by the standard Mu outcross tests to determine if such F1's would have a higher mutation rate than plants receiving Mu from only one parent. The results are in Table 1.

Table 1. Mu activity in F_1's from the Mu x Mu crosses compared to standard Mu (control) values.

Family	Total	Total Mutants	% Mutants	Total Different Mutants	% Different Mutants
9626	35	9	25.7	6	17.1
9627	42	1	2.4	1	2.4
9628	42	8	19.0	4	9.5
9629	38	5	13.2	4	10.5
9630	36	6	16.7	5	13.9
9631	40	1	2.5	1	2.5
9632	33	4	12.1	4	12.1
Total	266	34	12.8	25	9.4
Total Less 9627-9631	184	32	17.4	23	12.5
Previous standard Mu tests (control)	1541	171	11.1	98	6.4
X^2 Total Mu x Mu and control			.4916		2.6119
P =			.30-.50		.20-.10
X^2 Total Mu x Mu (minus 9627 & 9631) and control			4.3311		6.7924
P =			.02-.05		<.01

In the Mu x Mu crosses there appear to be two populations. One has a higher than standard Mu activity and the other appears to have the standard or lower Mu rate (families 9627 & 9631). These latter crosses may be instances where the Mu x Mu plant received Mu from only one parent (= loss of Mu). If these low rate families are removed from the population, then Mu x Mu plants have significantly higher mutation rates than plants that receive Mu from only a single parent. This is particularly obvious in the "% Different Mutants" class. In this class the rate is twice the control rate suggesting two Mu's have twice the effect of one. However, there is slightly less of a marked difference in the "% Mutants" class. In this case, the Mu x Mu lines have 1.6 times the mutation rate of the control. Additional Mu x Mu outcrosses are needed in order to obtain more reliable figures. Certainly, the preliminary data suggest that Mu effects may be additive in plants with Mu contributions from both parents.

Donald S. Robertson

Culturing of endosperm tissue

The culturing of endosperm tissue has been abetted by the use of inbred R168 (Illinois) as the background genotype (J. C. Shannon and J. W. Batey, 1973). These tissues have been cultured on modified MS medium in our continuing study of anthocyanin genes and controlling elements in tissue culture (M. B. Gorman and P. A. Peterson, 1978). Several conditions were varied in testing the efficacy of growth conditions for field-grown materials. These include culturing of different genotypes at different post-pollination stages and different times of collection

(7:00 a.m., Noon, and 8:00 p.m.). Assessing the hour of culturing was done in order to evaluate the effect of age difference on tissue growth and callus initiation in terms of hours rather than in days after pollination. Time effects (morning, noon, or evening) on the tissue performance in vitro could not be compared due to the confounding effect of age differences in hours from pollination, which is done normally at approximately 10:00 a.m.

The two phases of endosperm tissue growth: Two phases of tissue growth were recognized in vitro. The initial growth (first 7 to 10 days) resulted in organized and compact tissue which is comparable to the in vivo endosperm. In contrast, the second phase of growth (after 10 to 15 days) is disorganized and localized proliferations of growth appear.

The first phase can simply be identified as the growth phase, whereas the second phase can be considered the callus phase. The timing of appearance of the callus phase differed from genotype to genotype. Callus initiation seems to depend on the initial tissue growth.

Effect of age and genotype on tissue growth: Using an index method to assess tissue growth performance, it could be determined that the first and second phases of growth of different genotypes were better when cultured between 202 hours (8-days old at 8:00 p.m.) and 226 hours (9-days old at 8:00 p.m.) than when cultured at later stages after pollination. Genotypic differences were more noticeable for these two phases of growth with endosperms of earlier stages than with older endosperms. Also, the differences among genotypes were more significant in callus phase (15 days) than in growth phase (until a week).

In addition to the inbred R168 background, some genotypes in the present study contained the controlling element allele wx-m-8 which was backcrossed two to three times to R168 [wx-m-8(R168)]. The genotypes with R168 background showed better tissue growth and callus initiation than that of wx-m-8(R168). Inbred R168 by itself had been previously reported to be good for endosperm callus initiation (A. R. Reddy and P. A. Peterson, 1977) and was found to perform better than wx-m-8(R168) in the present study.

Considerable variation occurred within the progeny of a selfed ear in growth and callus phases. This may be attributed to the heterozygosity of the segregating alleles.

In conclusion, the conditions for the most efficient growth of callus include genotype and age of tissue (hours after pollination).

L. V. Reddy and P. A. Peterson

A case of non-reciprocal cross-incompatibility of maize

Frequently, maize geneticists encounter poor ear setting among their crosses. Often an environmental effect (hot summers) is suggested. When poor setting is found when there is a clear expectation of good setting, then one takes notice and investigates. Such a case was found in 1975 among crosses involving controlling elements.

When a1-m(pa-pu)/a1 sh2 genotypes (Peterson, 1970, TAG) or its derivatives are crossed by a1 et/a1 et males, ears with reduced seed set (RSS) are observed. Among RSS progenies, there is a consistent array of progeny types. Approximately 80 to 90 percent of the ears produce from 0 to 25 kernels per ear (class A), 6 to 23 percent produce 26 to 200 kernels per ear (class B) and 0 to 3 percent produce over 200 kernels per ear (class C). RSS occurs with specific male parents since crossing a1-m(pa-pu)/a1 sh2 by other male testers (a1 sh2/a1 sh2, a1-m(r)/a1-m-1) yields ears with normal seed set (NSS).

The reciprocal cross, a1 et/a1 et x a1-m(pa-pu)/a1 sh2, results in NSS. The resulting F1's of this NSS cross also give NSS when they are crossed by a1 et/a1 et males.

The RSS effect is heritable and is maintained through several successive crosses of a1-m(pa-pu)/a1 sh2 x a1 sh2/a1 sh2 males. No segregation of the RSS effect is observed in the progenies of these crosses nor in the selfed progenies of a1-m(pa-pu)/a1 sh2.

The accumulated results of these crosses have provoked the following hypothesis for RSS behavior. It is considered that the a1-m(pa-pu)/a1 sh2 lines carry a genetic factor controlling the incompatible condition of the flower (specifically the silks). The a1 et/a1 et plants carry a genetic factor controlling the incompatible condition of the pollen and interacting with the silks. The hypothesized interactions are as follows:

RSS female x RSS male = RSS
RSS female x N male = N
N female x RSS male = N
N female x N male = N

The transmission of RSS is complex and it appears that cytoplasmic-chromosomal interaction might be involved. Studies are in progress to test various aspects of this hypothesized interaction.

Kitisri Sukhapinda and Peter A. Peterson

The Uq controlling element system: Change in nomenclature

Due to the prior use of Ub to designate the unbranched tassel gene (see Neuffer, Jones and Zuber, 1968, The Mutants of Maize, Crop Sci. Soc. Amer., Madison, WI), the Ubiquitous-controlling element system (Friedemann and Peterson MNL 54:1) is now identified as the Uq-controlling element system. The regulatory element is designated Uq and the receptor allele, a1-ruq (for the a1 locus). The designation + indicates the absence of Uq.

Peter D. Friedemann and Peter A. Peterson

Dosage effect of Uq on the mutability pattern

Two types of mutability patterns are observed on kernels of the original source of the Uq controlling element system. One pattern type is distinguished by the appearance of relatively early and more frequent mutation events (larger and more numerous colored spots on a colorless aleurone background) and is designated coarse-high. A second type of pattern designated fine-low consists of later, infrequent events (relatively few small colored spots on a colorless aleurone background).

Progeny ears of the cross a1-ruq/a1-ruq +/+ x a1-ruq/a1-ruq Uq/Uq only contain kernels with a fine-low pattern of spots. In contrast, the reciprocal cross gives progeny with almost exclusively coarse-high spotting. Selfs or sibs of plants with the genotype a1-ruq/a1-ruq Uq/Uq again contain almost exclusively coarse-high spotted kernels. These data when correlated with the origin of the endosperm (female parent, 2 doses; the male parent, one dose to the triploid endosperm) indicate the following:

Aleurone genotype	Uq dose	Observed spotting pattern
a1-ruq/a1-ruq/a1-ruq Uq/+/+	1	fine-low
a1-ruq/a1-ruq/a1-ruq Uq/Uq/+	2	coarse-high
a1-ruq/a1-ruq/a1-ruq Uq/Uq/Uq	3	coarse-high

Visually, no consistent difference is observed between the coarse-high spotting pattern with 2 doses of Uq versus 3 doses of Uq. No dosage effect has been observed when the Uq dose is held constant and the dosage of a1-ruq is varied, i.e., a1-ruq at 1, 2 or 3 doses.

Peter D. Friedemann and Peter A. Peterson

AUSTIN, TEXAS
University of Texas

Apparent chiasma maintenance and terminalization across a region homoeologous for a segment derived from Tripsacum

In maize microsporocytes heterozygous for a chromosome 2 interchange chromosome which carries a homoeologous Tripsacum segment substituted for the distal half of its short arm, normal synapsis usually occurs at pachytene throughout the bivalent. Crossing over, however, is almost entirely restricted to the homologous proximal region of the arm, where it apparently occurs frequently (Genetics 45:195-209, 1960; Genetics 45:651-664; J. Heredity 53:87-88, 1962). Acetocarmine squash preparations of anthers from heterozygous plants were systematically scanned, and diakinesis stage cells were classified for presence or absence of a chiasma in the knob-carrying arm of chromosome 2 as well as for the position of the chiasma (when present) within this knob-carrying arm. The chromosome 2 bivalent was usually readily identifiable at diakinesis because of its terminal knob and relatively large size. Of 123 diakinesis cells so classified, 6% showed no chiasma in the knob-carrying arm, 33% were found to have a chiasma a substantial distance from the knob, 58% showed a chiasma immediately adjacent to the knob, and 3% had an apparently terminal chiasma, in the knob region. Thus in a very large proportion of the cells a chiasma presumed to have resulted from a necessarily more proximal crossover event (in the region of homology) was found to be located immediately adjacent to or at the knob by diakinesis. In these cases the amount of chromatin between the chiasma and the knob was so scant as to make the interpretation unreasonable that differentially, strongly condensed, more distal chromatin rendered the apparent position of the chiasma to be falsely nearly terminal. It is difficult to avoid the interpretation that many chiasmata had terminalized across most of the region where the two chromosomes of the bivalent shared only a homoeologous relationship, and that loss of chiasmata formed in the proximal half of the arm was rare at most. Such loss would produce a chromosome 2 bivalent with the ends of the knob-bearing arm free and with equational separation of the terminal knob at these ends. No such bivalent was seen.

Marjorie Maguire

A search for the synaptic adjustment phenomenon in maize

It has recently been suggested from several laboratories that complex synaptic configurations (required for homologous synapsis in the presence of heterozygosity for chromosome rearrangements, or resulting from multivalent formation in polyploids, or even resulting from interlocking of normal bivalents) may be formed at early pachytene, but are altered at later pachytene by dissolution of the central element of the synaptonemal complex, followed by its reinstatement in such a way that only free bivalents, typical of normal sequence homozygotes in diploids, are usually found at late pachytene. It has been suggested that the synaptic adjustment inferred may be a process of widespread occurrence (Moses, M. J. et al., J. Cell Biol. 79:123a, 1978; Rasmussen, S. W. and P. B. Holm, Carlsberg Res. Comm. 44:101-125, 1979). Maize microsporocytes heterozygous for a paracentric inversion

in the long arm of chromosome 1 (inversion 4305-25) were studied in this laboratory (in acetocarmine squashes) at early and late pachytene and also at early diplotene. Clear remnants of loop configurations typical of homologous synapsis of the inverted region were found in a number of cells at early diplotene, and synaptic failure of the inverted region was common at both early and late pachytene. In maize microsporocytes a synaptic adjustment process comparable to that which has been reported in mammals seems to be absent.

Marjorie Maguire

BLOOMINGTON, INDIANA
Indiana University

The wx locus is the structural gene for the Wx protein

The protein product of the wx locus has been identified and isolated. When starch granules from Wx endosperm are extracted by heating in SDS containing buffer and run on SDS polyacrylamide gels, five proteins are visualized by Coomassie Blue staining. One major protein is present which makes up about 85% of the total extracted proteins and has a molecular weight of approximately 60,000. The four other minor proteins are all of higher molecular weights. When the starch granules from endosperms of 29 wx alleles which produce no amylose were examined, 25 showed a complete lack of the major protein, termed the Wx protein, while the minor proteins were unaffected. This difference between Wx and wx endosperm was observed from 12 days to maturity. Also, starch granules from Wx pollen have the Wx protein while those from wx pollen do not. The other four alleles, B3 (an Mp controlling element mutation), C31, R and 90 all make the Wx protein. B3 and C31 show normal levels of the protein and R and 90 show reduced levels. All alleles which produce reduced amounts of amylose have some Wx protein. m-8, an Spm mutation, has less than 3% the normal level, wx-a has about 5%, and S5 and S15, two stable partial revertants of the Ds mutant m-1, obtained from O. Nelson, have full levels.

That the Wx protein is coded for by the wx locus is demonstrated by the facts that the Wx protein varies linearly with Wx allele dosage and that Wx proteins with altered isoelectric points are produced by the wx alleles 90, C31 and R. Our results indicate that the Wx protein is the starch granule-bound NDP sugar-starch glucosyl transferase since this enzyme activity is also absent in wx endosperm (Nelson and Rines, Biochem. Biophys. Res. Comm. 9:297) and varies linearly with Wx dosage (Tsai, MGNL 39:153).

The data also show that wx is the locus of the structural gene. Since altered proteins are produced by alleles mapping near both ends of the locus (C31, R and 90) the structural gene extends throughout most of the mapped region (Nelson, MGNL 50:109). Thus, the controlling element mutations B3 (Mp), m-1 (Ds) and m-6 (Ds), and probably also B4 (Ds) and m-8 (Spm) lie within the structural gene. It may be that some of them are in an internal control region (regulatory introns) but this certainly is not the case for B3, which produces the full level of an inactive transferase. The same is true for m-1 which, after presumed transposition of the Ds element away from the locus, gives rise to two fully expressed but only partially active Wx proteins, those specified by S5 and S15. No size differences have been detected on SDS gels among any of the allelic Wx proteins. Our analysis indicates some form of RNA processing for B3 and m-8.

Allele	Amylose content	% Wx protein (relative to Wx)	Controlling element
m-1	0	0	Ds
m-6	0	0	Ds
m-8	low	3	Spm
B3	0	100	Mp
B4	0	0	Ds
S5	low	100	Ds revertant
S15	low	100	Ds revertant
C31	0	100	--
R	0	30	--
90	0	15	--
wx-a	low	5	--

All of the other wx mutants mapped by Nelson, including the unmapped alleles I, P60 and BL3, lack the Wx protein. Alleles J and K were not tested.

Craig Echt and Drew Schwartz

Extraction of the Wx protein

The Wx protein and the four other minor starch bound proteins are firmly held in the starch granule by a combination of electrostatic forces and entrapment within the starch matrix. The proteins could not be extracted from intact granules without first swelling the starch granules past the gellation point by either heating or treatment with 8M urea. Once the matrix is opened the following conditions have been found to be effective for solubilizing the proteins: 2% SDS, 8M urea (swelling and dissociation are one step), and low molarity buffer (0.01 M) below pH 2 or above pH 7.5. pH extraction was not successful with 0.05M buffers. Extractions at pH 7.5 and above also required a reducing reagent such as 5% BME or 0.01M dithiothreitol. The efficiency of extraction increased with pH from 7.5 to 10.0. pH 2 is as efficient as pH 10 and both are nearly as efficient as SDS or urea.

Craig Echt

Further studies on the structure of abnormal chromosome 10

This contribution is a progress report of our cytogenetic studies on the eleven Df K10 chromosomes described in our article in the 1980 Maize News Letter. Five of the eleven are simple terminal deficiencies; the remaining six have a translocated chromosome involving abnormal 10 and a heterologous chromosome. All eleven are deficient for the Sr2 locus since loss of the dominant allele was used in screening for the deficient K10 chromosomes and all had lost the K10 knob. Of the five simple terminal deficiencies, two, Df K10(H) and Df K10(K), had the W2 locus while the remaining three, (C), (F), and (I), were deficient for both W2 and Sr2. The cytological length at pachynema of the two which were not deficient for the W2 locus was greater than that of the three deficient for W2 and Sr2. The (F) deficiency was not as extensive as (C) or (I). There was no transmission through the pollen of the (C) and (I) deficiencies while the (F), (H), and (K) deficiencies were transmitted although with reduced rates; as expected, the pollen transmission of (F) was lower than that of (H) or (K) since it was a longer deficiency.

Arm 10S and the portion of 10L from the centromere to a position just distal to the R locus are structurally similar in normal 10 and abnormal 10. The euchromatic distal 1/5 of the long arm of N10 to the right of R carries the W2, L13, and Sr2

loci with Sr2 closest to the tip of 10L. The portion of 10L in abnormal 10 corresponding in position to the distal 1/5 of N10 comprises what we have called the differential segment. It has three small knobs, the terminal one lying opposite the telomere of N10 in K10/N10 microsporocytes. No known genes have been assigned to the differential segment. Further, in K10/N10 heterozygotes there are no exchanges within the limits of the differential segment. In abnormal 10, adjacent to the right end of the differential segment (marked by the third of the small knobs) lies a euchromatic stretch of chromatin whose length approximates that of the differential segment. This euchromatic segment, extending beyond the tip of the N10 in K10/N10 pachytene bivalents, is homologous to the distal 1/5 of the long arm of N10. We have shown that it possesses the W2 and Sr2 loci and that their linear order in the transposed segment with respect to the R locus is unchanged. The genetic determiners in K10 responsible for such unique phenomena as preferential segregation and neocentromere formation have been shown by J. Miles and by M. H. Emmerling to be localized in the large heterochromatic knob, which is next in linear sequence along the long arm of K10.

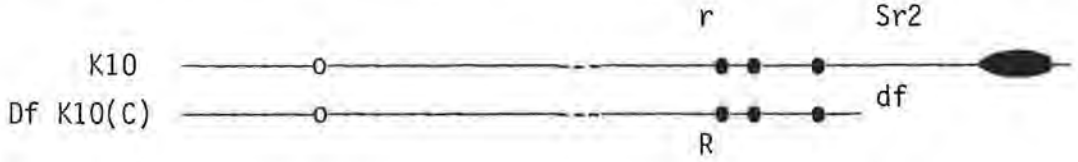
Recombination studies with the Df K10 chromosomes provided some interesting data. G. Y. Kikudome (Genetics, 1959) showed that in K10/N10 compounds the R Sr2 recombination was reduced from the normal frequency of 35% to 1-2% and all exchanges occurred in the segment between the R locus and the first of the three small knobs in the differential segment. Low R Sr2 values were also found in our Df K10/N10 heterozygotes. Although we attributed the great reduction in crossing over distal to R in K10/N10 heterozygotes to genetic dissimilarity of the differential segment with its three small knobs, an alternative explanation ascribes the reduction in crossing over to the large heterozygous heterochromatic K10 knob. We know from Kikudome's work that crossing over in the terminal segments of 9S is reduced in K9/k9 plants. A similar situation for chromosome 10 might obtain in K10/N10 sporocytes although we considered this eventuality unlikely since the K10 knob is known to enhance crossover values, particularly in structural heterozygotes. Discrimination between the two explanations came from crossing Df K10(F) R -/N10 r W2 heterozygotes with r W2/r w2 pollen parents. The Df K10(F) chromosome lacks the K10 knob as well as the W2 and Sr2 loci. The expected classes from noncrossover and crossover gametes in the female parent are given below:

$$\frac{\text{Df K10(F) R -}}{\text{N10}} \quad \frac{\text{r W2}}{\text{r W2}} \quad \times \quad \frac{\text{r W2}}{\text{r w2}}$$

	Male gametes	
Female gametes	r W2	r w2
nco R -	colored aleurone green seedlings	R-r spotted aleurone white seedlings
nco r W2	colorless aleurone green seedlings	colorless aleurone green seedlings
co R W2	colored aleurone green seedlings	colored aleurone green seedlings
co r -	colorless aleurone green seedlings	colorless aleurone white seedlings

As shown in the Punnett square, the expected proportion of colored:R-r spotted: colorless kernels is 1:1:2 from nonrecombinant gametes. Recombination distal to R gives colored kernels producing green seedlings which cannot be distinguished from noncrossovers. Recombination distal to R does not lead to a corresponding increase in the R-r spotted aleurone-white seedling class. The excess of the colored aleurone-green seedling class over the R-r spotted aleurone-white seedling class reflects the amount of recombination distal to R but deviations from expected ratios give an unreliable estimate of recombination. A much better determination of crossing over distal to R comes from a consideration of the kernels with colorless aleurone. With no crossing over distal to R, all colorless kernels produce green seedlings. White seedlings from colorless kernels arise only by crossing over. However, the percentage of recombination distal to R calculated from the relative proportion of green and white seedlings from colorless kernels is only one half the true value since in half of the cases a crossover gamete would be fertilized by a r W2 sperm and produce a green seedling. When 1936 colorless (r) kernels from the above cross were planted, 1862 green and 13 white seedlings (0.69%) were obtained. Twice this value gives 1.38% recombination distal to R in Df K10(F)/N10 heterozygotes, a percentage very close to that found in K10/N10 plants. Clearly, the low frequency of recombination distal to R cannot be ascribed to the K10 knob since comparable values were found when the K10 knob was present and when it was absent. The marked reduction must be caused by genic differences in the differential segment.

There are no mutant alleles distal to R in the K10 chromosome and this would ordinarily mean that crossover studies distal to R in K10/Df K10 compounds could not be carried out. However, all of our Df K10 chromosomes lack the Sr2 locus and since hemizygous Df/sr2 plants express the recessive striate phenotype, the deficiency for Sr2 can be used to genetically mark the terminus of the Df K10 chromosome. Df K10(C) pollen cannot compete successfully against N10 or K10 pollen. In K10 r Sr2/Df K10(C) R df plants, diagrammed below, the percent of R kernels found in pollen testcrosses is a measure of the amount of crossing over distal to R.



All single exchanges in this structurally homozygous region transfer the R allele to a pollen-transmissible chromosome. The frequency of R kernels was seven percent. The R-sr2 recombination value also measures the crossover frequency between R and the tip of Df K10(C). The two values proved to be identical. Approximately two percent of the observed seven percent should be ascribed to exchanges between R and the differential segment. We have no estimate of the frequency of crossing over in the short region distal to the differential segment. Even if it be zero, there would be only five percent recombination within the homozygous differential segment which is equal in length at pachynema to the distal fifth of the long arm of N10 where there is 35-36% recombination in N10/N10 sporocytes. It may be concluded that crossing over per unit length of chromatin is low in the differential segment. Indeed, our studies with K10 deficiencies (H) and (K) suggest that this region may be devoid of exchanges.

In testcross data from plants heterozygous for K10 r Sr2 and either Df K10(H) R - or Df K10(K) R -, there was 16% recombination between R and the end of the Df K10 chromosome. This interval includes the homozygous differential segment and the greater part of the adjacent euchromatin, which is homologous in gene content and linear order to the distal fifth of the long arm of N10. However, less than half as

much crossing over took place in this stretch of chromatin as in the R-sr2 interval of N10 which is physically approximately only one half as long. We have interpreted these data as indicating that exchanges in K10/Df K10 pairs take place only between R and the first of the three small knobs of the differential segment and in the euchromatin to the right. We suggest that there is no or little recombination in the differential segment in either structurally homozygous or heterozygous bivalents.

M. M. Rhoades and Ellen Dempsey

On the linear order of genes in the distal region of 10L

In the recent linkage map collated by Coe the order and map position in the distal part of 10L is given as follows:

R	Lc	Mst	w2	o7	sr2	12	K
57	61	(63)	73	80	(92)	(99)	

The map positions enclosed in parentheses indicate tentative assignments. Our data suggest that some revision be considered. First, 12 is not beyond sr2. The evidence for this statement comes from our studies with Df K10(H) and (K). Seedlings homozygous for either of these chromosomes are green; later they become green-white striped due to the deficiency of Sr2 but this phenotype is not expressed until the plants approach maturity. Homozygous deficient plants should manifest a mutant phenotype, similar to that produced by a recessive allele, for all loci included in the deficiency. For example, Df K10(F) is deficient for the segment containing W2 and Sr2. Homozygous deficient seedlings were white as are hemizygous w2/Df and w2/w2 seedlings. However, seedlings homozygous for Df K10(H) or for Df K10(K) are not white, virescent, glossy, luteus, or dwarf indicating that no dominant alleles of these seedling traits are in the segment of K10 distal to the Sr2 locus. The failure of the homozygous deficient plants to show the luteus phenotype demonstrates that the L2 locus is not distal to Sr2, at least in the K10 chromosome. The data also indicate that Sr2 is situated near the K10 knob since no mutant effects have been observed in seedlings homozygous deficient for any euchromatin which may be distal to Sr2.

Second, since the 12 mutant has been lost, we suggest that the 113 mutant, which was accurately located by P. Mascia (1978 Maize News Letter) 4.5 map units to the left of Sr2 at map position 87, replace 12. Whether or not L13 and L2 are allelic cannot be ascertained since no stocks with 12 are extant.

The o7 locus is given in the above map as 7 crossover units distal to w2. This may be the correct order in N10 chromosomes but we have some reservations in accepting this placement. The o7 locus may be flanked by w2 and sr2 but this order is based on 2-point data from crosses of different stocks which could well differ in recombination frequency. We attempted to order o7 with respect to R and w2 using F2 data where all three loci were segregating, but modifiers affecting the o7 phenotype made accurate scoring impossible. In our 1980 News Letter article we stated that the o7 locus appeared to lie to the left of w2 since the dominant allele was retained by the Df K10(F) chromosome when the W2 and Sr2 loci were lost. After three backcrosses to the o7 tester to eliminate modifying genes which inhibited the expression of the opaque trait, we are convinced that the Df K10(F) chromosome, deficient for W2 and Sr2, does indeed possess the dominant allele of the o7 locus and that the linear order in the K10 chromosome is R O7 W2 Sr2. Either the accepted linear order in N10 is wrong or the w2 o7 segment has been inverted in the K10 chromosome. Studies in progress involving three point linkage tests in N10 should reveal which alternative is correct.

M. M. Rhoades and Ellen Dempsey

Did abnormal 10 arise from a translocation between Tripsacum and Maize Chromosomes?

The two kinds of chromosomes 10 found in races of maize clearly differ structurally and genetically. Since N10 is much more frequently encountered, it presumably, although not necessarily, is the ancestral form. What can be said about the source of the differential segment and the large heterochromatic knob which characterize abnormal chromosome 10? Not much, but certain speculations may be fruitful. The K10 knob is unique in that it has specific genetic properties not possessed by any other knob found in races of maize. Although it contains the same highly repetitive 185 bp sequence of satellite DNA in all knobs of maize (Peacock, Dennis, Rhoades and Pryor, in press) it cannot be identical to them in DNA composition. It is not a typical maize knob. The origin of the differential segment is likewise obscure but its insertion into 10L and the translocation of the piece with the K10 knob may have taken place at the same time, both being contributed by the same chromosome. Of possible significance in this connection is the statement made years ago by L. F. Randolph that one of the pachytene chromosomes of a diploid Tripsacum dactyloides from Kansas had a terminal segment similar in appearance to abnormal 10. Randolph did not describe this chromosome in detail but he was fully cognizant of the appearance of abnormal 10 so it is a reasonable inference that it had both a segment comparable to the differential segment of K10 and a large subterminal knob. Walt Galinat has isolated as supernumeraries a number of chromosomes from diploid Tripsacum dactyloides in a maize background. Possibly the Tripsacum chromosome described by Randolph has already been isolated by Galinat. If not, it should be possible to extract it and study its synaptic behavior as a supernumerary in maize sporocytes with and without abnormal 10. If it pairs with the distal end of 10L of abnormal 10 but not with normal 10 and if this Tripsacum chromosome can induce preferential segregation and neocentromeres and also possesses the W2 and Sr2 loci, then abnormal 10 could have been produced in a maize-Tripsacum hybrid by a simple translocation. There are a lot of "ifs" in the above speculation but additional studies may be highly rewarding and indeed have a direct bearing on the evolutionary history of modern maize. There is in our opinion no convincing evidence that abnormal 10 originated from a translocation involving a B chromosome nor is there any evidence that another chromosome of the A complement donated the segment differentiating K10 from N10. The above hypothesis, which predicates Tripsacum as the source of this chromatin, is simple and we find it attractive because it is experimentally testable.

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Maize in India

The year 1978/79 was a sabbatical for me and I went to India on an Indo-American Research Fellowship to study genetic relationships and genetic distance in the older Indian landraces of maize. Specifically I was interested in the landraces grown in the Eastern Himalayas around Darjeeling and further east in Assam. Because of government policies I was denied access to most of the tribal maize growing areas of India on national security grounds but was able to obtain representative material by having Dr. J. K. S. Sachan of the Indian Agricultural Research Institute make collections for me. Much of the maize production is centered in the Indo-Gangetic plains of India and I was stationed at the Punjab Agricultural University where there is an active maize breeding program under the direction of Dr. A. S. Khehra.

The maize of India is extremely interesting from an evolutionary viewpoint because of its distance from the center of diversity for this crop and because once introduced to India small genetically isolated populations have been cultivated locally, sometimes for over a century. The oldest of the Indian landraces were probably introduced by the Portuguese (16c) and these flints have undergone considerable local adaptation. Within the last century there has been the arrival of United States germplasm via South Africa (Hickory King types) and direct introduction by American missionaries especially among tribal peoples in hill districts. India is too big and diverse a country to make generalizations but I was repeatedly impressed by how rigid is the selection of cultivators for crop uniformity. The differences between abutting cultivators could be as varied as differences between regions. Each one of these adjacent fields possessed its separate and distinct evolutionary history. The pattern of selection was the polar extreme of what I'd encountered in the Americas with indigenous cultivators and is worthy of further investigation. The racial diversity of maize in India is small when compared to the Americas but the selection for genetic uniformity and local adaptation indicate a potential for unique germplasm for the plant breeder, especially in the area of disease resistance.

I centered part of my research on the study of the landrace Sikkim Primitive (N. Dhawan, MNL 38:69-70, 1964), which was recognized as showing marked resemblance in its ear (but not plant type) to the reconstructed ancestor of Mangelsdorf. This little grown popcorn of Sikkim and adjoining areas occurs at mid-elevation, 6000-8000 feet, in moist tropical cloud forest region, and has been claimed to be a primitive sort of ancestral maize. Actually, it is a local adaptation to short day (tropical short day, flowering in September) of probably the commercial popcorn Ladyfinger. The resemblance to the reconstructed ancestor is not inappropriate since Ladyfinger was used in one of Mangelsdorf's reconstructions. The people of the region grow maize as a food crop (an eight or ten rowed semident/flint of the recognized race Tista Mendi [Bhag Singh, Races of Maize in India, 106 pages, Indian Council of Agricultural Research, 1977]), which is most probably a derivative of a Caribbean Flint/New England Flint from the plains below, but the popcorn Sikkim Primitive, or Murli, is totally distinct and used only as offerings in ceremonial use among the Buddhistic peoples of the region. These small popcorns make a much more to scale offering than the semident maize. This popcorn is not widely grown and the cultivators who do grow it do so for personal use in their own prayer rooms, which can be half the total floor space of the house (the cook house, because of the possibility of fire in these wooden structures, is separate and actually much of the living is done not in the house but in the cook house). Offerings of bowls of water and small ears of Murli with yellow (sacred color) endosperm are placed before a permanent altar in the prayer room. The people of this region cultivate steep hillsides with a winter crop of peas and potatoes, intercropped; and a summer crop of maize sometimes intercropped with finger millets. The maize is consumed either as a fermented beer-like beverage (Wilkes, Econ. Bot. 22:347-359, 1968) or parched and sometimes some actually popped. They grow excellent cool temperate vegetables and obtain a large fraction of their dietary protein from plant material. Livestock (cows, goats and pigs) are all pen fed and cornstalks are an important part of the ruminant feed. The house sites are in the middle of the cultivated fields and there is no village formation with distant fields. Maize is hung as ears from the headbutts of the rafters of the house and the stalks are kept dry under cover in an extension of the cow shed. The number of plants of Murli grown is small, certainly less than a hundred while the semident Tista Mendi population is large and may cover about two/three hectares (the average landholding).

A second area which I looked at closely in an indirect manner, and which is worthy of further studies, is the Eastern Region of the tribal areas in the states of Arunachal Pradesh, Nagaland, Assam, Manipur, and Tripura. Much of the maize, which is not typically Indian in the region is extremely interesting because it has been introduced by missionaries in the early part of this century. From an evolutionary viewpoint these are modified Reid Yellow Dents and Lancaster Sure Cropper which might be a wealth of disease resistant germplasm for present day temperate inbreds entering the tropics. Unfortunately I was denied access to the region and all the collections were made by Dr. Sachan.

A third area where older landraces are grown is in the foothills of South India, around 3000 to 5000 feet in elevation, seasonally dry with a tropical forest vegetation cover. These are modified New England Flints which are very rapid in their maturity and among tribal people in Andhra Pradesh and Orissa are called "hungry children food" because the crop is ready and eaten green (like a sweet corn) before the slower to mature rice crop is ready for harvest. The maize was planted in small garden plots along with squash (C. pepo) and beans, but the beans in this case were cowpeas (Vigna unguiculata) and Phaseolus lunatus, the "carob" group which is often toxic. Maize is no longer a principal crop in the region and is being displaced by the introduction of more rapidly growing, fertilizer responsive, earlier to mature rice varieties. This maize landrace most probably possesses germplasm for disease resistance because all the crops grown in the region showed signs of fungal infections.

I was surprised to find Tripsacum (T. laxum, the non-flowering "Guatemala Grass" that was widely used to stabilize soils on tea estates in Ceylon [Sri Lanka] between 1900 and 1920) growing as an escape in the tropical rain forest zone of Kerala, South India. It is still being used to stabilize soils in tea plantations and at Periyar, Kerala I observed elephants foraging on Tripsacum; this was a first.

The use of teosinte as a forage crop was much more widespread twenty years ago and instances of its present use were few and far between. In general the use of "Florida teosinte" on state run dairy farms has been replaced by sudan grass.

Most of the maize grown in India will be short day and difficult to grow in experimentation under U.S. conditions (assuming it has passed plant quarantine) without short day induction of flowering, but many of these local collections from tribal areas deserve screening for disease resistance and inclusion in the World Maize Germplasm Collections.

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Crosses of Zea diploperennis with corn

The purpose of the Argentine plantings (see item from Chapel Hill) was to complement the plantings in the United States and to take advantage of the fact that in the southern hemisphere, mid-summer corresponds to mid-winter in the northern. The plantings in both countries were designed to test the hypothesis of Garrison Wilkes, who postulated that several of the races of annual teosinte, which some students of corn's ancestry regard as the progenitors of cultivated corn, might instead be the progeny of the hybridization of Zea diploperennis with a cultivated corn in the early stages of domestication.

The plantings in Argentina, like those in the United States, began with crossed seed produced by Mangelsdorf. In a small garden in Chapel Hill, N.C., completely isolated from all other Maydeae, he crossed plants of Zea diploperennis, grown from seed obtained from Hugh Iltis, with a primitive Mexican popcorn race, Palomero Toluqueño. This popcorn race was chosen as the corn parent of the cross because it, or its precursor, is the race most likely to have been grown in Jalisco in the area where Z. perennis was discovered by Iltis et al. It was chosen also because it has small pointed kernels, like those of teosinte, so that relatively little segregation for kernel size and shape would be expected in later generations of the cross.

The F1 hybrids: F1 plants were grown at two localities: Buenos Aires, at latitude 34°35' and altitude 25 meters, and Tilcara in the province of Jujuy, at latitude 23°35' and altitude 2460 meters. The plants at Buenos Aires first flowered on February 15 from seed sown on September 13, an interval of 155 days. The planting at Tilcara first flowered on February 25, from a sowing made on September 25, an interval of 153 days. Since the average day lengths at Tilcara are not much shorter than those at Buenos Aires during this period, but the mean temperatures were very much lower, the fact that the interval from sowing to flowering was about the same in the two localities, 153 and 155 days respectively, suggests that differences in mean temperatures had no marked effect. In vegetative growth, however, the plants grown at Tilcara grew much less luxuriantly than those grown at Buenos Aires.

Annual growth habit dominant: None of the F1 plants in either planting had fully developed rhizomes like those of their teosinte parent, and in this respect habit of the corn parent may be considered as dominant. However, several plants had small strongly condensed rhizome-like structures, similar to those that in some species of perennial plants are called "bulbils."

Most of the F1 plants also had profuse and robust adventitious roots, perhaps one expression of perennialism. After a period of dormancy, several of the F1 plants at both Buenos Aires and Tilcara resumed growth. A dissection of the root system of one of these in the Tilcara planting showed that the new growth arose from a tiny bulbil. It can be said, however, that in the majority of F1 plants the annual growth habit of the corn parent was dominant.

Pollen of an F1 plant: The pollen of an F1 plant grown at Buenos Aires comprised well-filled grains approximately normal in size and smaller grains, some well-filled and others only partially so. The pollen does not resemble the semi-sterility characteristic of plants that are heterozygous for chromosome translocations or long inversions.

The F2 population: A population of 107 F2 plants was grown at Buenos Aires. Of these it was possible to classify 84 plants for the four characteristics under study: distichous vs. polystichous pistillate spikes, solitary vs. paired pistillate spikelets, fragile vs. tenacious rachis segments, and perennial vs. annual growth habits.

Although the population was too small to be reliable in revealing Mendelian ratios for all of the characteristics under study, the F2 population, like the F1, shows the annual growth habit to be dominant to the perennial. The numbers of annual and perennial plants were respectively 62:22, a close approximation to a 3:1 Mendelian ratio.

With respect to the remaining characteristics, the ratios are not clear-cut: polystichous vs. distichous, 41:43; paired vs. solitary, 68:16; tenacious vs. fragile, 37:47.

There are indications of linkage between several of the teosinte characteristics but the numbers are too small to establish these clearly. There is no indication that the inflorescence characteristics of teosinte are linked with the perennial growth habit.

Somewhat surprising is the relatively high frequency of phenotypes combining all of the parental characteristics. Of 84 plants, 23 had all of the botanical characteristics of the corn parent; 5 all of those of the teosinte parent. The results, so far as they go, suggest that not more than four major gene pairs distinguish the two parents of the cross in their principal botanical characteristics.

Perhaps even more surprising is the relatively high frequency of the recombinant phenotypes, annual teosintes and perennial corns. The numbers are respectively 10 and 5.

Unexpected characteristics in the F2: Two characteristics not apparent in either parent, red pericarp and pod corn, appeared in several of the F2 plants. These could not be attributed to contamination since the F1 plants were grown in a small botanical garden situated on the Faculty of Agronomy campus, far removed from any other corn plantings.

The red pericarp color may represent the interaction of the genes for brown pericarp color of the teosinte parent with the cloudy pericarp color, known as "dingy," of the popcorn parent.

A possible explanation of the pod corn is that the popcorn parent of the cross carries a lower allele of the Tu locus that is not expressed because it also carries the tunicate inhibiting gene, Ti. Recombination in the F1 allows the tunicate allele to be expressed.

A second F2 population: From the seeds of the same F1 plants, a second and much larger F2 population was grown at Calilegua, a locality in a subtropical, sugarcane growing area. The data from this planting have not yet been completely analyzed but a preliminary examination shows the results to be quite similar to those obtained from the first F2 population. Annual-type plants outnumbered perennial-type plants by a ratio of approximately 3:1, as they did in the Buenos Aires plantings. Apparently the inheritance of perennialism in Zea is far more simple than had earlier been generally supposed.

Also, in the Calilegua planting, the recombinant phenotypes, annual teosinte and perennial corn, occurred in about the same frequencies as in the Buenos Aires F2 populations.

A small backcross population: From a planting of 40 seeds of a backcross of the diploid perennial x F1, 32 plants were obtained. Of these, 10 were classified as annual and 22 as probably perennial. This is not a significant deviation from the 1:1 ratio expected if the perennialism of teosinte is recessive to the annual growth habit of corn as it seemed to be in the two F2 populations described above.

In this population no perennial-corn phenotypes were to be expected and none occurred, but the frequency of annual-teosinte phenotypes might be much higher than that occurring in F2 populations. Apparently it is. The pistillate spikes of all of the annual-type plants have not yet been examined but several of those that have resemble the spikes of known races of annual teosinte such as Central Plateau and Nobogame. The spikes of several of the plants classified as "probably perennial" resemble the annual teosinte race, Huehuetenango, in having trapezoidal instead of triangular rachis segments.

There appears to be no difficulty in producing annual teosintes from backcrosses of the diploid perennial parent by the F1. This may have been the manner in which annual teosinte races arose in Mexico.

Results support the Wilkes hypothesis: Our results from both F2 populations and one backcross population are consistent with the Wilkes hypothesis that annual teosintes could have been created by the hybridization of Zea diploperennis and a cultivated corn in the early stages of domestication.

They are also consistent with the suggestion of Iltis et al. that perennial corns might be produced by similar hybridizations.

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Allometric genetics

Let p be the frequency of a more favorable gene in tolerance to heat, say ltel; 1-p the frequency of a less favorable gene, Ltel, allelic to ltel; a, half the difference between the two homozygous genotypes; and d the degree of dominance; with K being the average value of the less favorable gene. The conventional representation of the basic genetic parameters is represented as follows:

Genotype	Frequency	Number of favorable genes	Genotypic value	
			Uncoded W'	Coded W=W'-K-a
ltel/ltel	p^2	2	K+2a	a
Ltel/ltel	2p(1-p)	1	K+a+da	da
Ltel/Ltel	$(1-p)^2$	0	K	-a

The problem is a. Suppose a represents the effect of one gene on survival, or fitness. In percent under no stress, a would be zero, and it could happen in the other extreme that one genotype survives 100%, the other 0%. In this case a would be 50%. In this model a is one point in space-time. The definition of a new a which takes into account space-time must be in terms of an angle. In the relationship of allometry, being X and Y two measures, they are usually related by $X=AY^{\alpha}$ (J. S. Huxley, Problems of Relative Growth, 1932), really related X-Y with Y. Relating X÷Y with Y leads to the allometric relationships shown in Fig. 1. It

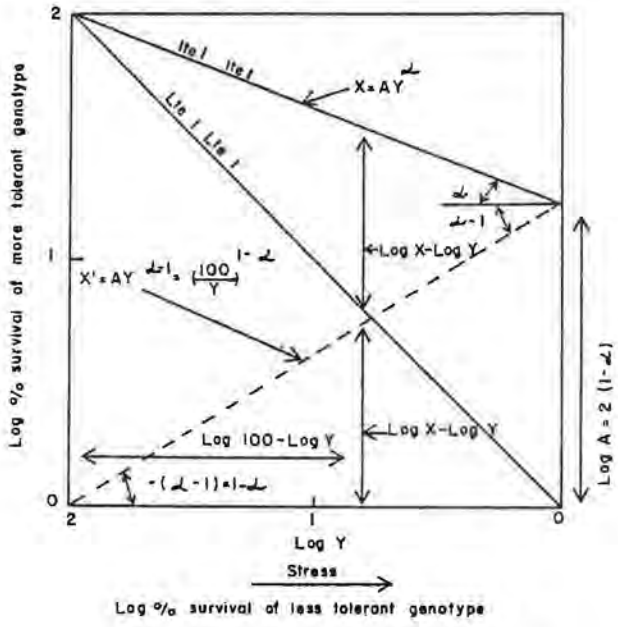

Fig. 1. Allometric relationships between the survival of two genotypes, x, say ltel ltel (latente), being more tolerant to heat and Y, Ltel Ltel, less tolerant. The scale ii in logs $X=AY^{\alpha}$, with X'=X÷Y, $X'=AY^{\alpha-1}=(100\div Y)^{1-\alpha}$.

shows that α and A are redundant, A being the antilog $2(1-\alpha)$ and the simplest representation being $X' = (100 \div Y)^{1-\alpha}$. The conventional interpretation is a point in those lines. Substituting $1-\alpha$ and δ for d in the conventional representation we have a genetic interpretation of the allometric relationships as follows:

Genotype	Frequency	Number of favorable genes	Genotypic value: Uncoded W'	Genotypic value: Coded W=W'-K-(1-α)
lte1/lte1	p^2	2	$K+2(1-\alpha)$	$1-\alpha$
Lte1/lte1	$2p(1-p)$	1	$K+(1-\alpha)+\delta(1-\alpha)$	$\delta(1-\alpha)$
Lte1/Lte1	$(1-p)^2$	0	K	$\alpha-1$*

*See in Fig. 1 that $-(\alpha-1) = 1-\alpha$.

This also opens the way to analyze, and to map, single genes with quantitative effects including survival or fitness. It should be warned that the best fit is gotten calculating by the minimum products method derived by G. Teissier (Biometrics No. 1, 4:14-53, 1948). The minimum squares method underestimates the absolute value of the coefficients. It is interesting to point out that L. I. Gripi-Papp (Dr. Thesis, ESALQ. Univ. of São Paulo, 1970) in a demonstration of $X=AY^{\alpha}$ arrived first at the form $X'=AY^{\alpha-1}$.

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Crosses of Zea diploperennis with corn

We crossed Zea diploperennis with a primitive popcorn race, Palomero Toluqueño, in a small isolated garden in Chapel Hill in the early summer of 1979. The teosinte proved not to carry the Ga cross-sterility factor and no other barriers to crossing were apparent. We obtained abundant crossed seed.

In order to obtain F1 and F2 populations as rapidly as possible, we arranged for two winter plantings of the F1 plants to be made in Homestead, Florida, and two additional ones in Argentina, in case the Florida plantings should be lost by an early winter freeze.

All four of the F1 plantings succeeded and from two of them, one in Florida and one in Argentina, seed was harvested for F2 plantings. The results of the Argentine plantings are reported in earlier pages of this Newsletter (see item from Buenos Aires). This report is concerned only with plantings made in the United States.

F2 populations in Florida: We grew two F2 populations in Homestead, Florida, one in the experimental plots of Pioneer Hi-Bred; the other in the fields of Agricultural Alumni Seed Improvement. For the special attention that they gave our plantings, we are indebted to Dean Wrucke of Pioneer Hi-Bred and Karalee Holden of Ag. Alumni.

The principal purpose of the Florida plantings was to get some idea of the variation that we might expect in F2 populations and to this extent, they were successful.

It had been suggested to us by several skeptics that the inheritance of growth habit would prove to be so complex that, combined with the segregation for the botanical characteristics distinguishing corn and teosinte, we might expect to find

annual teosintes, if they occurred at all, in such a low frequency that populations of many thousands of plants would be required to discover them.

The opposite proved to be true. In both of the Florida plantings, comprising only several hundred plants, a number of annual-teosinte phenotypes occurred. We photographed these as a matter of record. The Florida plantings were the first to show us that the inheritance of annual vs. perennial growth habit is not at all complex.

F2 populations in Texas: The Texas planting was made at a field station of Texas A and M University located in the Brazos River Bottom about 15 miles west of the city of Bryan. The main purpose of this planting was to grow an F2 population large enough to not only obtain numerous annual-teosinte phenotypes, but also to compare these with plantings of the presently-known races of annual teosinte and also to obtain photographs of such comparisons. Another purpose was to study the inheritance of the contrasting characteristics involved in the cross and to detect genetic linkages, if present.

An initial planting of about 4000 plants made in April was a total failure because of unprecedented hot, dry weather. Although irrigation was available and freely used, the F2 plants did not thrive, apparently suffering from the excessive heat. The first planting was useful only in showing that F2 populations derived from high-altitude parents will not ordinarily flourish under the hot, dry conditions that prevailed in the summer of 1980.

The second planting made in early August fared little better. It not only suffered from the continuing heat and drought but was also subject to the attacks of a disease, not ordinarily occurring on corn, as well as insect damage. Despite the application of pesticides, many plants were lost.

Among the plants that survived and finally flowered in late October, there were numerous annual-type plants with teosinte-type pistillate inflorescences. Thus, this planting agrees with F2 populations grown in Florida and Argentina in showing that the recombinant annual-teosinte phenotypes are not rare and that the number of gene pairs involved in the inheritance of the characteristics under study cannot be great.

A backcross population: Somewhat more successful was a small backcross population of the diploid perennial parent by the F1. This comprised 147 plants. We classified these into five categories with the following results:

Category	No. of Plants
Perennial	2
Weakly Perennial	58
Intermediate	66
Resembling F1	16
Duplicating F1	5

The first and last data are interesting in showing that the spectrum of variation in this population ranges between plants almost identical to the perennial parent and plants resembling the F1 hybrids. This has to be theoretically expected. No annual- or perennial-corn phenotypes were to be expected in this backcross population and none occurred.

If we count the plants classified as "intermediate" as annuals, as they probably are, since they lack rhizomes, the ratio of perennial to annual phenotypes is 60:87. This is not a highly significant deviation from a 1:1 ratio theoretically expected if one major gene pair is involved. The data at least fit a 1:1 ratio somewhat better than they fit the 3:1 ratio that would theoretically be expected if two gene pairs were involved in the inheritance of annual vs. perennial growth habit. Another possibility that should perhaps be considered is

that the cross may involve not one, but two genes for annual growth habit carried by the same chromosome.

This backcross population is most interesting because it may duplicate the manner in which annual-teosinte types arose in Mexico centuries ago as the progeny of natural crossing of Zea diploperennis and a cultivated corn in an early stage of domestication. The F1 hybrids that occurred in colonies of perennial teosinte would have pollinated the perennial teosinte and in subsequent generations, the colony would have contained both perennial and annual teosintes but no perennial corns.

All of the results of the Texas plantings are consistent with the Wilkes hypothesis on the origin of annual teosintes.

Paul C. Mangelsdorf, Lewis M. Roberts and John S. Rogers

CHESTNUT HILL, MASSACHUSETTS
Boston College

Meiotic observations of diploid perennial teosinte

Meiotic divisions in the microsporocytes of five clones of diploid perennial teosinte were examined with standard acetocarmine squash technique. At pachytene stage, it was consistently observed that there were knobs and large chromomeres on eight of the 10 chromosome pairs. Most of these knobs and chromomeres were homozygous. The knob size varied from small to medium. The knobs on the short arms of chromosomes 1 and 2 and the long arms of chromosomes 2 and 3 were small. The knobs on the short arm of chromosome 3, and on the long arms of chromosomes 4, 6, 7, 8 and 9 were medium-sized. All of these knobs were terminal. Chromosomes 5 and 10 were knobless. Several times, the knob on the long arm of chromosome 9 was found heterozygous and synaptic beyond the knob region. However, when the chromosomes were studied with Giemsa staining procedure, the knobs appeared larger than they did with the above technique.

The characteristics of the gross morphology of the pachytene chromosomes of diploid perennial teosinte are similar to those of the tetraploid perennial teosinte reported by Longley (1937), Ibrahim (1960) and Ting (1964), except for knob number and size. In addition, we have successfully crossed five different varieties of maize with this diploid perennial teosinte. All of them resulted in fertile F1 hybrids. In view of these, it seems reasonable to conclude that diploid and tetraploid perennial teosinte should be in one species instead of two separate species as proposed by Iltis et al. (Amer. J. Bot. 67:994-1004).

At diakinesis, among a total of 322 cells examined from 5 clones, it was found that 276 (85.7%) of them had 10 regular bivalents with both closed-ring and open-ring shaped configurations. Nine bivalents and two univalents were found in 41 (12.7%), eight bivalents and four univalents in 4 (1.7%), and seven bivalents and six univalents in 1 (0.3%). At anaphase I, only 61.3 percent of a total of 476 cells had normal 10 to 10 distributions of chromosomes. The other 39 percent showed irregularities in chromosome behavior:

Chromosome Behavior	Frequency	% of Total
Normal (no B or L)	292	61.3
1 B	9	1.8
1 L	7	1.4
2 L	48	10.0
4 L	120	25.2

These irregularities ranged from one bridge without fragment (B) to one or four laggards (L). This meiotic instability is probably caused by the long time accumulation of mutations due to vegetative propagation.

Y. C. Ting, M. K. Gu and Margaret Yu

Advances in anther culture of maize

a. Higher percent of callus-initiation and regeneration: Since the spring of this year over 4500 maize anthers were cultured in vitro on medium Zheng-14. The anthers were of maize Dan-Sun 91 which is a hybrid from Kirin province of the People's Republic of China. It was very encouraging to note that approximately 18.0 percent of these anthers responded favorably by growing into callus or embryoid about four weeks after inoculation. It is better than any previously reported results. It is an improvement.

After the calli had been transferred into regeneration medium, over 50 percent of them grew into certain form of plantlets. Now more than 200 healthy pollen-plants have been obtained. Many of them survived transplantation in the greenhouse. Without any doubt, they provide a new source of material for cytogenetic research.

b. Establishment of maize anther callus lines: In addition to Dan-Sun 91, maize varieties King Hwang 13, Stock 6, King Hwang 9, Chuen-Dan, Kwei-Dan, etc. were also employed for anther culture. Calli were obtained from anthers of most of them. Through examination and tests six haploid callus lines were established. They continued to grow on the original basal medium (Zheng-14), if they were transferred to newly prepared medium with a frequency of every four to six weeks. If it is needed, pollen-plants can be obtained by transferring these calli into regeneration medium.

Y. C. Ting, Wan-zhen Zheng and Margaret Yu

Fine structure of maize anther callus

By following anther culture procedure as stated in the foregoing section, calli were obtained from anthers of maize Dan-Sun 91. Before differentiation (three- to four-week old) some of the calli were fixed with 3% glutaraldehyde and postfixed with 1% buffered OsO_4. Then they were further prepared for electron microscopy by embedding in Epon.

Under the electron microscope, it was observed that two types of cells were discernible: one was filled with cytoplasm and the other was occupied mostly by vacuole. The former were in general smaller than the latter. Both were irregular in shape.

