MAIZE GENETICS COOPERATION

NEWS LETTER

49

April 15, 1975

Division of Biological Sciences
and
Agricultural Experiment Station
University of Missouri
Columbia, Missouri

INTERNATIONAL MAIZE SYMPOSIUM - GENETICS AND BREEDING '75

This unique Symposium will be held in Champaign-Urbana, Illinois, September 8-12, 1975. Registration is open to all interested parties.

The program will consist of three portions: 1) the Invitational Papers, to be presented in eight half-day sessions; 2) the Demonstration Papers, to be available for viewing throughout the week at the Symposium Headquarters, and the abstracts of which will appear in the registration portfolio; and 3) the Exhibits, which will be accessions of maize stocks (e.g., mutants, races, open-pollinated lines, resistant lines, etc.) planted on the Agronomy Farm at the University of Illinois. One half-day will be allocated to tours of the Exhibits.

The Invitational Papers Program, designed by the Program Committee, has been completed; the manuscripts will be published in full immediately following the Symposium. An invitation to submit abstracts for Demonstration Papers was extended in January in the general announcement of the Symposium. Abstracts should be sent immediately to the Executive Secretary.

The registration fee for the entire Symposium is $45.00. Registrants will receive a copy of the proceedings and the registration portfolio without additional charge. For further information about the Demonstration Papers, the Exhibits or pre-registration, contact the Executive Secretary:

Dr. D. E. Alexander
Department of Agronomy
University of Illinois
Station A, Box 2636
Champaign, Illinois 61820, U.S.A.

Dr. G. P. Redei, organizer of the STADLER GENETICS SYMPOSIA, requests announcement of the 7th Symposium, April 18-19, 1975, at Columbia, Missouri. The program includes the following:

E. Chargaff--Impact of Biochemistry on Genetics
R. B. Helling--Eukaryotic Genes in Prokaryotic Cells
O. L. Gamborg--New Advances in Somatic Cell Hybridization in Plants
R. Flavell--Genome Organization in Higher Plants
N. Sueoka--Chromosome Replication and Gene Expression in Bacillus subtilis
C. D. Miles--Genetic Analysis of Photosynthesis
A. C. Wilson--Relative Rates of Evolution of Organisms and Genes
G. B. Johnson--Enzyme Polymorphism and Adaptation
D. E. Metter--Natural Selection and Adaptive Resemblances

The detailed program can be obtained from Conferences and Short Courses, University of Missouri, Columbia, Missouri, 65201.

Proceedings of this and previous Symposia are available (Vols. 3-5 $4.00, Vols. 6 & 7 $4.50 each; postage and handling 50 cents per order) from Stadler Genetics Symposia, 117 Curtis Hall, University of Missouri, Columbia, Missouri 65201.

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I. FOREWORD

Cooperation is the reason that the News Letter has existed. We who work on the genetics, cytogenetics and biochemical genetics of maize have a tradition of freely exchanging our materials, data, interpretations and puzzles directly with each other or through this non-publication. If there have been any undesirable consequences, they have been only when the reporting of a substantial study has stopped with a News Letter note and has not been carried to the formal literature, with the result that the general scientific community has failed to learn of our information, ingenuity, insights, errors or flights of concept. It is vital that our informal means of communicating be maintained, and your new "Secretary" will strive to maintain it; in fact, ideas for ways by which the informality can be enhanced and formal publication facilitated would be most welcome. For example, Cooperators might appreciate in future News Letters brief items about manuscripts that have been submitted and are not yet in print, if these are given as "Report" items (author and title, with or without further text) contributed by the authors.

The costs of preparation, reproduction and mailing of this News Letter, as in recent years, are borne by a grant from the National Science Foundation. All of us can be grateful that this support is available, because it is indispensable.

Until this year's contributions were in hand and the editing was begun, we did not know how much attention Ellen Dempsey had been giving to the News Letter contributions; we send Ellen our encomia, based on the experience of only one cycle but aware that years of such excellent care have required exceptional dedication and patience. If in our editing for format, nomenclature and clarity we have marred the history of her delicate and exacting touch, we apologize to her more than to the contributors. If we have altered meanings or otherwise erred in our editing, we invite errata for the next issue.

Attention given by contributors to the new recommendations on nomenclature was very helpful; the recommendations are repeated this year. A number of new symbol assignments are listed in the report from the Maize Genetics Cooperation Stock Center.

A list of publications of E. G. Anderson and associates, including identification of those papers for which reprints are available, has been prepared and is included between the Stock Center report and the list of Recent Maize Publications.

Deadline for contributions for the next issue (Volume 50, 1976) will be January 1, 1976. While this deadline is substantially earlier than the customary one and may find some data unanalyzed, trial of a change seems desirable for a number of reasons, not the least of which is the possibility of moving the date for distribution to a time somewhat ahead of planting season.

Index corrections wanted: Toward a list of corrigenda for the 1962 symbol index and the 1970 author and name index, please pass along by letter, post card or notes on brown paper bags any corrections for the indexes that may have come to your attention.

Back issues wanted: Repeated requests are received for back issues, including appeals from newly developing maize laboratories in the U. S. and other countries, but also from some locations with resources too limited to purchase even a microfilm with U. S. exchange. If you come across unnecessary extra copies of back issues of any volumes, please consider sending them in for this type of distribution; we could supply postage on request. If you are interested in obtaining back issues, please see the back cover.

Archival materials needed: In attempting to assemble a "permanent set" of the News Letter for archival maintenance, single copies of Volumes 27, 28 and 36 are not in the files and will have to be photocopied from bound volumes to complete the set if copies cannot be located. Original copies of these three issues would be especially appreciated for this purpose.

Found on a weatherbeaten brown paper bag, written in heavy graphite pencil:

> "A couple of years ago Marcus Rhoades asked several of us to send seed stocks to Cornell to be maintained there for distribution, and to send in linkage data and other information to be mimeographed for distribution among those of us who wished to share our information. The notion was very helpful, and continues to be."

If you see Professor Rhoades before I do, please mention how well it has worked out.

I would like to thank M. G. Neuffer for help in planning and developing this volume. Preparation of the issue was much facilitated by the enthusiastic and systematic redaction of the copy by Karen Sheridan. M. D. Murray aided in the screening and compilation of the publication lists. Acknowledgement is due Paul Bolen, Kenneth Leto and William Rafaill for their help with proofing of the copy.

E. H. Coe, Jr.

II. REVISED GENETIC NOMENCLATURE FOR MAIZE
(Repeated from 1974 News Letter)

During the 1974 Allerton Park meetings, there was consideration of the proposed nomenclature changes (1973 MNL 47:229-230). Following discussion of possible difficulties, the group voted to accept the recommended changes outlined below. It is hoped that these changes will be implemented in all journal papers written after this date.

RECOMMENDATION 1: Each locus is designated by a lower case italicized symbol. Traditionally, this has been a one or two letter symbol, but some three letter symbols have been used. We recommend that all newly assigned symbols have three letters in the future.

RECOMMENDATION 2: As previously, different loci at which mutations produce the same general phenotype are distinguished by italicized numbers following the gene symbol, but the number one will be omitted in the designation of the first locus identified, i.e., the first locus identified would be *sh* and the second *sh2*. The number will appear on the line both when the gene name is written out and when the symbol is used, e.g.: brittle-2 and *bt2*.

RECOMMENDATION 3: A mutational site or event is designated by an isolation number, laboratory number or previous designation following the gene symbol and set off by a dash: e.g., *sh2-6801*.

The dominant allele at a locus should be designated by the gene symbol with a capital letter, as *Sh2*. Where it is desirable to designate a particular dominant, this can be done as *Sh2-W22*.

The mutation by which a locus was first detected should be designated by a capital R or Ref, as *sh2-R*, to indicate the reference allele.

The superscripts that currently indicate different alleles at a locus will be written after the dash following the locus designation. As examples, R^r would become *R-r* and P^{RR} would become *P-RR*.

RECOMMENDATION 4: A mutation at an unknown locus conditioning a phenotype similar to that conditioned by mutations at one or more known loci can be designated by an appropriate gene symbol, an asterisk (*) to indicate that the locus is unknown and a laboratory number, as *bt*-7011*. After tests establish allelism with mutations at a given locus, the number of that locus can be substituted for the * but the laboratory

isolation number retained, as bt2-7011. It would be preferable if the mutations within the locus that appear to represent independent mutational events were designated only by isolation numbers that do not purport to furnish any information about the characteristics of the allele.

Since these recommendations provide only a framework for changes, uncertainties in application are certain to arise. It is suggested that all queries be referred to Dr. R. J. Lambert, Maize Genetics Cooperation, University of Illinois, Urbana, Illinois 61801. Dr. Lambert has agreed to act as a clearinghouse for all questions relating to gene symbols.

C. R. Burnham
E. H. Coe
O. E. Nelson
E. B. Patterson
M. M. Rhoades

III. REPORTS FROM COOPERATORS

AGRICULTURAL RESEARCH INSTITUTE
Hungarian Academy of Sciences, Martonvásár, Hungary

Data on stalk breaking force and certain morphological characteristics of stalks in maize — Lodging has become a serious problem in overmaturing maize, especially during the past few years in Hungary. Higher plant populations, intensive nitrogen fertilization and the cultivation of maize mostly in monoculture along with the probable formation of more virulent forms of fungi cause as much as 40 to 60% lodging in the field. The objectives of these studies on lodging were (1) to investigate certain stalk characteristics including the resistance to breakage at different internode levels and (2) to study the relationships between breaking force and the length and diameter of the internodes.

We studied one hybrid, 156 x B14, which is resistant to lodging, and another, 156 x N6, which is susceptible to stalk lodging under natural conditions. Individual plants (70) from these hybrids were evaluated at overmaturity, at the end of November 1973. We used simple equipment to break the stalks. The inbred line 156 is Hungarian, while the lines B14 and N6 are of American origin.

The data in Table 1 show that the percent of lodging (natural lodging below the ear), the stalk dimensions and the resistance to breaking vary at different internode levels. Lodging was greatest at the third and fourth internodes in both hybrids.

In the hybrid 156 x B14 the short, thick internodes were the most resistant to breaking. The breaking force varied from 14.38 to 21.46 kg, a range of 7.08 kg. The mean values of breaking force of the hybrid 156 x N6 — which is susceptible to lodging — are rather low; there are no significant differences between the examined internodes. The extreme values for breaking force varied from 15.78 to 16.01 kg, a difference of only 0.22 kg.

On the basis of breaking force data for the lodging-resistant hybrid 156 x B14, it can be stated that the third node has a determinative effect on stalk breaking force; therefore it is enough to examine the characteristics of the stalk at the third internode only. The hybrid 156 x N6 exhibited no differences in breaking force at the different internodes.

We calculated correlations between breaking force and internode length and diameter at the first five internode levels of the hybrids 156 x B14 and 156 x N6. We have found a significant negative correlation between breaking force and the internode length at the second (-0.1552^{+++}, NS) and third (-0.3297^{++} and -0.3970^{+++}) internodes. Correlations of breaking force with internode diameter for hybrid

Table 1. Mean observations on breaking force and certain stalk characteristics of the single-cross hybrids 156 x B14 and 156 x N6.

Node number (from base)	Node length cm	Index*	Node diameter cm	Index*	Breaking force kg	Index*	Lodging percent	Index*
				156 x B14				
1	14.44	68.8	2.59	112.1	21.46	119.6	0.0	-
2	18.14	86.4	2.49	107.8	20.85	116.2	2.4	38.1
3	21.00	100.0	2.31	100.0	17.94	100.0	6.3	100.0
4	20.97	99.9	2.15	93.1	15.94	88.8	4.1	65.1
5	20.73	98.7	2.02	87.4	14.38	80.2	1.4	22.2
				156 x N6				
1	11.33	71.9	2.58	109.3	15.98	100.6	1.5	5.9
2	13.98	88.8	2.48	105.1	15.88	99.9	12.3	48.4
3	15.75	100.0	2.36	100.0	15.89	100.0	25.4	100.0
4	16.84	106.9	2.21	93.6	16.01	100.8	14.7	57.9
5	16.80	106.7	2.07	87.7	15.78	99.3	4.2	16.5

*Index (percent) in relation to third internode

156 x B14 were positive and highly significant at all five internode levels; these r values were: 0.7047^{+++}, 0.6559^{+++}, 0.6928^{+++}, 0.6243^{+++} and 0.6768^{+}. On the other hand, in the hybrid 156 x N6 the r value was significant only at the second internode level (0.4464^{+++}).

I. Kovács

Comparison of homozygous opaque-2, heterozygous and normal in hybrid 156 x B14 — We developed several heterozygous and homozygous opaque-2 hybrids and their normal analogues with the general formulae A x B, A x B o2 and A o2 x B o2. The yielding ability and other agronomic characteristics of the hybrid 156 x B14 and its two different opaque-2 forms are reported here.

One hundred plants of each hybrid were examined individually, and the data on the most important characteristics are presented in Table 1. It will be seen that the flowering time of the hybrids was practically the same; however, there was a significant difference in the earliness of normal and opaque forms as indicated by the moisture content at harvest. The moisture content of homozygous and heterozygous opaque was higher by 13.2% and 5.6%, respectively, than that of the normal analogue.

Table 1. Comparison of homozygous opaque-2, heterozygous and normal in hybrid 156 x B14.

Combinations	Days to 50% male flowering	Moisture content (%)	Shelling Percentage	Dry grain yield per plant (g)	1000-grain weight (g)	
					normal	opaque
156 x B14	83	30.2	83.5	203.0	294.9	-
156 x B14 o2	82	31.9	83.0	192.0	293.8	253.8
156 o2 x B14 o2	82	34.2	81.1	182.7	-	249.2
L.S.D. 5%				6.4		
Percent of the normal hybrid						
156 x B14	100.0	100.0	100.0	100.0	100.0	-
156 x B14 o2	98.8	105.6	99.4	94.6	99.6	86.1
156 o2 x B14 o2	98.8	113.2	97.1	90.0	-	84.5

The most important differences were found in the yielding ability of the hybrids. It can be seen in Table 1 that the dry grain yield of the heterozygous 156 x B14 o2 hybrid was nearer to the normal: the difference was 5.4%; the grain yield of 156 o2 x B14 o2 was 4.6% less than that of the heterozygous opaque hybrid and 10% less than that of the normal hybrid, a result of the joint effects of such agronomic characteristics as higher moisture content at harvest, lower kernel weight and poor shelling percentage.

I. Kovács

Effect of population density on the performance of opaque-2 maize and their normal analogues — It is known that the homozygous opaque-2 (high lysine) mutants of maize commonly give a 10 to 15% lower yield than their normal analogues. Maize well adapted for Martonvásár is commonly planted to a density of 40,000 plants per hectare (80 x 30 cm area per plant). An attempt was made to study the effect of doubled population density (80 x 15 cm) on the performance of 15 opaque-2 single-cross hybrids, their six parental inbred lines and their normal analogues in an experiment conducted during the year 1972 in a split-split plot design with three replications.

Mean observations for a number of characters are presented in Table 1 for the o2 and normal endosperm types. The population density was found to have a statis-

Table 1. Effect of population density (80,000 expressed as % of 40,000) on various characters of o2 and normal maize.

Character	o2	Normal
% moisture	100.00	101.44
Days to 50% pollen-shed	100.98	100.43
Days to 50% silking	102.29	101.21
Total leaves	99.00	99.49
% lodging	118.72	117.74
% Ustilago infection	106.25	50.00
% Helminthosporium infection	140.00	38.09
% frit fly infection	80.60	75.00
Grain yield per plot	155.05	162.56
Raw ear yield per plot	153.70	163.28
Ears per plant	91.26	92.93
Plant height	100.00	100.52
Ear height	102.02	101.09
Ear leaf area	91.74	94.91
Leaves above the ear	98.27	100.00
Tillers per plant	35.62	41.18
Ear length	91.72	91.38
Ear diameter	97.37	94.87
Kernel rows	97.39	97.42
Kernels per row	94.75	92.66
Kernels per ear	91.84	90.57
Drying percentage	100.00	98.64
Shelling percentage	99.17	101.24
Rachis weight	80.00	80.77
Rachis diameter	95.83	95.83
1000-grain weight	97.74	95.59
Kernel density	97.62	97.70
Kernel length	95.83	97.26
Kernel width	100.00	98.63
% water imbibition	103.50	97.28

tically significant effect on the days to 50% silking, grain yield, raw ear yield, ears per plant, ear height, ear leaf area, tillers per plant, ear length, ear

diameter, kernel rows, kernels per row, kernels per ear, rachis weight, rachis diameter and kernel length (Gupta and Kovács, Theoret. Appl. Genetics 45: 64-71, 1974 and Proc. VII Maize Sorghum Sec. EUCARPIA, 1973, in press).

It can be seen from the data in Table 1 that increasing the population density delayed female flowering time more for the o2 types than for their normal analogues and increased lodging, ear height, grain yield and raw ear yield; the increased density reduced the number of ears per plant, ear leaf area, tillers per plant, ear length, ear diameter, kernel rows, kernels per row, kernels per ear, rachis weight, rachis diameter and kernel length. However, grain yield, raw ear yield, ear length, ear diameter, kernels per row and kernels per ear are apparently less affected by density in homozygous opaque-2 populations. Increased density seems to have reduced infections due to Ustilago maydis and Helminthosporium turcicum in normal plants and increased them in opaque-2 types, and the frit fly infection was reduced less in the o2 types than in their normal analogues.

D. Gupta and I. Kovács

Additive genetic variance in opaque-2 and analogous normal triallels —All possible three-way cross-hybrids were made among six o2-converted inbred lines of maize (WF9 o2, R61 o2, N6 o2, HMv850-2 o2, C103 o2 and W187 o2) and their normal analogues. Observations on a number of characters were made on these hybrids in four replicate split-plot trials conducted during the years 1973 and 1974. Data obtained were analysed genetically using the procedure outlined by Rawlings and Cockerham (Crop Sci. 2: 228-231, 1962), and the expectations of eight components of genetic and environmental variance calculated for the o2 and normal hybrids for each year.

Variance attributable to additive and additive epistatic gene effects was expressed as a percentage of the total variance and combined over the 2 years (Table 1). It can be seen that 80.53% of the total variation observed for grain yield in the o2 hybrids was attributable to additive and additive epistatic gene effects, compared with 87.28% in the analogous normal triallel; the o2 hybrids have nearly 7% more non-additive gene effects than their normal analogues for the trait grain yield. It can further be seen that a number of characters had more variation attributable to additive and additive epistatic gene effects in the o2 forms than in their normal analogues. Thus, the days to 50% pollen-shed, days to 50% silking, total number of leaves, leaf area index, leaves above the ear, ear height, tillers per plant and yield components like drying percentage and shelling percentage had a greater proportion of their variance attributable to additive and additive epistatic gene effects if the o2 gene was present in recessive homozygous condition than if it was absent. However, plant height, water imbibition and such

Table 1. Total variation attributable to additive and additive epistatic gene effects in the o2 and analogous normal triallels.

Character	o2	Normal
Days to 50% pollen-shed	96.56	90.08
Days to 50% silking	96.34	83.96
Total leaves	91.63	77.80
Grain yield	80.53	87.28
Raw ear yield	88.83	88.23
Leaf area index	94.76	89.02
Leaves above the ear	93.23	90.26
Ears per plant	78.78	79.48
Plant height	91.14	93.01
Ear height	96.47	93.77
Tillers per plant*	78.11	71.08
Ear length	86.15	86.54
Ear diameter	90.13	93.25
Kernel rows	82.89	93.52
Kernels per row	76.70	85.12
Kernels per ear	78.96	85.36
Drying percentage	93.18	85.98
Shelling percentage	94.22	92.76
Rachis diameter	87.74	90.80
200-kernel weight	88.56	90.75
Kernel density	84.63	84.47
% water imbibition	72.48	80.27
Kernel length	86.92	87.42
Kernel width	83.98	92.34

*Data from one year (1973) only.

yield components as ear diameter, kernel rows, kernels per row, kernels per ear, rachis diameter, 200-kernel weight and kernel width had more variation due to additive and additive epistatic gene effects in the normal cross-hybrids than in their o2 counterparts. The proportion attributable to additive and additive epistatic gene effects appeared to be unaltered for such traits as raw ear yield, ears per plant, ear length, kernel density and kernel length.

D. Gupta

Investigation of some varietal hybrids developed at CIMMYT under our continental climatic conditions — In 1974 in collaboration with CIMMYT we studied the adaptation of 132 varietal crosses selected by CIMMYT's Dr. E. C. Johnson from many parts of the world and representing different latitudes and altitudes. The important geographical data for Martonvásár are: latitude 47°21', longitude 18°21', elevation 150 m. The general behavior of these crosses observed at Martonvásár can be summarized as follows: they have good early vigor and are very tall (3-4 m) with highly placed ears, an under-developed root system with a rather high percentage of root lodging and a significant susceptibility to stalk-rot and to Ustilago maydis.

Table 1. Relationships of two earliness characteristics in some of the CIMMYT varietal crosses.

Symbol of varietal crosses	Days to 50% male flowering Average number of leaves above the ear											
	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0	7.2
131 A	109											
130 A	108											
129 A		113										
39 A			107									
64 A				110								
108 A					110							
77 A						114						
127 A							116					
55 A					96							
76 A					99							
9 A						100						
18 A							100					
40 A								100				
1 A									100			
50 A											106	
4 A												106

Mean male flowering time: 104 days
Mean leaf number above the ear: 5.97

The adaptability to environmental factors can be evaluated on the basis of such earliness characteristics as the days to 50% male flowering and the number of leaves above the ear. We obtained a highly significant positive correlation ($r = 0.2989^{+++}$) between these two traits. Within this relationship, however, we have found several special responses to the climatic conditions, including the day length. It can be seen in Table 1 above that certain combinations having a lower number of leaves above the ear require more days to 50% male flowering; conversely, there are certain combinations which have relatively more leaves above the ear and at the same time have a short vegetative period.

I. Kovács

Heat requirement for germination of maize at low temperature — We have presented data in the 1973 News Letter (47:214-216) on the characteristic behavior of certain inbred lines of maize during the germination process and on their heat requirements at low temperatures (10 days at $8^{o}C$, followed by 21-22 days at $14^{o}C$, planted in a plastic box 5 cm deep in soil). In the present paper we have new experimental data from tests conducted in the incubators of the Martonvásár Phytotron.

Effect of growing conditions of different years: We found that seeds harvested in different years were very similar in their time of germination and heat requirements (Table 1), despite the variable quality of the seed, as indicated by

the germination percentages. We concluded that the heat energy required for germination was little affected by the environmental conditions of different years.

Table 1. Germination data for seeds of inbred lines B14, WP14 and N6 harvested in different years.

Inbred	Year of Harvest	Germination (%)	Days	Sum of temperatures (°C)
B14	1972	70	21	234
B14	1973	85	22	248
WP14	1966	80	22	248
WP14	1970	86	22	248
WP14	1972	56	21	234
N6	1969	70	25	290
N6	1973	56	25	290

Comparative tests on inbreds and hybrids: Forty-five inbred lines and 28 hybrids differed by only 3% in germination percentages, but by 3.5 days in germination time and 49°C in heat unit requirement, an average difference of 17%. We observed differences of 13 days among the various inbred lines and 10 days among the hybrids (about 10 cm growth). Greater differences could possibly have been observed, but most of the sweet corn samples had not germinated or had only started germination by the end of the one-month cold test.

Table 2. Heterosis in heat requirement.

Combinations	Sum of temperatures (°C)		
	$\overline{P}$	F_1	$\overline{P}$ (as % of F_1)
M5190 x B14	248	178	139
HMv1410 x B14	248	192	129
M5190 x HMv1311-1	227	192	118
HMv1366 x HMv1311	213	206	103
HMv1410 x W22R	220	220	100
156 x B14	248	220	113
HMv1410 x HMv1322	283	248	114
M5190 x A239	276	248	111
HMv1410 x OH05	269	248	108
HMv1410 x HMv424-e	311	318	98
Average	253.7	231.4	

Heterosis: Experimental data on the hybrids and their mid-parents are presented in Table 2 above; it is interesting to note that heterosis resulted in reduced heat requirements for all but two of the hybrids.

M. Herczegh

Comparison of cold test data with cold wave tolerance of young maize seedlings — Cold tests have commonly been used in maize to determine genotypes tolerant to low temperatures at the time of germination. The study reported herein was conducted to evaluate the growth behavior of three adapted hybrids of maize (MvTC290, MvSC429 and MvSC598) grown in a phytotron with three-day periods of 5 to 15°C temperatures starting on the 8th, 15th and 22nd days after germination and to compare these observations with the corresponding data on cold test germination.

Observations on ten seedlings of each of the three hybrids on the 36th day of growth in the chamber, along with the cold test data, have been presented in Table 1. It can be seen that the hybrid MvTC290, belonging to early maturity

Table 1. Mean observations on cold wave tolerance and cold test germination.

Character	Hybrid		
	MvTC290	MvSC429	MvSC598
	Cold wave tolerance		
Greenness counts	4.9	4.6	2.6
Total leaves	6.9	6.9	7.0
Plant height (cm)	56.4	59.2	54.3
Fresh weight (g)	12.2	13.5	10.7
Dry weight (g)	1.1	1.3	1.0
	Cold test germination*		
CT-value	2.2	3.3	1.6
Emergence (%)	46.0	66.0	40.0
Days of incubation	21.0	20.0	25.0

*For the procedure adapted see Gupta and Kovács (Euphytica 24, No. 1, 1975).

group, had maximum greenness counts (arbitrary scores from 0 for completely yellow to 5 for deep green) after having been cold-treated three times. The hybrid MvSC429, belonging to a medium maturity group, had a mean greenness count of 4.6, slightly lower than that of the early hybrid. The late hybrid MvSC598, however, had a mean greenness count of only 2.6, indicating poorer chlorophyll synthesis (i.e., far lower tolerance to cold temperatures).

The number of seedling leaves varied little if any among the hybrids. Plant height, fresh weight and dry weight measurements of the young seedlings demonstrated that the hybrid MvSC429 exhibited the most cold tolerance, followed by MvTC290 and MvSC598; this sequence corresponds to that observed in the low-temperature germination tests. Thus, there seems to be the same genetic mechanism

working for cold tolerance in maize both at the time of germination and at the seedling stage.

D. Gupta and I. Kovács

UNIVERSITY OF ARIZONA
Committee on Genetics, Tucson, Arizona

Morphological and physiological analysis of d alleles — To characterize the d alleles of maize, mature plants of d, d-Tall, the F_1 between d-Tall and d and the heterozygotes +/d and +/d-T were compared with respect to total height, leaf length and area, and internode length and diameter. The data suggest regression of the F_1 toward the d-T parent, even when heterosis is taken into account. It is interesting that the leaf area comparisons show that only d plants differ from the heterozygotes.

Data for sixth node down from tassel

	+/d-T	+/d	d-T	F_1	d
internode length (cm) (nodes 5-6)	16.79	15.41	6.08	8.25	6.15
internode diameter (cm) (node 6)	1.36	1.56	1.35	1.32	1.17
leaf length (cm)	88.29	81.13	60.00	79.33	58.17
leaf area (cm^2)	565.75	450.00	442.92	539.08	339.33

Total height (first node to tassel top) measurements show d-T plants to be 20 cm taller than d plants and the F_1 to be 13 cm taller than d-T; the +/d plants are 30 cm shorter than +/d-T plants. These data support the inference that d-T is a leaky mutant and that the function or structure of the protein involved is not as completely impaired as in d.

Morphological comparisons of four-day-old GA-treated coleoptiles and mesocotyls revealed a difference in the response of the two alleles to GA. The coleoptiles of d-T do not respond, but the mesocotyls do; in d, both respond. Measurements on 12-day-old GA-treated seedlings revealed similar responses by both alleles.

Biochemical analyses of coleoptiles and mesocotyls for RNA, amylases and peroxidases are in progress. Preliminary data indicate a difference in amylase activity when expressed as mg of starch converted per 20 minutes per mg of protein. Peroxidase electrophoretic patterns show a distinct difference between alleles and in response to GA. Ribosomal RNA shows no difference in the ratio of smaller molecular weight to larger molecular weight species.

Charles F. Mischke and Robert M. Harris

An unusual chloroplast mutant — An albino corn mutant, y*-4801, arose during the examination of the F_2 of dwarf d-Tall x d crosses. In a population of 3000 dwarf F_2 seedlings, segregating 1:2:1 for the dwarf alleles, there were 150 albino mutants.

The mutant is unusual in that there is incomplete penetrance of expression. The albino plants are able to develop green leaves or regions of green in the leaves. There are never yellow regions, and white areas do not occur in a "banded" pattern. Seedlings that emerge green sometimes subsequently produce white leaves or regions of white in green leaves. Plants that survive develop green in the first and second leaves; the remaining leaves either are entirely white, have green bundle sheaths or develop normally. Only 20 plants have survived to the five leaf stage, and only one plant produced a tassel.

The mutant appears to be chromosomal since the same type of albino mutant has appeared in populations of homozygous d plants. However, the mutant has not been observed in the F_2 of dwarf d x d-T. It is thought not to be a temperature sensitive mutant since it has appeared in both greenhouse and growth chamber plantings. At present, research is underway to develop purebred lines and to examine development under varying conditions of light and temperature.

Charles F. Mischke and Barbara S. Mischke

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Further studies on maize x perennial teosinte hybrids — Pachytene chromosomes of the F_1 plants of perennial teosinte x maize were again examined with the light microscope to see if the chromosome pairings occurred at random; particular attention was paid to the short chromosomes. Great difficulty was encountered in identifying the chromosomes because of their extreme entanglements. Limited data lead to a conclusion that teosinte chromosomes paired preferentially with teosinte chromosomes, and the maize homologue was left unpaired in most of the cases. The single chromosomes (the third homologue) frequently synapsed nonhomologously on themselves. At anaphase I the distributions of chromosomes were extremely irregular; among a few hundred microsporocytes studied, no 10-20 distributions of chromosomes were observed.

The fertility of the F_1 plants was, as expected, very poor. Only one well-developed kernel was obtained from more than 200 pollinations including both selfs and backcrosses to the maize parent. This was apparently due to the unbalanced chromosome constitutions in the gametes produced.

Phenotypically the F_1 plants were very similar to the teosinte parent when they were grown in the field, particularly with respect to the characteristics of fruits and flowers. When these F_1 hybrids were grown in the greenhouse it was even more difficult to distinguish their growth habit from that of the inbred perennial teosinte.

The microsporocytes of these F_1 hybrids are currently under study with the electron microscope to see if there is any difference in the structural organization of the synaptonemal complexes between the homologously associated chromosomes and the nonhomologously associated ones.

In order to facilitate backcrossing the F_1 hybrids to the parental species, clones of these hybrids were subjected to colchicine treatments. It appears hopeful that some of these plants will become hexaploid subsequent to these treatments, because they have thick leaves and slow growth.

Y. C. Ting

The fine structure of the bivalent chromosome 6 of Chalco-teosinte — A brief report on the gross structure of the nucleolus and nucleolar bodies of Chalco-teosinte was given last year (M.G.C.N.L. 48:17). Further studies with the electron microscope were carried out on these organelles and on the bivalent chromosome 6 (nucleolar chromosome). It was consistently found that there were nucleolar bodies, varying in size and number from cell to cell, in addition to the regular nucleolus. These bodies were always without a nucleolar cup and unattached to any chromosomes. No fiber-like structures were seen in them; however, granular substances embedded in the homogeneous matrix were always present. In contrast, fibers of 300-400 Å width in the form of a helical arrangement were present in the cup-like structure of the regular nucleolus. These are probably the nucleolonema. Connections between these fibers and the chromatin region of chromosome 6 were also observed. These connections appeared to consist of fine fibrils having an average width of 100 Å. Both the nucleolar bodies and the regular nucleolus possessed vacuoles, which also varied in number and size but were invariably spherical in shape.

At pachynema, the central element of the synaptonemal complex of bivalent chromosome 6 measured about 300 Å in width, which is less than that of diploid and haploid maize and Michoana-teosinte. It was also frequently found that the central element was composed of two components, each with a cross dimension of 100 Å. In the centromere region, fibers with a cross dimension of 300 Å were sometimes observed connecting the densely stained chromatin regions of the two arms. In addition the centromere region possessed a less darkly stained area flanking the fibers and extending into the nucleoplasm.

Up to the present no synaptonemal complex has been definitely identified in the

satellite segment of chromosome 6. Only darkly stained chromatin, sometimes divided by a clear region, was found in this segment.

Y. C. Ting

Effect of streptomycin on chloroplast structure and pollen fertility —The attempt to induce cytoplasmic male sterility in maize using streptomycin has been continued from last year. C103N seed was treated in 50 ml solutions of streptomycin (Petrov, Fokina and Zheleznova, U.S. Patent #3,594,152) for 24 hours at room temperature with dosages ranging from .0005 micrograms/milliliter to 10,000 micrograms/milliliter. At the same time, control seeds were soaked in distilled water.

At a dose of 50 ug/ml, bleaching of the leaves was noticed, and none of the plants which had been treated with at least 500 ug/ml survived past the seedling stage. However, the most profound effect on the surviving plants occurred at .001 ug/ml, with one of these plants exhibiting altered morphological characteristics. This plant was much shorter than the control plants, and it produced only one central spike.

The unshed pollen of all the plants was checked, using the conventional aceto-carmine staining, in order to ascertain if there had been any effect on pollen fertility. All the control and treated plants with the exception of the one abnormal plant had fertile pollen. When the unshed pollen from this plant was checked it was found that the anthers from the top two-thirds of the spike contained mostly fertile pollen; the anthers from the lower one-third of the spike contained all sterile pollen. Thus, this plant was sectorially sterile.

Chloroplasts of the treated plants were studied in leaf sections prepared for electron microscope observation. This was done in an attempt to correlate pollen sterility with a change in the chloroplasts. The leaf sections from the sectorially sterile plant showed normal sized chloroplasts with a much higher number of osmiophilic granules. As the dose of streptomycin was increased to 50 ug/ml, the chloroplasts appeared shrunken and no longer had the characteristic grana. At a dose of 500 ug/ml the whole lamellar structure had disintegrated, and the chloroplasts were greatly reduced in size.

It is encouraging that at least partial sterility can be induced by streptomycin. Further studies are being done using this drug, and more examinations of chloroplast structure in both maintainer and cytoplasmic male sterile plants are being conducted. Hopefully, these studies will yield new information on the possibility of involvement of the chloroplasts and the other organelles in the phenomenon of cytoplasmic male sterility.

Rita M. Ryan

Acridine orange banding of maize chromosomes — Haploid and diploid maize seeds from the same strain were germinated at 23°C for four to seven days. A modification of Dutrillaux's technique for human chromosomes was applied to root-tips using BuDr and acridine orange.

When viewed with blue light fluorescence, the chromosomes appeared yellow/green with red/orange bands. Chromosome 1 had three red/orange regions, one on the short arm and two on the long arm. Chromosome 4 had one on the short arm and two on the long arm. Chromosome 6 had a red/orange band at the nucleolar organizer region and two bands on the long arm, and chromosome 7 had a red/orange band on the long arm that corresponds to the regular knob region shown by acetocarmine squashes of microsporocytes at pachytene stage. Further studies of the other chromosomes are in progress.

The regions banded by the acridine orange-BuDr technique appear to correspond to the Giemsa-banded regions reported last year in the News Letter. The red/orange bands are late-replicating, indicating that there are more heterochromatic regions revealed by acridine orange than by the conventional acetocarmine technique. If acridine orange bands are the same as G bands, then the G bands are also late-replicating.

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Ultrastructure of the pollen grain ektexine of maize and its relatives — The present investigation using electron microscope methods has revealed that the pollen grain ektexines of "pure races" of maize and teosinte have very similar patterns of evenly distributed ektexine spinules at the ultrastructural level. This ektexine pattern was also found among some re-investigated fossil pollen grains (approximately 80,000 years old) from the deep-core samples from Mexico City (U. C. Banerjee, Ph.D. Thesis, Harvard Univ., 1973); these fossil pollen grains were previously described by Barghoorn and Wolfe (M.G.C.N.L. 27:17, 1953) and by Barghoorn, Wolfe and Clisby (Harvard Bot. Mus. Leaflet 16:229, 1954). Similar ektexine patterns were also recorded in fossil maize pollen from Gatun Basin, Panama, by A. S. Bartlett (Ph.D. Thesis, Harvard Univ., 1967) and by Bartlett, Barghoorn and Berger (Science 165:389, 1969) and in some archaeological pollen grain samples from Tehuacán Valley, Mexico, and from surface level at the site near

Huarmey, Peru, by Banerjee (1973). However, when introgression of teosinte occurs with maize or vice versa, the pollen grain ektexines of the hybrid progeny show a new "spinule-loss" type of ektexine pattern, easily recognizable ultrastructurally (Banerjee and Barghoorn, 30th Ann. Proc. Electron Micr. Soc. Amer., p. 226, 1972). This "spinule-loss" pattern was also found with the pollen grain ektexine of maize from Bat Cave, New Mexico, as reported by Banerjee (1973).

The ektexine patterns of pollen grains of Tripsacum spp. (both diploids and tetraploids) show a distinct ektexine spinule-clumping represented by the "negatively-reticuloid" pattern. This phenotypic ektexine pattern is dominant over the ektexine patterns of maize and teosinte (Banerjee and Barghoorn, Abstr. Amer. Assoc. Stratigr. Palyn., 1972). The introgression of Tripsacum with maize or teosinte can be detected by the presence of some degree of spinule-clumping if pollen grains are derived from the hybrid progeny. The oldest convincing evidence of Tripsacum introgression with maize was found in some archaeological maize samples recovered from the lower levels of the site near Huarmey, Peru, approximately dated 2000 to 1600 B.C. (this date is estimated by the archaeologists--personal communication with Professor Mangelsdorf, and Mangelsdorf and Cámara-Hernández, M.G.C.N.L. 41:47, 1967). The ultrastructural characters of the ektexine also show that Cuzco maize (Zea mays L.) from Peru, and Florida teosinte (Euchlaena luxurians Durieu.) from southern Guatemala, are possibly contaminated with Tripsacum germplasm.

The palynological investigations with Mangelsdorf's genetic stocks of maize also suggest that "teosinte" is not a hybrid of maize and Tripsacum, as it was considered previously (Mangelsdorf, P.C., Corn: Its Origin, Evolution and Improvement. Harvard Univ. Press, 1974).

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In situ staining of pollen grains for alcohol dehydrogenase activity — The cytochemical reduction of p-nitroblue tetrazolium chloride is a well-known assay for NAD(P)-linked dehydrogenases in the primary substrate (oxidized) to primary substrate (reduced) reaction direction. Here, the specificity of the assay lies in the enzyme's specificity for primary substrate. We have adapted the methods of Hauser and Morrison (1964; Amer. J. Bot. 51, 748) to semi-quantitate the level of ethanol dehydrogenase in shed pollen.

Procedures:

1. Pollen is collected for a three-hour interval in a paper bag. Take whatever precautions necessary to insure healthy (stainable) pollen. In our hands, pollen

may be stored dessicated at 4°C for at least 2 hours without lowering stainability or *in vitro* germination.

2. After shaking-away most of the anthers, about 10^6 grains are dispersed onto 50 ml 0.1 M sodium phosphate buffer, pH 7.3 in a standard petri dish. After about 10 mins healthy grains will sink.

3. Freeze the pollen sample at -20°C for three hours on an iron plate. Presumably, this slow freezing procedure perforates the pollen wall and membranes, yielding 10^6 tiny dialysis bags.

4. After no more than six hours of freezing, remove the surface of the ice with running tap-distilled water and with it anthers, nonsunken pollen, and flotsam. Then defrost at room temperature on an iron plate rotating at about 30 rpm for 45-60 mins. Endogenous dehydrogenase substrates are presumed to dialyze into the buffer.

5. Remove the buffer (dialysate) with a pasteur pipet connected to an aspirator bottle, and immediately replace with dehydrogenase stain at 10-15 ml per 10^6 grains.

6. For 100 ml of *alcohol* dehydrogenase stain:

Stock	ml per 100
0.1 M sodium phosphate, pH 7.3	86.0
0.01 M p-nitroblue tetrazolium chloride (NBC) in 100% methanol (AR)	3.0
0.01 M NAD^+ (NBC; ethanol free)	10.0
95% ethanol (the primary substrate)	1.0

When tightly-capped, this stain is stable at 4°C for at least 24 hrs. Malic acid, sorbitol, sodium lactate and succinic acid also serve as primary substrates under these conditions.

7. Stain for 3±1 (± range that we use for absolutely unambiguous results) hrs with slow rotation. Stop the reaction by replacing stain with 100% technical-grade methanol and/or cooling the reaction to 4°C. The advantage of the latter method is that it may be done automatically.

In order to estimate the total number of grains in a sample, we suspend pollen at 4-6 x 10^3 grains per ml (by eyeball estimation) in 40% glycerine, remove aliquots for dilution and particle counts using millipore techniques, and calculate the exact grains per ml suspension. Known volumes are then dispensed into large gridded petri plates for screening, where pollen does not change position as the plate is moved; use incident light and about 16X. Screening is accompanied by motion sickness in some people; call collect with a more humane method.

Comments:

These procedures were devised using pollen segregating *Adh*$^+$/*Adh*$^-$, where the mutant *Adh* (from Drew Schwartz) is CRM^-. Omitting ethanol yields 100% of 10^7

yellow, translucent grains, but only if the freeze-dialysis procedure is followed. Using lactate as a primary substrate, 97-100% of the grains stain blue and opaque. With ethanol, 50% stain blue and opaque and 50% stain yellow and translucent with zero statistically significant overlap; do not overstain. One of us (MF) has screened almost 200,000,000 pollen grains using these methods; the method works. We also know that the stain is able to detect as light blue grains 5% of wild-type ADH levels.

Adh is about 1.5 mu from lw (Schwartz) and less than 1 mu from Kn (Freeling) on the long arm of chromosome one. Like wx, Adh should be of general utility. Unfortunately, simultaneous scoring for waxy and ADH may prove difficult, especially since ADH is stained in shed pollen.

The power of pollen analysis (per Oliver Nelson's prototype work with wx) as a means for recombinational frequency or topological mapping within the Adh cistron would be greatly increased if we had flanking pollen markers. Small pollen, fluorescent pollen, oblong pollen and the like would be ideal if they prove transmissible; they need not specify competitive gametophytes. If anyone has a potential marker within 20 mu of lw your cooperation is requested.

Michael Freeling and Elvin Brown*

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Effects of plant density and spacing on the grain yield of hybrids — In Szeged in 1973, the effect of different plant densities and of the cutting of the leaf surfaces on yield were examined. Two hybrids were sown with two spacings in a randomized block layout. After fertilization leaves were cut upwards from below in three different ways. Table 1 shows the extent of leaf cutting.

Table 1. Extent of leaf cutting.

	Treatments	Surface of leaves (cm^2) A90 x 153R		W64A x Oh43	
		b_1	b_2	b_1	b_2
a_1	control (without cutting)	4913.2	4251.3	5562.3	4944.7
a_2	plants with leaves cut below ear	2241.4	2119.4	2781.8	2337.1
a_3	plants with half of leaves cut above ear	820.6	753.2	1017.9	786.0

b_1 = 5 plants/m^2; b_2 = 10 plants/m^2

The size of leaf surface was established with the aid of the Montgomery formula. Seeds were planted on May 15.

In 1973 during the growing season there was less precipitation compared with the 20-year mean (Table 2).

Table 2. Monthly precipitation sums (mm).

	April	May	June	July	August	September
Mean of 20 years	40.7	53.8	65.7	50.0	48.2	32.4
1973	59.9	33.9	79.9	43.5	18.4	12.2

The other ecological factors (temperature, hours of sunshine, etc.) did not show a significant difference from the 20-year mean.

The experiment was analyzed by variance analysis. Each of twenty plants represents a separate replication. Table 3 shows the effects of different plant densities on leaf surface and the change of leaf surface per hybrid.

Table 3. Change of leaf surface (cm^2) with plant density.

Genotype	Plant density b_1	b_2
A90 x 153R	4913.19	4251.28
W64A x Oh43	5562.30	4944.69

$SD_{1\%}$ 376.48; $SD_{0.1\%}$ 501.01

Table 4 gives the grain yield per plant adjusted to 14% moisture and yield per 100 cm^2 leaf surface, according to the extent of leaf cutting.

Table 4. Changes in grain yield (gr) with plant density and cutting of leaf surface.

Extent of leaf cutting	A90 x 153R				W64A x Oh43			
	gr/plant		gr/100 cm^2 leaf surface		gr/plant		gr/100 cm^2 leaf surface	
	b_1	b_2	b_1	b_2	b_1	b_2	b_1	b_2
a_1	111.7	79.7	2.30	1.90	90.0	75.0	2.67	2.37
a_2	96.5	70.9	4.35	3.39	70.9	59.6	2.59	2.64
a_3	56.7	58.5	7.03	7.93	54.4	43.0	5.49	5.94
$SD_{1\%}$			0.71				0.72	
$SD_{0.1\%}$			0.92				0.93	

Results:

1. Leaf surface per plant decreases significantly as the result of higher plant density.
2. There is a considerable difference in the leaf surface between the two investigated combinations.
3. When all leaves were cut below the ear, the grain yield per plant decreased less than when half of the leaves above the ear were cut.
4. The amount of grain produced per 100 cm^2 leaf surface above the ear is significantly higher than that for leaves below the ear.

