MAIZE GENETICS COOPERATION

NEWS LETTER

50

March 1, 1976

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

This 50th volume is dedicated to

Marcus M. Rhoades

TABLE OF CONTENTS

I. FOREWORD

Fifty volumes of informal cooperation in maize genetics, totalling over 5000 pages, constitute a remarkable history. This golden volume represents an idea whose time came early and whose fruits are evident in the rich fund of knowledge, manipulations and tools available today for genetic and cytogenetic research, for crop improvement and for study of evolutionary processes, morphogenesis, physiology, metabolism, biochemistry and molecular biology with this species. This issue includes diverse reports across all of these disciplines. Yet it is our common interest in genetics and cytogenetics and our desire to further this area of knowledge that fosters the cooperation.

If all goes as well as intended, this volume will be in your hands well before the planting season for most locations. According to some cooperators the deadline came before completion of some types of data collection and analysis; of course that has always been the case for any deadline with research proceeding at full tilt, but if the result seems to be less data and more verbosity this year, please offer suggestions.

I have compiled a chronological listing (Section II) of those distributions and promulgations in Maize Genetics Cooperation that we have on file. Supplies of copies of most of these items are exhausted, although most recent News Letters and Indexes are still available. A look at the listing highlights the contributions of those who have nurtured this cooperation.

For the report on the Stock Center and the Stock Catalogue, camera-ready copy was provided by R. J. Lambert; we are most grateful for that easing of the editing work.

The list of Recent Maize Publications is substantially larger than usual this year. Not only was our search system wider, but the literature is exploding with papers in biochemistry and metabolism that are of increasing genetic interest; agronomic and quantitative genetic studies of increasing theoretical importance continue to develop internationally; and the genetics of pest and stress response continues to expand. Y. C. Ting kindly provided some hard-to-catch items.

An Author-Name Index for volumes 44 through 50 constitutes the back portion of this volume. The task of scanning these volumes for citations, along with the professional detective work, was undertaken by Sheila McCormick.

Users have been patient not to complain at the fragility of the cover on volume 49. (Does this mean it is not being used?) We are trying a sturdier material this time and will appreciate comments.

The costs of preparation, reproduction and mailing of this News Letter are borne by a grant from the National Science Foundation. We are grateful for this indispensable support.

Deadline for contributions for the next issue (volume 51, 1977) is January 1, 1977.

Index corrections are wanted from the 1962 symbol index.

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

Exhausted issues could be reproduced (2/3-size, unbound) for $2.00 per issue if there is enough interest in them. Please identify those volumes you would like to acquire in reproduction, so that we can plan a run.

Found on a stained and tattered sheet of bibulous paper, written in acetocarmine: "Mystifying genetic data -- about 50% sterile pollen; progenies from self-fertilization segregate about half normal and half 50%; some normal individuals, when crossed to standard strains, give all 50%. Get new teasing needles, cover sl....."

I would like to thank M. G. Neuffer for help in planning and developing this volume, and J. B. Beckett and R. L. Larson for help with parts of the copy. Karen Sheridan gave exacting and systematic attention to parts of the editing, composing and proofing. Marion D. Murray aided in the publication-searching, and Sheila McCormick and William S. Rafaill helped proof the copy.

E. H. Coe, Jr.

II. NEWS LETTER FILES

Following is a chronological ("archival") list of materials of the Maize News Letter and related cooperation, maintained on file at the University of Missouri. Extensive files of individual correspondence are also being maintained. R. L. Cushing, E. Dempsey, L. J. Gundy, A. Manwiller, R. L. Plaisted, M. M. Rhoades and H. H. Smith kindly provided help and parts of the materials needed toward completing the files. Copies of items that are starred have not been located and are requested from cooperators.

Vol.	Date	From	Pp.	Contents
	12 Apr 29	R. A. Emerson, Cornell	30	Letter referring to "cornfab" held in N.Y. during winter science meetings, transmitting compilation of linkage data and maps.
	17 Apr 30	R. A. Emerson, Cornell	17	Revised maps.
	26 Jul 30	R. A. Emerson, Cornell	23	Linkage data for above maps.
	* ?	?	?	Cooperation planned at Sixth Congress.
	5 Oct 32	M. M. Rhoades, Cornell	3	Report of meeting at Congress; request for seed stocks to be maintained at Cornell; list of stocks.
	12 Dec 32	M. M. Rhoades, Cornell	1	Call for stocks, want lists and data.
	* ?	?	?	Correspondence about possible grant.
3	23 Jan 33	M. M. Rhoades, Cornell	16	Want lists; symbolization; stocks; gene list.
	13 Nov 33	M. M. Rhoades, Cornell	2	Call for news items.
4	18 Dec 33	M. M. Rhoades, Cornell	7	News items.
5	25 Jan 34	M. M. Rhoades, Cornell	12	Proposed nomenclatorial system; stock list.
6	21 Feb 34	M. M. Rhoades, Cornell	4	Nomenclatorial comments and revisions.
	* 1 Apr 34	?	?	Rockefeller Grant available.
7	13 Sep 34	M. M. Rhoades, Cornell	11	Call; news items; communications from USSR; addendum to gene list; mailing list.
8	24 Nov 34	M. M. Rhoades, Cornell	18	News items.
	21 Jan 35	M. M. Rhoades, Cornell	1	Call.
9	6 Mar 35	M. M. Rhoades, Cornell	22	Stocks; news items; map.
	30 Nov 35	R. A. Emerson, Cornell	3	Call.
10	4 Mar 36	R. A. Emerson, Cornell	22	News items; linkage data; stocks; inbred tests.
	21 Nov 36	D. G. Langham, Cornell	1	Call.
	1 Jan 37	D. G. Langham, Cornell	1	Call.
11	23 Mar 37	D. G. Langham, Cornell	26	News items; stocks; inbred tests.
	17 Nov 37	D. G. Langham, Cornell	2	Call.
	22 Jan 38	D. G. Langham, Cornell	1	Call.
12	6 Mar 38	D. G. Langham, Cornell	40	News items; stocks; symbol index; map.
	21 Jan 39	D. G. Langham, Cornell	1	Call.
13	15 Apr 39	D. G. Langham, Cornell	22	News items; stocks; publications; mailing list.
	31 Oct 39	G. A. Lebedeff, Cornell	1	Call.
	8 Jan 40	R. A. Emerson, Cornell	1	Call.