The cells with full cytoplasm appeared to be actively growing. Their chloroplasts were well differentiated and starch grains were developed. However, grana-thylakoids and stroma thylakoids were unclear. Mitochondria were also present and they were in general much smaller than chloroplasts. In most of the mitochondria, christae or inner membranes were well organized. In addition, these cells also had abundant endoplasmic reticulum with clearly defined ribosomes. The nuclei were located in the center of the cells or nearly so. On the other hand, those cells which had a large vacuole in the center appeared senescent. Their nuclei were apparently pushed to the periphery of the cells. Cytoplasms were dense and more darkly stained than those of the other group of cells described in the above. Organelles such as chloroplasts, mitochondria and endoplasmic reticulum were less developed. No starch grains were observed in the chloroplasts and no grana thylakoid and stroma thylakoid were present. Further studies on the ultrastructure of anther calli at various stages of development are in progress.

Margaret Yu

Continued studies on the chromosomes of maize from China

During last year F1 hybrids of nine crosses between Wilbur's Flint and maize from China were grown. Microsporocytes of these hybrids were examined with light microscope by the same technique as what was previously reported (MGCNL 54:106). At pachytene stage, it was consistently observed that all the chromosomes synapsed regularly except the short arm of chromosome 10 of maize variety Peking-2. Asynaptic configuration was frequently found in this chromosome. The number of knobs varied from one to six (Table 1). For example, maize Peking-4 had only one terminal knob on the short arm of chromosome 9, while Peking-8 had six knobs. None of these had any knobs on chromosomes 2, 3 and 10.

Table 1. Numbers and positions of chromosome knobs in maize from China (K indicates homozygous knob, k heterozygous knob).

	Chromosomes																			
	1		2		3		4		5		6		7		8		9		10	
Varieties	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
Ying-64	-	-	-	-	-	-	K	-	-	-	K	-	K	-	-	-	-	K	-	-
Tich-133	-	-	-	-	-	-	-	-	-	-	K	-	K	-	-	-	-	K	-	-
Henan-8	-	-	-	-	-	-	KK	-	-	-	-	-	-	-	-	-	-	-	-	-
Henan-9	-	-	-	-	-	-	K	-	-	-	-	-	K	-	-	-	-	-	-	-
Peking-2	-	-	-	-	-	-	K	-	-	-	K	-	K	-	K	-	-	K	-	-
Peking-4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	K	-	-
Peking-6	-	-	-	-	-	-	-	k	-	-	KK	-	K	-	K	-	-	K	-	-
Peking-7	-	-	-	-	-	-	-	-	K	-	-	-	K	-	-	-	-	K	-	-
Peking-8	-	K	-	-	-	-	K	-	-	-	K	-	K	-	K	-	-	K	-	-

At diakinesis, 10 bivalents were regularly formed in most of the hybrids. However, hybrids involving maize variety Henan-8 had about five percent of the cells showing 20 univalents. The implication of this is under investigation.

Y. C. Ting and Margaret Yu

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Studies with a cDNA clone for endosperm sucrose synthase

We are studying the gene for endosperm sucrose synthase with the aim to isolate and characterize McClintock's "controlling element" Ds which is found in the vicinity of gene Sh and has given rise to mutable sh alleles, probably by the formation of adjacent deletions which bring gene Sh into closer contact with Ds.

mRNA of 23-day-old maize endosperm was translated both in wheat germ extracts and rabbit reticulocyte lysates. A protein with an apparent molecular weight of 88,000 comigrates in SDS polyacrylamide electrophoresis with sucrose synthase. This protein is precipitated with an anitserum against sucrose synthase, and shows the same protease digestion pattern as the enzyme. It is not synthesized with mRNA extracted from sh/sh mutant kernels lacking sucrose synthase. By these criteria, the protein is the in vitro translation product of sucrose synthase mRNA.

The separation of mRNA in methylmercury hydroxide agarose gels and subsequent translation indicates a length of sucrose synthase mRNA of 2,800 nucleotides, which is compatible with the coding length necessary for a protein of a molecular weight of 88,000 and untranslated sequences.

A cDNA clone for maize endosperm sucrose synthase of 620 nucleotide pairs length was obtained by cloning double stranded DNA obtained from the total maize endosperm poly(A)RNA in pBR322, and identifying the appropriate clone by hybrid-promoted translation.

Plasmid DNA containing the cloned cDNA was nick-translated and used as a probe for Southern blots against DNA obtained from wildtype maize and mutants. Using restriction endonucleases EcoRI and BamHI, we obtained a single band hybridizing to a probe from the wildtype and each of three mutant DNAs. In the case of EcoRI, the size of the band was different in each case. No hybridization was obtained with the DNA of a mutable bz, which according to the hypothesis advanced above should be a deletion extending from Ds beyond Sh to the beginning of Bz. These findings support an earlier report by B. Burr and F. Burr.

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Inheritance of trapped-silk trait

We observed silk strands "trapped" in the outer perimeter of the cob upon breaking a mature ear of inbred line Mo17 into two halves. Subsequently, we examined ears of certain other inbred lines and did not observe this characteristic. Here, we report preliminary results of a study of this trait. The genotypes used in this study are listed in Table 1.

Table 1. Trapped-silk channel (TSC) data for 22 genotypes.

Set	Genotype	% Mo17	No. ears observed	% ears		Ave. % TSC per ear
				Normal	Trapped-silk	
	Mo17*	100	10	0	100	100
	N104	0	10	100	0	0
1	N104 x Mo17	50	10	30	70	14.9
	Mo17 x N104	50	9	22	78	14.2
	Mo17(Mo17 x N104)	75	16	6	94	25.9
	N104(Mo17 x N104)	25	9	67	33	4.3
	N28	0	10	100	0	0
	Mo17 x N28	50	11	0	100	15.8
2	Mo17(Mo17 x N28)	75	12	0	100	31.6
	N28(Mo17 x N28)	25	7	14	86	21.9
	H84	0	10	100	0	0
	Mo17 x H84	50	13	8	92	12.9
3	Mo17(Mo17 x H84)	75	7	0	100	26.0
	H84(Mo17 x H84)	25	9	100	0	0
	Oh545*	0	10	0	100	29.0
	Mo17 x Oh545	50	4	0	100	41.3
4	Mo17(Mo17 x Oh545)	75	4	0	100	34.0
	Oh545(Mo17 x Oh545)	25	7	0	100	31.4
	Mo5	0	10	100	0	0
	Mo17 x Mo5	50	12	17	83	8.6
5	Mo17(Mo17 x Mo5)	75	6	0	100	26.3
	Mo5(Mo17 x Mo5)	25	5	80	20	3.4

*Related through C.I. 187-2.

All the genotypes were grown in one-row plots (13 plants per plot) with the exception of the two backcrosses in set 1 which had two rows each, and were allowed to open-pollinate. Usable ears were harvested and examined for trapped silks. Data on total number of ears observed per genotype, % ears with all normal silk channels and with trapped-silk channels, and average % trapped-silk channels per ear are given in Table 1. All the observed ears of both Mo17 and Oh545 had trapped-silk channels, the average % trapped-silk channels per ear being 100% and 29%, respectively. This may be explained by the fact that both Mo17 and Oh545 are related through C.I. 187-2 parentage.

In set 1, data on N104 x Mo17 and the reciprocal cross Mo17 x N104 indicated no reciprocal effect for this trait. Sets 1, 2, 3, and 5 showed an increasing dosage effect for average % trapped-silk channels per ear as the genetic complement of Mo17 increased, with the exception of Mo17 x N28, which had a lower value than that of N28(Mo17 x N28). However, in all cases the percentage of ears with trapped-silk channels increased additively with increased dosages of Mo17.

In set 4, all the ears of both the inbreds involved, the F1 cross, and both backcrosses showed trapped-silk channels. Average % trapped-silk channels per ear was the highest for Mo17 x Oh545 when compared with the other F1 crosses.

The data on the average % trapped-silk channels per ear in relation to the genetic complement of Mo17 are shown in Figure 1. Preliminary indications are that

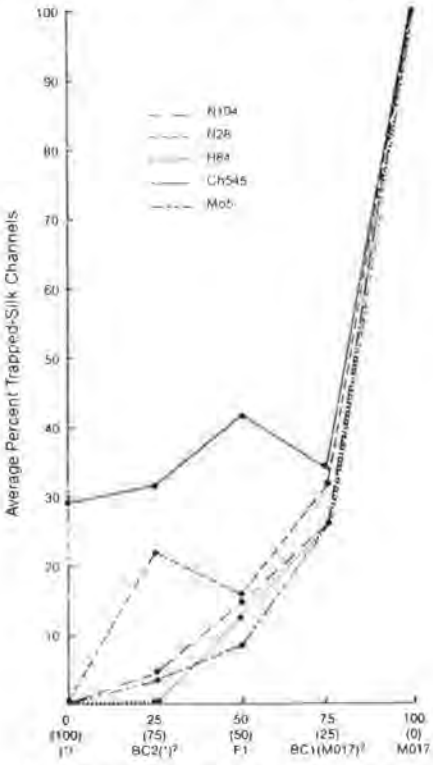

Fig. 1 Percent trapped-silk channels as related to genetic complement of M017.

the trapped-silk trait is quantitatively inherited. Further studies are needed to verify these results with a larger sample size and to determine the anatomical development of this trait. The benefit of this trait to a genotype is not known at this time.

M. S. Kang and M. S. Zuber

Inheritance of brittle node

Inbred line B73 derived from Iowa Stiff Stalk Synthetic C5 has a tendency to break at upper nodes during the tassel-bagging operation. Crosses of B73 with four different inbred lines (non-brittle types) were made and F2 progenies were obtained. The F1 plants in each cross were normal (non-brittle). The F2 data given below indicated a 3:1 segregation for normal:brittle node in each cross:

	F2 Plants		χ^2 for	
Cross No.	Normal	Brittle Node	3:1 Ratio	P
1	95	22	2.247	0.2-0.1
2	94	20	3.38	0.1-0.05
3	90	28	0.101	0.8-0.7
4	98	34	0.04	0.9-0.8

Therefore, brittle node trait appears to be controlled by a single recessive gene. Tests for allelism with bk2 (brittle stalk) and a study to locate the brittle node gene using waxy-marked translocations are planned. The brittle stalk (bk2) mutant has been described as "Leaves and stalk very brittle, easily broken. Plant shows [in picture] leaves shattered by moderate winds" (Neuffer, M. G., L. Jones and M. S. Zuber, 1968, The Mutants of Maize). The brittle node trait is different from brittle stalk in that leaves remain intact even against strong winds, but breakage occurs at the node when the tassel is handled. If tests for allelism with bk2 are negative, the new gene will be designated btn1.

This information may be useful to breeders in manipulating the brittle node trait depending upon their objectives (for example to facilitate detasseling in seed production fields).

M. S. Kang

The iojap gene reverts to normal

In certain backgrounds, especially in that of Tr inbred, ij ij plants are only slightly white-sectored but have very pale green ("light grainy") leaves and tassels. These pale green leaves occasionally have dark green, normal-appearing sectors, some as large as 1/8 to 1/4 of the leaf width. Green sectors could represent mutations of ij or other nuclear genes to normal, or changes in state or mutation of the chloroplasts. In one such plant in 1979, a green sector occurred in the tassel, encompassing 3 or 4 branches. Progeny from these branches were obtained as follows:

Female	Male	Progeny
ij ij	green branches	22 green, 21 iojap
ij ij	iojap branches	3 green, 45 iojap
+ +	green branches	4 +/+, 6 +/ij
+ +	iojap branches	0 +/+, 8 +/ij

Progeny were identified as +/ij from F2 families, which segregated in a 3:1 ratio in each instance. The sector in the tassel was due to mutation from ij to +, and presumably reflects the same event occurring in the leaves.

E. H. Coe

The occurrence of maternal white seedlings in ears from iojap x normal

From the cross of ij ij x + + (with Oh51a as male parent--see MNL 52:82), a large number of ear maps are being derived. Certain features of these maps are surprising. Maternal white seedlings occur on ears in non-Poisson distributions, suggesting clustering arising from clonally proliferated events, but in arrays that are not homogenous clonal groups (see MNL 54:28-30), and their grouping on ear maps is inconsistent with ear morphogenesis as derived by M. M. Johri (see note in this Newsletter), in which both of two embryo cells contributing to the ear are represented at the base. Maternal white seedlings are found in large arrays mostly in the distal portion of the ear. Taken with the fact that scattered green seedlings occur in mainly white areas, and vice versa, the implication is that location (or cell growth rate or attenuation) influences the occurrence of exceptional white seedlings more than sorting-out and clonal proliferation.

E. H. Coe

The sh-bz-x1 mutation may include the C locus

Ears of plants heterozygous for + +/sh-bz-x1 were crossed by c sh Bz tester. The resulting kernels segregated about half colored non-shrunken and half colorless shrunken, while self-pollinations on other ears of the same plants gave only colored non-shrunken and crosses by C sh bz tester gave half non-shrunken purple and half shrunken bronze. The mutant, as characterized by J. P. Mottinger (Genetics 64:259, 1970), is transmitted infrequently through the male parent and affects pollen size; it also results in reduced seed size when heterozygous. The above results identify that the sh-bz-x1 chromosome is also c. No recombinants (c Sh or C sh) were observed in a few small tests. Since the original irradiated pollen parent from which sh-bz-x1 arose was a colored-seeded standard (i.e., C Sh Bz), it appears that the C locus was deleted at the same time as Sh and Bz, and that the deletion extends through all three loci. Tests show that Yg2 is not included in the deletion.

E. H. Coe

Placement of vp1 near lg2 on the long arm of chromosome 3

Two +/vp1 ears and four +/+ x +/vp1 ears failed to segregate viviparous kernels after pollination by confirmed +/TB-3Lc plants. All eight ears of +/vp1 x TB-3Ld segregated viviparous grains. Therefore, the vp1 locus must lie between the two translocations in the vicinity of lg2 (see Coe, MNL 54:130). These results confirm Robertson's reports (MNL 27:9 and 39:104) that vp1 is proximal rather than distal to a1.

J. B. Beckett

Progress on the allotetraploidization of maize as indicated by declines in quadrivalent frequencies

This project has been described recently (MNL 54:24-26). Briefly, three synthetic populations (A, B, and C) are maintained by random crossing within themselves and have been subjected to x-irradiation (10,000 r to the kernels) for six generations. Synthetic B is the population that will eventually contribute the restructured genome for the allotetraploid and Synthetic D will contribute the normal genome. Synthetic D is composed of 4n material that has never been irradiated. It is derived from 20 maize inbred lines with a large admixture of Alexander's Syn. B. Synthetic A and C are homozygous for a different group of 5 recessive markers: bz2 lg y v16 wx and a su pr gl g. These have been crossed

with plants from the B synthetic. Progress toward allotetraploidization will be determined by changes in genetic ratios. This will be reported on next year.

Cytological evidence for allotetraploidization has been found by examining the quadrivalent frequencies of Syn. D, Syn. B, and Syn. BxD plants. The data are given in the accompanying table. The Syn. B plants were derived from the 4th cycle of recurrent radiation. They were self-fertilized once and then crossed with Syn. D plants which were self-fertilized once. The Syn. B plants for the cytological examinations were from the S2 generation.

Pairing Configurations

	0 20II	1IV 18II	2IV 16II	3IV 14II	4IV 12II	5IV 10II	6IV 8II	7IV 6II	8IV 4II	9IV 2II	10IV 0II	Total	Ave. IV	χ^2	Other
Syn. D															
1	0	0	0	0	1	3	13	22	28	22	14	103	7.89	2.86	1†(a)
2	0	0	0	0	0	3	4	19	28	20	7	81	7.98	0.81	0
3	0	0	0	0	2	3	9	20	44	41	12	131	8.08	0.05	1(b)
4	0	0	0	0	1	1	8	19	30	35	15	109	8.21	0.86	0
5	0	0	0	1	1	0	10	25	37	43	25	142	8.27	2.81	0
Total	0	0	0	1	5	10	44	105	167	161	73	566	8.10		
Syn. B															
1	0	0	0	0	2	8	22	37	29	25	6	129	7.41	39.81**	0
2	0	0	0	0	2	9	23	25	24	25	7	115	7.42	34.82**	0
3	0	0	0	0	0	6	16	17	31	22	6	98	7.66	12.14**	3(c)
4	0	0	0	0	1	3	15	27	37	23	13	119	7.82	5.91	3(d)
5	0	0	0	0	0	3	4	29	53	32	11	132	8.06	0.13	0
Total	0	0	0	0	5	29	80	135	174	127	43	593	7.68		
Syn. B Syn. D															
1	0	0	0	5	9	20	28	25	18	6	0	111	6.23	251.07**	2(e)
2	0	0	0	3	13	25	30	23	19	8	2	123	6.27	268.15**	0
3	0	0	1	1	8	18	27	31	19	12	3	120	6.63	167.73**	0
4	0	0	0	0	2	21	31	33	30	19	5	141	7.03	105.21**	2(b)
5	0	0	0	0	3	10	21	23	33	13	4	107	7.03	79.89**	0
6	0	0	0	0	1	8	22	30	28	20	5	114	7.36	39.64**	0
7	0	0	0	0	2	11	16	25	35	25	8	122	7.53	25.50**	0
8	0	0	0	0	1	5	16	25	34	24	12	117	7.76	8.75*	0
9	0	0	0	0	0	4	12	23	30	25	8	102	7.82	5.06	1(g)
10	0	0	0	0	0	4	11	26	39	33	11	124	7.96	1.58	0
11	0	0	0	0	1	3	8	19	33	23	14	101	8.03	0.32	0
12	0	0	0	0	1	1	6	23	46	21	16	114	8.10	0.00	0
Total	0	0	1	9	41	130	228	306	364	229	88	1396	7.31		

†Along with the configurations in the table there were other ones: (a) 7IV 5II 2I, (b) 8IV 3II 2I, (c) 2 (7IV 1III 4II 1I), 5IV 1III 8II 1I, (d) 2 (6IV 7II 2I), (e) 3IV 1III 12II 1I, 5IV 1III 8II 1I, (f) 6IV 7II 2I, 7IV 5II 2I, and (g) 5IV 1III 8II 1I

**significant at .01

*significant at .05

The pairing configurations were determined at diakinesis. Most configurations were combinations of quadrivalents and bivalents. However, there were a few trivalents and univalents found. These cases were not included in the totals.

The five Syn. D plants had frequencies ranging from 7.89 to 8.27 quadrivalents per cell. There is some variability but it is not significant from the average value of 8.10.

Four out of five Syn. B plants had statistically significant reductions in quadrivalent frequencies as did nine out of twelve Syn. B x Syn. D hybrids. While the declines in quadrivalent frequencies are not great (1.87 quadrivalents at most), the data indicate that allotetraploidization is taking place.

Because the Syn. B plants used were not homozygous the full expression of preferential pairing is not possible. If we symbolize the unaltered chromosomes of Syn. D as S (for standard) and the altered chromosomes of Syn. B as R (for restructured), there are many types of restructuring. Thus there are R_1, R_2, . . . R_n chromosomes. Many of the chromosomes in Syn. B may not have been altered and thus Syn. B is a mixture of S and R chromosomes. The full expression of preferential pairing is found in balanced ditypes (SSR_1R_1, SSR_2R_2 etc.). These would be expected to be rare in the Syn. B or Syn. B x Syn. D hybrids. Most of these plants would be unbalanced ditypes ($SSSR_1$) in which preferential pairing is not possible. Preferential pairing would be possible in tritypes (SSR_1R_2) but it would be reduced from that found in SSR_1R_1 or SSR_2R_2 types. The affinity of R_1 for R_2 chromosomes may be the same as that of R_1 for S or R_2 for S. This has been discussed in TAG 54:161-168.

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A group of new mutants defective in kernel development--the dek mutants

During the last several years we have examined a large collection of EMS-induced mutants all of which are disturbed in their endosperm and embryo development. We have referred to these as defective kernel mutants as a generalization of the defective seed and germless terms of D. F. Jones (1920) and M. Demerec (1923) and we have reported on some of their genetic and morphological characteristics (M. G. Neuffer and W. F. Sheridan, 1980, Genetics 95:929-944; W. F. Sheridan and M. G. Neuffer, 1980, Genetics 95:945-960). The defective kernel mutants are designated by the gene symbol dek. Listed below are 15 dek mutants with their chromosome arm location and certain other characteristics. These mutants have been referred to in our previous communications by reference to the E number, a laboratory designation; this E number is included below.

Symbol	E No.	Chrom. arm	Mature kernel pheno.	Lethality or seedling phenotype	Culture phenotype	Carot. synth.**	Antho. synth.
dek1	792	1S	clf	L	-	B	B
dek2	1315A	1L	dsc scr	L	gr	N	-
dek3	1289	2S	gm	L	w-gs	N	-
dek4	1024A	2L	cp fl	L	gr-nl	N	N
dek5	874A	3S	sh	w-gs*	w-gs	N	N
dek6	627D	3L	o sh	L	n	N	-
dek7	211C	4S	sh su	gs	w-gs	N	N
dek8	1156A	4L	sh	?	gr-sml	N	-
dek9	1365	5L	crp	L	gr	dil	dil
dek10	1176A	6L	cp	L	gr-crl-stb	N	N
dek11	788	7L	et	L	-	N	N
dek12	873	9S	cp	L	gr-nl-crl	N	N
dek13	744	9L	de o	L	pg-gs	N	N
dek14	1435	10S	cp	L	yg	N	-
dek15	1427A	10L	cp fl	L	gr	N	N

*w, white; gs, green striped. **B, blocked; N, normal; dil, dilute; -, undetermined.

Note that the mutant dek1 (E792) was first described by Neuffer (1977) and designated as clf and was subsequently termed gay by Dooner (MGNL 54:79). Additional details on the above mutants as well as the definitions of the abbreviations used above are presented in Neuffer and Sheridan (1980) and Sheridan and Neuffer (1980).

These 15 mutants are clearly non-allelic inasmuch as they are located on 15 different chromosome arms. Among our collection of defective kernel mutants are many that have been located to these same chromosome arms. Allelism tests are in progress and those mutants that prove to be non-allelic will be given dek number designations, i.e., dek16, dek17, etc.

We have begun to transfer the above dek mutants from the original genetic stocks in which they were isolated to a large-embryo strain (Alexander's high oil) and also to Black Mexican sweet corn. We will be pleased to share these mutants with other investigators.

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The phenotype of iojap plants: sorting-out of plastids vs. incoordination

Iojap is generally treated as a "striping" factor with sectored leaves, but the phenotype of ij ij plants as described and pictured by M. T. Jenkins (J. Hered. 15:467, 1924) and M. M. Rhoades (Unités Biol. Douées de Continuité Génétique, 1949, pp. 37-44) is variable and quite different from conventional striping (see MNL 53:30). We have converged ij into 6 different inbreds and can compare the expression of ij ij in seedlings according to several parameters, as follows:

Inbred	White tissue %	Green areas	Pattern of White Tissue: First leaf	Pattern of White Tissue: Second leaf	Morphology
Oh51a	80-100	light green	symm. margins	scattered	normal
W23 R-g	5-90	medium green	scattered	scattered	normal
Tr	5-50	light grainy*	symm. margins	scattered	normal
Mo17	20-90	dark green	symm. margins	symm. midribs	normal
K55	10-20	dark green	symm. margins	symm. midribs	bladeless**
Ky21	5-60	light grainy	symm. margins	symm. midribs	normal

*Light grainy signifies pale green leaves (finely "spatter-painted"), usually with darker veins.

**Bladeless refers to the absence of lamina proliferation on later leaves, except for irregular, knotted or gnarled "remnants."

On a number of ij ij plants in Tr background this summer, tillers developed rapidly as a result of fortuitous death of the shoot apex at the 5-10 leaf stage. Such tillers were initially pure white in sharp contrast to the light grainy phenotype of neighboring plants. As they advanced further, however, a few of the leaves showed patches of grainy tissue, suggesting that the competence to become green was present in the plastids but perhaps was overwhelmed by unusually rapid proliferation at high temperatures. One such white tiller carried a dark green sector in two successive leaves, more than 1/4 of the width of the leaf (see accompanying note on reversion of ij).

Some observations suggest that seasonal variation may be elicited during maturation of the seeds. In particular, progeny matured in Florida in the winter (versus in Missouri in the summer) tend to have much more white tissue.

These diverse expressions were defined in derivatives with their cytoplasmic constitutions derived from the inbreds; preliminary observations indicate that cytoplasmic differences are not responsible for the variations.

The diverse expressions found in ij ij plants are difficult to square with expectations from sorting-out of plastids in morphogenetic lineages (see MNL 53: 30). Among observations that tend to separate the phenotype from sorting-out are the following:

1. The light grainy expression in Tr and Ky21 backgrounds, which is extremely reduced in chlorophyll yet virtually unsectored.
2. Occurrence of green plastids cryptically in apparently pure white areas (manuscript in preparation).
3. Symmetrically patterned white areas contrary to morphogenetic lineages.
4. Stage-specific sectors, originating separately in leaf or stem initials (Walbot and Coe, PNAS 76:2760, 1979).
5. Variations in expression that appear to be related to seasonal conditions during cell-determination phases.
6. Expressions in tillers that appear to be related to sudden changes in growth.
7. "Running out" of green color, and aborted spikelets, in distal parts of tassels.
8. Localization of white seedlings in ear maps from ij ij x + + at the distal tip of the ear (see accompanying note), contrary to morphogenetic lineages.

While sorting-out may contribute to these expressions, incoordination between the cells and the proplastids (in replication, reproduction, determination, differentiation) must play a larger role than sorting-out.

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Clonal analysis of development in corn

Through clonal analysis, we have been investigating the destiny of embryonal cells in corn (M. M. Johri and E. H. Coe, MNL 54:80). The basic strategy is to use the anthocyanin markers, eliminate the dominant allele by x-raying and then examine the clones in various parts of the corn plant. Clones originating from the outermost cell layer (L-I) of the embryonic meristem can be easily distinguished. By analyzing the clones, E. H. Coe and M. G. Neuffer (1978, pp. 113ff. in The Clonal Basis of Development, eds. Subtelny and Sussex, Academic Press) have traced the development of nodes 7 through 20, tassel and ear shoot.

Initials for the first few internodes are present in the dry embryo: In the first six or seven internodes the sectors cannot be distinguished easily because these nodes do not elongate. These nodes were found to elongate upon application of gibberellic acid (100 µg/plant) to the seedling when the second leaf was unfolding. This technique has now enabled us to trace the development of the first few lower internodes also. As shown in Table 1, the sectors occupied only part of an internode for nodes 2 and 3, but a complete internode for nodes 4 through 7.

Table 1. Length of internode (mm), apparent cell number (ACN) and extent of sectors (in nodes) for material x-rayed at dry seed stage. 100 µg GA_3 per plant was applied at the 2-leaf stage.

Node Level	Length of internode mean ± S.E.M.	ACN	Extent
7	-	27	1
6	60±9	31	1
5	67±7	30	1
4	111±11	61	1
3	32±10	69	0.88
2	3.7±0.5	99	0.41
1	-	-	-

Though no sectors could be observed in the first internode, minute and microscopic sectors were observed in the second internode. These were 4 cells in width and about 16 to 20 cells in length. These data show that, in the meristem of the dry embryo, internodes 2 and 3 are represented by at least 2 layers of cells and internodes 4 through 7 by a single layer of cells (see Fig. 1). These results are

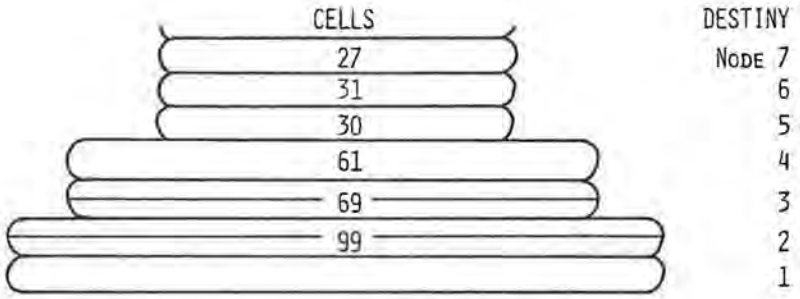


Fig. 1. Number of cells generating the lower 7 internodes.

also in agreement with the model proposed by Coe and Neuffer (1978). They found that at the dry embryo stage nodes 8 through 14 were represented by three levels of 32 cells each (the 32 cells at a given level developed into 2 or 3 nodes). The data of Table 1 further indicate that determination of individual lower internodes occurs when there are 32 initials in the L-I. These initials divide once generating 64 cells and then the cell divisions leading to the widening and lengthening of the internode axis occur.

Clonal relationship between spikes and spikelets in the tassel: The tassel sectors described earlier (Johri and Coe, 1980 MNL 54:80) were examined further in order to determine the proliferation pattern of the clones constituting the tassel. Despite considerable variability in results, the size of the tassel seems to be independent of ACN or the number of clones. In the different families investigated about 60% of the tassels developed from 4±1 cells of the dry embryo, and tassels with a small or a large number of branches developed from more or less the same number of embryonic cells (Fig. 2). This observation indicates that in the tassel initials the rate of cell division and the time when spikes get determined are quite different in sparsely branched tassels as compared to highly branched ones. Whether these two processes are coupled is not known at present but these parameters are worthy of consideration in the future if we wish to modify the size of tassel.

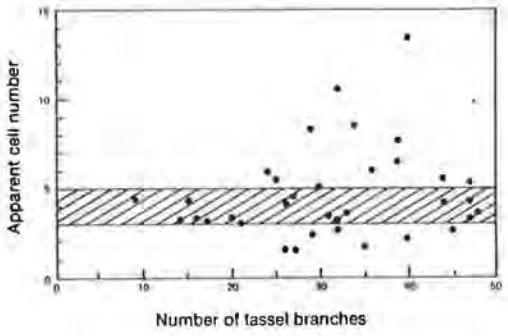
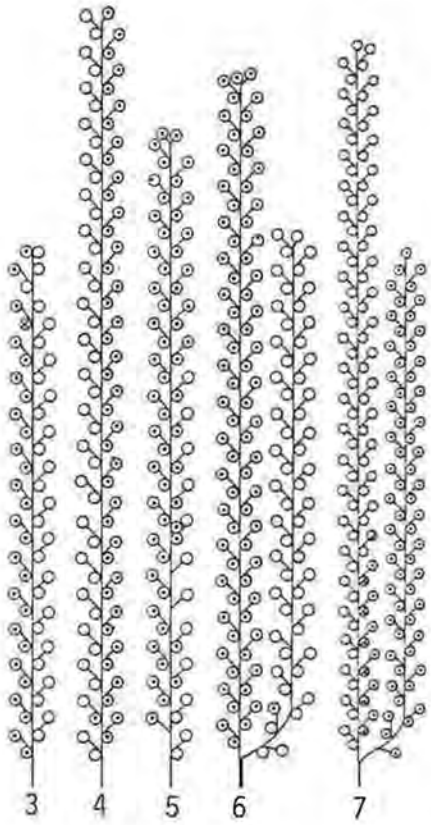


Fig. 2. Relationship between ACN and number of tassel branches. Crossed area designates the tassels developing from 4±1 cells.

The lineages of all four cells are present at the base of tassel, but their relative proliferation is highly variable and finally only two lineages extend into the central spike. The individual first order branches were either completely or partially included in the sector (Figs. 3-5). The latter situation was observed especially in the spikes at the border. The second order spikes were always of one phenotype, completely included in the sector (Figs. 6 and 7). The first order



Figs. 3 to 7.

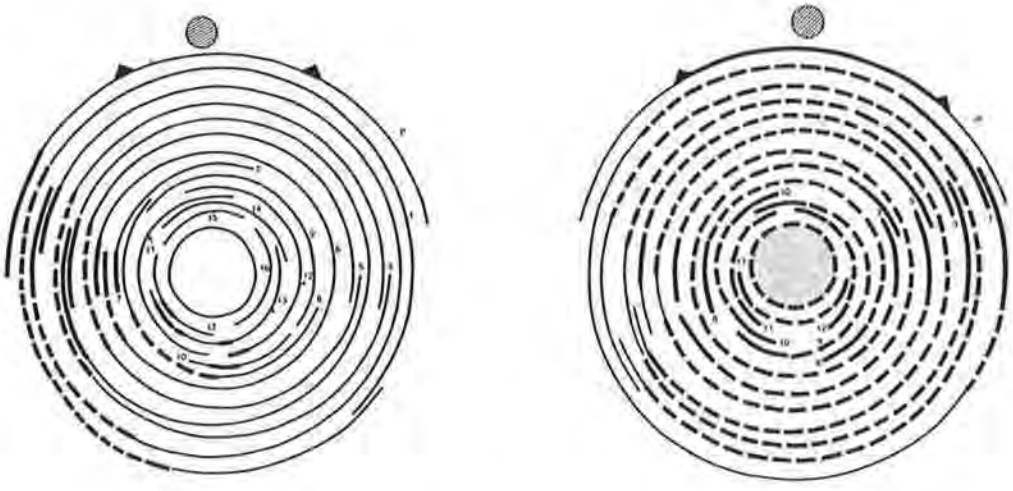
Clonal relationship between spikes and spikelets. Figs. 3-6 show distribution of spikelets without glumes (o) and with glumes (ø) in the first and second order spikes. These spikes are from tassels showing sectors due to loss of Vg. Fig. 7 illustrates distribution of spikelets with green (r-g, ø) and colored anthers (R-r, o) in a spike from tassel showing a sector for the loss of R-r.

branches can therefore develop from the lineages of two cells but only one of these usually continues into the second order spike. Only rarely one or two spikelets situated at the base of the second order spike were found to have developed from the lineage of a second cell (Fig. 6). The proliferation of a cell lineage in the first order spike is quite ordered and generates a linear file of cells. Often the same lineage developed into several sessile or pedicellate spikelets along one side of a spike. At the border, a single spikelet on a first order branch was occasionally half sectored (Fig. 7), and in such spikelets one floret showed all the three anthers either green (r-g) or colored (R-r); or bronze (bz2) or purple (Pl). A single spikelet can thus develop from two cell lineages but the stamens of a floret develop from a single cell lineage.

Sectoring pattern in ear shoots: The ear sectors observed earlier (Johri and Coe, 1980, MNL 54:80) were studied further and four distinct but related patterns of the proliferation of clones have been found.

1. In 20% of ears with a sector, the edges of all the husks were observed to be colorless (non-purple). The shank and the husks between the edges were pale purple. The shank lacked any external features to suggest the continuity of colorless edges from one husk to the next. The entire cob was included in the sector. The meristem of these ear shoots can be interpreted as a periclinical chimera in which the L-I layer (or layers) originated from a single L-I cell lacking the dominant allele (B, Pl or C2). The L-II layer in these chimeric meristems was genetically purple. Since we are seeing the underlying purple L-II layers through the colorless L-I cell layers, the shank appears pale purple.

2. In 35% of ears, the sectored region represented between 20 and 90% of an ear shoot. In the ear shown in Fig. 8, the sector consisted of about 25% of the width of the first two husks, then gradually diminished and terminated in the last husk. The sectors in other ears occupied as much as 90% of the ear shoot (Fig. 9) and the progression of the sector from one husk to the next could be easily followed externally on the shank. The L-I in the ear shoots of this class seems to originate from two L-I cells and the extent of proliferation of these cell lineages is highly variable.



Figs. 8, 9. Diagrammatic representation of sectors in ear shoots. The prophyll (P) and husks (1-16) have been drawn in the same orientation as their arrangement on the shank. Colorless (——), pale purple (----) and purple (——) regions of husks.

3. The third category of sectors was similar to the second one, but showed colorless stripes in the pale purple regions of husks and shank. Some 25% of ears with a sector showed this pattern. These stripes did not follow a clonal relationship from one husk to the next and seemed to represent a displacement of genetically purple L-II by colorless L-I in local areas. Replacement of the genetically colorless L-I cell layers (except the epidermis) by purple L-II cells was also observed and in such cases, purple stripes occurred against a background of pale purple or colorless. The proliferation of two cell layers is thus quite variable and due to periclinal divisions one cell layer can displace the other in local areas.

4. In the remaining 20% of ears, the sector lacked purple color through the depth of the husk. There was no indication that husks in such ears developed from cells derived from both L-I and L-II of the embryonic meristem. Very early during the formation of the ear shoot meristem, one of the initial L-I cells may have divided periclinally so that the L-II was displaced by a L-I daughter cell in the meristem. Alternatively only L-I cells may have formed the bud meristem.

Proliferation of cell lineages in the cob: The clonal boundaries showed no relationship to rows even though a pair of rows develops from a single branch primordium. The clonal tissue switched a complete row or often only half a row laterally as determined on the basis of glume color (Figs. 10, 11). A row of branch primordia does not originate from the lineage of the same cell through the entire length of the cob. Each row can develop from cells derived from two different but adjacent cell lineages. In many instances the florets at the border showed half-sectored glumes.

Fig. 10. Ear showing a sector due to loss of C2.

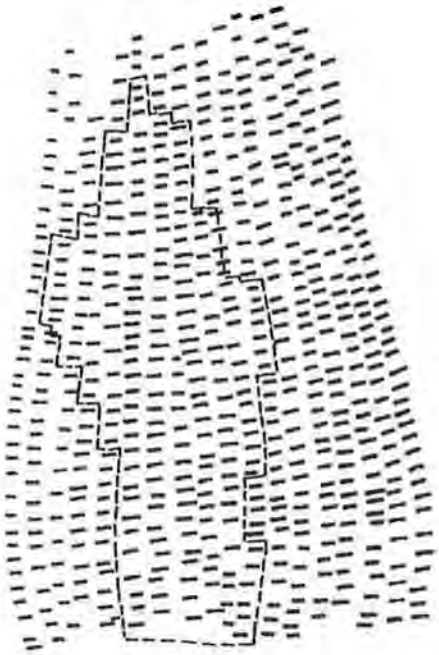


Fig. 11. Map showing the relationship between clonal boundary and rows of kernels in the cob shown in Fig. 10.

These results show that the number of times a cell divides is not predetermined. A cell lineage can contribute anywhere between 5 and 90% of husks and/or cob and less frequently only a single cell lineage will extend into a cob. As with the four cell lineages present at the base of the tassel, the lineages of two cells entering the ear are present at the base of the ear. As opposed to the tassel, however, the cob was not divisible into two lateral halves based on clonal restriction. The clonal boundary that runs along the midrib of leaves and through the central spike in the tassel, dividing the corn plant into front and back halves, was not distinguishable in the ear shoot. This seems to be due to a variable proliferation of cell lineages, in which the initials of an ear shoot may be occasionally derived either from the front half or the back half.

Polyembryonic and sectored plants from embryos x-rayed during early developmental stages: In the first part, we described the results which showed that the initials of the first few internodes were already present in the dry embryos. To determine if these individual nodes were also initially produced as a group, the developing kernels were x-rayed at different stages of maturation. Plants homozygous for anthocyanin and chlorophyll markers (B Pl Wd) were pollinated with wd pollen (male plants were b pl wd with ring-9S carrying C-I Wd). At various intervals (see Table 2) the ear shoots were x-rayed (1000 rad/ear shoot), the plants were returned to the greenhouse and the kernels were allowed to mature. In each family, variegated and unvariegated kernels were sown separately and sectors were scored in the seedlings and mature plants.

Among the different F1 families, about 20 to 60% of the kernels developed into viable seedlings. In the population examined, a few polyembryonic seedlings were also observed. Nine such seedlings arose from kernels x-rayed 43, 144 and 168 hr after pollination. Each of these seedlings exhibited a single coleoptile but two

Table 2. Distribution of Polyembryonic and Sectored plants from kernels x-rayed at various intervals after pollination

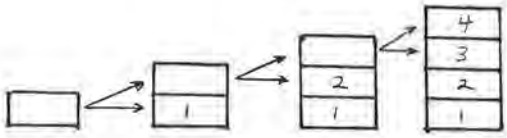
Family	Time x-rayed (hr)	Kernels planted	Plants observed	Polyembryonic seedlings	Sectored seedlings Fraction (leaf no.)	Other losses (no. of plants)
923[1]	35	10	6			
924	43	17	6	1		
925	43	16	4		1/8(2)	
926	58.5	52	26			Loss of B(2)
927	58.5	63	39			Loss of Pl(1),-g(1)
928	72	80	54			
929	96	77	62			
930	120	25	21			
931	120	38	30			
932	144	109	87	4		Loss of Pl(2)
933	168	129	91	4	1/8(1,2)	
934	192	22	14		1/16(each in 1,2,3) 1/16(each in 1,2) 1/16(1)	
935	192	120	84	2	1/8(each in 2,3) 1/8(2,3)-1/16(4) 1/16(1) 1/8(1)	
936[2]	35	5	3			
937	43	6	2			
939	58.5	9	4			
940	58.5	43	25			Loss of C2(1),B(1)
941	72	29	18			
942	96	31	18			
943	120	4	1			
944	120	47	26		1/4(1) 1/2(1)-1/4(2,3)-1/8(4,5)-1/16(6)-1/32(7)	
945	144	17	8			
946	168	22	15			
947	192	1	1			
948	192	31	12			

[1]Kernels not variegated 923-935 [2]Kernels variegated 936-948

separate and complete axes beginning with the first or second leaf, each having independent sets of leaves and a shoot apex. The two seedlings arising from kernels x-rayed at 192 hr showed a single coleoptile, a single first leaf and a single second leaf. The third leaves were free in one seedling but partially fused in the other.

Polyembryonic seedlings in x-rayed material have been described earlier (D. T. Morgan, 1956, MNL 30:83). Corn embryos show enormous plasticity during development and even the use of x-rayed pollen increases the frequency of polyembryonic seedlings (D. T. Morgan and R. D. Rappleye, J. Hered. 42:90, 1951). The pattern of plasticity suggests to us that possibly the determination of the first and second leaves has already occurred by 192 hr. This can explain the type of polyembryonic seedlings observed in family J935.

The distribution of sectors in leaves strongly supports this interpretation. Most of the seedlings with sectors were present in families J933-935 and J944. White deficiency sectors were present in the first two to seven leaves, suggesting that during development a group of nodes (two to seven) is first produced. In the seedlings of family J935, the sectors were present either only in the first leaf or in leaves two to four. Individual nodes are thus generated starting from the first one (the first node is the lowermost one). Though the data are fragmentary, the most plausible trend indicates that during embryogeny 8 or 16 initials destined to produce a group of nodes are first produced. A single initial cell of this group divides in such a way that it generates a specific nodal initial and an undifferentiated cell. The latter in turn follows the same pattern of cell division and finally all the nodes are formed as shown below:



Proposed cell division pattern of a group initial cell. Numbers 1 to 4 refer to lower four nodes. It is assumed that this initial cell is destined to produce four nodes.

In addition to these plants, sectors representing losses of B, P1 or C2 were also observed. The sectoring pattern of J932-81 will be described. This plant showed a p1 sector beginning in the culm below the tassel and continuing up to the 17th leaf from top. It occupied about 25 to 30% of the culm perimeter. The relative distribution of P1 and p1 parts as determined on the basis of the sheaths of the top 11 leaves is shown in Fig. 12. At the time of x-raying (144 hr after pollination), there could be three or four cells in the transverse plane in the apical dome of the embryo and one of these presumably lost the P1 marker. The lineage of the p1 cell seems to have proliferated in a somewhat random manner. This lineage started left of the midrib in leaves 1 to 7, but was found to be present on the other side of the midrib in leaves 9 and 11.

The first vertical division in the terminal cell of the 2- or 3-celled proembryo has been reported to separate the front and back halves of a corn plant in such a way that the axis of bilateral symmetry is defined by the position of midrib in the leaves (Steffensen, 1968, American J. Bot. 55:354). Our observations suggest that this determination is not absolute and, though the two cells separated by this vertical division usually generate the front and back halves, there is

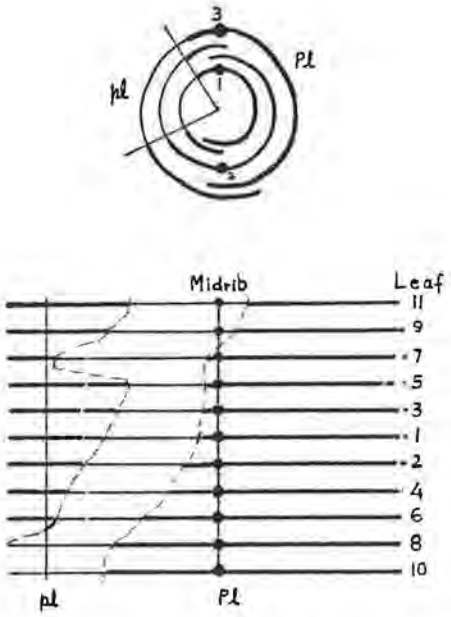


Fig. 12. Distribution of pl and Pl regions in the top 11 leaves. In the diagram on top the relative orientation of the first three leaves is shown. In the lower diagram leaves have been drawn in a linear orientation to show the proliferation of the pl cell lineage.

nothing which prevents one cell from contributing lineage to the other side. In the plant under discussion, the lineages of Pl cells on the right may have proliferated much less and consequently the lineage of the pl cell from the left of the midrib contributed to the tissues on the right. These observations clearly demonstrate that the proliferation of individual cell lineages is highly variable and spatial location rather than lineal descent is the deciding factor in determining the final fate of a cell.

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Determination of breakpoints in B-A chromosome translocations

The determination of breakpoints in hyperploid stocks with translocations between B and A chromosomes can be a different kind of challenge than the breakpoint analyses of A chromosome translocations. In cytological studies of different hyperploid stocks containing B-A translocations, good cross-configurations were almost impossible to find. In fact, most of the pachytene cells showed separate associations of $B^{A}B^{A}$ and $A^{B}A$ figures, rather than a complex of the four chromosomes. A second concern in translocation breakpoint analyses of any type

is the usual inability to place a measure of confidence on the estimates. Often, the cytologist is fortunate to obtain one good cross-configuration, or very few of them. Even if a number of measurements can be made, ratios are being calculated and reported. Ratios cannot be handled by the usual statistical tests.

The following discussion outlines some attempts to overcome all three of the problems mentioned above. Firstly, a cytological technique was needed in which the pachytene chromosomes could be observed with enough resolution to discern the points of exchange without cross-configurations. Briefly, squashes were made with propionic carmine followed by an exaggerated de-staining process. Combined with phase contrast microscopy, one consistently obtains preparations which show very distinct chromomere patterns. Photomicrography and printing upon ultra high contrast paper yield the desired results (See Figure 1). A more detailed description of the entire technique will be reported later.

An example of the method for calculating the breakpoints and providing confidence intervals will be given for the TB-10Lb stock. Figure 2 shows several of many photomicrographs obtained of the normal B, and Figure 3 shows several photomicrographs of the normal chromosome 10. The $B^{10}B^{10}$ figures are much easier to find in hyperploid stocks than the $10^{B}10$ figures. Actually, the $B^{10}B^{10}$ figures are so conspicuous that one can usually obtain numerous observations of at least part of the configuration. Figure 4 shows several of many representative $B^{10}B^{10}$ figures with the probable breakpoints indicated by arrows.

Measurements were made of the various chromosome regions by utilizing photomicrography, enlargement onto printing paper, and measuring with a cartographic map measurer. Identical conditions and magnifications were used throughout. The pertinent measurements needed are actually the result of different figures in different cells, and in some cases, in different squash preparations. Nonetheless, one can generate an abundance of data with relative ease, and therefore, calculate means for the lengths of the various regions. For an example of the precision, six different B chromosomes measured in this manner gave the following measurements in arbitrary units: 9.1, 9.0, 9.2, 9.1, 8.4, 9.9. In conclusion, the lack of cross-configurations is overcome by chromomere pattern analyses, and the rarity of cells distinctly showing all of the pertinent regions is overcome by gaining many figures of each component, and then calculating the means. These steps also tend to overcome the problems of non-homologous pairing, synapsis, and other cytological discrepancies.

Lastly, several statistical techniques can be used so as to place confidence intervals with the results. Again, the data obtained for the TB-10Lb stock will be used as an example. Measurements were made for both the B chromosome and the chromosome 10 regions. Those of the B chromosome will be shown as representative of the technique.

B chromosome calculations (means and standard errors):

Centromere to breakpoint:	7.1 units $\pm$ .3344	(n=15)
Centromere to chromosome end:	8.9 units $\pm$ .2169	(n=6)

Breakpoint location = 7.1/8.9 = .80

Several different methods might be used for calculating a confidence interval for a ratio:

Method I (use of extremes):

Lower limit = (7.1 - .3344)/(8.9 + .2169) = .7421
Upper limit = (7.1 + .3344)/(8.9 + .2169) = .8562

Figure 1.

Figure 2.

Figure 3.

Figure 4.

It can be stated that at least 68% of the means would fall within the ratios of .7421 and .8562. For various mathematical reasons, this is a conservative interval. However, one can also relate the breakpoint ratio to the standard error of the difference of means through the use of the square root law. This calculation is slightly less conservative.

Method II (standard error of the difference between means):

$$S.E.D. = \sqrt{.3344^2 + .2169^2} = .3985$$

Also, the ratio of $\bar{X}_1/\bar{X}_2$ is equal to $1 + (\bar{X}_1 - \bar{X}_2) / \bar{X}_2$.

By inserting the difference between the means $(\bar{X}_1 - \bar{X}_2)$ with the calculation, one can again calculate the upper and lower limits:

$$\text{Lower limit} = 1 + (-1.8 - .3985)/(8.9 - .2169) = .7467$$
$$\text{Upper limit} = 1 + (-1.8 + .3985)/(8.9 + .2169) = .8462$$

Note that these results are slightly tighter than those from above. Again, it can be stated that at least 68% of the means will fall within the ratios of .7467 and .8462.

Method III (approximate variance of the error of the ratios):

$$\text{variance} \doteq S.E._1{}^2/\bar{X}_2{}^2 + (\bar{X}_1{}^2/\bar{X}_2{}^4)S.E._2{}^2$$

$$\doteq .3344^2/8.9^2 + (7.1^2/8.9^4).2169^2$$

$$\doteq .00177$$

$$\text{and the S.E.} = \sqrt{.00177} = .0421$$

Then,

$$\text{Lower limit} = .80 - .0421 = .7579$$
$$\text{Upper limit} = .80 + .0421 + .8421$$

and again, 68% of the means would fall within the ratios of .7579 and .8421.

In summary,

	Lower limit	Upper limit	Size of Interval
Method I	.7421	.8562	.1141
Method II	.7467	.8462	.0995
Method III	.7579	.8421	.0842

The pattern that occurs is obvious. Method III, of course, yields the smallest confidence interval and should be preferred. If a 95% confidence interval is desired, the same method can be used with the S.E.'s simply multiplied by 2. And the breakpoint in the other chromosome can be calculated next in the same way.

A total of 255 photomicrographs of 10 different TB stocks are presently being analyzed using these procedures. These data will be reported at a later time. These techniques might also be useful for the standard A translocation analyses.

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Hydroxamates (DIMBOA) in relation to resistance to corn leaf aphids

The following inbreds and single crosses were grown in replicated plots in the field and scored visually at tassel emergence for reaction to aphids:

C131A	OH43	B14	Bx x C131A
B37	C103	Bx Bx	B37 x WF9
B49	WF9	bx bx	N28 x B37

They were evaluated following natural infestation on the basis of 1 = no infestation to 4 = heavily infested. Hydroxamate concentration was determined by use of the rapid procedure (Crop Sci. 14:601-603, 1974). A significant correlation ($r = 0.58$) was obtained between hydroxamate concentration and aphid resistance. These results agree with our previous work (Crop Sci. 7:55-58, 1977).

Recent work with the rapid procedure seems to indicate that the concentration of $FeCl_3$ used previously (0.1N) may not be sufficient to react with all the hydroxamic acids in high DIMBOA lines. We are currently testing the effects of different concentrations of $FeCl_3$ (0.1N, 0.3N and 0.5N) on the colorimetric reaction. It also appears that anthocyanin pigments which often develop at the base of the stem of corn seedlings may be greatly reduced by wrapping the basal stem in aluminum foil. These pigments may interfere with the colorimetric reaction.

G. M. Dunn, D. G. Routley and David Beck

Selection for an early ornamental flint corn

Work is in progress on selection for an early ornamental flint corn. Inbreeding and hybridization for the past several years has not been particularly effective since DC hybrids usually provide little variation in colors. Furthermore, potential seed sales may not justify maintenance of numerous inbreds plus other production costs. We have recently tried crosses of the type (1) broad based synthetic x white inbred and (2) op x op. Several strains of both types are now under advanced testing. Some of these have good vigor, excellent colors, and are at least three weeks earlier than currently available strains. We feel such material can be used in short season areas for both decoration and for corn meal. Corn bread made from freshly ground flint corn has a unique nutty flavor.

G. M. Dunn and David Beck

GRAND FORKS, NORTH DAKOTA
University of North Dakota
COLUMBIA, MISSOURI
University of Missouri

Developmental mutants--a group of defective kernel mutants blocked in early embryo development

An examination of embryonic development of 150 defective kernel mutants has revealed 15 lethal mutants that are blocked in their embryonic development at a stage prior to the formation of the first leaf primordium (only one of these mutants, E792, is described in the report by Neuffer and Sheridan in this issue). These mutants were examined early and late in kernel development by dissection of mutant kernels on self-pollinated segregating ears. There are nine mutants blocked at the proembryo stage and five of these are allelic. Four mutants are blocked in the transition stage and two mutants in the coleoptilar stage of embryo development. These stages are those defined by E. C. Abbe and O. L. Stein (1954). Since preliminary results indicate that eleven of the mutants are located on six different chromosome arms, it appears that several gene loci can result in stage-specific blocks in embryogenesis. Additional details on these mutants are reported in Sheridan and Neuffer (1981, to be published in the 39th Annual Symposium of the Society for Developmental Biology, S. Subtelny, editor).