J. Németh and L. Pintér

Investigation into the relationship between moisture content and severity of infection in maize —In 1973 in Szeged the changing of moisture was examined for 36 different-maturity inbred lines and 44 hybrids. The samples were taken at 10-day intervals from August 23 to October 16. On September 5 artificial inoculations were made with Fusarium graminearum by inserting an inoculum-laden toothpick into each ear of 15 plants. A numerical rating of 1 to 5 constituted a linear scale of percent rot in the inoculated ear. These values were a measure of the intensity of infection. The results obtained are, for the relationship between moisture content and severity of infection:

Inbred lines	$r = +0.53^{***}$	n = 36
Hybrids	$r = +0.46^{**}$	n = 44

For the relationship between silking date and severity of infection:

Inbred lines	$r = +0.53^{***}$	n = 36
Hybrids	$r = +0.46^{**}$	n = 44

From the data the following conclusions may be drawn:

1. We obtained a significant correlation coefficient between the moisture content and the severity of infection for both inbred lines and hybrids.
2. The correlations between days to mid-silk and the severity of infection of the ears were also significant.

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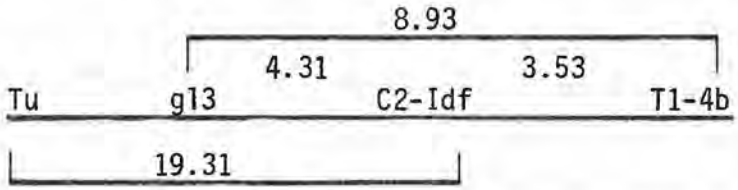
Linkage relations of the diffuse factor on chromosome 4 — Prior written reports have disclosed that the diffuse factor is located on chromosome 4, but its exact position, relative to other marker sites, has not been given in any written form. Linkage studies are continuing and the following statements can now be made:

a. Diffuse, which in the highly unstable state conditions a high frequency of somatic sectoring in pericarp tissue, has been located between glossy-3 and the

breakpoint of the reciprocal translocation T1-4b. The order concluded on the basis of two point tests is presented in Table 1 along with the sample size and percent recombination.

Table 1. Recombination values and linkage of markers on chromosome 4.

Chromosome interval	Sample size	Recombination %
Tu-C2-Idf	3933	19.31
gl3-C2-Idf	1034	4.31
C2-Idf-T1-4b	2141	3.53
gl3-T1-4b	524	8.93



b. The stable, fully active form of diffuse, which inhibits pigment in all plant tissues even in single dose, was tested individually against two other markers on chromosome 4: distal pale (dp) and c2. In a population of 970 individuals dp and diffuse showed 23.0 percent recombination. No data relative to the other chromosome 4 markers and dp are available from these current matings, but Dr. E. G. Anderson, who supplied the distal pale stocks for these studies, indicated that dp was "really far out on chromosome 4." Most probably, distal pale is more distal than diffuse. Since no direct confirmation of the direction is yet available, its position in Table 1 has been omitted.

c. In a population of more than 5000 individuals c2 and diffuse showed no proven recombinants. Since c2 c2 c2 conditions colorless aleurone and the active form of diffuse produces an indistinguishable phenotype, crossover tests required that only 1/2 of the recombinant types in the total population would be detectable, and phenotypically they would be colored aleurone. All seeds from the mating C2 diffuse/c2 nondiffuse x c2 nondiffuse/same that exhibited any detectable level of pigment were tested as presumptive C2 nondiffuse chromosomes resulting from crossing over. All such individuals proved to be variations in the expression of the active form of diffuse; thus, no recombinants were recorded.

Is diffuse an allele of C2 or does diffuse restrict exchange in its vicinity? In order to check these possibilities, tests were made to measure the recombinational rate between glossy-3 and two translocations, T1-4b and T4-9b, with and without the diffuse character inserted between them. The data are clear (Table 2);

diffuse in the form tested, the highly unstable state, does not reduce recombination between the outside markers. Thus, C2 and diffuse are situated at the same chromosomal site. Are they alleles? Operationally, since there has been no observed recombination between C2 and diffuse they must be at least very close to each other in a physical sense. However, functionally they are quite different. For one, diffuse in the active state suppresses pigment in every tissue of the corn plant including the pith and roots, while c2 has so far been found to stop pigment formation in the aleurone only. On the other hand, there are those states of diffuse which apparently suppress pigment formation in the aleurone but not detectably in the pericarp. This latter grouping at first looks like a c2 effect but with one important difference. When this form of diffuse, called very dark diffuse, is in three doses in the aleurone, the aleurone is not colorless but rather exhibits modest levels of aleurone pigment. Since pigment suppression

Table 2. Recombination between glossy-3, diffuse and reciprocal translocations T1-4b and T4-9b.

gl3 — 18.49 — T4-9b	(N = 173)
gl3 — 5.43 — C2-Idf — 15.6 — T4-9b	(N=423)
gl3 — 11.01 — T1-4b	(N=218)
gl3 — 4.25 — C2-Idf — 5.23 — T1-4b	(N=306)

in a clear dominant fashion is a constant characteristic of diffuse, it is suggested that the symbol C2-Idf be used. The nondiffuse situation would then by symbolized C2 or C2-idf. With such a symbol the individual characteristics will be noted while expressing the zero recombination result.

Irwin M. Greenblatt

A major modifier of diffuse instability — The somatic sectoring rate conditioned in the pericarp by C2-Idf, while variable in different pedigrees, exhibits a rather repeatable average number of stripes in a specific line. The heterozygote produces, on the average, one-half as many stripes as the homozygote. In one pedigree, Inbred W22R C2-Idf heterozygotes averaged 32 stripes on an area of 50 kernels, and the homozygote averaged 64 stripes in the same area.

A discrete variant of the above rates has also been found. It is known as very dark diffuse and in the same W22R background produced only 0.10 stripes per 50 kernels. The single stripe found in the entire pericarp of an individual of this

variant phenotype is typically of the diffuse type, i.e., a diffuse border of pigment is present along the somatic sector in the pericarp (A/A, P-RR/P-RR, C2-Idf/C2-Idf.

During the linkage studies conducted with C2-Idf and glossy-3 it was noted that almost all new cases of the very dark diffuse phenotype were associated with recombination between glossy-3 and diffuse. When an exchange occurred between gl3 and C2-Idf, the phenotype of diffuse altered from the standard high rate to the very dark diffuse level. Therefore, it seems highly likely that a major modifier of diffuse striping exists and is located just the other side of gl3 from C2-Idf. The relevant data using T4-9b and T1-4b are given in Table 1. From the data in

Table 1. Linkage estimates for markers on chromosome 4 in which a modifier of diffuse instability is recognized.

Sample size	Translocation	Percent recombination		
		Mod —— gl3	—— C2-Idf	—— T
306	T1-4b	0.68	4.25	3.92
212	T1-4b	0.94	1.89	1.89
Average		0.77	3.28	3.09
579	T4-9b	0.34	7.94	12.09
423	T4-9b	0.48	6.15	15.60
Average		0.40	7.19	12.97

Table 1 it can be seen that the modifier is less than one unit from gl3. Since it also appears that the translocation breaks are affecting the exchange rate, these values are only to be viewed as relative and not as absolute values. Apropos, from an additional recombinational test utilizing Tu as the proximal marker in a population of 3197 plants, the modifier was located 11.21 units proximal to C2-Idf and 16.44 units distal to Tu. The modifier-to-C2-Idf interval in this latter test without translocation interference is significantly higher than those calculated from the values in Table 1.

The modifier is much like the one found by B. Ashman on chromosome 10 modifying R-st action. It is definitely not any of the elements involved in the Ac Ds, Spm or Dt systems. Test of interaction with each system has given negative results.

A study of the modifier in stocks homozygous for the C2-Idf chromosome — and thus the modifier — has produced the notion that the modifier is transposable. The very dark diffuse types occur in the homozygotes at a rate of 0.5 percent.

But when phenotypic selection is made for strong aleurone pigment reduction due to C2-Idf action among the homozygotes that are unstable, the rate of very dark diffuse types was 11 percent. It thus appears that the modifier is transposing and in addition that the very dark diffuse refers to pericarp striping only. In the aleurone it may be more active. These latter studies are in progress.

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Resistance to European corn borers and sugarcane borers in maize — Resistance to the European corn borer, Ostrinia nubilalis (Hubner), and the sugarcane borer, Diatrea saccharalis (F.), has been confirmed in exotic maize varieties from the world maize germplasm collection of CIMMYT. Advancement in levels of resistance and adaptability to New York growing conditions has been obtained using full sib recurrent selection with alternate cycles in New York and Mexico. Promising lines with resistance to first and second generation O. nubilalis are being developed.

The mechanism for first-generation leaf-feeding resistance appears different from the antibiosis mechanism due to DIMBOA, which is responsible for resistance in most U.S. lines. DIMBOA content was analyzed by a combination of thin-layer chromatography and colorimetric techniques. The exotic lines had DIMBOA levels as low as or lower than susceptible U.S. lines and far below that of resistant U.S. lines, yet their resistance to the borer in the field under conditions of artificial infestation was as high as or higher than the most resistant U.S. lines.

Larvae were reared on artificial diets into which were incorporated ground freeze-dried corn leaves of the various lines to determine if any other antibiosis factor was present in the exotic lines. Larvae reared on exotic lines had lower mortality, higher pupation and equal or faster rates of development than larvae reared on a susceptible, low-DIMBOA line, while larvae reared on a resistant, high-DIMBOA line had greater mortality, lower pupation and a delayed development. This suggests, but does not prove, that there is no other toxic component present in freeze-dried leaves of these exotic maize lines that accounts for their resistance.

Larval feeding preference was tested by giving newly-hatched larvae a choice of feeding on agar discs of freeze-dried leaves of two corn lines. The exotic lines and the resistant, high-DIMBOA line were tested against the susceptible, low-DIMBOA line. In general, larvae did not show any non-preference toward the exotic lines. However, extreme non-preference was evident toward the high-DIMBOA line, with the degree of non-preference roughly proportional to the DIMBOA level in the tissue. This supports the suggestion that resistance in the exotic lines is not conditioned

by the same mechanism as that in the high-DIMBOA lines. Non-preference as a mechanism cannot be ruled out by this study since freeze drying removes any volatiles from the leaves that might be involved in non-preference.

V. E. Gracen, A. C. Bellotti and S. L. Sullivan

Male sterile cytoplasm evaluation and development — We initially collected 38 sources of cytoplasmic male sterility and transferred these cytoplasms to a series of inbred lines. By growing one generation a year in New York and two successive generations in Florida we were able to complete the transfer of the cytoplasms to the inbreds in just over two years. By using the HmT toxin-injection technique we were able to rate the resistance to H. maydis race T of all of the inbred-by-cytoplasm combinations in the field in each successive generation without fear of fungal contamination and spread. We also have rated the cytoplasm-by-inbred combinations for fertility restoration reactions. We realized early in our conversion process that many of the cytoplasms we tested could be assigned to three groups (T, C and S groups), as Duvick and Beckett have previously reported, by fertility restoration reactions. We discovered that although many of the cytoplasms fit into the three groups, there was significant variation between cytoplasms within groups, especially within the S group. A characterization and regrouping of the different cytoplasms as well as an evaluation of which cytoplasms seem best suited for hybrid development in each inbred background has been published (Agron. J. 65:654). A total of 247 cytoplasm-by-inbred combinations was released to the public in March, 1974.

C. O. Grogan and V. E. Gracen

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Cryptic lateness in maize — Shaver (MNL 46:24) and Shaver & Prior (MNL 48:24) have described the phenomenon of "cryptic earliness" in maize wherein id/id lines, although having a medium or late phenotype, nevertheless contribute extreme earliness to hybrids when the other parent is Id/Id (normal).

The opposite phenomenon could be called cryptic lateness, where a homozygous recessive line has an early phenotype but contributes lateness to a hybrid when the other parent is normal. Conversions of inbreds to the recessive state could find use in practical seed production because early x late crosses could be made in straightaway plantings. If the incorporated gene is completely recessive, the resulting hybrid would not be changed. If pollen production is good, then the use of a converted, cryptically late male might be preferable to incurring the hazards

and expenses of split planting which might otherwise be necessary to consummate a "nick".

Cryptic lateness was observed as a side effect in the recessive phenotypes of one of our routine conversions. The alteration in days to ½-silk was noted in the 1975 Hawaii winter nursery:

Inbred	Normal version days to ½-silk	Homozygous recessive conversion days to ½-silk	Stage of recovery
Fr3	63	56	BC_1I_2
Mo16	67	61	BC_3I_2
K55	66	57	BC_3I_2
659	63	56	BC_3I_2
907	67	60	BC_3I_2
Average	65.2	58.0	

These data indicate that converted lines are 7.2 days earlier to ½-silk and that, extrapolating to a seedfield situation, the use of a converted line could avert the need for a one leaf split in planting male and female.

It should be noted that in making "cryptically late" conversions, recoveries can be made as exactly as for any other normal conversion. This is not the case with "cryptically early" conversions based upon id/id, since this genotype is normally ear-barren, and an undetermined number of complementary loci would have to be transferred along with id in order to restore workable ear-fertility.

D. L. Shaver

DEFIANCE COLLEGE
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Flavonoid analysis of Zea mays tissues at different developmental stages — Much work has been devoted to flavonoids associated with gene action in maize. However, most work has centered on flavonoids found in the aleurone. It is the purpose of this report to survey flavonoids found in three tissues at two different developmental stages.

Flavonoids were extracted from roots, sheaths and leaves of two-week- and four-week-old plants with the following genetic background: R R W22 (A, A2, C, C2, R, Pr). The two-week-old plants were grown in a growth chamber at 22°C. The four-week-old plants were grown in a growth chamber for two weeks and transferred to a greenhouse for the remaining time.

Table 1. Identity, color reactions and spectral maxima of Zea mays flavonoids.

Compound	Identity[a]	Color[b] in U.V.	Color[b] in $+NH_3$	R_f in TBA	R_f in HOAc	Spectra[c] in MeOH	Spectra[c] in $+AlCl_3$	Spectra[c] in +HCl	Spectra[c] in +NAOAc	Spectra[c] in $+H_3BO_3$
1	Quercetin 3,7-diglycoside	DP	YG	.42	.68	343,267, 255	420,328sh, 300sh,274	372,354, 293sh,272	394,266	372,261
2	Kaempferol 3-monoglycoside	DP	YG	.41	.35	344,265	417,296sh, 272	398,274	402,342sh, 268	372,268
3	Flavonol-glycoside	DP	YG	.40	.52	No spectra measured[d]				
4	Vitexin	DP	YG	.25	.48	328,274 266,260	378,344 300,280	372,344, 298,278	370,342, 292	402,354, 321,285
5	Flavonol 7-monoglycoside	DP	O	.28	.12	345,270	358,270	355,269	420,342, 297	360,269
6	Flavonol 7-monoglycoside	DP	O	.16	.23	344,268	359,282	354,267	424,343, 290	358,265
7	Flavonol-glycoside	Y	Y	.48	.29	No spectra measured[d]				
8	Flavonol-glycoside	Y	Y	.53	.16	No spectra measured[d]				
9	Flavonol-glycoside	Y	Y	.63	.27	No spectra measured[d]				
10	Quercetin 3-monoglycoside	DP	YG	.54	.45	354,298sh, 256	404,358sh, 296sh,270	394,354, 296,264	404,310sh, 272	366,296sh, 258
11	Cyanidin 3,5-diglycoside	DP	DP	.35	.54	520,282	555,285			

a - tentative identification

b - DP, dark purple; YG, yellow green; O, orange; Y, yellow

c - spectra measured according to T.J. Mabry, The Systematic Identification of Flavonoids (1970)

d - only trace amounts present

A minimum of 1.0 g of fresh material was cut into small pieces, placed in a 50 ml Ten Broeck homogenizer and ground with 10 ml of 0.5% HCl in methanol (v/v). The homogenate and methanol washings were centrifuged for 5 min at 200 x g, and the methanolic supernatant was evaporated in vacuo to about 1 ml. The total methanolic extract and washings were applied to a 2.5 cm disk of Whatman No. 3 MM chromatography paper suspended on stainless steel pins. The disk was dried with the aid of a hairdryer and then inserted through four parallel slits, 5 mm apart, at the origin of a 46 cm x 57 cm sheet of Whatman No. 3 paper. Two-dimensional descending chromatography was used to separate the flavonoids. Chromatograms were developed in the long direction of the paper in t-butanol, acetic acid and water (3:1:1 v/v), and acetic acid (15%) was used in the second dimension.

Chromatograms were examined under long-wave ultraviolet light, and the flavonoids were readily detected as light-absorbing regions. The flavonoid-containing areas were cut from the chromatograms and extracted into high grade spectral methanol. Five spectra are reported for most compounds. The compounds were identified on the basis of R_f values, color reactions on the paper chromatogram and spectral analysis (Table 1). Anthocyanins were further characterized by hydrolyzing in 2N HCl for one and one-half hours and chromatographing the resulting sugar. The aglycone was also analyzed spectrophotometrically.

It is apparent from the results (Table 2) that there are differences in flavonoid composition between various tissues and that further differences are found

Table 2. Flavonoids in various tissues at different ages.

Tissue		Compound number*										
		1	2	3	4	5	6	7	8	9	10	11
Root	2 wk											+
	4 wk											+
Leaf	2 wk	+	+	+	+	+	+					
	4 wk	+	+		+	+	+					
Pigmented sheath	2 wk					+	+	+	+	+	+	+
	4 wk					+	+				+	+
Sheath	2 wk				+	+	+	+	+			
	4 wk				+	+	+	+	+	+		

\+ present

* corresponds to Table 1 compounds

between two week and four week old plants. The fact that differences exist between tissues is not surprising in view of other research as well as field observations which show that flavonoids are not uniformly distributed within the plant or even in all cells of a tissue. Differences in various developmental stages would seem to imply that their occurrence within a plant is sufficiently controlled to provide a basis for flavonoid regulation of biological systems. These experimental results are important in assigning a primary role for flavonoids, which are generally considered as secondary constituents, not absolutely essential to the life of individual cells or even to the plant as a whole.

John Trautman and B. C. Mikula

Flavonoids in chloroplasts of Zea mays — Early biological interest in the flavonoids was concerned largely with chemical characterization within a framework of genetic and taxonomic studies. Recent work has been concerned with physiological control and biosynthesis. This report is concerned with the localization of flavonoids in specific organelles for further insight into the biosynthetic processes and the likely physiological functions of flavonoids at the ultrastructural level.

A minimum of 100 g fresh weight of leaf material was used for plastid isolation. Midribs and petioles were discarded, the ramaining material washed in distilled water, and the sample chilled to $4^{o}C$.

The tissue was cut into 2 cm pieces and placed in a Waring blender, and from three to four volumes (w/v) isolating medium were added. The aqueous isolating medium contained 1.1 M sorbitol, 0.01 M magnesium chloride and 0.02 M EDTA in 0.15 M pH 6.8 Sorensen's buffer. The tissue was homogenized at about 23,000 rpm by three two-second bursts in a Waring blender. The homogenate was filtered through one layer of cheesecloth and two layers of "Miracloth." The filtrate was centrifuged for one minute at 200 x g at $4^{o}C$. The pellet was discarded and the supernatant recentrifuged at 2000 x g for one minute. The resulting chloroplast pellet was resuspended in a known volume of medium based on the number of centrifuge tubes used, and an aliquot was taken for plastid determination. Plastids were repelleted by centrifugation at 2000 x g for two minutes. This pellet served as the chloroplast preparation. Flavonoids were extracted from the chloroplasts with acidic 50% methanol (0.5% HCl in 50% aqueous methanol v/v) for 12 hours in a cold room. The extract was filtered through Whatman No. 1 filter paper in a Büchner funnel and evaporated to about 1 ml for paper chromatography. A paper chromatogram was also prepared from a standard methanol extract of the leaf (see part 1 of this report).

On comparison of the plastid extract chromatogram and the methanol extract chromatogram, it was determined that the flavonoids were the same in both samples. The paired chromatograms were analyzed under ultraviolet light, color changes in ammonia vapor noted, and the flavonoids eluted for spectrophotometric measurements (Table 3).

Table 3. Comparison of leaf and chloroplast flavonoids of Zea mays.

Compound number*	Identity	Leaf	Chloroplast
1	Kaempferol 3-monoglycoside	+	+
4	Vitexin	+	+
5	Flavonol 7-monoglycoside	+	+
6	Flavonol 7-monoglycoside	+	+

+ present

* corresponds to the compounds in Table 1 which are fully characterized

Recent research has shown that flavonoids are not end-products but are continuously synthesized and degraded in healthy tissues. The above evidence indicates that flavonoids are most likely synthesized within the chloroplast and transported to the vacuoles in most cells. It had been thought in the past that flavonoids were stable end-products of metabolism stored in the vacuole and thus removed from enzymatic activities associated with plant growth, differentiation, etc. It appears that this older view must be seriously questioned.

John Trautman

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Allotaxis in maize — We use the word "allotaxis," with the same value as "heterotaxis," to express in a general way that the plant material stands aside from the common or normal arrangement, such as the modifications in a maize stock reported by us on other occasions (IV Jornadas de Genética Luso-Espanholas, Oeiras, Portugal, 1967; Port. Acta Biol. 10: 289-300, 1968; An. Aula Dei 10: 716-723, 1969). This material is not only of the aberrant phyllotaxy type reported by Greyson and Walden (Amer. J. Bot. 59: 466-472, 1972), but also includes more

complicated types, not possible to consider only as modifications of phyllotaxis. Aberrant phyllotaxy could then be referred to as allophyllotaxis, an individual case of general allotaxis.

Determinations of length, width and area of leaves, height of plant and length of internodes, and number of nodes, leaves and ears, have been made in normal distichous plants of maize and in corresponding plants with allotactic modifications. Comparing decussate material (De) with distichous material (Di), the ratio De/Di results in different values depending on the character. The ratio is lower than 1 (De/Di = 0.75) for length of internodes and height of plant and for length, width and area of leaves. The ratio is near 1 (De/Di = 1.01) for mean number of nodes. The ratio is higher than 1 for the features total blade area per plant (De/Di = 1.28), total number of leaves per plant (De/Di = 2.03) and number of potential ears per plant (De/Di = 3.21).

There is an apparent positive correlation between length and area of leaves. The width of leaves tends to a constant value, different for distichous and for decussate material.

With increasing number of nodes and leaves, there follows a corresponding decrease in the length of leaves and the area of leaves. This fact may be considered as a natural tendency of the plant to hold its physiological stability irrespective of its apparent phenotype. The normal distichous phenotypes studied here have a practically constant total leaf blade area. In contrast, the decussate phenotypes, while positively correlated with the number of nodes, present rather important variability in the total leaf blade area, which signifies a different capability for trapping sunlight energy. One may conclude, therefore, that physiological stability for decussate material may be reached at a level different from that of distichous material.

The normal distichous plant seems to have reached its best equilibrium for height, as indicated by a constant length of internodes. Yet the decussate plant seems to be potentially operative, as indicated by the variable length of internodes. The distichous phenotype with opposite leaves has a potentiality similar to decussate plants.

The different behavior of phenotypes is displayed in the first stages of the living plant, at least as far as the current increase of the number of leaves is concerned. However, some defective characters dealing with shortness of the stem are not expressed until more advanced developmental stages have been reached.

M. Blanco, A. Lorenzo-Andreu, J. L. Blanco and A. Alvarez

FUNK SEEDS INTERNATIONAL
Bloomington, Illinois

Cytoplasmic male sterility research: M_3 generation from streptomycin treatments — Since the initial report (MNL 47:35-37) on treating maize seeds with streptomycin, there has been a generation-to-generation report. The principal objective of this research was to induce cytoplasmic male sterility in an inbred line. As reported last year (MNL 48:32-35), male sterile plants were obtained. The sterile plants were sibbed within the row, and these progeny were grown out this past summer. Many of the rows had plants that segregated for sterile:fertile plants. Some rows had plants that were all fertile. No rows had plants where all plants were sterile. The best genetic ratio to explain the results seems to be 1:1 for sterile:fertile plants since from the rows that segregated for sterile plants, the overall average was 45% steriles. This could be due to at least two things:

(1). A nuclear gene for male sterility in the heterozygous condition was present in some of the seeds that were initially treated with streptomycin. This gene segregated after selfing, and these plants were sibbed within the row by fertile plants which were either homozygous or heterozygous for genic male sterility. Homozygous plants used as the pollen source produced rows that were all fertile, and plants heterozygous for the male sterile gene used as the pollen source gave progeny segregating approximately 1:1 for sterility:fertility. If this is the case, it assumes that no cytoplasmic male sterile mutants were induced and only that spontaneous genes for male sterility were occasionally in the heterozygous condition in the seeds that were initially treated with streptomycin.

(2). Cytoplasmic mutants for male sterility could have been induced but the inbred population was segregating for restorer genes, which allowed the 1:1 ratio for sterility:fertility (MNL 47:35-37). To examine this theory further, as many as possible of the male sterile plants in each row were each crossed by pollen from any inbred in our field laboratory that had pollen available. Also, as many inbred pollen parents as possible were used on the sterile plants in each row. This was done in an attempt to bring in some non-restorer genes. This material will be grown in the next generation to observe for male sterile progeny.

This work has been continued using treatment procedures basically similar to the original report (MNL 47:35-37). In addition to streptomycin we are using erythromycin, acroflavine and ethidium bromide on maize seeds in an attempt to induce cytoplasmic male sterility.

Robert W. Briggs

Chemical pollen control by DPX 3778 — This compound is being evaluated for its ability to prevent pollen shed and thus facilitate hybrid corn production.

DPX 3778, an experimental compound from E. I. Dupont De Nemours and Company, Inc., was applied to inbred A632Ht as an over-the-top spray at rates of 0.06, 0.12, 0.25, 0.50, 1.0, 2.0 and 4.0 pounds/A at daily intervals beginning 30 days prior to anticipated pollen shed.

DPX 3778 at 1.0, 2.0 and 4.0 pounds/A applied 30 days prior to pollen shed induced a plant growth regulator response in the form of staminate production of silks and kernels in addition to normal ear development. DPX 3778 at 4.0 pounds/A produced undesirable plant growth for the duration of the experiment, ranging from bent or curved tassels when applied 5 days prior to pollen shed to the severe malformation already described at 30 days before pollen shed.

The maximum time interval between application and pollen shed for sterilization at the various rates tested was approximately 7 days at 0.5 pounds/A, 21 days for 1.0 pounds/A and 30 days for 2.0 and 4.0 pounds/A. The lower tested rates of DPX 3778 at 0.06, 0.12 and 0.25 pounds/A were ineffective in preventing pollen shed. Untreated plants shed pollen from two to ten days earlier than plants treated with 4.0 pounds/A. No data on ear morphology were obtained.

A water application study was conducted in which DPX 3778 at 1.0 and 2.0 pounds/A was applied to A632Ht as an over-the-top treatment at spray volumes of 5, 10, 20 and 40 gallons/A when tassels were beginning to show. Application of the compound at 1.0 and 2.0 pounds/A prevented pollen shed and was equally effective at all spray volumes. No immediate symptoms of phytotoxicity were observed with 1.0 or 2.0 pounds DPX 3778/A; however, one or two percent of the plants sprayed with 2.0 pounds/A remained permanently bent following windy weather (20 mph) five and six days after application. Untreated plants reached ten percent silk stage two to five days earlier than plants treated with 1.0 or 2.0 pounds/A DPX 3778.

Charles Laible and L. R. Kincaid*
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Bicentennial corn — There will be interest across the United States regarding the Bicentennial Birthday of our nation in 1976. A bicentennial O. P. variety of corn (Carswell White) that has been maintained by the Carswell family for 200 years was compared in 1974 with two hybrid checks.

The average yield of the hybrids was 52% more (130.6 vs 86.0 bu/a) than the Carswell White. The hybrid checks also yielded an average of 61% more corn than seven other long-time O.P. varieties of the Southeast. The average percent of

erect plants for the hybrids was 81%, compared with 54% for the O.P. varieties. These data indicate the progress that has been made in corn genetics and corn breeding.

A. A. Fleming

Bacterial leaf blight of corn — Bacterial Leaf Blight caused by Pseudomonas alboprecipitans is on the increase in the South. Some of the inbred lines that had resistance or tolerance under conditions of natural infection in 1974 were GA 222, GA 69:223, GA 69:244, GA 69:218, Mo 18W, CI 90C, Mo 20W and Oh 513.

A. A. Fleming

Cytoplasmic-genotypic effects in maize inbreds — Different cytoplasms were incorporated into well-established inbred lines through several generations of backcrossing. Significant differences were obtained among sources of cytoplasms within the inbreds for such characteristics as germination, vigor, color (chlorophyll), leaf rolling, plant height, ear height, silking, tasseling and yield. Certain combinations of cytoplasm and genomes gave more desirable agronomic performances than others.

A. P. Rao and A. A. Fleming

A cytoplasmic effect on the occurrence of northern corn leaf blight — Seed with the genotype of the long-time maize inbred CI 21 (Athens) was prepared with the cytoplasms of inbreds GA 199, GT 112 and CI 21 (A) in separate backcross programs; thus, each lot of seed had the same genotype but a different cytoplasm.

The cytoplasms were classified in the field for reaction to Helminthosporium turcicum Pass. on a 1 - 5 rating scale. The results indicated a highly significant difference between the GA 199 and GT 112 cytoplasms. All cytoplasms were moderately susceptible, but the ranking in order of resistance was GA 199, CI 21 (A) and GT 112. The GA 199 cytoplasm with CI 21 (A) nuclear genes offered more resistance, resulting in a favorable cytoplasmic-genotypic interaction.

A. P. Rao and A. A. Fleming

Differential reaction of four corn cytoplasms to a herbicide — Four maize cytoplasms with the genotype of inbred GT 112 were compared for reaction to the preemerge herbicide butylate (S-ethyl di-isobutylthiocarbamate) applied at the rate of 3.5 kg/ha. Herbicidal injury was measured on 12-day-old seedlings. Differences were significant in three paired comparisons. GA 199 cytoplasm in the GT 112 genotype was more susceptible to injury than GA 172 and GT 112 cytoplasms.

The susceptibilities occurring here may be due to plasmon-sensitive effects. The tolerance in certain cytoplasms may be due to a favorable cytoplasmic-genotypic interaction and the cytoplasm's ability in the plant cells to absorb lesser amounts of the herbicide.

A. P. Rao and A. A. Fleming

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The template for 5S ribosomal RNA is not necessary for formation of a nucleolus — Ribosomes in eukaryotic organisms (excluding ribosomes in mitochondria and chloroplasts) are 80S and are composed of a 60S subunit and a 40S subunit. The 60S subunit contains a 28S rRNA (ribosomal RNA) molecule and the 40S subunit contains an 18S rRNA molecule. The templates for 18S and 28S rRNAs are at the nucleolar organizing region in all eukaryotic organisms analyzed including maize (Phillips, Kleese and Wang 1971, Chromosoma (Berl.) 36:79-88). McClintock (1934, Zeitschr. Zellf. U. Mikr. Anat. 21:294-328) demonstrated that the nucleolar organizing region on chromosome 6 is necessary for formation of the nucleolus in maize.

In addition, each 60S ribosomal subunit contains a 5S and a 7S rRNA molecule. Recently, the location of the template for 5S rRNA has been determined in maize using in-situ hybridization of ^{125}I-labeled 5S maize rRNA with maize pachytene chromosomes (Wimber, Duffey, Steffensen and Prensky 1974, Chromosoma (Berl.) 47:353-359). The template for 5S rRNA is located on the long arm of chromosome 2.

The purpose of the current study was to determine if the template for 5S rRNA is also necessary for the formation of a normal nucleolus. In other words, is the 5S rRNA template also a nucleolar organizing region? For this purpose, meiosis in plants monosomic for the chromosome bearing the 5S template (monosomic 2 plants) was studied.

The monosomic 2 plants were selected from progeny of a cross between R/r-X1 plants in inbred W22 with Mangelsdorf's Multiple Chromosome Tester (see Weber 1973, Theoret. Appl. Genetics 43:167-173). Microsporocyte samples were taken from monosomic 2 plants, fixed and analyzed by the propio-carmine squash technique. All monosomic 2 plants were analyzed at diakinesis to verify that an entire chromosome was missing.

A monosomic 2 plant contains only one chromosome 2; thus, no more than two microspores of a quartet of microspores could contain a chromosome 2. Since a univalent chromosome is often lost during meiosis, some of the quartets contain a chromosome 2 in only one member, and other quartets would not include any chromosome 2.

If the 5S rRNA template is necessary for formation of a normal nucleolus, then normal nucleoli would be present in no more than two of the four members of a quartet in a monosomic 2 plant. However, if the 5S rRNA is not necessary for the formation of a normal nucleolus, then normal-appearing nucleoli would be present in all four members.

Four monosomic 2 plants were analyzed, and the following results were obtained:

Plant Number	Quartets with normal nucleoli in		
	4 cells	3 cells	other
3549-31	200	0	0
3550-14	276	2	0
4374-53	278	0	0
4480-27	259	0	0
Total	1013	2	0

In each quartet the four nucleoli appeared identical. It is clear from these data that the 5S template is not necessary for formation of a normal-appearing nucleolus at the quartet stage. Thus, the 5S rRNA template is not a nucleolar-organizing region in these cells. [Research supported in part by U. S. Atomic Energy Commission Contract AT(11-1)-2121].

David F. Weber

A test of the effects of DPX 3778 on the meiotic cytology in Zea mays — DPX 3778, an experimental compound from E. I. DuPont De Nemours and Co., Inc., appears to have promise as a pollen control agent. Extensive tests in several laboratories (Laible and Kincaid in this Newsletter, and others) indicate that relatively low amounts of this compound (as low as 0.5 lb/A) can prevent pollen release in corn, so that use of this compound might be an alternative for detasseling in commercial seed production.

In addition, this compound can induce production of silks and kernels in the staminate inflorescence, cause bent or curved tassels, induce both flowers in some spikelets to function and delay silking time (Laible and Kincaid in this News Letter; Charles Laible, personal communication).

Because this compound has such a wide spectrum of effects, and because it is effective in preventing pollen release if it is applied near the time that meiosis is taking place, it was felt that this chemical might also affect meiosis. At the time this study was carried out, the most effective time to treat plants was believed to be at the time meiosis was taking place. However, it is now known that if plants are treated 7 days before anthesis (long after meiosis is completed), the chemical is effective as a pollen control agent.

Plants of the inbred KYS were sprayed with DPX 3778 as an over-the-top spray at a rate of 5 lb/A. Microsporocyte samples were taken at 4, 8.5 and 48.5 hours after treatment. The microsporocyte samples were fixed and prepared for slides by the propio-carmine squash method. Pachytene, diakinesis, metaphase I, anaphase I,

metaphase II, anaphase II and the quartet stage were analyzed in each sample as well as from untreated sibling controls to detect any abnormalities which might be caused by DPX 3778.

At each stage, almost all of the cells were normal. Although a very low frequency of abnormal cells was detected at certain stages in these samples, a similar frequency of these abnormal cell types was also observed in untreated control plants.

Plants of the inbred A632 were also treated in a similar way at a rate of 4 lb/A, and microsporocyte samples were taken at 30 and 105 hours after treatment. Meiosis in these samples also appeared no different from meiosis in control, untreated sibling plants.

Thus, meiosis in DPX 3778-treated plants does not appear to differ from meiosis in untreated control sibling plants. (I would like to express my thanks to Dr. Charles Laible for treating the plants utilized in this study. I would also like to thank Funk's Seeds International for providing nursery space in which these and other plants were grown).

David F. Weber

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A maize-microbe bioassay for the detection of proximal mutagenicity of agricultural chemicals — We have devised a bioassay to detect the presence of proximal mutagens of agricultural chemicals. A proximal mutagen is a mutagen that arises from the host metabolism of a non-mutagenic substance or "promutagen" (Brusick, D. J., and V. W. Mayer, Environ. Health Perspec. Experimental Issue No. 6:83-96, 1973). Although we believe the wide use of pesticides is necessary, we suggest that the present monitoring systems used to detect genetic damage are inadequate. Since the possibility exists that mutagenic agents may be passed along the food chain, we contend that additional genetic monitoring systems should be developed and tested for their accuracy and economic feasibility. The recent citation of aldrin and dieldrin as carcinogenic compounds (Carter, L. J., Science 186:239-242, 1974) amplifies our concern, especially since many scientists hypothesize that carcinogens cause cancer by somatic mutations (Ames, B. N., Genetics 78:91-95, 1974). Thus a rapid method to detect mutagens arising from the use of agricultural chemicals is urgently needed.

This bioassay is based on the host-mediated scheme. In this experiment we used a maize-yeast system. The chemical studied was atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine].

One hundred kernels of inbred H51 were planted in each of eight trays filled with equal amounts of vermiculite. Into each tray a final volume of 1.5 l of distilled water plus a known concentration of atrazine was added. The concentrations of atrazine used were 0 ppm (control), 1 ppm, 5 ppm, 10 ppm, 15 ppm, 20 ppm, 25 ppm and 30 ppm. This concentration gradient encompasses the concentrations of atrazine used in commercial applications (0.5-5 ppm). The trays were put into an environmental chamber set to days with a 14 h photoperiod. The day temperature was 30^{o} C and 20^{o} C at night. The plants were allowed to grow for one week. Once during this period 500 ml of distilled water was added to each tray.

The seedlings were harvested after one week, and root tips were collected for chromosome analysis. The roots, stems and leaves were collected and placed on ice. Approximately 50 g of tissue from each tray was gathered. Tissues from the plants of each of the trays were homogenized separately with a Virtis blender in 200 ml of sterile water. The material was filtered through "Miracloth" and the filtrate was passed through No. 4 filter paper. The filtrate was centrifuged at 1000xg for 20 min. The supernatant fluid (1S fraction) was saved and lyophilized. Each sample, in powder form, was placed into a vial, whiffed with nitrogen and sealed. The vials were coded to introduce a blind, and the reversion tests were conducted using Saccharomyces cerevisiae.

The presence of a proximal mutagen in the 1S fraction was tested by reversion analysis using three S. cerevisiae strains. H201.14.4 is a haploid ade^{-} base pair substitution auxotroph; D4 is a diploid ade^{-} base pair substitution heteroallele; and DW844 is a haploid frameshift nuclear petite. Each strain was plated on complete media at a population density of 10^{7} cells/plate. The plates were incubated at 30^{o} C for 6 h. After incubation there was a confluent growth of cells covering each plate.

Each lyophilized 1S fraction was sterilized and diluted in sterile distilled water to a concentration of 12 mg/ml. 0.1 ml of the sterile 1S fraction was placed onto the middle of each plate and incubated for 18 h at 30^{o} C. Each plate was then replica-plated onto minimal media, incubated at 30^{o} C for 72 h and scored. A 0.1 ml, 1000 ppm solution of atrazine was also tested on H201.14.4 as described above.

The data concerning the reversion and induced recombination analysis are presented in Table 1. The data indicate that a mutagen is present in the 1S fraction of plants exposed to various concentrations of atrazine. That the

Table 1. Summary of yeast reversion or recombination data and maize chromosome observations.

1S fraction	*S. cerevisiae* strains			Chromosome morphology of maize root tips
	H201.14.1	D4	DW844	
CONTROL (0 ppm)	0	37	0[a]	CONTROL[b]
1 ppm	++	1000	0	normal
5 ppm	++	700	0	normal
10 ppm	+	900	0	normal
15 ppm	+++	2000	0	normal
20 ppm	++++	55	0	normal
25 ppm	+++	20	0	normal
30 ppm	+++	30	0	normal
Atrazine (1000 ppm) applied to plate	+	NA[c]	NA	NA

[a]Zero indicates that the reversion rate was not above the spontaneous reversion rate.

[b]The control was considered the "normal" chromosome morphology and was compared with the morphology of the chromosomes from plants exposed to the various concentrations of atrazine.

[c]Not applicable.

mutagen is not a natural component of maize is shown by the control. The very high concentration of atrazine applied directly to the yeast cells did induce a low reversion rate; however, the general increase in the amount of reversion of H201.14.4 is directly related to the amount of atrazine to which the maize plants were exposed. D4 also shows a high recombination rate up to the 15 ppm 1S fraction. The recombinants were confined to an area within the drop of the 1S fraction. The lack of recombinants above the spontaneous rate in 1S fractions above 15 ppm may be due to lethality.

In both base pair substitution mutant stocks, H201.14.4 and D4, there is an increase in the reversion or recombination rate induced by the 1S fraction of plants exposed to atrazine. However, DW844, a frameshift mutant reverted by ICR-170, does not revert by the proximal mutagen present in the 1S fractions. From these data we suggest that the proximal mutagen derived from atrazine primarily induces base pair substitution mutations.

We were unable to detect any chromosome damage induced by atrazine in exposed seedlings. Breaks induced by atrazine in meiotic chromosomes of barley have been reported; however, the plants were exposed to 1000 ppm (Wuu, K. D., and W. F. Grant, Cytologia 32:31-41, 1967).

We propose to extend this bioassay to include the effects of long term growth after an initial exposure to a pesticide. Maize pollen grains can be used to detect chromosome damage and forward and reverse mutation rates. The amount of pollen abortion can be used as an index of chromosome aberrations; if a proximal mutagen causes breaks in meiotic chromosomes, we could monitor these effects over an exposure concentration gradient by the increase in pollen abortion. Forward and reverse mutation rates could be measured on populations based on 10^5 to 10^6 pollen grains by studying mutation rates at the waxy locus. We have experiments in progress that should determine whether or not the above suggestions are feasible.

We contend that this bioassay could be used routinely by industry to test the agricultural chemicals they produce prior to their introduction into the environment. We believe that such information is essential in making rational decisions concerning agriculture and its ecological impact. (Partially funded by a D. F. Jones Fellowship, Research Corporation, New York).

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Topographical structure of the R region in R-ch complexes — Recombination studies involving a number of R-ch isolates revealed that the R region in these stocks consists of a number of closely linked discrete genetic units, each controlling anthocyanin pigmentation in a plant part or tissue. Recombinational analyses in the testcross progenies from G R-ch/g r-g heterozygotes of five cherry isolates show the following linkage relationships among the anthocyanin traits: pigmentation in aleurone (S), anther (P), silk (Si) and pericarp (Ch) (Table 1). Probable gene sequences in these isolates can be constructed as:

Ecuador R-ch: G - S - P - Ch - Si

New Mexican R-ch: G - Si - S - Ch - P, or g - P - Ch - Si - S

Standard R-ch: G - Si - Ch - S - P

Pueblo R-ch: G - S - Ch - Si - P

P.C. 150 R-ch: G - S - Ch - Si

In addition to these four anthocyanin traits, pigmentation in glume (Glm), auricle (Au), leaf margin (Lm), nodal ring (Nr) and coleoptile (Co) appear to be controlled by independent discrete units. Leaf color factor (Lc) expression was poor and

Table 1. Recombination percentages among g and four anthocyanin traits in five R-ch isolates.

Interval	Ecuador R-ch	New Mexico R-ch	Standard R-ch	Pueblo R-ch	Peru Corongo R-ch*
g-S	15.13	14.71	13.58	15.02	12.43
g-P	16.52	13.97	16.02	16.06	-
g-Si	17.83	13.54	13.21	14.36	13.09
g-Ch	17.23	14.84	16.17	14.55	14.34
S-P	0.55	1.32	0.89	2.60	-
S-Si	2.00	0.39	1.19	1.03	2.39
S-Ch	1.52	0.72	0.97	1.06	2.20
P-Si	1.68	1.14	2.36	1.71	-
P-Ch	1.25	0.99	2.65	1.94	-
Si-Ch	1.07	0.42	0.64	0.46	0.39

*Peru Corongo #150 R-g, no anther color.

erratic in Delhi conditions and its relationship with these anthocyanin traits could not be established. However, recombinations among these traits and between these and the four established components P, S, Si and Ch were regularly obtained (Table 2). Intercrosses between different isolates or between segregant classes

Table 2. Recombination percentages among various anthocyanin distribution traits in two R-ch isolates.

	Ecuador R-ch	New Mexico R-ch1		Ecuador R-ch	New Mexico R-ch1
Population	13,750	3,072	Ch-Nr	0.77	0.54
S-Glm	0.93	1.40	Glm-Au	0.85	0.59
S-Au	1.06	0.46	Glm-Lm	0.65	1.22
S-Lm	0.87	0.89	Glm-Nr	0.84	1.57
S-Nr	1.17	0.95	Au-Lm	0.51	0.16
P-Glm	0.33	1.16	Au-Nr	0.57	0.73
P-Lm	0.65	1.37	Lm-Nr	0.55	1.33
P-Au	0.87	0.77	S-Co	0.72	-
P-Nr	0.86	1.70	P-Co	0.80	
Si-Glm	1.65	0.84	Si-Co	1.61	
Si-Au	1.33	0.06	Ch-Co	1.12	
Si-Lm	1.35	0.87	Glm-Co	0.80	
Ch-Glm	1.20	0.75	Au-Co	0.72	
Ch-Au	0.89	0.49	Lm-Co	0.58	
Ch-Lm	0.98	0.38	Nr-Co	0.68	

of the same isolate result in complementation in "trans" position, indicating that this cluster of genes does not form a pseudoallelic series. They are rather independent but closely linked genes carrying out the same function with different times of action. They may be termed "para-allelic" (Laughnan, J. R., Am. Nat. 86:109, 1952). Mutation studies to examine these findings are in progress.