*Not on file; identified in historical notes in MNL 14:56.

Vol.	Date	From	Pp.	Contents
14	5 Mar 40	R. A. Emerson, Cornell	56	News items; publications; stocks; historical notes.
	21 Jan 41	A. C. Fraser, Cornell	1	Call.
15	1 Apr 41	A. C. Fraser, Cornell	56	News items; publications.
	10 Dec 41	R. A. Emerson, Cornell	1	Call.
16	10 Feb 42	R. A. Emerson, Cornell	59	Reports; publications; stocks.
	10 Dec 42	R. A. Emerson, Cornell	1	Call.
17	15 Feb 43	R. A. Emerson, Cornell	51	Reports; publications; stocks.
	** ?	?	?	Call.
18	31 Jan 44	R. A. Emerson, Cornell	32	Reports; publications; stocks.
	** ?	?	?	Call.
19	15 Feb 45	R. L. Cushing, Cornell	50	Reports; publications; stocks.
	** ?	?	?	Call.
20	15 Apr 46	R. L. Cushing, Cornell	35	Reports; publications; stocks.
	26 Dec 46	H. H. Smith, Cornell	1	Call.
21	1 Mar 47	H. H. Smith, Cornell	59	Reports; publications.
	17 Dec 47	H. H. Smith, Cornell	1	Call.
22	8 Mar 48	H. H. Smith, Cornell	72	Reports; publications; stocks.
	28 Dec 48	H. H. Smith, Cornell	1	Call.
23	10 Mar 49	H. H. Smith, Cornell	78	Reports; publications; stocks.
	** ?	?	?	Call.
24	17 Mar 50	H. H. Smith, Cornell	81	Reports; publications; stocks.
	** ?	?	?	Call.
25	17 Mar 51	H. H. Smith, Cornell	68	Reports; News Letter chronology; author index; publications; stocks.
	2 Jan 52	H. H. Smith, Cornell	1	Call.
26	17 Mar 52	H. H. Smith, Cornell	76	Report of meeting concerning support; reports; publications; stocks.
	26 Sep 52	M. M. Rhoades, Illinois	4	Establishment of stock center; project outline.
	30 Dec 52	H. H. Smith, Cornell	1	Call.
27	17 Mar 53	H. L. Everett, Cornell	90	Report of meeting concerning support; reports; publications.
	5 Jan 54	H. H. Smith, Cornell	1	Call.
28	17 Mar 54	H. H. Smith, Cornell	94	Stocks; reports; publications.
	15 Dec 54	H. H. Smith, Cornell		Call.
29	17 Mar 55	H. H. Smith, Cornell	100	Reports; stocks; publications.
	7 Dec 55	M. M. Rhoades, Illinois	1	Call; announcement of transfer of responsibility.
30	15 Mar 56	M. M. Rhoades, Illinois		Minutes of meeting regarding cooperation.
	7 Dec 56	M. M. Rhoades, Illinois	1	Call.
31	15 Mar 57	M. M. Rhoades, Illinois	173	Nomenclatural summary; reports; stocks; publications.
	12 Dec 57	M. M. Rhoades, Illinois	1	Call.
32	15 Mar 58	M. M. Rhoades, Illinois	156	Reports; stocks; publications.
	8 Dec 58	M. M. Rhoades, Indiana	1	Call.
33	1 Apr 59	M. M. Rhoades, Indiana	168	Reports; stocks; publications; mailing list.
	8 Dec 59	M. M. Rhoades, Indiana	1	Call.