William F. Sheridan and M. G. Neuffer

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University of Hawaii

Peroxidase isozymes in maize: characterization of locus Px7

The peroxidase system in maize is characterized by a large number of isozymes whose expression depends both on tissue and developmental stage of the plant. Thirteen zones of peroxidase activity are recognized electrophoretically, and nine genetic loci which control the inheritance of individual peroxidase isozymes have been described (Brewbaker and Hamill-Johnson, 1972, MCGN 46:29-33; Brewbaker and Hasegawa, 1974, MCGN 48:35-37). The number of genes responsible for the coding of peroxidase isozymes, all basically heme containing glycoproteins, suggests that although these multiple enzyme forms are closely related evolutionarily they may have distinct physiological functions.

Px7 is a major form of peroxidase in many maize tissues, including coleoptile, leaf, husk, silk, pericarp, and roots. It is absent in embryo, endosperm, pollen, anther and tassel initial. In leaf tissue Px7 accounts for about one-third of the total peroxidase activity. In silk, Px7 is the predominant form of the enzyme, and accounts for over half the total peroxidase in this tissue.

The migration of Px7 in an electric field is quite slow. In normal electrophoretic separations, Px7 does not move out of the origin. Lowering acrylamide gel concentration to 6% at pH 8.4 and extending electrophoresis time to 40 hours results in migration of Px7 toward the anode and good resolution of allelic variants. Increasing pH to 9.1 accelerates anodal migration but resolution of variants suffers.

Two major alleles of Px7 have been observed (Table 1). The slow variant, Px7-S, is common. A fast variant, Px7-F, has been observed in three lines of

Table 1. Allelic variants of Px7 in Zea mays.

Variant	Lines
Px7-S	A632, C123, N28, 38-11, 245, 318a, 442a, 677A, 2277, 5446, 5490, 6053, L289, F6, F8, FR9, Mo5, PH9, Oh07A, R168, R182, AA1 - AA7, AA9 - AA13, AA15 - AA23, C1230$_2$, Hi27, CM105, H94, M113, P39, R177, W6462, WQ6A, A619, CM111, Mo17, Oh43, Va35, B14A, CI64, Oh51A, AA8, AA14, H95, M14, Oh545, T20.
Px7-F	T24, T36, T55, Carioca 338.
null in all tissues	B73, CI66.
null in some tissues, present in others.	B37, H84, W64A

sweet corn and Carioca 338. Backcrosses suggest these alleles are inherited in a co-dominant manner:

Cross	SF	F
71-1285 (S/F) x 71-1258 (F/F)	14	17

Several inbred lines have been observed which are null at the Px7 locus. These fall into two classes: those which are null in all tissues, and those where the enzyme is absent in one tissue, silk, and present in others such as leaves. Obviously the mechanisms by which nulls arise in these classes are quite different.

Px7 has a tendency to streak on acrylamide gels, which suggests that it might be bound to some heterogeneous component. The molecular weight of Px7, as determined by Sephadex chromatography, is about 75,000. The molecular weights of the other maize peroxidases range from 33,000-50,000. Although Px7 is the largest of the maize peroxidase isozymes, it is retained within the pore structure of the molecular sieve gels Sephadex G-100 and Sephadex G-200:

Gel Pore Type	Exclusion MW	Elution Volume/Void Volume
G-75	75,000	1.05
G-100	100,000	1.22
G-200	200,000	1.50

This indicates that it is not attached to large cellular structures such as cell walls or membranes. The F1 heterozygotes in crosses between Px7-F and Px7-S lines have only two bands which co-migrate with each of the parental alleles. The absence of a third intermediate heteromultimer band suggests that Px7 despite its large molecular weight behaves as a monomer.

Edwin H. Liu, Chifumi Nagai, and James L. Brewbaker

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Osmania University

Feeding studies with c1 and c2

The use of genetically blocked markers provides a powerful tool in analyzing the gene action sequence of the anthocyanin pathway. Homozygous recessive kernels of c1 and c2, 20-25 days after pollination, with exposed aleurone were used. These were placed directly on filter paper or 0.8% agar containing cinnamic acid, caffeic acid, naringenin and quercetin (1 mg/100 ml of dist. water). Anthocyanin was observed in about 25% of c1 kernels, fed with cinnamic acid and caffeic acid. In the case of c2, the kernels developed anthocyanin only with naringenin. The c2 kernels showed pigment on the crown, spreading gradually to the sides. In the case of c1 the crown which was in contact with the substrate showed very pale to almost no pigment, whereas lateral sides, which were directly exposed to light, developed pigment. Chromatographic and spectrophotometric studies of hydrolyzed samples suggest that the pigment is cyanidin.

Padma Balaravi and G. M. Reddy

Light requirements in anthocyanin synthesis

Kernels of c1 and c2 developed pigments, with some of the substrates, only in the presence of light. The c1 kernels treated with cinnamic acid and caffeic acid failed to show any response when placed in the dark for 72 hours. These kernels were then exposed to light for about 20-24 hours and developed pigment, suggesting that light is essential for pigment synthesis. Anthocyanin synthesis was generally seen on the sides that were directly exposed to light. When kernels were placed in a uniform field of light, the pigment was observed on all sides.

Padma Balaravi and G. M. Reddy

Role of c2 in the gene action sequence

The c2 mutant aleurone extracts were analyzed by paper, TLC and spectrophotometrically. The Rf values obtained with BAW and Forestal (0.40 and 0.81) and U.V. absorption maxima at 270 μ and 222 μ suggest that the unknown sample may be cinnamic acid.

The fact that c1 can synthesize cyanidin with cinnamic acid and caffeic acid and c2 with naringenin suggests that the c1 block may be before cinnamic acid, whereas c2 may be after cinnamic acid but before the flavanone/C-15 intermediate step. The fact that c2 accumulates cinnamic acid suggests that c2 may be blocking before the C-15 intermediate stage.

These observations independently confirm the earlier gene action sequence of Reddy & Coe (1961 MGCNL) where it was suggested that c2 follows c1 in the sequence. Since c1 can utilize cinnamic acid (without hydroxyl groups) to synthesize cyanidin (with 3' and 4' hydroxyl groups) it may be possible that 3' and 4' hydroxylation (controlled by the Pr/pr gene) may be occurring after c1 in the sequence and probably after the C-15 intermediate formation.

Padma Balaravi and G. M. Reddy

IRKUTSK, USSR
Siberian Inst. Plant Physiol. and Biochem., USSR Acad. Sci.

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* Dedicated to the memory of *
*
*   Prof. M. I. Khadzhinov   *
*
(deceased November 21, 1980)
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Isozymes of 6-phosphogluconate dehydrogenase (6PGD): a presumable mode of control

Three phenotypic variants of 6PGD spectra have been previously described in the scutella of 3-day-old maize seedlings (Fig. 1). Most frequently, the pattern consists of two adjacent bands (class A spectrum), while in class B two more distant bands are supplemented with the third weakly staining and more mobile band. Class C spectrum is rather rare: it has been observed in the scutella of Palomero Toluqueño maize as well as in the leaves of all teosinte species, except teosinte Chalco. B and C patterns differ only in their staining distribution (MNL 54:55, 1980).

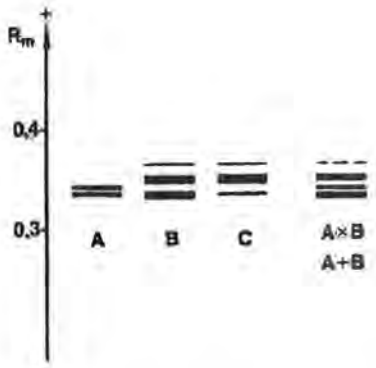

Fig. 1. 6PGD phenotypes A, B, and C of maize and teosinte. AxB, hybrids of class A and B maize inbreds; A+B, mixed A and B samples.

The probability that the variants of 6PGD patterns are conformers is excluded by the dissociation-association test, by extraction in the presence of increasing 2-mercaptoethanol concentrations, and by separation of isozymes in polyacrylamide gels of different porosity.

To discriminate plastid and cytosol isozymes (allozymes) of 6PGD, we separated a 900 g particulate fraction from the scutella and leaves of seedlings and washed the sediment with hypertonic extraction medium. Twice-washed plastids were found to be microscopically intact and virtually free of alcohol dehydrogenase, which served as a sensitive marker for cytosol impurities. In contrast to the class A pattern, in class B inbreds 6PGD spectra of the cell-free extract (plastids plus cytosol) and the twice-washed particulate fraction (plastids) differed quite distinctly: plastids lacked the most mobile band, while the staining of the second band diminished (Fig. 2). By

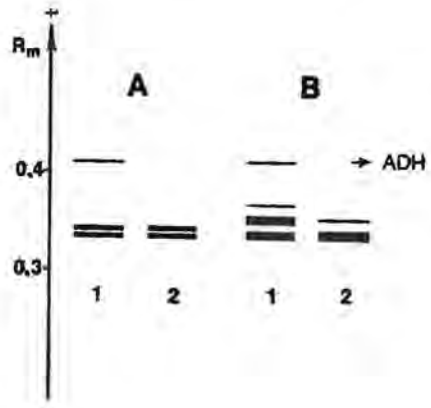

Fig. 2. 6PGD spectra (classes A and B) in the course of plastid purification from maize scutella and leaves: (1) the cell-free extract; (2) the purified particulate fraction free of cytosol (ADH-free plastids).

successive double-dilutions (Klebe, Biochem. Genet. 13:805, 1975) of the particulate fraction extract, the activity of this isozyme was shown to exceed two-fold that of the plastids. We suggest that the class B pattern is formed by such coincidence of two cytosol and two plastid bands that the staining of the more mobile plastid isozyme is intensified by the slower cytosol isozyme. The respective cytosol and plastid bands in the class A pattern apparently do not differ in their mobility (Fig. 2), and therefore two bands are formed in the cell-free extract samples.

Segregation studies (based upon the dimeric structure of 6PGD, see Gasperi et al., Biochem. Genet. 17:855, 1979) suggest that classes A and B differ in alleles of a single locus, while the second monomorphic locus controls the band common both to the A and B patterns:

	Phenotype				
	AA	BB	AB	Chi-square*	P
AAxAA	10	-	-	-	-
BBxBB	-	10	-	-	-
AAxBB	-	-	25	-	-
BBxAA	-	-	25	-	-
ABxAB	20	25	40	0.877	0.50-0.75
BAxBA	23	21	46	0.133	0.90-0.95
ABxAA	24	-	18	0.856	0.25-0.50
ABxBB	-	21	22	0.022	0.90
BAxAA	24	-	34	1.72	0.10-0.25
BAxBB	-	22	22	-	0.999

*Theoretically expected ratios 1:1:2, 1:1:2, 1:1, 1:1, 1:1, respectively.

Hybrid spectra AxB and BxA are similar to the patterns in A+B mixtures and in AB heterozygotes from the collection of maize races (MNL 54:55, 1980). No additional bands of different mobility due to hybridization of subunits have been observed in F1, F2, and backcrosses among the maize races and teosinte. These data seem to exclude the existence of interallelic heterodimers.

Quite recently, C. W. Stuber and M. M. Goodman (MNL 54:99, 1980) proposed another two-loci model of 6PGD control comprising nine alleles at the Pgd1 locus and three alleles at the Pgd2 locus, and formation of heterodimers between allelic and non-allelic isozymes. To overcome the discrepancies of the two models, we apparently need some additional data that, in particular, would help to interpret the staining distribution in the class B and C patterns.

T. B. Sukhorzhevskaia and E. E. Khavkin

Isozymes of NAD-dependent glutamate dehydrogenase (GDH) mark cell epigenotypes in roots of different origin

Two-gene control has been suggested previously from analysis of GDH spectra in scutella of maize seedlings (MNL 53:45, 1979). The products of two loci, by free association into hexamers, would produce the seven-band spectrum with binomial staining distribution. However, the latter was found only in developing and mature anthers, while all the other organ-specific GDH patterns deviated widely from the

binomial prototype. We therefore suggest that the organ-specific GDH spectra are determined both by differential activity of two genes and by post-translational modification of gene products changing the activities of the associates.

The five-band GDH pattern in the coleorhiza and in the primary and lateral roots of the seedling differ widely from the seven-band pattern in the adventitious roots similar to that of the shoot (Fig. 1, lanes 1 and 2). The adventitious (seminal) roots arise near the top of the scutellar node (Sass, Corn and

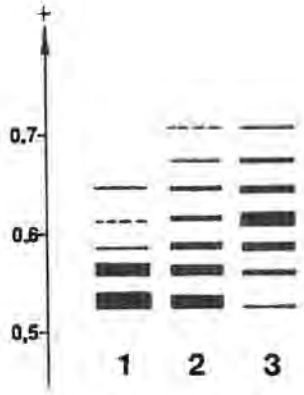

Fig. 1. GDH isozymes in (1) the primary and lateral roots of the seedling; (2) the adventitious roots and the shoot of the seedling; and (3) roots induced in the calli derived from the coleoptile node of the embryo (inbred W155).

Corn Improvement, 2nd ed., 1977, p. 97); that is, they are shoot-derivatives. It therefore appears that the GDH epigenotype is determined rather by the origin of the initial cells (stem-cell lineage) than by the further fate of the cells derived from these initials.

Calli derived from the developing and mature maize embryos are regarded as homologues of root and shoot meristems: while M. Freeling et al. (Maydica 21: 97, 1976) interpret these calli to be the apical and lateral root and shoot meristem derivatives, R. L. Mott and W. W. Cure (Physiol. Plant. 42:139, 1978) consider these embryo-derived calli to be abnormally growing adventitious roots. Apparently GDH spectra may help to resolve this discrepancy. Two variants of GDH spectra, that is the scutellum- and the shoot-specific patterns, were found in the calli derived from the coleoptile node of embryos (for details of callus initiation and culture see Khavkin et al., Planta 145:245, 1979). While staining distribution in GDH patterns somewhat varied in the successive subcultures of these calli, yet in none of the cases did we observe the five-band GDH pattern characteristic of the primary or lateral roots. The scutellum-derived calli also produced the seven-band GDH patterns intermediate between the scutellum and the shoot spectra by staining distribution.

By lowering 2,4-D concentration in the agar medium, root formation was induced in the calli derived from the coleoptile node of the embryo. Quite unexpectedly, these roots exhibited the seven-band GDH pattern with the binomial staining distribution (Fig. 1, lane 3), that is, the prototype GDH spectrum free of any subsequent modifications.

The embryo-callus-root transformations may apparently provide a hopeful approach to studies both of the somatic heredity as related to the stem-cell concept and of the modification of maize isozymes in the course of cell and tissue differentiation.

T. B. Sukhorzhevskaia and E. E. Khavkin

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Cornell University

Increase of inbreds in several cytoplasms

An additional backcross generation was made to increase seed of several standard inbreds in a number of designated cytoplasms, e.g.:

Minn. A239 in C, CA, D, EK, EP, G, J, K, L, LF, M, ME, ML, MY, OY, P, PS, RB, S, SD, SG, T, TA, TC, 181, 234, and Q;
Minn. A495 in B, C, D, EK, F, G, H, HA, I, IA, J, ML, MY, PS, R, RB, RS, SG, T, TA, TC, VG, W, 181, and 234;
Minn. A619 in Bb, B, C, CA, CH, D, EK, EP, ES, F, G, H, HA, I, IA, J, K, L, LF, M, ME, ML, MY, NT, P, PR, R, RB, RS, S, SD, SG, TA, TC, VG, W, 181, 234, and Q;
Minn. A632 in Bb, CA, CH, D, EK, EP, ES, G, HA, I, IA, J, K, L, LF, M, ME, ML, MY, NT, OY, PR, PS, RB, S, SD, SG, TA, TC, 181, 234, and Q;
Minn. A636 in CA, CH, EK, EP, F, G, HA, IA, J, K, L, M, ME, ML, MY, NT, OY, PS, RB, RS, SD, SG, TA, TC, 181, 234, and Q;
Io. B8 in B, C, CA, CH, D, EK, EP, F, G, H, HA, I, IA, J, L, LF, M, ME, ML, MY, NT, OY, P, PS, R, S, SD, SG, TA, TC, VG, W, 181, 234, and Q.

Other inbred seed increased in diverse cytoplasms include: NY AyX65, NY AyX138, NY AyX157, NY AyX187y-1, NY AyX187y-2, NY Ay499, NY Ay191-71, NY Ay303E, NY Ay490-2A, and Conn. C153. All inbreds have been back-crossed to the individual cytoplasms a minimum of eight times and, thus, are essentially isogenic. Sample lots are available upon request and a charge will be made for company orders.

V. Gracen, H. Everett, W. Tracy and C. Manchester

Iojap crosses

In the 1979 nursery iojap plants grown from the Illinois Seed Stock line were crossed as males (pollinators) to the following inbreds as females: SD10, Oh51A, C0107, R181, and W182BN. The F1 (Ij ij) hybrids were selfed in the 1979-80 Winter nursery in Florida. Segregating iojap plants (ij·ij) were backcrossed as females to SD10, Oh51A, C0107, I11R181, and W182BN as males. Plants from this BC1 generation will be observed in Florida and a BC2 is planned for the New York nursery in 1981. The inbreds were selected as strong non-restorers of cytoplasmic sterility in the S, C, and T cytoplasmic groups. All BC generations will be carefully checked for manifestations of cytoplasmic pollen sterility.

H. Everett

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Failure to verify the Ga9 locus on chromosome 4

J. Jimenez and O. E. Nelson (J. Hered 56:259-263, 1965) described a new gametophyte factor isolated from the popcorn variety White Rice. Their data showed that the factor was located on chromosome 4 but was not an allele of Ga1, which has been placed at position 71 in the short arm, 28 crossover units to the left of su1. The new Ga factor showed 30% recombination with su1 but assorted independently of Ga1. The locus was designated Ga9 and placed 30 units to the right of su1. The Ga9 allele was described as interacting with Ga1 alleles--Ga9 pollen had a competitive advantage over ga9 pollen on silks carrying the Ga1-s allele.

In conjunction with studies on cross-sterility in popcorn, we made several tests designed to place Ga9 relative to other chromosome 4 loci. su is in the short arm but very close to the centromere, and 30 units to the right of su would place Ga9 near position 101 on the long arm. C2 has been placed at position 123 and might reasonably be expected to show linkage with Ga9. Pollen from ga1 Su Ga9 C2/ga1 su ga9 c2 plants was used to pollinate ears homozygous Ga1-s su ga9 c2 and ears homozygous ga1 su ga9 c2. Since Ga9 pollen has a competitive advantage over ga9 on Ga1-s Ga1-s silks, crosses to this tester gave a reduced frequency of sugary kernels, 5504 Su:1647 su (23.0% su). Assuming no ga9 gametes functioned, 23.0 is a measure of the distance between su and Ga9. Ga9 pollen does not have a competitive advantage on ga1 ga1 silks, and the crosses to this tester did not give a reduced frequency of sugary kernels, 753 Su:956 su (55.9% su). The difference in frequency of sugary kernels on the two testers verifies the presence of a segregating Ga factor in the test stock.

The aleurone pigmentation intensity was quite variable in the above crosses, and only the non-sugary kernels could be classified for C2. The frequency of c2 kernels in crosses to the Ga1-s Ga1-s tester was 46.9% (2534/5404) and in crosses to the ga1 ga1 tester was 53.0% (399/753). The frequency of c2 kernels was slightly less on the Ga1-s Ga1-s tester, but the Ga9 and C2 loci assorted nearly independently.

Three chromosome interchange stocks with breakpoints at 4 cent, 4L.30, and 4L.63 were crossed to a Ga9 stock, and the plants heterozygous for the interchange were used as males in crosses to plants homozygous Ga1-s ga9: Ga1-s N ga9 x ga1 T ga9/ga1 N Ga9. The ears on plants from these crosses were scored for ovule abortion (semi-sterility). The percent semi-sterile ears (T ga9 crossovers) for each interchange was: 4 cent - 23.1%, 4L.30 - 26.6%, and 4L.63 - 45.7%. The distal breakpoints were less closely linked with the Ga factor than the centromere breakpoint.

Jimenez and Nelson hypothesized Ga9 on the basis of isolation of ga1 ga9 gametes from Ga1-s ga9/ga1 Ga9 heterozygotes. Because of our failure to place Ga9 on the long arm of chromosome 4, a retest was made for the occurrence of ga1 ga9 gametes in the above heterozygote. Plants from the cross Ga1-s Su ga9/ga1 Su Ga9 x ga1 su ga9 were selfed and test crossed on Ga1-s su/ga1 su ears, essentially the same test made by Jimenez and Nelson. Since ga1 and ga9 assort independently, 1/4 of the gametes from the heterozygote in the above cross would be expected to be ga1 Su ga9 crossovers, which when selfed would give ears with 25% sugary kernels and when test crossed would give ears with 50% sugary kernels. The parental and all other crossover classes would give a reduced frequency of sugary kernels on either or both the selfs and test crosses. Forty-four plants were selfed and test crossed and none gave the sugary segregations expected from a ga1 ga9 gamete.

The data from our tests have failed to verify the Ga9 locus on the long arm of chromosome 4. All our data are consistent with the interpretation that the Ga action in the variety White Rice is due to a Ga1 locus allele that has action in

the pollen but not in the silks. Such action is essentially that of the cross-neutral allele, Ga1. Ga1 Ga1 silks do not give a competitive advantage to either Ga1-s or Ga1 pollen over ga1 pollen, but Ga1 pollen has a competitive advantage over ga1 pollen on Ga1-s Ga1-s silks.

R. B. Ashman

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Instituto Fitotecnico de Santa Catalina

Relative DNA content in isogenic lines of maize in their own cytoplasm and in annual teosinte cytoplasm

Microspectrophotometric measurements of DNA were made in the interphase nucleus of root-tip cells and interphase nucleus of tapetum cells in isogenic lines of maize (Zea mays L. genotype), in different cytoplasms (Zea mays L. and Euchlaena mexicana Schrad. cytoplasms). For the interphase nucleus of root-tip cells, Zea mays genotype in its own cytoplasm has 33.21 A.U. of DNA content (average of 42 individuals), and in annual teosinte cytoplasm has 35.55 A.U. of DNA content (average of 48 individuals). These results show no significant differences between cytoplasms. In the interphase nucleus of tapetum cells, Zea mays genotype in its own cytoplasm has 27.82 A.U. of DNA content (average of 83 individuals) and Zea mays nucleus in annual teosinte cytoplasm has DNA content of 17.82 A.U. (average of 67 individuals). Significant differences between cytoplasms were found ($P > 0.01$). According to our results we may conclude that Euchlaena mexicana cytoplasm changes the DNA content in the nucleus of tapetum cells, but not in the nucleus of root-tip cells.

Ida Graciela Palacios

Cytogenetic studies on Zea diploperennis

Zea diploperennis Iltis, Doebley and Guzmán is a new species of the Maydeae tribe which has 2n = 20 chromosome number. The meiotic configuration shows either 10 bivalent chromosomes or 9 bivalent + 2 monovalent chromosomes. In addition there has been found a Zea diploperennis plant with 2n = 20 + 1 chromosomes. Apparently this extra chromosome is a B chromosome and according to Mangelsdorf (personal communication) it may be a plant of Zea diploperennis with introgression of Zea mays.

The length of the chromosomes (Fig. 1) in the state of intermediate pachynema is as follows:

Chromosome	Relative lengths (μ)	Ratio of arms (L/S)
1	107	1.07
2	107	1.11
3	101.3	1.27
4	95	1.62
5	87	--
6	63.6	2.78
7	67.6	2.18
8	64.9	4
9	62.2	1.41
10	50.6	5.66
Extra (possible B) chromosome	15.4	

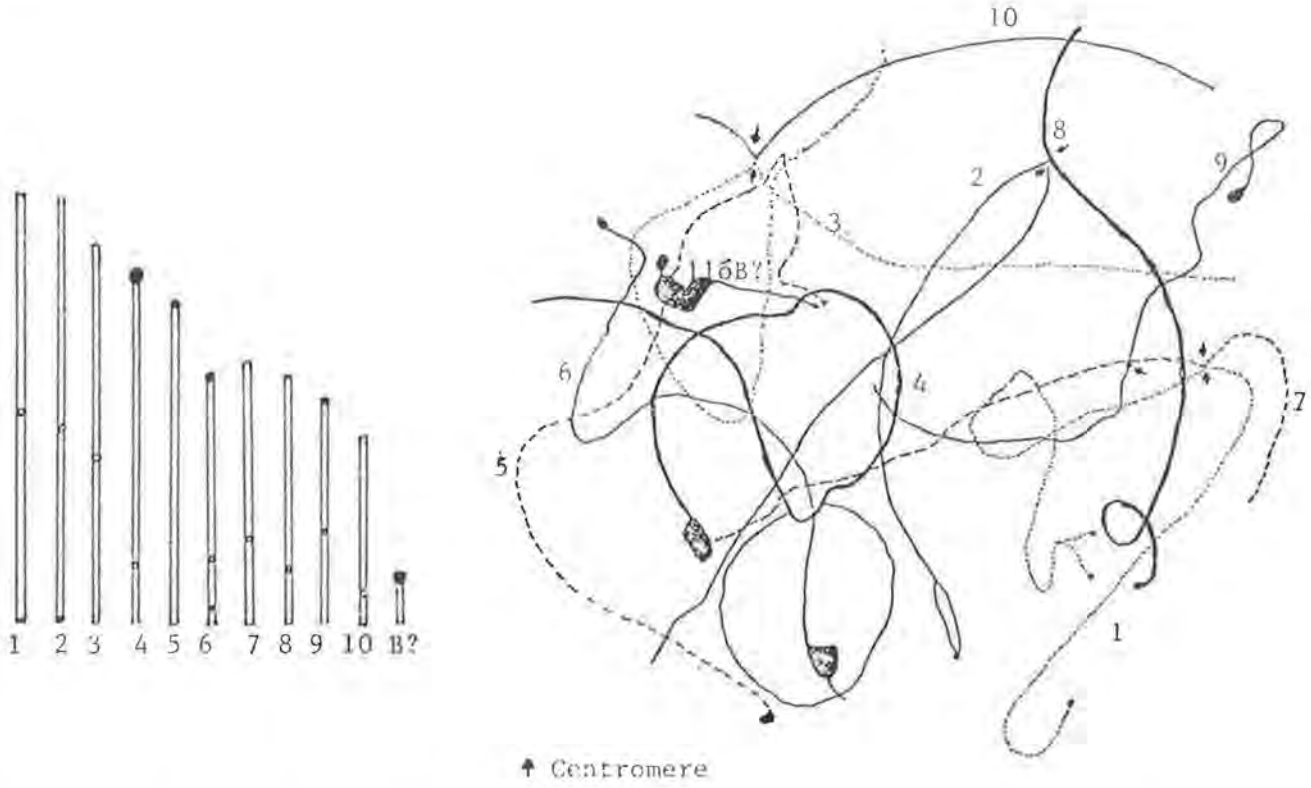


Fig. 1. Diagram of Zea diploperennis chromosomes showing relative lengths, centromeres and knob positions.

Zea diploperennis is characterized by very small terminal knobs in chromosomes 1, 2 and 6; medium size terminal knobs in chromosomes 5, 8 and 9, a very large one in both chromosome 4 and the extra chromosome or possible B chromosome. It does not have knobs in chromosomes 3, 7 and 10.

In 3% of the cells, the nucleolus is detached from its organizer either in advanced pachynema, diplonema and diakinesis. In that case the organizer begins to form one or more additional nucleoli. This phenomenon has been previously observed by the author in Zea perennis x Zea mays hybrids.

María del Carmen Molina

A new hybrid between Zea diploperennis and Zea perennis

In the Instituto Fitotécnico de Santa Catalina a new hybrid, Zea diploperennis (2n = 20) x Zea perennis (2n = 40) with 2n = 40 was obtained. When Zea diploperennis is used as female hybrids are easy to get. In that case near 60% of the grains are hybrid, with 90% fertility. In reciprocal crosses, using Zea perennis as female the results were negative in most cases, since just one hybrid grain was obtained. Plants originating from the cross Zea diploperennis x Zea perennis are either semicreeping or erect, have a strong root system and short, thick rhizomes and look very vigorous. A mean of 25 tillers per plant 3 months from planting was found. The only plant from the reciprocal cross is more erect with leaves tending to roll. This leaf character is not found in the parent species. The differences between reciprocal crosses may be due to either cytoplasmic interactions or differential gametic viability.

María del Carmen Molina

Effects of aspartate derived amino acids on floury-a maize embryos

Embryo growth inhibition by certain combinations of aspartate derived amino acids has been reported for several cereal species (C. E. Green and R. L. Phillips, Crop Sci. 14:827, 1974). Thus, the embryo growth of normal maize is severely inhibited in a medium containing lysine plus threonine (LT) at 1 mM concentration (Green and Donovan, Crop Sci. 20:358, 1980). Embryos and callus of mutant lines of maize, such as o2 and su1, are an exception to the rule (Ciampi and DaSilva, Ciencia e Cultura, 29:701, 1977, and Sysoev et al., Fiz. Biok. Kult. Rast. 11:318, 1979). In addition to such mutants, we present here evidence of the lack of inhibition by LT on excised mature embryos of the fl1-a high quality protein maize.

Simultaneous addition to the culture medium of LT 1 mM is not enough to block the normal growth and development of excised mature fl1-a embryos. Increasing the concentration of amino acids to 2.5 mM resulted in growth inhibition which averaged 50% reduction in relation to the control (Table 1). The maximum inhibition observed was in the root length either at 1 mM or 2.5 mM of LT in the medium. Neither amino acids alone nor other combinations caused embryo growth inhibition.

Table 1. LT growth inhibition: % of inhibition in respect to the control (without amino acids)

Parameter	LT 1 mM	LT 2.5 mM
Primary root length	35.69	87.13
Shoot length	17.78	57.58
Seedling fresh weight	17.69	47.71
Roots fresh weight	10.00	72.78
Shoots fresh weight	9.52	57.14
Seedling dry weight	6.67	40.00
Roots dry weight	9.50	50.00
Shoots dry weight	8.34	34.00

The growth inhibition observed in the fl1-a embryos is strongly different from the normal-embryo one. Thus, we suppose that either (1) an internal metabolic alteration of the embryo due to an increasing content of free amino acids and/or methionine, not due to a direct effect of the fl1-a gene, or (2) a desensitization of the aspartokinase enzyme to its specific modulator lysine due to a direct effect of the fl1-a gene, could explain the differences.

The accumulated evidence up to now about the way of action of the high quality protein maize mutants gives more weight to the first hypothesis than the second.

Although the finding of an inbred normal maize line with less sensitivity to LT inhibition (see this MNL, below) shows that the presence of floury or opaque mutant genes in the background is not strictly necessary for obtaining partial desensitization to the LT inhibition, new proofs from our laboratory show that changes in the sensitivity of homoserine dehydrogenase enzyme to its specific inhibitor, threonine, could play a more important role than the previously suspected differences between normal and mutant behavior (Rapela, submitted to Experientia).

Nevertheless, whatever be the explanation, the lack of whole inhibition on the growth and development of fl1-a embryos may be converted as a useful tool for isolating ones growing on these selective culture mediums.

Miguel Angel Rapela

Suggesting a new use of LT inhibition

A normal inbred line of maize, BP, partially insensitive to lysine plus threonine (LT) embryo growth inhibition, was found among several inbred lines of the Instituto Fitotécnico de Santa Catalina. The kernel of the BP lines has a higher lysine content than the common normal lines and has a high level of free amino acids (Magoja, personal communication). This high level of free amino acids and also probably high level of methionine could reverse "in vivo" the external LT growth inhibition. Another explanation rests on the fact that the BP embryo could have a particular amino acid uptake; that is to say a slow uptake of LT. But we think that is not the case. Probably the high free amino acid level is correlated with a high free methionine level. This would be possible if the biosynthesis rate of each amino acid is not higher than the biosynthesis rate of the other amino acids, like the case of free lysine in the o2 kernel (Chibber et al., Cereal Chem. 54:558, 1977).

If this is true, the LT selective method would have another use in the isolating and screening of free amino acid overproducer inbred lines and segregants.

Miguel Angel Rapela

Isolating LT insensitive normal maize embryos: an induction-selection model

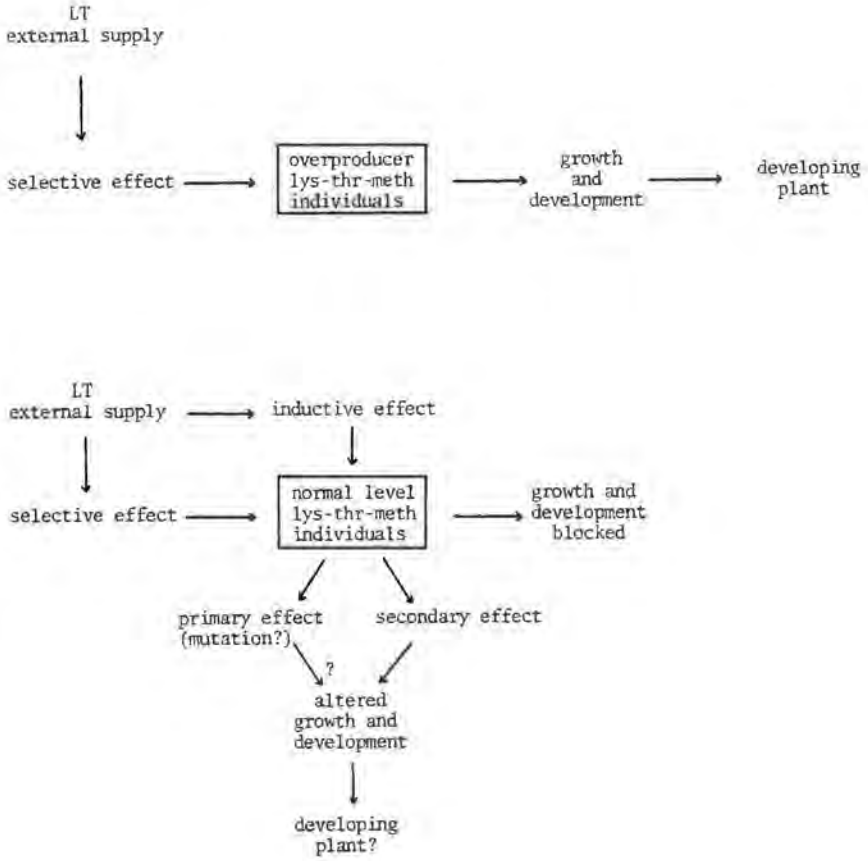
In our screening of more than 150 embryos of the inbred normal line of maize BP, it was possible to isolate 2 wholly insensitive to cumulative LT 2.5 mM growth inhibition. The embryos were submitted to two inhibitory culture cycles, 10 days each, and then were transplanted to an aerated sterilized organic culture medium without asepsis. The first inhibitory cycle was carried out in total darkness at 30 C, and the second was carried out with a photoperiod of approximately 12 hours, also at 30 C. One of the isolated embryos (mutant?) died in the second inhibitory culture cycle, and the other died after 10 days of culturing in the organic unaseptic medium. This is another case in which the desirable isolated plant is not capable of completing its whole life cycle. The results obtained by us were less successful than those of Hibberd et al. (Planta, 148:183, 1980), since these authors used the isolated callus technique and then by tissue redifferentiation were able to obtain developing, although infertile, plants.

It is evident that in addition to the selective (selective?) effect the LT method causes several unexpected effects that alter normal plant metabolism. We call the selective effect the primary LT effect, and the metabolic alterations the secondary LT effects.

In our case, the BP line has more than 30 years of inbreeding, is a stable line, and no apparent mutations have been found (Magoja, personal communication). The isolated possible mutants were morphologically different from "normal" counterparts; both possible mutants had root and shoot lengths similar to normal counterparts growing in control mediums (without amino acids); both had long coleoptiles; both were thinner than normal counterparts and less green, and none of them showed the typical swollen roots caused by LT inhibition.

So, it is clear that these isolated seedlings were not BP seedlings with less sensitivity to the LT inhibition and they could have been possible BP mutants. Thus, the striking point to discuss is how these possible mutants appeared provided the mutational stability of the BP line. The only logical answer is to think that an external effect was responsible for the differences and not that the differences (genetic or not) could appear in the presence of the external effect. In other words, we suggest that in certain cases the LT effect is an inductive means of aspartate derived amino acid overproducer individuals rather than a means to select them. The term inductive is not used here as synonymous to mutagenic in the strict sense of the word. The inductive effect (= LT primary growth inhibitory effect) would be the result of an "external pressure" that could affect certain genomal places or produce epigenetic changes.

Obviously, this is not the case for the natural overproducers of essential amino acids, because such individuals do not show inhibition with the LT effect and this method is only selective on them. But the most exciting fact is that these individuals grow normally to physiological maturity (Rapela, unpublished results). A whole view of the problem can be seen as an induction-selection model:



The inductive LT hypothesis does not necessarily involve that the secondary effect always escorts the primary effect. Although up to now there is no evidence of the dissociation between primary and secondary effects, there is sufficient evidence that secondary effects do not act in the same way on all genetic backgrounds (compare Hibberd's results and this). So, the successful possibility would be in the search of a genetic material stable to the secondary LT effect but inducible by the primary LT effect.

Miguel Angel Rapela

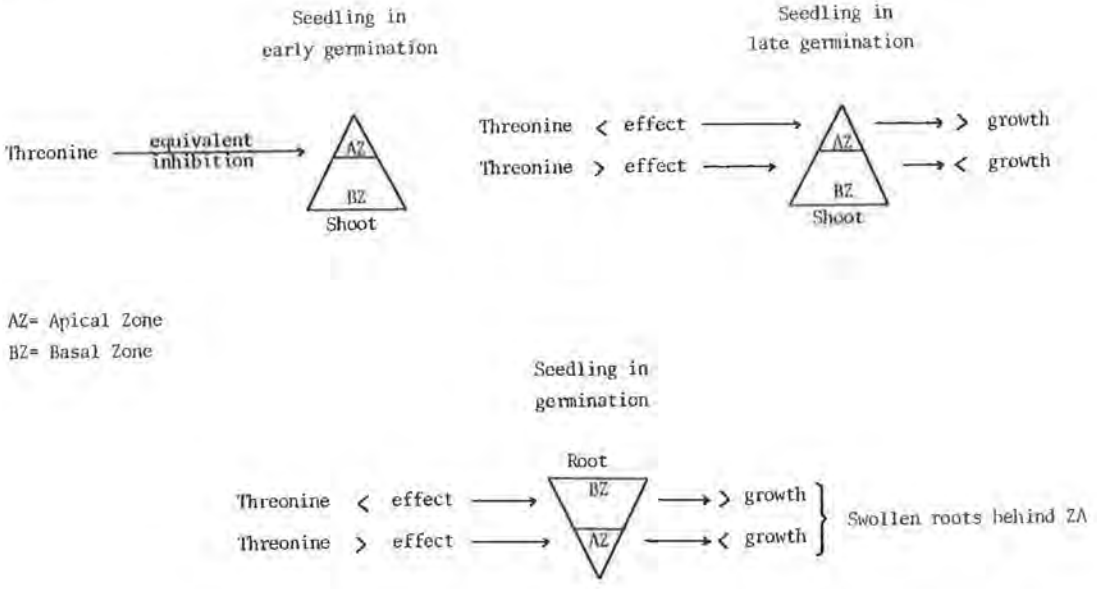
Threonine inhibitory root growth effects: encircling the problem and a new point of discussion

In our studies on the effect of aspartate derived amino acids on the growth of excised mature embryos of normal lines of maize, we have observed that threonine alone either at 1 mM or 2.5 mM in the medium caused slight inhibition of root growth especially when such growth was determined by length. Reduced root growth by a threonine effect was observed previously by Green and Donovan (Crop Sci. 20: 358, 1980) and our results confirm this report. The threonine effect on root growth was not observed in fl1-a seedlings, and this fact was the basis of our

hypothesis suggesting that the differences between the behavior of mutant and normal embryos under LT inhibition could be located at the level of homoserine dehydrogenase enzyme (Rapela, 1980, submitted to Experientia).

The slight growth inhibitory effect of threonine was observed by us in roots of several seedlings of inbred lines and hybrids of maize and also in the BP inbred line (see this MNL, above). Since this line has less sensitivity to LT inhibition, it was a good material for studying the effect of such amino acids because BP embryos grow and develop in these inhibitory mediums. Confirming Green and Donovan's report, the LT inhibitory effect was much more marked in the root zone than in the shoot zone. These differences could be explained if root and shoot zones differ in the rate of translocation of the amino acids or differ in the sensitivity of the regulator enzymes to their specific inhibitors. The first point remains to be studied, but the second one is very interesting to focus.

Two enzymes are implicated in the flow regulation of aspartate derived amino acids: aspartokinase and homoserine dehydrogenase. Between both, homoserine has unusual properties and characteristics and allows some physiological and genetic speculations about its regulation. Thus, based on the findings of Bryan's group (Biochim. Biophys. Acta 171:205, 1969; Plant Physiol. 55:991, 1975 and 55:999, 1975) about the changes in the regulation of homoserine dehydrogenase during growth of maize, we attempt to give an extension of these ideas applied to the behavior of a maize seedling growing in an inhibitory LT medium. This extension is based on features of the spatial variation of sensitivity of the homoserine dehydrogenase to threonine inhibition in roots, as well as spatial and temporal variation in shoots. Since lysine alone did not have visible inhibitory effects on root and shoot growths, this extension can be applied to the conjunct LT inhibition:



As we can see in the figure, the root zone would be much more affected than the shoot zone by LT inhibition. The maximum inhibition is located in the apical root zone, and the lowest in the basal root zone. Thus, the lengthening of roots would be strikingly inhibited while the weight increase of roots would be less inhibited.

The cumulative LT inhibition is certainly the external cause of the lack of embryo growth. But we suggest that threonine alone is responsible for the unlike root-shoot behavior under LT inhibition, despite the aforementioned translocating problems. The unlike root-shoot behavior also appears in fl1-a seedlings (see Table 1 in this MNL, above), and we think that it occurs the same way. This fact does not invalidate the supposition of differences in homoserine dehydrogenase, since such enzyme probably differs more in the high-low sensitivity than in the whole sensitivity-insensitivity to the threonine effect.

The use of slight threonine root inhibition for isolating possible overproducer lysine-threonine-methionine individuals is very attractive but very difficult to put into practice. The degree of difference between root inhibition and no inhibition is low. So, this method could never replace the LT selection method, but it would be very important for isolating individuals with homoserine dehydrogenase less sensitive to threonine.

Miguel Angel Rapela

Behavior of the nuclear elements in Zea mays

Material: Line X - Genotype C*-IE7002 A1 A2 C R Pr B Pl homozygous (#1877 Dr. Randolph, 1933), phenotype A C R Pr B Pl; Line Y - Genotype A1 A2 C R Pr homozygous (originating from the cross between c-tester and gl ij tester from Cornell University, 1934), phenotype A C R Pr.

Operation 1: (Line X x Line Y) x Line Y. F1 Phenotype A C R Pr B Pl; BC1 40 progenies, grains Pr = 10084, Pr dilute = 3179, colorless = 256; total = 13519; colorless grains = 1.8%. The percentage of variability of colorless grains between progenies was very small since 50% of the progenies fell within 1 to 2% colorless grains. The amplitude for colorless grains fell between 0.5 and 4%. The mean is 1.8%.

Interpretation: Mendelian interpretation is possible due to the homogeneity of the segregation among 40 BC1 progenies. The gene C*-IE7002 of Line Y with activators would produce free replicates (amplification) that would inhibit the aleurone color. Line X would carry the genes E1 E2 E3 E4 E5 besides the genes A1 A2 C R Pr B Pl C*-IE7002, each of them (E*) would degrade the free replicates of the gene C*-IE7002. The operations and experimental results with the genotypes previously mentioned are:

C*-IE7002 E1 E2 E3 E4 E5 A1 A2 C R Pr B Pl x + e1 e2 e3 e4 e5 A1 A2 C R Pr

Phenotype = A C R Pr B Pl by degradation of the replicates C*-IE7002

Phenotype = A C R Pr

F1 = C*IE7002 + E1 e1 E2 e2 E3 e3 E4 e4 E5 e5 A1 A1 A2 A2 C C R R B B Pl Pl

Phenotype = A C R Pr B Pl

All grains have aleurone color because of degradations of the replicates C*-IE7002.

Previously mentioned BC1 will segregate 1/2 C*-IE7002 +, and only 1/32 will carry genotype e1 e1 e2 e2 e3 e3 e4 e4 e5 e5, which do not degrade the replicate C*-IE7002 and for that reason will segregate 1/2 x 1/32 = 1/56% colorless grains according to experimental data.

Operation 2: From 256 grains colorless aleurone (Operation 1) were obtained 134 plants which were self-fertilized. Segregation for colorless grains between progenies from S1 showed a very large variability which is indicated in the following table:

51 progenies did not segregate colorless grains
15 progenies segregated 1 to 10% colorless
27 progenies segregated 11 to 20% colorless
13 progenies segregated 21 to 30% colorless
14 progenies segregated 31 to 40% colorless
4 progenies segregated 41 to 50% colorless
4 progenies segregated 51 to 60% colorless
2 progenies segregated 61 to 70% colorless
0 progenies segregated 71 to 80% colorless
1 progeny segregated 81 to 90% colorless
0 progenies segregated 91 to 100% colorless

All grains analyzed from the segregating progenies gave the following results: Pr = 8843, Pr dilute = 8307 and colorless = 5081. Besides the large variability in the segregations of colorless grains between progenies were produced spurious segregations such as large colorless areas in ears alternating with colored areas; variable segregations of colorless grains according to considered area; big glumes, viviparity, big grains and grains more reduced than brittle, scattered anthocyanic spots in the stalk and anthers; stiff leaf with distic position, zig-zag stalk and male sterile.

Interpretation: Perhaps free replicates of the C*-IE7002 gene in synaptic labile position (episomic) with diverse loci would produce spurious segregations.

Operation 3: Colorless grains from 51 progenies (5081 grains) in Operation 2 were self-fertilized and the 52 ears with colorless grains were crossed x Line Y, and then were self-fertilized. The F1 had all colorless grains with good expression. In F2 was obtained great variability in the segregation and expression of aleurone color; the dominant character of the aleurone color in F1 was changed to recessive in F2.

Interpretation: In S2 the dominant free elements for colorless aleurone would stabilize in some progenies because of allelic synaptic phenomena. In the F1 of the cross between the previously mentioned S2 (colorless grains) x Line Y, the colorless character is dominant, but in F2 new synaptic phenomena are produced along the Line Y loci with free C*-IE7002 elements. The new synaptic phenomena would change dominant inhibitor character of the aleurone color to recessive.

Operation 4: (Line X x Line Y) x Line Y (BC1) gave colorless = 6, Pr dilute = 65, Pr = 205. From the colorless class, sub-line (a) gave in S1 colorless = 27, Pr = 250; in S2 from the colorless, colorless = 195, Pr = 75; in S3 from the colorless, colorless = 133, Pr = 42 (good expression). From the BC1 Pr class, sub-line (b) gave in S1 colorless = 69, Pr = 273; in S2 from the colorless, 5 ears gave all grains colorless and 5 ears segr. 3/4 colorless:1/4 colored (good expression).

Interpretation: One among 200 backcrosses has a free C*-IE7002 replicate able to produce a permanent chromosomal insertion or episomic transitionary state. The above phenomenon is produced in sub-lines (a) and (b) independently and both lines answer to mendelian monogenic segregation of the dominant inhibitory character of the aleurone color.

Luis Mazoti

Inheritance of some characters in maize-perennial teosinte hybrids

Crosses between Gaspé line (Zea mays L.) and perennial teosinte (Euchlaena perennis Hitch.) were performed (MNL 52:37, 1978), showing high genetic affinity between the two species according to the fertility of the cross (82.5%).

The parents differ from each other in their photoperiodic response, since Gaspé blooms on the 28th day after emergence and perennial teosinte after 193 days, thus indicating a strong response to photoperiod. The hybrid F1 plants bloomed at 61.6 ± 7.2 days, showing a partial dominance of the earliness of Gaspé over its relative; furthermore the low variability is an index of uniform behavior of the F1 individuals, with low environmental modification.

The average evolutive cycle for the F2 individuals was 90.4 days, somewhat superior to the F1 but always under the average of its parents (110 days). The heritability of this character is high (0.88). On the other hand there was no recovery of the paternal extremes in the F2 population (245 plants) analyzed, indicating that the character is conditioned by several factors. The minimum number of genes that would determine earliness would be nine.

Other characters studied (pollen fertility, number of tillers per plant, and days to silking) were related among themselves and with days to blooming of the tassel (Figure 1). It is important to point out the inverse correlation, contrary to what was expected, between the number of tillers per plant and days to tassel. The relations among all the characters are highly significant, demonstrating that the earliest plants and those which have a higher number of tillers are more fertile.

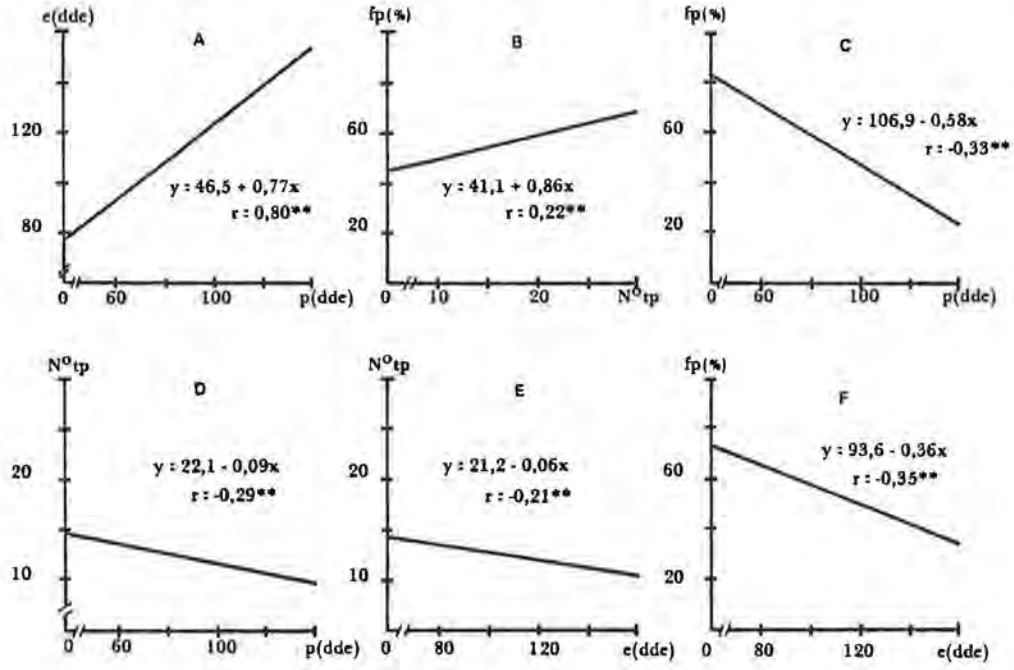


Fig. 1. Correlation between some characters of F2 plants. A--relationship between days to silking (e) and days to tassel (p). B--relationship between pollen fertility (fp) and number of tillers per plant (tp). C--relationship between pollen fertility (fp) and days to tassel (p). D--relationship between number of tillers per plant (tp) and days to tassel (p). E--relationship between number of tillers per plant (tp) and days to silking (e). F--relationship between pollen fertility (fp) and days to silking (e). All correlation coefficients (r) significant at 1% level. The mensurations were made on 245 plants.

As regards the character of the inflorescence, distichous ear is completely dominant over polystichous ear and pistillate spikelets unpaired are dominant over paired. Hence, there is a different genetic behavior between the annual teosintes and the perennial, since E. perennis would have a different genetic action for its specific characters with respect to annual teosinte, also showing a high prepotency in the transmission of its characters in the hybrids and descendants.

Another important aspect was the extraordinary hybrid vigor, not only in the F1 individuals but also in the F2. The high heterosis of these hybrids was quantified by comparing the characters of the F1 with those of its parents (see Table 1).

Table 1. Heterosis of F1 plants (E. perennis x Gaspé). FC/E--number of fruit cases per ear; PN--number of productive nodes; EUN--number of ears in the uppermost node; E/T--number of ears per tiller; E/PN--number of ears per productive node.

	E. perennis	Gaspé	F1	Difference	
	(a)	(b)	(c)	(c-a)	(c-b)
FC/E	5.1	-	9.3	+ 4.2	-
PN	2.8	1.6	4.7	+ 1.9	+ 3.1
EUN	1.0	1.0	4.8	+ 3.8	+ 3.8
E/T	2.9	1.6	25.7	+ 22.8	+ 24.1
E/PN	1.0	1.0	5.5	+ 4.5	+ 4.5

The hybrids have a higher number of productive nodes, a higher number of ears in the uppermost node, a higher number of ears per tiller and a higher number of fruit cases per ear than the parents.

Jorge Luis Magoja and Gabriela Nora Benito

Inheritance of endosperm storage proteins in reciprocal hybrids between maize and perennial teosinte

The protein patterns of Euchlaena perennis Hitch., Gaspé line (maize) and its reciprocal F1 and F2 (MNL 52:37, 1978) were studied. It was also considered interesting to compare them with Tripsacum dactyloides.

Endosperm proteins were fractioned according to the method of Landry-Moureaux (1970). When the proteins of the maize endosperm, of E. perennis and Tripsacum are fractioned, the protein patterns which are obtained differ (Table 1). In the

Table 1. Endosperm protein pattern of Gaspé (Gs), Euchlaena perennis (Ep) and Tripsacum dactyloides (Td). SS--saline (albumins, globulins); Z--zein; G1--glutelin-1; G2--glutelin-2; G3--glutelin-3.

Fraction	Soluble nitrogen (percent of total)		
	Gs	Ep	Td
SS	5.3	1.8	1.8
Z	53.1	57.1	55.2
G1	9.8	20.7	26.9
G2	6.9	3.3	5.1
G3	14.1	9.2	9.7
protein %	12.5	21.0	27.4

close relatives of maize albumins and globulins are very low. This coincides with the results found by J. W. Paulis and J. S. Wall (J. Agric. Food Chem. 25:267-270, 1977), who ascribe these differences to the small size of the germs of Euchlaena and Tripsacum. The results obtained in our work, performed on endosperm, show that there is no influence of the germ size; this smaller ratio of albumins and globulins must be the result of a specific differentiation as a consequence of genetic differences among the species.