Strong negative interference and consequent high coincidence values were obtained in the majority of the three-point tests. This may be explained by a high degree of effective pairing in this region due to homology of the component segments. It can be postulated that various members of the gene cluster at the R region in R-ch complexes might have originated as tandem repeats through unequal crossing over. Two or more genes thus assembled together would acquire altered functions through mutation or position effect. On the basis of three-point data, tentative maps for the R region in Ecuador R-ch and New Mexican R-ch1 isolates are constructed as below:

....	0.55	0.33	0.80	0.58	0.51	0.57	0.77	1.07	
g	S	P	Glm	Co	Lm	Au	Nr	Ch	Si

Ecuador R-ch

....	1.32	0.39	0.84	0.59	0.16	0.38	0.54	...	
g	P	S	Si	Glm	Au	Lm	Ch	Nr	K

New Mexican R-ch1

K. R. Sarkar, J. K. S. Sachan and Gita Guha

Characterization of the Spf and Dil factors of the spotted-dilute R system —

To explain the aleurone spotting behavior in the unstable R alleles designated as "spotted-dilutes" (R-sd), Sastry and Kurmi (MNL 44:101) postulated the presence of two dominant modifiers, Dil (diluting factor) and Spf (spotting factor). Our studies involving two isolates, R-sd2 and R-sd4, confirm these postulations. Homozygous R-sd plants on selfing occasionally yield intense, spotted and dilute kernels in addition to the spotted-dilute kernels. Data from selfing and testcrossing heterozygous R-sd/r plants involving isolates R-sd-4 are presented in Tables 1 and 2.

Segregation of Dil was regular in the majority of ears, showing 3:1 ratios on selfing and 1:1 on testcrossing. The other factor, Spf, however, did not exhibit regular Mendelian behavior and consideration of its linkage with R does not fully explain the erratic segregation pattern. Segregation of both Dil and Spf in R-sd2 stocks was more irregular, not conforming to the 1:1 ratio in most of the ears obtained in the testcrosses.

Selfing of heterozygous dilutes of the R-sd4 isolate (R Dil/R dil) yielded dilute and non-dilute (intense) kernels in a 3:1 ratio, confirming that the diluting factor is a dominant independent modifier of the S component of the R locus and is not concerned with the spotting phenomenon. Linkage data obtained by crossing R-sd stocks with the waxy translocation series and selfing or testcrossing

Table 1. Segregation on selfing of R-sd4/r plants.

Pedigree	Types of kernels							χ^2 3:1 for color	χ^2 3:1 for spotted: non-spotted	χ^2 3:1 for dilute: non-dilute
	Spotted-dilute	Colored				Color-less	Total			
		Spotted	Dilute	Intense	Total					
129.2-1	87	15	3	10	115	39	154	0.008	11.49	0.65
129.2-2	150	48	120	42	360	105	465	1.45	76.80	0.00
130.2-1	130	2	44	58	234	85	319	0.46	43.12	0.04
130.2-2	120	15	10	28	173	63	236	0.36	0.84	0.002
131.2-1	179	9	68	81	337	99	436	1.22	66.34	0.52
131.2-4	150	42	111	34	337	121	458	0.49	58.40	1.07
134.1-1	114	33	89	35	271	98	369	0.47	62.24	0.001
135.1-2	140	38	110	32	320	117	437	0.73	64.04	1.66
Total	1070	202	555	320	2147	727	2874	0.13	284.20	0.54

Table 2. Segregation in R-sd4/r x rr test crosses.

Pedigree	Types of kernels							χ^2 1:1 for color	χ^2 1:1 for spotted: non-spotted	χ^2 1:1 for dilute: non dilute
	Spotted-dilute	Colored				Color-less	Total			
		Spotted	Dilute	Intense	Total					
129.2-6 x 100 B.1	104	85	28	6	223	227	450	0.03	107.72	7.52
129.2-7 x 100 B.1	60	40	30	35	165	140	305	2.05	7.42	1.36
129.2-8 x 100 B.1	103	151	23	31	308	315	623	0.79	129.86	10.18
132-1 x 100 B.2	40	35	20	15	110	98	208	0.69	14.54	0.90
132-3 x 100 C	58	41	33	38	170	168	338	0.01	4.60	0.84
132-5 x 100 C	38	51	85	15	189	194	383	0.06	0.64	17.18
132-6 x 100 C	100	138	15	25	278	301	579	0.91	141.02	8.28
132-7 x 100 C	87	132	16	19	254	249	503	0.05	133.28	9.06
133.2-3 x 100 A	119	115	23	35	292	299	591	0.08	106.08	0.22
133.2-4 x 100 A	68	93	26	5	192	210	402	0.81	88.02	0.08
Total	777	881	299	224	2181	2201	4382	0.09	5.90	0.38

the translocation heterozygotes indicated that Dil is most probably located on chromosome 10. A relative estimation of anthocyanin content for kernels in segregating ears showed that dilute kernels contain 4-10 times less anthocyanin than the normally pigmented ones.

Spf failed to produce any response in standard R. It may be suggested that the R allele in R-sd isolates carries a controlling element conditioning it for Spf response. In crosses of R-sd4 with 15 geographical R isolates, only two produced any response in F_1. In the rest of the crosses solid-colored kernels were obtained. In F_2, nine of these crosses yielded a 13:3 (non-spotted:spotted) ratio, indicating no response of these R alleles to Spf. Six isolates, however, showed a 3:1 (spotted:non-spotted) segregation, suggesting that these alleles are responsive to Spf action.

Spotting patterns in the isolates are distinct and can be easily identified. Spotted-dilute phenotypes could be reconstituted by crossing "spotted only" (Spf, no Dil) derivatives from R-sd4 with "dilute only" (Dil, no Spf) individuals from R-sd2, R-sd6 and R-ch. Spf and Dil seem to be autonomous and the two phenotypes are superimposed in spotted-dilute kernels. However, spotting patterns in these reconstituted types were not the same as in R-sd4, indicating that Spf is the general regulator and that distinguishable phenotypes are due to different "states" of the R locus in these responsive alleles.

Spf and Spm show close parallelism in behavior. However, when Spf was crossed with c2-m2 (no Spm) to observe whether it can induce Spm, only spotted-dilute phenotype was recovered. Crosses between R-sd and a Dt produced overlapping patterns of the two phenotypes in F_1. Testcross with a a gave a 1:1:1:1 segregation for intense, spotted, dotted and colorless kernels, suggesting that these systems operate independently of each other.

A dosage effect study of Spf revealed that the number of spots (mutations) per kernel increases on increasing Spf dose from one to three, the relationship being almost linear. Average numbers of spots per kernel with 1, 2, and 3 doses were 39, 227 and 300 respectively. The size of the spots also showed an increase with increased dosage, although their shape and pigmentation intensity were relatively unaltered.

In crosses between R-mb and R-sd, it was further observed that the R-sd allele is not paramutable. The number of spots on R-sd kernels and their shape, size and intensity of pigment remained unaltered following association with the paramutagenic R-mb allele. The heterochromatic knob, K, on chromosome 10 was found to repress the action of Spf to some extent, reducing the number of spotted

kernels. In the testcross ears from r K/R-sd k and r k/R-sd k heterozygotes, the percentage of spotted kernels among colored kernels in the former was 46.8% and 81.0% in the latter.

In order to establish linkage relationships of Spf and Dil, the two spotted-dilute isolates were crossed with golden plant, colorless seed testers (g r-g). From the testcross segregations the following linkage values were estimated:

	R-sd2	R-sd4
g-R	12.83 ± 0.99	14.16 ± 0.98
g-Spf	35.86 ± 1.42	27.84 ± 1.26
g-Dil	33.51 ± 1.39	49.32 ± 1.41
R-Spf	41.62 ± 1.46	32.61 ± 1.32
R-Dil	34.29 ± 1.40	48.53 ± 1.41
Spf-Dil	46.07 ± 1.47	51.07 ± 1.41

Indira Singh, J.K.S. Sachan, Gita Guha and K.R. Sarkar

Induction of mutations with tassel and pollen treatments — In a search for a suitable technique for induction of mutations, a number of chemicals were tried for seed, tassel and pollen treatments in an inbred, stock 2. Seed treatments were not very effective, as the concentrations used were rather low. The chemical mutagens were EMS (ethyl methane sulfonate), DES (diethyl sulfate), NMU (nitroso methyl urea), NEU (nitroso ethyl urea), BMS (butyl methane sulfonate) and NG (nitroso guanidine). Tassel treatments involved dipping the cut end of

Table 1. Mutation frequencies in tassel and pollen treatments.

Treatment	Percentage of M2 families segregating		
	Chlorophyll mutants	Endosperm mutants	Floral & ear Abnormalities
EMS 0.03% T	1.7	16.5	23.1
0.05% T	3.9	16.5	9.3
DES 0.03% T	0.0	3.8	21.8
0.05% T	4.0	10.6	14.1
NMU 0.005% T	0.9	5.4	20.5
0.0075% T	2.1	8.4	17.6
NEU 0.005% T	0.06	12.3	6.1
0.0075% T	0.0	12.0	9.0
BMS 0.03% P	12.5	0.0	25.0
NG 0.35% P	7.3	20.2	7.13

T = tassel treatment; P = pollen treatment

a tassel for 48 hours in the mutagen solution, which was replaced periodically (6 hours interval), and collecting pollen from these tassels for pollination. For pollen treatment mineral oil was used for suspension of the chemicals. Concentrations and mutation frequencies are presented in Table 1 (see preceding page). NG appears to be the best treatment in these studies.

J.K.S. Sachan and K.R. Sarkar

Interesting chlorophyll mutants — In the course of our mutagenesis studies, we came across two interesting chlorophyll mutants. The first one was luteus type, having fine green spots on shining lemon yellow leaves. It originated from 15 Kr gamma ray seed treatment. The spots were sharp and present in all leaves, and the mutants survived up to the 4 to 5 leaf stage only. Number of green spots per leaf varied from 5 to 15. The mutant segregated in a 3:1 ratio in M2 (116 normal:34 mutant seedlings) and was maintained in heterozygous condition. In M3 and M4 families this mutant also appeared, but in addition to the spotted-luteus (1*-sp) types, luteus (no spots) and albino seedlings were also obtained. This may be a case of an unstable gene under the influence of controlling elements. In an attempt to locate this mutant, crosses with waxy translocation lines were made. Linkage indications with Wx were obtained in crosses involving T4-9g, T5-9a and T6-9 4505.

We called the second mutant "yellow virescent," as it differed from yellow-green and virescent. In M2, it was very weak with narrow leaves, unbranched tassels and no silk. There was 50% mortality before flowering, but the appearance and performance improved in M3 and M4. This mutant was crossed with the waxy translocation series and linkage data showed significance in crosses with T4-9c, T4-9b and T9-10b.

J.K.S. Sachan and K.R. Sarkar

Pollen grain diameter in maize — Studies on the pollen grain size in a number of inbred lines of maize revealed some interesting findings. Fully mature anthers which would shed pollen in an hour's time were collected from the main axis of the tassel on the second day of pollen shedding and preserved in 70% alcohol. Pollen samples from ten anthers from a tassel were stained in acetocarmine, and 25 random grains were measured. Thus, means of 50 observations from two plants constituted the pollen grain size of each inbred. Mean pollen diameter in two separate sets of inbreds, the first set comprising 41 lines grown in the summer at Delhi and the second set of 73 inbreds grown in the winter at Hyderabad, showed wide and significant line-to-line differences. Pollen diameter in these lines ranged from 81.9 to 114.1 micra. The frequency distribution was quite normal.

There was no significant difference in pollen size measurements of fresh pollen and pollen from anthers stored in 70% alcohol for 3 months and measured at fortnightly intervals. Plant-to-plant differences within the same inbred were not significant. There was no statistically significant difference in pollen size for samples collected from the same plant on subsequent days of shedding or from different branches of the same tassel. These results contradict an earlier report on pollen size in maize (Banerjee and Barghoorn, MNL 45:244-45). However, the influence of environmental factors on pollen size was confirmed in a study where 8 inbreds were grown in two locations and for two years in each location. Analysis of variance of the data showed that variations due to lines and years were significant at the 1% level and those due to location were significant at the 5% level. These suggest that pollen size in maize is controlled by both genotype and environment.

Crosses between large and small pollen inbreds were studied in F_1 and F_2. Within-plant variability in both generations was not significant, whereas plant-to-plant variability for pollen diameter was significant in F_2 but not in F_1. These results would suggest that the pollen grain size is determined by the genotype of the mother plant (sporophytic control) and not by the gene content of the haploid pollen nuclei (gametophytic control). Pollen size of the F_1 plants was not always intermediate between the two parents, but F_2 plants in general had smaller pollen diameter than in F_1. F_1's between small and large pollen parents, when backcrossed to small and large pollen parents, produced progeny with, respectively, smaller pollen and larger pollen than the F_1 plants.

D. Kumar and K.R. Sarkar

Inheritance of pollen grain size in maize — Two sets of diallel crosses were made from the two groups of inbred lines mentioned in the preceding report. The first set of 8x8 diallel included the inbred parents and the F_1's, grown in two locations with two replications. The second set of 9x9 diallel included parents, F_1 crosses and reciprocals, grown in only one location with two replications. Five random plants from each plot and 50 measurements for pollen size from each plant were taken for each entry.

Analysis of variance for general and specific combining ability indicated highly significant differences among the parents for both general and specific combining ability effects for both the locations in the 1st diallel. Similar results were obtained in the 2nd diallel. The analysis for the 2nd diallel is summarized in Table 1.

Table 1. Analysis of variance for pollen grain diameter.

Source	d.f.	m.s.
General combining ability	8	60.25**
Specific combining ability	36	10.39**
Reciprocal effects	36	3.55
Error	80	3.38

Homogeneity of Wr-Vr (nonsignificance of t^2 - B.I. Hayman, Genetics 39:789, 1954) indicated that an additive-dominance model with independent gene distribution was adequate to explain the data. Variance component analysis was, therefore, carried out. The components of variation are presented in Table 2, and some proportions of the components in Table 3.

Table 2. Components of variation for pollen diameter in maize.

Component	Estimate	Standard error
$\hat{D}$	27.98	0.98
$\hat{F}$	21.08	2.30
$\hat{H}_1$	11.74	2.18
$\hat{H}_2$	7.60	1.87
$\hat{h}_2$	115.74	1.25
$\hat{E}$	3.38	0.29

Table 3. Proportions of components of variation for pollen grain size.

Proportions	Estimate
$(H_1/D)^{\frac{1}{2}}$	0.64
$H_2/4H_1$	0.16
$[(4DH_1)^{\frac{1}{2}} + F]/[(4DH_1)^{\frac{1}{2}} - F]$	3.78
h_2/H_2	15.23
heritability (narrow)	0.51

The high level of significance of D, H_1, H_2 and h_2 indicates the operation of additive and dominant genes in respect to this character. Pollen size was highly sensitive to environmental variations, as E was significant. The overall degree of dominance was 0.64, indicating the operation of partial dominance in the expression of this trait. $H_2/4H_1$ suggested asymmetry of gene distribution for pollen size.

D. Kumar and K.R. Sarkar

Pollen tube growth in vitro and in vivo — Fresh pollen grains were germinated in cavity slides in aqueous culture medium consisting of 0.45M sucrose supplemented with Ca, B and Mg. More than 50% of pollen grains germinated, and mean pollen tube lengths were obtained for the parents and F_1's of the 8x8 diallel at ½, 1, 2 and 3 hours. Pollen tube growth in live silks was studied with the help of radioactive ^{32}P (House and Nelson, J. Hered. 69:18, 1958). Actively shedding tassels were removed from plants and the cut stalk end was immediately immersed in water in a conical flask. Radioactive ^{32}P in the form of H_3PO_4 of 350 μCi activity was administered in water. Radioactive pollen from the tassels was collected after 24 hours and used for pollination on silks specially prepared by cutting back on the previous afternoon. At 2, 4 and 6 hours after pollination cobs were harvested and the tips of the silks washed to remove ungerminated hot pollen. Silks were removed, dried by pressing between blotting paper sheets, and mounted in autoradiographic frames with X-ray film in direct contact. The films were developed after 5 weeks and the lengths of pollen tubes were measured.

Significant variability for rate of pollen tube growth both in vitro and in vivo was observed in the eight lines. The ranges were 1.50 - 3.69 μ per minute in vitro and 33 - 108 micra per minute for in vivo studies. In most of the crosses pollen from the hybrids had shown either intermediate rate or slower than either parent. Heterotic effects in rate of tube growth were obtained in a few crosses only.

Correlation studies involving pollen size and rate of pollen tube growth in artificial medium revealed that larger pollen showed a higher rate of pollen tube growth than the smaller pollen. A correlation coefficient for pollen tube growth in vitro computed over two hours after inoculation was 0.84 and significant. On the other hand, negative but non-significant correlation coefficients were obtained between pollen size and rate of tube growth in live silks. There was no correspondence between rates of pollen tube growth in vivo and in vitro.

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Stabilization of freshly broken chromosome ends in the endosperm mitoses — We have previously shown that B chromosomes cause loss of knobbed segments of members of the regular chromosome complement. We hypothesized that replication of the heterochromatic knobs was delayed at, and only at, the second microspore mitosis. We suggested that a dicentric chromosome is formed at anaphase; following bridge breakage, a broken chromatid passes to one sperm cell and an intact chromatid goes to the other sperm. Data from high-loss plants carrying a knobbed chromosome 9

are particularly instructive because 9S has marker genes (C and Wx) affecting the endosperm that are situated some distance apart. When pollen from a high-loss plant with a large terminal knob on 9S and the C and Wx alleles was used in crosses to c wx female lines, a number of distinctive kernel phenotypes were produced following breaks in 9S at the second microspore anaphase. Let region (1) be the knob-C interval, region (2) the C-Wx segment and region (3) the Wx-centromere interval. Breaks in (1) followed by a bridge-breakage-fusion cycle in the endosperm mitoses give kernels variegated for C-c and for Wx-wx. A break in (2) produces a kernel with colorless aleurone and an endosperm mosaic for Wx and wx sectors. Rupture in region (3) yields a colorless (c) kernel with all wx starch. Data from such a cross are given below:

Distribution of breaks in the short arm of chromosome 9 based on the frequency of whole loss and variegation for the C and Wx markers.

C-c, Wx-wx kernels from breaks in (1)	c, Wx-wx kernels from breaks in (2)	c, Wx kernels from breaks in (2) No Wx-wx mosaicism	c, wx kernels from breaks in (3)	Total kernels examined
30	20	14	601	3483

The unexpected feature of the above data is the occurrence of the 14 stable c Wx kernels. We postulated in our 1973 paper (J. Heredity) that these c Wx kernels could arise in the following ways:

(1) if there is a break between C and Wx followed by healing to form stable ends, as occurs in the embryo; (2) if chromosome 9 underwent a cryptic bridge-breakage-fusion cycle throughout endosperm development but, owing to a weak fusion of the broken ends, the dicentric bridges broke at the same position at every anaphase; (3) if a mutation of C to c occurred; or (4) if there was an internal deletion of the C locus. We tentatively concluded that the c Wx class was best accounted for by assuming a weak or imperfect union of broken ends. More recent observations suggest that none of the four mechanisms was correct and that a new type of structural modification is responsible. The pertinent data follow.

Crosses were made in which pollen from a high-loss strain with a terminal knob on 9S and the Yg2, C and Wx alleles was placed on silks of yg2 C wx testers. A deficiency of the Yg locus in a sperm fertilizing the yg egg would yield a yg seedling. Scores of exceptional yg seedlings arising from the above cross were grown and testcrossed as the female parent by Yg c wx pollen. The great majority of the exceptional yg plants had, in addition to a normal chromosome 9 with the yg C wx alleles, a chromosome 9 deficient for all of the markers on 9S, which was not transmitted. Some, however, had a chromosome 9 deficient for Yg but carrying

the C and Wx loci in some instances and only the Wx locus in others. When one of these exceptional yg plants (33016-1, which had a low percentage of aborted pollen) was pollinated by a Yg c wx plant, it gave an ear with 242 C Wx and 106 C wx kernels. Since the Wx allele carried by the deficient chromosome 9 was recovered more frequently than the wx allele on the normal chromosome, this situation was deemed worthy of further study. Plant 33016-1 was not examined cytologically, and all that could be inferred from the genetic data was that it had a deficiency for the Yg allele and that some unknown mechanism was responsible for the excess of Wx kernels. C Wx kernels from the above cross were planted as family 33356, and several individuals were backcrossed reciprocally; PMC's were also taken for cytological examination.

The cytogenetic analysis of individual plants of 33356 revealed the presence of four chromosomal classes.

Class I had:
- 2 normal chromosomes 4 with no marker genes
- 1 normal chromosome 9 with the Yg c wx alleles
- 1 chromosome 9 deficient for the tip of 9S including the Yg locus but capped by a terminal piece of 4L consisting of the segment from the knob to the tip

Since the deficient segment of 9S included McClintock's wd locus, this 9-4 translocated chromosome is designated T9(wd)-4 to indicate that it is a translocated chromosome with an internal deficiency for the tip of 9S. The deficient chromosome in Class I carried the dominant C and Wx alleles.

Two classes of gametes are produced by Class I plants: N9 N4 and T9 (wd)-4 N4. Class I plants were testcrossed reciprocally. When used as the female parent, a 1:1 ratio was found for the segregating C:c and Wx:wx alleles, indicating that megaspores with the T9(wd)-4 chromosome functioned as well as those with a N9. The T9(wd)-4 N4 megaspores have a duplication for the terminal piece of 4L and are deficient for the tip of 9S, but transmission is normal despite the genic imbalance. However, when Class I plants were used as the pollen parent in testcrosses, the following data were obtained:

C Wx	C wx	c Wx	c wx	Σ
46	9	116	1081	1252

If none of the T9(wd)-4 N4 pollen functioned in competition with N9 N4 pollen, the frequency of C kernels (4.4%) measures the amount of crossing over between C and the Wd deficiency. Two male testcrosses made onto yg c wx silks gave:

(1) Yg C Wx	(0) yg C Wx	(1-2) Yg C wx	(2) yg C wx	(2) Yg c Wx	(1-2) yg c Wx	(0) Yg c wx	(1) yg c wx	Σ
4	11	1	1	35	0	310	2	364

The estimated amount of wd-C crossing over, based on the assumption of no functioning of T9(wd)-4 N4 pollen, is 4.7%. That some T9(wd)-4 N4 pollen does achieve fertilization in competition with N9 N4 grains is indicated by the occurrence of yg plants in the above table. These amount to 3.8% of the total population, i.e., the T9(wd)-4 N4 pollen functions only 4.0% (14/350) as well as does N9 N4 pollen. The amount of wd-C recombination is 1.9% (7/364). The C-Wx recombination of 10.0% is comparable to the value found in the reciprocal cross.

Class II had: 1 normal chromosome 4
1 chromosome 4 deficient for a terminal piece of 4L
1 T9(wd)-4 chromosome carrying C and Wx
1 N9 chromosome carrying Yg c wx

Four kinds of gametes are produced: N9 N4; T9-4 N4; T9-4 Df4; and N9 Df4. The latter will abort. Class II plants used as the pollen parent in crosses with c wx females gave:

C Wx	C wx	c Wx	c wx	Σ
1014	90	135	1074	2313

C-Wx recombination = 9.7%

The ratios of C:c (1104:1209) and of Wx:wx (1149:1164) indicate a high percentage of functioning of T9-4 Df4 pollen since we know from the data of Class I plants that there is a low functioning of T9-4 N4 pollen. This is expected since there is no duplication and only a small terminal deficiency of 9S including the Yg and Wd loci.

Some crosses of Class II individuals to yg c wx females provided the following data:

(1) Yg C Wx	(0) yg C Wx	(1-2) Yg C wx	(2) yg C wx	(2) Yg c Wx	(1-2) yg c Wx	(0) Yg c wx	(1) yg c wx	Σ
5	271	1	20	34	1	290	7	629

The wd-C interval has 2.2% recombination, and that for C-Wx is 8.9%.

The following data came from testcrosses using Class II plants as the female parent:

C Wx	C wx	c Wx	c wx	Σ
267	30	25	131	453

The ratios of 297 C:156 c and of 292 Wx:161 wx approximate the 242 Wx:106 wx ratio found in the original yg exceptional plant. The C-Wx recombination value is 12.1%.

Class III had: 2 normal chromosomes 4
1 normal chromosome 9 carrying C and Wx
1 normal chromosome 9 carrying c and wx

Only one plant of this constitution has been studied. Reciprocal testcrosses gave 1:1 ratios for both C:c and Wx:wx. The high C-Wx recombination value of 25%

determined from limited data is a reflection of the structural homozygosity of the two chromosomes 9.

Class IV had:
1 normal chromosome 4
1 deficient chromosome 4
1 normal chromosome 9 carrying yg C wx
1 T9(wd)-4 chromosome carrying C and Wx
1 normal chromosome 9 carrying Yg c wx

This class includes infrequent trisomics arising from nondisjunction of the N9 and T9-4 chromosomes in plant 33016-1. A single plant was studied (33356-14). When used as the female parent in testcrosses, it gave 88.4% C and 70.4% Wx kernels. The reciprocal cross gave 61.1% C and 23.6% Wx kernels. Without knowledge of the chromosomal constitution of 33356-14, the above genetic data defy comprehension, but they are readily understood on the basis of cytological observations. In the absence of crossing over in 9S the following kinds of meiotic products are formed on the assumption of random segregation:

n spores		n + 1 spores	
1. N9 (C wx)	N4	7. $\frac{\text{T9-4 (wd C Wx)}}{\text{N9 (c wx)}}$	N4
2. N9 (C wx)	Df4 aborts	8. $\frac{\text{T9-4 (wd C Wx)}}{\text{N9 (c wx)}}$	Df4
3. N9 (c wx)	N4	9. $\frac{\text{N9 (C wx)}}{\text{T9-4 (wd C Wx)}}$	N4
4. N9 (c wx)	Df4 aborts	10. $\frac{\text{N9 (C Wx)}}{\text{T9-4 (wd C Wx)}}$	Df4
5. T9-4 (wd C Wx)	N4 low in ♂	11. $\frac{\text{N9 (C wx)}}{\text{N9 (c wx)}}$	N4
6. T9-4 (wd C Wx)	Df4	12. $\frac{\text{N9 (C wx)}}{\text{N9 (c wx)}}$	Df4 aborts

Of the n spores, one-third will abort (2 and 4) while T9-4 (wd C Wx) N4 pollen will have a low transmission rate even though filled with starch. If none of the n+1 spores function in male crosses, the C:c ratio should approximate 2:1 (61% C was observed), while the percentage of wx kernels should be greater than that of Wx (76% wx was observed). When class IV plants were used as the female parent in testcrosses, where we may assume equal viability of all megaspores except those of the aborted types (2, 4 and 12), the percentage of C kernels should be greater than in the male data since all of the functioning n + 1 spores have the C allele. The observed percentage of C in the female data is 88.4% as compared with 61% in the male gametes. With the Wx gene, 70.4% Wx was observed in female tests and 23.6% in the male backcrosses. The greatly different frequencies of Wx:wx in the reciprocal crosses could be accounted for by a number of speculative hypotheses,

but they are readily explained by the predicted array of gamete types given above. Ascertainment of the true mechanism came only from cytology.

The establishment of the four classes in the offspring of 33016-1 makes it possible to reconstruct its genotype and the events occurring at the second microspore division. 33016-1 had a N9 and a N4 contributed by its female parent. The fertilizing sperm possessed a Df4 and the T9(wd)-4 chromosome. These two structurally changed chromosomes arose at one second microspore division when both chromosomes 9 and 4 formed dicentric bridges. Chromosome 9 was ruptured in anaphase close to the terminal knob, producing a freshly broken end which united with a freshly broken end of an acentric fragment derived from breakage of the dicentric chromosome 4.

Plant 33016-1 therefore had a N9, a N4, a T9(wd)-4 and a Df4. It was pollinated by a N9 N4 strain. Class I came from an egg with a N4 and the T9(wd)-4 chromosomes to give a N9 T9(wd)-4 N4 N4 zygote. Class II arose from an egg with the Df4 and T9(wd)-4 chromosomes. Class III was derived from a N9 N4 egg, and Class IV originated following nondisjunction of the N9 and T9(wd)-4 chromosomes, which passed to the same pole at anaphase I of meiosis as did the Df4 chromosome. Nondisjunction of the N9 and T9(wd)-4 chromosomes presumably would be increased by the piece of 4L on the T9(wd)-4 chromosome.

While the above account is a good example of how a combined cytological and genetical attack led to the elucidation of a complex genetic situation, the demonstration that chromosomes comparable to the T9(wd)-4 chromosome can arise suggests a new explanation of the stable C Wx class discussed in the introduction of this note. Let us assume that the dicentric bridge involving chromosome 9 broke between the C and Wx loci. The C allele would be eliminated in the acentric fragment. Further assume that another chromosome of the complement was involved in a dicentric bridge, because it too was knobbed, and that breakage produced an acentric fragment with a broken end. The union of the two freshly broken ends produced a translocated chromosome deficient for C, possessing the Wx allele and capped by a piece from the heterologous chromosome. If such a chromosome were present in the endosperm, it would not undergo a bridge-breakage-fusion cycle, and the mature endosperm would be colorless and would not show Wx-wx mosaicism. Such a mechanism is, we believe, responsible for the stable C Wx class.

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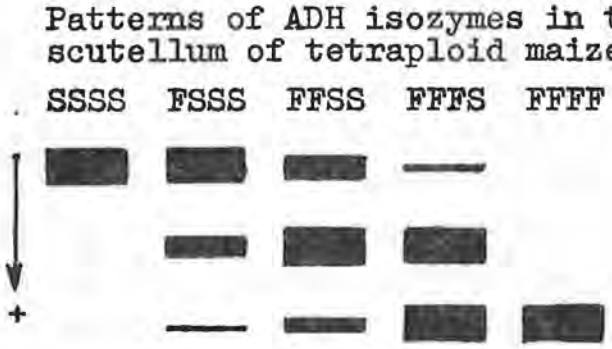
Comparative studies on the expression of Adh in the scutellum of diploid and tetraploid maize — The tetraploid of Adh-F Adh-F/Adh-S Adh-S genotype is an advantageous experimental model for investigation of the regulation of activity at the Adh locus, which controls alcohol dehydrogenase (Schwartz, D., Science 164:585, 1969). When the duplex FFSS is self-pollinated, the offspring are of five genotypic and phenotypic classes which segregate in a 1:8:18:8:1 ratio. On zymograms each of the five genotypic classes is identified by the comparative staining intensity of isozyme bands (Figure). At equal activities of the F and S alleles,



which specify ADH-F and ADH-S protomers, the dimer molecules ADH-F ADH-F, ADH-F ADH-S and ADH-S ADH-S should be formed in a ratio of 56.3:37.5:7.2 percent (9:6:1) for the FFFS triplex, a ratio of 7.2:37.5:56.3 percent (1:6:9) for the FSSS triplex and a ratio of 25:50:25 percent (1:2:1) for the duplex. Quantitative densitometer measurements of zymograms showed a ratio of 49:42.3:8.7 percent for the FFFS triplex, a ratio of 4.1:31:64.9 percent for the FSSS triplex and a ratio of 32.1:50:17.9 percent for the duplex. These ratios are easily explained on the assumption that the S allele is 1.3 times more active than the F allele; that is, the activity of the enzyme is regulated at the level of transcription. This explanation is in accordance with Schwartz' hypothesis on a limiting factor that is necessary for transcription and for which the alleles compete with different degrees of effectiveness (Schwartz, D., Genetics 67:411, 1971). It was shown that the intensities of the isozyme bands in the duplex FFSS and the diploid heterozygotes FS are identical. This demonstrates that the ratio of the activities of the alleles does not change when cells are transferred to another level of ploidy. The presence of all five phenotypic classes indicates that all four alleles of the Adh locus are active in a tetraploid cell. We have reported elsewhere (Levites,

E. V., and S. I. Maletzky, M.G.C.N.L. 48:63, 1974) that the activity of ADH in diploid and tetraploid plants homozygous for the F allele is the same. However, because the cell volume in tetraploid plants is about twice that in diploid plants, the enzyme activity per tetraploid cell should be twice as high.

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Genetic control of meiosis: mutations affecting meiosis — Meiotic mutants should help to focus attention on single events in the process of meiosis and on specific aspects of the regulation of meiotic systems. Two meiotic mutants controlled by recessive genes were investigated. They were obtained after seed treatment with chemical mutagens (N-nitrosomethyl urea).

Desynaptic mutant: The 44 normal:15 desynaptic plants in the M_3-M_4 segregating progenies indicated that the meiotic irregularities are under the control of a single recessive mutant gene (dy*-G). (Ed. note: Dr. Golubovskaya proposed to use the symbol ds, which would be subject to confusion with Ds; dy*-G is suggested in view of parallel effects with the mutant described by Nelson and Clary, J. Hered. 43:205-210, 1952). Analysis of meiotic prophase I demonstrated all stages: leptotene, zygotene and pachytene. However, as early as zygotene the pairing chromosomes had desynaptic regions, which were more distinct at pachytene. It was found that at diakinesis most homologous chromosomes lie apart and very few open bivalents are formed. The mean numbers of bivalents and univalents at MI were 0.6 and 18.8, respectively.

Chromosome distribution at AI was irregular. Ten + ten chromosome distributions were observed in only 15.2% of 131 cells examined. Other cells showed no regularity in chromosome distribution. Second meiotic division was normal, and all the observed irregularities were the consequences of anomalies in chromosome segregation during first division.

Only 15% of the tetrads looked normal at the end of meiosis. The mutant plants were completely sterile. This desynaptic type of meiotic mutant is frequently observed among different plant species.

Mutation causing the absence of first division (Genetica, in press, 1975): Mutant plants exhibit characteristic meiotic peculiarities. (1) Prophase I of meiosis (leptotene, zygotene, pachytene and diplotene), including the pairing of homologous chromosomes, is absent. At the stage which presumably is diakinesis, all 20 chromosomes lie separately, resembling the mitotic condition. (2) The first meiotic division is of a mitotic type; the 20 univalents are arranged in an orderly manner along the equatorial plate at MI, and the 20 chromatids separate and pass to each pole at AI. (3) Although the centromeres have divided in the first division,

the second meiotic division takes place; the chromatids are randomly distributed at AII, giving rise to 100% anomalous tetrads. Mutant plants are completely male- and female-sterile.

This meiotic mutation is controlled by a single recessive gene (the segregation in M_3-M_4 plants heterozygous for this mutation was 64 normal:15 mutant plants, $\chi^2 = 1.52$, $P = 0.1 - 0.15$).

This mutation causing meiotic sterility was designated "the absence of the first division," and its symbol is afd-W23 (W23 is line Wisconsin 23 where this mutation first appeared). This new type of meiotic mutation has not been described in the literature. Meiotic mutants in plant and animal species are listed in a reference (Ontogenesis 6: 2, 1975). However, the first division was experimentally substituted by the second division by Astaurov (Cytogenetica razhvitiya tutovogo shelkopryada, M. "Nauka," 1968) in Bombyx mori and by Maguire (Chromosoma 48:2, 1974) in Zea mays L. The mechanisms of the substitutions are different from the mechanism we describe for afd-W23.

This type of meiotic mutation might have been involved in the course of evolution of apomictic plants as a cytogenetic mechanism underlying the gradual transition from meiosis to mitosis.

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Location of gl12 — A-B chromosome translocations were used to locate gl12 in a mutant stock received from the Maize Genetics Coop.

The data from the F_1 progenies presented in Table 1 clearly indicate the long arm of chromosome 3 as the carrier of the gl12 locus. After this result we looked to relate gl12 with Rg, lg2 and ra2.

Table 1. Results of the F_1 from gl12 gl12 x the A-B translocations.

Translocations	Breakpoint	Gl12	gl12	Total
B-1a	1L.2	37	0	37
B-1b	1S.05	169	0	169
B-3a	3L.1	88	15	103
B-4a	4S.25	232	0	232
B-7b	7L.3	62	0	62
B-8a	8L.7	119	0	119
B-9a	9L.5	121	0	121
B-9b	9S.4	146	0	146
B-10a	10L.35	59	0	59

Table 2. Backcross segregation: G112 g112 Rg rg x g112 rg.

G112 Rg	G112 rg	g112 Rg	g112 rg	Total
84	12	3	116	215

Recombination = $\frac{15}{215}$ = 0.07.

Table 3. F_2 segregation: G112 g112 Lg2 lg2 selfed.

F_2 families	a_1 G112 Lg2	a_2 G112 lg2	a_3 g112 Lg2	a_4 g112 lg2
73.1049	67	31	20	1
73.1050	65	22	20	1
Total	132	53	40	2

$c = \frac{a_1 \times a_4}{a_2 \times a_3} = \frac{264}{2120} = 0.1245$; recombination fraction = 0.23.

Table 4. F_2 segregation: G112 g112 Ra2 ra2 selfed.

F_2 family	G112 Ra2	g112 Ra2	G112 ra2	g112 ra2	Total
73.1051	63	23	18	1	105

$c = \frac{a_1 \times a_4}{a_2 \times a_3} = 0.1521$; recombination fraction = 0.25.

Livia B. de Lares and Dora M. de Zerpa

Location of g114 — Homozygous g114 from the Maize Genetics Coop was crossed with A-B and reciprocal interchanges. The F_1 and testcross data are presented in Tables 1 and 2.

Table 1. F_1 progenies (g114 x A-B translocations).

Translocation	Breakpoint	G114	g114
B-1b	1L.05	226	0
B-3a	3L.01	115	0
B-4a	4S.25	56	0
B-7b	7L.3	24	0
B-8a	8L.7	28	0
B-9a	9L.5	77	0
B-9b	9S.4	9	0
B-10a	10L.35	124	0

Table 2. Backcross segregations: (A-translocations x gl14) x gl14.

Reciprocal translocation	Breakpoint	Gl gl Tt*	Gl gl tt	gl gl Tt	gl gl tt
wx 1-9c	1S.48; 9L.22	1	3	12	7
wx 1-9(8389)	1L.74; 9L.13	21	12	4	3
wx 2-9b	2S.18; 9L.22	37	17	2	22
2-9c	2S.49; 9S.33	26	17	1	7
		53	36	21	39
wx 3-9a	3L.11; 9L.16	2	3	0	0
wx 3-9b	3L.48; 9L.53	6	5	5	6
wx 3-9c	3L.09; 9L.12	6	9	5	14
3-9e	3L.02; 9L.29	17	9	6	13
wx 4-9b	4L.90; 9L.29	14	15	2	6
wx 4-9g	4S.27; 9L.27	3	2	3	2
wx 4-9(5657)	4L.33; 9S.25	15	14	17	13
wx 5-9a	5L.69; 9S.17	11	18	9	3
wx 5-9c	5S.07; 9L.10	3	3	3	2
wx 6-9a	6S.79; 9L.40	7	5	3	7
wx 6-9b	6S.10; 9S.37	17	8	15	10
wx 7-9a	7L.63; 9S.07	9	18	23	18
7-9c	7L.14; 9L.22	26	22	13	10
wx 7-9(4363)	7 cent; 9 cent.	11	8	25	18
wx 8-9(6673)	8L.35; 9S.31	8	11	20	16

*Tt = heterozygous translocation, semisterile; tt = homozygous for normal chromosomes, fertile.

Table 3. Backcross progenies: (gl14 x wx 2-9b) x gl14; (gl14 x 2-9c) x gl14; (gl14 x 2-9d) x gl14.

Translocation	Breakpoint	Gl gl Tt*	Gl gl tt	gl gl Tt	gl gl tt
wx 2-9b	2S.18; 9L.22	37	17	2	22
		10	5	5	6
		19	1	17	42
		48	12	4	25
		28	4	3	19
2-9c	2S.49; 9S.33	26	17	1	7
		27	13	11	11
		26	23	10	28
		26	19	13	25
		8	7	3	8
2-9d	2L.83; 9L.27	11	17	9	32
		18	14	19	36

*Tt = heterozygous translocation, semisterile; tt = homozygous for normal chromosomes, fertile.

The data indicated linkage between gl14 and T wx 2-9b and 2-9c, both with break points on short arm of chromosome 2; consequently, additional backcross progenies (Table 3. on previous page) were raised involving the named interchanges plus T2-9d (2L.83; 9L.27).

We found the classification of gl14 to be difficult and not always satisfactory because of the frequent doubtful expression of the character. The detection of linkage and the χ^2 partition of its components showed that Gl14-gl14 segregation constituted an important source of deviation (Tables 4 and 6). Notwithstanding, backcross progenies involving T wx 2-9b showed significant deviation from independent inheritance due to joint segregation (Table 4).

Table 4. Detection of linkage between gl14 and T wx 2-9b: analysis of χ^2 by orthogonal functions.*

	Gl14 gl14 Tt	Gl14 gl14 tt	gl14 gl14 Tt	gl14 gl14 tt	Total
Observed	142 (a_1)	39 (a_2)	31 (a_3)	114 (a_4)	326
Expected (with no linkage)	81.5	81.5	81.5	81.5	326

		χ^2	DF	Probability
Segregation for Gl14-gl14: $\chi^2_{gl} = \frac{(a_1 + a_2 - a_3 - a_4)^2}{n} = \frac{(36)^2}{326} = \frac{1296}{326}$		3.97	1	0.05- 0.02
Segregation for Tt: $\chi^2_T = \frac{(a_1 - a_2 + a_3 - a_4)^2}{n} = \frac{(20)^2}{326} = \frac{400}{326}$		1.22	1	0.30 - 0.20
Joint segregation: $\chi^2_L = \frac{(a_1 - a_2 - a_3 + a_4)^2}{n} = \frac{(186)^2}{326} = \frac{34596}{326}$		106.12	1	Extremely small
	Total	111.31	3	Extremely small

*Mather K., 1938. The measurement of linkage in heredity. London: Methuen & Co. Ltd.

The linkage relationship between gl14 and the wx 2-9b breakpoint indicated by the backcross data in Table 4 was confirmed by information obtained from F_2 families (Tables 5 and 6). Classification of F_2 kernels for waxy and normal endosperm corresponds with the separation of TT from tt; both genotypes are fully fertile, but TT can be identified by its association with waxy endosperm. In this way we were able to ascribe a genotype to each class of the F_2 (Table 5) and detect linkage (Table 6).

Table 5. Families of the F_2: wx 2-9b x gl14 selfed.

Classes		73-1013	73-1014	73-1015	Total
	TT*	17	14	0	
Gl14	Tt**	48	46	49	180 (a_1)
	tt***	11	9	1	21 (a_2)
	TT*	5	6	7	
gl14	Tt**	10	11	10	49 (a_3)
	tt***	27	12	22	61 (a_4)

*waxy endosperm and fully fertile

**normal endosperm and semisterile

***normal endosperm and fertile

Table 6. Detection of linkage from the F_2: gl14 x wx 2-9b selfed and X^2 analysis.

	a_1	a_2	a_3	a_4	Total
Observed	180	21	49	61	311
Expected (with no linkage)	174.935	58.315	58.315	19.435	311

$$X^2_{gl} = \frac{(a_1 + a_2 - 3a_3 - 3a_4)^2}{3n} \qquad X^2_{T} = \frac{(a_1 - 3a_2 + a_3 - 3a_4)^2}{3n}$$

$$X^2_{L} = \frac{(a_1 - 3a_2 - 3a_3 + 9a_4)^2}{9n}$$

	X^2	DF	Probability
Segregation for Gl14 gl14	17.83	1	0.01
Segregation for Tt	0.30	1	0.70 - 0.50
Joint segregation	96.23	1	Extremely small

Backcross and F_2 data and analyses indicate that gl14 is located on chromosome 2, probably on the short arm .

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Hereditable character conditioned by nuclear units and genes that do not respond to mendelian inheritance — One multiple dominant line, A C R Pr B Pl, derived from Doctor Randolph's pedigree 1877 (year 1933), was maintained by inbreeding in the Instituto Fitotécnico de Santa Catalina. This subline was considered in 1953 as inductive of mutations (Mazoti, Caryologia VI, Suppl. pp. 709-715, 1954) It gave origin, by crossing, to the dominant inhibitor of aleurone color C-I-7001 (referred to in MNL 40:62 as C^{IP}) which is an allele of gene C, at locus 26 of chromosome 9. The "multiple dominant" subline produced a new dominant inhibitor mutant of aleurone color located near the gene wx at an approximate distance of 26 units from C-I-7001. The presence of a dominant activator Ac* and a recessive li* is necessary for the gene, C*-IE-7002, to manifest its dominant inhibitor action of the aleurone color; for this reason I think that this gene has originated from the transposition of the structural genes of a possible operon C to a contiguous place of a foreign operator.

In Table 1, (published in MNL 41:88) we find that the data manifest the relation of 0.685 colorless aleurone, 0.315 aleurone color, for repulsion association of two inhibitor dominant genes of aleurone color, C-I-7001 and C*-IE-7002 at a distance of approximately 26% of crossing-over, having in backcross the recessive activator gene Li* and having present in all cases the dominant activator Ac*.

The location of gene C*-IE-7002 was done by the cross indicated in Table 2. From the analysis of Table 2 we can judge that in the majority of the classes the deviations are not significant and that the great deviations which manifest themselves in the less frequent classes (0.1% double crossingover) were a mistake in the classification into normal kernels and shrunken endosperm which would greatly modity the value of χ^2.

In progenies derived from the same progenitors, both having the same isogenic constitution and the same mendelian relation, 3/4 aleurone color and 1/4 colorless aleurone should be obtained in all progenies; however, here we obtained variable segregations in the ear according to the different areas (1/2 right or 1/2 left of the ear) and in other cases an excess of colorless aleurone kernels.