**Not on file; assumed.

Vol.	Date	From	Pp.	Contents
34	1 May 60	M. M. Rhoades, Indiana	154	Reports; stocks; publications.
	9 Dec 60	M. M. Rhoades, Indiana	1	Call.
35	15 Apr 61	M. M. Rhoades, Indiana	183	Reports; stocks; publications.
	8 Dec 61	M. M. Rhoades, Indiana	1	Call.
36	15 Apr 62	M. M. Rhoades, Indiana	122	Reports; stocks; publications.
	1 Jul 62	E. H. Coe,Jr., Missouri	45	Symbol index to volumes 12-35.
	1 Dec 62	M. M. Rhoades, Indiana	1	Call
37	15 Apr 63	M. M. Rhoades, Indiana	196	Reports; chromosome 1 linkage data; stocks; publications.
	6 Dec 63	M. M. Rhoades, Indiana	1	Call.
38	15 Apr 64	M. M. Rhoades, Indiana	150	Reports; stocks; publications.
	14 Dec 64	M. M. Rhoades, Indiana	1	Call.
39	15 Apr 65	M. M. Rhoades, Indiana	210	Reports; stocks; publications.
	14 Dec 65	M. M. Rhoades, Indiana	1	Call.
40	15 Apr 66	M. M. Rhoades, Indiana	205	Reports; map; stocks; publications.
	21 Dec 66	M. M. Rhoades, Indiana	1	Call.
41	15 Apr 67	M. M. Rhoades, Indiana	233	Reports; stocks; publications.
	15 Dec 67	M. M. Rhoades, Indiana	1	Call.
42	15 Apr 68	M. M. Rhoades, Indiana	208	Reports; stocks; publications.
	18 Dec 68	M. M. Rhoades, Indiana	1	Call.
43	15 Apr 69	M. M. Rhoades, Indiana	242	Reports; stocks; publications.
	18 Dec 69	M. M. Rhoades, Indiana	1	Call.
44	15 Apr 70	M. M. Rhoades, Indiana	232	Reports; stocks; publications.
	15 Apr 70	E. H. Coe,Jr., Missouri	51	Author and name index to volumes 3-43.
	18 Dec 70	M. M. Rhoades, Indiana	1	Call.
45	15 Apr 71	M. M. Rhoades, Indiana	287	Reports; stocks; publications.
	6 Dec 71	M. M. Rhoades, Indiana	1	Call.
46	15 Apr 72	M. M. Rhoades, Indiana	245	Reports; stocks; publications.
	12 Dec 72	M. M. Rhoades, Indiana	1	Call.
47	15 Apr 73	M. M. Rhoades, Indiana	277	Reports; nomenclatural recommendations; stocks; mailing list; publications.
	12 Dec 73	M. M. Rhoades, Indiana	1	Call.
48	15 May 74	M. M. Rhoades, Indiana	244	Foreword with historical notes; reports; revised nomenclature; stocks; publications.
	13 Jan 75	E. H. Coe,Jr., Missouri	1	Call.
49	15 Apr 75	E. H. Coe,Jr., Missouri	183	Revised nomenclature; reports; stocks; publications.
	1 Nov 75	E. H. Coe,Jr., Missouri	1	Call.

III. REPORTS FROM COOPERATORS

UNIVERSITY OF ARIZONA
Committee on Genetics, Tucson, Arizona

Cyclic AMP as a growth promoter of dwarf (d)

Seeds of dwarf (d) were soaked and planted in either GA_3 (2.6×10^{-6}M, K salt), GA_7 (2.6×10^{-6}M, K salt), cyclic AMP (1×10^{-6}M) or distilled water in a growth chamber at 25±1C. Once every 24 hr the germinating seeds were subjected to one hr of red light. The lengths of coleoptiles and mesocotyls were measured 108 hr after planting (Table 1). The lengths of both coleoptile and mesocotyl of GA_3-, GA_7- or

Table 1. Mean lengths for tissues of 108-hr seedlings (expressed in mm).

Tissue	Treatment			
	Control	GA_3	GA_7	cAMP
Coleoptile	22.64	31.58	25.11	29.32
Mesocotyl	9.01	16.97	20.92	11.98

cAMP-treated seeds are significantly greater than the controls, although the increase in mesocotyl length of cAMP-treatments is significantly less than that of GA_3 or GA_7 treatments. There is no evidence of a synergistic effect for GA_3 and cAMP in increasing the length of the coleoptile or mesocotyl.

Auxin production, as measured by the Avena section test, is increased significantly in GA_3-treated coleoptiles, but not in cAMP-treated ones. Amylase activity is increased in treated coleoptiles, but only GA_3 elicits increased amylase activity in the mesocotyl.

Charles F. Mischke and R. M. Harris

BHABHA ATOMIC RESEARCH CENTRE
Biology and Agriculture Division, Bombay, India

Further studies on the EMS-induced dominant mutant "curled entangled"

Curled entangled (Ce) gene expression (MNL 48:15) at different stages of plant growth was studied in the progenies of selfed plants and their crosses as pollen parent to normal plants. Curling expression was noted every fifth day after germination. The homozygous plants did not survive till maturity. Plants in the selfed progenies expressed the mutant character continuously from the fifth to the twenty-fifth day; two peaks were observed, one on the tenth and the other on the twentieth day. On the other hand, in the crossed progenies about 90 percent of the plants expressed the mutant features within ten days (Table 1). In the selfed progenies

Table 1. Curled entangled gene expression in selfed and crossed progenies (figures within parentheses represent percentages).

Progeny	Family Number	Total Plants	Number of plants: Days after germination 5th	10th	15th	20th	25th
Ce/+ ⊗	22	1192	124 (10.41)	392 (32.88)	204 (17.12)	336 (28.18)	136 (11.41)
N x Ce/+	24	1335	829 (62.09)	356 (26.66)	125 (9.36)	16 (1.21)	9 (0.68)

more than 1/3 of the plants were late in expression and were found to be heterozygotes; most of the plants which expressed the mutant character earlier did not survive, since they were homozygotes. The expression was very effective and conspicuous in the crossed progenies. It seems possible that the induced mutant line might have some unknown factors that are influencing the mutant expression.