Another differential characteristic of the protein patterns studied is the high ratio of glutelin-1 in E. perennis and Tripsacum. It seems that if the ratio of glutelin-1 were a specific character, E. perennis would be genetically closer to Tripsacum than the annual species of teosinte.

Finally, other differences among the protein patterns of the three species are the different ratio of glutelin-3 (less in E. perennis and Tripsacum than in maize).

The protein patterns of the F1 endosperms obtained by the crossing of Gaspé and perennial teosinte differ according to the way of crossing (Table 2). The protein pattern found for the first F1 (Gaspé x E. perennis) shows a significant modification with respect to the maize that acted as mother. This would explain the small

Table 2. Endosperm protein pattern of Gaspé (Gs), Euchlaena perennis (Ep) and their F1 and F2 reciprocal crosses. SS--saline (albumins, globulins); Z--zein; G1--glutelin-1; G2--glutelin-2; G3--glutelin-3.

Fraction	Gs	Ep	Gs x Ep	Ep x Gs	Gs x Ep F2	Ep x Gs F2
SS	5.3	1.8	11.7	3.8	5.0	4.3
Z	53.1	57.1	46.6	63.9	47.7	44.6
G1	9.8	20.7	8.5	10.9	25.3	22.4
G2	6.9	3.3	11.3	5.1	9.5	9.9
G3	14.1	9.2	14.4	7.1	11.3	10.3
protein %	12.5	21.0	15.8	21.2	18.2	19.1

viability of the grains which was indicated earlier (MNL 52:37, 1978). In addition to the characteristics pointed out, the levels of glutelin-1 and glutelin-3 are similar to those of the mother line. The reciprocal F1 (E. perennis x Gaspé) presents differential peculiarities in its protein pattern. It appears that in the cross of Gaspé x E. perennis, Zea arises as dominant for the ratio of glutelin-1 and 3. In the reciprocal E. perennis x Gaspé, Zea also appears as dominant for glutelin-1, in spite of the fact that the ratio of genomes in the endosperm is 4 to 1 in favor of Euchlaena. The protein patterns of the reciprocal F2 endosperms are very similar among themselves.

Although there is no evidence on the chromosomal behavior of both species as regards the numeric participation in the F1 gametes, it may be considered that certain maize chromosomes that carry regulatory genes which would control the relative level of the glutelin-1 fraction would be eliminated by the preferential formation of gametes. This fact would explain why the character of Euchlaena (high glutelin-1) is restored in the F2 endosperms in spite of being recessive in the reciprocal F1.

Angel Alberto Nivio and Jorge Luis Magoja

Influence of perennial teosinte germplasm on polypeptidic pattern of maize endosperm proteins

The molecular patterns of zein and glutelin-1 obtained according to Landry-Moureaux (1970) were studied in Gaspé line, Euchlaena perennis, their reciprocal F1 and F2 and Tripsacum dactyloides. Patterns of the proteins of the defatted endosperm were obtained by polyacrylamide gel electrophoresis, using aluminum lactate buffer pH 3.1, and gels 8M in urea (see Figures 1 and 2).

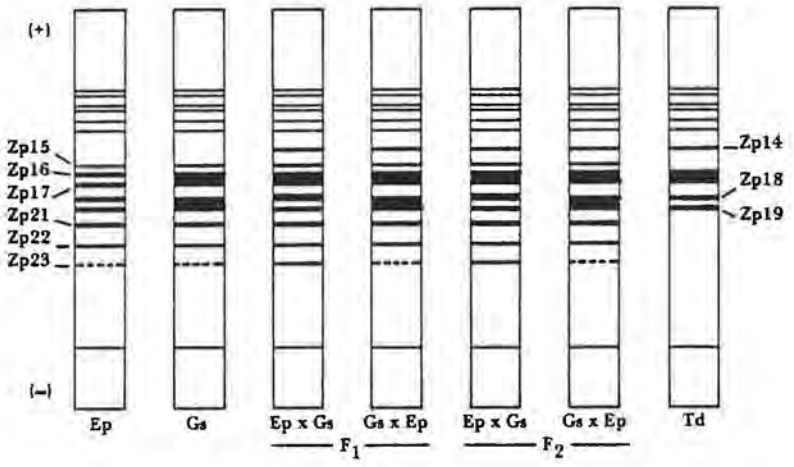


Fig. 1. Polyacrylamide gel electrophoretic pattern of zein polypeptides (Zp) in E. perennis (Ep), Gaspé (Gs), their reciprocal F1 and F2, and Tripsacum dactyloides (Td).

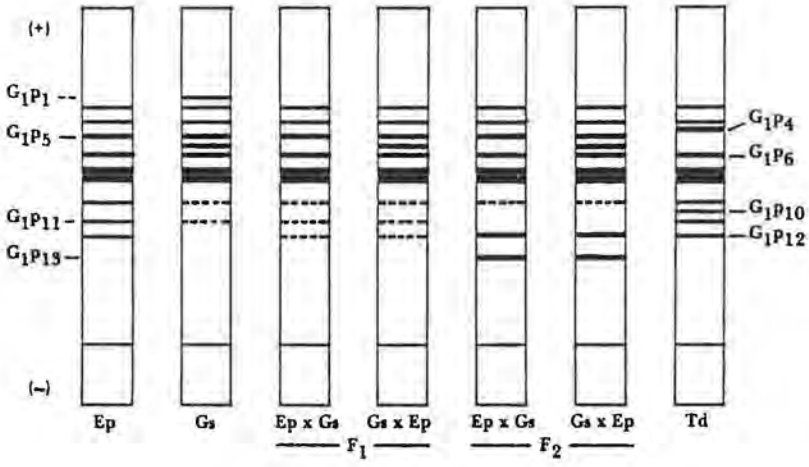


Fig. 2. Polyacrylamide gel electrophoretic pattern of glutelin-1 polypeptides (Glp) in E. perennis (Ep), Gaspé (Gs), their reciprocal F1 and F2; and Tripsacum dactyloides (Td).

If we compare the zein polypeptidic pattern of maize with perennial teosinte and Tripsacum, the latter differs from the first two in the absence of the polypeptides of greater mobility. These results coincide with those obtained by J. W. Paulis and J. S. Wall (J. Agric. Food Chem. 25:267-270, 1977) and they indicate a greater phylogenetic distance between Tripsacum and maize than between maize and teosinte. The zein pattern of Gaspé is practically equal to that of Euchlaena. This great similarity could be indicative of the high genetic affinity between them. The patterns of zein in reciprocal F1 endosperms are very similar and the most noteworthy fact is the appearance of a new polypeptide (Zp 14) which was not found in any of its parents. However, this polypeptide is found in Tripsacum. The patterns of the reciprocal F2 endosperms are equal to those of the reciprocal F1 endosperms from which they derive.

The molecular patterns of Gaspé, Euchlaena and Tripsacum show some differences for glutelin-1. However, Gaspé resembles Euchlaena far more than Tripsacum. As with zein the reciprocal F1 endosperms show differences in their patterns according to the direction of the cross. The F2 reciprocals resemble those of the F1 from which they derive; moreover a new polypeptide (Glp 13) appears, which is not found in its parents.

It may be concluded that there is a cytoplasmic influence over the molecular patterns of the storage proteins in the offspring of Gaspé and Euchlaena. We may say that the cytoplasm of Euchlaena perennis shows an influence in the expression, at a molecular level, of some of the components of the storage proteins of the grains and, probably, over other characters in the hybrids of this species with maize.

When storage protein polypeptide patterns of maize are compared between Euchlaena perennis and Tripsacum, certain differences are evident although they cannot be indicated as being greater than those existing among different types of maize (Zea mays). However, the endosperm protein patterns (ratios between different types of proteins) are very constant and characteristic of the species, and for this reason we may primarily declare that the greater differentiation between Maydeae species, as regards grain storage proteins, is more due to the action of regulatory units controlling synthesis of the different proteins than to structural units coding the molecular components. In other words, it is probable that regulatory genes rather than structural genes have been differentiated between species in the control process of protein synthesis, since the evidence presented in the current paper and by other authors suggests a reasonable similarity between the taxa at a molecular level (protein polypeptidic components) and a greater differentiation in the ratios in which the storage proteins are found, as a consequence of a different control in their synthesis regulation.

Jorge Luis Magoja and Angel Alberto Nivio

Inheritance of modified endosperm structure in floury-a maize

By means of selection from the cross between floury-a and normal lines, it is possible to obtain a floury-a line with completely flint phenotype. Likewise among the offspring of other crosses later on, between lines carrying floury-a gene and normal lines, a relatively fast conversion to normal phenotype through selection was observed. This phenomenon led to the opinion that possibly the suppressor action on the floury-a phenotypic expression was conditioned by few genes.

The flint floury-a line has the floury nucleus of the kernel in greater proportion than the normal lines, however, all the periphery of the kernel has a thick portion of hard endosperm. Crosses between modified floury-a and normal lines were carried out, but only crosses with DY normal line are reported in this paper.

Ears with F2 kernels were obtained and parallel backcrosses were carried out with modified floury-a, with the purpose of studying the genetic condition of the floury-a phenotypic suppression.

The F2 grains and the backcrosses show endosperm structure segregation. The kernels have been visually classified in two types: (1) those of flint, hard structure, which are vitreous and translucent and are regarded as having normal phenotype, and (2) those of floury structure, which are soft and opaque, of a floury phenotype conditioned by the floury-a gene (recessive in two doses). In general the phenotypic expression of floury-a is good, not presenting major difficulties in the classification of floury and flint kernels.

The experimental results obtained from the first crossing (modified floury-a x normal DY) are indicated in Table 1. It may be observed that in the 15 ears analyzed the number of F2 kernels with flint phenotype differs significantly from the 3:1 ratio. The results show an evident excess of kernels with normal phenotype, which presupposes the phenotypic suppression of the floury-a gene.

Table 1. Cross 1 (modified floury-a x normal DY)

Pedigree	Obs.		Exp. (3:1)				Exp. (13:3)			
	Flint	Floury	Flint	Floury	χ^2	P	Flint	Floury	χ^2	P
77-07531(1)	118	20	103.5	34.5	8.1256	<0.01	112.1	25.9	1.6417	0.20-0.30
77-07531(2)	139	35	130.5	43.5	2.2145	0.10-0.20	141.4	32.6	0.2126	0.50-0.70
77-07531(3)	192	50	181.5	60.5	2.4297	0.10-0.20	196.6	45.4	0.5801	0.30-0.50
77-07531(4)	173	40	159.8	53.2	4.3958	0.02-0.05	173.1	39.9	0.0001	>0.99
77-07531(5)	104	21	93.8	31.2	4.4826	0.02-0.05	101.6	23.4	0.3118	0.50-0.70
77-07532(1)	174	27	150.8	50.2	14.3432	<0.01	163.3	37.7	3.7301	0.05-0.10
77-07532(2)	109	16	93.8	31.2	9.9226	<0.01	101.6	23.4	2.9047	0.05-0.10
77-07532(3)	186	41	170.3	56.7	5.8281	0.01-0.02	184.4	42.6	0.0705	0.70-0.80
77-07532(4)	107	21	96	32	5.0416	0.02-0.05	104	24	0.4615	0.30-0.50
77-7707(1)	185	39	168	56	6.8809	<0.01	182	42	0.2636	0.50-0.70
77-7708(1)	125	29	115.5	38.5	3.1254	0.05-0.10	125.1	28.9	0.0006	0.95-0.98
78-07503(1)	251	64	236.3	78.7	3.6834	0.05-0.10	255.9	59.1	0.5079	0.30-0.50
78-07503(2)	299	78	282.8	94.2	3.7356	0.05-0.10	306.3	70.7	0.9309	0.30-0.50
78-07503(3)	259	61	240	80	6.0166	0.01-0.02	260	60	0.0204	0.80-0.90
78-07503(4)	169	43	159	53	2.5156	0.10-0.20	172.3	39.7	0.3270	0.50-0.70

The segregation observed between flint and floury kernels suggests a 13 flint: 3 floury ratio. This type of segregation may be conditioned by a recessive suppressor in two doses, or by two complementary recessive genes dominating in two doses. The expected values were calculated both for a segregation of 3:1 and for one of 13:3. As may be seen in cross 1, the 13:3 ratio fits better than the 3:1 ratio, but also, in most cases, the hypothesis of a 3:1 segregation can not be accepted.

In order to establish whether the suppressor effect is conditioned by only one recessive gene in two doses, or by two complementary recessive genes dominating in two doses, the backcross of the F1 by the modified floury-a was carried out. If one were dealing with only one recessive gene in two doses, the backcross should show a proportion of 3 flint kernels to one floury kernel, whereas if it were due to two complementary recessive genes dominating in two doses the proportion would be 5 flint kernels for every 3 floury kernels. The experimental results strongly suggest that the nearest proportion is that of 5:3, with which the hypothesis of two complementary genes dominating in two doses is accepted (see Table 2).

Table 2. Backcross 1 (modified floury-a x normal DY) x modified floury-a

Pedigree	Obs. Flint	Obs. Floury	Exp. (5:3) Flint	Exp. (5:3) Floury	χ^2	P
78-07503 x -07549(1)	154	98	157.5	94.5	0.2073	0.50-0.70
78-07503 x -07549(2)	131	85	135	81	0.3160	0.50-0.70
78-07503 x -07550(1)	99	66	103.1	61.9	0.4400	0.50-0.70

Control experiments were carried out by crossing floury-a line with floury phenotype with DY normal line, and also backcrosses were made (see Tables 3 and 4). In these crosses the 3:1 ratio occurs invariably between F2 kernels and 1:1 ratio in the backcrosses, that is, the phenotypic expression of the floury-a gene in this genetic background is good and behaves as a recessive in two doses.

Table 3. Cross 2 (normal DY x floury-a)

Pedigree	Obs. Flint	Obs. Floury	Exp. (3:1) Flint	Exp. (3:1) Floury	χ^2	P	Exp. (13:3) Flint	Exp. (13:3) Floury	χ^2	P
76-7720(3)	135	52	140.3	46.7	0.7860	0.30-0.50	151.9	35.1	10.0700	<0.01
77-7720(5)	171	51	166.5	55.5	0.4864	0.30-0.50	180.4	41.6	2.5986	0.10-0.20
77-7721(1)	162	54	162	54	0.0000	1.00	175.5	40.5	7.0295	<0.01
77-7722(1)	275	96	278.3	92.7	0.1517	0.50-0.70	301.4	69.6	12.3662	<0.01
77-7722(2)	240	90	247.5	82.5	0.9090	0.30-0.50	268.1	61.9	15.7341	<0.01

Table 4. Backcross 2 (normal DY x floury-a) x floury-a

Pedigree	Obs. Flint	Obs. Floury	Exp. (1:1) Flint	Exp. (1:1) Floury	χ^2	P
76-7722 x -7554(1)	217	232	224.5	224.5	0.5011	0.30-0.50

The results suggest that the suppression of the floury-a expression in the material tested is conditioned by two complementary recessive genes dominating in two doses, which are referred to as suppressor-1 floury-a (sfa) and suppressor-2 floury-a (sfa2).

Jorge Luis Magoja

High-quality protein maize with normal genotype: changes in endosperm protein pattern

Earlier (MNL 52:37, 1978) it was reported that from the progenies of crosses between high-quality protein floury-a line and normal inbreds it was possible to isolate maizes with normal endosperm phenotype and genotype with high-quality protein. The kernels of the high lysine maizes with "normal genotype" have normal phenotype because their endosperms are vitreous and translucent, and are of the red flint type. The maizes also have "normal genotype" for they do not carry in their genetic background any floury mutant.

From ears selected with high lysine-tryptophan levels, the endosperm proteins were fractioned according to the Landry-Moureaux method and compared with normal inbreds; we found the following results:

Table 1. Endosperm protein pattern of normal inbred (DY) and high lysine "normal genotype" inbred (AL24). SS--saline (albumins, globulins); Z--zein; G1--glutelin-a; G2--glutelin-2; G3--glutelin-3.

	Soluble nitrogen (percent of total)	
Fraction	DY	AL24
SS	6.8	12.2
Z	51.7	35.7
G1	13.9	16.4
G2	12.5	9.9
G3	11.1	23.9
protein %	12.9	8.3
lysine (g/16g N)	1.9	3.5

If it is kept in mind that the primary effect of known mutants which condition high lysine is to repress the zein synthesis and to stimulate albumins, globulins and glutelin-3 synthesis, it was to be expected that the high lysine level of the "normal genotype" maizes would also be a consequence of the same phenomenon. In effect, high lysine and tryptophan levels are the consequence of a profound modification of the protein pattern compared with those of normal lines. Thus, these results suggest that the "normal genotype" represses the zein and stimulates the accumulation of saline fraction (albumins, globulins) and glutelin-3.

Recently we have obtained uniform inbred strains for the high lysine character. These lines were crossed with normal inbreds in order to establish the inheritance of this character.

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Selection for resistance to brown stripe downy mildew in maize-- study of original and improved populations in crosses

A maize cultivar 'Makki Safed-1' (MS1) suffered heavily due to an epiphytotic of brownstripe downy mildew during the kharif of 1975. The disease is caused by Sclerophthora rayasiae var. zeae Payak and Renfro (Phytopath. 57:394-397).

However, considerable variability was observed within the cultivar for the reaction to this disease. This cultivar was, therefore, subjected to mass selection before as well as after flowering. The original and improved version, MS1 (ms)C1, were evaluated in some cross combinations at Gurdaspur in a randomized block design with four replications. A plot consisted of two rows, each of 6 meters length. Row-to-row distance was 75 cm and plant-to-plant spacing was 25 cm. The experiment was planted in a sick plot created by putting on powdered infected leaf debris. Disease incidence was recorded on a 1-5 scale, which was adapted from Miller et al. (Pl. Dis. Reptr. 54:1134-1136, 1970). The grain yield performance and disease reaction were as follows:

Pedigree	Reaction to BSDM* (1-5)	Grain Yield (kg/ha)
MS1 (Original)	3.1	2731
MS1 (ms)C1	2.2	4103
(CM 400 x CM 300) x MS1 (Original)	2.0	4126
(CM 400 x CM 300) x MS1 (ms)C1	1.5	4253
H 301 x MS1 (Original)	2.4	2995
H 301 x MS1 (ms)C1	2.2	3185
(Syn P200 x Kisan) x MS1 (Original)	1.6	4485
(Syn P200 x Kisan) x MS1 (ms)C1	1.1	4774
Tuxpeno Planta Baja x MS1 (Original)	1.6	4311
Tuxpeno Planta Baja x MS1 (ms)C1	1.1	4667
C.D. at 5 percent	0.8	1063

*BSDM means brown stripe downy mildew and 1 means highly resistant and 5 highly susceptible.

The improved population was significantly better than the original population for reaction to brown stripe downy mildew. Better resistance to disease in the improved population was also evident in all the crosses. For grain yield also an appreciable gain is apparent in the crosses involving MS1 (ms)C1. The improved version has given consistently better yield performance in all the crosses.

The performance of crosses shows that the gain made in the population is at the genetic level and the superiority is transmitted to the crosses. Significant gains in the population in a cycle of mass selection indicate that inheritance of this disease may be largely under additive genetic control.

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Erratum

In the 1980 MNL 54:80-84, we (K. Shimamoto and O. Nelson) reported the translocation of various radioactive (^{14}C) compounds into seeds being grown in vitro. Table 1 (page 81) of that report gives erroneous estimates of the specific activity (cpm/nmol) of the labelled compounds in the growth medium. There is a constant error of 10^6. The correct specific activities (cpm/nmol) are sucrose, 3.8; fructose, 3.7 x 10^5; leucine, 1.1 x 10^5; phenylalanine, 9.6 x 10^5; proline, 5.7 x 10^5; adenine, 1.1 x 10^5; thymine, 1.1 x 10^5; thiamine, 3.9 x 10^4; nicotinic acid, 1.2 x 10^5.

Oliver Nelson

The mutants opaque-9 through opaque-13

There are numerous loci at which mutations condition an opaque phenotype. We report here five additional mutants that are not allelic to previously reported opaque mutants nor to each other. Four of these mutants were provided by Robert Brawn of Funk Seeds International and one by M. G. Neuffer of the University of Missouri. All five of these mutants are simple recessives. The mutants from Brawn, o9, o11, o12, and o13, are spontaneous in origin while o10 from Neuffer is a presumptive EMS-induced mutant.

opaque-9: From Brawn and formerly designated as ox-74120. The mutant kernels have fully opaque crowns which are light in color. There may be patches of corneous starch on the abgerminal side of the kernel or the entire base of the kernel may be corneous. There is frequently a cavity in the center of the kernel. Several other spontaneous mutants from Brawn are allelic to opaque-9. The dye-binding capacity of opaque-9 in the Udy test (a measure of the content of basic amino acids) is slightly higher than that of nonmutant kernels.

opaque-10: From Neuffer (E-1356) and formerly designated by us as ox-7747. This is a solid opaque which is phenotypically much like opaque-1. The dye-binding capacity is not higher than nonmutant kernels.

opaque-11: From Brawn and formerly designated as ox-7455. The mutant kernels are thin, somewhat shrunken, and have a greyish cast. There is usually a cavity in the center of the endosperm. The dye-binding capacity is high--equal to or greater than opaque-2.

opaque-12: From Brawn and formerly ox-7638. The mutant kernels are thin, variable in size, and are etched or scarred. On germination, the mutant kernels give rise to plants that are very chlorophyll-deficient. In some genetic backgrounds, these plants survive and develop good color as they become older, but they never become more than 75 cm tall. The mutant plants will shed pollen but don't often produce ears. The dye-binding capacity of mutant kernels is intermediate between nonmutant kernels and opaque-2 kernels. The amount of alcohol-soluble proteins is only slightly reduced in the mutant kernels as compared to nonmutant sibs.

opaque-13: From Brawn and formerly ox-7729. The mutant kernels are etched and may have a thin rim of corneous starch on the abgerminal side. The dye-binding capacity of the mutant kernels is only slightly greater than nonmutant kernels.

Seeds of these five mutants are being sent to the Maize Genetics Stock Center.

Oliver Nelson

A reexamination of the Aberrant Ratio phenomenon

The report of aberrant ratios for various marker genes in the advanced progenies of maize plants infected as seedlings with barley stripe mosaic virus (G. F. Sprague and H. H. McKinney, 1971, Genetics 67:533) has elicited considerable interest among geneticists. Attempts have been initiated in several laboratories to investigate the phenomenon further. In a recent paper, R. G. Samson et al. (1979, Genetics 92:1231) reported that the results of their investigations of a Sprague Aberrant Ratio (AR) A/a* stock [a stock supposedly homozygous dominant for all the aleurone factors other than A and in which sib matings in either direction between plants grown from colored seeds (presumed to be A/a) and plants from colorless seeds (presumed to be a/a) yielded an excess of colorless kernels over the 50% expected in such matings] suggested that such stocks might be heterozygous at another locus necessary for aleurone color. They presented no data verifying this hypothesis, however. Our data show by several types of evidence including direct tests of such stocks that two A/a* stocks are indeed heterozygous at other color factor loci. It should be noted that after the initial identification of an

aberrant ratio in a self-pollinated plant (e.g., an excess of colorless kernels in a plant of the presumed genotype A/a, A2/A2, C/C, C2/C2, R/R) Sprague and McKinney maintained the AR stocks by sib-matings between plants from colored kernels and plants from colorless kernels. For two other instances of AR, an A*/a stock [in which sib matings between plants grown from colored seeds (presumed to be A/a) and plants grown from colorless seeds (presumed to be a/a) yielded an excess of colored kernels over the 50 percent expected] and an Su/su* stock [in which sib matings between plants from Su kernels (Su/su) and those from su kernels (su/su) yielded an excess of sugary kernels], other explanations suggest themselves.

In 1977, we received from G. F. Sprague seeds of the cross, a-p/a x a/a [Sprague 1976 441(1) x 442(1)]. This stock gave aberrant ratios of colored (pale) to colorless (an excess of colorless) in sib-matings between plants from colored and plants from colorless seeds. Two types of crosses were made--sib-matings in both directions between plants from colored kernels and plants from colorless kernels and crosses in both directions between our W22 a tester and the plants from colored kernels. The purpose of these crosses was to verify the observations of Sprague and McKinney that (1) there was an excess of colorless kernels in crosses between plants from colored and colorless kernels from the cross of presumed A/a or (a-p/a) x presumed a/a regardless of the direction in which the cross is made; (2) one observes expected proportions (0.5) of colorless kernels when plants from colored kernels (from A/a x a/a) are crossed either as male or female by an a tester; (3) one can recover aberrant ratio stocks after such an outcross.

Table 1. The percentage of colorless kernels observed in various crosses involving Aberrant Ratio stocks

Year, row	Presumed Genotype	Source of Stock	Pollinations Made	Percent Colorless Kernels
1977, 17687-89	a-p/a	Sprague 1976 441(1) x 442(1) Colored (pale)	X17690-92 X17695-91	51, 62, 58, 59, 70, 59 54, 51, 44
1977, 17690-92	a/a	Sprague 1976 441(1) x 442(1) Colorless	X17687-89	66, 65, 61, 69, 62, 59
1977, 17695-96	a/a tester	Nelson 1974 10429 selfed	X17687-89	44, 50, 47, 46, 49, 50, 52
Fla 1978, 7824-25	a-p/a	17687 x 695 Colored kernels	selfed	22, 46, 27, 43, 28, 21, 22, 24, 24, 47, 26, 46, 26, 25, 43, 26, 29, 26, 43, 29, 42
Fla 1978, 7829	a-p/a	17695 x 687 Colored kernels	selfed	26, 27, 25, 43, 24, 40, 33, 26, 30, 28, 24, 22
1978, 19472-3	a-p/a	F7825-2 selfed (47% Colorless) Colored kernels	selfed	21, 21, 45, 40, 29, 27, 29, 0, 40, 46, 46, 41, 43, 44, 42, 27, 0
1978, 19475-6	a-p/a	F7829-6 selfed (40% Colorless) Colored kernels	selfed	18, 42, 27, 28, 25, 22, 24, 30, 43, 23, 0, 0, 27, 45, 24, 20, 21, 43, 28, 40, 46, 25, 48, 23, 0, 0

Table 1 records the results of investigations made with this Aberrant Ratio stock from Sprague. The sib crosses between plants grown from colored kernels and those grown from colorless kernels did yield an excess of colorless kernels in most crosses, and crosses of the plants from colored kernels times our a tester did give approximately 50% colorless kernels. However, when colored kernels from this cross (presumed A/a x a tester) were planted in Florida (1978) and the plants selfed, plants giving an excess of colorless were found to occur frequently (Table 1, lines 4 and 5). The percentages of colorless kernels in various plants showed a distinctly bimodal distribution with means of 25.8 and 43.7 for the two classes.

These progenies were followed for one more generation by planting colored kernels from two self-pollinated plants that gave high percentages of colorless kernels in Florida and self-pollinating the resulting plants. The results are given in Table 1, lines 6 and 7. There was a trimodal distribution with respect to the percentages of colorless kernels--those ears with no colorless kernels; those distributed about 25% colorless kernels ($\bar{x}$ = 24.7%); and those distributed about a modal value in the low 40's ($\bar{x}$ = 43.4%). By this time, it was clear that all observations could be explained if the original accession from Sprague were, in addition to being heterozygous (A/a), heterozygous at another of the complementary loci necessary for aleurone anthocyanin production. The mean values of 43.7% colorless kernels for selfed plants in Florida (1978) and 43.4% colorless kernels in Wisconsin (1978) on the high colorless plants are close to the 43.75% colorless expected when selfing a plant of the constitution A/a; X/x where either a/a/a or x/x/x conditions a colorless seed phenotype. The mean value of 62.7% colorless in the original sib crosses (Table 1, lines 1 and 3, excluding the value of 51% colorless) is close to the 62.5% colorless expected from a cross of a plant from a colored seed (A/a; X/x) times a plant from a colorless seed (a/a; X/x or A/a; x/x) with either a/a/a or x/x/x conditioning a colorless seed phenotype.

Direct confirmation of the genotype is necessary, however, and this was provided in 1979. Colorless seeds from 19473-5 selfed (43% colorless) were planted, and the resulting plants crossed onto all the color testers. The five plants proved to be uniformly A2/A2; C2/C2; R/R but to be of various constitutions (A/A, A/a, a/a) at the A locus and homozygous recessive c/c at the C locus. A second test demonstrated that colorless seeds within a progeny derived from a cross of the original AR stock (a-p/a) times our a tester could be colorless for reasons other than their genetic constitution at the A locus. Plants from colorless seeds of 19473-6 selfed (44% colorless) were pollinated by our a tester. Of 68 plants thus tested, 38 were a/a, 20 were A/a, and 10 were A/A. Therefore, it is clear that seeds within this progeny could be colorless without being a/a and that alleles at a second color factor locus were segregating. We already know that that locus is C in this line of descent.

A second AR stock was received from Sprague in 1979. This was A/a* x a/a [Sprague 1978 211(1) x 210(1)]. The colored and colorless seeds were planted in adjacent rows, and the plants from the colored seeds were either selfed or crossed reciprocally in paired pollinations with the plants derived from colorless seeds. The results are presented in Table 2. At the same time, 4 plants from colored seeds were used as pollinators onto all color testers. These four plants were all shown to be A/a, A2/A2, C/C, C2/c2, and R/R.

Table 2. The results from sib-matings between plants from colored and colorless seeds derived from A/a* x a/a, Sprague 1978, 211(1) x 210(1), or self-pollinations of plants from colored kernels

Year, row	Presumed Genotype	Source of Stock	Pollinations Made	Percent Colorless Kernels
1979, 21551	A/a	211(1) x 210(1) Colored kernels	- 1 selfed	40
			- 3 x 552-9	74
			- 4 selfed	44
			- 5 x 552-3	76
			- 8 x 552-6	65
			- 9 selfed	42
			-10 x 552-7	57
			-11 x 552-8	75
			-13 x 552-1	71
			-15 x 552-2	59
1979, 21552	a/a	211(1) x 210(1) Colorless kernels	- 1 x 551-13	72
			- 2 x 551-15	57
			- 3 x 551-5	75
			- 6 x 551-8	66
			- 7 x 551-10	62
			- 8 x 551-11	78

With the knowledge that alleles at two color factor loci are segregating in the tested plants from colored seeds, it is clear that the colorless seeds from a sib mating might be a/a, C2/c2; a/a, c2/c2; or A/a, c2/c2. This enables one to interpret the results of the sib-matings given in Table 2. These fall into two groups --one with a mean of 61% colorless kernels and one with a mean of 74% colorless kernels. The group with the lower percentage of colorless kernels ($\bar{x}$ = 61%) almost certainly represents crosses of A/a, C2/c2 plants with plants that are A/a, c2/c2 or a/a, C2/c2. In such crosses, 62.5% of the kernels are expected to be colorless. The second group of crosses ($\bar{x}$ = 74% colorless kernels) are matings between plants that are A/a, C2/c2 and those that are a/a, c2/c2. In these crosses, 75% of the kernels are expected to be colorless.

A subsection of this progeny was followed in 1980. The colored and colorless kernels from 21551-11 x 21552-8 (75% colorless kernels) were planted in adjacent rows. The plants from the colored kernels were crossed onto the color factor testers, self-pollinated, and used as males onto plants from the colorless kernels in a few instances. The results are given in Table 3. All plants tested were A/a, C2/c2. When selfed, the percentages of colorless kernels were close to the

Table 3. The genotypes and pollination results of plants grown from colored kernels from 21551-11 x 21552-8 (75% colorless kernels)

Year, row	Genotype[a]	Pollination Results (% Colorless) Selfed	on 23266[b]
1980, 23265 - 1	A/a, -----, C/C, C2/c2, R/R	43	--
- 5	A/a, A2/A2, ---, C2/c2, R/R	46	61
- 8	A/a, A2/A2, C/C, C2/c2, R/R	--	62
-11	A/a, A2/A2, C/C, C2/c2, R/R	44	77
-12	A/a, -----, C/C, C2/c2, R/R	--	61
-13	A/a, -----, C/C, C2/c2, R/R	45	75

[a] A blank means that the genotype at that locus is unknown.

[b] 23266 contained sib plants grown from the colorless seeds of 21551-11 x 21552-8.

expected 43.75%. When crossed to their colorless sibs, the percentages of colorless kernels were close either to the 62.5% colorless expected if the colorless seed were A/a, c2/c2 (or a/a, C2/c2) or to the 75% colorless kernels expected if the colorless seed were a/a, c2/c2.

In summary, two Aberrant Ratio stocks giving higher than expected percentages of colorless kernels in sib-matings between plants of the presumed genotypes A/a and a/a were followed for several generations. In each case, the stock was found to be heterozygous at a second color factor locus (C/c in one instance and C2/c2 in the second). The excess of colorless kernels results from segregation of alleles at a second color factor locus. It is unnecessary to postulate any anomalous genetic behavior in these stocks.

Two other Aberrant Ratio stocks have also been received from Sprague and investigated to some extent. The existence of anomalous ratios has been confirmed and the investigations have been sufficient to show that the basis(es) is(are) different than that in the two cases already discussed. The first stock is one in which sib-matings of plants from colored kernels (presumed to be A/a) with plants from colorless kernels (presumed a/a) produce an excess of colored kernels over the 50% expected. One such stock was received from Sprague [1976 433(5) x 434(9)]. It has been most difficult to obtain satisfactory seed sets on this stock so that no adequate data have been collected. In 1979, a plant from a colorless seed crossed as a female with a plant from a colored seed produced 50%

colored seeds. Of two plants from colored seeds crossed as females with plants from colorless seeds, one gave 61% colored kernels and the other 51% colored seeds. Although an excess of colored kernels can result from segregation at two color factor loci given the requisite genotypes, that does not account for the results here. In 1980, a number of plants from the colored kernels of the cross that in 1981 produced 61% colored kernels were tested for their allelic constitution at the color factor loci. All such plants were A/a, A2/A2, C/C, C2/C2, and R/R. It is possible that a gametophyte factor linked to A accounts for the excess of colored kernels in sib-matings in this stock. There is a gametophyte factor, Ga7, located 17 map units distal to the a locus. The possibility of the involvement of this or another gametophyte factor previously unidentified should be ruled out before proceeding to alternative suggestions.

Another Aberrant Ratio stock is one in which sib-matings between plants from Su/su kernels and su/su kernels give an excess of sugary kernels. In their 1971 paper (Genetics 67:533-542) Sprague and McKinney suggest that they had found stocks giving aberrant ratios for sugary without supplying any data. In 1979, such an AR stock was received from Sprague [1978, 208(2) x 209(1)]. This was again a sib-mating (Su/su x su/su). The nonsugary (Su/su) kernels were planted and the plants selfed as well as crossed as males to Golden Cross Bantam. The results are presented in Table 4. It should be noticed that contrary to the observations with

Table 4. The percentages of sugary kernels when plants from the nonsugary kernels from Sprague 1978, 209(2) x 209(1) were self-pollinated or crossed onto Golden Cross Bantam

Year, row	Percent Sugary Kernels Selfed	Onto GCB
1979, 21522 - 1	38	55
- 2	40	--
- 3	45	--
- 4	34	58
- 5	37	56
- 7	27	59
-11	36	64
-12	39	--
-13	38	67
-14	39	61

the (A/a*) AR stocks giving an excess of colorless kernels that outcrosses to a control stock (Sprague and McKinney) or our a tester (Table 1) showed expected ratios (i.e., 50% colorless), outcrosses to a sugary hybrid not previously involved in these crosses still produced an excess of sugary kernels. However, the excess over expectations is greater in the self-pollinations than in outcrosses.

In 1980, nonsugary kernels from 21522-5 selfed (an Su/su plant that gave 37% sugary kernels when selfed in 1979) were planted. The resulting plants were pollinated by pollen from Golden Cross Bantam (GCB) Hybrid plants and crossed as males onto GCB plants. The results are recorded in Table 5. The data are somewhat incomplete in that both crosses are not available for all plants. It is clear, however, that when the Su/su plants from the AR stock are crossed as females by the su/su GCB hybrid, the percentages of sugary kernels observed in the various ears group about the expected 50%. The reciprocal crosses where the Su/su plants were used as males show marked deviations from 50% suggesting that a gametophyte factor could be involved. There is a gametophyte factor locus, Ga1, on the 4th chromosome linked to the su locus which could produce excess sugary kernels when plants of the constitution Ga su/ga Su were self-pollinated or used as males on a Ga su/Ga su tester. No excess sugary kernels would be expected if Ga su/ga su

Table 5. The percentages of sugary kernels produced when plants from nonsugary kernels (Su/su) of 1979 21522-5 x are crossed as males and females with GCB plants

Year, row	Percent Sugary Kernels XGCB	on GCB
1980, 23397 - 3	--	65
- 5	--	57
- 8	42	--
- 9	51	--
-10	47	58
-12	53	62, 63
-13	52	70
-14	53	--

plants were pollinated by an su/su tester. However, this locus does not seem to be implicated for several reasons: (1) Ga pollen grains have a competitive advantage over ga pollen grains only on the silks of plants which are Ga/Ga or Ga/ga. The GCB hybrid is apparently ga/ga, and Ga pollen grains should not have a competitive advantage over ga pollen grains on GCB silks yet marked departures from 50% sugary are observed when GCB plants are pollinated by Su/su plants from the AR stock; (2) if the AR Su/su plants were ga Su/Ga su, they should be capable of pollinating Ga-s/Ga-s plants, and this was not the case in our tests. Using the term "gametophyte factor" in its broadest sense, there are factors on chromosome 4 capable of distorting segregation ratios for sugary without requiring any specific genetic constitution on the female side. W. R. Singleton and P. C. Mangelsdorf (1940, Genetics 25:366-390) reported small pollen (sp) to be 6 crossover units from su. The sp pollen grains rarely function in competition with Sp pollen grains. Carangal (1958, MS Thesis, Purdue University) reported that lethal pollen (lp) is about 14 crossover units from su. No lp pollen functions in competition with Lp pollen, and the lp pollen cannot be distinguished from Lp by size nor any stain tested. Thus, there is considerable precedent for gametophyte factors on chromosome 4 capable of distorting sugary percentages when pollen from a Su/su plant is used to pollinate an su/su tester if the Su/su plant were Su sp/su Sp or Su lp/su Lp.

As in the previous cases of AR discussed, the deviation from expectation with the Su/su* stock may well have a prosaic explanation.

I appreciate the cooperation of George Sprague in supplying the various AR stocks used.

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Correlation between certain characters for earliness in hybrids produced on systematic heterozygous series

Characters for earliness were studied on hybrids produced on two heterozygous series with different vegetation periods (F564 x HMv404 and CE187 x A632), using 4 pollinator lines (W117, A340, HMv 09 and B37) in each case. The experiments were set up at Martonvásár in a random block design in 4 replications in 1979 and 1980. For each heterozygous series 1920 plant data were evaluated for the following characters:

1. Number of days from sowing to 50% tasseling
2. Number of days from sowing to 50% silking
3. Moisture content at harvest
4. Total number of leaves
5. Number of leaves above the ear.

The mean values of the characters examined are shown in Table 1. The effect of the year was significant at the 0.1% level for the number of days from sowing to 50% tasseling and 50% silking and for the moisture content at harvest, but was not

Table 1. Mean values of earliness indices.

Character	F564 x HMv404		CE187 x A632	
	1979	1980	1979	1980
No. days to 50% tasseling	70.59	85.67	73.36	88.35
No. days to 50% silking	73.79	88.71	75.59	90.80
Moisture at harvest, %	30.16	34.83	29.66	35.64
Total no. of leaves	15.81	15.78	16.99	16.99
No. of leaves above ear	5.02	5.04	5.81	5.85

significant for the total number of leaves or the number of leaves above the ear. The interaction of heterozygous series x year was only significant at the P = 0.1% level for the moisture content at harvest, while this interaction cannot be demonstrated for the other characters. The data show that in both years there was considerable deviation in the earliness indices. In 1980 flowering was an average

Table 2. Correlation between certain characters for earliness in hybrids produced on systematic heterozygous series. Martonvásár, 1979, 1980.

Pairs of Characters for Earliness	Heterozygous Series			
	F564 x HMv404		CE187 x A632	
	1979	1980	1979	1980
1. No. days to 50% tasseling				
- No. days to 50% silking	0.963	0.944	0.971	0.900
- Moisture at harvest, %	0.901	0.786	0.870	0.807
- Total no. of leaves	0.758	0.895	0.581	0.825
- No. of leaves above ear	0.673	0.714	0.602	0.765
2. No. days to 50% silking				
- Moisture at harvest, %	0.903	0.764	0.894	0.787
- Total no. of leaves	0.758	0.859	0.472	0.822
- No. of leaves above ear	0.654	0.653	0.502	0.731
3. Moisture at harvest, %				
- Total no. of leaves	0.603	0.676	0.516	0.699
- No. of leaves above ear	0.378*	0.545	0.508	0.641
4. Total no. of leaves				
- No. of leaves above ear	0.768	0.772	0.817	0.927

*Significant at the 1% level; (all others significant at 0.1% level).

of 15 days later than in 1979. The delay in flowering was associated with an increase in the moisture content at harvest, but there was little change in the total number of leaves or the number of leaves above the ear. It is interesting to note that for the hybrids produced on both heterozygous series the characters examined changed in a similar manner due to the effect of the year.

The correlation between the different characters for earliness can be seen in Table 2. The correlation is highly significant for both years and for hybrids produced on both heterozygous series. The number of days from sowing to 50% tasseling and 50% silking and the moisture content at harvest show a closer correlation with the total number of leaves than with the number of leaves above the ear. Years with different weather conditions had little or no effect on the correlation between the earliness indices.

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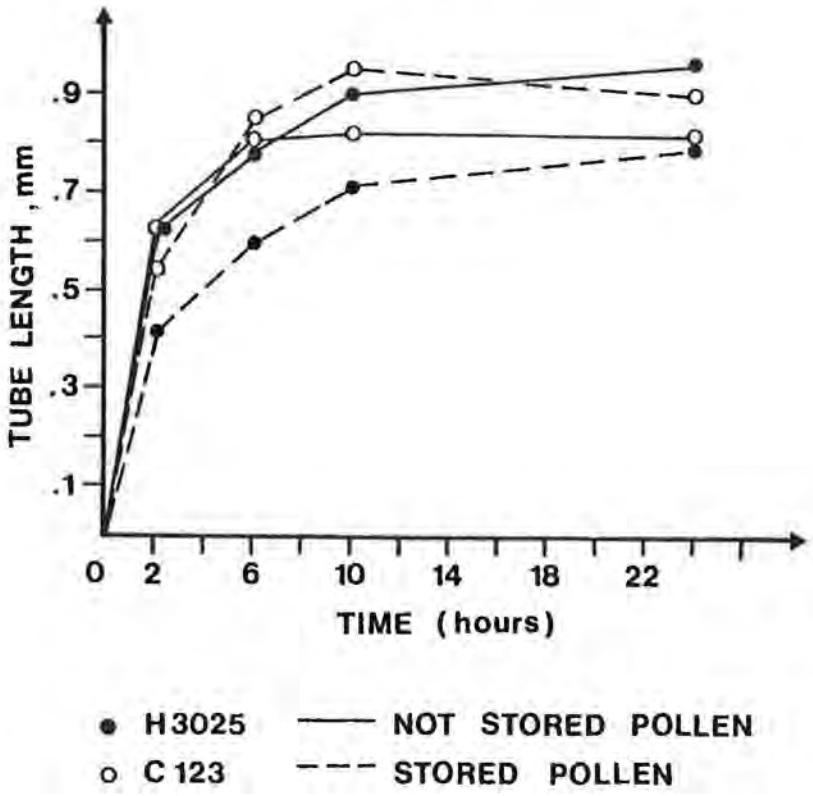
In vitro germination and tube growth of maize pollen

Maize pollen grows with difficulty on artificial media. A good germination percentage is obtained on agar media, while in liquid media, probably because the water uptake is unregulated, the grains generally burst. The total tube length reached in vitro is very limited, compared with the length in natural conditions, probably owing to the lack of the metabolic support furnished in vivo by the style.

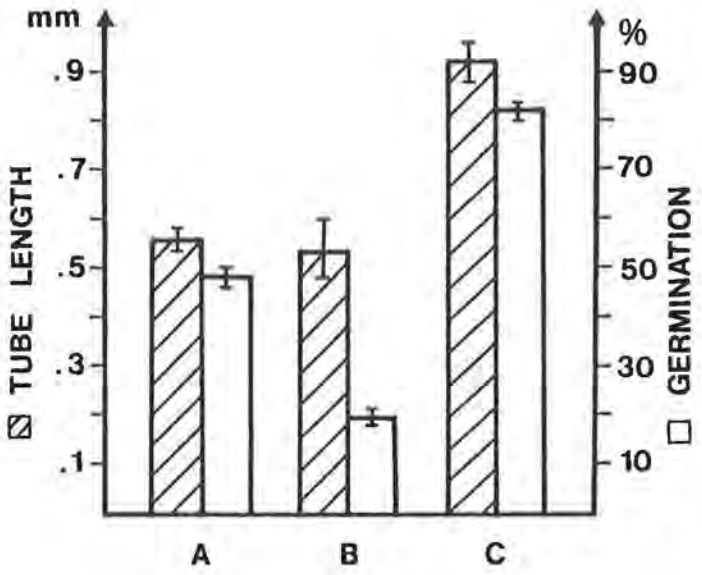
Most of the tube growth is observed in vitro in the first two hours, and within about six hours the growth stops. This trend is observed also when the pollen is stored for 24 hours at 4 C immediately after collection. Fig. 1 shows the tube growth during 24 hours of two inbred lines on standard medium (P. L. Pfahler, Genetics 52:513, 1965; D. Cheng and M. Freeling, MGCNL 50:11, 1976). The growth

Fig. 1



was measured after 2, 6, 10 and 24 hours. Storage appeared to have a favorable effect on the C123 line, not on the H3025. A favorable response to storage has been reported by P. L. Pfahler and H. F. Linskens (Theor. Appl. Gen. 42:136, 1972) and by C. Frova and W. A. Feder (Ann. Bot. 43:75, 1979), but it is clearly dependent also on the pollen genotype involved.

In order to obtain pollen germination and growth in liquid medium for particular experimental requirements, such as pollen treatment with hydrosoluble compounds, we tested a more complex medium (J. P. Mascarenhas, Am. J. Bot. 53:563, 1966). In Fig. 2 pollen germination percentage and tube length of the W22 line after four hours of incubation on standard medium, agarized and liquid Mascarenhas medium, are reported.



A= STANDARD MEDIUM

B= AGARIZED MASCARENHAS MEDIUM

C= LIQUID MASCARENHAS MEDIUM

Fig. 2

The result is clearly better in the last condition; however, we observed a great variability in the number of burst grains from one experiment to another.

We investigated the stylar component effect on pollen tube growth by supplementing the medium with water and ether silk extracts, or directly with stylar fragments. Since the contribution of stylar tissues to gametophyte development may derive from the metabolites present in the mature silks, or from those mobilized only as a response to the tube growth itself, we used both pollinated and not pollinated silks. Moreover, in order to verify the effect of pollen grains, which were present in the first treatment, pollen extracts were also added. In Fig. 3, as indicative data, the results concerning one of the tested lines (H3025), are reported. Similar results were obtained for the other lines (WF9, C123, B14). In general the silk extracts had an unfavorable effect on pollen growth for all the genotypes. Pollen extracts acted differently according to the pollen source used in the extract: in some cases growth was inhibited, whereas the B14 pollen seemed to have a favorable effect on the development of all the lines except H3025.

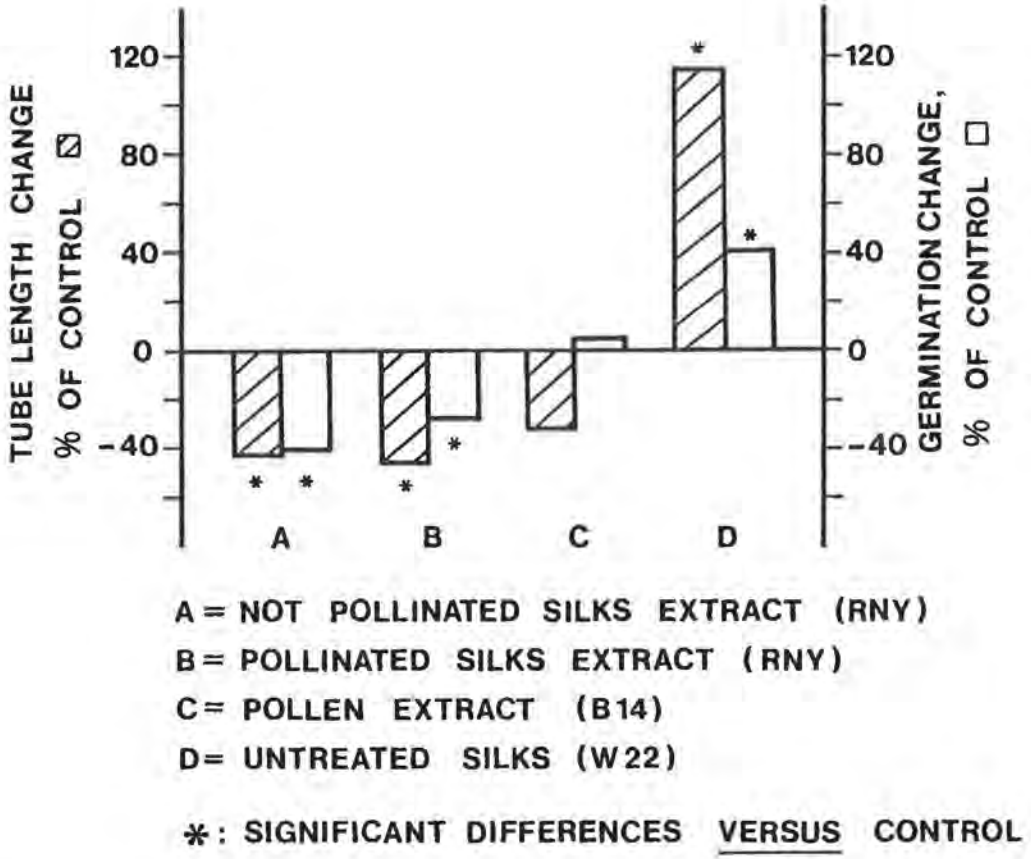


Fig. 3

The silk fragments directly soaked in the medium revealed a clearly favorable effect on germination and particularly on pollen tube growth, even if the pollen was not in direct contact with them. In fact the silks were deposed on the bottom of the petri dish and covered with a thin layer of medium. Thus, it appears that the silks diffuse some growth factor, which is inactivated during the extractive manipulations, or that these extractive manipulations induce the production of some inhibitor substance.

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Levels of starch branching enzyme IIb and gene dosage at the ae locus

Branching enzyme (α-1,4-glucan:α-1,4-glucan-6-glycosyl transferase; E.C. 2.4.1.18) is one of the enzymes directly involved in the synthesis of starch. Branching enzyme modifies the developing α-1,4 polyglucan by the hydrolysis of an internal α-1,4 bond, followed by subsequent reattachment of the small α-1,4 glucan chain to the remaining or another α-1,4 glucan chain by an α-1,6 bond. This creates branch points as well as additional non-reducing ends where further

synthesis of α-1,4 glucan chains can occur. Multiple forms of branching enzyme in developing maize kernel have been detected using DEAE-cellulose chromatography (C. D. Boyer and J. Preiss, 1978, Carbohyd. Res. 61:321). In addition, studies have shown the DEAE-cellulose profile of branching enzymes from kernels homozygous for amylose-extender (ae) to have no detectable quantities of branching enzyme IIb, while branching enzymes I and IIa remain unaltered (Boyer and Preiss, 1978, Biochem. Biophys. Res. Comm. 80:169). We have now examined the levels of branching enzyme from maize kernels with endosperm with 0, 1, 2 and 3 doses of the recessive ae allele.

Characterization of branching enzyme levels present in 22-day-old maize kernels (inbred W64A) involved partial purification consisting of homogenization, centrifugation, precipitation with 40% ammonium sulfate, and DEAE-cellulose chromatography. All procedures were performed at 4 C. DEAE-cellulose fractions were assayed for branching enzyme activity according to the rate of α-glucan formation from glucose-1-phosphate by phosphorylase a, and further characterized by the branching of amylose. Levels of individual branching enzyme fractions were corrected for differential rates of recovery of total branching enzyme activity. Results showed an inverse relationship between increasing dosage of the recessive ae allele and branching enzyme IIb levels in the endosperm:

Dose of recessive ae allele	Relative activity	Activity/kernel (μmoles/min)	Activity/gm F.W. (μmoles/min)
3	0	0	0
2	12.2	0.21	0.99
1	35.8	1.03	5.15
0	49.8	1.41	6.43

Levels and properties of branching enzymes I and IIa did not vary as a function of ae dosage. Despite different recoveries of activity in different enzyme preparations, we still obtain a fairly linear relationship of enzyme level and dose of the dominant ae allele. These results are consistent with the possibility that ae is the structural gene for branching enzyme IIb.

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Genetic control of chromosome segregation during the first meiotic division

Analysis of allelic relationships of mutations affecting the same process makes it possible to establish some features of the genetic control of this process. We have studied relationships between meiotic mutations which affect the segregation of homologous chromosomes in maize. The mutation "divergent spindle" (dv), first described by F. J. Clark (1940), was kindly provided by Dr. R. J. Lambert for our investigations. Three other mutations (ms43 A344, ms28 A344, mei 025 W64A) have been described by us elsewhere (MNL 53, 1979; Int. Rev. Cytol. 58, 1979; Genetika No. 4, 1980).