Table 1. C-I-7001 +/C C*-IE-7002, Li* li* X C +/C +, li* li*.

Progeny	Phenotype: Colorless aleurone	Phenotype: Colored aleurone	N-1	χ^2 relation 0.685:0.315	P
1	219	116	1	1.51	ns
2	98	47	1	0.05	ns
3	234	117	1	0.54	ns
4	276	123	1	0.08	ns
5	266	116	1	0.22	ns
6	128	54	1	0.28	ns
7	256	123	1	0.15	ns
8	213	100	1	0.02	ns
9	228	101	1	0.09	ns
10	189	117	1	6.43	<0.01
11	266	109	1	1.02	ns
Total χ^2			11	10.46	ns
Deviation	2.373	1.121	1	0.55	ns
Heterogeneity			10	9.91	ns

Table 2. C-I-7001 + + +/C sh wx C*-IE-7002, Li* li* X C sh wx, li* li*.

Phenotype	Frequency calculation	Observed	Calculated	P
Colorless + +	0.37750	190	212.5	ns
Colorless sh wx	0.20575	98	115.63	ns
Color sh wx	0.18875	104	106.07	ns
Colorless + wx	0.10525	91	59.15	<0.001
Color sh +	0.10500	62	59.01	ns
Color + +	0.01700	9	9.55	ns
Colorless sh +	0.00050	4	0.28	<0.001
Color + wx	0.00025	4	0.14	<0.001
		562	561.98	

Tables 3 and 4 show the variable segregation according to the different sectors or areas of the ear in progenies derived from the backcross +/C*-IE-7002, Li* li* X li* li*.

In Table 5 we can observe a great variability in the segregation of colored and colorless kernels.

Table 3. +/C*-IE-7002, Li* li* X +/+, li* li*: Area (1), seven rows of the middle left side of the ear; (2), seven rows of the middle right side.

Progeny		Aleurone Colored	Colorless	Total	Deviation from mendelian segregation χ^2	P
1	I(1)	120	98	218	46.2	<0.001
	D(2)	156	46	202	0.5	ns
		276	144	420	19.3	<0.001

Discrepancy between middle left side and middle right side of the ear $\chi^2 = 22.89$; P<0.001.

Table 4. +/C*-IE-7002, Li* li* X +/+, li* li*: Areas as in Table 3.

Progeny		Aleurone Colored	Colorless	Total	Deviation from mendelian segregation χ^2	P
	I(1)	128	90	218	30.8	<0.001
	D(2)	148	56	204	0.79	ns
		276	146	422		

Discrepancy between middle left side and middle right side of the ear $\chi^2 = 8.91$; P<0.01.

Table 5. Backcross +/C*-IE-7002, Li* li* X +/+, li* li*.

Progeny	Phenotype Colored aleurone	Colorless aleurone	Deviation from mendelian segregation χ^2	P
74-7950	192	62	0.04	ns
74-7122	227	150	43.96	<0.001
74-7122	171	155	88.38	<0.001
72-7952	217	117	17.92	<0.001
72-7000	262	178	56.48	<0.001
72-7000	289	137	11.64	<0.001
(a)			218.01	

These variable deviations are attributed to the gene or a chromosomic sector of the locus C*-IE-7002 that produces its active replies with a frequency not synchronized with the chromosomic division; for this reason it would stay free in the cellule, and its distribution during the cellular multiplication would be a matter of hazard, with the activator genes Ac* and Ii* necessary to manifest its activity. In M.N.L. (40:62-63, 1966; 41:87-91, 1967) the hypothesis based on replies of DNA was suggested in order to interpret this phenomenon; however, at that time we had neither located the gene C*-IE-7002 nor found genes Ac* and Ii*. For this reason the actual interpretation differs from the previous ones, for the gene C-I-7001 (C^{IP}) would not have had its origin in teosinte, but in the subline derived from Dr. Randolph's dominant multiple pedigree 1877 (1933).

The gene that would produce "replies" would not be the gene C-I-7001, but it could be the gene C*-IE-7002, linked to the preceding one. In order to explain the hypothesis based on replies of DNA it is not essential that the "bits" of DNA be autoduplicable; it is sufficient for it to be produced by a chromosomic sector which corresponds to the gene C*-IE-7002.

The hypothesis that those free units of DNA would explain the contiguous phenomena of apparent paramutation, mosaicism, no mendelian segregations and genetic instability is affirmed in this work.

I think that the locus C could be a "normal" operon (Jacob, F., Science 152: 1470-78, 1966) in which its structural genes are capable of producing an enzyme that would inhibit the aleurone color but are repressed by the normal regulator in an inducible system that does not have the "inducer." The recessive gene c would be the operon C with the regulator genes which are suppressed or absent. The gene C-I would be the operon C with the operator suppressed or absent. This hypothesis would satisfy the degree of dominance of the series of alleles of the C locus. From its analysis we could interpret that the gene C*-IE-7002 is a translocation of structural genes to a contiguous place of a foreign active operator; for this reason it would not act as the dominant gene C-I, which cannot be repressed since it lacks an operator. In this case the gene C*-IE-7002, which has an operator, would need the genes Ac* and Ii* for its regulation. This hypothesis would be true if the aleurone color manifested itself in the presence of a deficiency at the C locus. This could not be true according to McClintock (Cold Spring Harbor Symp. Quant. Biology XVI:13-44, 1951) but the hypothesis would be possible according to Coe (Genetics 47:779-783, 1962).

I think that it is possible that Dr. Randolph's line can be related to the one studied by McClintock (material which was never introduced in this Institute) and that the transposition phenomenon based on the breakage-fusion-bridge cycle may have given rise to many sublines with structural changes. In the light of the genetic regulation phenomena which are now known, such position effects could turn a character conditioned by only one gene of good expression and penetration into a fluctuating character, offering advantages in the evolution and selection of the organisms (Mazoti, 1945, Revista Argentina de Agronomía t.12, No. 3, p. 181). Perhaps with this system of transposition of chromosomic sectors the regulation of the reply of the genes or of a little sector of DNA can also be altered, causing a "self-infection" of unpredictable consequences for the organism that may change the concept about the basis of selection (Rendel, Proc. Nat. Acad. Sci. 64: 578-583, 1969) or perhaps may annul the normal inhibition of the cellular multiplication (Mazoti, 1963, Revista Facultad de Agronomía, 3a época, t. XXXIX, pp. 63-68).

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Information or seed for lines Ind.AH83 and CI617 — Iowa Stiff Stalk Synthetic was developed in 1933 and 1934 by recombining 16 lines selected by various corn breeders as being stiff stalked (Sprague, G. F., J. Amer. Soc. Agron. 38:108-117, 1946). The 16 lines recombined to form Iowa Stiff Stalk Synthetic were: Ia.I159, Ia.I224, Ia.Os420, Ia.WD456, Ind.461-3, Ill.12E, CI617, CI540, Ill. Hy, Oh3167B, Ind.AH83, Ind.Tr9-1-1-6, F1B1-7-1, A3G-3-1-3, CI187-2 and LE23. Iowa Stiff Stalk Synthetic has been used extensively in the Iowa Corn Breeding Program in basic breeding studies evaluating recurrent selection procedures for the improvement of breeding populations. It has been shown to be good for general combining ability in crosses with other varieties and also as a source population for lines having good general combining ability (e.g., B14, B37, B73 and N28).

Iowa Stiff Stalk Synthetic was developed about 40 years ago, and it is impossible to determine how many times the synthetic has been reproduced to maintain its viability. Consequently, I have been attempting to reassemble the original lines used in the formation of the synthetic variety. I am interested in resynthesizing Iowa Stiff Stalk Synthetic from the original lines to determine how its

mean performance and variability compare with the 'original' version of the variety we presently have in cold storage.

I have been able to recover 13 of the 16 lines from seed stocks at Iowa State University (Ia.I159, Ia.I224, Ia.Os420, Ia.WD456, Ill. Hy and CI187-2), Funk Brothers Seed Company (CI540, Ind.Tr9-1-1-6, A3G3-1-3 and Ill.12E), Pioneer Hi-Bred International, Inc. (LE23 and Ind.461-3) and Ohio Research and Development Center (Oh.3167B). In addition Mr. Baker of Pioneer Hi-Bred gave me seed of the parents (Fe and B2) of F1B1-1-7-1. I have not been successful in obtaining either seed for or information about Ind.AH83 and CI617-3-4. Dr. G. F. Sprague (personal communication) thought CI617-3-4 was a line developed by Dr. F. D. Richey from an Illinois variety; this is the extent of my information for Ind.AH83 and CI617-3-4.

If anyone can provide me with any information, suggestions or seed of Ind.AH83 and CI617-3-4, it would be appreciated. One or both of the lines may have been renumbered, or they may not have survived subsequent evaluation.

Arnel R. Hallauer

Differences in absorption of foliar-applied high molecular weight phosphate among corn inbreds with three different cytoplasms — The Texas male-sterile cytoplasm (cms-T) has been shown to absorb a foliar-applied high molecular weight phosphate (HMP) more than its isoline with normal cytoplasm. In a similar experiment with the S cytoplasmic male-sterile (cms-S) and the C cytoplasmic male-sterile (cms-C), it was found that cms-C is similar to cms-T in its absorption of the HMP; cms-S showed no difference in absorption when compared with its normal isoline. In none of the three comparisons of each of the cytoplasmic male-sterile lines with its normal isoline was there a difference in orthophosphate absorption, nor did any of the lines show a difference in the translocation of either source of phosphorus inside the plant ten days after application. These results show that the three known cytoplasms are not similar in the property of absorption of foliar-applied HMP. Further, differences were found among lines in the rates of absorption of foliar-applied phosphorus.

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Gametophytic factor (ga10) on chromosome 5 distal to A2 — Reciprocal crosses of an A2 Bt/a2 bt stock with a homozygous a2 bt tester revealed a deficiency of colored kernels when the heterozygous plants were used as males (Table 1) compared to the results of crosses when the same plants were used as females (Table 2).

Table 1. The cross a2 bt/a2 bt X A2 Bt/a2 bt (4 3408 and 3409).

Male	a2 bt (%)	A2 Bt (%)	a2 Bt (%)	A2 bt (%)	Total
4 3408-4	276 (79.1)	50 (14.3)	23 (6.6)	0 (0.0)	349
-6	308 (79.0)	68 (17.4)	12 (3.3)	1 (0.3)	390
-7	126 (77.8)	31 (19.1)	3 (1.9)	2 (1.2)	162
-8	185 (79.1)	30 (12.8)	17 (7.3)	2 (0.8)	234
-9	507 (85.6)	61 (10.3)	24 (4.1)	0 (0.0)	592
-11	121 (72.4)	37 (22.2)	9 (5.4)	0 (0.0)	167
4 3409-1	343 (87.5)	39 (9.9)	10 (2.6)	0 (0.0)	392
-7	287 (77.6)	62 (16.8)	19 (5.1)	2 (0.5)	370
Average	(79.7)	(15.4)	(4.5)	(0.4)	
Average % A2		(15.4)		(0.4)	

Table 2. The cross A2 Bt/a2 bt (4 3408) and 3409) X a2 bt/a2 bt.

Female	at bt (%)	A2 Bt (%)	a2 Bt (%)	A2 bt (%)	Total
4 3408-4	161 (46.1)	167 (47.9)	11 (3.1)	10 (2.9)	349
-6	156 (44.2)	172 (48.7)	15 (4.3)	10 (2.8)	353
-7	52 (46.4)	52 (46.4)	3 (2.7)	5 (4.5)	112
-8	61 (44.9)	66 (48.5)	5 (3.7)	4 (2.9)	136
-9	150 (51.2)	135 (46.0)	4 (1.4)	4 (1.4)	293
-11	42 (45.2)	47 (50.5)	3 (3.2)	1 (1.1)	93
4 3409-1	204 (45.5)	207 (46.2)	23 (5.1)	14 (3.1)	448
-7	142 (48.3)	132 (44.9)	10 (3.4)	10 (3.4)	294
Average	(46.4)	(47.4)	(3.4)	(2.8)	
Average % A2		(47.4)		(2.8)	
Average % a2-bt c/o			(6.13)		

In view of the deficiency of A2 Bt kernels, it is assumed that the ga allele is linked with A2 and Bt. It does not appear, however, to be the same as ga2 (chromosome 5, distal to bt), based on the following. If the order on chromosome 5 of the parental genotype had been A2-Bt-ga, crossing over between A2 and Bt would have resulted in an excess number of the colored-brittle class (A2-bt-Ga) when compared to the colorless-round class (a2-Bt-ga). This was not observed. The excess crossover class was colorless-round (Ga-a2-Bt) rather than colored-brittle (Table 1). This would place the ga locus distal to A2, and the order would be ga-A2-Bt.

Since data are unavailable on the competitive disadvantage of the recessive ga10 allele, ga10 can tentatively be located 31 crossover units (15.4 x 2) from A2.

Jaime Gonella and Peter A. Peterson

The presence of En among some maize lines from Mexico, Colombia, Bolivia and Venezuela — In tests of an assortment of maize lines from Bolivia, Colombia, Mexico and Venezuela, five lines have been shown to possess En (Table 1). In the same tests the presence of r (or other distinguishable allele) and the color suppressor C-I was noted. The 23 lines tested can be grouped into five divisions with respect to the r allele, En and C-I (Table 2).

Table 2. Summary of the grouping of three characters.

	Presence of r	Presence of C-I	Presence of En	No. lines
1	Yes	Yes	No	12
2	Yes	No	No	3
3	Yes	Yes	Yes	4
4	R-st	No	Yes*	1
5	Yes	No	Yes*(a)	3
				23

*Presence of En being confirmed.
(a) One of these already confirmed.

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Studies of a mutator locus on chromosome 10 — In the 1971 News Letter (45:81-87, 1971) I reported on an elevated spontaneous mutation rate that seemed to be under the control of a factor(s) at or near the y9 locus in chromosome 10. In genetic studies with y9 we had the opportunity to observe the self-progeny of numerous outcrosses involving heterozygous y9 plants as male parents; in these outcrosses there was an approximate 15-fold increase in mutation as compared to similar outcrosses not involving y9. The mutations occurred with equal frequency in outcross plants that received the y9 allele and those that did not; thus, they are not restricted to the chromosome carrying the y9 gene. A given outcross family frequently would have several plants that segregated for mutants which were quite similar in phenotype. If these represent identical mutants, it would suggest

Table 1. The distribution of En, r-allele and C-I among maize lines from various geographical areas.

Population	Origin	Race	Presence r	Presence C-I	Presence En**
Oaxaca 40	Tepalcingo, Morelos (Mexico)	Bolita	Yes	Yes	No
Chiapas 223	" " "	Zapalote Grande	Yes	Yes	No
Chiapas 225	" " "	Tepecintle	Yes	Yes	No
Chiapas 13	" " "	Oloton	Yes	Yes	No
Chiapas 171	" " "	Tehua	Yes	Yes	No
Nayarit 15	" " "	Reventador	Yes	Yes	Yes
Oaxaca 48	Tlaltizapan, Morelos (Mexico)	Zapalote Chico	Yes	Yes	No
Nayarit 72	" " "	Jala	Yes	Yes	No
Sonora 54	" " "	Harinoso de Ocho	Yes	No	No
Guanajuato 21	Leon, Guanajuato (Mexico)	Conico Norteno	Yes	Yes	No
Puebla 91	Chapingo (Mexico)	Arrocillo Amarillo	Yes	Yes	No
Mexico 72	" "	Conico	Yes	Yes	Yes
Mexico 55	" "	Palomero Toluqueno	Yes	Yes	Yes
Mexico 7	Batan (Mexico)	Cacahuacintle	Yes	Yes	Yes
Venezuela 341	Venezuela	Cariaco	Yes	No	No
Venezuela 870	"	Negrito	Yes	Yes	No
Santander Sur. 340	Colombia	Cacao	Yes	Yes	No
Choco 306	"	Chococeno	Yes	Yes	No
?	"	Chococeno	Yes	No	*
Bolivia 809	Bolivia	Pohoso	Yes	No	*
Bolivia 705	"	Cholito	Yes	No	No
Bolivia 707	"	Cholito	Yes	No	Yes
?	"	Cholito	R-st	No	*

* Presence of En being confirmed.
** Tests made with the standard En tester, a-m(r)/a-m-1 sh2.
? Population unknown.

that the mutator gene was acting in mitotic stages resulting in tassel sectors carrying a new mutation.

Three lines carrying y9 were observed in which limited tests seemed to indicate that there was not an elevated mutation rate. If these observations were confirmed, it would suggest either (1) that the mutator effect was controlled not by the y9 locus but by a separable factor or (2) that y9 is responsible for the mutator effect but can become inactive. The three lines tested consisted of one in which y9 had been crossed with the inbred M14 five times, one in which y9 had been crossed with the inbred W22 four times and one involving a cross to a bf2 stock. (In this report all lines tested were the result of crosses of heterozygous y9 plants as males to non-y9 lines; hence the tested family will consist of ½ heterozygous y9 plants and ½ +/+ plants). Plants of these lines (tested families) were grown, self-pollinated (to test for the presence of y9 and any new mutations) and outcrossed to a standard line (M14/W22). Only outcrosses from plants in which the selfed progeny did not segregate for new mutations were tested further. Fifty seeds from each outcross were planted, the resulting plants self-pollinated and the selfed ears seedling-tested for the presence of seedling mutations. The results of these tests are given in Table 1. For controls, selfs of outcrosses of M14, W22 and Standard (M14/W22) to Standard (M14/W22) were used. Since there was no obvious increase in mutation rate in these three y9 stocks, it would appear that y9 lines can lose the ability to induce mutation, either by recombination or by some inactivation of the mutator factor.

Table 1. Mutation rate in apparent non-mutator y9 lines.

Line	No. of outcrosses tested	Total plants for all outcrosses	No. of mutations	% mutation
M14/y9	17	755	4	0.5
W22/y9	14	685	1	0.1
bf2/y9	13	565	3	0.5
Control	20	880	2	0.2

The observations reported in the 1971 News Letter were made only incidentally to linkage studies that were being carried on at the time, and there was thus a possibility that some mutations might have been overlooked. In 1971 three lines that had shown increased mutation rates were tested again by the procedure outlined above for the non-mutator lines. The three lines tested derived from

crosses of y9 to purple aleurone (pl aleur), g and bf2 (not the same bf2 line listed above). The results of tests involving the outcrosses of plants heterozygous for y9 from the tested families are given in Table 2. Column 4 includes all mutations that occurred. When more than one ear of an outcross family segregated for a mutant of a given phenotype, it was assumed that these were derived from a single mutational event that gave rise to a tassel sector.

Table 2. Mutation rates in mutator y9 lines heterozygous for y9.

Line	No. of outcrosses tested	Total plants for all outcrosses	Total mutants	Total mutants %	Total different mutants	Total different mutants %
pl aleur/y9	7	280	34	12.1%	20	7.1%
g/y9	4	168	16	9.5%	6	3.6%
bf2/y9	3	119	18	15.1%	10	8.4%
Total mutator	14	567	68	12.0%	36	6.3%
Control	20	880	2	0.2%	2	0.2%

Such mutants were counted only once in determining the number of different mutants that had occurred (column 6). For example, in one outcross family one plant segregated for a yellow-green necrotic mutant, another segregated for a pale yellow mutant and two plants segregated for a yellow-green mutant. The total number of mutants observed was 4 (column 4), but there were only three different mutants (column 6). The assumption that mutants with similar phenotypes are derived from the same mutational event has not been proved, since for the most part such mutants have not been tested for allelism. However, one test in 1972 involving two albinos segregating in sibling ears of one outcross family did prove that they were allelic, so the assumption is not unreasonable. There is always the possibility of two mutants with similar phenotypes arising independently; since this undoubtedly occurs, the mutation rate based on total different mutants (column 6) is a minimal estimate. An increase in mutation rate is obvious in these lines; there is an 18- to 42- fold increase in mutation over the control lines with a 31.5-fold increase observed for the total mutator progeny.

In the tests reported in the 1971 News Letter only the outcrosses of plants that were heterozygous for y9 were considered since we were concerned only with following this gene. However, in 1971 outcrosses from sibling plants of the

tested families not carrying y9 were tested as well; the results of these tests are given in Table 3. It is obvious that the non-y9-bearing plants have a mutation rate of the same magnitude as that observed in the y9-bearing plants.

Table 3. Mutator rates from plants not carrying y9 (siblings of plants listed in Table 2).

Line	No. of outcrosses tested	Total plants for all outcrosses	Total mutants	Total mutants %	Total different mutants	Total different mutants %
pl aleur/y9	9	352	40	11.4%	16	4.5%
g/y9	3	131	14	10.7%	8	6.1%
bf2/y9	1	38	4	10.5%	4	10.5%
Total mutator	13	521	58	11.1%	28	5.4%
Control	20	880	2	0.2%	2	0.2%

Such results could be expected if the female parents (non-y9) of the tested families were homozygous for a mutator gene. When heterozygous y9 plants were crossed with such a line, all the plants (whether or not they received y9) would exhibit an increased mutation rate. This seems to be an unlikely explanation since three genetically unrelated lines were used as female parents in these crosses (i.e., g, bf2 and purple aleurone). Included in the 1971 report was the finding of mutability in a line in which the female parent carried T9-10b; in this case at least four different lines would have had to be homozygous for a mutator factor. The one thing these four tested lines had in common was that the male parent of each was heterozygous for y9, and it would seem that mutability is being transmitted in association with y9. Since only 13 plants not segregating for y9 were involved in these tests, since two of the 13 plants tested had no mutations and since we have shown that the mutable locus can be separate from y9, the 11 plants with an elevated mutation rate may represent crossovers in which the mutator gene has been transferred to the non-y9 chromosome in the heterozygous y9 parent of the tested families. Larger numbers of non-y9-bearing plants will have to be tested to determine if they consistently exhibit an increased mutation rate. If they do, it is possible that the y9-bearing chromosome is having an effect that is transmitted to the next generation through the non-y9 gamete. If such is the case, the effect may be either permanent or transitory. Further

tests will be necessary to distinguish between the two possibilities. If the mutator phenotype is the result of a cytoplasmic factor that is pollen transmissible, non-y9 mutator plants would be expected. Although male transmission of cytoplasmic factors has been demonstrated in other plants, it has not been established in corn.

If the mutability is associated with y9, the individual plants of the tested families should segregate for new mutations when self-pollinated. This would be expected since these families have been produced by outcrossing heterozygous y9 plants. Samples of the tested families were grown and self-pollinated and the resulting ears scored for the segregation of new mutants. The results are given in Table 4 along with the results of the mutation tests of the outcrosses of the tested families. It is obvious that the mutation rate within the tested families is of the same order of magnitude as that observed when these families are outcrossed. These results demonstrate that the elevated mutation rate has remained constant for at least two generations.

Table 4. Mutation rates found in the families of plants tested for the transmission of mutations (compared with the mutation rate found in the outcrosses of these families).

	Results from selfs of tested families			Results from selfs of outcrosses of tested families (Tables 2 & 3 combined).		
Tested progeny	No. of plants tested	Total different mutants	Total mutants %	No. of plants tested	Total different mutants	Total different mutants %
pl aleur/y9	56	3	5.4%	271	18	6.6%
pl aleur/y9	68	3	4.4%	361	18	5.0%
g/y9	109	7	6.4%	299	14	4.7%
bf2/y9	73	5	6.8%	157	14	8.9%
Total	306	18	5.9%	1088	64	5.9%

If a mutator factor is closely associated with y9, homozygous y9 plants might be homozygous for the factor; such homozygosity might result in a higher mutation rate. Four homozygous y9 plants were self-pollinated and outcrossed to standard; the resulting outcross plants were self-pollinated and their ears scored for the segregation of new mutants. The results are presented in Table 5. The outcross

Table 5. Mutations in outcrosses of homozygous y9 plants.

Family	Total plants	Total mutants	Total mutants %	Total different mutants	Total different mutants %	Total different mutants from outcrosses of ear parent providing the homozygous y9 %
7501-02	85	0	0	0	0	0
7503-04	85	3	3.5%	3	3.5%	8.9%
7505-06	58	10	17.2%	4	6.9%	7.1%
7507-08	89	13	14.6%	7	7.9%	2.3%
Total	317	26	8.2%	14	4.4%	6.9%

of one plant produced no mutations, while the outcrosses of the rest had three or more different mutants. There is no consistent evidence that homozygous y9 plants have a higher mutation rate than heterozygous y9 plants. If the mutator factor is loosely linked to y9, it may be that three of these homozygotes have lost the factor by crossing over in one of the two gametes and the fourth from both. In the homozygous y9 families, most plants were weak and were not usable for selfing and outcrossing; only the stronger plants were used in these tests, and these might have lost, through crossing over, one or more of the mutator factors. Homozygosity for the mutator factor might be responsible for the weakness exhibited by many homozygous y9 plants.

Donald S. Robertson

A new compound A-B translocation, TB-5S,1L(8041) — Several compound A-B translocations have been produced by crossing over between the original set of A-B translocations produced by Roman (Roman and Ullstrup, Agron. J. 43:450-454, 1951) and selected reciprocal A translocations. Rakha and Robertson (Genetics 65:223-240, 1970) describe eight such translocations. These translocations have a portion of two A chromosomes attached to the B centromere; proximally there is a piece of the A chromosome carried by the original A-B translocation and distally a segment of one of the A chromosomes which was involved in the reciprocal A translocation.

In 1973, F_1's between TB-1a (1L.2) and T1-5(8041) (1L.80,5S.10) were crossed as males to an a2 tester. Many of the ears on the a2 plants segregated for small yellow seeds, which ranged in size from very small, almost empty, pericarps to seeds about one-eighth the size of the plump purple seeds on the ear. It was assumed that these seeds were the result of fertilizations by gametes from a

pollen grain carrying a new compound A-B translocation which consisted of a proximal segment of the long arm of chromosome one (from L.2 to L.80) with the distal 90% of the short arm of chromosome 5. The small yellow seeds were assumed to have endosperms that were deficient (hypoploid) and embryos that were hyperploid for this new translocation.

In 1974 the largest yellow seeds were planted. From the 110 seeds planted, only 55 mature plants were obtained. The seeds were sown directly into the field, and a better yield would undoubtedly have been realized if the seeds had been germinated in petri dishes and later transplanted to the field. The plants that were obtained were reasonably vigorous, and most produced ears when self-pollinated. Pollen examination revealed sterility ranging from 15% to 50%; the majority of the plants had 15-25% abortive pollen grains. All the self-pollinated ears segregated for purple seeds, as is expected if the embryos of the small seeds were hyperploid for the new translocation ($5/B^5$ B^5, a2/A2 A2). To confirm hyperploidy these plants were also crossed to a balanced lethal stock heterozygous for vp2 and ps, which are known to be proximal to a2 in the short arm of chromosome 5. All of these outcrosses segregated for very small ps and/or vp2 seeds which were non-viviparous. Also segregating on these ears were large purple viviparous seeds. The latter are expected when the deficient sperm fertilizes the egg nucleus of a vp2 or ps embryo sac and the hyperploid sperm fertilizes the polar nuclei. The presence of purple seeds on the selfed ears, in addition to the small seeds with vp2 and ps endosperms and the large purple viviparous kernels in the outcrosses, confirmed that a new compound translocation had been produced. These tests also place the three genes a2, vp2 and ps in the distal 90% of the short arm of chromosome 5.

Five of the same plants that were crossed to the vp2/ps stock were crossed to a homozygous bz2 line; in all these crosses bronze seeds were observed to be segregating. None of the ears from the self-pollinated A-B plants segregated for bronze seeds. These results indicate that bz2 is in that segment of chromosome 1 that remains in the translocation (1L.2 to 8L.80). The bronze seeds in these crosses were not as small as those observed when this new translocation was crossed to the a2 tester or to the vp2/ps stock. The bronze seeds ranged in size from about a fourth as large to fully as large as the purple seeds on the same ears.

Small seeds are characteristic of kernels with hypoploid endosperms resulting from crosses with TB-1a. However, the seeds are not nearly as small as those

observed when the new compound translocation is used in crosses with the a2 tester and the vp2/ps stock. The occurrence of small seeds in the latter crosses would suggest that both the long arm of chromosome one and the short arm of chromosome 5 have genes that affect seed size, and the small seeds observed are the result of the cumulative effect of these seed-size genes. Since the seeds with hypoploid endosperms from the crosses with the bz2 stock are consistently larger, there is a possibility that it carries seed-size genes in this region that are more active in the hemizygous condition than allelic genes in the a2 and vp2/ps lines. Alternatively, the bz2 stock may have modifier genes elsewhere in the genome that partially suppress the action of the hemizygous seed-size genes in the hypoploid segment.

I now have seed of this translocation available for anyone that might desire some.

Donald S. Robertson

An A-B translocation with segments from three different A chromosomes — As the preceding article indicates, it is possible to produce compound A-B translocations in which segments from two A chromosomes are attached to the B centromere. The B^A element of such compound translocations undergoes nondisjunction in the division of the generative nucleus of the pollen grain. Will nondisjunction continue to be observed if additional chromosomal material is added to the B^A chromosome?

To test this, the A-B translocation TB-2L,1S(4464) and the reciprocal translocation T2-4f were used to synthesize an A-B translocation consisting of segments from chromosomes one, two and four. TB-2L,1S(4464) was generated by crossing over between TB-1b (1S.05) and TB-2(4464) (1S.53,2L.28) and carries 48% of the short arm of chromosome 1 (1S.05-1S.53) and 72% of the long arm of chromosome two. The T2-4f translocation has breakpoints at 2L.75 and 4L.12. F_1's between TB-2L,1S (4464) and T2-4f were used to pollinate a c2 tester stock. With the proper chromosome pairing, the right crossing over (in the region between 2L.28 and 2L.75) and the right chromosomal segregation (1^B,$B^{1,2,4}$, 2^1, 4^2), a balanced microspore will be produced that carries the new tripartite A-B translocation. If this new translocation undergoes nondisjunction in the division of the generative nucleus, non-purple (yellow) seeds should be observed in the crosses with the c2 tester; these seeds would be expected to have endosperms hypoploid and embryos that were hyperploid for the new translocation. A homozygous c2 contaminant seed would be confused with one carrying the translocation. I have frequently observed

mottled seeds in crosses with c2; if the mottling was extremely weak, such seed might be mistakenly classified as a seed with a hypoploid endosperm.

Thirty putative A-B translocation seeds were planted, and twenty-three of these produced mature plants. Many of the plants were medium height, and some of these had short, pointed leaves. Eight plants were tall. All plants were examined for pollen sterility, self-pollinated and as many as possible crossed to gl3. Four of the tall plants had normal pollen and segregated for purple seeds when self-pollinated; since plants with the new compound A-B translocation would be expected to show pollen sterility, these were not tested on gl3. Of the remaining four tall plants, two were semi-sterile and two showed about 75% sterility. The crosses of these with gl3 did not segregate for the mutant. Of the eight tall plants only two did not segregate for purple seeds and were probably c2 contaminants. The yellow seeds from which the remaining six plants came were probably either the result of heterofertilization or of weak purple pigment synthesis in a C2 c2 c2 genotype. Five medium height plants that were crossed as males to gl3 segregated for glossy seedlings in a frequency expected for plants carrying an A-B translocation. Three of these five plants were semi-sterile, and two had about 75% sterility. The selfed ears of four segregated for purple seeds, while the fifth plant did not produce an ear.

On the basis of plant phenotype (medium height), pollen sterility, segregation of purple seeds on the selfed ears and segregation of gl3 in the outcrosses, it would seem reasonable to assume that these five plants carry an A-B translocation in which three segments of nonhomologous A chromosomes have been transferred to the B centromere. Attached to the B centromere are 48% of the short arm of chromosome 1 (S.05-S.53), 47% of the long arm of chromosome 2 (L.28-L.75) and 82% of the long arm of chromosome 4. Using the chromosomal unit length values given in the "Mutants of Maize," there would be attached to this centromere a segment of chromosome equal to a unit length of 192. This is approximately the length of chromosome two (196). This long segment of A chromosomal material attached to the B centromere does not seem to interfere with nondisjunction, as evidenced by the yellow seeds in the testcross on the c2 tester and by the presence of gl3 seedlings in the outcrosses of putative A-B translocation plants.

Seeds of this translocation are available.

Donald S. Robertson

Tester stocks for A-B translocations — To use A-B translocations (TB's) efficiently for locating genes, it is necessary to know that crosses have been made with plants carrying the translocation. One sure way to do this is to use a homozygous translocation line. I am not aware, however, of many homozygous A-B translocation stocks; most lines have been propagated by outcrossing. It is best to use the TB parents as females, thereby producing heterozygous TB plants of A A^B B^A constitution. If the TB plants are used as males, most of the heterozygotes will be hyperploid (i.e., A A^B B^A B^A). The euploid heterozygotes have slightly higher pollen sterility than the hyperploid and are thus easier to classify. The compound TB's are exceptions to the general use of female propagation; it is better to propagate these as males. Because the pairing relationships in the hyperploid plants are more likely to be AA^B and B^AB^A, there is less likelihood of a crossover occurring that would disrupt the compound TB than in euploid heterozygotes where the B^A element is more likely to pair with the homologous A chromosomes.

Pollen sterility is one way of picking out plants carrying TB's, but it is not a foolproof method since sterility is frequently low and will overlap the range observed in normal siblings. For euploid heterozygotes 15-25% defective pollen can be expected, while hyperploid heterozygotes will exhibit 10-20%. Hyperploid compound TB's have pollen sterility that ranges from 15% to nearly 50%, although the most commonly observed value is about 25%. Because these stocks carry a reciprocal A translocation some plants with high sterility (e.g., up to 50%) may not carry the TB. Therefore, all compound TB's must be confirmed by crossing to a marker gene (see below). If the TB parent (simple or compound) is crossed as a male, some deficient plants will be produced which show approximately 50% sterility; these are of no use in locating genes or in propagating the TB.

A more reliable way to pick plants which are known to carry a given TB is to use endosperm marker genes. If the TB is propagated in the absence of the marker gene, subsequent crosses to the marked stock will generate seeds segregating for the marker. Such seeds will have a deficient (hypoploid) endosperm and a hyperploid embryo and thus carry the desired TB. Table 1 lists the TB's I have worked with and the marker stocks that can be used to generate known heterozygotes. This list is made up of those TB's originally produced by Roman (Agron. J. 43:450-454, 1951), some of those more recently developed by Beckett (MGNL 45:144-146, 1971) and compound TB's developed by Rakha and Robertson (Genetics 65:223-240, 1970).

Table 1. Suggested marker genes for producing known TB heterozygotes.

TB	Source	Chromosome arm(s)	Endosperm tester gene	Hypoploid endosperm phenotype	Comments
1a	Roman	1L	lw	Pale yellow &/or white	Crosses will segregate large and small seeds. Small seeds will have hyperploid embryos.
1b	Roman	1S	vp5	Pale yellow &/or white	Crosses will segregate large and small seeds. Small seeds will have hyperploid embryos.
1c	Beckett	1L	lw	Pale yellow &/or white	
2S,3L (6270)	Rakha & Robertson	2S & 3L	al	Pale yellow &/or white	Compound TB
2L,1Sc	Rakha & Robertson	2L & 1S	w3	Pale yellow &/or white	Compound TB
2L,1S (4464)	Rakha & Robertson	2L & 1S	w3	Pale yellow &/or white	Compound TB. I have a homozygous stock of this translocation.
2L,3L (7285)	Rakha & Robertson	2L & 3L	w3	Pale yellow &/or white	Compound TB
3a	Roman	3L	a or sh2	Non-purple or Shrunken	
3b	Beckett	3S	cl	Pale yellow &/or white	
4a	Roman	4S	su	Sugary	
4L,9S (6222)	Rakha & Robertson	4L & 9S	c2	Non-purple	Compound TB
4L,9S (6504)	Rakha & Robertson	4L & 9S	c2	Non-purple	Compound TB
4L,1L (4692)	Rakha & Robertson	4L & 1L	c2	Non-purple	Compound TB

Table 1. (continued)

TB	Source	Chromosome arm(s)	Endosperm tester gene	Hypoploid endosperm phenotype	Comments
4L,7L (4698)	Rakha & Robertson	4L & 7L	c2	Non-purple	Compound TB
5S,1L (8041)	Robertson	5S & 1L	a	Non-purple	Compound TB
5a	Beckett	5L	lw2 or pr	Pale yellow &/or white; red seeds	
6b	Beckett	6L	none		Crosses with w14 (w_{8657}) can be used to confirm the presence of the TB but they cannot be used to select TB plants. Use pollen sterility.
7b	Roman	7L	o5	Opaque-shrunken	
8a	Roman	8L	none		Crosses with v21 can be used to confirm the presence of the TB but cannot be used to select TB plants. Use pollen sterility
9a	Roman	9L	none		Crosses with Bf can be used to confirm the presence of the TB but cannot be used to select TB plants. Use pollen sterility.
9b	Roman	9S	c or sh	Non-purple or Shrunken	
9c	Beckett	9L	none		Crosses with Bf can be used to confirm the presence of the TB but cannot be used to select TB plants. Use pollen sterility.

Table 1. (continued)

TB	Source	Chromosome arm(s)	Endosperm tester gene	Hypoploid endosperm phenotype	Comments
10a	Roman	10L	r	Non-purple (purple scutellum, see comments)	I have a homozygous TB stock, homozygous for purple aleurone and the R-scm2 allele that colors the scutellum.
10b	Beckett	10L	r	Non-purple	
10c	Beckett	10S	y9	Pale yellow	

Tester genes lw, vp5, w3, lw2 and cl are all white-albino mutants and cannot be made homozygous. Thus, segregating populations must be used, and it is best to cross each putative TB plant with several plants suspected of carrying the marker gene. The al, y9 and o5 marker genes produce weak homozygotes, and it would be more efficient if a tester line were established by crossing homozygotes of these markers (as males) to a standard line to develop stocks of known heterozygotes.

Donald S. Robertson

Additional studies on the differential recovery of crossover products from male and female in plants hypoploid for TB-10a — In 1970, I reported that more crossover products were recovered through the pollen than through the eggs of TB-10a hypoploid (deficient) plants (MGCNL 44:84-91, 1970). In these tests plants hypoploid for TB-10a and heterozygous for y9 were reciprocally crossed with homozygous y9 plants. The hypoploid plants carried y9 on the normal chromosome and the + allele on the deficient 10^{B} chromosome; most of the functional gametes from such plants will be expected to carry y9, but a few + gametes will be produced as a result of crossing over between the breakpoint and y9. The frequency of + (yellow endosperm) seeds in crosses involving hypoploid plants will therefore be a measure of the crossing over.

The crosses in the 1970 report (1969 crosses) were not exact reciprocals. In 1970 and 1971 paired reciprocal crosses were made so that in each set of crosses the two plants involved functioned as both male and female parents with respect to each other. The results of these tests (Table 1) are in agreement with those reported in 1970.

Table 1. Transmission of crossover products through pollen and ovules when exact reciprocal crosses were made between hypoploid $10/10^B$ (y9/+) plants and homozygous y9 plants.

Year	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
1970	679	9.7	1018	21.0	11.3	37.05**
1971	564	13.7	692	20.8	7.1	10.5**
Total	1243	11.5	1710	20.9	9.4	44.5**

**Significant at the 1% level of probability.

When the crossover values of 1969, 1970 and 1971 are examined they are found to vary from year to year. This variation is systematically compared in Table 2. The only significant between-year variation occurred for the female crosses. In no cases were the differences in male crosses significant. From this limited test, it would appear that female transmission of crossovers is more sensitive to environmental factors than is the male transmission.

Table 2. Comparisons of the female crosses in 1969, 1970 and 1971 of hypoploid 10^B plants and of the male crosses for the same years.

Years compared	Total 1st year	% C.O. 1st year	Total 2nd year	% C.O. 2nd year	% Difference	Chi square
♀ Crosses						
1969 vs. 1970	1168	15.2	679	9.7	5.5	10.6**
1969 vs. 1971	1168	15.2	564	13.7	1.5	$0.6^{N.S.}$
1970 vs. 1971	679	9.7	564	13.7	4.0	4.3*
♂ Crosses						
1969 vs. 1970	2779	22.8	1018	21.0	1.8	$1.2^{N.S.}$
1969 vs. 1971	2779	22.8	692	20.8	2.0	$1.1^{N.S.}$
1970 vs. 1971	1018	21.0	692	20.8	0.2	$0.002^{N.S.}$

*Significant at the 5% level of probability.
**Significant at the 1% level of proability.
N.S. Not significant.

The different transmission rates of crossovers observed in male and female plants in these studies may be the result of some intrinsic factor in the normal chromosome 10 and have nothing to do with the hypoploid TB-10a condition. Previous studies on crossing over in normal chromosome 10 by other workers have

not revealed such differences. New crossover studies were made involving the y9-bf2 and bf2-g regions, which include the region being tested in the hypoploid crosses; the results of these crosses are given in Tables 3, 4, 5, 6 and 7. In none of the tests was there observed a significant difference in the male and female transmission of crossovers. For the whole region y9-g (Table 5) there is no indication of preferential transmission. There is apparently no differential transmission of crossovers that occur in the right hand portion of this segment of chromosome 10 (i.e., bf2-g, Tables 4, 5 and 7); however, the region closest to the breakpoint (i.e., y9-bf2, Tables 3, 5 and 6) exhibits a consistently higher transmission rate for male crossovers than for female crossovers. Although the difference is not significant (Table 6, Chi square 3.1), it comes very close to being significant at the 5% level (Chi square 3.8). If comparisons are made of the crossover and chi square values for this region in Tables 3, 5 and 6, it will be noted that male-transmitted crossovers are always higher; and as the numbers increase, so do the Chi square values. If this trend truly characterizes what is taking place in this region, one would expect a significant difference to be found if larger numbers of plants were tested.

Table 3. Male and female transmission of crossovers in the y9-bf2 region (two point tests) involving exact reciprocal crosses.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
183	9.8%	195	14.4%	4.6	1.4 N.S.

N.S. Not significant.

Table 4. Male and female transmission of crossovers in bf2-g region (two point tests) involving exact reciprocal crosses.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
357	16.5%	296	16.9%	0.4	.004 N.S.

Table 5. Male and female transmission of crossovers in a three-point test with y9, bf2 and g loci involving exact reciprocal crosses.

Region	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
y9-bf2	322	2.8%	259	4.4%	1.6	0.8 N.S.
bf2-g	322	18.0%	295	18.3%	0.3	0.0 N.S.

Table 5. (continued)

Region	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
y9-g*	322	20.8%	295	22.7%	1.9	0.2 N.S.

*Total crossing over in the y9-g region (double crossovers have been included twice).

N.S. Not significant.

Table 6. Total male and female transmission in y9-bf2 region from two-point tests (Table 3) and three-point tests (Table 5).

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
505	5.3%	490	8.3%	3.0	3.1 N.S.

N.S. Not significant.

Table 7. Total male and female transmission of crossovers in the bf2-g region from two-point tests (Table 4) and three-point tests (Table 5).

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
679	17.2%	591	17.6%	0.4	.01 N.S.

N.S. Not significant.

The y9-bf2 region is located proximally to the TB-10a breakpoint and involves the region tested in the original hypoploid tests. There is a possibility that the preferential transmission of male crossovers in hypoploid plants may be characteristic of any crossing over in this region (y9-bf2 = "critical region") and may not be due to anything unique about the hypoploid condition. If the increased transmission of crossovers through the male in hypoploid plants carrying y9 is due to activity in the "critical region," then crossing over between bf2 and the breakpoint would lie outside the "critical region" and there would be no difference in male and female transmission of crossovers in this region. The results of such a test are given in Table 8. There is observed a significantly higher transmission of crossovers through the male, which would be expected if the "critical region"

extended beyond bf2 to the vicinity of the breakpoint; if this were the case, two-thirds of the bf2-g region would be included in the "critical region." However, there is no evidence for a higher transmission of crossovers through the male

Table 8. Male and female transmission of crossovers between bf2 and the TB-10a breakpoint in crosses involving hypoploid plants.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
1612	9.1%	4093	12.3%	3.2	11.1**

**Significant at the 1% level.

when this region is tested in the absence of any rearrangements (Tables 4, 5 and 7); if there is a "critical region" it does not seem to include the bf2 breakpoint region. In that case the higher male transmission of crossovers between bf2 and the breakpoint may be due to the hypoploid condition of the tested plants.

One additional test of crossover transmission in the TB-10a hypoploid was made with oy, which is about 12 crossover-units to the left of y9. The results of these tests are found in Table 9. Again a significantly higher transmission of crossovers through the male is observed. Crossing over in the oy-y9 region in normal chromosomes has not been tested for male and female transmission, and until such tests have been made it is perhaps too early to speculate on the significance of the data in Table 9.

Table 9. Male and female transmission of crossovers between oy and the TB-10a breakpoint in crosses involving hypoploid plants.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
481	22.9%	664	32.5%	9.6	12.3**

**Significant at the 1% level.

Conclusion:

In tests of hypoploid plants carrying y9, bf2 or oy, male transmission of crossovers is consistently higher than female transmission; these results suggest that the hypoploid condition might be responsible for the differential transmission ("hypoploid effect"). However, tests of male and female transmission of crossovers by plants with normal chromosomes suggest that there might be a

"critical region" between y9 and bf2 that could account for some of the observed differential transmission. Whether or not this "critical region" really exists will require further tests. If it does exist, it will be necessary to determine how much of the "hypoploid effect" is due to events within this region and how much is due to hypoploidy per se.