Earlier it was reported that the mutant trait was expressed only on the leaves, which are rolled from side to side in the form of a hollow cylinder. The expression starts between the first and fourth leaf stages and continues until the termination of the growth period. The leaves, being rolled, get entangled with each other, thus affecting their arrangement on the stem. Four types of phyllotaxy were observed in the progenies (Table 2). When all the entangled leaves of the mutant

Table 2. The effect of Ce on phyllotaxy.

Family	Handling	Total plants	Leaf arrangement: Distichous	Irregular	Perpendicular	One-sided
24	Control	668	172 (25.75%)	116 (17.35%)	244 (36.55%)	136 (20.35%)
	Leaves disentangled	667	642 (96.25%)	13 (1.95%)	8 (1.20%)	4 (0.60%)

were separated during the growth period, normal distichous phyllotaxy was discernible in nearly all the plants. In plants which did not receive this treatment, only 25% of the population showed a distichous arrangement. This segregation indicates the influence of another gene for the appearance of leaf orientation. A high percentage of perpendicular types was also noted in the control. This clearly demonstrates a pseudo-effect of the Ce gene on the plant type.

The Ce gene interacts with a recessive trait, liguleless (lg). Ce expression was at the one- or two-leaf stage in the majority (84.54%) of the growing seedlings carrying the liguleless marker in homozygous condition. However, in the liguled plants the expression was delayed to the three- or four-leaf stage (Table 3).

Table 3. The effect of lg on Ce expression.

Growth stage	Number of plants: Liguled (%)	Liguleless (%)
First leaf stage	31 (8.37)	186 (67.41)
Second " "	45 (12.16)	88 (27.16)
Third " "	197 (53.25)	42 (12.96)
Fourth " "	49 (13.25)	6 (1.85)
Fifth " "	48 (12.97)	2 (0.62)

Chandra Mouli

Leafy mutant

A recessive mutant appeared as a segregant in a population of an ear produced by a colourless kernel. This kernel was obtained following EMS treatment of A C R seeds; the plants were pollinated by c sh wx tester stock. This mutant had a few main features, of which one character proved to be monogenic. The recessive homozygous plants were taller than both the inbred lines (i.e., untreated) and the pollen parents. The mutant had increased numbers of leaves, ranging from 20 to 24 as

against 12 to 15 in both the parents. This behaved as a recessive trait. The tassel emergence took place after 65 to 70 days, compared to 45 to 50 days in controls. These mutant traits were associated with increased numbers of ears (4 to 6) at each base, but had very few seeds. Tassel seeds also were present occasionally.

When the mutant was crossed with both parents, the F_1 had uniformly 16 to 18 leaves and flowered more or less at the same time as the parents, showing intermediate dominance expression for number of leaves. F_1 plants were crossed as female parent with normal and mutant pollen. F_2 segregation and backcross ratios (Table 1) indicate that mutant expression is governed by a single recessive gene. F_1 plants crossed with mutant pollen had F_1 types and mutant types in equal numbers, while F_1 plants crossed with normal pollen had F_1 types and normal ones in the same proportion. The segregation for plant height and ear number did not follow any specific pattern.

Table 1. Segregation of leafy mutant.

Cross	No. of progenies	Number of plants		
		Normal	F_1 type	Mutant
Mutant x ACR	5	-	96	-
" ⊗	27	122	209	144
ACR x Mutant	6	-	82	-
" ⊗	32	154	329	170
" x Mutant	8		335	379
Mutant x c sh wx	6	-	38	-
" ⊗	36	234	436	193
c sh wx x Mutant	9	-	34	-
" ♀	32	306	539	289
" x c sh wx	8	179	204	

Chandra Mouli

EMS-induced jointed seed syndrome

An induced heritable character, "jointed seed syndrome" (MNL 48:14) continued to be expressed in the succeeding generations. In F_3 generation the following observations were noted; a brief summary of the previous generation is also included.

F_1: EMS treated seed. Silks crossed with normal pollen (2.5% Jointed seeds).
F_2: 51 plants expressed jointed seeds (0.3 to 5.4%). 21 plants normal.
F_3: 23 (Possible homozygotes); Jointed seeds in each plant (0.3 to 12.50%); 28 (Possible heterozygotes) segregated for mutant trait. From the 21 normals of the F_2, 10 plants (Possible heterozygotes) segregated for mutant trait, 11 plants (Homozygotes) gave normal.

The F_3 segregation ratio and the occurrence of the segregation of mutant type plants from normal plants suggests that the mutant expression is controlled by a single dominant factor and is possible maternally inherited.

Some of the plants which were considered to be homozygous were further selfed for two more generations. Individual plants in these progenies expressed the mutant trait ranging between 0.35 and about 12.50 percent. The frequency of jointed seeds obtained in some of the selfed plants in F_5 generation was quite high compared to the F_1 plant (Table 1).

From plants which had more than one ear, one was selfed and another was utilized for reciprocal crosses with normal plants; this revealed that the mutant expression was only in the female plant (Table 2).