Mutation mei 025 exhibits its phenotypic effect earlier than ms43 and ms28. It forms a sticky cluster of chromosomes at metaphase I. Thus mei 025 is similar to the well known mutation "sticky" (G. W. Beadle 1937), with the difference that the latter produces chromosome sticking at prophase I of meiosis. The sticky chromosomes in both mutants lose their capacity to pass regularly to the poles.

In mutants ms43 and ms28, the pairing of chromosomes is normal, but the process of segregation of homologues during anaphase I of meiosis is disturbed.

We have also thoroughly studied mutation dv, which is known as a mutation with divergent spindle shape (D. Mazia, Mitosis and the Physiology of Cell Division, Academic Press, 1961; Baker et al., Ann. Rev. Genet. 10, 1976). We found that, in mutant dv, chromosomes at metaphase I gather in the center of the cell, and there is no strict co-orientation of the centromeres. For this reason, an oriented metaphase plate is not formed and the result is disorderly disjunction of homologous chromosomes at anaphase I. Each chromosome seems to move towards its "own" pole independently of the movement of the other chromosomes.

Phenotypically the above mentioned meiotic mutants are male sterile and female fertile.

We analyzed the allelic relationships in a series of diallelic crosses. The criterion of allelism was appearance of near 50% sterile plants in crosses like mei 025/mei 025 x ms28/+ and so on. The pattern of allelic relationships appeared to be complex:

	Male			
Female	mei 025/+	ms43/+	ms28/+	dv/+
mei 025/mei 025	--	not done	24f:18st	33f:44st
ms43/ms43	3f:1st	--	27f:0st	20f:0st
ms28/ms28	not done	20f:0st	--	17f:0st

f = fertile st = sterile

When ms43, ms28 and dv were crossed to mutant mei 025, the F1 contained male sterile plants (additional data bearing on ms43 are given later). This provides evidence for their allelism. Because ms43, ms28 and dv can be considered to be allelic to mei 025, we expected that heteroallelic combinations ms43/ms28, ms43/dv, and ms28/dv must also be sterile. However, all F1 tested plants from crosses ms28/ms28 x dv/+, ms43/ms43 x dv/+, ms43/ms43 x ms28/+ and ms28/ms28 x ms43/+ were fertile.

Two explanations of the genetic data are tentatively offered: (1) either mei 025 is a deletion, and ms43, ms28, and dv are closely linked genes, or (2) all the four mutations are a series of multiple alleles at the same locus but belonging to three different complementation groups.

The first explanation seems unlikely judging by the meiotic pattern of male sterile mei 025/dv plants, which we investigated cytologically in detail. If there were a deletion, meiosis would be of type dv in mei 025/dv plants, but this was not the case. Meiosis in these plants is of mei 025 type with the only difference that the sticking of chromosomes starts immediately after pachytene and continues to metaphase I. It means that the effect of mei 025 is enhanced in genotype mei 025/dv.

Additional preliminary cytogenetic data were obtained supporting the second explanation. The F1 plants from the cross mei 025/dv x ms43/+ were grown in greenhouses and cytologically studied. Among 22 tested F1 plants three types of meiosis were distinguished: (1) regular meiosis (6 plants), (2) enhanced effect of mei 025, similar to that observed in mei 025/dv (12 plants); (3) meiosis of mei 025 type, but with weaker chromatin condensation at metaphase I promoting more regular homologous disjunction (4 plants). Two plants with the third type of meiosis had fertile pollen grains. We propose to deal with the phenomenon of interallelic complementation in combinations of ms43/dv, ms43/ms28 and ms28/dv.

From the point of genetical control of meiosis preliminary conclusions may be issued: (1) the appearance of meiotic abnormalities at prophase I in mei 025/dv combination allows us to suggest that gene(s) responsible for disjunction and function of the spindle apparatus start to act much earlier than their phenotypic effect is manifest; (2) genetic control of chromosome segregation in maize is a relatively simple process that may be controlled by one gene with a series of alleles which are capable of complementation; (3) the mutation "sticky" is possibly concerned with spindle function and is also a member of the same allelic series.

I. N. Golubovskaya and A. S. Mashnenkov

Allelic relationships between meiotic mutations with similar disturbances of meiosis

We have conducted genetical and cytological analysis of allelic relationships between some phenotypically similar monogenic recessive meiotic mutants in maize.

Table 1. Tests for allelism and segregation pattern of meiosis in meiotic mutants

	Segregation Pattern					
	F1		F2			
Cross	Fertile, regular meiosis	Sterile, irregular meiosis	Fertile, regular meiosis	Sterile, irregular meiosis	$\chi^2_{9:7}$	Conclusion
dsy2/dsy2 x dsy A/+	41	0	---	--		not allelic
as/as x dsy A/+	4	0	107	97	1.56	not allelic
pam A/pam A x pam2/+	2	0	50	39	0.15	not allelic
ms4/ms4 x po/+	2	1				allelic

Allelism was studied between four mutations which impair the pairing of homologous chromosomes and the beginning of meiosis (Table 1). Two desynaptic mutants (dsy A, dsy2) isolated by us in different years from the same line of maize, A344, appeared to be non-allelic. In addition, dsy A was non-allelic to the mutation afd (absence of first division) isolated from W23 (Table 2) and to as (asynaptic), found by G. W. Beadle in 1930 (Table 1). This information confirms other data that the first stages of meiosis are controlled by many different genes.

Table 2. Cytological data on meiotic patterns in F2 segregants obtained from dsy/+ +/+ x +/+ afd/+ cross

	F2 Segregants Obtained after Self-pollination of F1			Meiotic Pattern			
Expected genotype Ratios in F1	No. of Families	Fertile	Sterile	Normal	afd	dsy	χ^2
1/4 + +/+ +	4	343	0	60	-	-	
1/4 + +/dsy +	2	84	25	84	-	25	0.95
1/4 + +/afd +	5	346	106	64	23	-	0.13
1/4 afd +/dsy +	2	179	141	179	77	64	0.40

Two mutations causing plural anomalies of meiosis, pam A A344 and pam2 W64A, were also non-allelic (Table 1).

However, possible allelism was found for mutations characterized by precocious postmeiotic mitoses: po (polymitotic), discovered by Beadle in 1933, and ms4, induced with treatment with N-nitroso-N-methylurea by us in A344 line. In po/po plants one or some mitotic divisions take place in sporads having reduced chromosome number (Beadle, 1933). In ms4/ms4 homozygotes the postmeiotic mitoses in the majority of tetrads fail to end; sporads scatter during anaphase and pollen envelopes are formed around them. Meiosis in heteroallelic po/ms4 is similar to ms4/ms4 homozygotes. It is suggested that entrance into the postmeiotic mitoses is controlled by only one recessive gene with a series of alleles.

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A procedure for detailed cytogenetic localizations and the production of small interstitial duplications

Improved procedures for the genetic detection of dosage series and cytogenetic localizations have previously been developed (J. L. Birchler, MNL 1979, 1980; Genetics 94:687; J. L. Birchler, M. Alleman and M. Freeling, Maydica, in press). These methods for chromosomal manipulation could be advanced further with the ability to induce and selectively recognize particular reciprocal translocations that are broken in predetermined regions of the genome. Here a system is described that will allow the recognition of newly induced translocations which will saturate a pre-selected chromosomal segment and provide the basis for finely detailed cytogenetic definition of practically any region of the maize chromosomes.

The procedure involves inducing the appropriate translocations to produce the desired aneuploids that include the alcohol dehydrogenase-1 gene as a marker and another region of interest. The system is possible because each segmental trisomic includes portions of two chromosome arms. The first requirement is the previous existence of one translocation broken in 1L and in the other chromosome arm at the appropriate point. If such exists, the second translocation, satisfying the necessary conditions to segregate segmental trisomics, can be induced and easily selected. These conditions have been outlined by Birchler (Genetics, 1980).

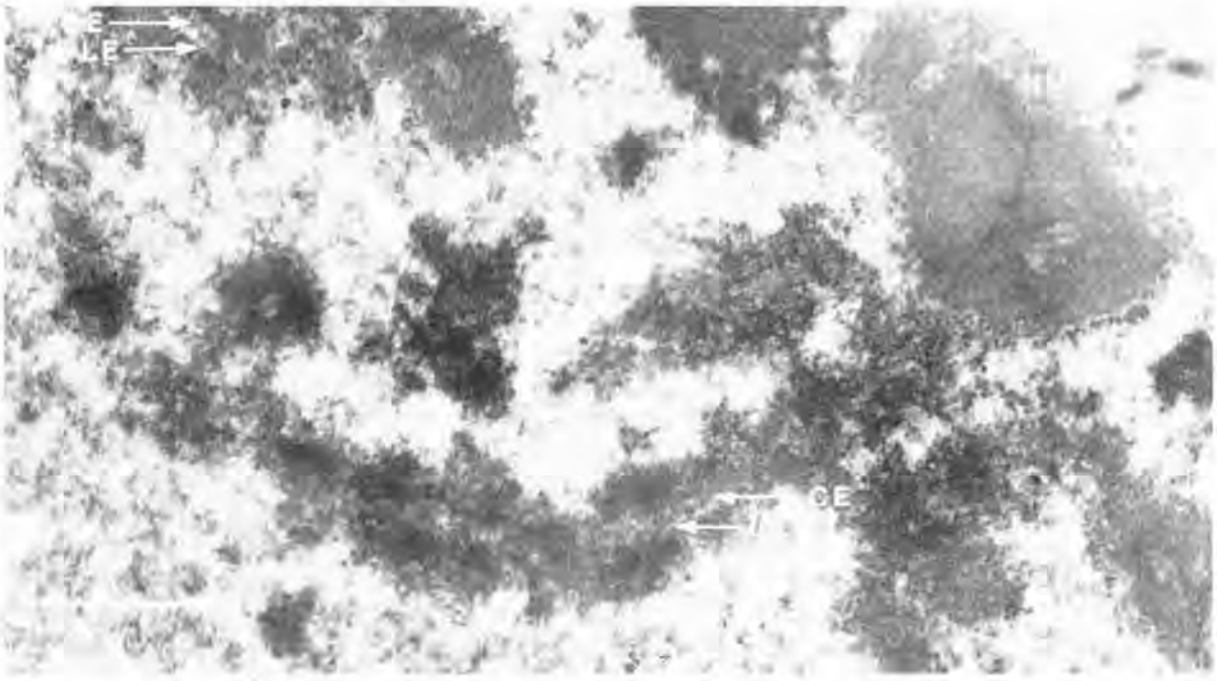
This is accomplished by using the translocation homozygote as a female for X-irradiated pollen from plants homozygous for Adh-Cm. This allele produces a polypeptide that is enzymatically very inactive and has a rare electrophoretic mobility. In pollen the in situ staining reaction (Freeling, Genetics 1976) for Cm is weak compared to normal, allowing ready classification. If no translocation or one involving another chromosome is induced, the F1 plants will segregate 1:1 for ADH positive and negative in the unaborted pollen grains. If, however, a translocation is induced that allows the production of overlapping segmental duplications including Adh, the ratio of ADH positive to ADH negative unaborted pollen will be 2:1. Skewed ratios might also be produced if a linked translocation is formed that segregates duplications adjacent to but excluding Adh. Whether these would be skewed toward positive or negative grains depends upon the relative position of the translocations used in the selection and the newly induced one. The two types of duplications, i.e., including or excluding Adh, can be discerned by subjecting an extract of the pollen to electrophoresis. If Adh is present in duplicated form, the Cm subunit will form dimers with the other allele present in the same gametophyte. Since pollen ADH is formed after meiosis (D. Schwartz,

Genetics 1971), the presence of heterodimers is indicative of duplicated gametes. The remaining situations that produce skewed ratios of + and - grains would not result in heterodimer formation. Thus, the appropriate breakpoints can be recognized. After selection of the F1 plants on the basis of pollen phenotype, the Cm allele will serve as a marker in embryo classification. Although this polypeptide lacks normal levels of activity, it forms a distinct active heterodimer that is sufficient for genetic manipulation. This approach shows promise for genetic dissection in maize because it will allow the genetic (as opposed to cytological) recognition and marking of segmental aneuploids with previously defined cytological limits for any region of the genome. Using this protocol one can induce and recover a host of aberrations in a region of interest that can be subsequently used for very precise cytological study of selected chromosomal segments.

J. A. Birchler

Early appearance of the synaptonemal complex in maize

If the synaptonemal complex (SC) is assumed to be a measure of exchange pairing during meiosis, then the time of appearance of this structure marks the earliest opportunity for exchange to occur. Recent studies report that the SC is seen during the meiotic S phase in Drosophila (R. F. Grell and J. W. Day, in Mechanisms in Recombination, R. F. Grell, ed.; J. W. Day and R. F. Grell, Genetics 83:67, 1976), wheat (H. A. McQuade and D. G. Pickles, Amer. J. Bot. 67:1361, 1980) and yeast (J. G. Petersen, L. W. Olson and D. Zickler, Carlsberg Res. Commun. 43:241, 1978). To define this period in the meiosis of Zea mays an electron microscopic study of microsporocytes in various stages of meiosis I was done. Meiotic stage of the anthers was determined by standard acetocarmine squash of one anther from each flower at the time of fixation and confirmed by thick sections for light microscopy.



Long twisted SC in leptotene nucleus. LE--lateral element, CE--central element, NM--nuclear membrane.

Electron microscopic observation of thin sections immediately adjacent to the thick sections revealed synaptonemal complexes at pachytene, zygotene and leptotene. Complete complexes had previously been reported only as early as zygotene (C. B. Gilles, Carlsberg Res. Commun. 43:241, 1974). The complexes seen at leptotene were morphologically very similar to those seen at pachytene although the central element appeared less distinct (see micrograph). Short "complex-like" structures were seen at interphase with clear lateral elements. However, the central element was visible only rarely in interphase nuclei. The relative decondensation of maize interphase chromosomes probably obscures these structures.

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Genetical studies of a collection of maize samples

During 1963-1979 a collection of maize germplasm consisting of 1905 samples from 45 countries was studied. The results in detail are included in the book, V. E. Micu, "The Genetical Studies of Maize," published by "Shtiintsa," Kishinev, Mold. S.S.R., U.S.S.R., in 1980. For the Newsletter, a summary of these studies is presented.

In 16,000 progenies from selfing of samples of the collection a very large number of mutants were observed. It is important to note that there were no chemicals applied on seeds or plants, but the old seeds were used for the growing of primary material for selfing. All observed mutants were divided into 5 groups and 86 phenotypical classes, which correspond to well-known mutants. The absolute majority of detected mutants are of the well-known types (Table 1). All the same,

Table 1. List and classification of mutants

1. Kernel Form & Texture		2. Pigmentation		3. Leaf Structure		4. Stalk Structure		5. Reproductive Syst. Structure & Function	
Type	No. Cases	Type	No. Cases	Type	No. Cases	Type	No. Cases	Type	No. Cases
bt, sh	27	al	5	ad	36	bk	12	an	28
cp	4	bm	24	cr	19	br	15	ba	64
de	83	f	27	gl	80	bv	1	bd	4
du	2	g	33	Hs	4	d	11	bs	21
et	10	gs	22	Kn	1	dlb	6	dep	6
mn	23	ij, j	30	lg	32	la	28	lo, zl	85
o, fl	85	l	91	nl	9	na	2	ms, CMS	44
su	33	li	3	Rg	5	py	4	Pn	2
wx	5	Og	3	Rs	19	zg	8	Pt	4
	272	oy	1	sl	16	others	47	ra	57
		pg	3	others	65		134	Rf1, Rf2	15
		pm	18		286			rf1, rf2	91
		sr	18					Rf3	11
		v	21					rf3	130
		vp	57					si, pi	15
		yg	7					sk	13
		ys	44					tb	1
		w, lw	140					tl	4
		wd	1					ts	21
		ws	3					ub	8
		zb	19					others	17
		zn	11						641
			581						

several new or little-known phenotypes are also revealed: defective pistils (dep); dichotomously branched plants (dib), absence of tassel (tl); short husks; short leaf sheath; and others. Note should be taken that the frequency of the mutants is clearly lower in dent than in flint samples.

In order to determine the inheritance of observed phenotypes the 1446 mutants were examined by elementary genetical analysis. More detailed genetical analyses, including tests for allelism, were conducted for 469 stocks, and clear-cut results were obtained for 428 of them (Table 2).

Table 2. The list of identified mutants

Locus	No. Cases	Locus	No. Cases	Locus	No. Cases	Locus	No. Cases
ad	5	d1	5	mn	1	sk	13
ba1	7	dib	1	o2	5	su1	27
ba2	5	dep	4	ra1	10	tb	1
bd	1	fl2	2	ra2	8	tl	2
bm1	13	g1	7	Rf1, Rf2	15	ts1	2
bm2	1	la	5	rf1, rf2	91	ts2	7
bm3	3	lg1	18	Rf3	11	ts4	3
bt1	8	lg2	7	rf3	130	wx	3
cms-S	4	Lg3	3				

In general, this research proves once again that local varieties and samples contain great genetic variability which may be used both for further studies and for the improvement of maize.

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Plasmid-like mitochondrial DNAs from Latin American maize races

There are two unique plasmid-like mitochondrial DNA (mtDNA) molecules associated with the S-type of cytoplasmic male-sterile (cms) maize (PNAS 74:2904-2908, 1977). These molecules have terminal sequences repeated once in reverse polarity (MGCNL 52:96-98, 1978), a characteristic often involved with insertional events in lower organisms. The spontaneous reversion of cms-S maize to fertility, correlated with the disappearance of these two molecules and changes in the mtDNA, has been associated with a transpositional event (Science 209:1021-1023, 1980).

Mitochondrial DNAs from 61 accessions of Latin American maize races were examined by agarose gel electrophoresis, BamHI restriction endonuclease fragment analyses, and electron microscopy of molecules under denature/renature and heteroduplex conditions.

The Mexican race, Cónico Norteño, contained two molecules which we cannot distinguish from the S-1 and S-2 molecules of cms-S. Test crosses to establish the identity of this cytoplasm as cms-S are not yet complete, but about one-half the

In situ hybridization was carried out with the 12 days post-pollination endosperm interphase nuclei. The nuclei were hybridized with ^{125}I-rRNA (sp. act. $5x10^7$ dpm/ug) and exposed for 7 days at 4 C. Silver grain number was correlated with nuclear and nucleolar volume (Figs. 2 and 3). The average number of silver

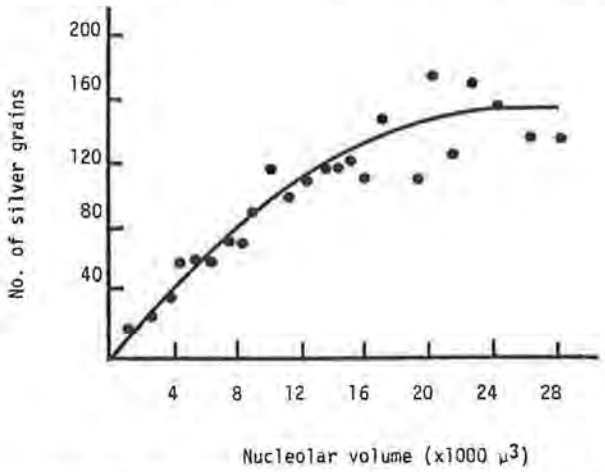

Fig. 3. Relationship between nucleolar volume and silver grains in hybrid Wf9xB37 (self-pollinated). Each value represents the average of up to 200 nucleoli.

grains per nucleolus ranged from 10 to 175. The observations suggest that the amount of rDNA increases with increases in nuclear and nucleolar volume. The silver grains were scattered over the entire nucleolus and were not localized over a particular region. This is different from the situation found in pachytene cells of the microspore mother cell, in which the silver grains are localized only over the NOR. The result indicates that the endosperm nucleolus contains dispersed rDNA, and agrees with our previous report that the amount of rDNA and nucleolar size are correlated (Chromosoma 36:79-88).

R. L. Phillips and A. S. Wang

An in vitro detection system for monoploid maize tissue cultures

Our objective was to develop a reliable system of obtaining monoploid maize tissue cultures using the ig system to generate paternal monoploids. Immature embryos of certain genotypes will readily initiate cultures capable of regenerating plants (C. E. Green and R. L. Phillips, 1975, Crop Sci. 15:417). The R-sc locus scutellar pigmentation system and Adh1 isozymes were chosen as genetic markers to detect haploidy.

This scheme has several improvements over other systems of obtaining monoploid cultures (C. E. Green and C. M. Donovan, 1979, Abstract 1714, 3rd Intl. Cong. PTCC, Calgary; H. S. Dhaliwal and P. J. King, 1979, TAG 55:257). The substitution of R-sc for the R-nj allele resulted in a consistently high color response which was easier to score because of the pigment location. The male parent's r-r allele was replaced with r-g, which eliminated pigmentation that could confuse the scoring of scutellum color. A second genetic marker (Adh1) was incorporated, which increased the screening efficiency for monoploids. Adh1-F and -S isozymes do not affect culture initiation and analysis requires only a small amount of tissue. Even if paternal monoploid tissue has spontaneously doubled prior to the cytogenetic analysis, the Adh1 pattern reveals the initial monoploid level. Maternal monoploidy versus accidental self-pollination cannot be differentiated.

Two major attempts were made to initiate monoploid cultures. Ears from crosses of W23 R-sc/R-sc Adh1-F/Adh1-F ig/ x [A188/Hayes White] ⊗ r-g/r-g Adh1-S/Adh1-S were harvested 12-18 days post-pollination. Embryos were isolated and placed sequentially on standard media (0.5 mg/l 2,4-D MS). After three days of light exposure ($95W/m^2$), pigment response was scored and the colorless embryos were transferred for a three-week period of culture initiation. Tissue samples of these cultures were assayed for Adh1 isozymes.

A consistently high proportion (93.5%) of the embryos expressed scutellar pigment. Six paternal monoploids were identified out of 7241 embryos, which was much fewer than expected. Several factors could have contributed to this discrepancy: (a) twenty-two of the colorless embryos did not grow after isolation and could not be analyzed for Adh1 isozymes; (b) embryos could not be readily found in about 6% of the normally developing kernels; (c) heterozygosity for ig in the maternal parent would have reduced the expected frequency of paternal monoploids; (d) the paternal genotype also might have influenced this frequency.

Variations of genetic and environmental factors of the basic embryo isolation procedure were tested in an attempt to improve the percent of embryos which expressed the scutellum pigment marker. Immature R embryos were placed on MS media, exposed to light and scored daily for pigmentation. After three days, the explanted embryos were either frozen and later quantitatively assayed for anthocyanins or incubated for 2-3 weeks for culture initiation.

A comparison of different R alleles showed that R-nj embryos gave a more variable response than either R-scm:2 or R-scm:3 embryos at similar stages of development. Pigment appeared on the upper surface of the scutellum with R-sc, R-scm:2 and R-scm:3, which was more easily seen than the R-nj pattern. Established diploid cultures with the R-sc allele often produced darkly pigmented tissues that resembled scutella. Cultures of the paternal genotype (both haploid and diploid) produced similar structures that were never pigmented. This apparent expression of R-sc in established cultures increases its effectiveness as a genetic marker in this system.

Increased irradiance did not alter the final percentage of pigmented embryos, but it did result in more anthocyanin per embryo. Color response increased with longer periods of light exposure although culture initiation decreased. Embryos with a colorless genotype showed the same decline in frequency of culture initiation under the same light treatments; thus the reduced culture initiation frequency was not an effect of pigmentation.

The cytokinins BAP, zeatin, and 2iP at 10^{-6}, 10^{-7}, and 10^{-8} M in the media did not affect the final color response of the embryos, although BAP increased coleoptilar anthocyanin content. All three cytokinins promoted growth of the coleoptile, which usually indicates poor culture initiation. There were no differences in color response among 2,4-D treatments of 0, 0.5, or 2.0 mg/l.

Abscisic acid (ABA) at concentrations of 1.0 mg/l or more resulted in a higher proportion of pigmented embryos, and more pigment per embryo, as well as inhibiting culture initiation. Lower doses of ABA (0.1, 0.25, 0.5 mg/l) did not promote pigmentation as much and still reduced culture initiation. Transfer of the embryos to media without ABA after 6, 12, or 24 hours avoided some of this inhibitory ABA effect, but the transfer procedure itself appeared to depress culture initiation. There was no correlation between pigmentation and culture initiation.

The combination of R-sc scutellar pigmentation with a second marker for Adh1 isozymes allowed identification of monoploid cultures from immature maize embryos under standard culture initiation conditions. Two of the six paternal monoploid cultures were capable of regenerating plants. The optimum size for culture initiation from monoploid embryos might differ from diploids because of their differences in ploidy and heterozygosity.

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Tissue culture potential of inbreds from the People's Republic of China

The primary factors influencing establishment of regenerable tissue cultures in maize are genotype, source and stage of donor tissue, and culture media composition (C. E. Green, Hort. Sci. 12:131-134, 1977). During the summer of 1980, 48 inbred lines from The People's Republic of China were planted at 2 dates (9 May and 24 May) and grown in the field at St. Paul, MN. Plants were selfed or sibbed and 12 to 16 days later 2 ears of each line were used as a source of immature embryos for tissue culture initiation. Embryos were isolated aseptically according to the standard procedure (C. E. Green and R. L. Phillips, Crop Sci. 15:645-649, 1975) and placed scutellar-side-up on Murashige and Skoog media containing 0.75 mg 2,4-D per liter. For most lines 30 embryos from each of 4 ears were tested (2 plants from the early and late planting dates); however, only 2 ears (1 date) were used for 4 genotypes.

The resultant tissue culture growth from each embryo was evaluated 4-5 weeks after initiation according to the following:

1. Mixed callus - lobular tissue proliferation from the scutellum, mixed with areas of leaf morphogenesis.
2. Callus - lobular tissue proliferation only, no areas of leaf morphogenesis.
3. Enlarged scutellum - smooth enlarged embryo, little to no tissue proliferation, no areas of leaf morphogenesis.
4. Developing embryo - highly organized, root and/or shoot emergence, no tissue proliferation.
5. Senescent embryo - no germination, no visible change in embryo morphology.

Two weeks after the first classification the cultures were examined again to confirm the initial observations. Data from the final classification are reported here as the distribution of 48 inbred lines according to their frequency of response within each of the 5 classes.

The mixed callus response is the most appropriate for the establishment of tissue cultures capable of organogenesis and plant regeneration. The data in Table 1 first were broken out according to the frequency of mixed callus formation and then according to the frequency of the other 4 response classes. Five lines

Table 1. Tissue Culture Response of Immature Embryos from 48 Inbred Lines from China.

Distribution of 48 inbred lines according to frequency of mixed callus			Response Classification									
			(1) Mixed callus		(2) Callus		(3) Enlarged scutellum		(4) Developing embryo		(5) Senescent embryo	
% Range	No. Emb	No. Lines	% Emb[a]	No. Lines[b]	% Emb[a]	No. Lines[b]	% Emb[a]	No. Lines[b]	% Emb[a]	No. Lines[b]	% Emb[a]	No. Lines[b]
0	1924	18	0	0	17	3	34	5	44	9	5	1
1-20	2273	21	8	0	13	2	26	4	51	15	1	0
21-40	432	4	28	0	4	0	13	0	55	4	0	0
41-60	348	3	47	3	9	0	18	0	25	0	2	0
61-80	180	2	77	2	2	0	10	0	8	0	2	0
Total	5157	48	12[c]	5	11[c]	5	27[c]	9	45[c]	28	3[c]	1

[a]Percent of embryos from all inbred lines within the range indicated in left-most column.

[b]Number of inbred lines for which that class was the most frequent response.

[c]Average of all embryos.

formed mixed callus cultures more frequently than any other class; however, the average frequency for all lines was only 12% and embryos of 18 lines did not form any mixed callus cultures. The most frequent response (class 4) was that which led only to shoot and/or root emergence from the embryo axis. This result suggested that the interaction of 2,4-D concentration (.75 mg/l) and embryo size might not have been appropriate for mixed callus formation from some lines. An examination of average embryo sizes recorded at the time of isolation for individual ears revealed that the 18 poorest lines (0% class 1) and the 9 best lines (21-80% class 1) had similar ranges (.9-3.1 mm vs. 1.3-3.7 mm) and identical overall mean embryo length (2.0 mm). Moreover, a range of embryo sizes had been obtained for most inbred lines by sampling embryos from different ears. These observations indicate that there was a pronounced genotypic effect, which for most of the 48 inbred lines did not favor mixed callus formation.

Inocula from 15 mixed callus cultures were transferred to media lacking 2,4-D to determine the frequency of plantlet regeneration (Table 2). White Fung Kur 1 and Chi 31 were the best lines both for the formation of mixed callus cultures and

Table 2. Designation and performance of inbred lines tested for plant regeneration.

Inbred Lines	Embryo size range[1]	% Mixed callus	% Regeneration
White Fung Kur 1 (白风可1)	2.2 - 2.6 mm	80	93
Chi 31 (齐31)	1.9 - 2.4	76	82
White Golden 03 (白金03)	1.5 - 2.2	53	17
Lai 1029 (莱1029)	1.7 - 1.9	45	40
North 01-4 (北01-4)	1.3 - 2.1	42	0
Wu 105 (武105)	1.3 - 2.0	33	17
Ong 13 (翁13)	1.9 - 2.8	29	72
(Twun x Tzuh 330)S6 (墩x自330)S_6	1.5 - 2.0	27	59
Twun 23 (墩23)	1.9 - 3.7	23	0
Twun 034 (墩034)	1.6 - 2.5	18	67
Yellow 94-1-2 (黄94-1-2)	2.0 - 3.0	18	56
Selection 100 (自选)	1.9 - 2.6	16	33
Group 105 (群105)	1.6 - 2.1	14	8
North 7 (北7)	1.5 - 1.7	11	33
East 028 (东028)	2.5 - 3.2	10	67

[1]Values are means for individual ears based on 5 embryos/ear.

for the frequency of recovery of plantlets from cultures. Plants were not recovered from 2 lines, but the frequency of plantlet recovery from the other 11 lines did not seem related to the frequency with which mixed callus cultures had been established.

These results suggest that the 2 lines, White Fung Kur 1 and Chi 31, would be appropriate genotypes to use in maize tissue culture work. Other lines among the 48 tested also could be used but the conditions employed for the culture procedure may need to be altered for satisfactory performance. The 18 lines that were not cultured successfully seem to have a strong genotypic effect against culturability, although suitable combinations of embryo size and developmental stage and media composition might be found upon further experimentation. These 18 lines apparently are not closely related as they were obtained from different locations in China. All 48 lines have been maintained and small amounts of seed are available by contacting BGG.

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Cytological observations and measurements of endosperm nuclei

Investigations of the nuclei in the developing endosperm have been initiated. The ultimate goals of these studies are (1) to elucidate the cytological and molecular behavior of this tissue, and (2) to determine the feasibility of using this system for in situ hybridization. Mitotic index calculations, nuclear volume measurements, microspectrophotometer measurements of DNA, and cytological observations were made from A188 endosperms every two days following pollination. In addition, tritiated thymidine, chemical pretreatments, and in situ hybridization studies were performed using several different strains.

Generally, the 3N endosperm nucleus begins dividing within hours after fusion, and continues dividing rapidly for several days. At about the third or fourth day after fertilization, cell wall formation takes place. By the fifth day, the endosperm is entirely cellular. Cell and nuclear divisions eventually cease in the central region of the endosperm, and persist the longest time in the peripheral regions. The nuclei then become very large in the innermost region. Considerable starch formation can be noted by the twelfth post-pollination day. Any nuclear division during these later stages is found only in the outer aleurone region.

Mitotic index was determined for every two-day period of post-pollination from A188 selfs by making propionic carmine squashes of endosperm tissue fixed in Farmer's solution. The tissue was always taken from the central region of the endosperm. Random transects of the slide preparations were made, and all endosperm nuclei encountered in the microscopic field were tabulated. From 194 to 1150 cells were counted for each two days of post-pollination through day 20 (Fig. 1). Not a single endosperm nucleus was observed in mitosis after post-pollination day 12. It is not known if the data for day 2 and day 4 are biologically significant or simply the results of aberrant samples. The collection of data at these stages will be repeated.

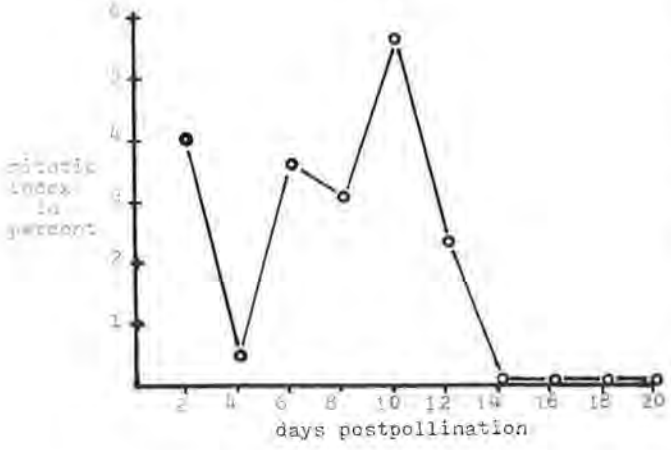

Figure 1.

Nuclear volumes in cubic microns were obtained from propionic carmine preparations which were made in the same manner as described above. Care was taken so as to prevent manual pressure to the nuclei, other than the placement of the cover glass. The nuclei in the endosperm tissue from A188 selfs were measured for every 2 days of post-pollination through day 20. Measurements were made with a Zeiss multiple operations processor MOP-3 system, and its units were subsequently converted to micron units. Random transects were again made, and all whole nuclei encountered in the microscopic field were measured until n equalled 60 at each stage. The diameter was determined by measuring the nucleus in both the longest and shortest directions and then averaging the two figures. Volumes were calculated assuming a spherical shape. A large range in nuclear size was noted within the tissue at each of the post-pollinated stages, especially within the older dates. The mean nuclear volume at two post-pollination days was 937.0 cubic

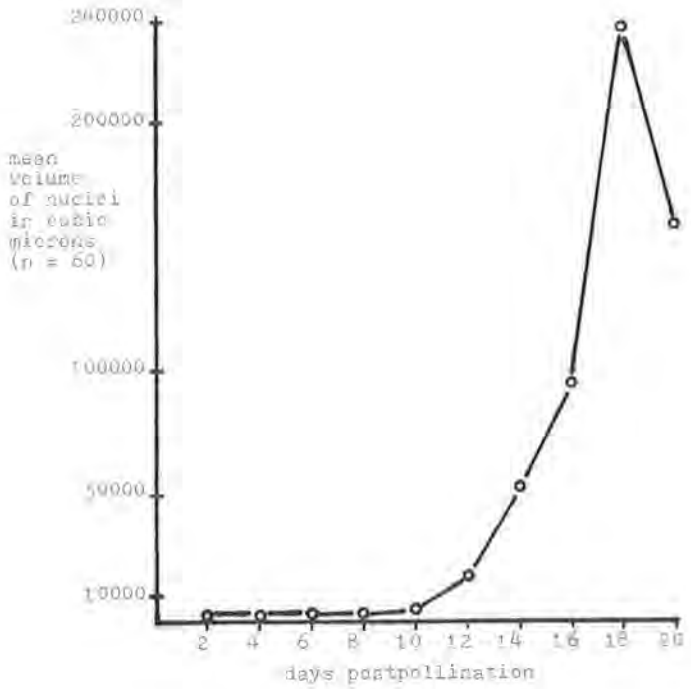

Figure 2.

microns, and at 18 post-pollination days the mean was 230,195.0 cubic microns (Fig. 2). This constitutes a mean volume increase of 255-fold, with some individual nuclei increasing as much as 975-fold. These increases also constitute a mean growth rate of 10.3 cubic microns per minute during the time period between day 2 and day 18. The decrease in mean volume at day 20 appears to be due to a nuclear breakdown that begins to occur in these older stages, with the larger nuclei being the most vulnerable. Generally, the nuclei after about 12 post-pollination days do not have a surrounding cytoplasm; rather they exist as naked entities. A marked increase in nuclear volume occurs after about 10 days. The mean growth rate from day 10 to day 18 was determined to be 20.3 cubic microns per minute.

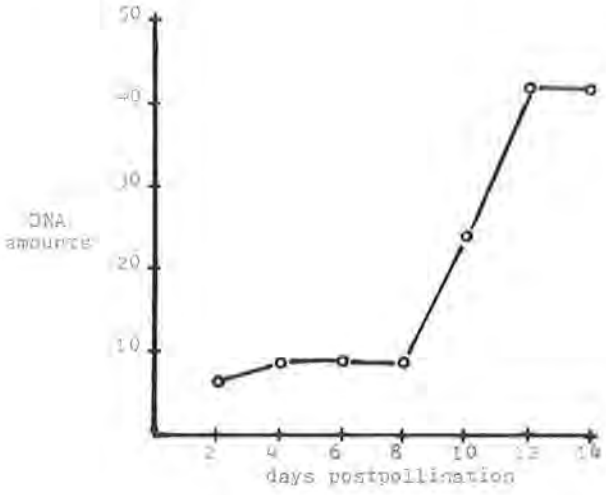

Figure 3.

Means for the DNA amounts per nucleus were determined for each two-day post-pollination period from day 2 through day 14. Feulgen technique was applied to the nuclei and the two-wavelength method was used with a Zeiss microspectrophotometer to gain the DNA measurements. A total of 30 nuclei were measured at each post-pollination stage. A mean increase in DNA amounts of 6.8-fold was calculated for the period between day 2 and day 14 (Fig. 3). A very sharp incline was observed after day 8.

The following linear correlation coefficients have been calculated from these data:

	Nuclear volumes	DNA amounts
Days post-pollination	.829	.906
Nuclear volumes	--	.730

All of the linear correlation coefficients are highly significant, statistically. In addition, a multiple correlation among all three variables shows a .906 correlation coefficient which is also highly significant. In this calculation, relative DNA amounts served as the dependent variable, and the nuclear volumes and days post-pollination were the independent variables.

Regardless of these high correlation coefficients, it can be noted that the nuclear volume increases at a much higher rate than does the DNA amount per nucleus. Figure 4 plots the ratio of nuclear volume to DNA amounts against days post-pollination.

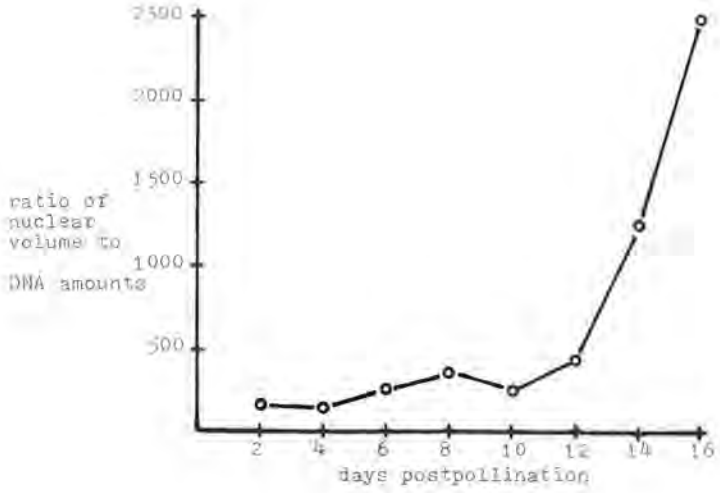

Figure 4.

These data prompt several conclusions and several more speculations. In the first place, there seems to be little question that the amount of DNA per nucleus increases as the endosperm develops. Feulgen photometry shows this DNA increase occurring somewhat concomitantly with nuclear volume increases. In addition, no mitoses are observed after 12 post-pollination days. In conjunction with this latter observation, tritiated thymidine autoradiographic experiments resulted in silver grain production directly over the chromatin of the nuclei, at stages later than 12 days. It appears that polyteny, endopolyploidy, or some other form of gene amplification is occurring. Since the DNA increase from day 2 to day 14 is approximately only seven-fold, the possibility exists that only certain regions of the chromatin complement are amplified. This amplification of a limited number of areas, however, may have to be immense to reach the seven-fold DNA increase that has been noted. Such conditions, if they do exist, may be ideal for in situ hybridization analyses of genes that are unique, or with few copies, in normal diploid tissue.

In situ hybridization with ^{125}I-labeled rRNA was successfully accomplished with these nuclei. A major drawback is the inability to recognize specific chromosomes because of the very diffuse state of the chromatin. Sixteen different chemical pretreatments at two different temperatures have not alleviated this problem.

Additional experimentation is presently being carried out and planned (1) to further elucidate the genetic system of the endosperm nuclei, and (2) to determine the feasibility of the system for in situ hybridization experiments. In this regard, cytological analyses, additional pretreatments, the use of cytological markers such as B chromosome translocations, and more autoradiographic studies are in progress. (Supported in part by NSF Grant PCM-7912069 A01 and administered through the University of Minnesota.)

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Inheritance of resistance to race 3 of Cochliobolus carbonum

Preliminary evidence has suggested that resistance to the maize disease caused by Cochliobolus carbonum race 3 is characterized by a reduced rate of disease increase and is quantitatively inherited. This study was designed to determine the nature of gene action governing resistance in maize to this disease.

Three sets of diallel crosses were made. In each of the first 2 sets, 7 maize inbred lines with different levels of resistance were crossed in all possible combinations. Three inbreds from each of these crosses were used as parents for the third cross. A total of 134 F1 and selfed progenies were screened for resistance to the pathogen in the growth chamber when seedlings were approximately 3 weeks old. Assessments for resistance were based on disease efficiency (DE), lesion length (LL), and sporulation capacity (SC).

The underlying genetic model in the diallel analysis assumes diploid segregation, no reciprocal differences between the progeny families, homozygous parents, no genotype-environment interactions, 2 alleles per locus, and absence of non-allelic gene interactions as well as linkage. The variance within each array of the diallel table and the parent-offspring covariance were calculated for each of the 3 replications by averaging the values of the F1's including reciprocals. The difference between the parent-offspring covariance and array variance was calculated for each replicate and averaged over the 3 replicates. Scaling tests were carried out to determine if the assumptions made for the diallel analysis were met. Regression of the parent-offspring covariances on array variances were computed to determine an appropriate model for the 3 characters in the study.

Analyses of variance of the diallel tables, similar to that of K. Mather and J. L. Jinks (1971, Biometrical Genetics), were computed to test the significance of the main genetic components, and to detect the presence of reciprocal differences among the progeny families.

The difference in parent-offspring covariance and array variance in crosses involving 2 parents in the one diallel were not homogenous. Therefore, they were removed from the analysis. The results of regression analyses of parent-offspring covariances on array variances indicated that a simple additive-dominance model with additive environmental effects and absence of gene interaction is adequate to describe the data. Only additive effects of genes were of primary importance in the inheritance of DE, LL, and SC. Average heterosis, line heterosis, specific combining ability effects, and maternal effects were occasionally significant, but were always much smaller than additive effect.

The only genetic variance estimate that exceeded twice its standard error was D, the additive genetic effect (Table 1). Other components H_1 (estimates of the dominance effects), H_2 (dominance effects measuring asymmetry of positive and

plants of Cónico Norteño in those plantings were completely or partially male-sterile. Fertile and nonfertile pollen on the partially sterile plants is indicative of gametophytic control, a characteristic of the cms-S system. Cónico Norteño was the only race, of the 17 Meso-American races examined, to exhibit the cms-S like traits. This observation has important implications. It establishes that a male-sterile system can exist and be maintained in indigenous populations of maize.

From the 44 South American accessions, 12 races (Coroico, Racimo de Uva, Kcello, Marron, Mochero, Guaribero, Morotí, Mishca, Araqüito, Pollo, Enano, and Chirimito) exhibited the same distinctive digestion fragment pattern, and each contained two plasmid-like DNAs similar to those of cms-S cytoplasm. We have temporarily designated this cytoplasm S*.

One of these molecules, S-2*, appears identical to the S-2 molecule in cms-S, although there may be micromolecular heterogeneity. Each has a molecular length of about 5450 nucleotides, the same BamHI cleavage sites, and terminal inverted repeats of about 155 nucleotides.

The other molecule, S-1*, has a length of about 7460 nucleotides whereas S-1 of cms-S has a length of about 6450 nucleotides. BamHI digestion of S-1* produces fragments of about 4560 and 2420 nucleotides, while S-1 of cms-S has no BamHI cleavage site. Heteroduplex analyses of S-1 and S-1* showed that these molecules have terminal homologous sequences of about 165 at one end and a homologous region of about 4719 nucleotides at the other end. Within the ends of S-1* is a terminal inverted repeat of about 152 nucleotides (Fig. 1).

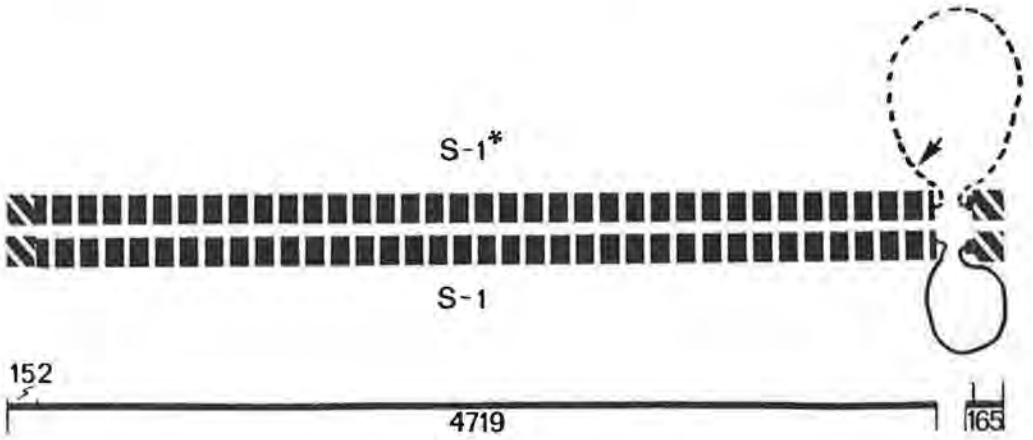

Fig. 1. Illustration of heteroduplexed mtDNA S-1* and S-1 molecules from S* and cms-S cytoplasms, respectively. DNA homologies are indicated by slashed, barred, and small-solid segments. Nonhomologous regions are indicated by thin solid or dotted lines. Approximate nucleotide length is indicated by numbers, and the BamHI restriction site is noted by the arrow.

The similarities of the S* plasmid-like molecules to, and partial homologies with, those of cms-S could imply their involvement in a male-sterile mechanism. However, we have found no male-sterility in the 12 races having the S* cytoplasm. Neither have we observed other phenotypic traits associated with this cytoplasm.

These molecules contain terminal inverted repeats, a characteristic common to transposable elements. They may have been derived by sequence excision from the large circular molecules of the mt genome. It is possible that these 12 races acquired the plasmid-like DNAs independently of each other. However, the disjunct distribution, geographically and racially, of the S* cytoplasm cannot preclude the possibility that these 12 races share a common ancestral cytoplasm. Finally, we have demonstrated that the presence of plasmid-like DNAs in maize is not a unique phenomenon, restricted to a single cytoplasm, the cms-S.

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Sequence rearrangements occur frequently in the evolution of mitochondrial DNA of maize and teosinte

In contrast with animal mitochondrial DNA (mtDNA), which is typically 10 megadaltons (Md) per mitochondrial genome, plant mtDNA is far more complex (Stadler Symp. 10:77-94). The maize mitochondrial genome has been estimated to be 320 Md (B. L. Ward, R. S. Anderson and A. J. Bendich, personal communication). In addition to larger size, plant mtDNAs are characterized by molecular heterogeneity (in Extrachromosomal DNA: ICN-UCLA Symposium on Molecular and Cellular Biology 15:63-73, Academic Press), observed as classes of circular chromosomes which vary in size, relative abundance and sequence (Devel. Genetics 1:363-378). In order to learn about the molecular events which have occurred in the evolution of these unusual DNAs, we have directed our attention to the mtDNA of maize and its closest relatives, the teosintes.

Three races of teosinte have been chosen for this analysis, based on systematic relationships and diversity of the restriction patterns of the mtDNA (PNAS 76: 4220-4224). Races Central Plateau (CP), Guatemala (GU) and perennial teosinte (ZP) were selected. CP is closely related to maize and was selected as a representative of annual teosintes. GU and ZP were selected because their mtDNAs are distinct from each other and each differs greatly from maize and the other teosintes.

Restriction enzyme analysis has been combined with DNA transfer techniques and molecular hybridization to follow molecular events which have occurred in the evolution of mtDNA. We have used cloned DNA fragments from normal (N) maize mtDNA as labeled DNA probes to detect the presence and size of specific sequences in restriction digests. Following electrophoresis and DNA transfer (using either nitrocellulose or DBM paper) labeled DNA from cloned probes was hybridized to the restriction digests. The number and size of the fragments with sequence homology were detected by autoradiography.

When single cloned fragments from N mtDNA are labeled by nick translation and hybridized to teosinte mtDNA, a complex variety of patterns appears. The results indicate a far more complex mode of evolution in mtDNA of maize and its relatives than has been observed in mtDNA of animals.

Twenty-three cloned fragments of N mtDNA were selected for this study. Each clone contains a single fragment of N mtDNA. All clones showed homology with specific fragments in all three races of teosinte, indicating general conservation of homologous sequences. Eight clones hybridized identically to N mtDNA and all three races of teosinte. However, most clones hybridized to bands of teosinte mtDNA which varied in position, number or intensity.

Only one cloned fragment demonstrated a change in teosinte which indicated a change in a single restriction site. In this case, clone 542, two bands appeared in GU and ZP which sum to the molecular weight of the fragment in N and CP. This type of change is typical of those observed in animal mtDNA (PNAS 77:3605-3609) but is relatively rare in the species examined in this study. Most patterns observed were more consistent with rearrangements rather than with site mutations.

The simplest kinds of rearrangement seen are inversion-type changes and insertion-deletion type changes. Other patterns observed are so complex that it would be hard to retain sequence homology if base substitution mutation were sufficiently extensive to generate such changes. DNA methylation could potentially result in patterns which could mimic both site changes and rearrangements, but extensive studies have shown that methylation does not occur to such an extent in mtDNA (B. L. Ward, R. S. Anderson and A. J. Bendich, personal communication; PNAS 77:6415-6519).

An interesting class of variation observed is that of intensity variants. In these cases, a given band is present in both species, but is greatly reduced in intensity. We propose that the restriction fragment has changed its relative abundance in the mtDNA because different classes of circular DNAs are known to vary in relative abundance (in Extrachromosomal DNA, Academic Press). Recombination or rearrangements involving different circle classes could generate a change in the abundance of a specific restriction fragment.

Our results indicate that the models of mtDNA evolution used for animal systems (PNAS 76:5269-5273) do not apply to plant mtDNA since rearrangements feature prominently in the evolution of sequence organization.

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Resistance to Helminthosporium turcicum from Tripsacum floridanum incorporated into corn

Many years ago Walton Galinat provided me with seed of a corn inbred crossed with T. floridanum. The hybrid expressed chlorotic-lesions (resistance) to the leaf blight caused by H. turcicum. The corn inbred was susceptible. The resistance persisted through backcrosses to susceptible corn. Resistant plants, however, were poor plant type and often partially fertile. After more generations of backcrossing and selfing with selection for resistance, normal looking and fertile corn plants with resistance were obtained. These can be identified as corn-T. floridanum (CTf) selections. The CTf selections have been used in backcross breeding and several inbreds with resistance from CTf obtained.

When crossed with susceptible inbreds, such as Hy-2 and Oh43, segregation for resistant (R), intermediate resistant (R-), or susceptible (S) lesion types has been regular and that of a single dominant gene as shown by the following data:

Population	Observed Ratio R	R-	S	Expected Ratio	P Value
Hy-2 x CTf F2	54	105	56	1:2:1	0.90 - 0.95
Oh43 x CTf F2	103	183	98	1:2:1	0.50 - 0.70
(Hy-2 x CTf) Hy-2	0	101	112	0:1:1	0.30 - 0.50
(Oh43 x CTf) Oh43	0	95	105	0:1:1	0.30 - 0.50
(Hy-2 x CTf) CTf	226	224	0	1:1:0	0.90 - 0.95

Homozygous plants are the most resistant.

Two other dominant gene loci, Ht and Ht2 (A. L. Hooker, Crop Science 17:132-135, 1977), for chlorotic lesion resistance to H. turcicum are known. When inbreds having Ht or Ht2 are crossed with CTf the CTf resistance segregates independently as shown by the following data:

Population	Observed Ratio R	Observed Ratio S	Expected Ratio	P Value
Ht Ht x CTf F2	211	15	15:1	0.80 - 0.90
(Ht Ht x CTf) Oh43	150	58	3:1	0.30 - 0.50
Ht2 Ht2 x CTf F2	284	17	15:1	0.50 - 0.70
(Ht2 Ht2 x CTf) Oh43	282	95	3:1	0.90 - 0.95

All evidence indicates that the resistance in CTf came from T. floridanum and that it segregates in a manner similar to that of a single dominant gene. I propose that it be given the symbol Ht3.

A. L. Hooker

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Breeding behavior of plants with a ring of ten or twelve chromosomes

The goal of continuing work is to produce a multiple interchange stock which will produce F1's with a ring of 20 chromosomes. Progress continues on the plan using the Inman convergent scheme of making crosses between lines that have interchanges in common, thus avoiding increases in sterility as interchanges are added (see pp. 113-114 in "Discussions in Cytogenetics").

A second plan was to utilize stocks which, when crossed with each other, would produce F1's with two rings with ten chromosomes each. From backcrosses to either parent, followed by selfing and selection, the goal was to establish a stock which combined the two. An interchange needed to produce the ring with 20 chromosomes would be produced by x-rays. In spite of considerable testing, no stock was established that would produce two rings of ten when crossed with normal. The problem appeared to be a high frequency of crossovers which reduced the number of chromosomes in the rings.