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A case of genetic instability at the opaque-2 locus — In a 1971 field trial all the ears of the hybrid (FR 123 o2 x R 103 o2) x A 619 o2 segregated variegated kernels. This phenotypic variegation appeared particularly clear on the kernel surface, where sharply bordered horny and opaque patches were present side by side. In the last two years we have accumulated genetic data suggesting the existence in our material of a mutable system responsible for the somatic variegations observed. The attributes of the system, even though not carefully quantified, may be synthesized from the following data from two selected progenies (Tables 1 and 2).

1. Mutability is either autonomous or under the control of an independent factor. With some exceptions the segregation ratios of Table 1 are consistent with the 3:1 ratio expected in the case of autonomous control. The ratios of Table 2, on the other hand, imply the existence of a two-factor interaction.
2. A particular variegation pattern is not stable. Kernels of c or m phenotype (see Table 1) frequently produce N or c variegated kernels, respectively. For example, the 3472-1 plant was clearly heterozygous, bearing a mutable and a non-mutable o2 allele. This plant, when outcrossed to standard o2, gave 345 opaque and 347 variegated seeds (232 of c or m type and 115 N type). The N phenotype has been maintained in the subsequent generation (class 3 of Table 1).
3. When heterozygous with an unstable o2 allele, o2-R may segregate at unexpectedly low frequencies. This is the case with ears 5, 7, 13, 23 and 27 in Table 1. Abnormal segregation ratios have also been observed in progenies with independent control of mutability (i.e., ears 4, 17 and 18 selfed and 5/o2-R and 16/o2-R in Table 2).

Table 1. Segregation ratios of a progeny with autonomous control of mutability. In 1973 a plant (3472-1) bearing a mutable o2 allele was outcrossed to a plant homozygous for a standard o2 allele (hereafter designated as o2-R). From this cross originated 345 opaque seeds (non variegated; class 1), 232 variegated seeds (class 2), and 115 subnormal seeds (class 3). In 1974 the three classes, after self-fertilization, gave the indicated segregation ratios.

Class	Selfed ear number	Number of variegated kernels	Type of variegation*	Number of opaque kernels	χ^2 (3:1)
1	1-12		-	all	-
2	1	294	c + m + f	94	0.12
	2	232	m + f	70	0.53
	3	140	c + m	48	0.03
	4	134	c + m	51	0.65
	5	159	c + m	60	0.67
	6	235	c + m	92	1.71
	7	386	c + m	105	3.42
	8	501	c + m + f	110	15.95
	9	213	c + m	67	0.17
	11	210	c + m	83	1.73
	12	149	c + m	53	0.16
	14	119	c + m	37	0.14
	16	199	c + m	57	1.02
	17	72	c + m	28	0.48
	18	108	c + m	43	0.97
	19	184	c + m + f	65	0.16
	20	98	c + m	27	0.77
	21	134	c + m	48	0.18
	22	210	c + m + f	70	0.00
	24	169	c + m + f	47	1.21
	25	185	c + m	55	0.55
	26	199	c + m	50	3.21
	13	240	N + c	4	71.02
	23	106	N + c	7	31.31
	27	224	c + m	25	29.72
3	1	211	c + m	96	2.31
	2	108	N	37	0.02
	3	100	N	42	1.59
	4	105	N + c	43	1.30
	6	99	N	29	0.37
	8	96	N + c	14	8.84
	9	95	N	31	0.01
	10	167	N	52	0.18
	11	102	N	26	1.50
	5	180	N + f	18	26.63
	7	263	N + f	15	56.98

*c Variegated phenotype with normal tissue prevailing.
m Variegated phenotype with 50% normal tissue.
f Variegated phenotype with opaque tissue prevailing.
N Subnormal phenotype: may appear either as a true normal or as a normal with very few spots of opaque tissue.

Table 2. Segregation ratios of a progeny with independent control of the o2 mutability. In 1973 the 3466-1 plant was pollinated with o2-R pollen. All the seeds obtained were variegated (c or f type). The plants from the f seeds, when self-fertilized or outcrossed, gave ears showing the following segregation ratios.

Ear number	Number of variegated kernels	Number of opaque kernels	χ^2 (9:7)	χ^2 (1:3)	χ^2 (1:1)
1 self	259	187	0.60		
2 self	211	136	2.93		
3 self	383	236	7.95		
4 self	418	221	21.80		
6 self	196	142	2.93		
7 self	156	120	0.01		
17 self	312	176	11.60		
18 self	350	205	10.46		
5/o2-R	132	249		18.90	
8/o2-R	127	337		1.53	
9/o2-R	64	232		1.80	
11/o2-R	62	128		5.90	
12/o2-R	64	160		1.52	
19/o2-R	59	179		0.00	
16/o2-R	211	207			0.04

4. The system of mutability acting at the o2 locus seems independent from the previously described Ac Ds and Spm systems. An Ac activity test has been carried out by crossing a C-I Ds/C Ds female with a male bearing a mutable o2 allele; no B-F-B cycles appeared in the F_1 kernels. The F_2 progeny segregated normal and variegated kernels, but B-F-B cycles were still absent. An Spm activity test was achieved by crossing a female a-m1/a-m1 wx-m8/wx-m8 with an o2 mutable male. The F_1 kernels were phenotypically a-m1 without the Spm-induced variegations, and the F_2 ears segregated opaque-2 variegated kernels without Spm activity at the A or Wx locus.

The o2 mutable system here described promises exciting developments. An analysis of a mutable gene system at a biochemical level is now feasible; moreover, the foreseen recovery of a wide spectrum of new o2 alleles will be useful in breeding maize for protein quality.

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The role of the male parent in the occurrence of matroclinous haploids — There exist some contradicting considerations concerning the genetic role of the male parent in the occurrence of matroclinous haploids in maize (MHM). Some students consider the effect of the pollen parent on the MHM frequency to be of a physiological nature (i.e., mostly the result of disturbances of the normal pollination and fertilization processes caused by different times of flowering of the ear and pollen parents and by delayed pollination); when studying this phenomenon it is therefore necessary to exclude this factor.

Two marker systems were utilized as male parents in this experiment: A B Pl C R-g (purple aleurone, purple seedling roots) and A C R-nj-cudu (red aleurone, purple embryo); line WF9 was used as the female parent.

In order to eliminate the possible influence of delayed pollination on the frequency of haploids produced, female inflorescences of the same age were pollinated on one and the same day, using both testers; some ears of the female parent were pollinated with a mixture (1:1) of pollen from both male parents. Such an experiment was possible because the alleles R-g and R-nj-cudu produce different kinds of aleurone coloring, and the seeds obtained from crosses with one marked parent are readily distinguishable from those obtained from crosses with the other.

According to the data in Table 1, we may conclude that the pollen parent influences the process of haploid formation even when the effect of delayed pollination is excluded (not only by means of pollinating the female flowers of

Table 1. Frequency of matroclinous haploids from WF9 depending on marked pollen parents.

A B Pl C R-g		A C R-nj-cudu		
Number of seeds	Number of haploids	Number of seeds	Number of haploids	χ^2
	Separate pollen sources			
18,300	178 (0.97%)	19,960	59 (0.30%)	63.4***
	Pollen mixture (1:1)			
14,740	102 (0.70%)	16,910	46 (0.27%)	38.9***

the same age at the same time, but also by means of pollinating with a pollen mixture, which permits excluding the influence of separate female plants on the MHM frequency).

Thus, we are inclined to agree with those students who consider the genetical features of the male parent to influence the MHM frequency. We agree also on the necessity of screening for this feature when creating the marker strains.

M. V. Tchumak

A mutation interfering with the ear formation process — Among 32 J_1 progenies of the line Sg25 TRf in 1972 we have found a family clearly different from all others in having late silking and unusual ear shapes. During the harvest we found that all plants of this family produced mutant ears provisionally classified into three types. (Figure 1). (Ed. note: the expressions can be seen very well in two prints provided by the author; they will be loaned to interested cooperators on request).

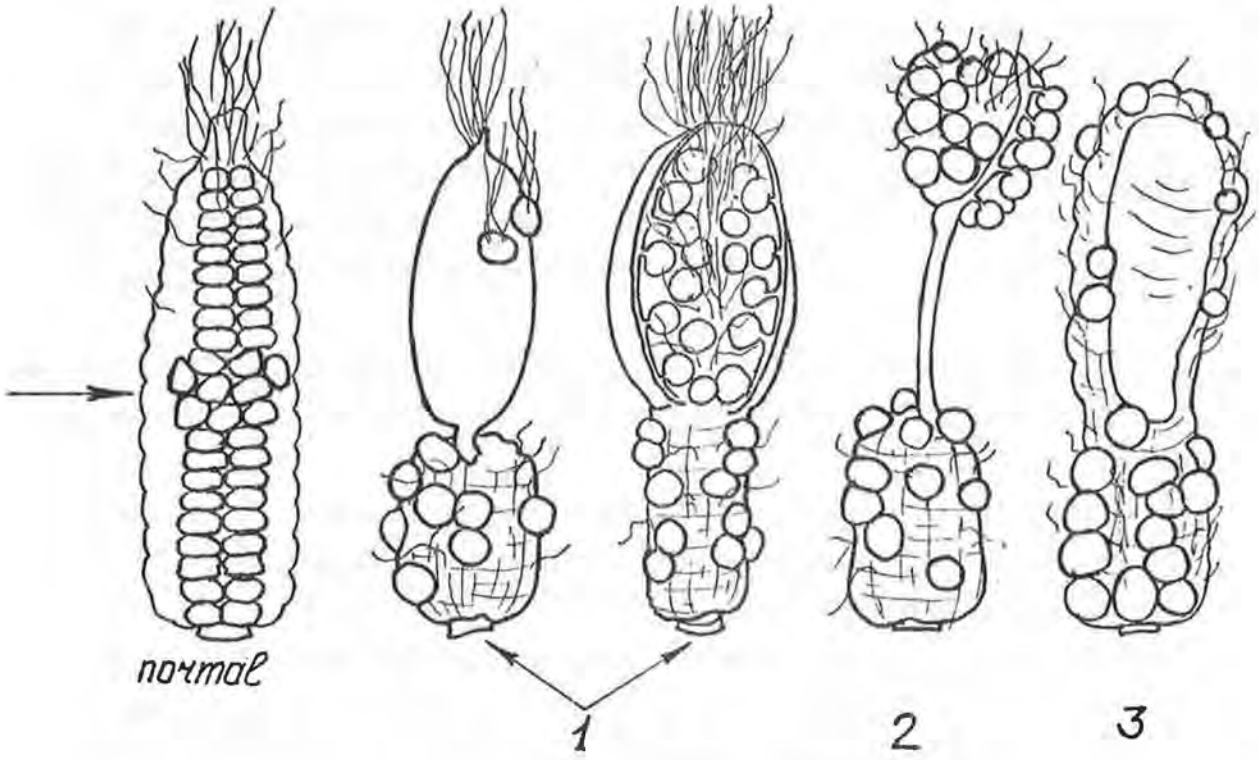

Fig. 1

Type 1. The upper tip of the ear is turned from inside out and resembles a leather tube with an opening on its end from which the silks emerge. The seeds are fixed onto the inner side of the wall, and pairs or paired rows of female spikelets sometimes occur on the external wall of the tube. The bottom part of the ear appears to be normal. We have observed 120 Type 1 ears (50%).

Type 2. The normal bottom part of the ear abruptly forms a thin stalk like a male panicle stem, ending with a short tube or a labiate sheet. Female spikelets and seeds are fixed inside the tube or from one or both sides of the sheet. We have observed 70 Type 2 ears (30%).

Type 3. The ear is almost normal except that its upper part has an area without spikelets. We have observed 49 Type 3 ears (20%).

The typical ears of the line Sg25 produce "uneven" rows in the middle part of the ear and tend to assume a fasciate shape; the ear tip has a reduced number of seeds, and the male panicles have spikeless spots on the central stem. The panicles of the mutant form are like the original ones but have no spikeless spots.

The F_1 progeny from crosses with unrelated forms showed normal ears. The F_1 progeny from the cross Sg25TRf mutant X Sg25TRf normal showed ears, not typical for the original line, that were greatly fasciated or very much cone-shaped.

Among 129 F_2 plants from the cross W64-1 X Sg25TRf mutant 10% of the plants had mutant ears; another 10% of the ears were non-typical, impossible to classify into any mutant type. The F_2 progeny from the cross W64-2 X Sg25TRf mutant gave only normal ears.

In F_2 of the cross Sg25TRf mutant X Sg25TRf normal, 67 plants out of a total of 243 (27.6%) showed mutant ears but the three types were less obvious than in the 1972 progenies.

J_2 and J_3 progeny of the mutant plants have also been studied. In J_3 some families showed mutant ears of the three types separately. However, no ear strictly reproduced the ear shape observed in 1972.

Having studied F_1, F_2, J_2 and J_3 we may conclude that the above described mutation interfering with the ear formation process is controlled by a single recessive gene; its clear development depends on the genetic background and on the growing conditions. We have named this mutation "cob turned out" (cto). It slightly resembles the mutation described by P. Sarvella and C. O. Grogan (J. Hered. 57:211-212, 1966) and designated by them as inverted ear; however, the ie mutation showed some deviation not only in the ear but in the panicle as well.

The cto mutation shows a high degree of polymorphism and thus may be of interest for embryologists. Further studies of this mutation are in progress.

E. I. Vahrusheva

A mutation causing the absence of the first division in meiosis — After treating the seeds of line W23 with a 0.012% solution of N-nitroso N-methylurea for 24 hours at 20-22° C, we have obtained in F_3 a recessive monogenic mutation showing total male and female sterility.

While studying meiosis in homozygous mutants the following pecularities of chromosome behavior have been found:

(a) Premature spiralization of the chromosomes. A dense chromatin layer forms around the nucleolus and later divides into 20 strongly reduced univalents.

(b) Absence of all prophase I stages (leptotene, zygotene, pachytene, diplotene and diakinesis).

(c) Absence of chromosome conjugation.

(d) Division of the centromeres of sister chromatids in metaphase I and the strict separation of 20 chromosomes in anaphase I towards each pole.

(e) Random distribution of the chromosomes during division II, resulting in sterility.

We have designated this mutation as the absence of the first division (afd-W23).

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Possible sporophytic expression of the waxy gene — It is widely understood that the phenotypic influences of the waxy genotype are limited to the pollen and the endosperm. Ericksson (Hereditas 63:187, 1969), however, has presented the following summary of several studies:

Cross	Total kernels	Waxy kernels
wx wx x Wx wx	79,381	39,173
Wx wx x Wx wx	152,871	36,523

The expected ratio of non-waxy to waxy should be 2:2 in the first cross and 3:1 in the second. If the totals were equal in the two crosses, the numbers of waxy kernels in the first and second crosses would then be in the ratio 2:1. The totals are not equal, however, and this ratio should be corrected to 2:(152,871/79,381) or 2:1.9257, if we assume that the disadvantage of the wx pollen is equal whether the genotype of the maternal parent is wx wx or Wx wx.

The assumption can be tested with the chi-square test:

Observed	39,713	36,523
Expected	75,696(2/3.9257) = 38,564.33	75,696/(1.9257/3.9257 = 37,131.67

Chi-square = 19.5728, df=1, P <.005

The result suggests, first of all, that waxy may have an effect on stylar tissues. If further studies support this suggestion, an interesting interaction between pollen tubes and stylar tissues will be indicated. These further studies must, of course, test for an alternative explanation: the possible influence of the ga8 locus, which is within 15 map-units of wx on chromosome 9. Perhaps some of the material summarized by Ericksson showed the influence of this locus. This too could have caused the deviations observed.

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The practical use of high quality but defective endosperm traits — Various recessive endosperm mutants (e.g., shrunken, brittle, opaque, waxy, etc.) which improve the quality (sweetness, flavor, nutritive value) of the endosperm are often impractical for large scale commercial use because they are associated with undesirable production traits such as reduced germination and disease susceptibility. However, if they enter a corn hybrid from just the pollen parent, which constitutes only every fifth row in a crossing field and which may come from nurtured means, the desired recessive traits will still segregate out in 25% of the F_2 kernels scattered at random on each ear of the farmer's crop. Thus, there will be normal seed quality for the seedsman, and the recessive mutants will still have a significant although reduced effect on the quality blend of the farmer's crop.

The popular bi-color (Y vs. y) sweet corn hybrids are an established example of the concept. In the case of shrunken-2 now used in combination with starchy (Su Su, sh2 sh2), the double recessive (su su, sh2 sh2) would be in the pollen

parent with any desired sugary inbred as seed parent. This permits high quality seed with good germination rates. The farmer gets a crop ear with a sprinkling (25%) of extra sweet kernels, usually just the correct amount for the many people who find 100% shrunken-2 kernels too sweet for their taste preference.

The propagation of the double recessive su sh2 in the pollen parent may be facilitated by the use of an extra Tripsacum chromosome carrying the dominant allele of one or the other of the recessive. When present as an extra pair of alien chromosomes, the transmission to daughter gametes is the normal 50-50. But when reduced to a single extra alien chromosome in the farmer's crop, its transmission drops down to about 8%, leaving the recessive trait largely uncovered to the benefit of the quality connoisseur. At present this system would have to be restricted to the use of Tr7 carrying the Su locus. The Tripsacum chromosome marked by Sh2 has not been isolated.

A side advantage of bisweet hybrids, as with bicolor hybrids, is that they are a source of "grow-it-yourself" ears exhibiting F_2 ratios. With the segregation of both bi-sweet and bi-color factors on a single ear, independent assortment may be demonstrated for students.

Walton C. Galinat

Three systems for two-ranked ears in corn — Depauperate type: The eight-rowed Northern Flints, when grown under stress, frequently produce two-ranked ears with paired spikelets giving a four-rowed ear. The tendency toward this type of two-ranking is stronger in eight-rowed strains having an inherited reduction in the vascular system of the cob. When such a reduction in vascular system is combined with the mutant for single female spikelets, the styles may fail to elongate, as in the "silkless" mutant.

Elongation type: When condensation is relaxed sufficiently, ranking continues to drop until the two-ranked state is achieved. The two-ranked level of condensation was selected from among the F_2 segregants of a cross between a string cob sweet corn inbred (MW401) and an "interlocked" derivative of Coroico corn by eight-rowed Northern Flint corn. The two-ranked cobs of this selection are sometimes four-ranked at the base or in the lower half of the rachis. The degree of condensation upon which this is based is polygenically controlled between extremes like that of kernel row number.

Tripsacum-teosinte type: A dominant factor for two-ranked spikes, first discovered as one of the effects of a Tripsacum chromosome (Tr9) when present

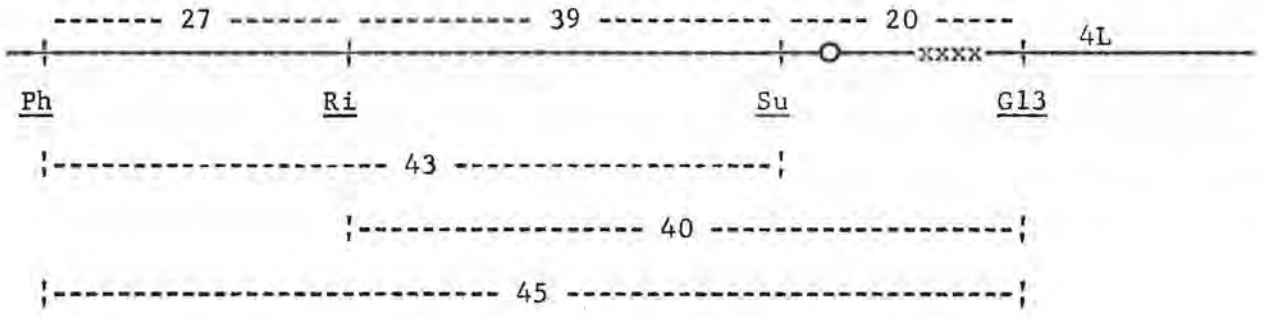
in an eight-rowed background, has been transferred to maize on a corn-Tripsacum interchange chromosome (M2-Tr9). In a row-number background higher than eight-rowed, the effect is only a reduction in row number. This dominant factor from Tripsacum is allelic to two-ranking from teosinte, as shown by a hybrid with a two-ranked teosinte derivative that failed to segregate the many-ranked condition through the F_3. At first the dominant factor was unstable regarding the point at which its phenotype was manifest. However, in due course a factor, possibly from teosinte, was selected which synchronized its expression with the onset of rachis formation. The nature of this synchronizing factor is unknown.

As one of the essential traits which distinguishes corn from teosinte, the inheritance of the two-ranked spike has special significance. The development of two-ranked, string cob sweet corn is possible and well underway.

Walton C. Galinat

Abscission layer development in the rachis of Zea: its nature, inheritance and linkage — Abscission occurs independently in two regions of the rachis, namely the rind and the pith, as seen in longitudinal sections of cobs from corn-teosinte derivatives. Our studies reveal that development of the abscission layer in these two regions is controlled by two different genes on chromosome 4 (Tables 1 and 2). These genes, hereby designated as Ph for pith abscission and Ri for rind abscission, are placed on the short arm as shown in Figure 1.

Figure 1. Placement on chromosome 4 of factors for abscission layer development in maize-teosinte derivatives.



xxxx = possible small inversion in the Su-G13 region

Table 1. Backcross segregation data for rind and pith abscission layer development from Nobogame teosinte with chromosome 4 markers from corn.

	Su G13	Su g13	su G13	su g13	Total
Ph Ri	205	51	31	119	406
Ph ri	52	32	24	78	186
ph Ri	58	14	6	38	116
ph ri	118	31	29	213	391
Total	433	128	90	448	1099

Table 2. Four-factor linkage analysis of Su, G13, Ph and Ri.

	Combinations	Frequencies	Total	Recombination
Parental	Su G13 + su g13	433 + 448	881	
Recomb.	Su g13 + su G13	128 + 90	218	20%
Parental	Su Ph + su ph	340 + 286	626	
Recomb.	Su ph + su Ph	221 + 252	473	43%
Parental	Su Ri + su ri	328 + 344	672	
Recomb.	Su ri + su Ri	233 + 194	427	39%
Parental	G13 Ph + g13 ph	312 + 296	608	
Recomb.	g13 Ph + G13 ph	280 + 211	491	45%
Parental	G13 Ri + g13 ri	300 + 354	654	
Recomb.	G13 ri + g13 Ri	223 + 222	445	40%
Parental	Ph Ri + ph ri	406 + 391	797	
Recomb.	Ph ri + ph Ri	186 + 116	302	27%

In the corn background of the backcross segregation reported here, abscission in the rind portion of the rachis was partially suppressed in the sense that its expression in most specimens required special treatment. After longitudinal sections of 1099 cobs from the backcross were soaked in water and then spread out, cut surface uppermost, on the greenhouse bench for a period of one year, some previously obscure abscission layers in the rind were revealed. In some of the shorter, more condensed cobs the expression of rind abscission was apparently completely suppressed despite this year-long treatment because of the tight fusion of the apex of the cupule to the glume cushion of the spikelet pairs above; this resulted in a slight deficiency in the rind abscission phenotype despite all efforts to observe it. With either gene the expression of abscission layers in the heterozygote is intermittent and more frequent toward the tip of the ear where condensation is slightly relaxed.

The non-shattering rachis becomes semi-lethal in teosinte because it inhibits seed dispersal. But the reciprocal condition, partial abscission layers in the corn cob, may be tolerated because a comparatively high level of condensation in corn prevents complete rind abscission through a fusion of the apex of the cupule to the glume cushion above. Pith abscission is ineffectual in the absence of complete rind abscission, so modern corn can cope with some gene flow from teosinte for these two abscission factors because of their usual neutral effect on the corn cob.

The reduction in crossing over between Su and G13 in this segregation from the usual 34 percent to 20 percent is interpreted as being due to interference from a small heterozygous inversion.

Walton C. Galinat

Adaptiveness of knobs in teosinte — The chromosome knob constitutions of 310 plants from 54 collections of Mexican teosinte and 88 plants from 7 collections of Guatemalan teosinte have been determined. The analysis of the regional distribution of knob types showed that they occur in combinations that are characteristic for each population.

There are two general knob categories in Mexico: (1) knobs that are widely distributed in almost all local populations, and (2) knobs that have a more specific regional distribution; furthermore, within each of these groups the knobs of different size generally do not show the same frequencies within and between regions. Some of the data illustrating these points are given in Tables 1 and 2 in terms of the relative frequencies found in each of the geographical regions.

The knobs found at the 3L1, 5L1 and 9S positions are representative of the first group. The 5L1 position is predominated by the large knobs in all regions except Nobogame in northern Mexico; the medium knobs and the knobless positions are always present but in relatively lower frequencies than the large knobs. On the other hand, although all the regional populations have knobs in the 3L1 and the 9S positions, their frequency varies according to the region. The 3L1 position is predominated by large knobs in the Chalco region; in the regions of Guerrero-S.E. Michoacan-W. Mexico, this position is predominantly knobless. There are higher knob frequencies in the Guanajuato-N. Michoacan region than in the regions farther south where the large and medium knobs and the knobless

Table 1. Relative frequencies (percent of the total number of chromosomes examined) for the different knob types found at the indicated positions in teosinte populations from various Mexican regions. The number of collections used from each region is given in the last column.

Region	Knob position and size												Total	Coll.
	3L1				5L1				9S					
	l	m	s	o	l	m	s	o	l	m	s	o		
Nobogame	3.1			96.9	15.6		6.2	78.1	6.2		3.1	90.6	32	2
Gto.-N.Mich.	40.7	23.7	0.8	34.7	73.7	11.8		14.4	13.5	10.1	8.4	67.8	118	12
N.E.Mich.	71.4	3.6		25.0	85.7	7.1		7.1	10.7	7.1	14.3	67.8	28	3
E.Mich.-W.Mex.	5.1	10.2		84.7	63.2	7.1		29.6	62.2	10.2	5.1	22.4	98	9
Huetamo, Mich.	2.0	10.0	2.0	86.0	90.0	4.0		6.0	80.0	6.0	2.0	12.0	50	4
N. Guerrero	31.6	14.5	1.3	52.6	75.0	13.1		11.8	50.0	13.1	10.5	26.3	76	5
Central Gro.	9.6	3.8		86.5	71.1	1.9		26.9	51.9	13.4	3.8	30.8	52	5
Chalco, Mex.	79.5	6.0	1.8	12.6	80.1	9.6		10.8	51.8	7.8	3.0	37.3	166	14
	4S2				5S1				9L2					
	l	m	s	o	l	m	s	o	l	m	s	o		
Nobogame				100.0				100.0				100.0	32	2
Gto.-N.Mich.	0.8			99.1				100.0	13.5	16.1	7.6	62.7	118	12
N.E.Mich.			3.6	96.4	25.0			75.0	7.1		10.7	82.1	28	3
E.Mich.-W.Mex.		2.0	7.1	90.8		2.0		97.9		4.1	3.0	92.8	98	9
Huetamo, Mich.	14.0	30.0	16.0	40.0	2.0			98.0			4.0	96.0	50	4
N. Guerrero	9.2	18.4	3.9	68.4	2.6			97.3	7.9	15.8		76.3	76	5
Central Gro.	23.1	17.3	3.8	55.8	13.4			86.5	3.8			96.1	52	5
Chalco, Mex.	18.7	5.4	1.2	74.7	36.7	12.0	0.6	50.6				100.0	166	14
	1L1				6L1									
	l	m	s	o	l	m	s	o						
Nobogame			46.9	53.1				100.0					32	2
Gto.-N.Mich.	47.4	16.9	5.1	30.5	18.6	8.5		72.9					118	12
N.E.Mich.	57.1	14.3		28.6	10.7	7.1		82.1					28	3
E.Mich.-W.Mex.				100.0				100.0					98	9
Huetamo, Mich.	4.0	4.0	6.0	86.0				100.0					50	4
N. Guerrero		11.8	11.8	76.3				100.0					76	5
Central Gro.	17.3	9.6	1.9	71.1			1.9	98.1					52	5
Chalco, Mex.	78.9	4.8	1.2	15.0	76.5	6.6	1.2	15.7					166	14

Table 2. Relative frequencies (percent of the total number of chromosomes examined) for the different knob types found at the 2L2, 5S2 and 8S terminal positions in teosinte populations from northern and southern Guatemalan regions. The number of collections from each region is given in the last column.

Region	Knob position and size												Total	Coll.
	2L2				5S2				8S					
	l	m	s	o	l	m	s	o	l	m	s	o		
Northern Guatemala	1.9	15.4	36.5	46.1	71.1	11.5	1.9	15.4	61.5	21.1	5.8	11.5	52	3
Southern Guatemala	47.2	13.9	11.1	27.8	69.4	5.5	2.8	22.2				100.0	36	4

positions are present in similar frequencies. In Chalco, large knobs occur at relatively high frequencies in the 3L1, 5L1 and to a lesser extent in the 9S position. In the Guanajuato-N. Michoacan region the large knobs are even lower in frequency in the 9S position but remain high in the 3L1 and 5L1 positions. In the S.E. Michoacan-Mexico-Guerrero region the reverse situation occurs, with a high frequency of large knobs in the 9S position and a low frequency in the 3L1 position. Nobogame teosinte is almost knobless in all positions.

Three positions are given illustrating the second group of knobs. The 4S2 and 5S1 positions illustrate the case where teosinte from the Chalco region has shown knobs at these positions, while the Guanajuato-N. Michoacan populations are usually knobless in these positions. In the Guerrero-S.E. Michoacan-W. Mexico region knobs were present at 4S2 in rather low frequencies and almost entirely lacking at the 5S1 position. In this regard the 9L2 position seems to show a reverse situation with relation to the knob distribution at the 4S2 and 5S1 positions. The knobs are present in Guanajuato-N. Michoacan and also (in an irregular fashion) throughout the Guerrero-S.E. Michoacan-W. Mexico region but are completely absent in populations from the Chalco region.

The 1L1 and 6L1 positions illustrate another pattern. Teosinte populations from both the Chalco region and the Guanajuato-N. Michoacan region exhibit a high frequency of knobs, especially the large knobs, while the plants from other regions either have completely knobless chromosome segments (as for 6L1) or carry a mixture of knobbed and knobless segments (as in the 1L1 position).

Three general knob distribution patterns were found in northern and southern Guatemala (Table 2). One of the patterns is exemplified by the terminal knobs in the 2L2 position. In the northern teosintes the knobless condition predominates, and the frequencies go down as the knob size increases; whereas in the south the situation is reversed, with a predominance of the large knobs. The second pattern is illustrated by the knobs at the 5S2 position; teosinte populations from both regions show similar tendencies in the relative frequencies of their knobs. The third pattern is illustrated by the knob data from the 8S position; in the northern region the large knobs usually predominate with variable but always lower frequencies for other knob types, while in the southern populations the knobs are absent.

These results seem to show quite clearly that the knobs found at different positions on the chromosomes are not distributed at random among the teosinte populations of different regions. This non-randomness would seem to indicate

that they are not only active chromosomal structures but also that they have highly developed selective values.

There is experimental evidence that the knobs in maize are closely linked to genes controlling the development of different morphological or physiological characteristics. There is also evidence that the presence of knobs reduces recombination in the chromosome segments where they are located, at least when they are present in a heterozygous condition, and that this reduction in recombination is inversely related to the knob size. Consequently, it seems clear that the selective value of a given knob depends on the kind of genes that the knob is closely linked with. The knob itself might be one of the important factors in developing a specific linked gene complex (supergene) since the reduction of recombination, in concert with natural selection, favors the development of gene complexes better co-adapted to the particular sets of factors imposed upon the population by different selective pressures.

Takeo A. Kato Y. and Walton C. Galinat

Maize-teosinte introgression — The basic problem is how these two sympatric species intercross freely and yet maintain their specific identities. This study shows how chromosome structures including the knobs can account for this anomalous situation.

It has been found that some knob types present in relatively high frequencies in teosinte populations are absent or nearly so from maize populations that usually grow in close sympatry; however, the knobs in these same positions have been found in relatively high frequencies in the races of maize Zapalote Chico and Zapalote Grande in regions of Oaxaca and Chiapas of southern Mexico, where no teosinte populations have yet been found. This is the case for the knobs at the 4S2, 5S1 and 7S positions in populations of maize and teosinte from Chalco in southeastern state of Mexico and from the Mazatlán area in central Guerrero (Table 1). The single medium knob on 4S2 and the large one on 7S found in maize from Mazatlán are interpreted as having their origin from the Zapalote of Oaxaca rather than from teosinte. There are two main reasons for this conclusion: (1) there is no indication of introgression of these knobs in the Chalco region where it is known that hybridization occurs at a higher frequency than in Guerrero, and (2) the large knobs on 7S were found to be absent in teosinte from the Mazatlán region. These results seem to indicate that at least these knobs are not introgressing between maize and teosinte populations.

On the other hand, the knobs at 1L1 and 3S1 are present in both the maize and the teosinte populations from the Chalco region, but absent in maize and present

Table 1. Knob frequencies for the indicated positions on several chromosomes of maize and teosinte populations from two Mexican regions, Chalco in the southeastern part of the state of Mexico and Mazatlán in central Guerrero, where both plant species grow in close sympatry. The knob frequencies of maize populations from another region are included for comparative purposes.

Species/ region	Collec- tions	Knob position and size																Total chrom
		1L1				3S1				4S2				5S1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
MAIZE																		
Chalco, Mex.	10	4	5	3	114	3	8	0	115	0	0	0	126	0	0	0	126	126
Mazatlán, Gro.	4	0	0	0	124	0	0	0	124	0	1	0	123	0	0	0	124	124
Oaxaca-Chiapas	13*	0	5	8	135	18	22	7	101	4	29	16	99	17	13	0	118	148
TEOSINTE																		
Chalco, Mex.	14	131	8	2	25	1	21	0	144	31	9	2	124	61	20	1	84	166
Mazatlán, Gro.	5	9	5	1	37	18	1	0	33	12	9	2	29	7	7	0	45	52
		6L2				6L3				7S				7L1				
		l	m	s	o	l	m	s	o	l	m	s	o	l	m	s	o	
MAIZE																		
Chalco, Mex.	10	0	0	4	122	0	1	15	110	0	0	0	126	72	9	1	44	126
Mazatlán, Gro.	4	0	2	28	94	1	28	23	72	1	0	0	123	51	24	4	45	124
Oaxaca-Chiapas	13*	4	49	70	25	0	21	91	36	69	24	7	48	118	19	4	7	148
TEOSINTE																		
Chalco, Mex.	14	0	0	31	135	0	0	20	146	42	27	6	91	131	20	0	15	166
Mazatlán, Gro.	5	0	0	21	31	40	4	0	8	0	2	1	49	45	0	0	7	52

* Collections of the races Zapalote Chico and Zapalote Grande (from unpublished data of McClintock, Blumenschein and Kato)

in teosinte from Mazatlán. It is also known that all 1L1 knob types are frequently found in the Palomero Toluqueño race of maize and that those at the 3S1 position occur in populations from western Mexico, the Bajio region and the Central Mesa where Chalco is located and in the Zapalotes of Oaxaca. Teosinte populations of other regions also possess relatively high frequencies of these knobs; it is therefore difficult to be certain whether the knobs present in maize from Chalco represent introgression from teosinte or not. The fact that these knobs were absent in maize from Mazatlán seems to suggest that the knobs present in Chalco maize are not the result of introgression unless it is argued that in Mazatlán conditions of temporal and spacial isolation exist that prevent hybridization.

The 6L2 and 6L3 positions show knobs suggesting probable introgression in both directions (see the small knobs of 6L2 and the large and medium knobs of 6L3 in Mazatlán material). However, the small knobs of 6L3 in maize from Mazatlán most probably come not from teosinte but from some maize source, such as the Pepitilla race from northern Guerrero or the Zapalote from Oaxaca; considering these knobs introgressive also conflicts with the argument that introgression does not occur in Mazatlán due to differential flowering and/or fertilization.

The knobs at the 7L1 position show that the large size knobs are present in maize (including the Zapalotes) in frequencies similar to those found in teosintes from the two regions considered here; however, data on the smaller knobs indicate that introgression might be occurring in the Chalco region but (again) not in Mazatlán.

It is well known (and confirmed in these studies) that the Guatemalan teosintes have knobs only at the terminal positions of the long and the short arms of their chromosomes. With the exception of the 4S2, 7S and 9S knobs, none are known to occur at the other 14 positions in maize populations from Guatemala or in any other maize populations so far examined. It is also know that maize and teosinte hybridize with some frequency in Guatemala, generally producing highly fertile hybrids, but it seems clear, in spite of this, that no common introgression (of at least 14 chromosomal segments) occurs.

The results given above could be interpreted in at least two ways: (1) No introgression occurs at all between teosinte and maize populations, in spite of the constant formation of fertile hybrids; if so, the isolating mechanism is probably a complex of different components. (2) Different maize and teosinte populations and chromosomal segments behave differently so that populations

growing in one region introgress some chromosomal segments and those of other regions may introgress other segments.

The fact is that the available data show that at least several chromosome segments are not introgressing in populations of maize and teosinte; whether other segments are introgressing or not is a question that is not possible to answer at the present time and further more critical investigations are needed in order to discriminate among different possibilities.

Takeo A. Kato Y. and Walton C. Galinat

Abnormal chromosome 10 — Two types of abnormal chromosome 10 are known in teosinte, but only one of these types has been found in maize populations. In the type that is common to both species chromosome 10 has an extra distal segment of chromatin which possesses a large subterminal knob. The second type, which is found only in teosinte populations, differs from the first type only in that the extra segment having the subterminal knob also has a small or medium terminal knob. In order to facilitate the discussion of these two types of abnormal chromosome 10, the first is designated type I and the second, type II.

The geographical distribution and frequencies of the two different types of abnormal chromosome 10 in populations of maize and teosinte from regions of central Mexico are given in Table 1. The frequency with which the abnormal chromosome 10 appears in populations of maize and teosinte is very low; however, the type I abnormal chromosome 10 is scattered in maize populations throughout the whole region concerned. These data also show not only that the type I abnormal chromosome 10 is found in both species and the type II only in teosinte, but also indicates that the two types occur separately in populations of teosinte from different regions. Type I was found only in teosinte plants from eastern and southeastern Michoacan and the western part of the state of Mexico, while type II was found in one collection from southern Guanajuato, in collections from Guerrero and in the Chalco region in southeastern Mexico state. This differential distribution of these chromosome types in teosinte might indicate that they possess genetic constitutions which make each of them become better co-adapted to gene complexes of different populations growing under different environments.

When the data from maize and teosinte are compared, especially those from Chalco in the state of Mexico and from Mazatlán in central Guerrero, it becomes clear that these chromosomal segments are not introgressing from maize to teosinte or vice versa. Therefore, the fact that both types of abnormal

chromosome 10 are present in teosinte indicates that the ancestral teosinte population complex had them and they later segregated into the populations of different regions because of changes in the selective forces acting on them. An alternative view would be that type I is derived from type II by loss of the distal knob.

Table 1. Geographical distribution of the two types of abnormal chromosome 10 in collections of maize and teosinte from various regions of central Mexico.

	Collections			Chromosomes		
	With	Without	Total	Type I	Type II	Total
MAIZE						
Guanajuato	2	15	17	4	0	196
Guerrero	4	25	29	9	0	366
Hidalgo	2	9	11	4	0	108
Mexico	7	20	27	15	0	384
Michoacan	4	10	14	9	0	144
Morelos	1	12	13	9	0	108
Puebla	2	4	6	2	0	42
Gueretaro	1	11	12	3	0	120
San Luis Potosi	1	14	5	1	0	52
Tlaxcala	1	2	3	1	0	34
Veracruz	0	1	1	0	0	1
TEOSINTE						
Nobogame, Chihuahua	0	2	2	0	0	32
Guanajuato-N.Michoacan	1	11	12	0	2	118
Guerendaro-Cd.Hidalgo, Michoacan	0	3	3	0	0	28
E.Michoacan-W.Mexico	3	6	9	4	0	98
Huetamo, Michoacan	2	2	4	2	0	50
Iguala-Arcelia, Guerrero	5	0	5	0	5	76
Mazatlán, Guerrero	2	3	5	0	5	52
Chalco, Mexico	6	8	14	0	11	166

(This and the previous two investigations have been financially supported by Research Corporation of New York, A.N.U.I.E.S. of Mexico City, Funk Bros. International, Inc. of Bloomington, Illinois, a Mass. Agric. Exper. Sta. Project (Hatch 352), the Graduate School of the National School of Agriculture of Chapingo, Mexico, and C.I.M.M.Y.T. of El Batan, Texcoco, Mexico).

Takeo A. Kato Y. and Walton C. Galinat

Cytological analysis of the hybrid su gl3 x bt2 gl4 — There has been some evidence of duplicate genes in corn (Rhoades, 1951), and their bearing on chromosome repatterning and evolution has thus far been only a matter of speculation; the following experiment was carried out in the hope of obtaining some concrete evidence in this direction.

The progeny from a cross between the su gl3 and bt2 gl4 chromosome 4 marker gene stocks was cytologically analyzed. The F_1 plants were all non-glossy and were studied at pachytene for possible chromosomal aberrations. An attempt was made to determine if the similar genes, gl3 and gl4, were separated by an inversion or if there was any indication of a duplication of a segment. In all the observations meiosis was regular. Chromosome 4 at pachytene was normal and did not show any heteromorphic structural differences.

The presence of duplicate genes is usually attributed to certain chromosomal aberrations in some ancestral generation. But in the above experiment where similar genes were introduced into the hybrid plant there was no indication of any such abnormalities. Therefore in this case there is now, at least, no evidence for a common origin of these two glossy loci.

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Fertilization ability of four inbred lines — Variability of male gametophyte competition in maize appears to be a widespread phenomenon not limited to the effects of the well known Ga genes (Pfahler, Genetics 52:513, 1965 and Genetics 57:513, 1967; Mulcahy, Nature 249:491, 1974). It has been observed that this character shows a variability which is typical of quantitative traits and that the differences between genotypes, at least in the case of pollen grown on synthetic medium, depend on genes that are expressed in the gametophytic phase (Sari Gorla et al., in press).

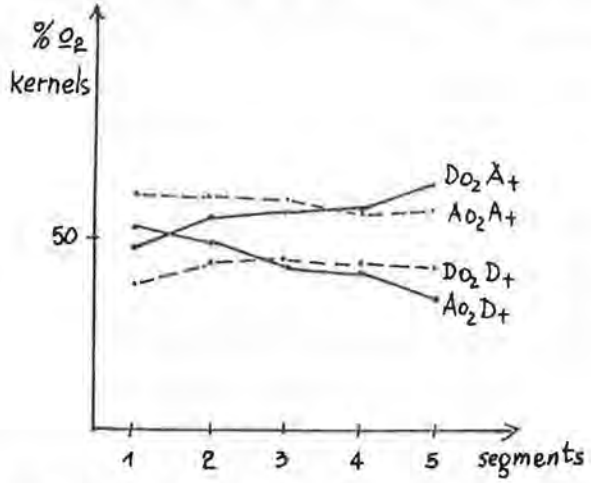
Competitive ability of pollen can be measured as the relative fertilization frequency of pollen of two different genotypes on the same ear; the competitive ability of four inbred lines was studied in this way.

The inbred lines RNY, B37, WF9 and C123 (which, for the sake of brevity, will be indicated as A, B, C and D, respectively) were compared, two by two, in all possible combinations. Mixtures were made with equal quantities of two different types of pollen, each marked for the presence of the normal or mutant allele

of the opaque-2 gene, which can be recognized on the kernels. The mixture was used to pollinate a hybrid obtained from two opaque-2 inbred lines.

For each line-pair tested four pollen mixtures were made: A+ Ao2 and B+ Bo2 (i.e., opaque and normal versions of the same line), which would test the effect of the marker gene and also the ability of both pollen types to reach the base of the ear; and A+ Bo2 and Ao2 B+, which would test the competitive ability of A versus B. The ears obtained were divided transversely into five segments in which the relative frequency of normal and opaque kernels was computed; the increase in fertilization frequency from the apex to the base of the ear (where the styles are the longest) by one of the two pollen types is an index of its relatively greater rate of growth. The results obtained for each pair can be expressed as the percentage of opaque kernels in the segments of ear from the apex (first segment) to the base (fifth segment). Figure 1 gives the A versus D comparison as an example.

Figure 1. A comparison of the competitive ability of pollen from two inbred lines.



The A+ Ao2 and D+ Do2 mixtures did not show any significant differences in the frequencies of the two kernel types in the different segments; this indicates that o2 does not influence pollen tube growth. The same finding was obtained for lines C and D. In contrast, the A+ Do2 combination revealed a significant increase of o2 kernels from the first to the fifth segment, and when the o2 version was the A line the opposite effect was observed. Thus, D line pollen has a greater competitive ability than that of the A line.

Results obtained from all line combinations are summarized in Table 1, in which A' and A" stand for normal and opaque versions of the same line, and the results of the comparisons are indicated in the conventional manner. The four lines included in this experiment revealed different fertilization abilities;

differences between these same lines were also observed with regard to pollen tube growth rates on artificial medium, which was in fact why they were chosen.

Table 1. Summary of the competitive abilities of pollen from four inbred lines.