Table 1. Frequency of jointed seeds in homozygous plants.

Progeny No.	Normal seeds	Jointed seed (%)
74-55b-44	135	17 (11.18)
" -56a-48	98	11 (10.09)
" -55b-12	130	14 (9.27)
" -53f-9	280	26 (8.49)
" -55b-8	190	16 (7.76)
" -55c-9	194	16 (7.61)
" -53f-1	176	14 (7.36)
" -54c-4	136	10 (6.84)
" -54C-4	280	19 (6.35)
" -53f-4	133	9 (6.33)
Total	1752	152 (8.68)

Table 2. Jointed seed mutant expression through female parent.

Pedigree No.	Number of seeds					
	Ear I Selfed		Ear II x Normal		Normal x Mutant	
	Normal seeds	Jointed seeds	Normal seeds	Jointed seeds	Normal seeds	Jointed seeds
74-56a-12	78	5	251	6	250	Nil
" -56b-1	85	4	165	9	257	"
" -53f-4	253	15	295	17	250	"
" -55c-2	266	10	178	4	300	"
" -55c-11	203	10	146	6	200	"
" -55E-5	153	2	96	4	250	"
" -55b-12	240	26	88	1	200	"
" -54E-10	183	6	62	3	200	"
" -56a-57	92	3	156	4	300	"
" -55b-9	91	5	182	5	300	"

The F_1 plants were crossed with mutant and normal pollen. Again, depending upon the female parent, in some progenies all plants were mutant type and in others there were normal plants. These plants, when crossed with both the parents, showed segregations (Table 3).

Table 3. Segregation of jointed seed mutant in the crosses.

Cross	No. of progenies	Number of plants	
		Normal	Mutant
(F_1 Mutant-type x N) x N	10	136	152
(F_1 Mutant-type x M) x M	10	121	146
(F_1 Normal x N) x N	10	143	162
(F_1 Normal x M) x M	10	96	114

The jointed seeds of both homozygous and heterozygous lines gave rise to twin plants. However, mutant expression was observed in either one, both, or none of them, depending upon the genotype of the plant (Table 4).

All these data clearly indicate the induction of a dominant gene which is maternally inherited and which governs the formation of twin seeds. This gene in homozygous condition is expressed in the range of 0.5 to 12.5 percent.

Table 4. Behaviour of twin seedlings originating from jointed seeds.

Pedigree No. Jointed seed	Number of seeds			
	Plant One		Plant two	
	Normal	Jointed	Normal	Jointed
74-53E-10	289	5	183	6
54d-9	273	4	135	3
54d-4	71	2	146	9
55b-9	91	5	125	5
55b-12	240	26	108	1
55b-4	114	2	94	1
55b-1	85	4	121	2
53b-2	173	-	92	-
53b-8	226	-	136	-
53E-4	192	-	241	-

Examination of mature seeds as well as seeds at early stages of development had revealed that the occurrence was due to the development of another carpel along with the fertile carpel of the normal flowers. Although the seeds were separated internally, the same pericarp layer surrounded both the seeds. Also, the twin seeds had only a single silk scar which indicated the development of twin seeds from a single ovary. All the three styles of the ovary of both the mutant and the normal plants were fused from the base upwards and in many cases only two styles were distinct. In the mutant, compared to normal, one of the styles was shorter and this was connected to the fertile carpel. One style, being short and therefore not fully exposed, gave a low percent of jointed seeds.

Experimentally cutting the ear at different levels and delaying pollination resulted in the increased frequency of jointed seeds (Table 5).

Table 5. Effect of cutting the ear and delaying pollination on the production of jointed seeds.

Operation	No. of plants	Number of kernels		Percent
		Normal	Jointed	
Routine cut				
Pollination 2nd day	24	5291	73	1.37
" 3rd day	28	3252	48	1.47
" 4th day	30	3645	66	1.51
Cut up to pith				
Pollination 2nd day	22	4610	86	1.87
" 3rd day	24	5898	130	2.21
" 4th day	32	6962	248	3.44

If it is possible to obtain a mutant of multi-carpellary type in maize then induction of all the three carpels to fertility may be visualized. This may help in explaining the nature and origin in evolution of this mutant condition from the wild ancestor where tricarpellary condition is a rule in monocots.

Chandra Mouli

BOSTON COLLEGE
Department of Biology, Chestnut Hill, Massachusetts

Additional study on the fine structure of maize microsporocytes

During the last year microsporocytes of a diploid maize inbred, maintainer of a cytoplasmic male sterile line, were examined with the standard techniques of electron microscopy. Particular effort was made to investigate the fine structures of bivalents, centromeres, the secondary constriction region, nucleolus and knobs of various chromosomes if available. At pachytene stage the synaptonemal complex was easily identified. By frontal view the diameter of the complex was approximately 2200 A.

Since the role of the synaptonemal complex in crossing over has been a subject of dispute, I had paid special attention to the finding of the existence of cross-elements in the complex. Up to the present, even though a large number of bivalents had been examined no cross-elements of any kind were definitely identified. If the synaptonemal complex is responsible for laying the ground for physical exchanges or crossing over between the two homologues, evidence of the formation of cross-elements between the two lateral elements should be expected. In view of this, once again the theory that the synaptonemal complex plays an important role in meiotic crossing over is questioned.