Since these multiple interchange stocks may have other uses, information on the kinds of progeny and their frequency are reported here. For this purpose, F1's with the big rings were crossed with normal stocks and the open pollinated progeny classified for ear sterilities similar to the parental types (either fertile or with very, very high sterility) and new combinations with lower sterility roughly corresponding to that for a ring of 8, 6, or 4 chromosomes. The results are:

Heterozygote Tested	Ear Sterility on Progeny: Parental F	Parental v.v.H.S.	Lower Sterility 0 8	Lower Sterility 0 6	Lower Sterility 0 4	v. low	% parental
1-5-6-7-8	58	69	39	18	20		62
3-2-4-9-10	66	63	23	44	31	2	56
5-7-1-9-10	28	70	33	26	30		52
6-3-2-4-8	81	83	56	53	62	4	49
5-7-1-9-10-8	32	34	11	7	7		75

The frequency of parental types from parents with a ring of ten ranged from 49 to 62%. For all except the 5-7-1-9-10 ring of ten, the two parental classes were roughly 1:1. Plants in the fertile class should have received from the normal parent the normal homologues of the interchange chromosomes, except for crossovers which had occurred in segments distal to the interchange breakpoints, thus contributing segments from the interchange chromosomes.

Seeds of the homozygous multiple interchange stocks and crosses are available.

Charles R. Burnham

Discussions in Cytogenetics

A sixth reprinting of "Discussions in Cytogenetics" @ $14.00 each, postpaid with stamps, not metered postage, is available from me at 1539 Branston Street, St. Paul, MN 55108.

Charles R. Burnham

Distribution of rRNA genes in the nucleolus organizer region

Twenty-three homozygous interchange stocks with a break in the short arm of chromosome 6 were used to study the distribution of rRNA genes in various segments of the nucleolus organizer region (NOR). Labeled rRNA was prepared either by iodination of 18S rRNA with ^{125}I-rRNA or by cRNA transcribed from cloned maize rDNA using ^{3}H-nucleoside triphosphates. In situ hybridization (Table 1) with ^{125}I-rRNA and ^{3}H-cRNA of interchanges T5-6d, T4-6(7328) and T2-6(001-15), all with a break in the chromosome 6 satellite (MGCNL 51:52), indicated that rRNA genes are not prevalent beyond the first chromomere of the satellite; no silver grains were observed over the second or third chromomere when translocated to other chromosomes. Interchange T1-6d has a break between the centromere and the NOR in the short arm of chromosome 6. Hybridization of T1-6d revealed the expected distribution of rRNA genes; all silver grains were localized over the NOR.

The cloned rDNA includes the non-transcribed spacer region (Benton, Ph.D. Thesis, Univ. Minn.). The ^{3}H-cRNA hybridized only to the NOR of the 15 homozygous interchanges and the inbred line A188. This observation suggests that the spacer sequence is probably not present at genomic locations other than the NOR.

At least part of the NOR-secondary constriction was separated from the NOR heterochromatin in 11 homozygous interchanges, namely T1-6(8415), T3-6(030-8), T1-6(4986-7), T2-6(027-4), T5-6f, T1-6(5495), T4-6Li (previously listed as T1-6Li), T3-6(032-3), T2-6(5419), T6-7(035-3) and T5-6(8696) (in Maize Breeding and Genetics, edited by Walden, 1978). Silver grains were observed over both segments after hybridizing with labeled rRNA. This indicates that the NOR-secondary constriction contains rRNA genes.

The cytological placement of breakpoints agrees well with the hybridization data. Cytology placed the break of T5-6f midway in the secondary constriction. Hybridization data suggested the break was in the proximal portion. This minor discrepancy was probably due to the difficulty in assigning the exact cytological breakpoint.

Interchange T6-10(5519) has a break at .90 in the NOR-heterochromatin and in situ hybridization revealed 70% of the silver grains over the proximal 90% of the NOR-heterochromatin (P/(P+D) ratio of .70). Interchanges T1-6(8415) and T3-6(030-8) both have a break in the proximal segment of the NOR-secondary constriction and also gave a 70% P/(P+D) ratio. These results suggest that 70% of the rRNA genes are localized in the NOR-heterochromatin and 30% in the NOR-secondary constriction.

Table 1. ^{3}H-cRNA/DNA and ^{125}I-rRNA/DNA *in situ* hybridization to interchanged chromosomes.

Interchange and Chromosome 6 Breakpoint	No. Silver Grains P (1)	No. Silver Grains D	P(2) / (P + D) (4,5)
T1-6 (6189) NOR Het. 0.10	9.30 ± 4.46	35.29 ± 12.10	0.21 ± 0.07 (67) c
T6-7 (4964) " " 0.32	6.70 ± 4.00	21.80 ± 11.60	0.24 ± 0.07 (40) I
T6-9d " " 0.46	5.72 ± 3.52	8.70 ± 5.08	0.40 ± 0.14 (120) I
T4-6 (4341) " " 0.50	13.33 ± 5.49	14.85 ± 5.72	0.47 ± 0.12 (149) cI
T6-9a " " 0.67	11.70 ± 6.40	7.50 ± 4.40	0.60 ± 0.09 (52) I
T6-7 (5181) " " 0.71	19.40 ± 12.40	10.00 ± 5.90	0.62 ± 0.11 (100) I
T2-6 (8786) " " 0.88	13.02 ± 5.33	6.14 ± 2.88	0.68 ± 0.09 (155) cI
T6-10 (5519)" " 0.90	16.00 ± 7.76	6.40 ± 3.34	0.70 ± 0.10 (51) c
T1-6 (8415) NOR S.C. Proximal	13.47 ± 5.91	5.07 ± 3.23	0.70 ± 0.10 (168) cI
T3-6 (030-8)" " "	13.85 ± 5.24	6.00 ± 3.18	0.70 ± 0.10 (101) I
T1-6 (4986·7)" " "	8.56 ± 3.44	3.61 ± 1.32	0.71 ± 0.06 (137) cI
T2-6 (027-4) " " "	11.42 ± 4.80	4.77 ± 3.62	0.71 ± 0.12 (163) cI
T5-6f NOR S.C. Midway	13.83 ± 8.29	3.94 ± 2.13	0.78 ± 0.10 (172) cI
T1-6 (5495) NOR S.C. Proximal	16.57 ± 6.27	4.49 ± 2.82	0.79 ± 0.10 (93) c
T4-6 Li(3) NOR S.C. Proximal	16.67 ± 7.95	4.41 ± 3.04	0.79 ± 0.11 (107) c
T3-6 (032-3) NOR S.C. Midway	18.20 ± 8.80	4.90 ± 2.80	0.79 ± 0.07 (20) I
T2-6 (5419) NOR S.C. Midway	21.74 ± 12.36	2.54 ± 1.38	0.90 ± 0.09 (120) c
T6-7 (035-3) " " "	18.11 ± 10.70	1.89 ± 1.37	0.91 ± 0.08 (26) c
T5-6 (8696) NOR S.C. Midway	19.40 ± 12.40	0.30 ± 1.00	0.99 ± 0.02 (42) I
T5-6d Satellite	16.60 ± 4.90	0	1.00 (35) I
T4-6 (7328) "	17.61 ± 4.28	0	1.00 (35) c
T2-6 (001-15) "	15.24 ± 5.45	0	1.00 (35) c
T1-6d 6S.74 (between cent & NOR)	0	18.24 ± 3.10	0 (35) c

1). P= proximal NOR segment, D= distal NOR segment, means and standard deviations are listed.

2). P/(P+D)= number silver grains associated with proximal NOR segment divided by sum of silver grains over proximal and distal NOR segments.

3). Previously listed as 1-6 Li.

4). Number of cells counted is given in parenthesis.

5). c=Cells were hybridized with ^{3}H-c RNA with a specific activity of 1.4 x 10^{8} dpm/ug. ^{3}H-cRNA was transcribed from cloned rDNA *in vitro* (cloned rDNA was a gift from Drs. G. Hagen and I. Rubenstein). Exposure time was 15 days.

I=Cells were hybridized with ^{125}I-rRNA with a specific activity of 5 x 10^{7} dpm/ug. Exposure time was 3-10 days.

cI=Pooled data of ^{3}H-cRNA and ^{125}I-rRNA hybridization.

The conclusion that 70% of the rRNA genes reside in the NOR-heterochromatin is in contrast to the 90% estimate of Givens and Phillips (Chromosoma 57:103-117), obtained by filter DNA/rRNA saturation hybridization. The discrepancy may be due to differential accessibility of the DNA for in situ hybridization between the NOR-heterochromatin and NOR-secondary constriction. The NOR-secondary constriction may be more readily hybridized than the NOR-heterochromatin.

R. L. Phillips and A. S. Wang

Nuclear volume, nucleolar volume and rDNA changes during endosperm development

Hybrid Wf9 x B37 plants were self-pollinated and the developing endosperm periodically collected, fixed overnight in 3 parts 95% alcohol and 1 part glacial acetic acid, and then stored at 4 C. A small piece of tissue was dissected from the central portion of the endosperm and squashed in propionic carmine. Nuclear and nucleolar areas were obtained using a Zeiss Multiple Operations Processor (MOP-3). Nuclear and nucleolar volumes were obtained from the following formulas: $V = 4/3\ \pi r^3$, $r = (\text{area}/\pi)^{\frac{1}{2}}$.

Mitoses were not observed on or after 16 days post-pollination (Table 1). Nuclei larger than 3,000 μ^3 were not observed undergoing mitosis. The frequency of telophase was much higher than other mitotic stages in 2 to 8 days post-pollination endosperm indicating that telophase is unusually long in young endosperm tissue.

Table 1. Number of endosperm cells at various mitotic stages during endosperm development of Wf9xB37 (self-pollinated). Cells were collected from the central portion of the endosperm.

Mitotic Stage	Days post-pollination												
	2	4	6	8	10	12	14	16	18	20	22	25	29
Prophase	20	4	8	27	22	5	16	0	0	0	0	0	0
Metaphase	8	4	2	3	3	0	3	0	0	0	0	0	0
Anaphase	10	2	2	2	2	1	2	0	0	0	0	0	0
Telophase	296	156	234	288	33	8	32	0	0	0	2	2	0
Interphase	192	274	116	157	400	520	491	513	560	567	633	696	692
Total	526	440	362	477	460	534	544	513	560	567	635	698	692

Number of nucleoli per nucleus at different developmental times is presented in Table 2. Diffuse nucleoli were observed in the majority of the nuclei at the earlier stages of endosperm development, namely 2 to 8 days post-pollination. A single nucleolus/cell was found to be the predominant type at later stages. Diffuse nucleoli were detected only in telophase nuclei suggesting that the telophase nucleolus requires considerable time to become organized in endosperm tissue.

Table 2. Number of cells with the indicated number of nucleoli/nucleus in endosperm cells of Wf9xB37 (self-pollinated). Cells were collected from the central portion of the endosperm.

No. Nucleoli	Days post-pollination												
	2	4	6	8	10	12	14	16	18	20	22	25	29
1	158	184	134	192	429	441	363	480	492	538	571	675	663
2	46	90	68	39	71	72	128	27	60	18	52	19	28
3	2	12	6	11	8	7	21	2	8	11	10	2	1
diffuse	258	138	258	282	26	2	24	0	0	0	2	2	0
Total	444	424	466	524	534	522	536	509	560	567	635	698	692

The nuclear volume increases 244-fold, from 368 μ^3 to 90,000 μ^3 at 2 to 22 days post-pollination (Fig. 1). The most substantial increase was observed between 16 and 22 days post-pollination even though no mitoses were observed during this period.

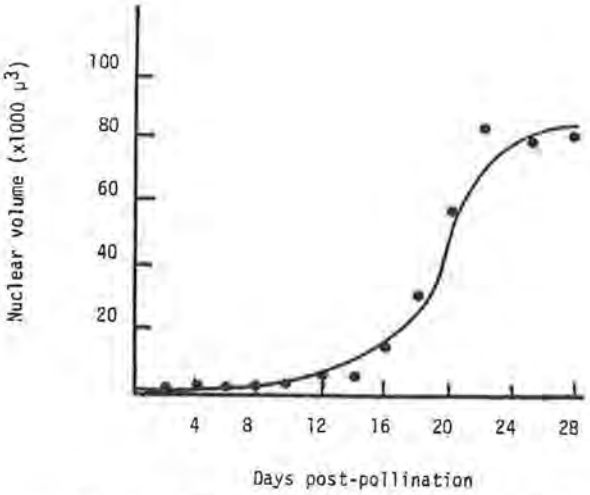

Fig. 1. Nuclear volume and endosperm age of hybrid Wf9xB37 (self-pollinated). Each value represents the average of 800 to 1000 endosperm cells.

Nuclei and nucleoli of interphase endosperm cells 12 days post-pollination were measured (Fig. 2). The nucleolar volume ranges from 50 μ^3 to 1900 μ^3. Nuclear and nucleolar volumes are closely related.

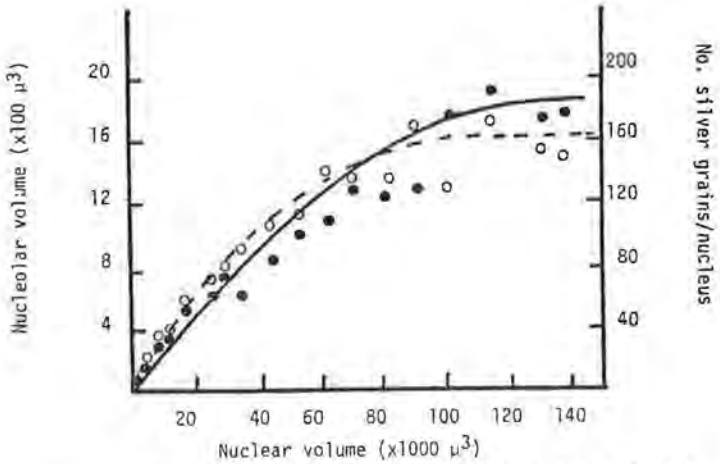

Fig. 2. Relationship between nuclear volume and nucleolar volume (closed circles) and between nuclear volume and number of silver grains from *in situ* hybridization with ^{125}I-rRNA (open circles). Each value represents the average of up to 200 nuclei.

Table 1. Estimates of the genetic varian-e components for DE, LL, and SC for the 3 diallel crosses sets A, B, and C.

Components	Estimates ± SE[a]		
	Set A	Set B	Set C
	Disease Efficiency (DE)		
D	6.0 ± 2.6	31.3 ± 8.5	18.5 ± 7.1
H_1	0.2 ± 9.9	1.2 ± 47.3	1.8 ± 24.7
H_2	1.7 ± 6.4	4.7 ± 27.4	5.4 ± 14.3
F	-1.3 ± 10.8	-0.8 ± 52.4	1.0 ± 29.5
E	0.3 ± 0.1	0.8 ± 0.1	0.7 ± 0.1
	Lesion Length (LL)		
D	3.0 ± 1.1	6.2 ± 3.6	5.7 ± 2.1
H_1	2.1 ± 3.6	3.4 ± 6.1	3.5 ± 7.9
H_2	1.6 ± 2.4	2.8 ± 3.0	4.3 ± 5.3
F	1.3 ± 4.0	5.1 ± 8.4	0.8 ± 0.4
E	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
	Sporulation Capacity (SC)		
D	13070 ± 6086	4604 ± 2264	14832 ± 9174
H_1	2615 ± 17103	968 ± 28363	5626 ± 19600
H_2	9721 ± 19967	2896 ± 28601	9684 ± 22522
F	1538 ± 27801	1466 ± 29242	6123 ± 15228
E	1495 ± 214	1495 ± 108	1054 ± 211

[a]SE = standard error.

negative effects of genes), and F (an indication of the covariance of additive and dominance effects) were smaller than their own standard error estimate and thus assumed not to be important. Environmental component of variation was symbolized by E.

The narrow-sense heritability estimates for DE, LL, and SC were 0.83, 0.60, and 0.37 respectively, indicating that it should be possible to select for resistance with reasonable success.

A. H. Hamid, J. E. Ayers and R. R. Hill, Jr.

The significance and analysis of host-pathogen interactions for polygenic resistance in maize

It is normally assumed that horizontal resistance in crop cultivars to different biotypes of plant pathogens is stable due to its polygenic inheritance. The durability of such resistance can be determined under constant exposure to the pathogen in replicated trials for a number of years under different environmental conditions. The cultivars that can sustain the original level of resistance are said to be stable. Such studies may not be feasible especially when financial constraints are imposed upon the breeders.

Our approach for estimating the stability of horizontal resistance to race 3 isolates of Cochliobolus carbonum was similar to that used by S. A. Eberhart and W. L. Russell (1966, Crop Sci. 6:36-40) to study yield performance of maize genotypes in different environments. In our model, maize inbred lines were exposed to various pathogen genotypes. Pathogen genotypes replaced "environments" in the Eberhart and Russell analysis.

Nine maize inbred lines with different levels of resistance were inoculated with six virulent isolates of C. carbonum and maintained in the growth chamber. Assessments for resistance were based on disease efficiency (DE), lesion length (LL), and sporulation capacity (SC). Analyses of variance demonstrated significant differences among host and among isolate genotypes. Since all interactions for the 3 resistance parameters were significant, generalizations could not be made on the relative performance of host lines over a wide range of pathogen genotypes.

A stability index for each isolate genotype was obtained as the difference between the mean of an isolate genotype on all host lines and the overall mean of all isolate genotypes on all host lines for DE, LL, and SC. Regression analysis was used for each host line with the stability index as the independent variable. The individual regression analyses were combined into an appropriate analysis of variance where the sum of squares measuring the isolates and host x isolate interactions were pooled and repartitioned into 3 items: common regression, residual, and pooled deviations (Table 1).

Table 1. Analyses of variance when stability parameters for DE, LL, and SC are estimated, based on six isolates of C. carbonum race 3.

Source	df	Mean Squares DE	LL	SC
Hosts (H)	8	57.8**	2.2**	84565**
Isolates (I) + Interactions (H x I)	45	28.5**	2.4**	45947**
Individual Regression	9	73.6**	8.7**	70089**
Common Regression	1	464.8**	73.3**	414249**
Residual	8	24.7**	0.6**	27069**
Pooled Deviation	36	27.2**	0.9**	39928**
Pooled Error	96	1.0	0.1	130

The results show that the mean square for common regression, the item which measures the difference between the slopes of the 9 regression lines, was significant (Table 1). The variation due to the residual component, which measures the scatter of points about the regression line, was also significant. The common regression indicated that host response is selected to average "fitness" of pathogen genotypes. Significant residual regression and pooled deviations mean squares indicated that large deviation from the average trend occurred. Thus, much of the variation was a host-pathogen genotype specific interaction.

The regression coefficients are in effect measures of response in the host to increased parasitic fitness of the isolates. Therefore, an inbred line has stable resistance when it has a low mean disease rating, a regression coefficient near zero, and small deviation from regression.

The regression coefficients for inbred line Va26 did not deviate significantly from zero, suggesting that this line is stable, by definition, for the 3 resistance parameters to all isolates (Table 2). The strikingly large standard error associated with the regression coefficient and the large deviation mean squares for DE and SC for this inbred line suggest that the individual points were in poor agreement with the fitted linear regressions. Lesion length response was somewhat

Table 2. Summary of stability parameters for DE, LL, and SC.

Hosts	DE $b_i \pm SE$	DE d^2_{ij}	LL $b_i \pm SE$	LL d^2_{ij}	SC $b_i \pm SE$	SC d^2_{ij}
Va26	0.4 ± 0.9	4.8	0.4 ± 1.6	2.8	0.0 ± 1.4	10971
B37	0.4 ± 0.7	3.5	1.2 ± 0.5*	0.3	0.6 ± 4.0	93255
H95	1.0 ± 1.2	10.1	1.2 ± 0.2*	0.5	1.8 ± 3.0	52552
MS72	0.8 ± 1.3	11.6	1.4 ± 0.3*	1.6	1.5 ± 2.9	59029
A632	-0.2 ± 1.1	8.0	1.6 ± 0.5*	0.5	1.6 ± 2.0	24658
Wf9	1.4 ± 1.4	13.6	1.2 ± 0.3*	0.1	1.9 ± 3.0	53034
B8B	1.7 ± 1.5*	15.1	1.3 ± 1.2*	1.7	0.2 ± 0.8	3328
W153R	1.9 ± 2.5	40.7	0.3 ± 0.2*	0.1	0.6 ± 3.1	55469
B14A	1.5 ± 2.6	44.4	0.8 ± 0.7*	0.6	0.3 ± 1.0	6155
Error		1.0		0.1		130

* regression coefficient deviates significantly from zero.

different from that with DE and SC (Table 1 and 2). Common regression was responsible for a large proportion of the total variation and regression coefficients often differed significantly from zero. Most regression coefficients did not differ significantly from 1.0. These results indicated that LL was largely determined by pathogen genotype. A high frequency of significant deviation mean squares indicated that specific host-pathogen interactions were also important. The large variation suggested that stable resistance will not be easily found. Further studies are needed on the limits within which these linear relationships are valid either by experimental investigations or by mathematical modelings.

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Probing photosystem II structure in maize mutants--herbicide binding studies

Several classes (chemical families) of herbicides are known to block photosystem II dependent electron transport at the level of the thylakoid membrane. The specificity of these herbicides for photosystem II makes them potentially powerful probes for elucidating the structure of the photosystem II complex. The mode of action of two such inhibitors, atrazine (a triazine herbicide) and diuron (a urea herbicide) have been extensively characterized; in both cases, these inhibitors act to block electron flow on the reducing side of photosystem II. Recently, K. Pfister, K. E. Steinback and C. J. Arntzen (Proc. Natl. Acad. Sci. USA, in press) have shown that a thylakoid membrane polypeptide with an apparent molecular weight between 32,000-34,000 becomes strongly labeled when stroma free thylakoids are incubated in the light with ^{14}C-azido atrazine, indicating that a polypeptide in this size range serves as at least a portion of the atrazine binding site, and further suggesting that this polypeptide is functionally associated with electron transport components located on the reducing side of photosystem II. We have previously reported that thylakoids isolated from the green photosystem II deficient maize mutant hcf*-3 exhibit the nearly specific loss of a thylakoid membrane polypeptide with an apparent molecular weight of 32,000, and we have hypothesized on the basis of electrophoretic and ultrastructural data that this polypeptide may be required for the assembly of (preexisting?) components of the photosystem II reaction center (K. Leto and C. D. Miles, Plant Physiol. 66:18-24; K. Leto and C. J. Arntzen, Biochim. Biophys. Acta, in press; MGCNL 54:117-118). Since both lines of evidence (inhibitor binding and mutant studies) suggest that the 32,000 dalton polypeptide is a component of the photosystem II reaction center, we have examined the binding of both atrazine and diuron to stroma-free thylakoids prepared from hcf*-3 and wild type control seedlings.

The binding of ^{14}C-atrazine and ^{14}C-diuron (both uniformly ring labeled) was performed as described by Pfister, Radosevitch, and Arntzen (Plant Physiol. 64:995-999). Basically, the procedure involves incubation of a known quantity of stroma-free thylakoid membranes (quantitated on a chlorophyll basis) with a known amount of ^{14}C-labeled inhibitor, followed by centrifugation to separate the membranes and bound inhibitor from the "free" (unbound) inhibitor remaining in the supernatant. The amount of free inhibitor was quantitated by liquid scintillation spectrometry, and the amount of inhibitor bound to the thylakoids calculated by subtraction. A hyperbolic plot of the data (free inhibitor vs. inhibitor bound/chl) was used to measure saturation of high affinity binding sites; the number of binding sites on a chlorophyll basis (chl/binding site, X_i) and the apparent binding constant (K_b) were determined from double reciprocal plots.

The binding constants and the number of binding sites for both atrazine and diuron in thylakoids isolated from hcf*-3 and control seedlings were as follows:

	Wild Type		hcf*-3	
Inhibitor	K_b	X_i	K_b	X_i
Atrazine	6.43×10^{-8}	340	1.68×10^{-7}	1800
Diuron	2.65×10^{-8}	300	1.13×10^{-7}	290

The values given for thylakoids obtained from control seedlings are in the range reported for other plant species similarly investigated. However, it is immediately apparent that the number of atrazine binding sites is greatly reduced in thylakoids prepared from hcf*-3 when compared to the number of sites observed in control thylakoids. In contrast, the number of diuron binding sites seen in thylakoids prepared from hcf*-3 was not reduced when compared to control membranes. Thylakoids prepared from hcf*-3 exhibited an increase in the binding constants for both atrazine and diuron, although the extent of this increase is small when compared to the extent of the loss of atrazine binding sites in these membranes. We conclude the following:

1) The loss of the 32,000 dalton lamellar polypeptide is accompanied by the parallel loss of photosystem II reaction centers and the loss of atrazine binding sites. Although alternative interpretations are possible, the data are consistent with the interpretations of Pfister et al. suggesting that a polypeptide in this size range is an integral part of the photosystem II complex and forms at least a portion of the atrazine binding site.

2) Although atrazine and diuron exhibit very similar modes of action at the level of the thylakoid membrane, the binding sites for the two are probably not identical, since thylakoids obtained from hcf*-3 contain a nearly normal number of diuron binding sites.

3) We have previously suggested that the 32,000 dalton thylakoid membrane polypeptide may be necessary for the organization of photosystem II, and that several of the polypeptides comprising the photosystem II reaction center complex may be present in an "unassembled" state in thylakoids obtained from hcf*-3. This hypothesis is supported by the discovery that thylakoids prepared from hcf*-3 contain a nearly normal number of diuron binding sites despite the loss of organized photosystem II reaction centers; diuron may be binding to photosystem II components which are present in these membranes but are not organized into functional reaction centers.

4) The observed increase in the herbicide binding constant for both atrazine and diuron in thylakoids isolated from hcf*-3 could be due to changes in the spatial orientation of the remaining photosystem II polypeptides, both with respect to each other and with respect to the lipid phase of the membrane.

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Flavonoids in maize pollen

We have made a broad survey of the flavonoids found in maize pollen and tested genotypes varying at the following loci (parentheses indicate the number of different alleles tested at each locus): A(5); A2(2); A3(2); B(2); Bz(2); Bz2(2); C(2); C2(3); In(2); P(4); Pl(2); Pr(2); R(6); and Sm(2). Pollen was extracted in methanol as some glycosides were unstable in acidified methanol. Duplicate extractions were made for genotypes with red or brown pollen, one in methanol and one in acidified methanol. The following is a summary of our findings to this point:

1) There were no flavones in any of the extracts.

2) Several Pl stocks had anthocyanins in the pollen, including some R-r B Pl lines, and most R-ch and r-ch Pl lines. The 'Chocolate pollen' of A. Tavcar (MGCNL 24:67) and the 'Pink pollen' of R. Brawn (MGCNL 29:33) were from purple anthered Pl stocks.

3) There were at least six pollen specific flavonol glycosides in most of the samples, and small amounts of quercetin 3-glucoside, the most common flavonol found in plant tissues. Some of the pollen specific flavonols are based on quercetin, others on isorhamnetin. Except for the compounds found in bz stocks (see below), all are glycosylated at the 3-position, and all are at least diglycosides.

4) In bz stocks, the concentrations of 3-glycosylated flavonols are markedly reduced, and they are replaced by at least three other glycosides that have the 3-hydroxyl free, and some aglycones. Bz/bz plants have normal amounts of the 3-glycosylated flavonols, and no flavonols with the 3-hydroxyl group free.

5) C2-Idf causes a marked reduction, but not a complete inhibition, of all flavonoids in both Bz and bz pollens. C2/C2-Idf plants have about 50% of the concentrations found in C2 C2.

6) Variations at the other loci had little if any qualitative or quantitative effects on the pollen glycoside patterns.

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Trisomics in Coix aquatica

Populations of C. aquatica (2n=10) are characterized by numerical and structural variations in chromosomes. Translocation hybridity, polysomy and polyploidy are often encountered, sometimes even as intraplant variation (P. N. Rao, 1976, Theoret. Appl. Genet. 48:179-184). In 314 trisomic plants isolated during a cytogenetic analysis of the species, the frequency of occurrence of different types of trisomics, their meiotic behavior and transmission of the trisomic character to the progeny were studied. In 147 of them the extra chromosome remained as univalent while the rest of the chromosomes formed 5 bivalents. 58 primary trisomics, 97 translocation trisomics and 12 tertiary trisomics were found. That all the 5 possible trisomics were encountered is evidenced by the differences in size and extent of heteropycnosis of the extra chromosome. The short chromosome trisomic was as frequent as the trisomic for the long chromosome. In all, trisomy involving the nucleolar chromosome was found in 66 cases. In translocation and tertiary trisomics, the higher associations involved up to 8 chromosomes in the former and 5 chromosomes in the latter. The extra chromosome, when unpaired with other

chromosomes, frequently paired within itself forming a ring. All the plants were pollen fertile to some extent, and a majority of them showed reasonable seed set. Transmission frequency of the extra chromosome to the progeny was variable (1.4% to 47.7%) and occurred both through male and female gametes in all the categories of trisomics.

Panuganti N. Rao

Inheritance of adherent seedling leaves in Coix

Adherence of seedling leaves in both C. aquatica (2n=10) and C. gigantea (2n=20) is governed by a single recessive gene designated as adh. The character is clearly seen at the 2-4 leaf stage. After 4-6 weeks, the adherence is resolved and the subsequent growth is normal. The heterozygous plants are phenotypically normal. All the 14 F1 interspecific hybrids (2n=15), between C. aquatica and C. gigantea, involving mutant parent plants, also showed adherent leaves in seedlings, indicating that genes controlling this character in the two species are allelic.

Panuganti N. Rao

Chromosome pairing in interspecific hybrids between Coix aquatica (2n=10) and C. lacryma-jobi (2n=20)

Reciprocal hybrids between C. aquatica and C. lacryma-jobi, obtained naturally and by deliberate crossing, showed 2n=15 chromosomes. Chromosome pairing was studied in these hybrids at diakinesis and metaphase I. Although at pachytene 6 of the chromosomes in C. lacryma-jobi are longer than the shortest chromosome in C. aquatica (J. Venkateswarlu, R. S. K. Chaganti, and P. N. Rao, 1976, Bot. Mus. Leafl. Harvard Univ. 14:205-224), in the hybrids, from diakinesis onwards, the 5 aquatica chromosomes appear distinctly longer than all the chromosomes of lacryma-jobi, due to differential levels of heteropycnosity and condensation of chromosomes in the two species. This distinction of chromosomes belonging to the two genomes is substantiated from chromosome behavior in triploid hybrids (3n=25) between induced tetraploid lacryma-jobi (4n=40) and C. aquatica (2n=10) in which the 20 small chromosomes of lacryma-jobi formed 10 bivalents and the 5 large chromosomes of aquatica mostly remained as univalents.

This distinctive feature of the chromosomes of the two species, when present in the same nucleus, facilitated the study of intergenomic and intragenomic pairing in the hybrids. The highest associations encountered were two associations of 3 chromosomes each (mostly comprising one aquatica and two lacryma-jobi chromosomes) with a mean of 0.328 per cell. Heteromorphic bivalents involving aquatica and lacryma-jobi chromosomes occurred with an average of 2.121 and a range of 0 to 5 per cell. These were mostly rods and occasionally rings. Intragenomic bivalents among aquatica chromosomes were predominantly rods, and occurred with an average of 0.155 per cell. The aquatica univalents ranged between 0 and 5 with a mean of 2.224 per cell. They occasionally showed inter-arm pairing. Pairing amongst lacryma-jobi chromosomes was quite rare, occurring with a frequency of not more than one bivalent per cell with a mean of 0.086. The lacryma-jobi univalents ranged between 2 and 10 with an average of 7.086 per cell. Further divisions of meiosis were very irregular, leading to near complete pollen sterility and meagre seed set even under open pollinated conditions.

The meiotic behavior in hybrids provides some understanding of the genomic constitution of the two species. The occurrence of 5 heteromorphic bivalents suggests that in C. lacryma-jobi there are 2 genomes of 5 chromosomes each and that one of them is apparently derived from C. aquatica. The formation of higher associations of 3 chromosomes and occasional intragenomic pairing in lacryma-jobi

chromosomes suggests that the second genome of 5 chromosomes is related to the first one. The occurrence of inter-arm pairing in univalent chromosomes and intragenomic bivalents in aquatica complement reveal the existence of both intra and interchromosomal duplications in the aquatica genome.

Panuganti N. Rao

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Evergreen stalks as an indicator of perennialism

The short growing season and long day-lengths during summer in Massachusetts make it a poor location compared to sub-tropical and tropical areas to study the inheritance and linkage of perennialism from diploperennis. After a series of killing frosts in late October and early November, the stalks of diploperennis as well as its F1 hybrid with maize and of a majority of plants in an F2 maize-teosinte segregation remained alive (green) with only the leaves being dead. In contrast both stalks and leaves of annual corn had been dead for about one month. Four of the evergreen stalk segregates from the F2 were dug from the field and transferred to the greenhouse. They have now developed a flush of basal shoots, indicating the validity of classifying for evergreen stalks as one component of perennialism.

Walton C. Galinat

The inheritance and linkage of perennialism derived from diploperennis

An F2 of the hybrid between diploperennis and WMT corn yielded 217 plants that were scored for Su su, Gl gl, Lg lg and evergreen vs. dead stalks. The data are as follows:

	Su	su	Gl	gl	Lg	lg	Observed Total	Expected 9:7	d^2/e
Evergreen	105	14	97	29	100	26	126	121	0.206
Dead	57	41	68	23	64	27	91	96	0.260
Totals	162	55	165	52	164	53	217	217	0.466

χ^2 = 0.466 with a probability of ca. 50% at 1 d.f. In other words, the observed does not differ significantly from a 9:7 ratio.

It is probable that the evergreen stalk is at least one component in perennialism and that its inheritance is at least partially controlled by two dominant complementary genes. Of the various WMT marker genes involved in the F2 segregation, three were scored (su, gl, lg) for possible linkage with perennialism. Glossy and liguleless segregated independently but the segregation of sugary-starchy is grossly distorted by the separation into the evergreen vs. dead classes. The sugary class is low in evergreen stalks and high in dead stalks while starchy is the reciprocal. Therefore it seems that one component of the perennial trait is located on chromosome 4.

Previously, D. L. Shaver (MNL 46:20, 1972) has suggested that three genes (id, gt, pe) may control perennialism. Perhaps a fourth trait of complex inheritance that produces vegetative dormancy under drought stress may be carried by diploperennis. This trait termed "latente" was first identified in Michoacan 21, as reviewed by Castleberry and Lerette (1979) of DeKalb AgResearch.

Walton C. Galinat

Preliminary observations on Zea diploperennis and its hybrid with Zea mays

Meiosis in Zea diploperennis Iltis, Doebley and Guzman is normal. At diakinesis ten bivalents are formed. The pachytene chromosomes show normal synapsis and are terminated by prominent chromomeres which may be referred to as small knobs. There are 11 to 13 terminal knob positions. Although these positions are constant in subtending one or both arms, they have knob-like structures ranging in size from that of a prominent chromomere up to that of a more obvious knob. Similar observations have been recorded for the tetraploid perennial teosinte (A. E. Longley 1941). In this feature they differ from maize chromosomes which have internal knobs.

The total lengths of the ten chromosomes of diploperennis in comparison with maize are slightly longer, especially three of them, namely chromosomes 2, 3 and 7 where the difference is significant. This was confirmed in the hybrid material where the teosinte chromosomes could be seen extending beyond their maize homologue. The arm ratios are almost the same for both maize and diploperennis. A table comparing the total lengths and arm ratios from a total of about 400 cells observed at pachytene is given below.

Total Lengths		Arm Ratios	
Maize*	Teosinte	Maize	Teosinte
65.49	68.35	1.2	1.3
56.06	64.35	1.4	1.8
51.19	61.49	2.0	2.0
50.05	52.91	1.6	1.6
50.05	48.62	1.1	1.1
34.89	40.04	3.2	3.2
40.04	51.48	2.6	2.3
40.04	44.33	3.0	3.3
34.89	37.18	2.0	2.0
28.60	32.89	2.6	2.7

*(Rhoades, 1950)

In the hybrid between maize and diploperennis meiosis was normal. At diakinesis in 90% of the cells ten bivalents were formed. But occasionally microsporocytes with two univalents were also seen. Pollen fertility was normal.

In almost all the teosintes, inversions have been reported in one chromosome or the other. The chromosomes of this hybrid showed two heterozygous inversions, a paracentric inversion loop in the long arm of chromosome 5 and a terminal inversion loop in the short arm of chromosome 9. In some cells the terminal inversion in chromosome 9 did not form a loop, but the inverted segments remained unpaired. Though the inversions were observed there was no sign of bridges or fragments in the 400 cells studied so far. This could be due to failure of recombination in the region of the inversion or due to infrequency of their occurrence.

It is significant that the tetraploid perennial teosinte (Z. perennis) has the same chromosome 9 inversion, reported by Y. C. Ting, as that reported here for the diploid. Thus, most of the cytological evidence supports the contention that the tetraploid is an ancient autotetraploid of the diploid and therefore that the two taxa should be considered as a single species.

C. V. Pasupuleti and W. C. Galinat

The reciprocal switching of binate vs. solitary female spikes and spikelets during a separation of teosinte and maize

Two of the changes from teosinte to maize seem to represent reciprocal differences. When the solitary female spikelets of teosinte became binate (paired) in maize, simultaneously the paired spikes of teosinte became solitary in maize. In the origin of paired female spikelets in maize, the rudimentary pedicellate member of the pair was reactivated. In the reciprocal switch to solitary spikes (ears) in maize, the sessile member is usually suppressed. Since these differences involve secondary sex traits within teosinte and maize as well as between these species, there is usually instability in switching the phenotype. When one transfers solitary female spikelets to modern maize, the expression is usually unstable. Paired ears in modern maize usually occur at a low frequency (one in 500?) and their expression is unstable. The combination of solitary spikelets with paired ears in maize should be both stable and successful in novelty types such as the square sweet corn.

Walton C. Galinat

Regulation of secondary sex traits in Zea

Teosinte and maize differ primarily in the secondary sex traits associated with female development. The programs for secondary female traits in these species have been genetically assembled by different selective pressures, a natural one in teosinte and a domestic one in maize. The various secondary traits include developmental modifications to various structures: the cupule (large to rudimentary); spikelets (single, paired); outer glumes (hard, soft); pith (small, large); condensation (relaxed, tight); apical dominance (weak, strong) and others.

Cupules in the female spikes of both teosinte and maize are adaptive but for different reasons. As the maize cob emerged, the cupule was preadapted to a transfer of function from protecting the grain to a mechanical support of the cob that prevents dry-cob shrinkage and, thereby, kernel shattering. When the non-cupulate condition of the male rachis in both species is genetically transferred to the female rachis, the new combination is incongruous in maize except when there is an absence of kernel crowding in certain low condensation strains. The non-cupulate condition is non-adaptive in the female spike of teosinte because it removes bird protection.

When the paired condition of male spikelets normal to both species also occurs with the female spikelets, it has opposite selective values. A change from solitary to paired female spikelets in teosinte opens its cupulate fruit case and, thereby, reduces its value as a protective device. Because such protection in maize comes from enclosing husk leaves borne below the ear, pairing of the kernels, like multi-ranking, results in the domestic advantage of increasing productivity per ear.

Walton C. Galinat

Reversal of dominance for two-ranking in hybrids with low condensation eight-rowed maize

The two-ranked or four-rowed ear of maize has always been reported as a recessive trait that is a common mutant or variant in eight-rowed maize. It is often unstable in expression in that only a portion of the ear, usually the upper part, will be four-rowed or with different ears on the same plant, one may be four-rowed and others eight-rowed. Seed from a four-rowed ear may produce eight-rowed ears and vice versa. The stunting of eight-rowed maize sometimes causes it to produce ears with only four rows.

As reported previously, we have stabilized the expression of two-ranking in maize through the transfer of a segment from Tripsacum chromosome 9 to the short arm of maize chromosome 2. In segregations with typical eight-rowed maize, two-ranking behaved as if controlled by a single recessive gene. But when hybrids of our two-ranking strains involved in our square-ear sweet corn breeding program were hybridized to our string cob inbred, W-401, the F1 hybrids were consistently two-ranked. Inbred W-401 was bred for a low condensation level approaching that of teosinte and similar to that of the oldest known archaeological maize cobs. Thus at this primitive state, two-ranking is dominant over four-ranking, as would be expected during the emergence of maize.

Walton C. Galinat

The small pollen of teosinte is coadaptive with the more slender, thin-walled styles of teosinte

There has been a question as to why modern teosinte, that is sympatric with maize, has pollen that is smaller than that of modern maize. Because of this fact, one group of researchers (P. C. Mangelsdorf, E. S. Barghoorn and U. C. Banerjee, 1978) claim that the large size of a few very ancient pollen grains proves that the ancestor of cultivated maize is a wild maize and not teosinte based on this one trait. They overlook the possibility that the large pollen could have come from a raw tetraploid of teosinte, as suggested by G. W. Beadle. In any case, the problem remains as to why the teosintes in contact with maize have small pollen while the teosintes more isolated from maize such as the Guatemala and Honduras races have pollen about the same size as that of primitive corn as represented by the race Chapalote.

It was previously known that at lengths greater than 2.5 cm in maize styles, the maize pollen tubes rapidly outgrow those of teosinte (Aquirre-Gonzalez, 1977). But the problem of teosinte protection from swamping by maize involves tube competition within teosinte styles. Preliminary studies of the teosinte styles by Dr. Chandra Pasupuleti indicate that they have fewer cells with thinner walls than maize styles. Therefore, there was reason to believe that the pollen competition in the two kinds of styles might have different results. Research plans include photographing the pollen tubes from the two sizes of pollen as they penetrate and grow in teosinte styles. A fluorescent stain (Martin's aniline blue) and a fluorescence microscope would be used.

In order to test out the possibility that the thinner pollen tubes from the smaller pollen of teosinte might worm their way more rapidly between the thinner smaller cells of the teosinte styles than the thicker tubes from the larger pollen of maize, we used the standard technique of pollen mixtures with only one stock carrying genes for aleurone color. In this case, a strain of Hopi flour corn with purple aleurone was used as the corn pollen and some of the teosinte's own pollen as the colorless teosinte source. The teosinte has a light brown pericarp which made it necessary to score the kernels for aleurone color on a fluorescent light table. Reserve samples of each mixture of pollen used were saved to eventually plot out the frequency distribution of large vs. small pollen that actually went into the mixture. We tried to get a 50-50 mixture of the two types of pollen but because of their unequal size, this may not have been achieved. In any case, the results obtained with fertilization rates will be compared to the pollen size distribution used. At this writing, we have not had time to plot out the distribution of pollen diameters for the various mixtures used and so only the kernel data are given here as follows:

Date	No. Spike Clusters	Aleurone color	
		None	Purple
8/23	4	23	8
8/27	18	154	8
8/30	3	33	2
8/31	7	134	56
9/1	5	35	8
Total	37	379	82
Expected	--	236	236

If the pollen mixture was approximately 50% corn and 50% teosinte, it is seen that there is a great excess of fertilization on teosinte styles by teosinte pollen. This is about the opposite to that which might have occurred had the same pollen mixture been placed on corn styles.

We are postulating that the small pollen and slender styles of teosinte that is sympatric with maize evolved as a protective device within teosinte to reduce the possibility of swamping by maize.

The teosinte kernels were cut from their fruit cases and scored for aleurone color by Mrs. Josephine Starbuck.

W. C. Galinat, J. S. Starbuck and C. V. Pasupuleti

Heterotic responses of maize hybrids containing alien germplasm

A synergistic effect, observable as a significant increase in yield, has been measured in several maize hybrid lines, each of which carried a different introgressed segment of genes from teosinte plus a short chromosomal segment from Tripsacum. These results are just part of the data collected from a three-year yield trial at Waltham. F1 hybrids were produced the summer before their being planted in the trial. Data were collected by lines, blocks and replications as shown in Table I.

TABLE I
Explanation of the hybrid pedigrees

PEDIGREE (Genotypes)	BLOCK I	BLOCK II	BLOCK III
INBRED:A158 w/homozygous teosinte chromosomal substitutions	INBRED:A158	INBRED:Havels-A158 (no Tripsacum)	INBRED:Havels-A158 w/extra Trips (Tr_7 disomic
t_1)Florida teos. sub 3	F_1:t_1xA158	F_1:t_1xHav-A158	F_1:t_1xHav-Tr7
t_2)Florida teos. sub 4	F_1:t_2xA158	F_1:t_2xHav-A158	F_1:t_2xHav-Tr7
t_3)Florida teos. sub 9	F_1:t_3xA158	F_1:t_3xHav-A158	F_1:t_3xHav-Tr7
t_4)Florida teos. sub 4,9	F_1:t_4xA158	F_1:t_4xHav-A158	F_1:t_4xHav-Tr7
t_5)Florida teos. sub 3,4,9	F_1:t_5xA158	F_1:t_5xHav-A158	F_1:t_5xHav-Tr7
t_6)Nobogame teos. sub 4	F_1:t_6xA158	F_1:t_6xHav-A158	F_1:t_6xHav-Tr7
t_7)Durango teos. sub 1,7,9	F_1:t_7xA158	F_1:t_7xHav-A158	F_1:t_7xHav-Tr7
t_8)A-158 No teos. Control	F_1:t_8xA158	F_1:t_8xHav-A158	F_1:t_8xHav-Tr7

By summing the data from the three trial replications, the yield of each of the 24 different lines can be compared. This tabulation is presented in Table II. As can be seen by the means in Block 1, the differing amounts of teosinte germplasm

TABLE II
Total and mean yields

BLOCKS	TOTAL YLD IN KG	LINE MEAN IN KG	BLOCK MEAN IN KG	OVERALL LINE
Blk 1	(n=6)	(n=6)	1.35	MEANS
Line a	7.50	1.25	(n=48)	1.67
Line b	8.03	1.39		1.78
Line c	8.97	1.49		1.97
Line d	7.32	1.22		1.83
Line e	8.25	1.37		1.84
Line f	7.47	1.24		1.47
Line g	10.58	1.76		1.95
Line h	6.78	1.13		1.59
Total	64.90			(n=18)
Blk 2			1.90	
Line a	10.50	1.75	(n=48)	
Line b	11.46	1.91		
Line c	12.63	2.10		
Line d	11.03	1.83		
Line e	12.82	2.13		
Line f	9.57	1.59		
Line g	12.28	2.04		
Line h	10.99	1.83		
Total	91.28			
Blk 3			2.04	
Line a	11.98	1.99	(n=48)	
Line b	12.40	2.10		
Line c	13.97	2.33		
Line d	14.60	2.43		
Line e	12.04	2.00		
Line f	9.47	1.57		
Line g	12.34	2.05		
Line h	10.96	1.82		
Total	97.76			
Overall Mean= 1.76 (n=144)				

have a significant effect in altering the yields about the mean of the control, 1.13 Kg. This becomes more evident in Block 2, but even more pronounced in Block 3 which contains the Tr-7 monosomic chromosomal segment.

The control mean (line h) in Block 3 is 1.82 Kg which is almost identical to the control mean of Block 2. It should be noted that these are the lines that have no introgressed teosinte present. However, in lines b, c, and d, which contain various teosinte segments plus the Tr-7 segment, the yield is higher than the related lines in Block 2 which have no Tripsacum. In other cases, such as in line g, the Tripsacum seemed to have made little if any difference.

A Duncan's Multiple Range test will be run on all of the line means and a more complete ANOVA covering 12 other dependent variables is yet to be done. Correlations between an increase in prolificacy and yield will also be studied.

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Genetic variation at the vp7 locus

Identification/isolation of certain maize mutants often depends upon or is made easier by observing one or more specific developmental stages. Prevalent among such mutants are those which delay but do not ultimately inhibit pigment development. Over the years, I have had occasion to "tide over" my hogs from one dry maize crop to the next by shucking and feeding immature ears. Thus I have had economic reason to observe a considerable number of immature endosperms of field maize wherein the major pigment is carotene. Several seed mutants with delayed carotene development have come to my attention. This report concerns a class which accumulates the pink carotene precursor, lycopene.

During the summer of 1979, out of about 30,000 dough stage ears from the high-lysine hybrid, "Pioneer 3369L," I found five with scattered pink endosperms. Two of these had mild vivipary (slight plumule elongation) associated with the pink endosperms, while three did not. As all five ears dried, the pink endosperms faded to an indistinguishable yellow. Embryos retained the pink color, though it was difficult to detect without sectioning them. Among about 250,000 additional ears from the same hybrid examined at maturity the same year, I found one with scattered pink endosperms and highly viviparous embryos (extensive plumule and radical elongation).

During the spring of 1980, all kernels from one non-viviparous ear, one mildly viviparous ear, and the highly viviparous ear were planted in separate isolation plots. Pink embryos from the non-viviparous ear produced albino seedlings which died at the three leaf stage. None of the mildly or highly viviparous seeds germinated. About half the open pollinated ears from each plot had scattered pink kernels in the late dough stage. Several plants in each plot were selfed, and approximately half of these produced a 3:1 yellow to pink endosperm ratio in the late dough stage. Bulk pollinations proved all three of my isolates to be alleles of one another and of vp7 supplied by Dr. R. J. Lambert. Mutant hybrid kernels expressed the degree of vivipary of the least viviparous parent. In other words, my non-viviparous allele suppressed vivipary when combined with either of my other two alleles or with Dr. Lambert's (mildly viviparous) allele. Likewise, my mildly viviparous allele attenuated vivipary when combined with my highly viviparous allele. The pink pigment of all three alleles was identified as lycopene by TLC.

Once genetic backgrounds have been stabilized, I intend to quantify the relative amounts of lycopene and other carotenoids and of abscisic acid produced by each allele. My family enjoyed "strawberries and cream" roasting ears left over from samplings for chromatography, and I have begun to move the non-viviparous allele into su and sh2 backgrounds. Homozygous vp7 seedlings produced from seed using the non-viviparous allele should prove to be of value in carotenoid pathway analysis.

Absalom F. Williams

Seed development on prematurely harvested maize ears

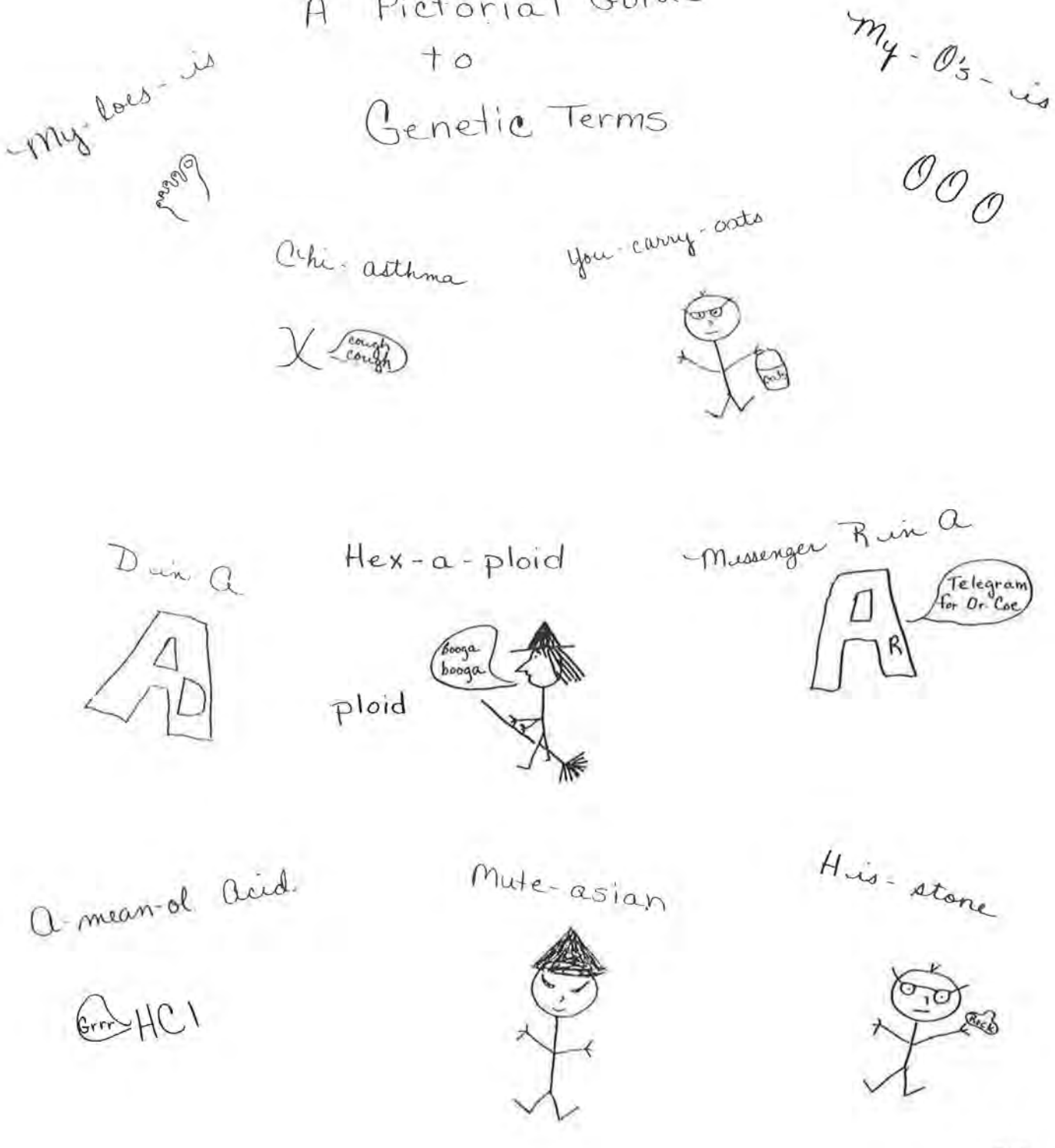
Up to 10% of the seeds on maize ears harvested while kernels are in early to mid-milk stage (ca. 10-20 days post-pollination) will develop to maturity if the ears are stored at July-August temperature and humidity. Mold growth and excess drying can be problems, though damaged ears without shucks, shanks, or tips work perfectly well under proper storage conditions. The most nearly ideal storage place I have found is a high shelf on a screened north porch. Onset of post-harvest development can be delayed for at least a couple of weeks by refrigerating ears (4 C) in a dry, air-tight container.