	A	B	C	D
A	A'=A''	A>B	A>C	D>A
B		B'=B''	C>B	D>B
C			C'=C''	C>D
D				D'=D''

D > A > C > B
C > D

If the direct comparison between C and D lines is not considered, it is possible to rank the four inbred lines according to their competitive ability (D, A, C, B). However, when the results obtained with a mixture of C and D pollen are taken into account, it is found that they do not conform to the linear order indicated. This fact is not very easy to explain, but since the same female genotype was used for every comparison, it may suggest that some kind of interaction exists between pollen tubes growing in the same silk.

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Spontaneous losses of dominant markers of chromosome 9 analyzed in maize endosperm — The consequences of chromosome breakage can be phenotypically observed in maize endosperm, if a multiple recessive tester is pollinated by a stock having the corresponding dominant alleles. Loss of dominant factors in a portion of the endosperm tissue is often due to breakage of the paternal chromosome in the tested region. This method was described by A. C. Fabergé (Z.i.A. Vererb. 87:392-420, 1956), who studied the effects of various agents on induced breakage of chromosome 9. The present report concerns the spontaneous breakage of this chromosome.

Two sets of crosses were made, and a sample of the progenies was examined. In cross #1 a single locus was considered. The stocks were those developed by E. H. Coe, Jr., which yield a high rate of maternal monoploids and are of the following genotypes:

$$\underline{C}\ \underline{C}\ ♀ \times \underline{C\text{-}I}\ \underline{C\text{-}I}\ ♂ .$$

(C-I = the dominant inhibitor factor of anthocyanin pigmentation of the aleurone). Since the endosperm genotype was C C C-I, the F_1 kernels showed a pale pigmentation due to incomplete inhibition by the single dose of C-I. In addition, both isolated and clustered spots of deep pigment could be observed. Since mutation rate C-I→C is negligible (Coe, MNL 32:104, 1956), each spot of pigment can be inferred to be the result of a breakage event that occurred proximal to C-I. The clusters of spots are probably the result of B-F-B cycles originating from a break distal to C-I. The pigmented spots in the aleurone layer were recorded in a sample of 200 kernels:

Number of spots/kernel	<10	11-13	14-16	17-19	20-22	23-25	26-28	29-31	32-34	35-37	>37
Frequency	2	11	23	37	48	36	23	11	5	3	1

Average frequency: 21.4 spots/kernel

The frequencies observed in this material follow the "normal" distribution.

The number of cells in smaller spots was also recorded:

Number of cells/spot	1	2	3	4	5	6	7	8	9	10	11	12
Frequency	719	402	92	196	74	62	45	69	37	32	25	18

One-cell spots result from chromatid breaks; the cell that inherited the deficiency did not divide further. Two-cell spots could result (a) from chromosome breakage prior to the last cell division; (b) from chromatid breakage during the penultimate cell division; or (c) from breakage in both sister chromatids during the last cell division. The origin of spots made up of three or more pigmented cells can only be guessed. The data reported above indicate that probably a majority of the breakage events occurred at the chromatid level. The relative peaks found for eight and four cells per spot indicate that a proportion of the cells underwent synchronous division during the last period of endosperm growth.

In cross #2 (with stocks of unrelated origin) three linked loci were considered:

C C bz bz wx wx ♀ x C-I C-I Bz Bz Wx Wx ♂

The pigmented spots in the aleurone layer were recorded in another sample of 200 kernels:

Number of spots/kernel	0	1	2	3	4	5	6	7	8	>8
Frequency	13	28	30	42	38	26	10	6	5	2

Average frequency: 3.3 spots/kernel

The frequencies observed in this material follow the Poisson distribution.

Three classes of spots (A, B and C) were compared on the basis of the location of breaks (distal or proximal to wx):

Class	Number of cells/spot	Number of spots examined	Loss of C-I Bz (break distal)	Loss of C-I Bz Wx (break proximal)
A	9-25	100	39	61
B	30-100	100	27	73
C	over 400	90	29	61

The spot size apparently was not affected by break location. When the phenotype of the spots was recorded for the three markers, spontaneous breakage frequencies were found to correspond satisfactorily to the physical distance of the relevant loci as indicated by the cytological map reported by Fabergé (1956). The data are summarized as follows:

Spontaneous breakage events in the short arm of chromosome 9

(SL = single losses; Cy = B-F-B cycles)

Region	I distal to C		II C-I-Bz		III Bz-Wx		IV proximal to Wx		
Breakage event	SL	Cy	SL	Cy	SL	Cy	SL	Cy	Total
Observed frequencies	—	14	6	0	34	15	143		212
Totals in regions II to IV			6		49		143		198
Expectations on the basis of physical distances			11.6		55.3		131.1		198

A comparison of the frequency of isolated spots (single losses) with the frequency of clusters of spots (B-F-B cycles) shows that a high proportion of spontaneous breaks can yield stable ends. Breaks induced in this region by UV and X-rays, according to Fabergé (1956), yielded no stable terminal deficiencies. The same author (Genetics 44:280-285, 1959), found that α particles could yield about 35% stable terminal deficiencies.

A. Ghidoni and N. Pogna

Giemsa staining of heteropycnotic regions in maize chromosomes — The study of longitudinal differentiation of chromosome regions has made considerable progress with the employment of denaturation-renaturation-Giemsa staining techniques (Pardue and Gall, Science 168:1356, 1970; Arrighi and Hsu, Cytogenetics 10:81-86, 1971). When these techniques were applied to maize chromosomes (Vosa et al., MNL 46:165-167, 1972; Sartori and Ting, Amer. J. Bot. 61,5 suppl.:63, 1974, abst.)

a correspondence was found between main Giemsa bands and knob locations. Centromeric bands were also observed with one of these methods (Filion, MNL 48:150-152, 1974).

The present investigation concerns a comparative study of Giemsa bands in mitotic metaphase chromosomes, and of chromocenters (condensed chromatin bodies) in resting nuclei, and the relation of these to known knob locations and to the presence of B chromosomes, in different maize stocks. The material is described below:

Stock 1: the inbred Black Mexican sweet corn, with and without B chromosomes. Plants with 0-4 B's were analyzed in the present study. This stock is nearly knobless, except for a medium-small size knob in position 6Ld.

Stock 2: a tester, outcrossed to related material and backcrossed to the same tester. Homozygous knobs were present in 4L and 8L and a heterozygous knob in 6L.

Stock 3: F_1 between a K10 stock (marked R-st) and a r tester. Homozygous knobs 4L, 6L; heterozygous knobs 2L, 8L, 10L (abn.).

Stock 4: inbred line KYS. All knobs homozygous in the following positions: 5L, 6L, 7L and 9St.

Stock 5: a r tester with the background of inbred line W22. All knobs homozygous in the following positions: 2L, 4L, 7L, 8L and 9St.

All of these stocks carry a knob-like heteropycnotic structure adjacent to the Nucleolus Organizer region (N.O.) in the short arm of chromosome 6.

Root tips were pre-treated with a saturated solution of α-bromonaphthalene or with .6% colchicine aqueous solution, for 5 to 6 hrs, and fixed overnight in 3:1 ethanol-acetic mixture. Then, a modified BSG (Barium hydroxide/Saline/Giemsa) technique described by Sumner et al. (Nature New Biol. 232:31-32, 1971) and by Vosa and Marchi (Nature New Biol. 237:191-192, 1972) was applied for the present study.

Chromocenters stained by Giemsa were observed in resting nuclei, and Giemsa bands in well-condensed metaphase chromosomes of root tips. The results are summarized on the following page.

The number and size of Giemsa bands and the number and size of chromocenters are correlated. Giemsa bands and chromocenters on one side, and knob numbers on the other side are also correlated. Some distortion was caused in the morphology of metaphase chromosomes by the denaturation treatment, but when individual chromosomes could be reasonably identified, Giemsa bands were found consistently at knob locations. Larger knobs were always observed as thick bands, and smaller

knobs as thinner bands, sometimes reduced to single granules. K10 invariably showed, besides a large chromocenter in resting nuclei, a thick band in metaphase chromosomes at the expected location. Occasionally, thin bands were observed in other locations such as telomeres, or close to centromeric regions.

Material	No. of B's	Average No. of chromocenters large or medium size	small size	Average No. of Giemsa bands thick	thin	No. of knobs* large or medium size	small size
Stock 1 (Black Mex.)	0	0	1-2	0	2	0	2
Stock 1 (")	1	0	1-3	0	2	0	2
"	2	0	2-4	0	2	0	2
"	3	0-1	2-3	0	2	0	2
"	4	0-1	2-3	0	2	0	2
Stock 2 (a/)	0	4	3-4	5	3-4	4	1-2
Stock 3 (K10/)	0	5-6	3-4	6	3-5	6	4
Stock 4 (KYS)	0	4	3-4	4	2-4	4	4
Stock 5 (W22)	0	8	2-4	8	2-4	8	4

*The knob-like structure adjacent to the N.O. is not included.

No large chromocenters were observed in the knobless stock with 0-2 B's. Occasionally, these were found in presence of 3-4 B's. The absence of large chromocenters in the presence of B chromosomes was also noted by D. T. Morgan, Jr. (J. Hered. 34: 194-198, 1943).

B chromosomes did not show prominent bands as a rule. A thin band was often observed near the centromeric region of the B chromosome; two more thin bands were occasionally observed in the median and/or in the distal portion of this chromosome.

A thin band was often observed in the distal tip of the satellite region of chromosome 6. Occasionally, a thin band was observed close to the N.O. region.

These observations suggest that the heterochromatin of knobs may differ from the heterochromatin of distal portions of the B chromosomes, although the two heterochromatin types appear indistinguishable by the conventional staining techniques. In this regard, the knob-like structure at the N.O. region also seems to differ from typical knobs of other chromosome regions.

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Nuclear male-sterility system of hybrid seed corn production — The extreme susceptibility of plants with T (Texas) cytoplasm to Southern Corn Leaf Blight race T has precluded the use of the T cytoplasmic male-sterility system in hybrid seed production. A return to stocks with normal cytoplasm that require hand or mechanical detasseling is the temporary solution, but alternate methods are needed to alleviate the problems and expense associated with detasseling. In order to use a nuclear (genic) form of male sterility, the system has to be modified in order that lines consisting of only male-sterile plants can be produced. This may be accomplished by preventing the pollen transmission of the normal allele as in the following cross: ms ms ♀ x ~~Ms~~ ms ♂. Incorporation of the stocks listed below into elite parental material with normal cytoplasm would provide a workable nuclear male-sterility system to replace hand or mechanical detasseling.

Stocks:

1) 5-6b translocation (5S.1, 6 sat); 2) nuclear male-sterile polymitotic (po); 3) 5-6b duplication-deficiency.

Utilization of the stocks:

1) Backcross both the translocation and the male-sterile gene into the appropriate female parental lines. Experience may allow the option of backcrossing the duplication-deficiency into the parental lines; this may be done in addition to or in lieu of backcrossing the translocation, a procedure which subsequently requires the additional step of extracting the duplication-deficiency.

2) Extract the genotype carrying both the duplication-deficiency and the male-sterile gene (po) in heterozygous condition (in repulsion).

3) Generate large supplies of the desired male-sterile female parent by crossing homozygous male-sterile plants with the corresponding duplication-deficiency genotype (step 2 above).

4) The production of hybrid seed would be accomplished by using the male steriles produced in step 3 as the female parent in combination with an appropriate fertile male parent. Any elite parental material can serve as male and accomplish fertility restoration.

Supporting data:

In the table below, the proportion of male-sterile (po) plants to total plants observed is given for eight independent extractions (ear cultures) of the 5-6b duplication-deficiency. Lines with only male-sterile plants (i.e., 100% male steriles) are the ultimate objective in any nuclear or cytoplasmic-genetic male-

sterility system. The 5-6b translocation is superior in this regard to other stocks tested against the male-sterile gene polymitotic (see lower part of table).

Translocation	Number times Dp-Df extracted	Progeny of po po x Po* po (ms plants/total)**	% male steriles
5-6b		145/145	100
"		119/119	100
"		104/104	100
"		96/97	99
"		26/26	100
"		17/17	100
"		10/10	100
"		8/8	100
	8	525/526	99.8
Others			
3-6b	31	3213/3311	97.0
4-6(5227)	12	950/987	96.3
5-6(8219)	1	132/139	95.0
5-6d	1	35/38	92.1
4-6c	17	679/763	88.6

*Po linked to duplication-deficiency and not usually pollen-transmitted.

**Only small samples of seed from several extractions have been grown thus far.

In extensive observations stocks carrying the polymitotic male-sterile gene have exhibited complete male sterility; such reliability is highly important in hybrid seed production.

Related issues:

1) The use of these stocks for commercial hybrid seed production would be subject to the patent recently granted to the University of Illinois Foundation, Urbana, Illinois.

2) The nuclear male-sterile stock available for release has a reduced seed set; a selection program is underway to develop an improved version of this stock.

Seed supplies and distribution:

Total available seed supply of the 5-6b translocation stock and the 5-6b duplication-deficiency stock is 1000 kernels each. Three thousand kernels of the male-sterile stock are available. Additional supplies are expected from current winter nurseries. Seed may be obtained at no charge from the Cytogenetics Project, Department of Agronomy and Plant Genetics, University of Minnesota.

R. L. Phillips

Progress report on three possible methods of producing an all male-sterile progeny —

Method 1: Tertiary trisomic. Two interchanges, T2-6a(2L.5-6S.0^{+}) and T4-6(055-8) (4L.26-6L.25), were crossed on plants trisomic for chromosome 6.

Low-sterile plants (25 to 35% pollen abortion) from those crosses were selected and crossed as females with ms heterozygotes. This was repeated for another generation, this time selecting for the 10-20% sterile class, which should have been tertiary trisomics. Some of the low-sterile plants among their progeny had a chance of having the desired constitution: two normal chromosomes, each carrying ms, and the extra interchange chromosome carrying the Ms allele. Crosses of such a plant on ms plants should produce all male-sterile progeny except for the transmission of n+1 through the pollen or the occurrence of crossovers between the interchange breakpoint and the ms locus.

In 1973 tests of the low-sterile plants crossed on ms were grown; the results of small scale tests in Hawaii were used to eliminate all but those crosses which appeared promising. From a few of the low-sterile plants descended from T2-6a, about 90% of the plants in the test cross were male sterile. In those from T4-6(055-8) about 80% of the plants were male sterile. Since all non-male sterile plants had about 15% pollen abortion, they were presumed to result from the functioning of n+1 pollen and, if so, should have been tertiaries similar to the parents. Eighteen of those Ms plants were selfed and test-crossed on ms, and all but three gave 1:1 ratios from the crosses on ms and 3:1 ratios from the selfs; the other three yielded an excess of ms plants, but nothing even approaching 90%. Based on ear sterility, the progeny in these tests also segregated for low sterile, 50% sterile and normal. Remnant seed is available and will be grown for cytological analysis.

In conclusion, those two interchanges are not satisfactory for the tertiary trisomic method. A clue for selecting an interchange more likely to be satisfactory is furnished by Dr. R. L. Phillips' results with T5-6b in which the transmission of a duplication for nearly all the short arm of 5 occurred only rarely, if at all. The T5-6(5765), with breaks at 5S.19-6L.32, and T5-6(5906), with breaks at 5S.15-6L.13, should be good sources of an interchange chromosome with a duplication for 5S for the desired tertiary trisomic.

Method 2: Internal deficiency linked with male-sterility but not pollen-transmissible. X-rayed pollen was applied to recessives or heterozygotes whose loci are linked with that of a genetic male sterile in that chromosome. The recessives that appeared among the progeny grown in 1972 were too weak to produce ears. In material from a similar test grown in 1974 a few recessives did produce an ear that was crossed with an inbred. Their progeny will be grown and tested for the presence of a deficiency, how it is transmitted, and its position with respect to the linked male sterility locus. A usable deficiency should be linked with the locus but should not include it.

Method 3: A male- and female-transmissible deficiency for a male sterility locus (proposed in M.N.L. 15:133, 1971). X-rayed pollen from an inbred was used on plants that were homozygous or heterozygous male sterile. The male-sterile plants among the progeny were increased by crossing them as females with an inbred. These male steriles should have carried a deficiency for the normal allele in the chromosome from the x-rayed inbred. If that deficiency were transmitted, at least through the female, part of the progeny from the F_1 male sterile x inbred should be heterozygous for the deficiency and should not segregate sterile plants when selfed. If the deficiency is not transmitted, all the progeny should segregate male steriles when selfed.

For six ms lines progeny of selfs from four to 14 different plants per line were grown in 1974. In four lines all the progenies tested by selfing segregated for ms, but three of 14 plants tested in one line and three of eight plants tested in another did not segregate. In a seventh ms line the only plant tested did not segregate. These three lines, plus one from earlier tests, may carry the desired type of deficiency. If the deficiency is transmissible through both the female and the male, progeny from the selfs should include the deficiency homozygote, recognizable by test crosses with ms. All that is known thus far is that the deficiency is transmissible; the original deficiency produced in x-rayed pollen was most likely transmitted in a sperm carried down by a normal pollen tube. Plants in those lines that did not segregate ms were selfed and also crossed on ms; unfortunately, many of the crosses on ms were unsuccessful for no known reason. The tests obtained will be grown this summer, and more plants will be test-crossed.

There were three lines from ms2, but seven or eight selfs from each all segregated ms2, indicating that those deficiencies were not even female-transmissible.

In 1974 the progeny from heterozygotes for other male steriles crossed with x-rayed pollen were grown. For ms10 (3859 seeds) there were 4 sterile plants, and for ms8 (4094 seeds) there were 2 sterile plants; these 6 ms plants were crossed with a normal inbred.

These tests were done on a small scale, but tests on a much larger scale may be needed to establish a usable line homozygous deficient for a male-sterile locus.

I wish to thank Dr. E. H. Rinke and Northrup, King and Co., Minneapolis, for their cooperation in growing and pollinating some of this material.

Note: Another reprinting of my book "Discussions in Cytogenetics" was made in September 1974. Paper costs were considerably higher, but printing a larger number lessened the needed increase in price (now $10.40 including postage).

Chas. R. Burnham, Emeritus Professor

Media for germinating seeds — Germination tests using different media were being run as a laboratory experiment in a class in Horticulture. Following a suggestion by C. R. Burnham, sand was included with the perlite and peat moss for three lots of corn seeds: Hayes white sweet corn (1973 crop), seed from ears of A188 not fully matured at the time of a heavy frost in September, 1974, and a dent corn cross at least 10 years old. The test was not replicated, and only nine seeds were planted in each trial; the daytime temperature was 80^{o} F, nighttime 70^{o}. After five days, 8 of the 9 Hayes white seeds planted in sand were up, only 4 of the 9 in peat moss and 5 of the 9 in perlite; of the A188, 4 of the 9 emerged in sand, none in perlite and 2 in peat moss. With the old seed there were no plants up at the end of five days; but at the end of eight days, four had emerged in the peat moss.

Steve Ruce

Additional notes on seed germination — For some time I have had excellent success using fresh sand in a greenhouse bench to start plants from very old seed or seed from ears only partially developed at the time of harvest, in many cases advanced little beyond the milk stage. By planting in the sand bench a few days after the field plantings, the plants were ready to transplant to the field a few days after emerging in the sand.

There is evidence that silica stimulates the germination of wheat stem rust spores. I am almost convinced that sand may stimulate seed germination, but it may be that the conditions regarding moisture and texture are better in sand. I have had better success with tests in sand than in petri dishes.

Chas. R. Burnham

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Division of Biological Sciences, Columbia, Missouri

A positive selection technique for photosynthesis mutants of maize — We have previously reported a screening technique to isolate mutants of the photosynthetic light reaction (MGCNL 46:127-29, 1972). That procedure was an adaptation of one used for green algae that simply monitors the level of chlorophyll fluorescence (P. Bennoun and R. P. Levine, Plant Physiology 42:1284, 1967). The fluorescence technique works well with maize but there is one class of mutants for which it would not select, namely those lacking activity on the oxidizing side of photosystem II. On culture plates of algae this class of mutants has a lower than normal fluorescence yield, but selection of low levels of fluorescence is not practical with whole leaves since the normal green plant has a low level of fluorescence to begin with.

In order to isolate this class of mutant which the fluorescence technique misses, we have employed photodynamic herbicides or other known photodynamic inhibitors of photosynthesis. This class of compounds is only toxic to the plant tissues when reduced or otherwise changed by the photochemical reactions of photosynthesis. The herbicide which gave the best, most reproducible results was a commercial preparation of Diquat (Chevron Chemical Company, San Francisco, California).

The usual treatment procedure for two to three-week-old seedlings grown in vermiculite was to spray the leaves evenly with a common insect spray gun containing 10mM solution of the active ingredient, 6,7-dihydrodipyrido (1,2-a:2',1'-c) pyrazinediium dibromide. After a light spraying the plants were either put into the dark or exposed to normal growth chamber light (500 watt/m^2). Following 12 to 24 hr. in the light, treated plants showed multiple, often isolated lesions on the leaves. The plants which were kept in the dark for the same amount of time looked nearly normal. If the treated plants were allowed to remain in the dark 12 to 24 hours after spraying but before light exposure, there was considerable translocation of the herbicide and uniform killing of the leaf tissue followed light exposure. Therefore our technique usually involved spraying followed by 12 hours dark, 12 hours light treatment. During all this time herbicide treated dark control plants showed little damage.

Next, families segregating the high chlorophyll fluorescence mutants hcf and hcf3 (Miles and Daniel, Plant Physiology 53:589, 1974) were sprayed with Diquat. After the above treatment all normal plants were dead and all high fluorescent mutants were unharmed, showing only a few necrotic spots. With the high concentration of Diquat (10mM) mutants eventually also died in the light, but not before they could be clearly distinguished from wild type. 1 mM Diquat will allow the mutants to survive longer but this concentration is less effective in killing wild type.

We can conclude that with a photodynamic herbicide we should be able to select those families segregating photosynthesis mutants of all types. These mutants can include those blocked on the oxidizing side of photosystem II, whereas the high fluorescence technique will only select mutants in photosystem I and on the reducing side of photosystem II.

This type of treatment is reported to be an effective screen in green algae for photosynthesis mutants as well (R. K. Togasaki, Indiana University, personal communication).

Donald Miles & Kenneth Leto

Temperature response of dominant disease lesion mutants — The disease lesion mimic mutants described previously (MNL 48:121) have been observed to be highly responsive to temperature. To establish the limits of the response kernels from backcross ears that would segregate 1:1 for Les and Les2 (previously designated Spt) and from an ear of the cross Les/+, + + x + +, Les2/+ were planted. Sixty kernels from each ear (20 seeds per treatment) were given a 48-hour germination period at room temperature (78°F) and then transferred to one of three growth chambers. All three chambers were regulated for 16 hours of maximum light and 8 hours of darkness; the temperatures were held constant at 72°F, 80°F and 84°F, respectively. Each leaf on each seedling was noted for lesions as it became fully extended, and a leaf was recorded as positive only when it had at least one large lesion or three small lesions. Leaf counts from the first nine plants showing lesions in each treatment are summarized in Table 1; additional mutant plants were excluded

Table 1. Effect of temperature on the occurrence of lesions on successive leaves of seedlings carrying Les, Les2 or both.

Family	Temp (°F)		Leaf number 1	2	3	4		5	6	7	8	Mut/N
						Large lesions (Les/+)						
37	72		9	9	9	8	//	1	0	0	0	9/20
	80		7	7	5	3		2				*8/20
	84		8	5	5	1		0				11/20
						Small lesions (Les2/+)						
38	72		7	7	5	6	//	5	8	9	8	9/18
	80		1	9	8	7		4				9/19
	84		9	9	9	9		5				10/19
						Les, Les2 or Les and Les2						
39	72	Large	9	9	9	9	//	7	1	1	0	11/20
		Small	0	1	0	0	//	1	9	9	8	10/20
	80	Large	9	9	8	4		2				10/19
		Small	4	3	6	5		5				*6/19
	84	Large	9	9	7	8		5				12/20
		Small	9	9	9	9		8				9/20

//Temperature changed from 72°F to 84° F at the four-leaf stage.

* Less than nine mutant plants, due to either poor expression or chance deviation from a 1:1 ratio.

to make the data from all three treatments directly comparable. Nonmutant plants were recorded as zero and have no weight in the table except in the two cases when less than nine mutant plants were found. If the reduced number is due to poor expression, the data are valid; if due to chance variation from a 1:1 ratio, a

slight bias (not enough to change the significance of the observations) is introduced.

The plants from the cross Les/+ x Les2/+ (family 39) included Les, Les2, Les Les2 and normal individuals. Since both mutants can be observed in the double heterozygote, the data were recorded separately for each type; thus, the double mutant plants were scored twice. To test for reversal of the temperature effect the plants in the 72° chamber were changed to 84° conditions after the four-leaf stage when lesion expression at 72° had stabilized. Table 2 summarizes the large and small lesion expression of only the double mutant plants in family 39 from Table 1.

Table 2. Effect of temperature on the occurrence of lesions on successive leaves of Les Les2 plants only.

Family	Temp (°F)	Lesion type	Leaf number 1	2	3	4		5	6	7	8	Mut/N
39	72	Large	4	4	4	2	//	2	0	0	0	4/20
		Small	0	0	0	0	//	0	3	4	2	
	80	Large	4	4	4	3		2				4/19
		Small	3	3	4	4		3				
	84	Large	6	6	6	6		5				6/20
		Small	6	6	6	6		6				

//Temperature changed from 72°F to 84°F at the four-leaf stage.

A number of significant facts are evident from the data presented here.

(1) Les is expressed strongly on nearly all of the leaves of plants grown at 72°. At higher temperatures the lesions appear on the first few leaves but become less frequent with each succeeding leaf. Not expressed in the tables is the fact that the frequency of lesions per leaf varies widely and is inversely proportional to the temperature.

(2) For Les a change in temperature from 72° to 84° causes an abrupt halt in lesion appearance on subsequent leaves. The occurrence of lesions on the first two or three leaves of plants grown at higher temperatures may result from evaporative cooling of the soil and the lower plant parts.

(3) Les2 is expressed most strongly at 84° (more lesions per leaf as well as on a higher proportion of leaves) and less strongly at 80° and 72°, in that order. The low numbers in family 38 for leaf 1 at 80° and for leaf 5 at all temperatures resulted from temporary careless culture practices. Drought and low soil fertility have been observed to suppress lesion formation.

(4) Changing the growth temperature from 72° to 84° improves the expression of Les2, both in the frequency of lesions and in the number of leaves affected.

(5) Observations not expressed in the table show that the double heterozygotes have an intermediate phenotype with fewer and less striking large lesions and fewer small lesions, although both are clearly expressed.

(6) A comparison of large lesion plants from family 37 with the same type in family 39 (Table 1) shows no appreciable difference at the lowest temperature (72^{o}) but a marked increase in the expression in family 39 at 84^{o}. Table 2 shows this to be mostly due to the expression in the double mutant plants.

(7) The same comparison for the small lesion mutant (Les2) shows a striking reduction in the lesions on plants from the Les x Les2 cross (family 39) as compared to the backcross (family 38) at low temperatures while at the highest temperature there is no appreciable difference.

(8) Changing the temperature from 72^{o} to 84^{o} for the Les x Les2 material produces a striking and opposite reversal of expression for both lesion types; the effect is more abrupt and complete than in either family carrying the single mutants.

From these observations it can be concluded that Les is expressed best at low temperatures (around 72^{o}) and not at high temperatures, while Les2 is expressed best at temperatures around 84^{o} and reduced at lower temperatures. Changes in temperature may abruptly alter the expression of either mutant according to its prescribed response. Double heterozygotes have an intermediate expression with both mutants expressed at lower levels. In the double heterozygote the expression of Les2 is restricted or reduced at lower temperatures, while the expression of Les is enhanced in the higher temperature range. The Les x Les2 material also shows differences suggesting parental influence on the interaction of Les and Les2.

M.G. Neuffer

Comparative efficiency of seed and pollen treatments in mutation experiments — An important aspect of the design of mutation experiments is economy in terms of the plants to be handled in each generation. A common practice with autogamous plant species such as barley or Arabidopsis is to treat seed with a mutagenic agent, grow an M_1, self that to produce M_2 seed, grow the M_2 and look for mutant segregants. The size of the experiment is usually determined by a trade-off between the number of M_2 plants required to provide a statistically adequate sample and the number of plants that can be handled. With corn, which has separate male and female flowers (geitonogamy), the M_1 may be selfed or outcrossed to untreated material and the progeny in either case may be selfed to produce an M_3, which is examined for segregating mutants. The economics of the numbers grown in each generation and the samples taken is often not properly understood, but

it is directly dependent on the developmental pattern of the species being studied.

The proportion of mutant individuals appearing in the M_2 will depend on the number of primordial cells in the seed which contributes to the germ line. As shown in Table 1, the combined seed progeny of an M_1 plant may segregate 7:1, 15:1 or 31:1 with a germ cell number of two, four or eight, respectively, for

Table 1. The frequency of mutant individuals in the M_2 of an M_1 in which a mutant has been induced in one primordial cell for autogamous vs. geitonogamous plants with different primordial germ cell numbers.

	Germ cell number					
	1	2	4	6	8	10
M_2 ratio (autogamous)	3:1	7:1	15:1	23:1	31:1	39:1
M_2 ratio (geitonogamous)	3:1	15:1	63:1	143:1	255:1	399:1

autogamous plants and 15:1, 63:1 or 255:1 for the same germ cell numbers in geitonogamous plants. According to Anderson et al. (Genetics 34:639-646, 1949) and Steffensen (Amer. J. Bot. 55:354-369, 1968), the primordial germ cell number for the corn tassel is between four and eight, probably nearer eight. Since it is unlikely that a recessive mutant would appear in the M_2, the M_2 must be grown, selfed and tested. It has not been established whether the same primordial cells produce both male and female gametes, in which case the gametes would be mutually concordant, or whether different primordial cells are involved. Treatments applied and effective at the seed stage may affect any one of the primordial cells independently and produce a sector generating half normal and half mutant gametes. Assuming eight primordial cells and concordance, the population treated will be 16 genomes times the number of seeds treated. For those mutants having no selective effects 1/16 of the gametes from an M_1 plant undergoing a mutational event will carry the mutant. The M_1 plants may be either crossed to a standard strain or selfed, with the results indicated in Table 2 and discussed below.

If one treats 100 kernels, each carrying eight diploid primordial germ cells, the resulting M_1 plants will carry 1600 treated genomes. If the treatment produces mutants in 25% of the genomes (a frequency somewhat higher than is characteristically found for treatment at the seed stage, but used here in order to make equivalent comparisons with pollen treatment), then 400 mutants will have

Table 2. Comparison of the efficiency of different methods of treatment and handling for mutagenesis.

Treatment and handling	M_1 plants	Treated genomes	Mutants produced at 25% effectiveness	M_2 selfed	Mutants detected	Plants grown $M_1 + M_2$	Efficiency (Mutants per plant)
Seed: M_1 crossed; large M_2	100	1600*	400	4700*	380	4800	0.08
Seed: M_1 selfed; large M_2							
Concordance	100	1600	400	2300	380	2400	0.16
Non-concordance	100	3200*	800	4700	760	4800	0.16
Seed: M_1 selfed; minimal M_2							
Concordance	1000	16000	4000	1000	500	2000	0.25
Non-concordance	1000	32000*	8000	1000	500	2000	0.25
Pollen: M_1 selfed	2000	2000	500	--	500	2000	0.25

*assuming eight non-concordant primordial cells each for the tassel and ear
**required to detect 95% of mutants; 7200 would be required to detect 99%

been produced. Crossing the M_1 plants as female by a standard strain will produce 100 ears that will preserve all the mutants. The frequency with which the gametes and kernels will carry a particular mutant will be one in 16. A planting of these seeds with a subsequent self-fertilization will be required to express any recessive mutants. According to Hanson (Agron. J. 51:711-15, 1959), a sample of 47 individuals is required in order to have 95% certainty of obtaining one individual occurring at a frequency of one in 16. Therefore, to detect 95% (380) of the 400 mutants in the 100 ears will require planting 47 kernels from each ear, a total of 4700 plants to be selfed. Thus, an input of 4800 plants (100 M_1 plus 4700 M_2) will produce 380 mutants, an efficiency of 0.08 mutants per cultured plant.

Selfing the M_1 is more efficient than crossing by a standard strain. Assuming concordance, a double sample (from the ear and the tassel) is provided by each selfed M_1 ear, and only 23 M_2 kernels, or 2300 M_2 plants will give an efficiency of 0.16. With non-concordance, a self will provide one test each from two 8-celled primordial sets (ear and tassel) for a total of 3200 treated genomes and 800 mutants. These will require 4700 individuals to detect 760 mutants, resulting in an efficiency of 0.16, identical to the value for concordance. The tendency is to try to save all of the mutants by taking a very large sample from the M_1 ears, but this is counterproductive; for example, a sample of 52 kernels (5200 plants) would be required to save 99.9% of the mutants (efficiency 0.075). An additional problem arises from maximal sampling, namely the duplication and confounding of mutants. A single mutational event in a primordial cell will be duplicated many times through cell divisions before gamete formation, and many copies of the same mutant will be produced. For this reason, only one mutant of a particular type can be accepted in the progeny of each M_1 plant as a unique mutant. This is of considerable consequence, inasmuch as there are many loci whose recessive alleles have similar, confoundable phenotypes.

A more efficient sampling method from studies with Arabidopsis but generalized in application (G. P. Redei, Z. Pflanzenzuchtg. 73:87-96, 1974) is to treat large numbers of seeds and grow a large M_1 and then take a minimal sample from each M_1 for the M_2 to be selfed. For maize the minimal sample would consist of a single seed from each M_1 ear. Following previous assumptions, treatment of 1000 seeds will affect 16,000 genomes and produce 1000 plants that will carry 4000 mutants. Planting one seed from each M_1 will test 2000 gametes and save 500 of the mutants. In terms of total input, an investment of 2000 selfed plants (1000 M_1 and 1000 M_2) will yield 500 mutants for an efficiency of 0.25. Furthermore, since only one sample of two gametes is taken from each M_1 plant the

problem of duplicate copies is eliminated; if by chance (one in 256, again assuming concordance) both gametes contribute the same mutant, it will be homozygous immediately and will be recognizable as such.

An equally efficient approach with some additional advantages over that just presented is to treat pollen; an investment of less than 100 plants for treatment plus a test by selfing of 2000 M_1 plants will produce 500 mutants for an efficiency of 0.25 (slightly less because of the plants needed for the original crosses with treated pollen). Pollen treatment has several advantages: (1) Each mutant seen is an independent event, so that except for normal attrition all mutants produced are saved--this allows easy comparison of mutation rates and of the relative frequencies of different mutant types. (2) Variations among different lines or between sexes in primordial cell number are not a concern in the estimation and comparison of mutation rates. (3) Dominant mutants are easily recognized as such and are ready for immediate testing.

The economic advantage described here for minimum sampling in mutation experiments applies equally well to the development of elite lines for breeding programs.

M.G. Neuffer

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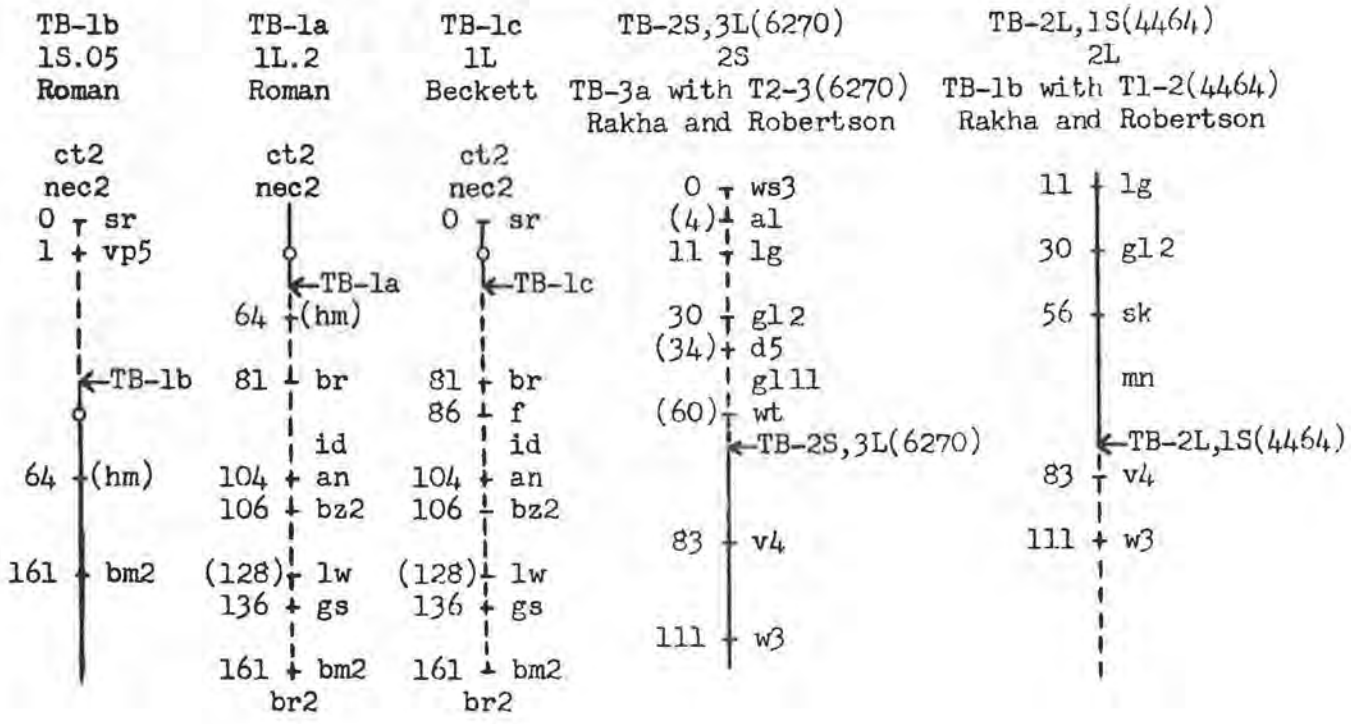
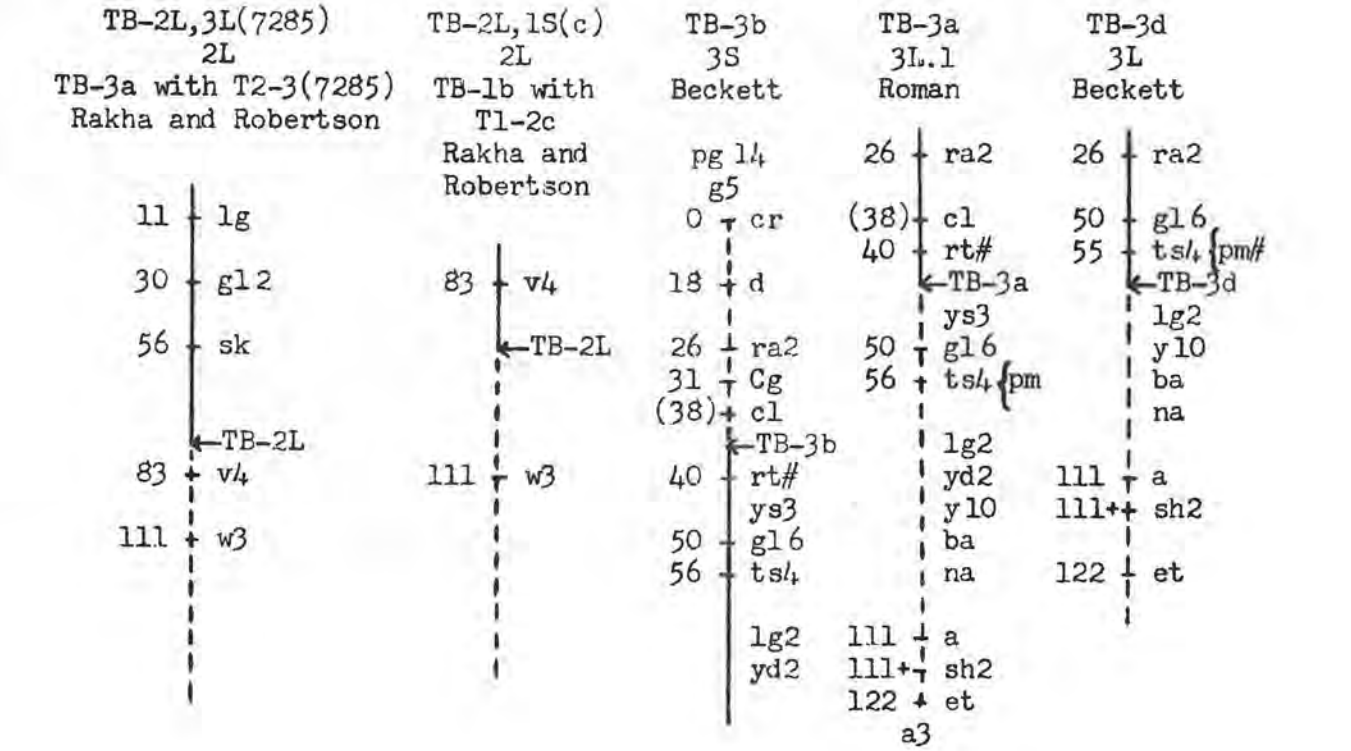
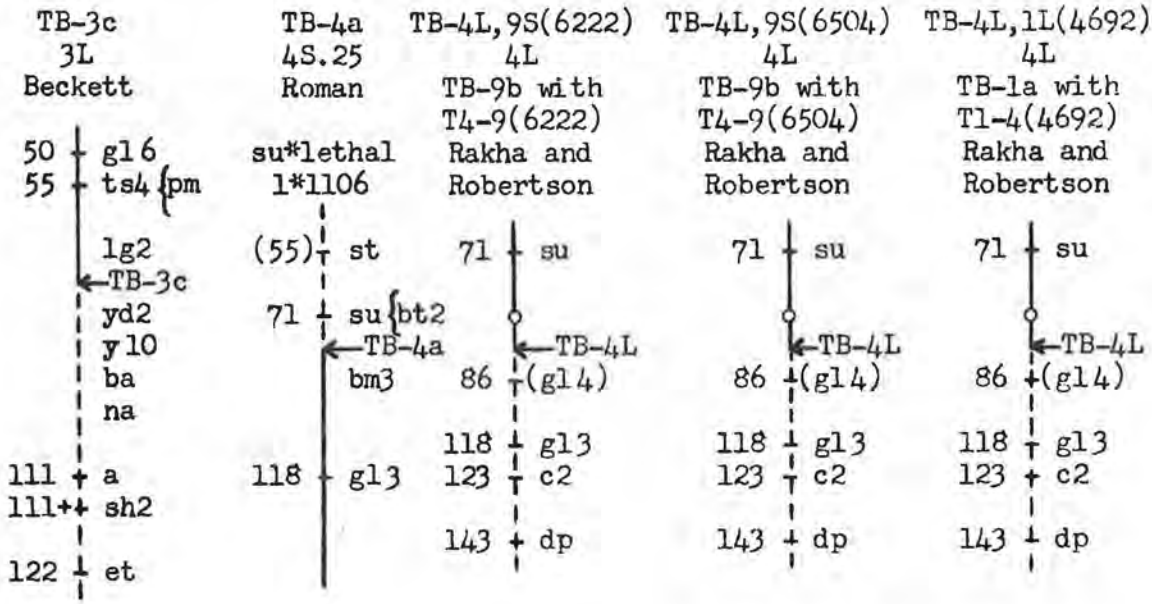
Genetic breakpoints of the B-A translocations of maize — The accompanying chromosome maps summarize the data I have collected on the genetic breakpoints of B-A translocations. The chromosome arm, cytological map position if known, and originator are given for each. The portion of each chromosome arm translocated to the centric segment of the B chromosome is shown as a broken line; therefore, all genes shown along the broken line were found to be "uncovered" by the translocation and all genes beside the solid portion were not uncovered.

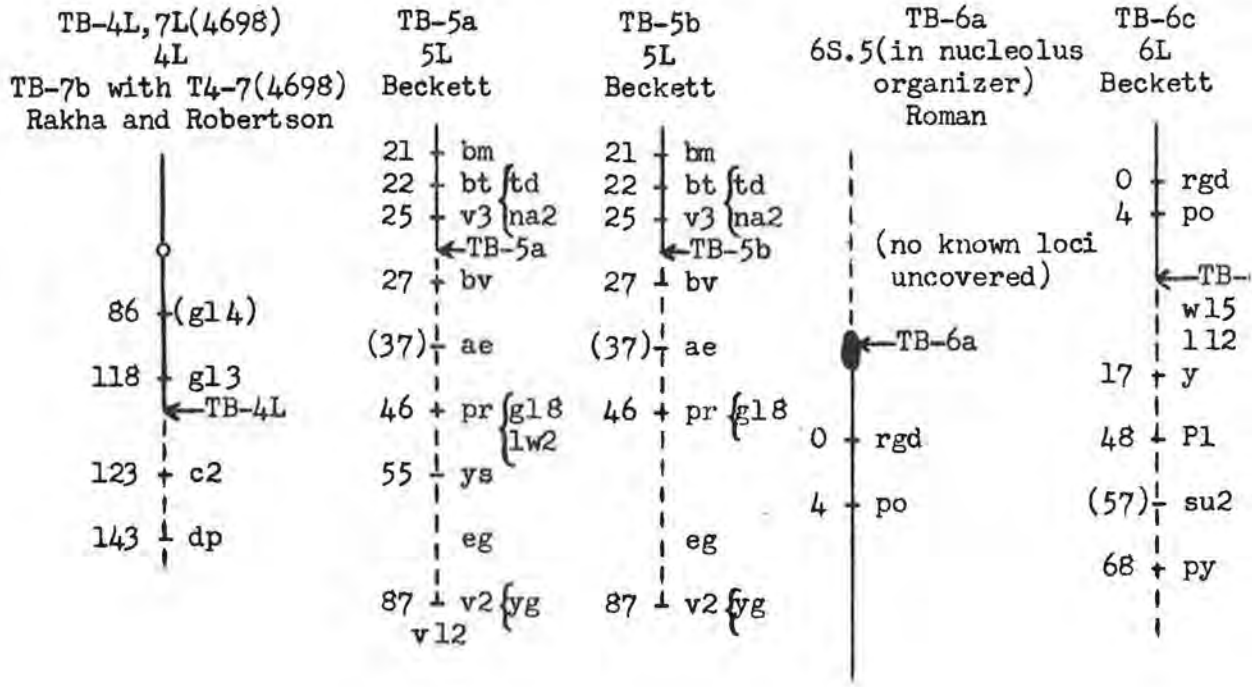
I have tested all loci listed with the exception of hm (tested by Roman and Ullstrup, Agron. Jour. 43:450-454, 1951), gl4 (tested by Rakha and Robertson, Genetics 65:223-240, 1970) and, for TB-10(18) and TB-10(19), zn and du (tested by Lin, MGCNL 48:182-184). Loci that should be retested for confirmation of position with respect to the B-A translocation are marked by the symbol "#". Map positions of loci are usually given, if known, and other factors are inserted in what is believed to be the proper place or listed at the end of the arm.