Chromosome 6, the nucleolar chromosome, is easily identified under both light and electron microscopes. It was observed that contrary to expectation, there was no synaptonemal complex beyond the secondary constriction region. Only darkly stained chromatin was shown in this region. As expected, synaptonemal complex was found in the rest of chromosome 6. In the centromere of this chromosome, only a lightly stained area was clearly observed. No microfibrils of any kind could be recognized. The synaptonemal complex was discontinuous in both the centromere and the secondary constriction regions.

In addition to the normal nucleolus, small nucleoli or nucleolar bodies varying in size and number from cell to cell were always present. These bodies were without any nucleolar cup and were unattached to any chromosomes. No fiber-like structures were seen in them; however, granular substances embedded in the homogeneous matrix were invariably observed. The appearance suggests their close relationship with ribosomes. Both the nucleolar bodies and the regular nucleolus possessed vacuoles which also varied in number and size but were always spherical in shape.

In the nucleolus of this inbred maize, two levels of structure could be revealed. One was the amorphous structure, the other, the fibrous. Fibers of the latter were about 350Å in diameter, and varied a great deal in length.

On the short arm of chromosome 9 there was a large terminal knob. This knob was frequently isolated and readily identifiable. No particular organizational characteristics were seen in the knob under the electron microscope. However, there were many fine fibrils radiating from the terminal region of the chromosome, and these fibrils measured less than 100Å in diameter. These fibrils are probably the basic components of the knob.

Y. C. Ting

Variations of maize anther callus in vitro

Since last summer 3950 maize anthers from 16 varieties have been cultured on defined medium. Callus growth from 201 anthers was observed. Morphological characteristics of these calli varied a great deal, from a size as small as 1-2 mm in diameter to as large as 3-5 times the original anther size. The small calli grew out from a part of the anthers, while the large ones grew out from the whole anthers. In the early stage of growth most of the calli were pale in appearance. When they were about two weeks old, they began to change from pale to brown. Chromosome constitutions of these calli have not yet been determined. However, it is expected that they vary from haploid to polyploid and aneuploid.

In order to induce embryoid development 182 calli of the above have been subcultured on an auxin-rich medium. It was found that after one week of subculture callus growth was almost completely stopped. Up to the present, no embryoid initiations were definitely identified. However, it is hoped that some of them will develop into plantlets before long. Previously it took 4-6 weeks for maize callus to differentiate into plantlets.

Nineteen of the calli were maintained by subculturing them on a 2, 4-D-containing medium.

It was also found that it did not make any difference in callus initiation and growth in the first four to six weeks of culture whether they were kept in dark or in light. Nevertheless, the calli were pale green if they were grown in light, while they were pale if they were grown in dark.

If this experiment will eventually lead to the production of plantlets, either haploid, diploid or aneuploid, it might become a new and useful technique in maize genetics, breeding, development and molecular biology.

Y. C. Ting and Robert McLellan

UNIVERSITY OF CALIFORNIA
Department of Genetics, Berkeley, California

Methods of maize pollen germination in vitro, collection, storage, and treatment with toxic chemicals; recovery of resistant mutants

One vigorous corn plant sheds over 10^7 haploid, trinucleate pollen grains. Waxy and alcohol dehydrogenase-1 are known to be expressed after meiotic anaphase II, and the many correlations of duplication-deficient gametes with pollen abortion suggest that much of the pollen phenotype is encoded by its haploid genotype rather than the genotype of its pollen mother cell. For this reason, Nelson (commencing in 1958, Science 130: 794 with wx) and later, Freeling (1976, Genetics, in press, with Adh) were able to study intracistronic recombination and reversion, and Schwartz (1975: lecture at the International Maize Symposium, Urbana) was able to select Adh-deficient mutants among allyl alcohol-resistant pollen grains. Over the last two years, this laboratory has perfected numerous procedures involving maize pollen. Following Schwartz's lead, we have also recovered mutants via pollen selection. The methods and recipes we use follow. We hope they prove generally useful.

In vitro germination using "David's Bread Loaf": We have revised the pollen germination medium and conditions reported by Cook and Walden (1965, Can. J. Bot. 43: 779). Our concoction--called the Cook and Walden Revised Medium (CWRM)--is composed of 17% w/v sucrose, 300 mg/l $CaCl_2 \cdot 2H_2O$, 100 mg/l H_3BO_3 and 0.7% w/v Difco Bactoagar, to a pH of 6.4 after the addition of agar but before heating. After heating until just clear (120 C for 8 min), this medium is gelled in a Griffin beaker of the desired diameter and stored at 4 C for at least four days without change. This column of gel is called "David's bread loaf", from which 2 mm slices are cut and immediately used for pollen germination at 25 C and low (uncontrolled) humidity within an unsealed petri dish. Our methods differ from Cook and Walden's in sucrose concentration, pH and humidity requirement; the major difference is that our pollen grains germinate on a newly-cut solid surface. We achieve 75-95% germination of healthy pollen after 30 min for all of the seven different lines and inbreds we have tried. Before we devised the "bread loaf" technique, we experienced dramatic genotype-specific fluctuations; pH and sucrose concentration had to be continuously adjusted. The "bread loaf" technique affords the reproducibility necessary for determining kill curves for pollen pretreatments, and slices with gametophytes are easily moved to other dishes for staining, counting, fixing and the like.