I have on occasion used this "poor man's embryo culture" technique to save stocks and crosses damaged by livestock or wildlife. Its all-or-none character for each kernel allows easy quantification and implies utility in physiological and genetic studies of seed development. Developing kernels tend to be scattered evenly among and within rows. Carbohydrates are apparently mobilized from arrested to developing kernels. Shallow injection of 0.1 ml .001% GA into the cob often stimulates development of a cluster of kernels around the injection site. Percentage of kernels undergoing post-harvest development drops almost to zero after about 20 days post-pollination, perhaps because assembly of starch synthesizing machinery reaches an "irreversible stage" at this time. Among viviparous non-alleles so far tested, only vp stimulates development of homozygous kernels on ears from heterozygous plants. Several defective-starch genes reduce propensity for development of homozygous kernels on heterozygous ears, but at least one (an

unmapped "collapsed endosperm" gene) favors development when heterozygous. I'm in the process of seeing if repeated selection based on post-harvest development can produce strains with improved efficiency of grain "nutrient sinks."

Absalom F. Williams

A Pictorial Guide to Genetic Terms



ADDENDUM

AMES, IOWA
Iowa State University

Seedling mutants l*-Blandy3 and l*-Blandy3drk: A clarification

It has come to my attention that there is some confusion with regard to the mutants l*-Blandy3, l*-Blandy3drk and l*-Blandy4. Stocks of l*-Blandy3 and l*-Blandy4 originally came from the Blandy Experimental Farm, Virginia. Mutant l*-Blandy3 is a medium yellow seedling mutant with some greening observed in older seedlings, l*-Blandy3drk is a mutant that occurred in stocks of l*-Blandy3 and l*-Blandy4 is a dark yellow luteus mutant. Seedlings of l*-Blandy3drk differed from l*-Blandy3 seedlings in that the former are much darker yellow. Originally l*-Blandy3drk was thought to be a dark yellow allele of l*-Blandy3, hence the symbol l*-Blandy3drk. Allele tests, however, showed that it was not allelic to l*-Blandy3. P. Mascia and D. S. Robertson (J. Hered. 71:19-24, 1980) established that it is allelic to l*-Blandy4, located on the short arm of chromosome 5. It is possible that the original l*-Blandy3drk was the result of contamination because the two lines were grown in close proximity for several generations. The mutant l*-Blandy3 is known to be on chromosome 6 (Robertson, MNL 47:82-87, 1973). The symbol l15 has recently been assigned to l*-Blandy3. There is a second allele at this locus, l15-Brawn.

Donald S. Robertson

COLUMBIA, MISSOURI
University of Missouri and U.S. Dept. of Agriculture

Linkage studies to locate whp

E. H. Coe and S. McCormick (MNL 53:29) have reported that a new locus, whp, acting as a duplicate factor with c2, causes sand-white, plump, non-functional pollen to be shed. TB lines have been or are being converted to either +/+, C2/c2 or +/+, c2/c2 constitution for crossing to a uniform strain that is whp/whp and either C2/c2 or c2/c2.

The first observations of critical crosses were done this past summer. Plants grown from colorless kernels derived from valid TB males were classified for hypoploids by greater than 50% pollen abortion and/or by gross plant phenotype.

Since all hypoploids scored shed yellow pollen, whp does not appear to be located on any of the following chromosome arm segments:

Arm segment	Total no. plants scored	No. of hypoploid plants
1La	109	15
3Sb	104	26
3La	38	11
4Sa	162	17
5La	190	34
6Lc	163	64
7Lb	155	37
8La	69	10
9Sb	106	14
9Lc	28	5

The tests are continuing.

S. A. Modena and E. H. Coe

LONDON, ONTARIO
University of Western Ontario

In vitro liquid culture of corn tassels

It is assumed that plant growth regulators (PGR's) are important, possibly causal, factors in the determination of sex expression in higher plants. There are, basically, three ways to test this hypothesis: measurement of endogenous levels of these substances, their exogenous application to the intact plant and their more direct addition in vitro. In some cases the consistency of data from these sources is striking and compelling. For corn, however, present information is incomplete and the relationship remains problematic.

We now report that Zea tassels (var. "Seneca-60") have been successfully cultured in sterile liquid medium. Immature tassels (approximately 1 cm long from 4-week-old plants) possessing spikelets with stamen and ovary primordia grow and differentiate over a 2-3 week period up to 20 cm and resemble normal tassels in many ways.

Maximum growth in the basal medium (BM) is expressed in plump florets with green, highly veined, papery and hairy glumes. Stamens differentiate into anthers and filaments and, occasionally, microspores, complete with wall, are obtained. Normal lodicule development is also observed. The conditions used for this surprisingly rapid response are simple. Tassels are dissected from surface sterilized stem-tips and explanted into 125 ml Erlenmeyer flasks containing 40 ml of liquid medium. The BM which supports this growth contains Murashige and Skoog minerals, White's vitamins and glycine, i-inositol and 3% sucrose. Flasks are shaken in a lighted growth chamber.

Addition of plant growth regulators to the basal medium induces interesting, and perhaps instructive, modifications. Better stamen development is achieved with IAA added to the basal medium. GA3 at 10^{-7} and 10^{-6} M enhances elongation of the main axis, branches and glumes but detracts from stamen and ovary differentiation, making these organs watery and filmy. A general proliferation of organs and also callus is obtained with cytokinins. In the presence of cytokinins, especially zeatin, ovary and silk differentiation is elicited.

These primary results indicate that despite difficulties with in vitro culture of other corn organs and tissues, the tassel possesses considerable potential for study via this technique. In addition to the tests on the sensitivity of the tassel to added PGR's these could include: (1) comparison of the sensitivities and requirements of tassel and ear, (2) analysis of the response and capacities of flower mutants such as an1, Tu, ts, Vg, etc., (3) the exploration of meiosis via various biochemical probes. The evaluation of some of these possibilities is under way.

Patricia L. Polowick, K. Raman and R. I. Greyson

Improved conditions for the extraction of maize polypeptides

Differences in the structure, physiology and biochemistry of plant tissues often do not allow (for the extraction of their polypeptides) the application of current or conventional animal buffers and/or maceration techniques. The more complex macro-molecular composition (and interaction) within plant tissues (e.g., phenolic, carbohydrate, and hydrocarbon compounds), and the mechanical strength afforded by the cell wall necessitate more stringent maceration and isolation methods in plant extract preparation to ensure the integrity of the polypeptides.

Current plant polypeptide extraction methods favor the preparation of sub-cellular (component) enriched fractions of various tissues. Few methods are available which allow extraction of whole plant tissue polypeptides. In contrast, a

number of more or less "universal" preparative techniques have been described for animal systems. In our hands, such methods proved to be unsuitable for the preparation of plant extracts. These methods are characterized by moderate ionic strength buffers, low detergent levels, disruption of tissue by osmotic shock with minimal mechanical maceration, and preparation at temperatures above 0 C.

We report below an improved method for the extraction of whole plant tissue which utilizes a modified buffer, a more rigorous protocol for tissue homogenization, and the use of polyacrylamide gradient pore gel electrophoresis.

Our methods evolved from an animal preparative technique outlined by Atkinson (Dept. of Zoology, Univ. of Western Ontario). The components of the animal buffer and the improved plant extraction buffer are contrasted below:

Animal Extraction Buffer (AEB)	Plant Extraction Buffer (PEB)
80 mM Tris-HCl	200 mM Tris-HCl
2% SDS	5% SDS
5% 2-mercaptoethanol	7.5% 2-mercaptoethanol
20% glycerol	10 mM phenylmethylsulfonylfluoride (PMSF)
pH 6.8	pH 7.5

Upon addition of buffer to the tissue, an extra mechanical grinding step employing a porcelain mortar and pestle was also found essential in obtaining a suitable yield of polypeptides from certain tissues (Baszczynski and Hughes, this Newsletter).

The increased PEB ionic strength has been found necessary in maintaining constant pH during extraction of plant polypeptides. Increased SDS and 2-mercaptoethanol concentrations resulted in heightened resolution of electropherograms (likely due to more complete denaturation/reduction of disulphide bonds and homogeneous detergent coating of protein subunits). Addition of the protease inhibitor PMSF to PEB decreased the amount of degradation products observed over time. The consistency of the tissue extract obtained with PEB made the addition of glycerol (used as an antioxidant and to increase the loading density of the samples) unnecessary. Use of a higher pH resulted in an increase in the number of polypeptides greater than 100 kilodaltons. The conditions described here were arrived at by the manipulation of each component individually until optimal results were obtained.

Polypeptides from maize pollen, primary root, shoot and mouse skeletal muscle tissues were extracted employing both PEB and AEB under identical conditions. These were separated simultaneously on 8.3% uniform concentration, 8.3-15% concave-exponential gradient and 3-15% linear gradient acrylamide gels in several replicates. In all cases the combination of more stringent maceration with PEB and use of gradient gels resulted in the heightened resolution of an increased number of bands. Differences in the relative amounts of polypeptides within tissues were noted.

These results are thought to be attributable to an increased polypeptide extraction efficiency or improved polypeptide solubilization, not achieved utilizing the corresponding animal method.

The conditions and methodology described in this contribution have allowed us to achieve improved polypeptide electrophoretic visualization from several tissues of such widely divergent species as corn, mouse and Neurospora crassa.

W. G. Hughes, C. L. Baszczynski and C. Ketola-Pirie

Tissue-specific electrophoretic differences in polypeptides from maize cultivars

Polypeptides from primary roots, shoots, pollen and leaf tissue of several maize cultivars were extracted and electrophoretically separated using a modified protocol (see MNL 54, 1980). Primary root and shoot polypeptide extracts were obtained by germinating seeds on moistened filter papers in the dark at 27-28 C for approximately 96 hours, excising 0.5-2.0 g of the terminal 0.5-1.0 cm tips of each tissue into porcelain mortars and homogenizing in two volumes of extraction buffer (200 mM Tris-HCl, pH 7.5, 5% SDS, 7.5% 2-mercaptoethanol and 10 mM phenylmethylsulfonylfluoride). All manipulations were carried out at 0-5 C. The homogenates were transferred to 10 ml glass tissue grinders, further extracted using a motorized homogenizer with a teflon pestle and placed on ice for 5-10 minutes. This last step was repeated and the homogenates were centrifuged in 15 ml corex tubes at 7,700xg for 20 minutes. The supernatants containing the polypeptide extracts were transferred to 5 ml glass tubes, boiled for three minutes and stored frozen at -20 C until required.

For preparation of leaf polypeptide extracts, plants were grown in flats under our standard greenhouse conditions for 21-28 days. After the seedlings were excised at soil level and sliced longitudinally, the young inner leaves were removed and cut up into small pieces prior to homogenization as described for roots and shoots.

For electrophoretic separation of polypeptides 8.3-15% concave-exponential gradient polyacrylamide gels were prepared as described by Laemmli (1970) and the Bio-Rad Gradient Former Instruction Manual (1978). The use of gradient gels resulted in better resolution of a larger number of polypeptides (especially in the 20-100 kilodalton range) than the previously used 8.3% acrylamide, uniform concentration gels.

Eight inbreds and two single-cross hybrids were used for electrophoretic comparison of polypeptides among cultivars and between different tissue sources of the same cultivar. In all cases, the overall pattern was similar for any tissue type. Differences in band position and/or intensity were noted primarily in two regions (34 to 37 kd and 80 to 90 kd) for both root and shoot (Fig. 1); prominent bands corresponding approximately to 27, 31, 47 and 51 kd common to all genotypes were present in both tissues. Pollen exhibited differences between cultivars in the bands at 80 to 90 kd (Hughes and Walden, this News Letter).

The polypeptide patterns of the four tissue types were compared for two inbreds (Fig. 2). Root and shoot patterns were similar with at least 85% of the bands apparently being common to both; leaf had 60-70% and pollen had less than 30% of bands in common with those of root or shoot. Bands with molecular weights of 44, 48 and 54 kd were noted in all four tissue types. Although these appear to have the same MW they may represent unique polypeptides in the different tissues. Two-dimensional electrophoretic analysis (currently in progress) should permit this discrimination.

The results indicate that differences may be detected in the electrophoretic phenotypes among cultivars or in various tissues (differing in ploidy level or developmental sequence) within a cultivar. Since culture conditions for any tissue were controlled, the observed differences between cultivars appear to be genotypically determined.

C. L. Baszczynski and W. G. Hughes

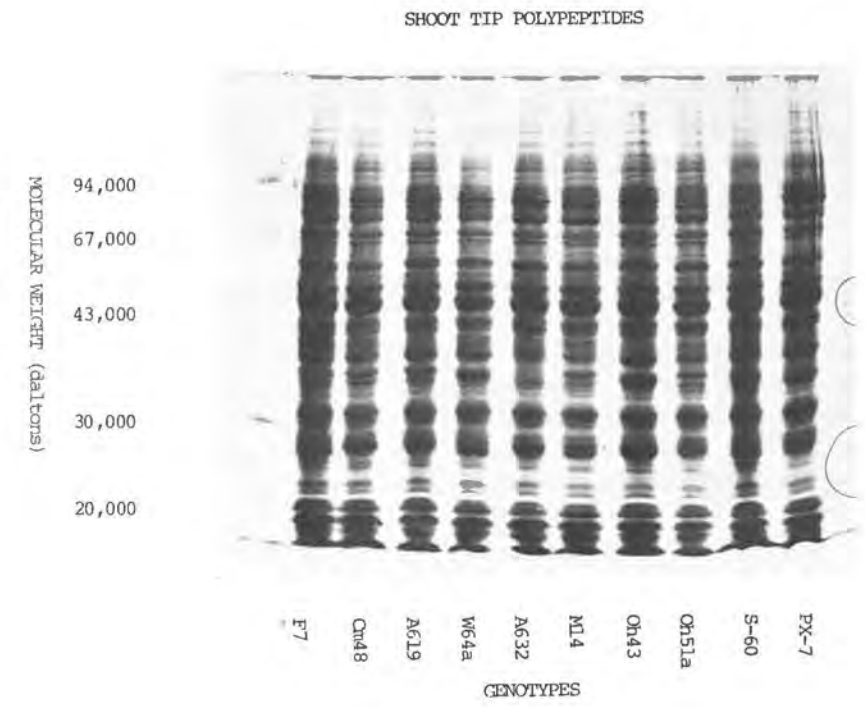


Figure 1.

Polypeptide patterns from four day shoots of the eight inbred and two hybrid (S-60 and PX-7) genotypes. Note differences in the MW range of 34-37 kd.

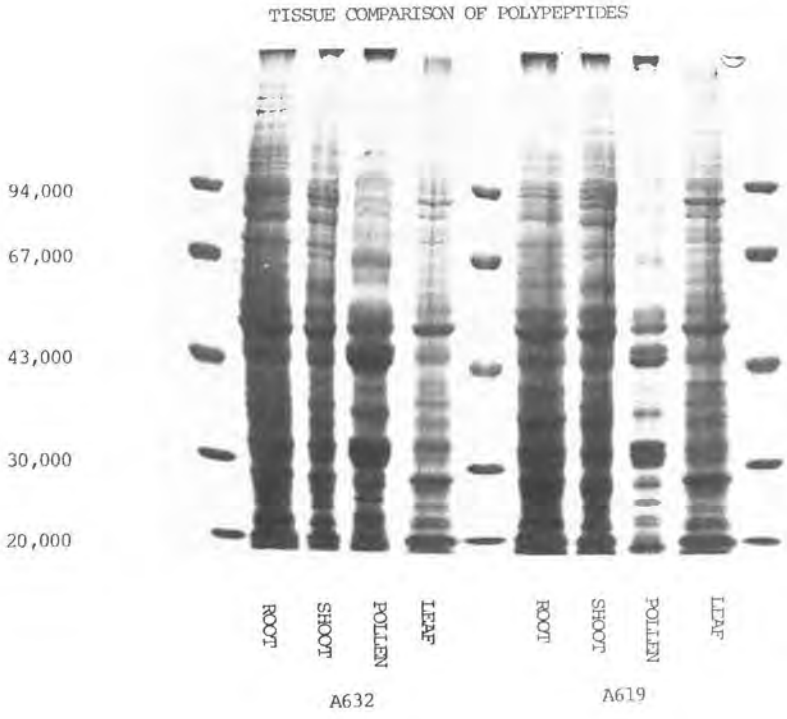


Figure 2.

Comparison of polypeptides from four tissues (as described in text) for two standard inbreds.

SDS-PAGE electrophoretic study of maize pollen polypeptides

Very little evidence is available which allows the identification of gametophyte genetic diversity. Review of the biochemical literature shows that approximately 100 enzymes have been assigned to the tissues of the corn plant but fewer than 40 of these have been identified in mature corn pollen. The techniques of molecular weight polypeptide electrophoresis in concert with computerized digital densitometry (MNL 54, 1980) provide a means by which additional gametophytic genetic diversity can be detected.

Freshly dehiscent pollen was collected from a number of field grown sporophytes and extracted according to the following regime (all operations on ice unless otherwise stated): Buffer added to tissue in the ratio of volume = (tissue fresh weight x 6.89/2 ml). The buffer: 200 mM TRIS-HCl, pH = 7.45; 5% sodium dodecylsulphate; 7.5% 2-mercaptoethanol; and 0.1 M phenylmethylsulphonylfluoride. The pollen/buffer mixture was vortexed and allowed to sit on ice for 20 minutes. The mixture was ground in a motorized tissue homogenizer (15 ml fitted with a teflon pestle), for 1.5 minutes. The homogenate was transferred to a 15 x 100 mm Corex tube and allowed to sit on ice for a further 20 minutes. The homogenate was centrifuged for 20 minutes at 8000 RPM (yields 7.71 Kg with SS-34 rotor on a Sorvall RC-2B centrifuge). The supernatant was decanted and allowed to warm to room temperature following which it was heated for 3 minutes in a boiling water bath, and stored (-20 C) until analyzed. The pellet from the last operation was resuspended in an equal volume of buffer, and stored at -20 C.

Electrophoresis was carried out on homogeneous 8.3% polyacrylamide gels prepared according to the method of Laemmli (1970). Approximately 100 micrograms of polypeptide were applied to each gel well and subjected to an electric field of 80 to 100 milliamp hours. Upon completion of the run, gels were fixed for two hours in 3:1:1, methanol-acetic acid water. Staining was carried out in 2% Coomassie Brilliant Blue R-250. Destaining was accomplished in 7% acetic acid. The stained electropherograms were photographed and subjected to digital densitometry.

Over one hundred pollen genotypes have been examined employing the above method. Five genotypes were selected as representative of diverse germplasm backgrounds: northern flints (RIW, WF, CM48) and corn belt inbreds (W64A, Oh43) and are described below.

The electropherogram in Figure 1 shows the resolution of polypeptides from the five genotypes of pollen. The mean number of peptides detected was 44 per well. In the 80 to 90 kilodalton range of each well, several peptide variants were detected. Each of the genotypes differ by at least four peptides within this region. The specific molecular weights (as obtained by regression and interpolation between standards, mean error 1.6 kilodaltons) were as follows:

MW	Oh43	W64a	CM48	WF	RIW
89,000			+		
88,742		+			
88,357					+
87,714			+	+	
86,685	+				
86,428		+		+	
86,171			+		
85,142	+	+			
84,500			+	+	+
84,114	+				+
83,857				+	
82,828	+				
80,642					+
80,000	+	+	+		

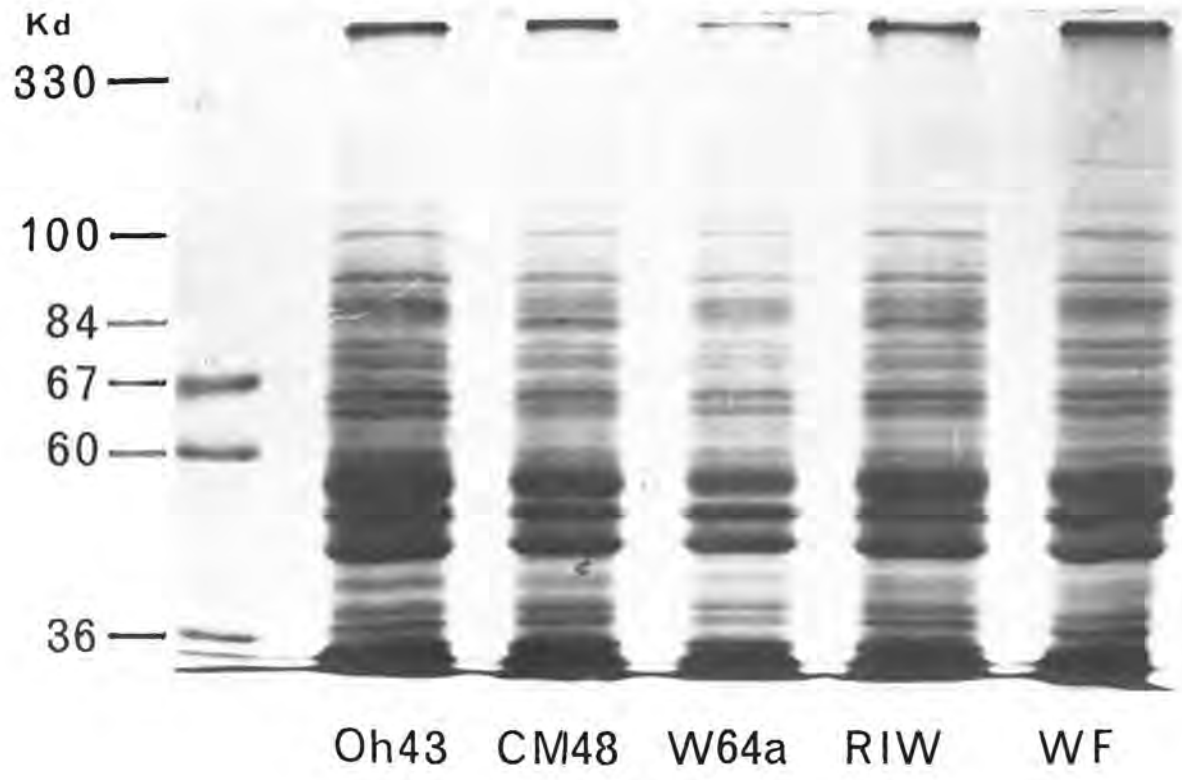


Figure 1. The above electropherogram shows the resolution of polypeptides from the five genotypes of pollen. The major area of peptide variation occurs between 80 and 90 kilodaltons.

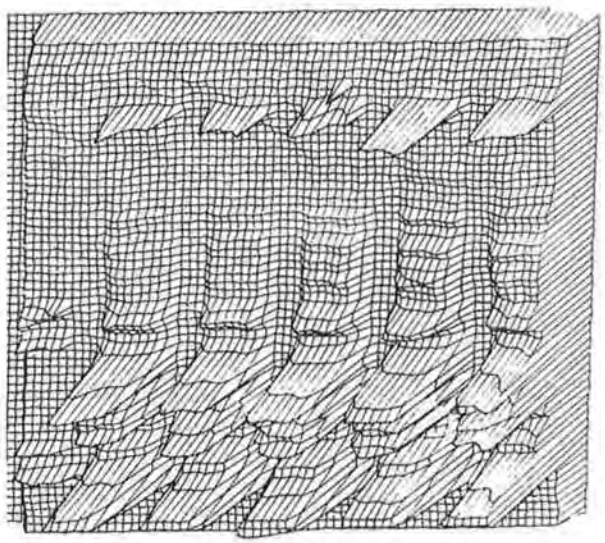


Figure 2. A densitometric representation of the electropherogram surface shown in figure one. Each square of the surface grid conotates a 1.6 mm portion of the original electropherogram. The plane is viewed from 75^{o} above the surface.

The presence of + indicates a particular polypeptide in the corresponding genotype. Note that each genotype differs relative to one another; however, grouping may be assigned according to the derivation of the germ source. The inference of such data is that variant peptides may differ by only a few amino acid constituents. Such variation is regarded as a reflection of genetic diversity in the gametophytic generation.

A three-dimensional densitometric "landscape" representation of the electropherogram is presented in Figure 2. The representation was arrived at by averaging 9 x 9 one hundred micron density surface squares to each grid square drawn in the figure. The ratio averaging of density is necessary in order to represent the gel surface in a reasonable size.

Our results from repeated electrophoresis of replicate pollen samples and plantings show very little variation among singular genotypes. This result is not surprising in that many of the stocks employed in the analyses have been subjected to several generations of inbreeding.

Among unrelated lines, electrophoretic analysis has produced consistent band variants (an average of 5-6 bands per genotype). We are now in the process of cataloging such variation (by one- and two-dimensional electrophoresis) in the hope that such data will be of value in characterizing and selecting desirable phenotypic expression. Although our examination of hybrids is only just proceeding, our preliminary results indicate that among intercrosses and F2 generations, segregation of most peptide variants proceeds in a predictable Mendelian fashion. Pollen from a number of plant/plant reciprocal crosses has not yet been processed.

These results demonstrate the feasibility of characterizing polypeptides from pollen. The employment of pollen from aneuploids, aberrations and polyploids will facilitate the opportunity to assign specific peptides to linkage groups. Since these methods can be used to characterize small amounts of tissue, it is now possible to study and compare "landscapes" from germinal and somatic sources by developmental and deterministic methods.

W. G. Hughes and D. B. Walden

Pollen germination influenced by genotype and/or agrichemicals

We reported (MNL 54:66) a pollen bioassay for agricultural chemicals and extended the use of this bioassay during the 1980 field season. A total of 48 genotypes were examined: (i) thirteen inbred lines were tested with all ten chemicals (MNL 54:66) in three concentrations; (ii) pollen from a further fifteen inbreds and twenty plant x plant reciprocal crosses was challenged with a selection of these chemicals. Oh43 was used as an hourly control for germination and tube elongation measurements. Forty-eight treatments/controls, each in triplicate with five samples per replicate, were scored daily. We report below preliminary results involving ten inbreds, two reciprocal crosses and seven agrichemicals (Tables 1 and 2). Percent germination for individual genotypes was calculated and averaged for all chemical treatments. These were then standardized to the control levels (Table 1). All genotypes germinated poorly at the field dose (manufacturer's recommendation for the sporophyte) level of the chemicals, while germination at the tenfold dilution was generally only slightly below the control level. Several genotypes demonstrated enhanced germination at the hundredfold dilution. The largest dose-responses were recorded for genotypes Oh43, F7 and A619 whereas CM48 and W23 appeared to be very sensitive to chemical treatment even at the hundredfold dilution. The reciprocals F7/Oh43 and Oh43/F7 were tolerant of all chemical treatments although some differential cytoplasmic effect was exhibited.

Table 1. Standardized mean germination of individual genotypes (21 chemical treatments)

Genotype	Control (no treatment)	FD x 10^{-2}	FD x 10^{-1}	FD*
CM48	1.0	0.6	0.1	0
Co220	1.0	1.2	1.0	0.5
F7	1.0	1.3	0.8	0.3
F2	1.0	1.1	0.7	0.2
W64A	1.0	0.9	0.5	0.1
A619	1.0	1.4	0.8	0.4
Oh43	1.0	1.7	1.1	0.4
A158	1.0	1.1	0.9	0.4
W401	1.0	0.9	1.1	0.6
A654	1.0	0.9	0.9	0.7
W23	1.0	0.4	0.3	0.1
F7/Oh43	1.0	1.2	1.0	0.8
Oh43/F7	1.0	0.7	0.7	0.8

*FD = Manufacturer's recommended field dose.

Mean percents germination of all 13 genotypes were standardized and grouped according to the chemicals tested (Table 2). In all cases, the control level of germination was less than that of the hundredfold dilution. Germination at the field dose approached 0 in all but three cases.

Table 2. Standardized mean germination (13 genotypes)

Chemical	Control (no treatment)	FD x 10^{-2}	FD x 10^{-1}	FD*
Atrazine	1.0	1.0	0.7	0
Banvel	1.0	1.3	1.1	0.9
Basudin	1.0	1.1	1.3	0.3
2,4-D	1.0	1.2	0.7	0
Lannate	1.0	1.1	1.0	1.0
Malathion	1.0	1.3	0.1	0
Roundup	1.0	1.1	0.1	0

*FD = Manufacturer's recommended field dose.

Dose response curves for all genotypes and chemicals have been constructed. Pronounced dose responses are stimulated by the chemicals Malathion, Roundup, 2,4-D and Atrazine with the field dose resulting in complete inhibition of germination. No genotype showed a dose response to the insecticide Lannate or the herbicide Banvel.

Further biometrical analysis of these and the remaining data are under way.

K. A. Startek and D. B. Walden

Affinity distance in maize: Effects of mitogens on chromosome orientation

The effects of anti-mitotic agents on the 'affinity-distances' of metaphase chromosomes of maize have been under study in this lab for several years (J. D. Horn, MNL 45:209, 1971; J. D. Horn and D. B. Walden, Genetics 88:181, 1978). The present investigation is an attempt to refine this analysis by employing new methods of data collection and analysis.

The earlier methodology involved using pair-wise comparisons of the mean distances between all possible combinations of homologous and non-homologous chromosomes in no fewer than twenty-five metaphase spreads for each experimental condition. These values, in addition to describing the mean distance between each pair of chromosomes, can be compared to the value derived by J. Hammersley (Ann. Math. Stat. 21:447, 1950) and R. D. Lord (Ann. Math. Stat. 25:794, 1954) for the mean distance between points randomly distributed in a sphere pressed into a circle. Random and non-random associations can thus be distinguished.

In our newer methodology, we record the positions of the chromosomes as the (x,y) coordinates of their centromeres and telomeres from "8x10" photographs of standard spreads. The recording is done on a computerized digitizer. As a point of reference, the centroid of the figure is calculated as are all distances between the centroid and the telomeres and centromeres. This allows the orientation of the chromosomes to be determined and offers another approach to the overall question of how the nucleus may be organized.

Seeds of the inbred Oh43 were germinated in the dark for 72 to 96 hours then divided into two groups for treatment with mitogens. Roots from group one were excised prior to treatment. In group two, the roots were not excised until treatment and fixation were complete. The treatments included cold (5 C for 24 hours), 8-hydroxyquinoline (0.003% for 3 hours), monobromonaphthalene (2.0% for 3 hours), and colchicine ($3x10^{-4}$ M for 3 hours). In both groups the controls consisted of untreated roots placed directly into fixative. No difference has been shown to occur between groups one and two.

The orientation of chromosomes 6 and 10 have been examined. Nearly 2/3 of the 6S arms are oriented toward the centroid of the spread. This orientation is not altered by a mitogen, confirming our earlier suggestion (Horn and Walden, 1978) that the position of chromosome 6, unlike all other chromosomes of the complement, was insensitive to an alteration in the microtubules. Chromosome 10S orientation towards the centroid, however, was markedly reduced in mitogen treated material as compared to the cold arrested treatment.

Additional pattern analysis of these data and data from cells with and without B chromosomes is underway. It is clear that both distance and position parameters of a pair of homologues are specific for that homologue and are in some cases altered by the action of one or more mitogens.

D. J. deKergommeaux and D. B. Walden

NORMAL, ILLINOIS
Illinois State University

Further localization of a dosage-dependent factor on 5L which alters lipid composition in maize embryos

We previously reported (MGNL 54:89-90) undertaking the production of a series of compound B-A translocations for the long arm of chromosome 5. At that time we had obtained presumptive compound translocation kernels for segments of 5L between breakpoints 0.1 (the breakpoint of TB-5La) and 0.21, 0.48, 0.57, 0.60, 0.61, 0.72 and 0.87. We have positively verified three of these (0.48, 0.57, 0.61) and feel

confident about two more (0.21 and 0.60). All of the compound B-A translocation kernels producing plants exhibiting partial sterility were backcrossed to their respective testers used to originally identify them, and also to various inbred and hybrid lines. Compound translocations for segments of 5L between 0.1 and 0.48, 0.57 and 0.61 were backcrossed to an a1 Dt tester. When ears from such crosses segregated for the marker, kernels with colorless endosperm and pigmented embryos consistently yielded chromosome counts of 22, while kernels with colorless endosperm and non-pigmented embryos yielded chromosome counts of 20. The former are interpreted to be hyperploids containing two copies of the compound B-A translocated chromosome, while the latter are interpreted to be diploids. Pachytene analysis of microsporocytes of the original 5-3 translocations used to generate the compounds were performed to verify the breakpoints previously catalogued by A. E. Longley. T3-5(5874), 5L 0.21, 3L 0.16, and T3-5(8351), 5L 0.60, 3L 0.75, were both confirmed to their approximate positions. T3-5(8528), 5L 0.72, 3L 0.06, turned out to involve a diminutive chromosome 9 with the breakpoints at or near the centromeres. T5-9(8386), 5L 0.87, 9S 0.13, turned out to have the breakpoint in 5S at approximately 0.8-0.9. The findings on the latter two translocations would explain the aberrant results obtained from the crosses involving presumptive compounds generated using those translocations.

Presumptive B-A translocation kernels for breakpoints in 5L at 0.08 and 0.14 have been obtained from the previous summer. The former possesses a breakpoint proximal to that of the original TB-5La chromosome. The compound could be generated if recombination followed mispairing between the B5La chromosome and the 5^3 chromosome. Alternatively the actual breakpoint in 5L for T3-5(8104) may be distal to 0.08. No pachytene analysis has been done for these two compounds. The genetic and cytological confirmation should come from crosses made in our winter nursery.

This series of compound B-A translocations for 5L is currently being used to locate the position of newly induced mutants in 5L between the individual breakpoints. We are also using it to position a dosage dependent factor previously located to 5L which alters the levels of oleic and linoleic acids in the embryo. The tables below show the data obtained (% ± standard error) when the dosage of 5L is altered between breakpoints 0.1 and 0.57 or 0.61. In both cases comparisons are made between sibling embryos either hyperploid or diploid for the designated segments.

S80 a1 Dt x 11 5-2 (B5L 0.1-0.57, 3L)

	#	C16:0	C18:0	C18:1	C18:2
20	(8)	12.82±0.37	2.89±0.12	34.49±0.31	49.42±0.61
22	(7)	12.66±0.24ns	3.16±0.20ns	33.67±0.35ns	50.08±0.47ns

S80 a1 Dt x 11 6a-4 (B5L 0.1-0.61, 3L)

	#	C16:0	C18:0	C18:1	C18:2
20	(10)	15.85±0.18	2.93±0.20	30.80±0.98	50.26±1.25
22	(10)	15.96±0.16ns	3.29±0.15ns	32.04±0.83ns	48.66±0.88ns

ns--Not significantly different from the diploid at p=0.05

Since no significant differences are found in these comparisons the dosage dependent factor must lie distal to the segments altered, beyond 5L 0.61.

J. D. Shadley and D. F. Weber

Identification of a dosage-dependent region on chromosome 10 in maize which alters lipid composition in maize embryos

We wish to report the possible identification of another dosage dependent factor affecting the fatty acid composition of embryos. Altering the dosage of the long arm of chromosome 10 using TB-10L(19) reveals differences between hyperploid and hypoploid embryos for both palmitic and stearic acids. The data in the table below (% ± standard error) show that hyperploid embryos have a significantly higher percentage of palmitic acid and a significantly lower percentage of stearic acid than their hypoploid siblings:

H75 310 x 103-6 TB-10L(19)

	#	C16:0	C18:0	C18:1	C18:2
20	(6)	12.44±0.52	2.55±0.12	25.61±0.99	59.04±1.15
22	(7)	16.29±0.72*	1.94±0.15***	25.34±0.68	56.11±0.58

*Significantly different from the hypoploid at p = 0.05.
***Significantly different from the hypoploid at p = 0.001.

TB-10L(19) with the breakpoint close to the centromere is one of a series of B-10 translocations generated by Bor-yaw Lin whose breakpoints lie throughout the entire length of 10L. This series can be used to further locate the dosage dependent factor discovered to specific chromosome regions between the individual breakpoints.

J. D. Shadley and D. F. Weber

RALEIGH, NORTH CAROLINA
North Carolina State University and U.S. Dept. of Agriculture

Compilation of isozyme genotypes for 342 inbred lines

A compilation of the isozyme genotypes at 21 enzyme loci as characterized using starch gel electrophoresis for 342 popular and historically important inbred lines of corn has been prepared by C. W. Stuber and M. M. Goodman. The allelic designations presented are those that were used in the laboratory scoring of the starch gels. A copy of this compilation can be obtained by writing to either of us at North Carolina State University.

C. W. Stuber and M. M. Goodman

RALEIGH, NORTH CAROLINA
North Carolina State University and U.S. Dept. of Agriculture
BLOOMINGTON, INDIANA
Indiana University

Linkage of several isozyme loci on chromosome 3

A five-point testcross involving 4 previously described isozyme loci (e.g., M. M. Goodman, C. W. Stuber, K. J. Newton and H. H. Weissinger, Genetics, in press, November 1980) has established that Me, Got1 and Pgd2 are linked to Mdh3, which has been localized to the long arm of chromosome 3 (K. J. Newton and D. Schwartz, Genetics 95:425-442, 1980). The data also suggest (Table 1) that a fifth locus, an

Table 1. Numbers of recombinant and parental chromosome types for a 5-point testcross

Region 1 (Est) — Region 2 (Pgd2) — Region 3 (Got1) — Region 4 (Me — Mdh3)

Cross tested*: $\frac{5 - B5 - L4 - R - C16}{5 - B5 - L4 - R - C16}$ ♀ × $\frac{4 - B2.8 - L4 - R - C18}{6 - B5 - L6 - SF - C16}$ ♂

	Parental Combinations†	Single Recombinants†				Double Recombinants†						Triple Recombinants†	Totals
Region:	0	1	2	3	4	1,2	1,3	1,4	2,3	2,4	3,4	1,2,4	
	24	14	8	2	6	7	1	4	1	2	0	1	70
	27	14	8	1	9	4	2	6	1	2	0	0	74
Totals	51	28	16	3	15	11	3	10	2	4	0	1	144

Recombination % ± S.E.

(Est) — 38.9 ± 4.1 — Pgd2 — 23.6 ± 3.5 — Got1 — 5.6 ± 1.9 — Me — 20.8 ± 3.4 — Mdh3

* Allele symbols listed from left to right correspond to loci spanning Regions 1 to 4.

† Each entry in upper row begins with upper, left allele listed for the male parent of the cross tested (viz. Est-4); each entry in the lower row begins with the lower, leftmost allele (viz. Est-6).

esterase locus (probably E8), may also belong to the same linkage group, although the esterase localization needs further confirmation. In this cross, there was approximately 39% recombination between the esterase locus and Pgd2. This suggests that E8 might be located in the short arm of chromosome 3.

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

Additional evidence for the unusual electrophoretic migration of a hybrid dimer

Numerous alleles have been studied at both the structural loci (Mdh4 and Mdh5 on chromosomes 1 and 5, respectively) encoding the cytosolic MDH isozymes (M. M. Goodman, C. W. Stuber, C-N. Lee and F. M. Johnson, Genetics 94:153-168, 1980; K. J. Newton and D. Schwartz, Genetics 95:425-442, 1980). With one exception (Goodman and Stuber, MGNL 54:100-101, 1980), each of these alleles ultimately results in the sorts of electrophoretic patterns commonly expected for dimeric isozymes. For example, both intralocus and interlocus heterodimers are formed and these have the customary staining intensities and expected migration distances intermediate (usually halfway) between those of their corresponding homodimers. However, in the case of the one exceptional allele, D8.5, which encodes a slow variant at Mdh4, the migration distances of all of the heterodimers which we have observed are skewed in the direction of slower migration. The result becomes most evident as D8.5 is crossed with variants carrying Mdh4 (or Mdh5) alleles which themselves encode slowly migrating isozymes. Then the hybrid band actually migrates more slowly than

either of the homodimers. These inferences were all derived from studies of numerous F1, F2 and backcross progeny. They have been reinforced by studies of pollen MDH. In F1 plants homozygous for a null allele at Mdh5 and heterozygous for D8/D8.5 at Mdh4, sporophytic tissues carry the D8 and D8.5 homodimers and a slower migrating band, the apparent D8·D8.5 hybrid band. Pollen samples carry only the D8 and D8.5 homodimers. This constitutes additional evidence that the slowest migrating cytosolic MDH band in D8/D8.5 heterozygotes is indeed the interallelic heterodimer, since MDH intralocus hybrid bands are not found in pollen (Newton, Ph.D. thesis, Indiana University, 1980). In order to eliminate any possible complications arising from comigrating mitochondrial MDH isozymes, anti-mitochondrial MDH antibodies (Newton, Ph.D. thesis) were used to specifically immuno-precipitate those isozymes prior to electrophoresis. The latter treatment allows an even clearer demonstration of the unusual behavior of these cytosolic MDH bands.

M. M. Goodman, K. J. Newton* and C. W. Stuber
*Currently at Stanford University, Stanford, CA

III. ZEALAND 1981

This list is based on new data reported in the current Recent Maize Publications (author, year) and in the Reports from Cooperators (name, 55). Recombination percentages and notes show genetic locations; new alleles and new loci are listed with descriptive words. Nonstandard symbols, overlaps of symbols, or differences in interpretation are identified by * preceding the symbol. Listings of organelle-genome designations and localizations have not yet been attempted, more because of the difficulty in defining firm standards for nomenclature and for mapping than because of any lack of solid data and observations [Applicants for open seats on the Extranuclear Regulatory Commission should send their reprints and suggestions to Zealand, 210 Curtis Hall, Univ. of Missouri, Columbia, MO 65211]. I accept responsibility for any errors and misses, and call upon your enthusiastic corrections and new observations.

Chromosome 1

Adh1-C-70-86	allele induced with EMS by D. Schwartz	Birchler, 1980
Adh1	between T1-3(5476) and T1-3(5242), 1L.66-.90	"
	" T1-3(5267) and T1-3(5242), 1L.72-.90	"
	" T1-8(6766) and T1-8(5821), 1L.54-.65?	"
	" T1-7(4891) and T1-7(5693), 1L.12-.92	"
	" T1-8b and T1-8(6697), 1L.59-.89	"
	order T1-10d - T1-10(8375) - T1-10(001-3) - Adh1 1L.50 1L.69 1L.86	"
	uncovered by TB-1La-3L5242 (1L.20-.90) but not by TB-1La-5S8041 (1L.20-.80) and others; located between 1L.80-.90.	"
	most probably located 1L.86-.89	"
	mutants induced by EMS from the FCm allele (FBm, FSm, SCm, UCm, F, Cm) arose independently in each of the two subunits of proposed duplication	Birchler &, 1979
*sMdh1	7.6+ 2.1 Amp1	McMillin &, 1980
	alleles -s1, -s5	"
mmm	TB-1La, TB-1La-3L5267 and TB-1La-5S8041 locate	Newton &, 1980
	27.5 Adh1	"
Mdh4	TB-1La and TB-1La-5S8041 locate	"
	28.9 Adh1	"
	alleles -D12, -E12, -D14.5	"
Cat2	TB-1Sb locates; TB-1Sb-2L4464 does not; alleles -Z, -P	Roupakias &, 1980
Cat3	TB-1La locates; TB-1La-5S8041 does not; alleles -A, -B	"
Amp1	replaces LapA; alleles -F, -S, -V	Vodkin &, 1980
Car1	37 Cat2	Scandalios &, 1980
Amp2	replaces LapD; alleles -F, -S	Vodkin &, 1980
dek1	E792; replaces c1f and gay; uncovered by TB-1Sb	Neuffer &, 55
dek2	E1315A; uncovered by TB-1La	"

Chromosome 2

dek3	E1289; uncovered by TB-3La-2S6270	Neuffer &, 55
dek4	E1024A; uncovered by TB-1Sb-2L4464	"
Tp-Trip9	segment transfer to 2S	Galinat, 55

Chromosome 3

Mdh3	TB-3La, TB-3Lc, TB-3Ld, TB-1La-3L5267 locate; alleles -C16, -C18	Newton &, 1980
	2.6 sh2	"
vp1	uncovered by TB-3Ld but not by TB-3Lc	Beckett, 55
dek5	E874A; uncovered by TB-3Sb	Neuffer &, 55
dek6	E627D; uncovered by TB-3La	"
Est (prob. E8)	38.9+4.1 Pgd2 23.6+3.5 Got1 5.6+1.9 Me 20.8+3.4 Mdh3	Goodman &, 55

Chromosome 4

zein	hybridization sites for mRNA or cDNA in 4L proximal portion and 4L distal	Viotti &, 1980
dek7	E211C; uncovered by TB-4Sa	Neuffer &, 55
dek8	E1156A; uncovered by TB-4L(?)	"
Ga9	failure to verify locus	Ashman, 55
ltel?	latente (see de Miranda, 55); association of evergreen stalk trait with Su from Z. diploperennis	Galinat, 55

Chromosome 5

1*-Blandy4	uncovered by TB-1La-5S8041; alleles -EMS1, -Blandy3drk	Mascia &, 1980
*sMdh2	4.5+1.9 Cat1; alleles -s8, -s0, -s4, -s1	McMillin &, 1980
Cat1	9.1 bt	Roupakias &, 1980
	5 Amy2	"
	3 Amp3	"
	TB-1La-5S8041 locates	"
	alleles -F, -K, -M, -S, -V, -V'	Scandalios, 1980
zein	hybridization sites for mRNA or cDNA in 5L distal portion	Viotti &, 1980
K5L	stained by banding methods in mitosis	Ward, 1980
Amp3	replaces LapC; alleles -F, -S, -I, -V	Vodkin &, 1980

(Chromosome 5, continued)

Mdh5	TB-1La-5S8041 locates; alleles -PF, -E12	Newton &, 1980
	19.7 a2	"
dek9	E1365; uncovered by TB-5La	Neuffer &, 55
Inv5L	in Z. diploperennis	Pasupuleti &, 55

Chromosome 6

Mdh2	trisomic 6, TB-6Lb and TB-6Lc locate; allele -null		Newton &, 1980
Enp1	replaces Ep1; alleles -A, -B, -C, -D, -E, -O		Vodkin &, 1980
dek10	E1176A; uncovered by TB-6Lb		Neuffer &, 55
115	replaces 1*-Blandy3; allele -Brawn		Robertson, 55
T1-6(6189)	6SNORhet.10	has 21% of rDNA proximal to break	Phillips &, 55
T6-9d	6SNORhet.46	40%	"
T4-6(4341)	6SNORhet.50	47%	"
T2-6(8786)	6SNORhet.88	68%	"
T6-10(5519)	6SNORhet.90	70%	"
T1-6(8415)	6SNORsec.constr.prox.	70%	"
T3-6(030-8)	"	70%	"
T1-6(4986-7)	"	71%	"
T5-6f	6SNORsec.constr.midway	78%	"
T1-6(5495)	6SNORsec.constr.prox.	79%	"
T4-6Li	"	79%	"
T2-6(5419)	6SNORsec.constr.midway	90%	"
T6-7(035-3)	"	91%	"
T4-6(7328)	6Ssat.	100%	"
T2-6(001-15)	6Ssat.	100%	"
T1-6d	6S.74(bet. cent. & NOR)	0%	"

Chromosome 7

Zp1	3.7±0.9 vp9 9.0±1.4 o2	Soave &, 1979
Zp2	" "	"
Zp3	" "	"
Zp21	0 o2 9.0±1.4 vp9	"
Zp29	" "	"
Zp6	linked to Zp21, Zp29	"
Zp16	linked to Zp1, Zp2, Zp3	"
De*-30	5 o2	"
zein	hybridization sites for mRNA or cDNA in 7S	Viotti &, 1980
K7L	stained by banding methods in mitosis	Ward, 1980
dek11	E788; uncovered by TB-7Lb	Neuffer &, 55

Chromosome 8

Mdh1	association with wx T8-9d and wx T8-9(6673); alleles -A1, -A6	Newton &, 1980

Chromosome 9

K9S	stained by banding methods in mitosis	Ward, 1980
wx	no-amylose alleles -B3 (Mp mutation), -C31, -R, -90 produce Wx protein	Echt &, 55
	intermediate alleles -m-8 (Spm mutation); -a; -S5 and -S15 (two revertants from -m-1, Ds mutation) produce Wx protein	"
	alleles -90, -C31, -R produce altered Wx protein	"
	no-amylose alleles -m-1 (Ds mutation), -m-6 (Ds), -B4 (Ds), -I, -P60, -BL3 and others lack Wx protein	"
sh-bz-x1	deficiency probably includes C1 but does not include Yg2	Coe, 55
dek12	E873; uncovered by TB-9Sb	Neuffer &, 55
dek13	E744; uncovered by TB-9Lc	"
Inv9S	in Z. diploperennis	Pasupuleti &, 55

Chromosome 10

1*-1039	allelic to oy	Mascia &, 1980
1*-1040	uncovered by TB-10Sc; allelic to oy	"
113	uncovered by TB-10L19; alleles 1*-Neuffer2(E59) and 1*-1050	"
	39.4 T5-10(4384)	"
	18.3 T5-10(5358)	"
	G 14.0±1.7 R 30.2±2.3 113 4.5±1.0 sr2	"
zein	hybridization sites for mRNA or cDNA in distal portion of 10L	Viotti &, 1980
K10	large knob and prominent chromomeres stained by banding methods in mitosis	Ward, 1980
Df-K10	(C), (F) and (I) terminal deficiencies lack W2 and Sr2	Rhoades &, 55
	(H) and (K) terminal deficiencies lack Sr2 but carry W2	"
	cytological extent of (C) and (I) greater than (F), (H) and (K)	"
	male transmission of (C) and (I) zero; of (F) greater than (H) and (K)	"
12	not expressed in DfK10(H) and (K) homozygotes; stock has been lost, suggest replacement with 113 on map (per Mascia), 4.5 to left of sr2	"

(Chromosome 10, continued)

R	1.4 DfK10(F) over N10	Rhoades &, 55
	5 DfK10(C) over K10	"
	16 DfK10(H) or (K) over K10	"
o7	not included in DFK10(F); order most likely R o7 w2 sr2	"
dek14	E1435; uncovered by TB-10Sc	Neuffer &, 55
dek15	E1422A; uncovered by TB-10L19	"
TB-10Lb	approx. breakpoints 10L.1, BL.8	Kowles &, 55

B chromosome

	centric heterochromatin (but not distal heterochromatin) stained by banding methods in mitosis	Ward, 1980

Unplaced

Rf4	restorer of C cytoplasm	Gracen, 1979
oro	alleles oro-4889, oro-8081, oro-6474, oro-64-4589-4	Mascia &, 1980
1*-4923	not allelic to oro or oro2 or sienna-yelnec	"
sienna-yelnec	not allelic to oro or oro2	"
Orom	orobanche modifier	"
de*-B1	defective endosperm	Manzocchi &, 1980
de*-B3, -B6, -B18, -B21, -B22, -B34, -B37, -B40, -B50, -B68, -B69, -B70, -B116, -B125, -B127, -B246		"
Amp4	replaces LapB; alleles -F, -S	Vodkin &, 1980
Uq	replaces Ub; ubiquitous controlling element	Friedemann &, 55
Ti	tunicate inhibitor	Camâra-H. &, 55
btn1	brittle node	Kang, 55
Px7	alleles -F, -S, -null	Liu &, 55
sfa1, sfa2	suppressor of floury-a; complementary pair	Magoja, 55
o9	replaces ox-74120; opaque endosperm crown	Nelson, 55
o10	replaces ox-7747; E-1356; opaque endosperm	"
o11	replaces ox-7455; opaque endosperm	"
o12	replaces ox-7638; opaque endosperm, chlorophyll-deficient	"
o13	replaces ox-7729; opaque endosperm	"
lp	lethal pollen (Carangal MS thesis)	"
AR	factorial constitutions sufficient to give observed phenomenon	"
whp	not uncovered by TB-1La, -3Sb, -3La, -4Sa, -5La, -6Lc, -7Lb, -8La, -9Sb, -9Lc	Modena &, 55
mei	allelism to dv, ms43 and ms28 is indicated; other tests inter se are negative	Golubovskaya &, 55
ms4	allelism to po is indicated	"
dsy	not allelic to dsy2, as or afd	"
pam	not allelic to pam2	"
dep	defective pistils	Micu, 55
dib	dichotomously branched	"
tl	absence of tassel	"
Ht3	H. turcicum resistance (chlorotic lesion); independent of Ht1 and Ht2	Hooker, 55

Lost and found

The following have been listed previously as lost, without response to the contrary:	Chrom. 1: ag, ga6, pa, Ts3, v19, zl; Chrom. 2: rp7; Chrom. 3: pg2; Chrom. 4: de1, de16, lo1, sp1; Chrom. 5: tn1; Chrom. 9: bp; Chrom. 10: 12, 18, sp2; Unplaced: b1, de17, gm, lu2, Pu1, Pu2, S1, S2, S3, S4, S5, so1, so2, w1	Cooperators
sy	was listed as lost (MNL 54); anticipate recovery from crosses	Beckett
y8	is it lost?	Beckett

Help wanted

*E5-I, E5-II	nonconforming symbols
Cytoplasms	standards for designations of "cms", "N", "cytopl", etc. are not keeping pace with new knowledge
Nomenclature	specifications of alleles (especially for isozymes) is falling behind our ability to make discriminations among "isoalleles" differing in strain of origin, isolation number, etc.

Assembled by

Prof Ligate

IV. QUESTIONNAIRE RESPONSE

Responses to the questionnaire distributed in November, 1981 totalled 124. Tallies are given in the following, with respondents' comments and abbreviated highlights after each.