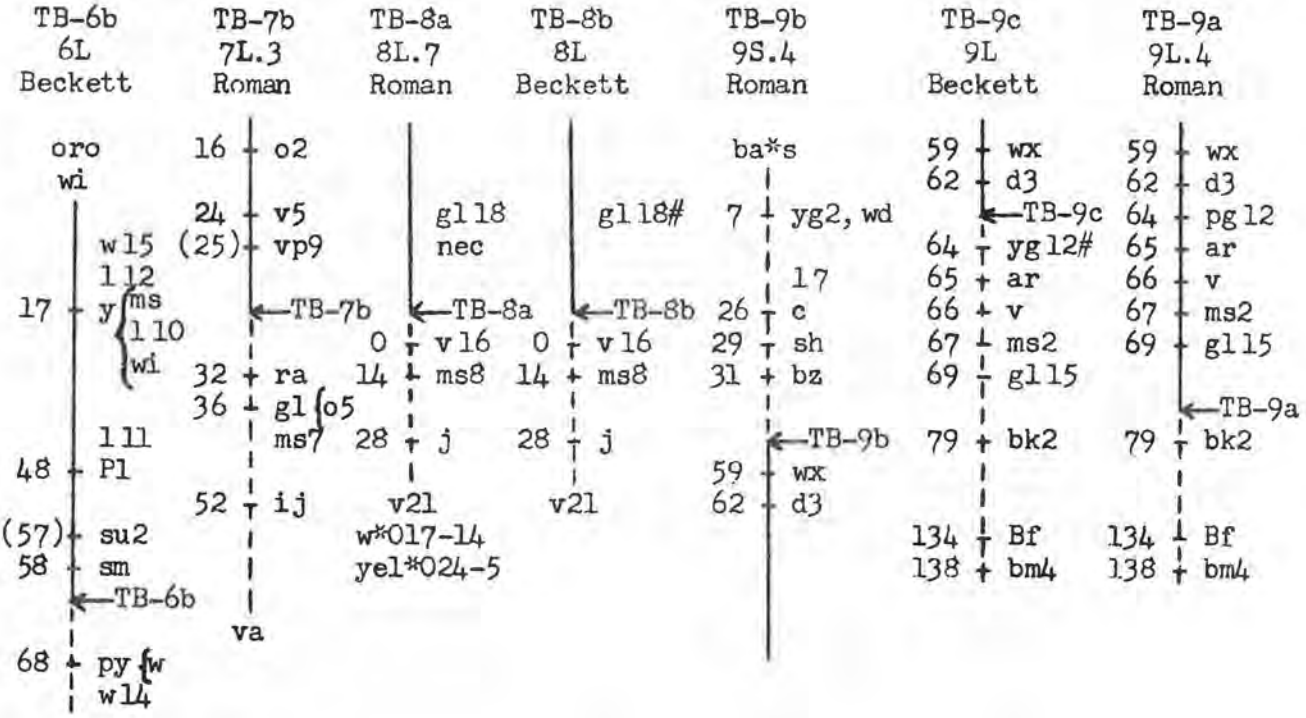
GENETIC BREAKPOINTS OF B-A TRANSLOCATIONS

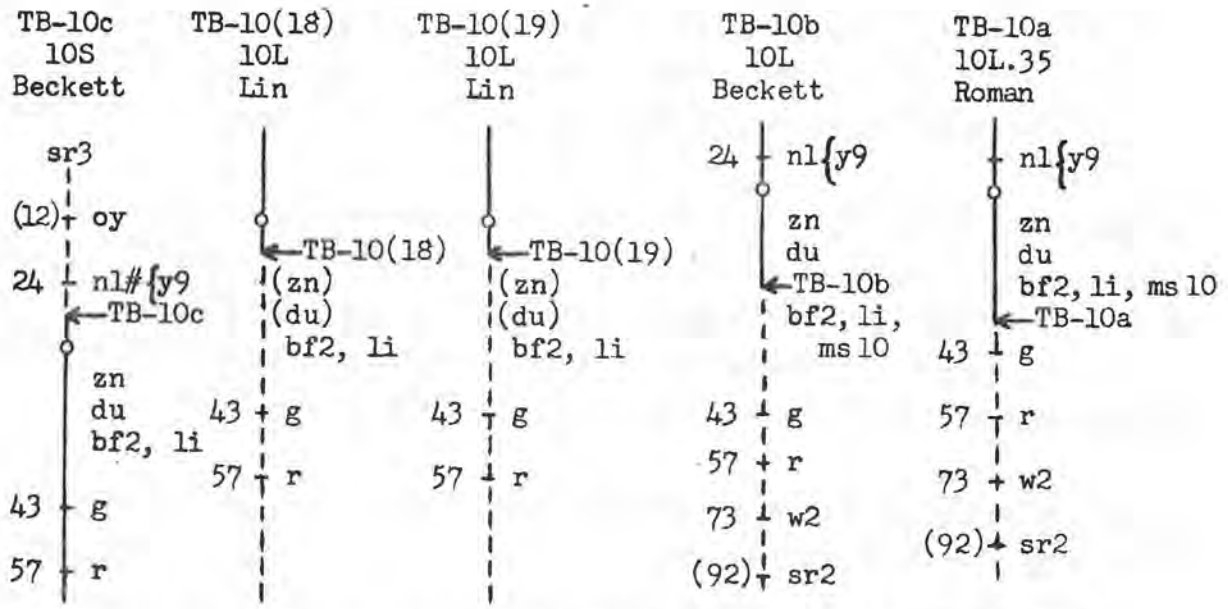





TB-3c
3L
Beckett
50 gl6
55 ts4 pm
lg2
TB-3c
yd2
y10
ba
na
111 a
111+ sh2
122 et
TB-4a
4S.25
Roman
su*lethal
1*1106
(55) st
71 su bt2
TB-4a
bm3
118 gl3
TB-4L,9S(6222)
4L
TB-9b with
T4-9(6222)
Rakha and
Robertson
71 su
TB-4L
86 (gl4)
118 gl3
123 c2
143 dp
TB-4L,9S(6504)
4L
TB-9b with
T4-9(6504)
Rakha and
Robertson
71 su
TB-4L
86 (gl4)
118 gl3
123 c2
143 dp
TB-4L,1L(4692)
4L
TB-1a with
T1-4(4692)
Rakha and
Robertson
71 su
TB-4L
86 (gl4)
118 gl3
123 c2
143 dp


TB-4L,7L(4698)
4L
TB-7b with T4-7(4698)
Rakha and Robertson
86 (gl4)
118 gl3
TB-4L
123 c2
143 dp
TB-5a
5L
Beckett
21 bm
22 bt td
25 v3 na2
TB-5a
27 bv
(37) ae
46 pr gl8 lw2
55 ys
eg
87 v2 yg
v12
TB-5b
5L
Beckett
21 bm
22 bt td
25 v3 na2
TB-5b
27 bv
(37) ae
46 pr gl8
eg
87 v2 yg
TB-6a
6S.5(in nucleolus organizer)
Roman
(no known loci uncovered)
TB-6a
0 rgd
4 po
TB-6c
6L
Beckett
0 rgd
4 po
TB-
w15
112
17 y
48 Pl
(57) su2
68 py





segment attached to centric portion of B chromosome (genes in this region are uncovered by the B-A translocation)

segment to which the distal portion of the B chromosome is attached (genes in this region are not uncovered by the B-A translocation)

o-centromere

●-nucleolus organizer

#-gene should be retested to confirm position

Herschel Roman's TB-7a (7L.95) is probably no longer extant. If anyone has viable seed, I would appreciate getting a small supply.

In addition to the translocations listed here, Lin (MGCNL 48:182-184) has reported 36 more B-A translocations on 10L.

Several changes in existing chromosome maps are required to accommodate the B-A translocation data; these changes are summarized as follows:

1. Although wt on chromosome 2 at map position 60 is uncovered by TB-2S,3L(6270), gs2 (position 54) is not, so the order of these 2 loci should be reversed. Tentative results indicate that sk may be uncovered, but the hypoploids produced by this translocation are often too weak to classify for this trait.

2. As reported in MGCNL 44:154-155, cl is uncovered by TB-3b, so the centromere must lie to the right of cl.

3. TB-3c uncovers ba (72) and y10(75), but not lg2(83), so lg2 must lie to the left of ba and y10.

4. As reported in MGCNL 47:145-147, tests with TB-10b and TB-10c place li in the long arm of chromosome 10. Lin's data (MGCNL 48:182-184) from TB-10(18), -(19) and -(26), establish that the order is centromere, zn, du; my data from TB-10b (MGCNL 47:145-147) establish that bf2, li and ms10 are next (the order within this group is still not known). Data from TB-10a and TB-10(32)(Lin) establish that g comes next, followed by r, as previously determined by ordinary linkage tests.

Although unlikely, it is possible that inversions on the translocated chromosomes may be present in some cases, giving an improper gene order. Therefore, appropriate linkage tests are needed to confirm the above conclusions.

I wish to thank R. H. Whalen for calling to my attention the need for bringing together my data on the genetic breakpoints of the B-A translocations.

J.B. Beckett

Knotted leaf mutants — Five new knotted leaf mutants have been identified. These mutants have been given the temporary designation of K-2, K-3, K-4, K-5 and K-6. K-2 and K-3 occurred as spontaneous mutations in the inbred line Mo14W. Both are similar in expression to the original knotted leaf mutant on chromosome 1 except that the severity of the knotting is much less. K-3 differs from K-2 by leaving large holes in the leaf surrounding the knotted areas.

K-4 knots only the ligule and occurred in a commercial hybrid. K-2, K-3 and K-4 behave as dominant genes. Allelism tests with the original knotted mutant so far have been inconclusive due in part to varying expressivity and penetrance.

The K-5 and K-6 mutants have small "cup like" intrusions parallel to the midrib on the upper leaves at about the time of tasseling. K-5 was found by

Dr. Grogan while he was at Mississippi State University, and he recently brought back the K-6 mutant from South Africa. K-5 behaves as a recessive gene, and Dr. Grogan observed K-6 to be partially dominant in some background genotypes.

We are converting seven inbred lines to the five new mutants along with the original knotted leaf mutant. Expressivity and penetrance of these mutants has been very unpredictable and appears to be highly affected by the environment. After we complete transferring these mutants into the same background genotypes, expressivity and penetrance studies are planned.

M.S. Zuber

Bz dosage effect on glucosyltransferase levels — In a previous note (MGNL 42:134) the presence of an enzyme uridine diphosphoglucose quercetin glucosyltransferase in maize pollen was reported. The enzyme catalyzes the addition of glucose to cyanidin or quercetin. In a second note enzymatic activity (MGNL 42:134) was found to depend on the presence of dominant Bz. Since that time the transferase has been extracted from mature seeds and seedlings of genotypes ranging from homozygous dominant to homozygous recessive. Table 1

Table 1. Glucosyltransferase activity.

Tissue and genotype	Specific activity[1]
Pollen Source	
Bz Bz	210
Bz bz	102
bz bz	0
Seedling[2]	
Bz Bz	308
Bz bz	157
bz Bz	151
bz bz	0
Embryo[2,3]	
Bz Bz	117
Bz bz	57
bz Bz	50
bz bz	0
Endosperm[3,4]	
Bz Bz Bz	2850
Bz Bz bz	921
bz bz Bz	484
bz bz bz	0

[1]Specific Activity = µgms. Isoquercitrin produced/hr/mg of protein.

[2]Heterozygotes derived from reciprocal crosses between homozygous strains; ♀ parent listed first.

[3]Endosperm and embryo samples derived from the same seeds.

[4]Heterozygotes derived from reciprocal crosses between homozygous strains; ♀ origin listed in first two symbols.

includes data for the various sources of enzyme and different genotypes. All enzymes are crude extracts except the seedling enzymes, which have been subjected to Sephadex G-50 gel filtration.

The data are quite conclusive in showing the same ratios for dosage of the dominant gene with specific-activity levels. The only exception to this is found in the homozygous dominant endosperm, where the gene dosage ratio is 3:2:1:0 and the specific activity ratio is essentially 6:2:1:0. The zero values for the homozygous recessive samples are real inasmuch as our procedures eliminate any contaminating nonspecific glucosyltransferase activity. In conclusion, Bz is clearly responsible for the glucosyltransferase activity and the activity follows a gene dosage ratio.

R.L. Larson and E.H. Coe, Jr.

Complex Glucosyltransferase Activity — Refinement of the purification processes for the glucosyltransferase (This MGNL, Larson and Coe) have led to several interesting discoveries: (1) non-specific contaminating glucosyltransferase activity could be eliminated; (2) the transferase exists in a complex with an as-yet-undetermined number of carbohydrate metabolizing enzymes; and (3) the complex appears to be large, with properties similar to an enzyme having a molecular weight in excess of 5×10^6.

Attempts to purify the transferase have yielded about a 40-fold purification and any efforts to improve on this have failed. Gel filtration using Sephadex G-50 or Bio-Gels A-.5m through A-15m all yield a single protein peak that elutes immediately following the void volume for that column. Centrifugation of the crude enzyme extract in water at 160,000 xg for 2 hours resulted in a 12 fold purification of the transferase, which remained in the supernatant. Centrifugation of this supernatant at 160,000 xg for 64 hours led to sedimentation of the enzyme complex and a supernatant devoid of any enzyme activity. This evidence strongly suggested a complex with possibly more than one enzymatic activity present. Acid phosphatase activity had been identified in our preparations prior to this time and subsequent studies have led to the identification of other activities.

Speculation as to what activities might be found associated with the transferase have focused on synthesis of the UDPG needed in the transferase reaction. Thus the enzymes assayed in the preparation included UDPG pyrophosphorylase for synthesis of the UDPG and enzymes needed to yield substrates for this reaction. These latter include nucleotide diphosphate kinase (UTP synthesis) and enzymes involved in synthesis of glucose-1-phosphate. The source of glucose remains a question as evidence has been obtained for phosphorylase activity that would

yield glucose-1-phosphate from starch and inorganic phosphate. In addition phosphohexoisomerase activity (fructose-6-phosphate⟶glucose-1-phosphate) and phosphoglucomutase (glucose-6-phosphate⟶glucose-1-phosphate) have been identified in our preparations. These enzymes would suggest possible utilization of sucrose as a source of glucose-1-phosphate, however the enzymes needed to cleave sucrose or sucrose phosphate to its monosaccharide components have not been identified. These activities have been identified chromatographically or by coupling the reactions with UDPG dehydrogenase or glucose-6-phosphate dehydrogenase. The activities described have been identified in pollen, seedling and seed preparations.

R.L. Larson

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Inheritance of susceptibility and tolerance to Leaf Freckles and Wilt (Corynebacterium nebraskense) of corn — A six-line diallel in 1973 and a seven-line diallel in 1974 were evaluated for reaction to Leaf Freckles and Wilt (LFW) disease, Corynebacterium nebraskense, in an effort to determine the mode of inheritance of resistance. Four resistant inbreds (B37, N10, N6 and H49), one intermediate (PC81) and one susceptible (B14A) comprised the 1973 experiment. Susceptible inbred A632 was added to the diallel in 1974.

The 1973 experiment was grown in two replications at each of three locations, Lincoln, Holdrege and Holbrook, in Nebraska. The latter two were planted on sites heavily infected with LFW in 1972 and were expected to become naturally infected. The Lincoln plots were artificially inoculated three times with a mixture of six isolates of the bacterium, and the Holdrege plots were inoculated once when no disease appeared by pollination time. Disease readings from individual plants in a plot were recorded on a 0 to 4 scale (0 represents no disease and 4 represents dead plant tissue) one to four weeks after inoculation in Lincoln and prior to desiccation at Holdrege and Holbrook. Means were computed for a maximum of 40 plants per plot. Considerable variation between inoculation dates was observed in Lincoln in terms of the overall disease level in the experiment, apparently due to environmental conditions following inoculation. Hot, dry environments at Holdrege and Holbrook resulted in very little disease development, even with the artificial inoculation at Holdrege.

The 1974 experiment was grown in two replications at Lincoln, and the plants were artificially multi-needle inoculated (See Calub et al., Crop Science 14:716-718, 1974) in the seedling stage with only the most virulent isolate rather

than with a mixture of isolates as used in 1973. Disease readings were based upon the same scale for 20 plants per plot in this experiment.

The inheritance of susceptibility and resistance appeared to be quantitative in nature, so the Gardner-Eberhart model was used to partition the variation among generation means into line effects (additive) and heterosis effects. When the analyses were conducted with parents included (Analysis II), heterosis effects were subdivided into average, line and specific heterosis effects. Without parents (Analysis III), general and specific effects were estimated.

Significant additive effects were detected in the analyses of the Lincoln data for both years and for the combined locations in 1973. This variation in parental contributions of homozygous loci amounted to 80.7-88.7% of the total variation among genotypes for the different analyses. Heterosis effects were significant only for the Lincoln data where syringe inoculation at pollination time was used, in which case specific heterosis effects accounted for 7.0% of the total variation. This was probably due to the specific effects of susceptible line B14A crossed onto the more resistant lines. Analyses with and without parents gave similar results.

Partial dominance for susceptibility to LFW is indicated by the fact that the F_1 readings of crosses between resistant and susceptible lines are generally greater than the midparent values.

Breeding techniques concentrating on additive gene effects should be effective in breeding for resistance to LFW. Testing over several locations is recommended due to significant genotype-by-location interactions. It appears, however, that LFW will become an economically serious disease only when plant injury occurs in conjunction with very warm and moist environmental conditions and the presence of the disease organism.

P.R. Martin, C.O. Gardner, A.G. Calub and M.L. Schuster

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Comparison of nuclear DNA from corn, Tripsacum and their hybrids — Tripsacum hybridizes with its relative, corn, and we have been able to characterize corn, Tripsacum and their hybrids for the buoyant density of nuclear DNA. It was of particular interest to determine if the parents of an intergeneric cross could vary in buoyant density and thus in their guanine + cytosine ratio. It was also important to make the rather novel comparison of parents versus hybrid with regard to buoyant density.

Corn-Tripsacum hybrids were made in the field by shortening the corn silks on the day preceding pollination with Tripsacum pollen. Harvested seeds were stored in a freezer and dusted with Arasan prior to germination in rolled paper towels. The germinated seeds were placed in expanded peat pellets until the plants were large enough to transplant to the field. Hybrids were easily identified by their gross and floral morphology.

Nuclear DNA was obtained and characterized for buoyant density as previously described (Shah and Levings, Crop Sci. 13:709-713, 1973). Nuclear DNA was isolated from purified nuclei to avoid contamination from organelle DNAs and to increase the yield. Buoyant densities were determined in neutral CsCl with Micrococcus luteus DNA as a marker on a Spinco model E analytical ultracentrifuge equipped with UV optics. Buoyant density values and the corresponding guanine + cytosine contents were calculated by using the equations described in the previous reference.

The corn parents involved in the cross were from the Bolivian race, Pororo, the nuclear DNA of which had a buoyant density of 1.702 g/cm^3 (Table 1).

Table 1. Buoyant density of nuclear DNA of corn, Tripsacum and their hybrids.

	Buoyant density g/cm^3
Parents	
Z. mays (Pororo)	1.702
T. dactyloides (64-48)	1.702
T. dactyloides (64-52)	1.701
Hybrids	
Z. mays (Pororo) x T. dactyloides (64-48)	1.702
Z. mays (Pororo) x T. dactyloides (64-52)	1.702

Previously, we had determined the mean density of DNA from several corn belt hybrids to be 1.702 g/cm^3, so Pororo appears to be typical of corn. Two different T. dactyloides parents, 64-48 (1.702 g/cm^3) and 64-52 (1.701 g/cm^3) were used in this study. The corn-Tripsacum hybrids both had densities of 1.702 g/cm^3. The difference between the 1.701 parent and the 1.702 hybrid was statistically significant at the 5% level. If it is assumed that these DNAs are composed of

only the four common bases, then buoyant densities of 1.701 and 1.702 g/cm^3 have molar percentages of guanine and cytosine of 41.8 and 42.8, respectively.

The nuclear DNAs of corn, Tripsacum and their hybrids consisted of single main bands with no satellites, as revealed by the neutral CsCl analytical centrifugation technique. This has been characteristic of all the grasses thus far studied.

The nuclear DNA of Tripsacum is similar to corn and other grasses in that they all have relatively high buoyant densities and thus guanine + cytosine contents. In one case, the intergeneric cross of corn and Tripsacum was successful despite the fact that its two parents differed by 1% in guanine and cytosine content; the hybrid between the two different parents resembled the high parent, corn,in buoyant density.

C.S. Levings, III, and D.H. Timothy

A fast renaturing fraction of nuclear DNA of corn — When DNA is melted and then allowed to renature for a short period of time, a fast renaturing fraction of the total DNA can be isolated. Using this technique we have isolated and partially characterized a fast renaturing fraction of nuclear DNA (nDNA) of corn.

Nuclear DNA was isolated and purified as previously described (Shah and Levings, Crop Sci. 13:709-713, 1973). The DNA was sheared, melted at 100^{o}C for 10 minutes and then allowed to renature (Cot = 1). Single- and double-stranded DNAs were separated by hydroxyapatite chromatography. Buoyant densities were determined in neutral CsCl with Micrococcus luteus DNA as a marker on a Spinco model E analytical ultracentrifuge (technique described in previous reference).

Under the conditions of this study (Cot = 1), a fast renaturing fraction of corn nDNA has been isolated which comprises about 11% of the total nDNA. Neutral CsCl analytical ultracentrifugation of this fraction revealed a single band with no satellite and a buoyant density of 1.708 g/cm^3; since total nDna has a density of 1.702 g/cm^3, the fast renaturing fraction is richer in guanine and cytosine than the main band.

C.S. Levings, III, and D.H. Timothy

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"Normal"-appearing sugary alleles — As part of my studies of kernel carbohydrates, I am incorporating various sugary alleles into the W64A inbred. During backcrossing I have been able to identify self-pollinated ears segregating for su-am or su-66. Both alleles have near-normal phenotypes but have a translucent halo-

appearance near the top of the kernel. Selection of these kernels with subsequent crosses of the plants to su-Ref have verified this observation. I would appreciate receiving any other independently occurring near-normal or semi-full su alleles to include in my investigation.

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C loss associated with bz-x3m — In the 1974 Newsletter it was reported that on C bz-x3m/c Bz kernels (bz-x3m was formerly bz-x3), colorless sectors and C-c breakage-fusion-bridge patterns were observed. This instability has been transmitted in a number of cases. The highest frequency of variegated kernels obtained so far was from ear #3234, a product of self-pollination on which the following classes were observed: 108 purple; 45 purple with few colorless sectors; 16 purple-colorless BFB patterns; 75 bz-x3m patterns; and 79 colorless. Some of the colorless kernels represented loss of the C allele in one sperm cell only since the scutellum was purple.

The expected phenotypic ratio if no loss of C is occurring is 1 bz-x3m pattern: 2 purple:1 colorless. If in the experimental population the purple and purple-colorless classes are combined, a 1:2:1 ratio results. Thus, the mosaic kernels do represent loss of the C allele on the C bz-x3m homolog.

Numerous additional ears exhibiting C loss on a chromosome 9 carrying bz-x3m have been observed. BFB patterns of Bz - bz-x3m have not been recovered, indicating that breakage is occurring only in the chromosome carrying C bz-x3m and not in the homolog with c Bz.

These observations suggest that an element (receptor) similar to Ds has become attached to chromosome 9 distal to the C locus. This element is responding to the regulator of bz-x3m by causing chromosome breakage. It is possible that the putative receptor element was originally part of the regulator and transposed away from the bronze locus.

In the self-pollinated progeny cited above, the frequency of C-c variegated kernels does not reflect the frequency of breakage in chromosome 9. Some of the kernels are c c C in constitution, resulting from fertilization of a c egg by a C sperm, but others are C C c produced by the reciprocal fertilization. In the c c C kernels breakage of the homolog carrying C will result in C-c variegation; but in the other class if loss of one C allele occurs the second is still there to produce pigment. Although a reduction in color intensity would result due to the

dosage effect of C, it is difficult to detect regularly.

Experiments are currently underway in which c Bz ear parents will be crossed with C bz-x3m individuals to produce c Bz/c Bz/C bz-x3m offspring. The frequency of C-c variegation in these progeny will represent the frequency of breakage in chromosome 9. Studies are also in progress to detect chromosome breakage cytologically.

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Purification and properties of genetically determined malate dehydrogenase isozymes — A large number of inbred lines have been examined, and eight strain-specific malate dehydrogenase (MDH) zymogram patterns have been found. The general isozyme pattern does not vary spatially or temporally within any given inbred strain, though quantitative differences are found. However, of the total number of isozymes present in any inbred strain, some are associated with the soluble cytoplasm (cytosol), some with mitochondria and some with glyoxysomes. The latter were found to be present only in scutella, while NADP-dependent MDH was found in leaf chloroplasts.

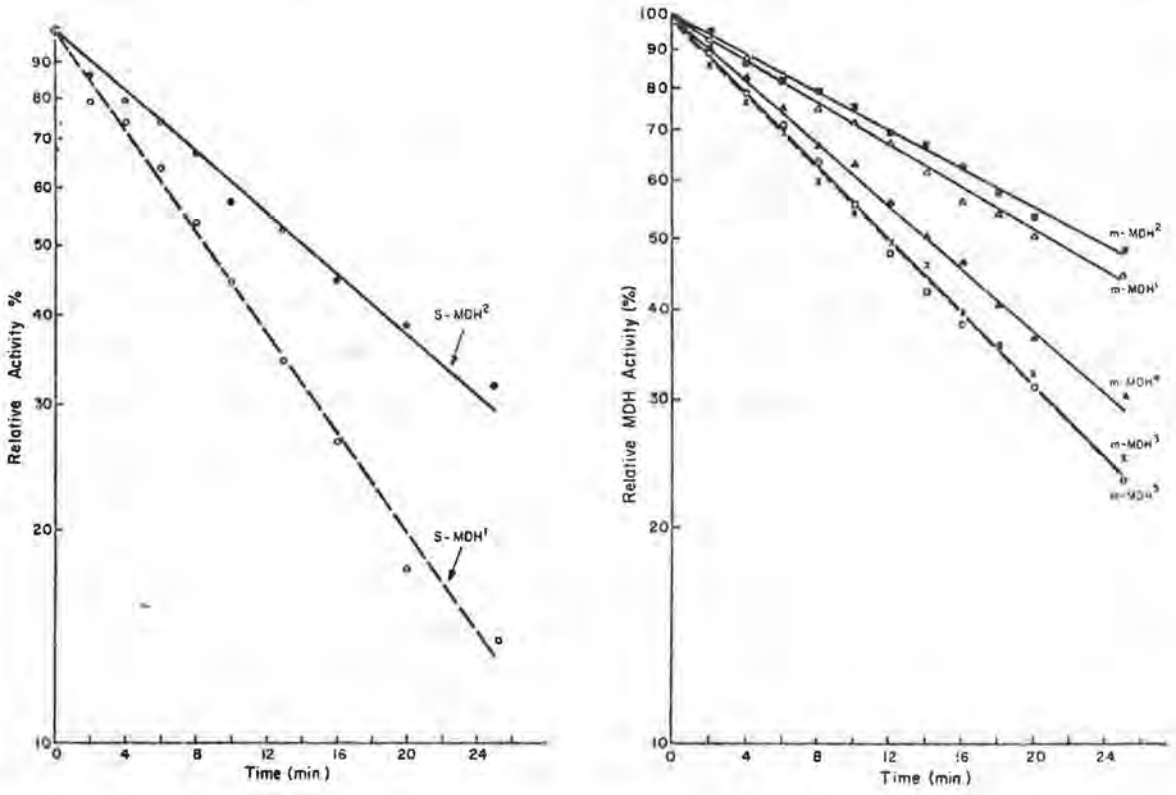
In strain W64A two soluble MDH isozymes (s-MDH), five mitochondrial MDH isozymes (m-MDH) and one glyoxysomal MDH (g-MDH) were found in scutella of etiolated seedlings. Both s-MDHs and m-MDHs were precipitated in 50-65% saturated ammonium sulfate. Fractionation on Sephadex G-150 columns shows that, by test tube assay, s-MDHs and m-MDHs come off as a single peak and therefore should have similar molecular weights. Detailed analyses of the MDH zymograms of the "peak fractions" indicate that m-MDHs come off a bit earlier than do the s-MDHs. The MDH isozymes thus partially purified were applied to DEAE cellulose columns. The seven MDH isozymes were separated into three major peaks by a linear salt gradient into two s-MDHs (s-MDH-1 and s-MDH-2), the three most anodal m-MDHs and the two most cathodal m-MDHs. The three peaks were then pooled separately and concentrated. Through the above mentioned purification steps the MDH isozymes in each peak were purified 200-300 fold. Using these three groups of partially purified MDH isozymes, experiments with reducing agents (100 mM mercaptoethanol), low pH treatments (pH 2.0) and high salt concentration treatments (7.5 M guanidine-HCl), along with

the genetic evidence so far obtained in our laboratory, have eliminated the possibility of conformational alterations to account for MDH multiplicity in maize. The isozymes of maize MDH are genetically determined. Molecular weight and isoelectric point determinations of the MDH isozymes were made on three highly concentrated MDH isozyme fractions. Using eight non-enzymatic protein molecular weight markers, gel filtration on Sephadex G-150 shows that s-MDHs and m-MDHs have molecular weights of 70,800 ± 1650 and 79,500 ± 1860, respectively. The pI for the different MDH isozymes ranges from pH 4.92 to pH 5.17.

The three MDH isozyme fractions were then subjected to starch gel electrophoresis; the MDH isozymes at the same peak on DEAE cellulose were thus separated clearly from one another. Each isozyme was then eluted from the gel by high-speed centrifugation. The seven isozymes were separated and highly purified in this manner; the biochemical properties of the seven forms were then examined.

It was found that both s-MDHs and the five m-MDHs have a pH optimum of about 8.5. Thermal inactivation curves indicate that the MDH isozymes vary in their thermolability (Figure 1). Michaelis constants (K_m) for OAA, malate, NAD^+ and

Fig. 1. Thermal inactivation of maize malate dehydrogenase isozymes at 53°C.
a) s-MDH's b) m-MDH's



and NADH of each isozyme were determined at pH 7.5, pH 8.5 and pH 9.5. In general the K_ms for OAA increase when pH increases, but the K_ms for OAA of the s-MDHs increase to a much greater extent than those of the m-MDHs. The K_ms for NADH are less dependent on pH. The K_ms for malate decrease when pH increases; however, the K_ms of m-MDHs are more affected by higher pH. For s-MDHs the K_ms for NAD^+ are almost independent of pH, but those of m-MDHs increase when pH increases. High concentrations of OAA (250 um) preferentially inhibit s-MDHs, but NAD^+ at high concentrations (500 um) seems to inhibit both s-MDHs and m-MDHs similarly. Both inhibitions are pH-dependent.

s-MDHs and m-MDHs are quite different in their capacity to use three NAD analogs as coenzymes (Table 1). Citric acid and isocitric acid inhibit only

Table 1. Catalytic activity of maize malate dehydrogenase isozymes in the presence of NAD or NAD analogs.

Coenzyme	Isozymes (Relative activity)*						
	s-MDH[1]	s-MDH[2]	m-MDH[1]	m-MDH[2]	m-MDH[3]	m-MDH[4]	m-MDH[5]
NAD^+	100	100	100	100	100	100	100
Deam-NAD^+	54.6	44.8	20.7	28.5	24.4	26.5	21.1
3-Ap-NAD^+	96.9	100.6	188	200	216.8	192.3	182.8
TN-NAD^+	241	253	18.3	21.4	21.8	21.1	21.5

*The data are the percentage of the reaction rates relative to NAD^+. Spectrophotometric assays were conducted with 0.75 mM NAD^+ or analog at 5 mM malate, 0.025 M Glycylglycine buffer pH 8.5.

m-MDHs; however, cis-aconitic acid and alpha-ketoglutaric acid inhibit both s-MDHs and m-MDHs. Reducing agents, chelating agents and monovalent metal ions are not required for the enzymatic activities of either s-MDHs or m-MDHs, but divalent metal ions may enhance MDH activities, especially for m-MDHs.

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On the regulation of alcohol dehydrogenase — The activity of many enzymes increases sharply after germination of maize seeds. However, alcohol dehydrogenase (ADH; EC 1.1.1.1) activity in the scutellum declines rapidly during this developmental period, indicating that there might be a unique mechanism for the control of ADH activity. Two possible ways for this to occur are (1) faster degradation (or inactivation) than formation of active enzyme molecules or

(2) only degradation (or inactivation) without further formation of active enzyme molecules.

We have noticed that the time-course of ADH activity after germination remains unchanged in the presence of a protein synthesis inhibitor (cycloheximide, 10ug/ml) or an RNA synthesis inhibitor (actinomycin D, 50ug/ml). This suggests that the control of ADH activity is independent of transcription and translation. Furthermore, by employing density labeling techniques we found that ADH molecules from seeds germinated in 70% D_2O and 10 mM $^{15}NH_4Cl$ for 36 hrs have exactly the same buoyant density as the ADH from seeds germinated in H_2O and $^{14}NH_4Cl$, clearly showing that there is no turnover of ADH molecules (at least for ADH-2, which is the most dominant ADH isozyme after germination). Thus, we have established that there is no de novo synthesis of active ADH molecules after germination. What then is the mechanism controlling the decrease in ADH activity? Is it due to degradation by a protease or the activation of a specific inhibitor? In reciprocal mixing experiments using the scutellar extract from early stages (e.g., 2 hr imbibed) and that from later stages of germination, we observed a significant decrease in the original ADH activity in the early stage extract, indicating the presence of an inhibitory substance(s) generated in the later stages of germination. The inhibition can be prevented by beta-mercaptoethanol; this in addition to other experiments eliminated the possibility that the inhibitor is a non-specific protease. The amount of inhibitor, assuming it is proportional to the extent of inhibition, increases steadily after 24 hrs of germination; simultaneously, ADH activity begins to decline. This fact leads us to propose that the generation of this inhibitor actually accounts for the decrease in ADH activity following germination.

The inhibitor is being purified by affinity chromatography, and preliminary data indicate that it is a protein of small molecular weight. A detailed account of the inhibitor and its role in ADH regulation is being published elsewhere.

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Substrate specificities and kinetic data for genetically defined maize aminopeptidases — Aminopeptidase isozymes from maize have been investigated with respect to substrate specificity and apparent K_ms. Four aminopeptidases — LAP-A, LAP-B, LAP-C and LAP-D — exist in maize and are resolved by starch gel electrophoresis; the maize aminopeptidases had earlier been designated by the restrictive name leucine aminopeptidase. A fast and a slow variant have been found for each isozyme. The direction of decreasing migration to the anode is A to D at pH 7.0.

Formal genetic analysis has shown that the LAP-A variants and the LAP-D variants are controlled by the LpA and LpD loci (Ed. note — Lp and Lp2 loci, respectively), and that the LpD and LpA genes are linked (Beckman, Scandalios and Brewbaker, Genetics 50:899-904, 1964).

Qualitative studies of the substrate specificities of the aminopeptidases were made by staining gel slices with various amino acid-naphthylamides as substrates. The source of enzyme was immature liquid endosperm from maize kernels collected 19 days after pollination. The LAP-A band preferentially cleaves the naphthylamide derivatives of the basic amino acids arginine and lysine. The B and C bands cleave the non-polar methionine, leucine and phenylalanine naphthylamide derivatives to the greatest extent as judged by the staining intensities of the zymogram bands. All other amino acid-naphthylamides are cleaved to lesser extents by one or more of the aminopeptidase forms except for the derivatives of histidine and the acidic amino acids and their amides, which are not hydrolysed.

In order to make quantitative measurements of aminopeptidase activity, the isozyme bands were cut individually from the starch gel; a 2mm gel slice was stained for aminopeptidase activity and then used as a template by placing it over the rest of the starch gel and cutting the stained regions out with a sharp scalpel. The starch strips were pressed through a syringe into a centrifuge tube and then spun at 35,000 g for 30 minutes. The supernatant was used as the source of aminopeptidase activity, which is assayed by a modification of the Goldbarg-Rutenburg method (Goldbarg and Rutenburg, Cancer 11:283-291, 1958).

Table 1-A shows the relative activities of the aminopeptidase isozymes separated in this manner toward arginyl-, leucyl- and alanyl-naphthylamide derivatives. For each isozyme the activity with the substrate most hydrolysed is given an arbitrary value of 100, and the activities toward the other two substrates are expressed relative to 100. The isozymes B_S and C_S run close together, and it is difficult to avoid cross-contamination completely when cutting the bands from the gels. This is probably the reason for the higher relative activity of the B_S variant toward leucine-NA and alanine-NA than B_F. Only data for the C_S variant are given because of lack of sufficient material from those lines having the C_F variant.

Table 1-B gives the apparent K_ms of the aminopeptidase forms. Where data are not available, the activity obtainable from the gel eluant was not high enough to make an accurate K_m determination for a particular substrate. The best fit linear regression line of substrate concentration^{-1} versus velocity^{-1} was used to calculate the apparent K_m; in most cases the values of two independent determinations are listed.

Table 1.

A. Relative activities of aminopeptidase isozymes toward three amino acid naphthylamides. The highest activity with a given substrate is expressed arbitrarily as 100 and the activities with the other substrates are given in values relative to 100.

B. Apparent K_ms for aminopeptidase isozymes for the given amino acid-naphthylamide.

A. % Relative Activity				B. Apparent K_ms		
Arginyl-NA	Leucyl-NA	Alanyl-NA	Isozyme*	Arginyl-NA	Leucyl-NA	Alanyl-NA
100.0	8.06	3.30	A_F	3.39×10^{-5} $2.58 \times$ "	---	---
100.0	7.66	4.93	A_S	$3.71 \times$ " $2.24 \times$ "	---	---
20.8	100.00	3.76	B_F	31.2×10^{-5} $22.4 \times$ "	8.14×10^{-5} $12.3 \times$ "	---
67.9	100.00	34.3	B_S	$29.3 \times$ " $28.2 \times$ "	$8.07 \times$ "	---
50.8	100.00	20.3	C_S	$29.3 \times$ " $26.4 \times$ "	$10.4 \times$ " $9.12 \times$ "	---
100.0	28.5	80.0	D_F	6.00×10^{-5} $4.81 \times$ "	---	57.9×10^{-5}
100.0	35.2	97.0	D_S	$5.88 \times$ "	---	$98.6 \times$ "

*The subscripts F and S refer to the fast and slow variants of the A, B, C and D aminopeptidases.

The aminopeptidases fall into three main groups. The LAP-A fast and slow variants, which hydrolyse arginine-NA and lysine-NA to the greatest extent, have a comparatively low K_m for arginine-NA. The B and C bands, which preferentially cleave non-polar amino acid-NA's, have consistently lower K_ms for leucine-NA than for the arginine derivative. The third group, LAP-D_F and LAP-D_S, have approximately equal maximal velocities for arginine-NA and alanyl-NA, but the K_m for alanyl-NA is considerably higher than for arginine-NA.

In addition to the relative velocities and K_ms for various substrates, we are also investigating the heat stabilities, pH optima and molecular weights of the isozymes and the effect of various chemicals on the aminopeptidases. The data obtained in these studies will be correlated with information concerning the genetic control of the aminopeptidases.

The LAP-A and LAP-D variants have a low K_m for arginyl-NA. This fact suggests that the A and D aminopeptidases possibly have a substrate-binding site that has

a high affinity for the basic amino acids. On the other hand, the B and C forms have lower K_ms and higher affinities for the non-polar side chains of some of the neutral amino acids. As mentioned previously, the LpA and LpD genes are linked (approximately 13 map units apart). The linkage relationships of the B and C loci and of the B and C loci to the A and D loci will be investigated, and we plan to determine the chromosomal locations of the aminopeptidase genes. The maize aminopeptidase system represents a potentially good system for correlating structural, biochemical and genetic information in an effort to understand possible evolutionary relationships between the aminopeptidase loci.

Lila A. Ott and John G. Scandalios

Quantitative catalase inhibitor variants — We have previously reported on a catalase-specific inhibitor in maize scutella which is involved in catalase regulation

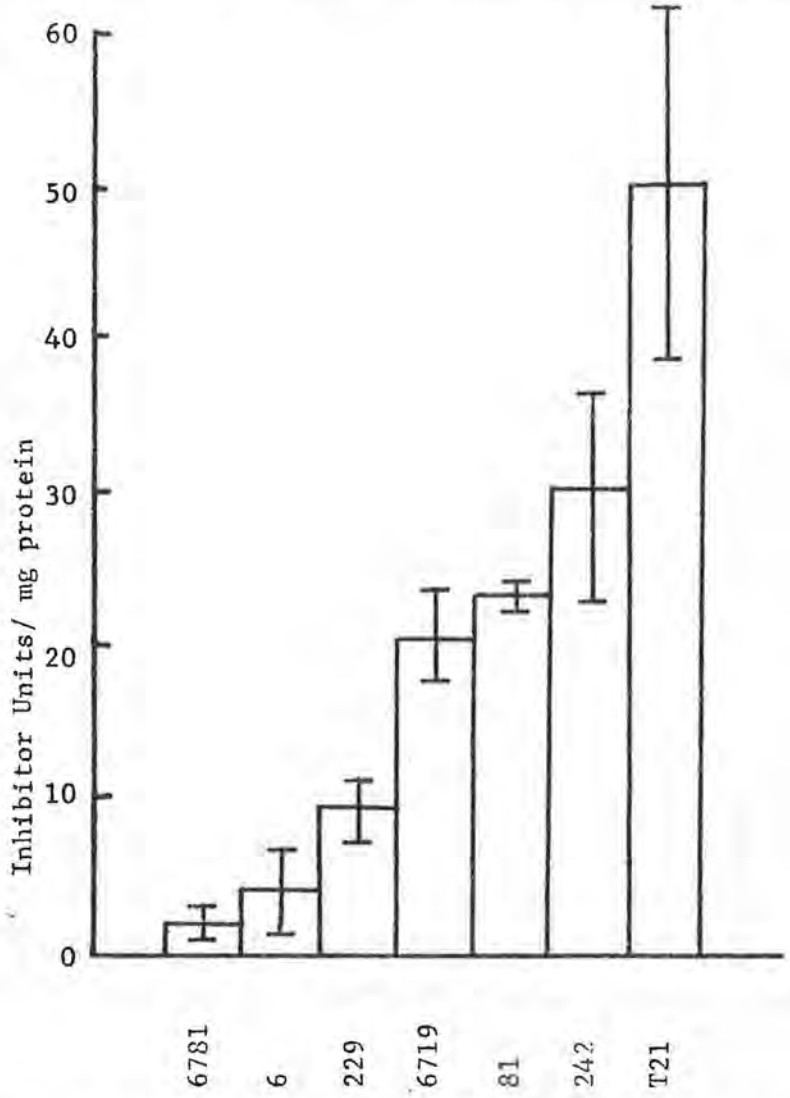

Fig. 1. Levels of inhibitor in various inbred maize strains. Error bars represent standard deviations of at least four replicates in two or three independent experiments.

during early seed germination (MGCNL Vols. 47, 48). The inhibitor has since been purified by affinity chromatography on immobilized catalase (Sorenson and Scandalios, Biochem. Biophys. Res. Comm., in press), and we have determined that it is a protein. We are currently screening inbred maize lines for quantitative inhibitor variants in hopes of defining the structural gene for the inhibitor. The results of the first screening series are shown in Figure 1 (preceding page). The inhibitor levels in these lines fall into three groups, 0-10 inhibitor units/mg protein, 20-30 i.u./mg and a high level group of approximately 50 i.u./mg for which the range has not yet been defined. Although there is only one inbred line in this category in the data presented, initial measurements of a second group of inbreds show several more lines which fall into the high inhibitor category.

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Effect of ethanol on meiotic chromosome behavior — Ethanol was introduced on filter paper into the tassel area at meiotic stages during a three-hour temperature elevation from about 25°C to 36°C. Microsporocyte samples were collected just before treatment, immediately following treatment, and at 5 hours, 7 hours, 24 hours and 48 hours following treatment initiation. Pre-treatment samples were found to be normal.