Pollen collection and storage: The majority of our pollen viability studies utilized a 23± 2 C greenhouse, low humidity and natural January to March lighting. We find that our typical plant sheds over a five-day period. First-day pollen usually germinates poorly; second-and third-day collections 2-4 hrs after dawn are

optimal; we avoid afternoon collections. Tassels should be stripped of anthers and pollen the evening prior to collection. Pollen is collected as shed in glassine bags, desiccated ($CaSO_4$) and stored at 4 C for 30 min to 4 hr. This cold storage-desiccation consistently elevates percent germination 5-10% to our modal 85%.

Berkeley's cool, dry summer permits routine collection of viable pollen from the field. Temperatures above 35 C or any discernible humidity greatly reduced the pollen's germinating ability. We typically collect 8 x 10^5 grains per plant in the late afternoon (2-5 p.m. PDT), subject them to chemical selective treatment, and pollinate at dusk. Our field pollen is from 50 to 90% viable. We suspect that the heat and humidity characterizing a corn belt summer might necessitate using cooled greenhouses for the male parents.

Pollen counting: Pollen samples were suspended in 40% technical glycerin in a 250 ml graduate cylinder to a final concentration of 4-6 x 10^3 pollen grains per ml by visual estimation. A 1.0 ml sample of homogeneous suspension was further diluted and the sample was layered evenly over a gridded Gelman filter (GA-6, 0.45 µm, 47 mm diam.) and quickly deposited by evacuation; circular currents were avoided in the layering process. The number of particles in four radial strips, each containing 5 squares (each square is one percent of the total area of the filter) were counted under incident light at a total magnification of 16X. In the rare instances where these numbers were significantly different from a 1:1:1:1: (by χ^2), the entire sampling process was repeated. For each original pollen sample, two filters were prepared, counted and preserved for further reference; this gave eight statistically equivalent numbers on which to base our estimates of total pollen grains per ml of original suspension. In general, 1 mg of our desiccated pollen contains about 2,000 grains.

When simply counting for percent germination, the slice of germination medium is placed over a grid of any desired color, or over a transparent grid if underlighting is desired.

Treatment with toxic vapor and recovery of resistant mutants: We have selected pollen grains resistant to various toxic vapors. Only allyl acohol (CH_2=CH-CH_2OH) resistance (rationale after Megnet, 1967, Arch. Biochem. Biophys. 121: 194, in yeast)--as it affects alcohol dehydrogenase activity--has been biochemically characterized: Megnet's scheme selectively kills ADH^+ cells owing to their capacity to oxidize relatively innocuous allyl alcohol to deadly acrolein. Megnet's selection is now being used in Drosophila and, as previously cited, Schwartz has reported success with maize ADH in pollen. Neither the selection scheme nor the strategy of using the male gametophyte are original to this laboratory, but the methods and results which follow are.

Pollen grains from a plant heterozygous for a gamma-induced ADH-deficient mutant (Adh-Fγ25, Freeling, unpublished), Adh^+/Adh^- were collected, stored, and dispensed in 20 mg lots (40,000 grains) onto glassine paper for vapor treatment in a 500 ml Mason jar with sealed lid containing 20 ml of $CaSO_4$ dessicant. In this experiment, methanol was used as an inert carrier. 0 - 50 µl 100% allyl alcohol was pipetted into the jar before sealing (1 µl allyl alcohol vapor/500 ml is ca. 7.4 x 10^{-5} M). After 40 min of treatment, the pollen was evenly dusted with a camel hair brush over a newly cut slice of CWRM and germinated as described. After the germination was complete, the slice was frozen at -23 C for 3 hr and defrosted for 30 min. ADH-specific stain was carefully layered over the gametophytes, left for 30 min, and replaced three times using methods of Freeling and Brown (1975, MGCNL 49:19). The 50% of the pollen grains that were ADH^+ stained blue and opaque; the other 50%, ADH^-, stained yellow and translucent. Thus the four phenotypes: blue with pollen tube, blue without tube, yellow with tube, and yellow without tube. The data tabulated below compare the allyl alcohol kill curves for sibling Adh^+ and Adh^- male gametophytes.

Allyl Alcohol µl/500 ml	Allyl Alcohol mM	Mean Relative Percent Germination* ADH^+ (blue)	ADH^- (yellow)
0	0	100 (78.5%)	100 (80.7%)
1	0.07	40	98
2	0.15	8.5	99
4	0.29	Zero	86
10	0.74	Zero	77.5
20	1.47	Zero	55.8
30	2.21	Zero	36.8
40	2.94	Zero	30.5
50	3.68	Zero	8.3

*The results of four independent experiments are averaged for each data point; mean absolute control was 79%; allyl alcohol was diluted with methanol such that 50 µl of foreign vapor were present; treated for 40 min.