The News Letter Please consider the following features in the News Letter and give your judgment of their value and utility.	Highly worthwhile	Worthwhile	Marginal	Not worthwhile	Needs explanation	Self-explanatory	This space for brickbats*
A. Cytogenetic working maps (see MNL 52:129)							
1. Tables of data documenting maps	38	45	22	0	7	8	
2. Maps with cytological markers placed on linkage map (format as in maps 1-4 & 8-10)	59	42	3	0	9	7	
3. Maps with genes placed on cytological map (format as in maps 5, 6, 7)	56	41	6	0	9	7	
B. Zealand 1980 (see MNL 54:127)							
1. Annual listings of new factors	64	35	1	0	7	7	
2. Annual listings of linkage information	48	45	3	0	5	9	
3. Requests	33	38	16	3	1	11	
4. Chromosome 3 (see MNL 54:130)	34	33	7	0	3	9	
5. Do you concur with the items listed as "lost"? Yes 34 No 1 Comments? "I have sy" (Beckett)							
C. Stock center report of activities	26	61	15	5	1	7	
D. Catalog of stocks	80	30	1	0	2	7	
E. "50 Years Ago" (Excerpts from MNL)	8	45	35	16	0	8	
F. Mailing list	36	48	17	0	1	7	
G. Index to authors and names (annual)							
1. To authors of contributed articles	68	40	1	2	0	8	
2. To authors cited in articles	25	33	38	12	0	7	
3. To authors of recent publications	49	44	10	6	0	8	
4. To names in the mailing list	21	36	30	20	0	7	
H. Index to symbols (annual)							
1. To gene symbols in articles	59	41	6	1	1	8	
2. To the catalog of stocks	46	46	11	4	1	7	
3. To chromosomal aberrations	46	45	13	2	2	7	
4. To aneuploids and chromosome additions	41	49	11	2	2	7	
5. To cytological markers	48	50	6	2	2	7	
6. To cytoplasms	50	45	7	2	2	7	
I. Recent publications section	71	25	5	1	0	6	

Please comment regarding listings of recent publications:

More than enough coverage of OK - 19

Needs more coverage of OK - 24; other - 5

Is the print size too small? OK - 45; other - 1

*Suggestions for improvement of the News Letter:

Comments (apart from a number of greatly appreciated compliments):

The Catalog of Stocks and the Mailing List need not be annual.
Change the deadline or do whatever is necessary to distribute by March.
Develop and share classroom applications--introduce future scientists to the "power" of auxiliary genetic analysis.
The Recent Maize Publications list would be enhanced by a subject or keyword index.
Some express a need for more coverage in Recent Maize Publications of insect and disease resistance, breeding aspects, biochemical and molecular areas.

Highlights of the tallied responses:

The Catalog of Stocks and the list of Recent Maize Publications are seen as the most worthwhile features (presumably outside of the Reports from Cooperators, about which no question was asked!).
Assembly of the annual Author and Name Index covering articles and publications is well justified by the strong interest in it (compilation of authors cited in articles is relatively simple and continues).
Assembly of the annual Symbol and Cytogenetic Index with comprehensive coverage is well justified.
The Mailing List is not necessary every year; annual change lists would be desirable (no update is attempted this year--a complete list will be provided in 1982).
The historical material of "50 Years Ago" is considered highly worthwhile by only a few (8) respondents (no materials are available from 1931, so no entries are given this year; this feature will be continued in the next few, modest years so long as resources permit).

The coverage in Recent Maize Publications is satisfactory (The many appreciative remarks were most welcome; see p. 145 for details on the criteria and sources used).

The Stock Center

Do you feel that the Stock Center should carry out the following functions?

	Yes Strongly		Neutral		No Strongly
Isolate new traits	21	17	38	18	12
Coordinate data on new traits	60	33	8	2	4
Test for allelism	22	26	37	11	7
Coordinate tests for allelism	47	39	14	2	2
Locate factors to chromosome	17	20	43	15	6
Coordinate locating factors	53	33	18	2	4
Map	25	21	36	10	9
Coordinate mapping	59	26	13	0	4
Solicit and sleuth for stocks	55	19	20	4	3
Construct marker stocks	41	30	20	8	4
Coordinate construction	50	36	10	1	0
Characterize stocks cytologically	10	22	39	25	10
Coordinate cytological characterizations	40	34	23	0	4
Maintain isozyme stocks	52	25	22	6	1
Characterize isozymes in stocks	8	15	40	23	15
Coordinate isozyme characterizations	27	31	32	5	5
Maintain stocks with defined pathogenetics	59	35	15	2	0
Characterize pathoreactions and genetics	14	19	46	14	12
Coordinate pathoreaction characterizations	41	31	22	4	4
Characterize inbred lines genetically	24	20	29	16	14
Coordinate characterizations of inbreds	48	31	16	5	6
Maintain converged stocks of selected variants	48	20	27	2	0
Converge selected variants to inbred lines	15	18	48	12	6
Coordinate converging of variants	39	39	24	5	2
Maintain cytoplasm types	82	21	7	0	1
Supply "standard" strains for physiological research	53	28	20	3	3
Recommend "standard" strains	57	24	18	4	0
Supply marked aneuploids (i.e., ready to use)	47	37	21	2	1
Supply diallel sets among inbred lines	17	11	42	13	19
Advise on genetic options and design	36	33	26	8	6
Other functions (specify)					

Comments:

Computerize information storage, retrieval and stock keeping.
Maintain multiple alleles and multiple occurrences of variants, for biochemical studies.
The Center's functions depend considerably on the Director's interests and capabilites.
The primary purpose of the Center is to maintain, improve and solicit stocks in order to aid genetic investigations by others.
Define the most useful genetic and cytological markers for mapping and other genetic purposes.
Seek funding (private?) for a summer training program for college students to learn maize genetics.
Become an international center for maize genetics.
Increase the range and variety of "representative" strains to go with the "exotics".
The Center may need to have (or at least to cooperate closely with) a rather extensive laboratory facility if it is to perform adequately its basic functions.
Markers present in some stocks might be presented more fully.

Highlights of the tallied responses:

Coordinating functions (and soliciting of stocks) are more appropriate than research functions; construction of marker stocks, however, is viewed as important, as are the definition and maintenance of genetic and cytogenetic accuracy.
Stocks of isozyme sources, defined pathogenetic materials, converged variants, and (especially) cytoplasms should be actively acquired and maintained.
"Standard" strains should be defined and made available.

Functions

Please consider the following functions. Rank your preference (increasing from 1-10) for the appropriate responsible party.

	Stock center	News letter editor	Open meeting	Elected czar	Volunteer committee	Elected committee	Other (specify)
Recommendations for nomenclatural standards	278	334	320	144	428	512	
Clearing house for symbols	454	523	168	162	294	298	
Coordination of linkage mapping	517	389	160	166	390	263	
Clearing house for linkage maps	435	514	106	130	320	225	
Coordination of cytogenetic mapping	379	447	120	117	388	230	
Clearing house for cytogenetic maps	417	522	91	139	303	210	
Clearing house for cytological data	430	480	112	129	347	184	
Clearing house for isozyme data	398	420	147	135	345	210	
Coordination/cataloguing of converged stocks	649	363	99	128	208	156	
Other (specify)_____							

Comments:

Clearing house functions carried out at the Stock Center depend heavily upon the Director.
Fund the above functions from grants.
Sequence and restriction maps are needed.
Volunteer committees should do the work; major needs should be discussed in open meeting; the Stock Center should serve a coordinating role.

Highlights of the tallied responses (the above tallies are cumulative rank points):
For nomenclatural standards, an elected or volunteer committee is favored, with some input by the editor and from open meeting.
For a symbol clearing house, either the editor or the Stock Center is favored.
Linkage mapping coordination is preferred by the Stock Center, with volunteer committee(s) and the editor involved.
Cytogenetic mapping coordination is preferred by the editor, volunteer committee(s) and the Stock Center.
A clearing house for linkage maps, cytogenetic maps, cytological data and isozyme data by either the editor or the Stock Center is favored, perhaps with volunteer committee(s).
Coordination of converged stocks is preferably to be done by the Stock Center, with the editor involved.

Cooperation

Please consider the following cooperations and indicate any for which you would be willing to take responsibility.

( ) Collection of linkage data for chomosome/arm/segment no._____
( ) Coordination of linkage mapping for_____
( ) Collection of cytogenetic/cytological data as follows:_____
_____
( ) Coordination of cytogenetic working map for_____
( ) Collection of aneuploid morphological data as follows:_____
_____
( ) Compilation of data on genetic and cytological constitutions of inbred lines.
( ) Indexing of inbred lines cited in the News Letter.
( ) Characterization of isozyme morphs in defined inbred lines and testers.
( ) Characterization of pathological reactions and/or factors in defined inbred lines and testers.
( ) Stockpiling or coordination of diallel sets of hybrids and backcrosses.

Other cooperation activities that need attention:

Highlights:

The response to this section is heartening, and the complexity and diversity will require some interaction and discussion.
For mapping, chromosomes 2, 4 and 10 drew no confessed interest (speak out soon if you have an interest in these or other chromosomes), though some have indicated interest in "any" chromosome responsibility.
There is strong interest in cooperation with pathogenetic work, on constitutions and indexing of inbred lines, on diallel sets, and on isozyme morphs, as well as diverse interest in many other cooperative areas. Anyone who would like to have names of others who are interested in cooperating in specific areas should feel free to write to me for information (or, of course, to proceed apace!). Undoubtedly we can develop a zeatropic solution to each of our high hopes.

E. H. C.

V. REPORT OF MAIZE GENETICS COOPERATION STOCK CENTER

During 1980 the stock center received a total of 104 seed requests. Eighty percent of the seed requests were from domestic users and twenty percent from foreign countries. The categories of seed requests were as follows: maize geneticists, 57.3%; maize breeders, 20.4%; plant physiologists, 17.5% and educational, 4.8%. A total of 1055 seed packets were sent to fill the 104 requests.

While it is difficult to establish trends in the number of seed requests received by the stock center, Table 1 indicates a reduction in the number of stock requests from 1975 to 1980.

Table 1. Number of seed requests for maize genetic stocks 1975-1980.

Year	Domestic	Foreign	Total
1975	121	36	157
1976	110	27	137
1977	107	36	143
1978	96	32	128
1979	79	25	104
1980	83	21	104

There has been a 34 percent decrease in the number of seed requests from 1975 to 1980.

The stock list this year includes the reciprocal translocation stocks that are in the stock center collection. Please use this list when requesting translocation stocks.

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

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*-5508
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
m1
D8
L1s
Les2
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 f1 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 f1 v4
ws3 lg gl2 b sk f1 v4
ws3 lg gl2 f1 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 f1 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 f1
lg gl2 b sk f1 v4
lg gl2 b sk v4
lg gl2 b wt v4
lg gl2 b f1
lg gl2 b f1 v4
lg gl2 b f1 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
f1
f1 v4 Ch

Chromosome 2 (continued)

f1 Ht v4
f1 Ht v4 Ch
f1 w3
f1 v4 w3
f1 w3 Ch
f1 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-Tall = 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 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
ig
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-d3l ; A2 C R
A-d3l ; A2 C R pr dt
A-d3l ; A2 C R B Pl dt
A-d3l ; A2 C R Dt
A-d3l ; A2 C R pr Dt
A-d3l sh2 ; A2 C R B Pl dt
A-d3l sh2 ; A2 C R Dt
A-d3l sh2 ; A2 C R B Pl Dt
A-d3l 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
ye1*-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
st
st Ts5
st 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
ms13
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 ; in 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
ms13
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 l10
y l11
y l12
y W15
y pb4
y pb4 pl
y pb4 Pl
y si
y wi Pl
Y Dt2 ; a-m A2 C R
y pgl1 ; Wx pgl2
y pgl1 wi ; wx pgl2
Y pgl1 ; Wx pgl2
y pgl1 ; wx pgl2
Y pgl1 ; wx pgl2
y pgl1 su2 ; wx pgl2
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 l10
Y l12
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
w14
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
f13
f13 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 bz wx ; A A2 R
yg2 c sh bz wx ; A A2 R
yg2 c sh wx ; A A2 R
yg2 c sh wx gl15 ; A A2 R
yg2 c sh 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-1 ; A A2 R
C ; A A2 R
C ; A A2 R B P1
C wx ; A A2 R
C wx ; A A2 R B P1
C wx ; A A2 R b P1
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 P1
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 pgl2 gl15 ; y pgl1
lo2
wx*
wx-a
wl1
wx d3
wx d3 wl1
wx d3 v gl15
wx d3 gl15
Wx pgl2 ; y pgl1
wx pgl2 ; y pgl1
Wx pgl2 ; Y pgl1
wx pgl2 ; Y pgl1
wx pgl2 bm4 ; y pgl1
wx v
wx v gl15 bk2 Bf bm4
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 P1
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 P1 ; 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
v18
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

Rs
v13
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 pr Y/y c bz wx r
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
WF9	rf rf2
R213	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 4-9e (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.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)

Reciprocal Translocation Stocks

Translocation		Break Points*	
1-2	7039	1S.90	2S.89
1-2	d	1S.78	2L.56
1-2	c	1S.77	2L.33
1-2	e	1S.61	2L.47
1-2	4464	1S.53	2L.28
1-2	b	1S.43	2S.36
1-2	036-7	1S.37	2L.33
1-2	5255	1S.25	2S.31
1-2	5896	1S.22	2S.30
1-2	004-11	1S.13	2S.36
1-2	8628	1ctr.	2L.49
1-2	5946	1ctr.	2ctr.
1-2	028-17	1ctr.	2ctr.
1-2	4937	1L.10	2S.15
1-2	5453	1L.11	2S.58
1-2	051-1	1L.16	2S.30
1-2	018-18	1L.16	2L.44
1-2	5539	1L.21	2L.61
1-2	5523	1L.27	2S.62
1-2	041-9	1L.27	2S.57
1-2	6892	1L.30	2L.35
1-2	6427	1L.43	2L.50
1-2	7211	1L.57	2L.79
1-2	6883	1L.63	2L.52
1-2	017-3	1L.67	2S.58
1-2	5376	1L.77	2L.08
1-3	5883	1S.88	3S.60
1-3	5597	1S.77	3L.48
1-3	5982	1S.77	3L.66
1-3	8995	1S.49	3L.06
1-3	k	1S.17	3L.34
1-3	a	1S.15	3L.17
1-3	c	1S.14	3L.14
1-3	h	1S.06	3L.04
1-3	013-9	1ctr.	3ctr.
1-3	6861	1L.04	3L.65
1-3	8048	1L.11	3S.18
1-3	j	1L.11	3L.13
1-3	6884	1L.17	3L.19
1-3	024-14	1L.27	3S.49
1-3	8637	1L.37	3S.50
1-3	4759	1L.39	3L.20
1-3	e	1L.58	3L.45
1-3	8405	1L.60	3L.31
1-3	d	1L.61	3S.75
1-3	5476	1L.66	3L.87
1-3	i	1L.68	3S.30
1-3	5267	1L.72	3L.73
1-3	4314	1L.81	3L.89
1-3	5242	1L.90	3L.65
1-4	h	1S.94	4L.52
1-4	002-19	1S.87	4L.42
1-4	5680	1S.87	4L.45
1-4	4308	1S.65	4L.58
1-4	b	1S.55	4L.83
1-4	8602	1S.41	4L.81
1-4	064-20	1S.23	4L.19
1-4	5566	1S.21	4L.26
1-4	8368	1S.14	4S.30
1-4	i	1S.13	4S.42
1-4	8663	1S.09	4S.36
1-4	5629	1L.10	4L.10
1-4	039-15	1L.14	4S.26
1-4	6422	1L.16	4S.11
1-4	5373	1L.17	4S.29
1-4	f	1L.25	4L.16
1-4	8249	1L.26	4L.63
1-4	d	1L.27	4L.30
1-4	c	1L.33	4S.23
1-4	8563	1L.39	4S.21
1-4	4692	1L.46	4L.15
1-4	a	1L.51	4S.69
1-4	5438	1L.93	4L.81
1-4	g	1L.95	4L.35
1-5	5045	1S.94	5L.50
1-5	058-2	1S.88	5S.62
1-5	4613	1S.78	5L.22
1-5	5525	1S.75	5S.53
1-5	i	1S.71	5S.74
1-5	6899	1S.32	5S.20
		1S.40	5L.10**
1-5	b	1S.17	5L.10
1-5	043-15	1S.10	5L.63
1-5	5512	1S.08	5L.70
1-5	6197	1S.02	5L.02
1-5	8782	1ctr.	5ctr.
		L-S or	S-L **
1-5	e	1L.03	5L.09
		1S.13	5S.24**
1-5	044-10	1L.05	5S.83
1-5	f	1L.07	5L.09
1-5	6401	1L.14	5S.20
1-5	7219	1L.15	5S.19
		1S.18	5L.39**
1-5	h	1L.18	5L.53
1-5	48-34-2	1L.19	5L.76
1-5	c	1L.34	5L.29
1-5	070-12	1L.39	5S.71
1-5	7212	1L.44	5S.28
1-5	4597	1L.52	5S.43
1-5	a	1L.52	5S.42
		1L.62	5L.44**
1-5	g	1L.58	5S.85
1-5	8041	1L.80	5L.15
		1L.80	5S.10**
1-5	7267	1L.92	5L.82
1-6	8452	1S.80	6L.52
1-6	8609	1S.79	6L.59
1-6	028-13	1S.56	6L.54
1-6	7097	1S.46	6L.62
1-6	7352	1S.40	6L.60
1-6	e	1S.37	6L.21
			6S **
1-6	055-10	1S.29	6L.48
1-6	5013	1S.26	6L.28
1-6	5495	1S.25	6S.80
1-6	c	1S.25	6L.27
1-6	6189	1S.23	6L.17
			6S **
1-6	4986	1S.21	6S.78
1-6	5077	1S.20	6L.60
1-6	h	1L.03	6L.17
1-6	d	1L.13	6S.74
1-6	g	1L.16	6L.84
1-6	a	1L.20	6L.54
1-6	8415	1L.29	6S.82
1-6	f	1L.32	6L.42
1-6	070-1	1L.40	6L.58
1-6	5225	1L.61	6L.72
1-6	4456	1L.71	6L.30
1-6	8658	1L.79	6L.91
1-7	4742	1S.95	7L.03
1-7	g	1S.79	7S.22
1-7	4837	1S.73	7L.55
1-7	f	1S.72	7L.80
1-7	4444	1S.65	7S.50
1-7	4405	1S.43	7S.46
1-7	6796	1S.40	7S.39
1-7	010-12	1S.35	7L.57
1-7	i	1S.31	7L.26
1-7	4302-31	1S.15	7L.12
1-7	k	1L.10	7L.56
1-7	5871	1L.12	7L.24
1-7	4891	1L.12	7L.69
1-7	j	1L.20	7L.61
1-7	5339	1L.24	7L.14
1-7	a	1L.28	7L.13
1-7	e	1L.39	7L.11
1-7	c	1L.39	7L.14
1-7	h	1L.46	7L.19
1-7	4420	1L.47	7L.90
1-7	b	1L.53	7S.12
			7L **
1-7	d	1L.81	7S.44
1-7	5693	1L.92	7L.18
1-8	8919	1S.53	8L.44
1-8	4307-4	1S.42	8L.61
1-8	001-13	1S.39	8L.67
1-8	4685	1S.20	8L.21
1-8	6591	1S.18	8S.43
1-8	008-17	1S.16	8L.20
1-8	5588	1S.10	8S.32
1-8	055-23	1ctr.	8ctr.
1-8	064-13	1ctr.	8ctr.
1-8	4676	1L.04	8S.06
1-8	5619	1L.07	8L.16
1-8	5634	1L.08	8S.28
1-8	5384	1L.10	8L.59
1-8	8683	1L.11	8ctr.
1-8	8640	1L.11	8L.16
1-8	020-19	1L.11	8L.38
1-8	4748	1L.12	8L.15
1-8	036-4	1L.18	8L.59
1-8	005-7	1L.22	8L.78
1-8	7509	1L.28	8L.21
1-8	5752	1L.36	8L.25
1-8	a	1L.41	8S.52
1-8	026-2	1L.49	8L.80
1-8	6766	1L.54	8L.77
1-8	b	1L.59	8L.82
1-8	5821	1L.65	8L.31
1-8	6697	1L.89	8L.52
1-8	5910	1L.93	8L.67
1-8	5704	1L.96	8S.67
1-8	055-4	(	)

* Break points taken from Longley, A. E.; Crops Research Bulletin, ARS 34-16, January, 1961.

** Break points determined by Dr. C. R. Burnham and students, University of Minnesota.

Translocation		Break Points*	
1-9	024-7	1S.71	9L.13
1-9	8302	1S.55	9L.29
1-9	8001	1S.51	9L.24
1-9	c	1S.48	9L.22
1-9	7535	1S.33	9S.27
1-9	8918	1S.21	9L.20
1-9	6762	1S.16	9L.53
1-9	a	1S.13	9L.15
1-9	8460	1S.13	9L.24
1-9	5622	1L.10	9L.12
1-9	4995	1L.19	9S.20
1-9	8886	1L.33	9L.23
1-9	4997	1L.37	9S.28
1-9	d	1L.42	9L.25
1-9	b	1L.50	9L.60
1-9	4398	1L.51	9S.19
1-9	8389	1L.74	9L.13
1-9	035-10	1L.89	9S.67
1-10	g	1S.80	10L.21
1-10	007-19	1S.07	10L.08
1-10	f	1S.04	10L.30
1-10	4885	1ctr.	10ctr.
1-10	8770	1L.09	10L.38
1-10	e	1L.16	10L.31
1-10	068-14	1L.16	10L.79
1-10	5273	1L.17	10L.69
1-10	h	1L.19	10S.39
1-10	a	1L.29	10L.33
1-10	c	1L.43	10L.74
1-10	8491	1L.45	10L.76
1-10	d	1L.50	10L.68
1-10	015-9	1L.67	10S.46
1-10	8375	1L.69	10L.64
1-10	001-3	1L.86	10L.48
2-3	023-5	2S.80	3L.70
2-3	8662	2S.78	3L.83
2-3	e	2S.76	3L.48
2-3	5800	2S.73	3S.81
2-3	5304	2S.62	3L.29
2-3	c	2S.46	3S.52
2-3	6270	2S.46	3L.60
2-3	014-12	2S.43	3L.51
2-3	6862	2S.39	3L.20
2-3	4369	2S.19	3S.26
2-3	010-10	2S.17	3L.13
2-3	4301-111	2ctr.	3ctr.
2-3	023-2	2ctr.	3ctr.
2-3	055-7	2L.10	3S.31
2-3	005-14	2L.12	3S.29
2-3	h	2L.14	3L.07
2-3	8483	2L.14	3L.12
2-3	i	2L.19	3S.51
2-3	g	2L.21	3S.21
2-3	7285	2L.26	3L.39
2-3	033-4	2L.27	3L.23
2-3	f	2L.35	3S.60
2-3	b	2L.45	3L.08
2-3	d	2L.67	3L.48
2-3	4303-74	2L.73	3L.68
2-3	6750	2L.76	3S.53
2-3	6284	2L.81	3L.75
2-4	5157	2S.86	4L.07
2-4	8865	2S.52	4L.27
2-4	060-8	2S.50	4L.37
2-4	018-3	2S.38	4L.47
2-4	5495	2S.27	4L.10
2-4	j	2ctr.	4ctr.
2-4	8407	2ctr.	4ctr.
2-4	g	2L.13	4S.31
2-4	010-4	2L.13	4S.31
2-4	k	2L.13	4L.04
2-4	004-13	2L.14	4S.51
2-4	4374	2L.15	4L.23
2-4	8027	2L.15	4L.43
2-4	d	2L.17	4L.45
2-4	5951	2L.18	4S.26
2-4	a	2L.30	4L.21
2-4	e	2L.31	4S.47
2-4	m	2L.34	4S.47
2-4	057-19	2L.35	4S.51
2-4	017-18	2L.39	4L.19
2-4	6266	2L.40	4L.27
2-4	011-7	2L.53	4L.76
2-4	l	2L.59	4S.40
2-4	f	2L.75	4L.12
2-4	052-15	2L.75	4L.66
2-4	c	2L.81	4S.09
2-4	b	2L.81	4L.53
2-5	g	2S.79	5S.24
2-5	059-17	2S.73	5S.61
2-5	019-1	2S.67	5S.51
2-5	4741	2S.47	5L.47
2-5	009-19	2S.29	5L.11
2-5	025-4	2S.26	5L.78
2-5	e	2S.19	5S.28
2-5	059-1	2ctr.	5S.84
2-5	b	2L.06	5S.09
2-5	6580	2L.09	5S.09
2-5	5098	2L.13	5S.23
2-5	a	2L.14	5L.15
2-5	c	2L.16	5S.48
2-5	015-3	2L.16	5S.69
2-5	002-16	2L.25	5L.35
2-5	023-15	2L.28	5S.30
2-5	032-9	2L.40	5S.31
2-5	062-3	2L.45	5S.34
2-5	5876	2L.47	5L.46
2-5	5645	2L.60	5S.85
2-5	6885	2L.63	5S.79
2-5	5602	2L.73	5L.77
2-5	8321	2L.86	5L.11
2-5	f	2L.91	5L.10
2-5	d	2L.91	5L.86
2-5	4578	2L.92	5S.71
2-6	8786	2S.90	6S.77
			6S.org.**
2-6	001-5	2S.72	6S.87
			org.**
2-6	b	2S.69	6L.49
2-6	060-5	2S.36	6L.18
2-6	027-4	2S.34	6L.11
		2L.10	6S.org.**
2-6	5472	2S.25	6L.15
2-6	e	2L.18	6L.20
			6S. **
2-6	6931	2L.24	6L.23
2-6	g	2L.24	6L.29
2-6	a	2L.28	6L.20
		2S.40	6S.50**
2-6	c	2L.37	6L.25
		2S	**
2-6	d	2L.41	6L.45
2-6	4717	2L.77	6L.27
2-6	5419	2L.82	6S.79
			6S.org.**
2-6	8414	2L.94	6S.79
			6S.org.**
2-7	5279	2S.93	7L.25
2-7	5144	2S.35	7L.08
2-7	022-4	2S.30	7L.24
2-7	8045	2S.12	7L.06
2-7	d	2L.16	7L.18
2-7	4400	2L.24	7L.32
2-7	f	2L.30	7L.68
2-7	b	2L.37	7L.12
2-7	c	2L.47	7S.34
2-7	4519	2L.65	7L.66
2-7	5783	2L.66	7L.10
2-7	038-12	2L.75	7S.68
2-7	8322	2L.76	7L.74
2-7	e	2L.82	7L.63
2-7	3692-1	2S.10	7L.02
2-8	013-17	2S.89	8L.61
2-8	4711	2S.86	8L.67
2-8	011-20	2S.58	8L.28
2-8	c	2S.15	8S.11
2-8	f	2ctr.	8ctr.
2-8	006-10	2ctr.	8ctr.
2-8	d	2L.05	8L.10
2-8	e	2L.07	8L.10
2-8	4414	2L.12	8L.14
2-8	7069	2L.13	8L.14
2-8	003-5	2L.19	8S.72
2-8	b	2L.20	8L.18
2-8	5454	2L.21	8S.39
2-8	h	2L.23	8L.22
2-8	5484	2L.24	8S.58
2-8	031-7	2L.30	8S.44
2-8	i	2L.32	8L.30
2-8	051-15	2L.62	8L.48
2-8	062-15	2L.70	8L.26
2-8	g	2L.71	8S.71
2-8	051-7	2L.83	8L.74
2-8	48-45-6	2L.84	8L.68
2-8	8376	2L.95	8L.03
2-8	037-5	2L.95	8L.54
2-9	7096	2S.57	9L.66
2-9	c	2S.49	9S.33
2-9	a	2S.36	9L.58
2-9	055-14	2S.28	9L.27
2-9	5711	2S.24	9L.23
2-9	b	2S.18	9L.22
2-9	062-11	2L.21	9S.53
2-9	5257	2L.28	9L.20
2-9	6656	2L.32	9S.31
2-9	5208	2L.76	9L.68
2-9	d	2L.83	9L.27
2-10	043-10	2S.89	10L.40
2-10	5651	2S.71	10L.62
2-10	b	2S.50	10L.75
2-10	8864	2S.10	10L.76
2-10	4484	2S.09	10L.14
2-10	5830	2L.12	10L.12
2-10	a	2L.16	10L.55
2-10	c	2L.30	10S.40
2-10	5561	2L.35	10S.16
2-10	8219	2L.50	10L.35
2-10	6853	2L.79	10L.86
2-10	035-2	2L.85	10L.49
3-4	8969	3S.75	4L.75
3-4	8397	3S.74	4S.55
3-4	8634	3S.71	4L.75
3-4	5156	3S.47	4L.67
3-4	5920	3S.28	4L.73
3-4	012-16	3S.27	4S.30

Translocation		Break Points*	
3-4	4662	3S.24	4S.67
3-4	4726	3S.16	4L.15
3-4	5891	3ctr.	4ctr.
3-4	5074-6	3ctr.	4ctr.
3-4	a	3L.07	4L.85
3-4	006-17	3L.10	4S.45
3-4	037-9	3L.10	4L.14
3-4	8443	3L.12	4L.13
3-4	6534	3L.48	4L.89
3-5	4635	3S.44	5S.48
3-5	e	3S.34	5S.16
3-5	6473	3S.32	5S.26
3-5	6462	3S.31	5L.47
3-5	4880	3ctr.	5ctr.
3-5	4898	3ctr.	5ctr.
3-5	6695	3ctr.	5ctr.
3-5	g	3L.01	5S.73
3-5	8104	3L.05	5L.08
3-5	8528	3L.06	5L.72
3-5	039-13	3L.13	5L.14
3-5	5874	3L.16	5L.21
3-5	i	3L.23	5L.20
3-5	5521	3L.17	5L.48
3-5	a	3L.28	5L.60
3-5	h	3L.55	5L.22
3-5	b	3L.61	5L.57
3-5	c	3L.62	5L.27
3-5	7043	3L.63	5L.61
3-5	8351	3L.75	5L.68
3-5	6346	3L.94	5L.83
3-6	b	3S.73	6S.82
			6S.org.**
3-6	060-4	3S.62	6L.08
3-6	4349	3S.58	6L.70
3-6	c	3S.56	6L.54
3-6	016-17	3S.48	6L.30
3-6	032-3	3S.41	6S.78
3-6	030-8	3S.27	6S.81
3-6	8963	3S.23	6L.14
3-6	a	3L.06	6L.30
3-6	7067	3L.07	6L.75
3-6	6349	3L.10	6L.15
3-6	8145	3L.17	6L.26
3-6	5368	3L.22	6L.20
3-6	d	3L.23	6L.82
3-6	5201	3L.26	6L.21
3-6	8672	3L.47	6L.87
3-6	7162	3L.52	6L.53
3-6	054-12	3L.72	6L.75
3-7	b	3S.92	7L.03
3-7	001-15	3S.38	7L.30
3-7	004-7	3S.38	7L.26
3-7	a	3S.25	7L.18
3-7	4670	3S.20	7L.76
3-7	4773	3S.11	7L.07
3-7	5724	3ctr.	7ctr.
3-7	5955	3L.10	7L.58
3-7	029-3	3L.11	7L.13
3-7	5378	3L.13	7L.73
3-7	e	3L.25	7S.56
3-7	6466	3L.36	7L.14
3-7	c	3L.46	7L.45
3-7	5471/	3L.64	7L.58
3-7	d	3L.64	7L.81
3-7	8006	3L.88	7L.90
3-8	024-11	3S.65	8L.49
3-8	6373	3S.53	8L.68
3-8	e	3S.36	8L.21

Translocation		Break Points*	
3-8	4626	3S.30	8L.31
3-8	6439	3S.30	8L.15
3-8	8666	3S.30	8L.14
3-8	8667	3S.30	8L.14
3-8	8670	3S.30	8L.14
3-8	8367	3S.28	8S.52
3-8	5558	3S.26	8S.74
3-8	c	3S.23	8L.85
3-8	4303-12	3ctr.	8ctr.
3-8	4872	3ctr.	8ctr.
3-8	043-14	3L.02	8S.40
3-8	7362	3L.07	8L.69
3-8	f	3L.08	8L.10
3-8	g	3L.12	8L.19
3-8	b	3L.16	8L.23
3-8	8023	3L.18	8L.16
3-8	4874	3L.28	8L.32
3-8	a	3L.41	8L.61
3-8	6261	3L.49	8L.40
3-8	h	3L.53	8S.46
3-8	8350	3L.75	8S.60
3-8	4340	3L.88	8L.72
3-8	4301-39	3L.92	8L.82
3-8	3687	3L.25	8L.88
3-9	054-18	3S.88	9L.82
3-9	6722	3S.66	9S.66
3-9	7041	3S.59	9L.70
3-9	5643	3S.55	9L.64
3-9	8447	3S.44	9L.14
3-9	030-2	3S.39	9L.30
3-9	8465	3S.27	9L.41
3-9	8032	3S.26	9L.96
3-9	020-5	3ctr.	9ctr.
3-9	e	3L.02	9L.29
3-9	5775	3L.09	9S.24
3-9	c	3L.09	9L.12
		3S.15	9S.20**
3-9	h	3L.09	9L.33
3-9	a	3L.11	9L.16
3-9	d	3L.13	9L.26
3-9	034-11	3L.46	9S.36
3-9	g	3L.40	9L.14
3-9	b	3L.48	9L.53
3-9	5285	3L.51	9L.49
3-9	4727	3L.54	9L.42
3-9	f	3L.63	9S.69
3-9	8562	3L.65	9L.22
3-9	4963	3L.76	9L.57
3-10	7464	3S.49	10L.60
3-10	8412	3S.39	10S.36
3-10	8349	3S.38	10ctr.
3-10	4382	3S.38	10L.29
3-10	5892	3S.17	10L.25
3-10	a	3L.16	10L.22
3-10	b	3L.19	10L.27
3-10	c	3L.22	10L.30
3-10	6691	3L.30	10L.87
3-10	036-15	3L.48	10L.64
3-10	044-10	3L.77	10L.72
4-5	e	4S.41	5S.32
4-5	g	4S.38	5L.30
4-5	8108	4S.37	5S.72
4-5	5529	4S.37	5L.46
4-5	8069	4S.34	5S.71
4-5	c	4S.34	5L.27
4-5	6831	4S.32	5S.59
4-5	6560	4S.32	5S.21
4-5	002-12	4S.29	5S.36
4-5	4305-8	4S.27	5L.28

Translocation		Break Points*	
4-5	4472	4S.25	5S.19
4-5	d	4S.21	5L.22
4-5	k	4S.06	5L.13
4-5	7078	4L.05	5L.10
4-5	i	4L.10	5S.15
4-5	h	4L.13	5L.08
4-5	a	4L.19	5S.29
4-5	j	4L.21	5L.36
4-5	8622	4L.30	5L.52
4-5	006-7	4L.43	5S.25
4-5	7136	4L.45	5L.33
4-5	f	4L.50	5L.80
4-5	6743	4L.56	5S.59
4-5	018-4	4L.61	5L.67
4-5	027-10	4L.61	5L.79
4-5	021-3	4L.62	5S.71
4-5	8395	4L.63	5L.82
4-5	b	4L.76	5L.68
4-6	b	4S.80	6L.16
4-6	e	4S.62	6L.56
4-6	7328	4S.53	6S.89
4-6	8380	4S.47	6L.18
4-6	5227	4S.46	6S.84
4-6	025-12	4S.44	6L.34
			6S. **
4-6	4341	4S.37	6S.81
4-6	c	4S.33	6S.83
4-6	011-16	4S.31	6L.33
			6S. **
4-6	4447	4S.28	6L.14
4-6	6623	4L.18	6L.31
4-6	8591	4L.17	6L.24
			6S. **
4-6	055-8	4L.29	6L.25
4-6	8428	4L.32	6L.28
4-6	8764	4L.32	6L.90
4-6	a	4L.37	6L.43
4-6	d	4L.49	6L.53
4-6	033-16	4L.50	6S.90
4-6	7037	4L.61	6S.77
4-6	8927	4L.70	6L.18
4-6	038-11	4L.78	6L.29
4-6	8339	4L.87	6L.79
4-7	8103	4S.81	7L.76
4-7	3686	4S.81	7S.06
4-7	6575	4S.38	7S.32
4-7	a	4S.32	7L.06
4-7	48-40-8	4S.32	7L.64
4-7	7347	4S.31	7L.66
4-7	7108	4S.17	7S.45
4-7	4698	4L.08	7L.74
4-7	7067	4L.17	7S.60
4-7	027-17	4L.17	7L.31
4-7	8374	4L.24	7L.55
4-7	4483	4L.39	7L.61
4-8	036-16	4S.66	8L.69
4-8	a	4S.59	8L.19
4-8	8987	4S.58	8L.76
4-8	8607	4S.42	8L.35
4-8	8004	4S.27	8L.84
4-8	5339	4S.22	8L.71
4-8	8456	4S.22	8L.75
4-8	b	4S.18	8L.16
4-8	6063	4S.02	8L.05
4-8	6926	4L.60	8L.71
4-8	6363	4L.76	8L.30
4-9	e	4S.53	9L.26
4-9	4307-12	4S.53	9L.55

Translocation		Break Points*	
4-9	g	4S.27	9L.27
4-9	5918	4S.24	9L.18
4-9	4304-82	4S.22	9L.37
4-9	6222	4L.03	9S.68
4-9	6504	4L.09	9S.83
4-9	d	4L.12	9L.17
4-9	a	4L.16	9L.58
4-9	004-7	4L.28	9L.26
4-9	4373	4L.29	9L.39
4-9	5657	4L.33	9S.25
4-9	5884	4L.40	9L.49
4-9	f	4L.55	9L.18
4-9	5574	4L.80	9L.87
4-9	c	4L.82	9L.29
4-9	b	4L.90	9L.29
4-9	8636	4L.94	9S.09
4-9	8649	4L.94	9S.09
4-10	c	4S.64	10L.18
4-10	9028	4S.57	10L.89
4-10	8541	4S.45	10ctr.
4-10	d	4S.36	10L.36
4-10	6662	4L.04	10L.03
4-10	e	4L.14	10L.14
4-10	b	4L.15	10L.60
4-10	021-5	4L.34	10L.33
4-10	073-8	4L.41	10S.74
4-10	6587	4L.55	10L.51
4-10	057-14	4L.56	10S.48
4-10	024-16	4L.75	10L.18
4-10	f	4L.94	10L.14
5-6	5622	5S.94	6L.92
		5S.87	6L.47**
5-6	8818	5S.91	6L.93
		5L.91	6L.93**
5-6	6522	5S.87	6L.70
5-6	6559	5S.72	6L.09
5-6	d	5S.64	6S.89
		5S.58	6S.Sat.**
5-6	040-1	5S.48	6S.82
5-6	6671	5S.49	6L.35
5-6	f	5S.37	6S.76
5-6	8590	5S.29	6L.25
		5S.25	6L.61**
5-6	4933	5S.23	6L.89
5-6	5765	5S.19	6L.32
5-6	5906	5S.15	6L.13
5-6	e	5L.11	6L.60
5-6	4669	5L.13	6L.40
5-6	6062	5L.20	6L.78
5-6	5685	5L.27	6L.20
		5S.24	6L.23**
5-6	4934	5L.34	6L.89
5-6	a	5L.35	6L.43
5-6	4666	5L.35	6L.86
5-6	004-17	5L.60	6L.24
5-6	b	5L.72	6L.21
5-6	8219	5L.76	6S.84
		5L.69	6S.Sat.**
5-6	c	5L.81	6L.08
		5L.89	6S.00**
5-6	8696	5L.89	6S.80
5-7	d	5S.63	7S.33
5-7	064-18	5S.61	7S.49
5-7	061-4	5S.54	7L.30
5-7	5143	5S.51	7L.10
5-7	3699	5S.46	7L.07
5-7	e	5S.40	7S.18

Translocation		Break Points*	
5-7	013-3	5S.36	7S.35
5-7	4306-4	5S.32	7L.35
5-7	3695	5S.27	7S.49
5-7	8679	5S.09	7S.26
5-7	062-18	5ctr.	7ctr.
5-7	023-13	5L.12	7L.15
5-7	3690	5L.17	7L.61
5-7	b	5L.18	7S.36
5-7	6293	5L.26	7L.63
5-7	8630	5L.38	7L.24
5-7	c	5L.42	7L.72
5-7	5179	5L.55	7L.73
5-7	a	5L.78	7L.72
5-7	f	5L.80	7L.85
5-7	8671	5L.96	7L.67
5-8	8420	5S.90	8L.33
5-8	8746	5S.84	8L.25
5-8	5013	5S.67	8L.59
5-8	6612	5S.59	8L.66
5-8	013-11	5S.59	8S.63
5-8	d	5S.55	8L.12
5-8	5570	5S.47	8S.35
5-8	c	5S.24	8L.20
5-8	b	5S.23	8L.23
5-8	5575	5S.21	8S.22
5-8	7068	5S.18	8L.18
5-8	5777	5S.13	8L.19
5-8	6402	5S.07	8L.07
5-8	A-50	5S.07	8L.11
5-8	6406	5ctr.	8ctr.
5-8	f	5L.02	8S.08
5-8	6289	5L.06	8L.54
5-8	045-6	5L.08	8L.13
5-8	002-17	5L.11	8L.28
5-8	8997	5L.16	8L.08
5-8	014-5	5L.19	8L.18
5-8	053-4	5L.21	8S.48
5-8	4636	5L.23	8L.79
5-8	g	5L.28	8S.44
5-8	007-17	5L.32	8S.47
5-8	5866	5L.32	8L.77
5-8	7102	5L.48	8S.10
5-8	030-1	5L.48	8L.78
5-8	a	5L.49	8S.58
5-8	8806	5L.72	8S.59
5-8	8796	5L.76	8L.11
5-8	055-20	5L.81	8L.67
5-9	8854	5S.33	9S.36
5-9	022-11	5S.30	9L.27
5-9	B-91	5S.23	9L.21
5-9	6057	5S.15	9S.52
5-9	8591	5S.09	9L.25
5-9	c	5S.07	9L.10
5-9	020-7	5ctr.	9ctr.
5-9	4817	5L.06	9S.07
5-9	5614	5L.09	9L.06
5-9	d	5L.14	9L.10
5-9	032-8	5L.19	9L.70
5-9	008-18	5L.29	9L.26
5-9	4790	5L.34	9L.45
5-9	8895	5L.37	9L.11
5-9	4305-22	5L.42	9L.15
5-9	e	5L.46	9L.74
5-9	4352	5L.48	9L.61
5-9	015-10	5L.50	9L.20
5-9	013-9	5L.51	9L.82
5-9	b	5L.68	9L.44
5-9	a	5L.69	9S.17
5-9	4871	5L.71	9S.38
5-9	8457	5L.78	9S.83

Translocation		Break Points*	
5-9	6200	5L.81	9L.71
5-9	8386	5L.87	9S.13
5-10	6760	5S.78	10S.40
5-10	5355	5S.77	10L.45
5-10	5653	5S.76	10L.71
5-10	031-18	5S.58	10S.55
5-10	X-57-16	5S.42	10L.42
5-10	5679	5S.16	10L.15
5-10	6830	5ctr.	10ctr.
5-10	b	5L.09	10S.25
5-10	5358	5L.10	10L.76
5-10	073-6	5L.13	10S.41
5-10	4384	5L.13	10L.79
5-10	a	5L.14	10S.54
5-10	5188	5L.37	10S.65
5-10	006-11	5L.49	10L.52
5-10	022-20	5L.65	10S.62
5-10	3693	5L.67	10L.51
5-10	7142	5L.73	10L.17
5-10	5290	5L.78	10S.49
5-10	5688	5L.78	10L.53
5-10	8345	5L.87	10S.61
5-10	4801	5L.91	10L.23
5-10	5557	5L.92	10S.39
6-7	7036	6S.90	7L.63
6-7	035-3	6S.80	7L.20
6-7	5181	6S.79	7L.86
		6S.Org.	7L.86**
6-7	4964	6S.76	7L.72
		6S.Org.	7L.63**
6-7	054-6	6L.10	7L.60
6-7	6498	6L.16	7S.48
		6L.23	7S.near ctr.**
6-7	4573	6L.22	7L.27
6-7	4545	6L.25	7S.73
		6L.07	7S.near ctr.**
6-7	7380	6L.29	7L.45
6-7	011-11	6L.29	7L.29
6-7	013-8	6L.31	7L.22
		6L.27	7L.63**
6-7	6885	6L.33	7S.58
6-7	8143	6L.35	7L.36
		6L.18	7L.16**
6-7	4337	6L.37	7L.13
6-7	6598	6L.43	7L.61
6-7	4594	6L.52	7S.67
6-7	027-6	6L.66	7L.97
6-7	a	6L.73	7L.68
6-7	7402	6L.97	7L.14
6-8	058-1	6ctr.	8L.46
6-8	6187	6L.19	8L.51
6-8	6873	6L.21	8L.29
6-8	5028	6L.21	8L.31
6-8	c	6L.27	8L.50
6-8	5605	6L.36	8L.22
6-8	a	6L.41	8L.80
6-8	024-1	6L.42	8L.74
6-8	d	6L.51	8L.77
6-8	b	6L.79	8S.76
6-9	017-14	6S.80	9L.50
6-9	4778	6S.80	9L.30
6-9	a	6S.79	9L.40
		6S.org.	**
6-9	d	6S.73	9L.82
6-9	067-6	6S.39	9L.47
6-9	5454	6ctr.	9S.75

Translocation		Break Points*	
6-9	6566	6ctr.	9L.90
6-9	84-39	6L.06	9S.73
6-9	b	6L.10	9S.37
6-9	4505	6L.13	9ctr.
6-9	c	6L.15	9L.29
6-9	8536	6L.18	9S.81
6-9	e	6L.18	9L.24
6-9	6270	6L.19	9L.28
6-9	6019	6L.27	9L.26
6-9	8906	6L.27	9L.59
6-9	043-1	6L.36	9L.36
6-9	5964	6L.47	9L.83
6-9	8768	6L.89	9S.61
6-10	f	6S.92	10S.28
6-10	5253	6S.80	10L.41
6-10	5519	6S.75	10L.17
6-10	b	6L.12	10L.29
6-10	e	6L.14	10S.43
6-10	d	6L.16	10L.29
6-10	8645	6L.21	10L.28
6-10	8651	6L.27	10L.48
6-10	h	6L.47	10L.87
6-10	044-8	6L.48	10L.51
6-10	c	6L.51	10S.36
6-10	8904	6L.51	10L.83
6-10	4307-12	6L.74	10S.71
6-10	a	6L.75	10L.15
6-10	4833	6L.83	10S.78
6-10	g	6L.85	10L.20
6-10	5780	6L.93	10L.13
7-8	5828	7S.31	8L.10
7-8	6531	7ctr.	8ctr.
7-8	6981	7ctr.	8ctr.
7-8	8580	7ctr.	8ctr.
7-8	004-3	7ctr.	8ctr.
7-8	016-15	7ctr.	8ctr.
7-8	034-17	7L.05	8S.59
7-8	5499	7L.05	8L.08
7-8	062-16	7L.15	8L.17
7-8	014-17	7L.18	8L.30
7-8	4536	7L.34	8L.47
7-8	038-8	7L.52	8L.46
7-8	7149	7L.56	8L.65
7-8	5479	7L.70	8S.21
7-8	021-1	7L.72	8L.49
7-8	4824	7L.83	8L.25
7-9	b	7S.76	9S.19
7-9	071-1	7S.70	9L.07
7-9	8659	7S.55	9S.35
7-9	053-8	7S.51	9L.77
7-9	5074	7S.48	9L.53
7-9	8558	7S.22	9L.16
7-9	4363	7ctr.	9ctr.
7-9	6225	7ctr.	9ctr.
7-9	8383	7ctr.	9ctr.
7-9	6482	7L.01	9S.97
7-9	7074	7L.03	9S.80
7-9	c	7L.14	9L.22
7-9	4713	7L.60	9ctr.
7-9	027-9	7L.61	9S.18
7-9	6978	7L.62	9S.83
7-9	a	7L.63	9S.07
7-9	032-13	7L.82	9L.88
7-10	7356	7S.75	10L.88
7-10	022-15	7ctr.	10ctr.
7-10	019-3	7L.17	10L.47
7-10	4422	7L.79	10ctr.
7-10	4356	7L.70	10S.37

Translocation		Break Points*	
8-9	b	8S.67	9L.75
8-9	4643	8S.37	9L.11
8-9	c	8ctr.	9ctr.
8-9	8525	8L.06	9S.63
8-9	5391	8L.07	9S.33
8-9	d	8L.09	9S.16
8-9	a	8L.13	9L.38
8-9	8951	8L.13	9L.77
8-9	043-6	8L.17	9S.34
8-9	e	8L.32	9L.25
8-9	6673	8L.35	9S.31
8-9	4775	8L.42	9L.68
8-9	4593	8L.69	9L.65
8-9	6921	8L.85	9L.15
8-9	5300	8L.85	9S.43
8-9	4453	8L.86	9S.68
8-10	b	8ctr.	10ctr.
8-10	5585	8ctr.	10ctr.
8-10	6653	8L.04	10L.06
8-10	3697	8L.10	10L.18
8-10	9020	8L.13	10S.50
8-10	6488	8L.14	10S.34
8-10	5287	8L.17	10S.33
8-10	034-19	8L.24	10L.28
8-10	001-5	8L.30	10S.57
8-10	d	8L.39	10L.16
8-10	c	8L.41	10S.56
8-10	6128	8L.43	10S.49
8-10	a	8L.48	10S.48
8-10	5944	8L.75	10L.40
8-10	e	8L.84	10S.37
9-10	059-10	9S.31	10L.53
9-10	3688	9S.49	10L.02
9-10	8630	9S.28	10L.37
9-10	b	9S.13	10S.40
9-10	4303-9	9L.26	10S.44
9-10	5488	9L.57	10L.89
9-10	041-4	9L.67	10L.92
9-10	041-6	9L.70	10L.90
9-10	7103	9L.73	10L.88

The following reciprocal translocation stocks do not involve the same chromosomes and/or breakpoints as originally reported. The new information was kindly supplied by Dr. C. R. Burnham and Associates of the University of Minnesota.

Translocation	Symbol	Breakpoint from Longley ARS-34-16		New information Burnham and Associates	
1-5	8347	1S.84	5L.51	1	2
1-5	8972	1S.56	5S.29		1 not correct
1-5	018-5	1S.53	5L.52	1	2
1-5	055-4	1S.32	5L.31	1 or	5 not correct
1-5	040-3	1S.17	5L.61	1 or	5 not correct
1-5	024-5	1S.09	5L.98	1	2
1-5	4331	1L.03	5S.02	7	10
1-5	6178	1L.04	5L.05	1	2
1-5	8388	1L.30	5S.25	1	2
2-6	4394	2S.91	6L.12	4	6
2-6	6671	2S.22	6L.22	5S.49	6L.35
2-6	5648	2L.25	6L.19	1	6
2-6	9002	2L.57	6L.56	1	6
2-6	f	2L.79	6L.87	1	6
5-6	8665	5L.58	6L.25	Independent of chrom. 5 genes	
5-10	6061	5S.60	10L.57	2	10

Also in the Maize Genetics Co-op collection are 48 cultures with no chromosome information and 27 cultures with chromosomes involved determined but no breakpoints. This seed is available to anyone who wishes to determine the chromsomes and breakpoints or would like to use the material as unknowns in cytogenetic courses.

VI. RECENT MAIZE PUBLICATIONS

The 469 references beginning on the next page have been compiled from the published literature primarily by screening Current Contents (Life Sciences; Agriculture . . .) for titles that include maize or its relatives and that deal with genetics, cytogenetics, breeding, evolution or molecular biology. Papers on biochemistry, physiology, culture, production, growth, development, anatomy, pathology and other areas are included if they seem to be relevant to genetic research. This screening is backed up by a most helpful computer search supplied by the National Agricultural Library, USDA, from Biological Abstracts sources. In addition, many papers are defined from listings supplied by Cooperators from their own publications and from sources not readily available. Abstracts and dissertations are not generally included, but other misses are unintentional; suggestions of items that may be missed, or of resources that are not covered, are earnestly desired.

I attempt to discover and include every publication that impacts on methods and knowledge toward improvement of the crop; that examines measurable or observational differences between strains for which there may be a genetic basis (e.g., pathology, stress, nutrient utilization, etc.); that defines methods of potential use in the field or the laboratory in genetics and related fields; or that characterizes "genetically significant" biochemical or physiological systems. The limited literature in some areas is surprising; in the recent questionnaire several respondents suggested more coverage of areas that are currently covered, which says that there is an expectation of more work in the field. Areas with surprisingly little research attention include genetic variation in major enzyme systems; genetics of pathogen/host; new perceptions in quantitative genetics relating to molecular biological surprises. These and similar areas suggest that those of us who are aware of the materials and of the genetic potential of this species might benefit science by being more vocal about its qualities and properties.

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VII. SYMBOL AND CYTOGENETIC INDEX

Contains symbols in the Reports from Cooperators and all other parts except the Catalogue of Stocks (see the symbol index in MNL 54 for access to the Stocks). Includes gene symbols and phenomenologic symbols (e.g., AR, NCS), aberrations and aneuploids and chromosomal features (e.g., B-chrom, Df, Dp, Inv, Iso, K, monosome, NOR, Ring, T, TB, Tp, trisome), and selected segments (ctDNA, mtDNA, rRNA). Chromosome additions or segments from relatives are generally included if they can be defined by symbols such as Trip (Td, Tf and Tr have been used in prior indexes covering from MNL 36 forward) or teos. Cytoplasms have been indexed under cms or cytopl. Suggestions are wanted for improving the usefulness of this index; so are corrections.

For the development of a tailor-made routine for sorting symbols and for index formatting, we are indebted to Manjit S. Kang.

Indexes are available to symbols for issues through No. 35 (Appendix available from Coe), for Nos. 36 through 53 (in No. 53), and from No. 54 to date annually in each issue.

VIII. AUTHOR AND NAME INDEX

References to all authors of Reports from Cooperators (underlined), to authors of Recent Publications, and to cited names in this issue (except the mailing list).
For the sort and index routine, we are indebted to Manjit Kang.

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