Desynapsis at synizesis and pachytene was common in all post-treatment samples, occurring with a distribution which suggests treatment damage of existing synaptonemal complexes. Decondensation was often found in chromosomes fixed at diplotene to metaphase I at all intervals following treatment. Bivalents were often dissociated to dyads or monads at metaphase I in 24-hour and 48-hour samples; nearly complete separation of bivalents to univalents was occasionally found at diakinesis in 24-hour samples. Polyspory was found at the quartet stage in a 24-hour sample.

Chromosome 10 rod bivalents at diakinesis were studied in material heterozygous for K10, collected and fixed immediately following treatment (material was therefore at late pachytene to diakinesis during treatment). In such rod bivalents open at the K10 end, the knob sometimes appeared to be disjunctionally separated and sometimes to be equationally separated (with a K10 knob at each end). This is considered to be evidence of treatment-induced chiasma failure following crossing

over between K10 and the centromere. It is not known whether treatment at pachytene reduces crossover frequency; further studies are in progress.

It is hoped that this report will draw attention to the apparent potential value of ethanol treatment techniques for the study of meiotic chromosome structure and behavior.

Stocks which have so far been subjected to ethanol treatment include KYS and Coop stocks heterozygous and homozygous for K10 and elongate (el). Similar effects were observed in all stocks with the following astonishing exception: frequent bivalent interlocking at diakinesis was found in a 24-hour sample from one el plant. This is described below.

Marjorie Maguire

Induced bivalent interlocking — In a sporocyte sample from a phenotypically el plant collected and fixed 24 hours after initiation of ethanol treatment (described above), clear bivalent interlocking at diakinesis was frequent. Diakinesis material collected from this plant before treatment appeared completely normal. From the affected sample 15 cells each showed two pairs of bivalents interlocking, four cells showed three pairs interlocking and four cells each had a chain of three interlocked bivalents; only nine cells were seen which had no evidence of interlocking at diakinesis. Many cells (119) contained chromosomes too clumped for analysis, and many of these may have been interlocked. Only five metaphase I cells were available in squash preparations from this sample; of these, one cell showed two sets of apparently interlocked bivalents, and one cell showed one pair of such bivalents.

It is unlikely that cells at diakinesis 24 hours after treatment initiation were less advanced than pachytene (complete synapsis) at the time of treatment initiation. Thus, bivalents probably already completely synapsed at treatment seem to have been induced somehow to interlock by diakinesis in many cells.

It is not known whether the el trait expression is in any way related to the bivalent interlocking seen. No such interlocking has been seen in diakinesis slides from another el plant similarly treated or from any other treated plants. Further studies are underway.

Marjorie Maguire

Possible clustering within anthers of sporocytes with crossovers in specific regions — A common impression among cytogeneticists who have examined large numbers of sporocytes in smear preparations is that cells with cytologically recognizable products of crossing over in specific regions tend to be found close together in pairs or larger clusters. This is unexpected since anther contents

are usually vigorously stirred in slide preparation, and there is no a priori expectation of similar crossover events in cells initially located close together. It seems very unlikely, however, that stirring during slide preparation actually produces order from randomness. Thus, true clustering of crossover cells in smear preparations is considered to be evidence of geographic clustering of such cells within the anther prior to slide preparation.

Data were collected on the distribution of anaphase I cells with the various observable crossover classes in smear preparations from plants heterozygous for paracentric inversion 5083. These classes include single crossovers within the inversion (single bridge and fragment), three-strand double crossovers within the inversion and proximal to it (fragment only) and 4-strand double crossovers within the inversion (double bridge and two fragments). The slides were systematically scanned and records were kept of the number of cells of each crossover class and of the number of cells of the no-observable-crossover class in each scan. A total of 1685 cells in 139 scans were scored. Results were subjected to analysis of variance. Variation between scans within anthers was found to be (1) significantly greater than random expectation for the proportion of cells with single crossovers within the inversion ($P < 0.01$), (2) borderline for the proportion of cells with three-strand double crossovers within and proximal to the inversion ($P \simeq 0.05$), and (3) well within random expectation for the proportion of cells with four-strand double crossovers within the inversion. For anthers with at least one event of the crossover class, variation between scans from the same anther was significantly greater than random expectation for the proportion of cells with three-strand double crossovers within and proximal to the inversion ($P < 0.01$), but not for the proportion of cells with four-strand double crossovers within the inversion (where error mean square was calculated to be greater than the mean square between scans within anthers).

Results thus support the interpretation that there is within-anther clustering of cells with crossing over within the inversion, at least of events of single crossing over within the inversion and of events of three-strand double crossing over within and proximal to the inversion.

The distribution of crossover classes with respect to each other within scans was also studied. Tests for within-scan correlations of frequencies for all combinations of crossover classes were negative. All estimates of r were close to zero. The three detectable classes of crossover events appear to be independently distributed with respect to each other within anthers. This is surprising since correlation of subsample frequencies for single and double crossovers would

be expected, with two obvious types of exceptions. One of these exceptions is the special case where effects on crossover frequencies in the two regions are approximately inversely related. In this case clustering of cells with double crossovers would not be expected, and variability in the frequency of doubles should be relatively small (both circumstances apparently contrary to present findings). The other type of exception results from the case where a large part of the variability in crossover frequency is due to factors which affect crossover interference with special constraints. The results are consistent with the suppositions (1) that classes of cells are somehow generated such that some are predisposed to crossing over within the inversion but not in the proximal region while others are predisposed to coincident crossing over in both regions and still others possibly to double crossovers within the inversion, and (2) that there is some tendency for cells of the same class to occur in groups of unknown size within the anther. Such a system accounts for clustering of cells of each crossover class in the absence of correlated distribution of cells of the various crossover classes. An economical alternative explanation (short of gross sampling error) has not yet been conceived by me.

Marjorie Maguire

UNIVERSITY OF TOLEDO
Department of Biology, Toledo, Ohio

An interchromosomal effect in maize — The effect of structural chromosome rearrangements on recombination in heterologous chromosomes has been well documented in a variety of organisms (see Lucchesi and Suzuki, Annual Review of Genetics, 1968, 2:53-87). Although this phenomenon, termed the interchromosomal effect, has been reported in maize (Bellini and Bianchi, 1963, Z. Vererbungslehre 94:126-132; Ting, 1963, Genetics 48:913-914), its properties and characteristics in corn remain to be explored.

We report preliminary data obtained with two paracentric inversions ($In2e^{S}$ and In3c), which were supplied by Dr. Greg Doyle. Recombination was studied in the short arm of chromosome 9, delineated by the markers c-sh-wx. Heterozygous inversion stocks were crossed to c sh wx. The resulting structural heterozygotes and their normal sibs were then backcrossed to the same tester.

In order to determine whether or not backcross differences were randomized, Chi-squares for heterogeneity were calculated. Among the normal sibs from either inversion, good homogeneous fit in both the c-sh and sh-wx regions was found. For the c-sh region, in the inversion heterozygotes homogeneity was also found.

However, for the sh-wx region the inversion heterozygotes from either $In2e^S$ or In3c proved to be heterogeneous.

For both regions the inversion heterozygotes and their normal sibs were pooled and tested for fit to a pooled $\overline{P}_{In2e^S+N2e^S}$ and $\overline{P}_{In3c+N3c}$. Among the pooled groups only two were not homogeneous, the c-sh region of In3c and the sh-wx region of $In2e^S$.

Table 1. Recombination and coincidence in testcrosses of inversion heterozygotes and normal sibs.

Inversion	Parental gametes	Reg. 1 singles	Reg. 2 singles	Doubles	Total	Recombination % Reg. 1	Recombination % Reg. 2	Coincidence
In3c	856	103	285	30	1274	8.1	22.4	1.30
Normal sibs	646	54	222	8	930	5.8	23.9	.62
$In2e^S$	575	45	157	9	786	5.7	20.0	1.01
Normal sibs	1359	86	361	10	1816	4.7	19.9	.59

Table 1 shows the backcross results. Although total recombination in the two regions tested was unaffected, multiple exchanges appear to be increased in the inversion heterozygotes. In order to determine whether or not the increase in multiple exchanges was significantly different from the number of multiples in the normal sibs, the probabilities of occurrence of the observed number of double exchanges in the inversion heterozygotes were calculated from Stevens' binomial-Poisson distributions. The frequency of double exchanges in the normal sibs was used as the expected number. For both inversions the number of multiple exchanges was significantly increased. In In3c heterozygotes the probability of obtaining the observed number of double exchanges was less than .005, and in $In2e^S$, 0.39.

C.M. McKinley and S.L. Goldman

UNIVERSITY OF VICTORIA
Department of Biology, Victoria, B.C., Canada

Brown pericarp — We presently have two stocks giving brown pericarp, phenotypically similar if not identical. One stock was obtained from the Coop as Sh bp wx P-RR, and the other segregated from stocks originally obtained (also from the Coop) as P1 a A2 C R B. After growing out and testing these stocks for two years, we have concluded that the brown pericarp phenotype requires a a for its expression. We would be interested in knowing whether anyone else has information that would confirm this. Flavanones are present in fresh cob and pericarp

tissue of these plants prior to the formation of the brown colour, but it is not yet clear how this flavanone build-up is related to the formation of the brown pigment. As expected from a a tissues, there are no 3-deoxyanthocyanins or 3-deoxyleucoanthocyanidins, but there are substantial amounts of C-glycosyl-flavones present.

E. Derek Styles and Oldriska Ceska

The action of P1 in maize (an hypothesis) — There appear to be three main phenotypic effects of the P1 gene in our W22 stocks: 1) P1 greatly enhances the amount of anthocyanins produced in the mature leaves of plants capable of producing pigment but by itself has no ability to produce anthocyanins. 2) In stocks capable of producing anthocyanin, as a given leaf matures, pigment production commences earlier in p1 stocks than in otherwise similar P1 stocks. This has been termed a repression of pigmentation of P1 (MGNL 48:153). 3) Anthocyanin-producing P1 stocks demonstrate a sunlight-independent production of anthocyanins in leaves and pericarp.

Further examination of the P1 action in leaf tissue of the mature plant has provided information suggesting a possible biochemical function of the P1 gene. We have measured the effects of P1 on leaf sheath pigmentation in r-g B and r-r B-b stocks by weekly analysis of each leaf from plants of two replicate families. Samples were taken from 3-4 weeks pre-anthesis to 4 weeks post-anthesis. Optical density measurements were made on acidic methanol extracts from each leaf and were corrected for weight differences between families. We found that the maximum P1 effect in individual leaves (in terms of percent increase over p1) increased in magnitude up to the time at which the eleventh leaf had reached its maximum pigment-producing capability. This corresponds with anthesis on a developmental time scale. In leaves developing later than this, the percent increase due to P1 remains constant, despite an overall decrease in the maximum amount of anthocyanin present in these leaves.

We have postulated and are presently testing the following hypothesis for the biochemical action of P1. P1 may constitute a "by-pass" loop along the normal pathway of anthocyanin production. In tissues without P1 pigment is being produced at a rate determined by the steps of the normal pathway beyond the by-pass loop branch point; in this case, precursors to the branch point would not be limiting. If P1 is present, however, the alternate loop is engaged and the precursors are preferentially fed into the loop at the expense of the normal pathway. Due to the increased flow of precursors through the loop, the precursor concentrations are now limiting and the flow through the normal pathway is reduced.

The flow through the by-pass loop must also involve systems that delay the production of the anthocyanin end product. The time-lag associated with the loop may be due to a secondary cycling pathway with developmental interactions or may simply be explained by enzyme kinetics. This suggests that the initial pigment-producing phenomenon may be due not to a repression by P1 but instead to a time lag in pigment production inherent in the by-pass loop system, coupled with a decrease in function of the normal pathway. The by-pass loop must rejoin the normal pathway before the point of action of the B gene because of two observations: 1) The magnitude of the P1 effect is proportional to the amount of pigment produced in the leaf tissue. 2) No leaf pigment is produced in b P1 plants. The sunlight-independent effect of P1 may result from the by-passing of a light-requiring reaction involved in the normal pathway of anthocyanin production.

In conclusion we suggest that an alternate biochemical pathway might explain the pleiotropic effects of P1 in repressing and enhancing anthocyanin production and at the same time allow for a single biochemical action initiated by P1.

David J. Kyle and E.D. Styles

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Primary non-homologue association among somatic chromosomes — From an extension of the study and refinement of the analysis presented earlier (MGCNL 48:165-167, 1974), we report evidence for primary non-homologue association. The "affinity distance values" (ADV) for the homologues and their grouping, based on the Tukey hsd procedure, from four cold-arrested stocks are:

Chromosome	ADV ± S.E.	Group*
X	34.9 ± 2.2	A
VII	35.7 ± 0.6	
II	35.9 ± 1.5	
III	37.9 ± 0.4	B
IV	38.4 ± 0.3	
IX	39.8 ± 0.3	
VI	41.2 ± 0.2	C
V	41.5 ± 0.8	
VIII	41.9 ± 0.4	
I	43.7 ± 1.0	D

*an hsd of 1.9 is required for $p \leq 0.05$

All non-homologue comparisons were also made. Eleven of 45 means exceeded the hsd value of 3.1 required to declare a mean significantly different from the

theoretical value of 45.3. This total of 11 means exceeds the two expected (5% level) and constitutes statistical argument for the presence in maize of primary non-homologue association.

In the presence of agents which disrupt microtubules, all the homologue ADV's were increased and the number of significant means of comparisons among non-homologues was reduced from 11 to one; i.e., the distributions became random.

J.D. Horn

Effects of cycloheximide on the frequency of somatic polar metaphase observed — We have found that a short pulse of cycloheximide resulted in a marked increase in the frequency of observed polar metaphase. The sensitivity of the cell to this treatment was cell-cycle time specific. A 15-minute cycloheximide treatment (75 ug/ml) at the beginning of prophase resulted in a marked increase in polar metaphases at 45-60 minutes post-treatment at 27°C and at 135 minutes post-treatment at 18°C (Table 1). We interpreted these results as being indicative of a cell-cycle time specific event.

Table 1. Dividing nuclei (%) following cycloheximide (15'; 75 ug/ml) treatment.

Control	Stage	Minutes following treatment							
		27°C				18°C			
		0	30	60	90	0	30	90	135
60	Prophase	42	61	55	68	57	68	76	63
21	Metaphase	36	18	15	5	24	18	18	6
6	Polar metaphase	6	15	25	27	7	6	6	31
7	Anaphase	8	4	3	0	6	4	0	0
6	Telophase	8	2	2	0	8	4	0	0

Cycloheximide is an inhibitor of protein synthesis. The proteins necessary for coiling of the somatic chromosomes are presumably already synthesized by the time of the onset of prophase since normal-appearing metaphase chromosome morphology is evident in cycloheximide-induced polar metaphase nuclei. Proteins necessary to uncouple the chromosomes from the nuclear membrane, for the breakdown of the nuclear membrane and for spindle fiber synthesis are not produced after the challenge with cycloheximide.

J.D. Horn

Description of chlorophyll mutants by in vivo spectrophotometry — Virescent chlorophyll mutants have long been recognized for their potential not only as genetic tools but also as vehicles for the study of development of the photo-

synthetic apparatus. Little of this potential has been realized, however, due in part to the absence of an adequate method for quantification of the greening process. Not only does the coloration of virescent mutants change with time, but both the rate and pattern of color development are subject to environmental control. We have found that there are limitations to the traditional methods by which the status of greening is determined by extractable chlorophyll. The purpose of this report is to describe a rapid and convenient method for description of virescent phenotypes, based on absorbance characteristics of chlorophyll in the tissue.

The method involves determination of an absorbance index (AI) calculated from an in vivo absorption spectrum and takes advantage of the increasing availability of spectrophotometers designed to accommodate dense, light-scattering samples. In our system a small disk (5 to 7 mm diameter) is punched from the leaf with a cork borer. The absorption spectrum of the disk is recorded over the range 650 nm to 750 nm, and the difference in absorbance is calculated between the chlorophyll peak (675 nm) and the long wave-length minimum (735 nm). The absorbance difference (read to 2 decimal places) is multiplied by 100 to remove the decimal and the resulting value is taken as an index of chlorophyll content.

In order to obtain valid absorbance measurements with dense, light-scattering tissue, it is necessary that the instrument have a high efficiency of light collection and a low-noise photomultiplier circuit (see Butler, W.L., Ann. Rev. Plant Physiol. 15:451-470, 1964). An increasing number of spectrophotometers which will accommodate light-scattering samples are commercially available. We use a Biospect 61 scanning spectrophotometer (Agricultural Specialties Co.) fitted with a Hewlett-Packard 7035B X-Y recorder. Stray light is limited by sample holder design which, while allowing the measuring beam to pass through the disk, restricts light leakage around the edge of the disk. Light collection is enhanced in that the sample is closely juxtaposed to the surface of a large (ca. 2-inch diameter) end-window photomultiplier tube. The Biospect is a single-beam instrument which employs an electronic compensation network for baseline adjustment. We use filter paper, which has approximately the same density and scatter properties as the corn leaf, as a reference for setting a flat baseline. Spectra are usually recorded over full scale ranges of 1.0 or 2.0 A. Total absorbance at the 675 nm peak frequently exceeds 3.0 A so that a zero offset must be used to bring the sample on scale. Thus, the absolute absorbance values at 675 nm and 735 nm include system response and have little meaning. However, subtraction of one from the other ($A_{675} - A_{735}$) cancels out the system response

and the resulting difference is an accurate and valid absorbance measurement.

Among the major advantages of this method is its speed. One minute or less is required for each sample, far less time than is required for traditional chlorophyll extractions.

There is, however, a significant correlation between the in vivo AI and extractable chlorophyll levels. In the experiment presented in Table 1 an AI was obtained for each of four disks harvested as a group from various leaf sources. The four disks were then pooled and chlorophyll extracted and quantified by Arnon's method, using absorbance at 652 nm (Arnon, D.I., Plant Physiol. 24:1-5, 1949). In Table 1 the extractable chlorophyll values are compared with the mean absorbance index (AI). A departure from linearity is observed above an AI of approximately 100 to 120, a deviation which is common with dense, light-scattering samples.

Table 1. Comparison of AI with extractable chlorophyll.

AI	60	74	83	107	123	138	148	196
Chl (mg/gfw)	0.75	0.90	0.98	1.36	1.63	2.00	2.20	3.93

The use of an in vivo AI to describe the status of a greening system provides an essentially non-destructive assay. For example, the very same tissue sample from which the AI has been obtained may itself be used for further analysis of interest to the investigator, such as in the experiment described above. Furthermore, small disks may be taken from leaves without injury to the plant. The same leaf or plant may then continue its development and be available for sampling again at a later date.

Finally, using the in vivo AI, it is possible to quickly and accurately construct a profile of a leaf or whole plant. We have done this with Oh 43 and with the virescent mutants v, v16 and v18 in the Oh 43 background. The results show quite clearly that the pattern of greening in leaves of both v16 and v18 is essentially like that of the wild type, in which the old cells near the tip accumulate the highest levels of chlorophyll with a gradual decrease in chlorophyll content toward the base of the leaf. In the v leaf, however, the pattern is essentially the opposite, indicating a significantly different developmental program. Thus, with this in vivo AI method we can now describe, with far greater simplicity and precision, the patterns of development in virescent and other

chlorophyll mutants and determine the influence of environmental parameters on the expression of the virescent (or chlorophyll deficient) phenotypes.

W.G. Hopkins, D.B. Hayden and D.B. Walden

Requests for seed — 1. We are interested in observing the 'ABPHYL' syndrome (AJB 59:466-472, 1972) in several different leaf size and leaf arrangement backgrounds. We would appreciate receiving a few seeds of such isolates, whether the isolates be specific mutant stocks or unique inbreds.

2. As indicated in the preceding report, we have techniques at hand which permit quantification of the greening processes in plants. Mutants such as virescents are now more amenable to analysis. We are interested in examining any virescent mutant and shall be prepared to perform tests of allelism with known mutants. I shall be grateful to colleagues if they would make available to us some seed of any virescent line unless they obtained the stock earlier from the Coop.

D.B. Walden

UNIVERSITY OF WINNIPEG
Biology Department, Winnipeg, Canada

The effect of K10 on chiasmata — It has been shown that K10 promotes crossing over in proximal regions of certain chromosomes, but the data are not yet inclusive enough to say that all chromosomes are affected similarly. A study of the effect of K10 on the number and distribution of chiasmata was undertaken to investigate the influence of this accessory chromatin on the total genome.

Sporocytes were taken from a line segregating k10 k10 and K10 k10, and chiasmata were studied at metaphase I. Data were collected from ten cells in nine plants each of k10 k10 and K10 k10. A chart was constructed with a schematic representation of tetrads having various numbers of proximal and distal exchanges, and a tally was made of the number of each of these tetrad types. For each genotype an average was obtained for the number of distal exchanges and proximal exchanges and the total number of chiasmata (Table 1). Statistical analysis was done by means of a t test.

Table 1. Effect of K10 on chiasmata.

	Average chiasmata per cell			Total number of chiasmata		
	distal	proximal	total	distal	proximal	total
k10 k10	7.73	11.06	18.78	696	995	1691
K10 k10	5.54	13.87	19.42	499	1249	1748
P	<.001	<.001	<.01			

The results suggest that K10 not only enhances chiasma formation but also causes a shift in chiasmata to more proximal positions. An increase in proximal exchanges would not be unexpected with the increase in total chiasmata, since any additional exchange would be more proximally located. However, the data indicate that the distal chiasmata are decreased under the influence of K10, demonstrating that normally distal exchanges have become proximal. Thus, these data confirm that K10 enhances chiasma frequency and causes a redistribution of chiasmata to more proximal positions.

These results do not indicate with certainty that all chromosomes are affected in the same way, because the chromosomes were not identifiable. However, they add substance to that interpretation.

Edward Ward

UNIVERSITY OF WISCONSIN
Laboratory of Genetics, Madison, Wisconsin

Enhanced phosphate content of amylose-extender starch — In 1928 R. A. Brink (Biochemical J. 22:1349-1361) reported that maize starch contained only one-twelfth as much organic phosphate (0.0015%) as did the starch from non-waxy seeds (0.0194%). This report prompted an examination of the phosphate content of the starches produced by seeds of several different genotypes.

The starches were prepared by the method of McGuire and Erlander (Die Staerke 18:337-341, 1966). The phosphate content was measured by the method of Ames (Methods in Enzymology 8:115), and the amylose content of the starches was measured by the method of Ulmann and Augustat (Z. Anal. Chem. 162:337-344, 1953). The results of the analyses are presented in Table 1.

Our results do not support the previous observation of a lower phosphate content in amylose-extender starch that is appreciably higher than that found in non-mutant starch or in the starch from other mutants with the possible exception of sugary. The ae mutants assayed here are derived from independent mutational events at the locus; neither is the reference ae allele.

It is not clear what this elevated phosphate content indicates since the starch components have not been separated to ascertain whether the increased phosphate content is confined to the amylose or amylopectin fraction or is characteristic of both. It may, however, provide a clue to those who are interested in the effect of the ae mutation on starch synthesis.

Table 1. The amylose and phosphate content of starch preparations from seeds of various genotypes.

	% Amylose	% Phosphate
+/+ (W64A x 182E)	25	0.007
wx-C/wx-C	0	0.006
du-6902/du-6902	33	0.010
du-6901/du-6901	31	0.012
ae-6901/ae-6901	49	0.019
ae-6902/ae-6902[a]	36	0.022
ae-6902/ae-6902[a]	32	0.022
de*-Kg/de*-Kg	22	0.006
de*-X-91/de*-X-91	25	0.003
de*-Ki/de*-Ki	19	0.006
su2-R/su2-R	36	0.009
cp/cp	27	0.005
o5/o5[b]	23	0.008
o5/o5[b]	22	0.009
su-R/su-R	24	0.017

[a]Separate isolations of starch from the same plant.

[b]Separate isolations of starch from two sib plants.

Oliver E. Nelson, Jr.

Sucrose synthetase in Sh and sh endosperms — A survey of starch biosynthesis enzymes from developing endosperms of Sh Sh and sh sh genotypes (chromosome #9) revealed that one enzyme, sucrose synthetase (sucrose-UDP glucosyltransferase), was considerably reduced in the latter but not in the former (Table 1). The possible influence of genetic background on the enzyme activity, if any, was considered minimal because both genotypes were in a W22 inbred background. Three additional sh sh mutants of independent and spontaneous origin have also shown reductions of similar magnitudes in sucrose synthetase activity in the endosperm. No such differences were observed in the embryos of 22-day-old kernels of normal and mutant genotypes. Although the enzyme assays reported here were made in the direction of sucrose synthesis (Tsai et al., Plant Phys. 46:299, 1970), assays in the direction of sucrose breakdown revealed similar differences between these two genotypes.

Table 1. Sucrose synthetase activity in developing endosperms and embryos.

Genotype	Stage	µmoles sucrose synthesized per mg protein per minute	Percent activity
Endosperm			
Sh Sh Sh(W22)	22-day	450	100.0
sh sh sh(W22)	22-day	50	11.0
Sh Sh Sh	31-day*	386	100.0
sh sh sh(sh #7205)	31-day*	44	11.4
sh sh sh(sh #7107)	31-day*	36	9.3
sh sh sh(sh #7321)	31-day*	46	11.9
Embryo			
Sh Sh	22-day	35	11.4**
sh sh	22 day	34	11.1**

*Obtained from greenhouse plants.
**Percent of Sh Sh Sh endosperm activity (307 µmoles sucrose per mg protein per min.)

The Sh locus is known to specify a protein designated as Sh protein in the developing endosperms (Schwartz, Genetics 45:1419, 1960; Chourey and Schwartz, Mutation Research 12:151, 1971). This protein is completely absent in sh sh genotypes, and its role in developing endosperms is not known. In order to test if sucrose synthetase activity is associated with Sh protein, attempts were made to visualize this enzyme on gels by zymogram techniques; such attempts have not been successful. However, Sh protein can be easily visualized after gel electrophoresis by using a protein stain and can be readily eluted from unstained starch gels. Sh protein eluates obtained from starch gels showed a single protein band on acrylamide gels which exhibited the same migration rate as the Sh protein band. This same preparation of Sh protein when assayed for sucrose synthetase activity gave a positive reaction. Eluates from all other areas of the gels showed no sucrose synthetase activity. These observations suggest that the Sh protein alone is associated with sucrose synthetase activity. Experiments are in progress to identify zones of sucrose synthetase activity in gels from sh sh endosperms.

Prem S. Chourey

IV. REPORT ON MAIZE COOPERATION

During 1974 the Maize Genetic Cooperation received 131 requests for maize genetic stocks. This is a 10 percent reduction in requests compared to 1973. There were 97 (47%) domestic and 34 (26%) foreign requests. Requests from geneticists were 47%, physiologists 24%, plant breeders 22% and educational 7% of the total number of requests received. A total of 1298 seed packets were sent to fill these requests.

Seed stocks of chromosome 2 and chromosome 7 were increased in 1974. Certain reciprocal translocation stocks were increased and testcrosses made to test for homozygosis. In addition, certain stocks were grown in observational nurseries to confirm pedigrees on mature plant traits, to test for homozygosity of reciprocal translocations increased in 1973 or to measure linkage of traits in certain cultures. In addition, backcross programs of incorporating the waxy reciprocal translocation series and plant color genes into two inbred lines were continued. A list of reciprocal translocation stocks available from the Co-op is published in the Co-op Newsletter report volume 43, 1969, or can be obtained upon request.

The following is a list of traits given permanent symbols by the Co-op or the person working with the particular trait.

Temporary Symbol	Permanent Symbol	Chromosome
codw	ct2	1
nec*-8147	nec2	1
v*-8983	v22	1
rp*-x	rp7	2
	w13-m	3
w*-7748	y10	3
pg*-m	pg14	3
v*-8914	v23	4
nec*-E409	nec3	5
l*-4120	l11	6
l*-4920	l12	6
w*-8657	w14	6
w*-8896	w15	6
gl*-g	gl18	8
nec*-6697	nec	8
v*-A552	v21	8
V*-m-1817	Vm	10

Requests for seed and correspondence relative to the stock program should be addressed to:

Dr. R. J. Lambert
S-116 Turner Hall
Department of Agronomy
University of Illinois
Urbana, Illinois 61801

Catalogue of Stocks

Chromosome 1

sr zb P-WW
sr P-WR
sr P-WR an gs bm2
sr P-WR an bm2
sr P-RR gs bm2
sr P-WR bm2
vp5
zb4 ms17 P-WW
zb4 ts2 P-WW br f bm2
zb4 ts2 P-WW bm2
zb4 P-WW
zb4 P-WW br
zb4 P-WW br f bm2
zb4 P-WW bm2
ts2 P-RR
ts2 P-WW br bm2
ts2 P-WW 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 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 ad bm2
P-WR br Vg
P-WR br f gs bm2
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

Chromosome 1 (continued)

P-WW br f bm2
P-WW br f an gs bm2
as
as rs2
rd-Hy
br f
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
an bm2
an-bz2-6923 (apparent deficiency including an and bz2)
br2
br2 bm2
tb-8963
Kn
Kn Ts6
1w
vp8
gs bm2
Ts6
bm2
id
nec2
ms9
ms12
ms14
mi
D8
TB-1a (1L.20)
TB-1b (1S.05)

Chromosome 2

ws3 lg gl2 B
ws3 lg gl2 B sk
ws3 lg gl2 B sk fl v4
ws3 lg gl2 B ts
ws3 lg gl2 b
ws3 lg gl2 b sk fl v4
ws3 lg gl2 fl v4
ws3 lg gl2 b ts
ws3 lg gl2 b v4
al
al lg
al lg gl2 B sk v4
al lg gl2 b sk v4
lg
lg gl2 B
lg gl2 B gl11
lg gl2 B gs2
lg gl2 B gs2 v4
lg gl2 B gs2 Ch
lg gl2 B sk v4
lg gl2 B v4
lg gl2 b
lg gl2 b gs2
lg gl2 b gs2 sk Ch
lg gl2 b gs2 v4
lg gl2 b gs2 v4 Ch
lg gl2 b sk
lg gl2 b sk fl v4
lg gl2 b sk v4
lg gl2 b wt v4
lg gl2 b fl v4
lg gl2 b fl v4 Ch
lg gl2 b v4
lg gl2 b v4 Ch
lg gl2 wt
lg gl2 w3
lg gl2 w3 Ch
lg gl2 Ch
lg b gs2 v4
lg Ch
d5 = d*-037-9
B gl11
B ts
gl11
wt
mn
fl
ts
v4
w3
w3 Ht
w3 Ch

Chromosome 2 (continued)

Ht (A & B source)
ba2
R2 ; r A A2 C
Ch
TB-2 6270 (2S)
TB-2 4463 (2L)
Primary Trisomic 2

Chromosome 3

cr
cr d
cr d Lg3
cr ts2 na
cr ts4 na
d-Tall = d*-6016
d rt Lg3
d Rf lg2
d ys3
d ys3 Rg
d Lg3
d Rg ts4 lg2
d pm
d ts4 lg2
d ts4 lg2 a-m ; A2 C R Dt
ra2
ra2 ys3 Lg3 Rg
ra2 ys3 Rg
ra2 Rg lg2
ra2 pm 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
Lg3
Lg3 Rg
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
ts4
ts4 ba na
ts4 lg2 a-m ; A2 C R Dt
ts4 lg2 gl7
ts4 na a-m et ; A2 C R Dt

Chromosome 3 (continued)

ts4 a-m ; A2 C R Dt
ba
y10
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
A sh2 ; A2 C R B Pl dt
A-d31 ; A2 C R
A-d31 ; A2 C R pr dt
A-d31 ; A2 C R B Pl dt
A-d31 ; A2 C R Dt
A-d31 ; A2 C R pr Dt
A-d31 sh2 ; A2 C R B Pl dt
A-d31 sh2 ; A2 C R Dt
A-d31 sh2 ; A2 C R B Pl Dt
A-d31 et ; A2 C R Dt
A-m ; A2 C R 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 et ; A2 C R Dt
a-st et ; A2 C R Dt
a-p et ; A2 C R dt
a-p et ; A2 C R B Pl Dt
a-x1
a Ga7 ; A2 C R
sh2
vp
Rp3
gl12
TB-3a (3L.10)
TB-3b(3S.50)
Primary Trisomic 3

Chromosome 4

Rp4
Ga
Ga su
Ga-S
Ga-S bt2
st
st Ts5
st fl2

Chromosome 4 (continued)

st Ts5 su
Ts5
Ts5 fl2
Ts5 su
Ts5 su zb6
Ts5 su zb6 o
Ts5 Tu
la su Tu gl3
la su gl3
la su gl3 c2 ; A A2 C R
la su gl3 o
fl2
fl2 su
su
su-am
su bm3
su zb6
su zb6 Tu
su zb6 C2-Idf (Active-1) ; A A2 C R
su gl4
su gl4 Tu
su gl4 j2
su gl4 o
su j2
su gl3
su gl3 o
su o
bt2
bt2 gl4
bt2 gl4 j2
gl4
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
v8
gl3
gl3 dp
c2 ; A A2 C R
C2 ; A A2 C R
C2-Idf (Active-1) ; A A2 C R
v17
gl7
ra3
TB-4a (4S.20)
TB-4 4692 (4L)
Primary Trisomic 4

Chromosome 5

lu
lu sh4
ms13
gl17
gl17 A2 pr ; A C R
gl17 a2 ; A C R
A2 vp7 pr ; 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 bt pr ; A C R
A2 bt pr ys ; in A C R
A2 v3 pr ; A C R
A2 pr na2 ; A C R
A2 pr ys ; A C R
a2 ; A C R
a2 ; A C R B Pl
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 ys ; 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 v2 ; A C R
a2 v3 pr ; A C R
a2 pr ; A C R
vp2
vp2 gl8
vp7
bm yg
bt
ms5
v3
td ae
ae
sh4
gl8
na2
lw2
ys
eg
v2
yg
ms13
v12
lw3 lw4
Primary Trisomic 5

Chromosome 6

rgd po y
rgd Y
po = ms6
po y pl
po Y pl
y = pb = w-m
y l10
y l12
y w15
y pb4
y pb4 pl
y pb4 Pl
y si
y wi Pl
y pg11 ; Wx pg12
Y pg11 ; Wx pg12
y pg11 ; Wx pg12
Y pg11 ; wx pg12
y pl
y Pl
y Pl Bh ; c sh wx A A2 R
y su2
Y l11
Y l10
Y pb4
Y wi pl
Y wi Pl
Y su2
wi
Pl Dt2 ; a-m A2 C R
pl sm ; P-RR
Pl sm ; P-RR
Pl sm py ; P-RR
Pt
w
w14
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 Tp
o2 v5 ra gl ij
o2 v5 gl
o2 ra gl ij
o2 gl
o2 gl sl
o2 bd
in ; A2 pr A C R
in gl ; A2 pr A C R

Chromosome 7 (continued)

v5
vp9
vp9 gl
ra gl ij bd
gl
gl-M
gl Tp
gl o5
gl g2
Tp
ij
Bn
bd
Pn
o5
g2
va
Dt3 ; a-m A2 C R
v*-8647
yel*-7748
TB-7b (7L.30)
Primary Trisomic 7

Chromosome 8

gl18
v16
v16 j
v16 ms8 j
nec
v16 ms8 j gl18
TB-8a (8L.70)
Primary Trisomic 8

Chromosome 9

yg2 C sh bz ; A A2 R
yg2 C sh bz wx ; A A2 R
yg2 C-I sh bz wx ; A A2 R
yg2 C sh bz wx K-L9 ; 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 gl15 bm4 ; A A2 R
C sh ; A A2 R
C sh wx ; A A2 R

Chromosome 9 (continued)

C wx ar ; A A2 R
C-I sh wx v ; 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 y
C Ds wx ; A A2 R pr
C-I Ds wx ; A A2 R
C-I ; A A2 R
C ; A A2 R
C ; A A2 R B Pl
C wx ; A A2 R
C wx ; A A2 R B Pl
C wx ; A A2 R b Pl
C wx ; A A2 R B pl
C-I wx ; A A2 R y
C-I wx ; A A2 R y B pl
C wx ar da ; A A2 R
C wx v ; A A2 R
C wx v ; A A2 R Pl
C wx gl15 ; A A2 R
C wx gl15 ; A A2 R pr
C wx Bf ; A A2 R
c 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
c wx bk2 ; A A2 R
sh
sh bp wx ; P-RR
sh bp wx ; P-RW
sh wx v
bp wx ; P-RR
bp wx ; P-RW
bp wx ; P-WW
lo2
wx
wx-a
wl1
wx d3
Wx pg12 ; y pg11
wx pg12 ; y pg11
Wx pg12 ; Y pg11

Chromosome 9 (continued)

wx pg12 ; Y pg11
wx v
wx bk2
wx bk2 bm4
wx Bf
wx Bf bm4
d3
v
gl15
gl15 bm4
bk2 Wc
Wc
bm4
l6
l6 ; l
l7
l7 ; l
yel*-034-16
w*-4889
w*-8889
w*-8951
w*-8950
w*-9000
TB-9a (9L.40)
TB-9b (9S.40)
Primary Trisomic 9

Chromosome 10

oy
oy bf2
oy bf2 R ; A A2 C
oy bf2 ms10
oy du R ; A A2 C
oy du r ; A A2 C
oy zn
Og
Og du R ; A A2 C
bf2
bf2 li g r ; A A2 C
bf2 g R sr2 ; A A2 C
bf2 g r sr2 ; A A2 C
nl g R ; A A2 C
y9
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
du g r ; A A2 C
zn
zn g r ; A A2 C
Tp2 g r ; A A2 C
g R sr2 ; A A2 C

Chromosome 10 (continued)

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-r 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-mb ; A A2 C
R-nj ; A A2 C
R-r ; A A2 C
R-r(Boone) ; 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
Lc
w2
w2 l
l
v18
Mst
du
l yel*-5344
yel*-8721
yel*-8454
yel*-8793
TB-10a (10L.35)
Primary Trisomic 10

Unplaced Genes

dv
dy
el
gl14
h
l3
l4
Rs
v13
ws ws2
ub
zb

Unplaced Genes (continued)

zb2
zb3
zn2
1*-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 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
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
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
Knobless Wilbur's Flint
Gaspe Flint
Gourdseed
Maiz chapolote
Papago Flour Corn
Parker's Flint
Tama Flint
Zapaluta chica

Tetraploid Stocks

P-RR
P-VV
Ch
B Pl
a A2 C R Dt
su
pr ; A A2 C R
y
gl
ij
Y sh wx
sh bz wx
wx
g A A2 C R
A A2 C R B Pl

Cytoplasmic Steriles and Restorers

WF9 - (T)	rf rf2
N6 (S)	
WF 9	rf rf2
N6	rf Rf2
R213	Rf rf2
Ky21	Rf Rf2

Waxy Reciprocal Translocations

wx1-9c (1S.48;9L.22)
wx1-9-4995 (1L.19;9S.20)
wx1-9-8389 (1L.74;9L.13)
wx2-9b (2S.18;9L.22)
wx3-9c (3L.09;9L.12)
wx4-9b (4L.90;9L.29)
wx4-9-5657 (4L.33;9S.25)
wx4-9g (4S.27;9L.27)
wx5-9a (5L.69;9S.17)

Waxy Reciprocal Translocations (continued)

wx5-9c (5S.07;9L.10)
wx6-9a (6S.79;9L.40)
wxy6-9b (6L.10;9S.37)
wx7-9a (7L.63;9S.07)
wx7-9-4363 (7 cent.;9 cent.)
wx8-9d (8L.09;9S.16)
wx8-9-6673 (8L.35;9S.31)
wx9-10b (9S.13;10S.40)

Inversions

gl2 Inv.2a (2S.70;2L.80)
wx Inv.9a (9S.70;9L.90)

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VII. AUTHOR INDEX

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I. FOREWORD

Cooperation is the reason that the News Letter has existed. We who work on the genetics, cytogenetics and biochemical genetics of maize have a tradition of freely exchanging our materials, data, interpretations and puzzles directly with each other or through this non-publication. If there have been any undesirable consequences, they have been only when the reporting of a substantial study has stopped with a News Letter note and has not been carried to the formal literature, with the result that the general scientific community has failed to learn of our information, ingenuity, insights, errors or flights of concept. It is vital that our informal means of communicating be maintained, and your new "Secretary" will strive to maintain it; in fact, ideas for ways by which the informality can be enhanced and formal publication facilitated would be most welcome. For example, Cooperators might appreciate in future News Letters brief items about manuscripts that have been submitted and are not yet in print, if these are given as "Report" items (author and title, with or without further text) contributed by the authors.

The costs of preparation, reproduction and mailing of this News Letter, as in recent years, are borne by a grant from the National Science Foundation. All of us can be grateful that this support is available, because it is indispensable.

Until this year's contributions were in hand and the editing was begun, we did not know how much attention Ellen Dempsey had been giving to the News Letter contributions; we send Ellen our encomia, based on the experience of only one cycle but aware that years of such excellent care have required exceptional dedication and patience. If in our editing for format, nomenclature and clarity we have marred the history of her delicate and exacting touch, we apologize to her more than to the contributors. If we have altered meanings or otherwise erred in our editing, we invite errata for the next issue.

Attention given by contributors to the new recommendations on nomenclature was very helpful; the recommendations are repeated this year. A number of new symbol assignments are listed in the report from the Maize Genetics Cooperation Stock Center.

A list of publications of E. G. Anderson and associates, including identification of those papers for which reprints are available, has been prepared and is included between the Stock Center report and the list of Recent Maize Publications.

Deadline for contributions for the next issue (Volume 50, 1976) will be January 1, 1976. While this deadline is substantially earlier than the customary one and may find some data unanalyzed, trial of a change seems desirable for a number of reasons, not the least of which is the possibility of moving the date for distribution to a time somewhat ahead of planting season.

Index corrections wanted: Toward a list of corrigenda for the 1962 symbol index and the 1970 author and name index, please pass along by letter, post card or notes on brown paper bags any corrections for the indexes that may have come to your attention.

Back issues wanted: Repeated requests are received for back issues, including appeals from newly developing maize laboratories in the U. S. and other countries, but also from some locations with resources too limited to purchase even a microfilm with U. S. exchange. If you come across unnecessary extra copies of back issues of any volumes, please consider sending them in for this type of distribution; we could supply postage on request. If you are interested in obtaining back issues, please see the back cover.

Archival materials needed: In attempting to assemble a "permanent set" of the News Letter for archival maintenance, single copies of Volumes 27, 28 and 36 are not in the files and will have to be photocopied from bound volumes to complete the set if copies cannot be located. Original copies of these three issues would be especially appreciated for this purpose.

Found on a weatherbeaten brown paper bag, written in heavy graphite pencil:

> "A couple of years ago Marcus Rhoades asked several of us to send seed stocks to Cornell to be maintained there for distribution, and to send in linkage data and other information to be mimeographed for distribution among those of us who wished to share our information. The notion was very helpful, and continues to be."

If you see Professor Rhoades before I do, please mention how well it has worked out.

I would like to thank M. G. Neuffer for help in planning and developing this volume. Preparation of the issue was much facilitated by the enthusiastic and systematic redaction of the copy by Karen Sheridan. M. D. Murray aided in the screening and compilation of the publication lists. Acknowledgement is due Paul Bolen, Kenneth Leto and William Rafaill for their help with proofing of the copy.

E. H. Coe, Jr.

Dr. D. L. Mulcahy directs our attention to an international symposium, GAMETE COMPETITION IN PLANTS AND ANIMALS: ITS BIOLOGICAL SIGNIFICANCE, to be held August 21-23, 1975, at the Villa Carlotta, Lake Como, Italy. The Symposium will deal with aspects of the influence of haploid and diploid genotypes on gametic competitive ability, competition within populations, the influence of gametic competition upon the diploid genotype, the feasibility of using reduced gametic competition to increase genetic variability in crops, and the possible use of gametic competition to influence the transmission of deleterious genetic factors in plants and animals, including man. The proceedings will be published. For details write Dr. D. L. Mulcahy, Universita di Milano, Istituto di Genetica, Via Celoria 10, 20133 Milano, Italy.

Dr. James C. Copeland requests announcement of the COLLOQUIUM ON REGULATORY BIOLOGY to be held on the Columbus campus of the Ohio State University September 4-6, 1975. Speakers will include W. Szybalski (U. Wisconsin), J. King (M.I.T.), M. Cashal (N.I.H.), S. Bourgeois (Salk Inst.), R. Goldberger (N.I.H.), J. C. Copeland (Ohio State U.), E. Zeuthen (Carlsberg Found.), G. Marzluf (Ohio State U.), T. Humphreys (U. Hawaii), and H. F. Lodish (M.I.T.). Contributed presentations will also be included. The proceedings of the Colloquium will be published. For further information write to Colloquium, College of Biol. Sci., The Ohio State Univ., Columbus, Ohio 43210.

Although supplies of most previous issues are exhausted or very limited, volumes 1-29 and volume 33 of the Newsletter have been microfilmed and are available for $9.50 U.S.; checks should be made out to E. H. Coe, Jr. If there is enough interest in other exhausted issues to justify a printing run, we anticipate that economical (2/3-size, unbound) reproductions could be supplied for about $2.00 per issue on a self-paying basis. Please inform us which issues you would want to acquire if reproduced in this way (of recent issues, volumes 39, 45 and 47 probably will have high priority).

Materials for volume 50 (1976) should be in our hands by January 1, 1976