According to the data, treatment under these conditions with about 0.3 mM allyl alcohol should let just a few ADH^+ gametophytes germinate. Does a positive germination assay indicate ability to fertilize an ovum successfully? Pollen samples treated exactly as above were brushed onto silks which had been cut back the previous day. Routine electrophoretic methods were used to ascertain whether $\underline{Adh^+}$ or $\underline{Adh^-}$ sperm participated in the fertilization. The results of these progeny tests were:

Allyl Alcohol (mM)	Seed Set	No. Seeds Receiving Allele* $\underline{Adh^+}$	$\underline{Adh^-}$
0.30	100%	0	72
0.30	100	0	70
0.22	100	3	65
0 Control	100	42	38

*Less than 25% of the seed set was genotyped.

We conclude that ability to germinate $\underline{in\ vitro}$ at least approximates ability to fertilize an ovum. However, when ADH^+ pollen is treated with higher concentrations of allyl alcohol, permitting fewer than 10^{-5} germinations, the vast majority of these survivors remain ADH^+. As might be expected, there are alternative ways to be resistant to any toxin.

$\underline{\text{Pollen Progaganda}}$: Since the recent dawn of "plant somatic cell genetics" much has been said of selecting mutants in haploid, totipotent suspension cultures. We submit that the tricks of "plant germ cell genetics" are not yet exhausted. Pollen is available in huge numbers; is haploid; mutants may be recovered in informationally normal cells; and pollen expresses many $\underline{\text{differentiated functions}}$, possibly permitting selection of agronomic traits. We see the pollen grain as a powerful genetic resource. We hereby grant permission to cite these methods.

David S. K. Cheng* and Michael Freeling
*Research Associate in Genetics Department

COMMONWEALTH SCIENTIFIC AND INDUSTRIAL
RESEARCH ORGANIZATION
Division of Plant Industry, Canberra, Australia

Characterization and distribution of GC-rich sequences in the DNA of maize

Satellite DNAs generated by Actinomycin D binding in CsCl density gradients were reported previously (MNL 47:28-30). The DNA from all corn lines examined apparently contained the same satellites but in different amounts. Subsequent work measuring the degree of hybridization of one of these satellites to total DNA from different lines confirmed this observation. It seems likely that the content of a particular satellite is positively correlated with the heterochromatin content of the particular line. Thus, in our continuing study of maize DNA it was important to characterize thoroughly the DNA from plants with the basic genome. Wilburs Flint Knobless has been used for these studies.

As a first step, thermal denaturation profiles were examined. These profiles were heterogeneous, indicating the presence of DNA species with a Tm about 10 C higher than the bulk of the DNA--i.e., DNA species with greater than 60% GC content compared to 42% for the bulk of the DNA. Reports of GC-rich sequences in maize DNA have been made previously (Brooks & Mans, Biochim. Biophys. Acta 312: 14, 1973; Pivec et al., Biochim. Biophys. Acta 340:199, 1974). In fact, this report describes GC-rich sequences that in all likelihood correspond to the same sequences first described by Brooks and Mans.

The GC-rich sequences are distributed throughout the genome. This was demonstrated by a comparison (3 methods) of unsheared and sheared DNA. Since GC-rich sequences have a higher melting temperature, under partial melting conditions these sequences will remain in a native double stranded condition, relative to the bulk of the DNA.

Method 1: If sheared (~500 bp) and unsheared (~30,000 bp) DNA molecules are partially denatured by heating and allowed to reassociate by cooling, the double stranded GC-rich regions will provide nucleation sites for the complete renaturation of those molecules containing GC-rich sequences. In this regard we have confirmed the observations of Brooks and Mans. About 70% of the hypochromicity was regained in the unsheared molecules compared to less than 10% for sheared DNA. Thus, the GC-rich sequences are distributed throughout the genome--i.e., 70% of unsheared molecules contain a GC-rich sequence.

Method 2: Thermal chromatography on hydroxyapatite (HAP). Under appropriate conditions double stranded DNA is bound to HAP, while single stranded denatured DNA may be eluted. By raising the temperature of a HAP column, DNA will be eluted unless it is covalently linked to a native double stranded region. Most sheared DNA was eluted at temperatures lower than were necessary to elute unsheared DNA, again demonstrating that most unsheared DNA molecules contained regions of higher thermal stability.

Method 3: Sheared and unsheared DNA were passed over a HAP column under partially denaturing conditions. Only those molecules containing native double stranded regions will be selectively retained on the column, and they can be recovered without further denaturation by elution with high salt. Under these conditions 70% of unsheared DNA was retained compared to 10% of the sheared DNA.

This third method was used to isolate preparatively DNA enriched for the GC-rich sequences. Further purification was achieved by denaturing and renaturing the DNA. Unpaired regions and single stranded tails were removed by digestion (to completion) with a single strand specific nuclease (S_1). The resultant double stranded DNA molecules had a size of about 200 b.p. (as judged by comparison with known-size fragments of ϕ80 phage DNA on agarose gel electrophoresis). A high GC content was confirmed by the Tm measured in thermal denaturation and the density

in neutral CsCl density gradients. A $Cot_{\frac{1}{2}}$ of 4×10^{-2} $M \cdot s \cdot l^{-1}$ was measured from renaturation kinetics. This value indicated the presence of repeated sequences in the GC-rich fraction. However, this rate is too slow for a single repeating unit of 200 bases. Thus, the GC-rich fraction represents either a family of repeated sequences or fragments of a larger, less-repeated sequence. Studies are continuing to distinguish these possibilities and to determine the length and distribution of these sequences.

Tony Pryor

Glucosidase in maize seedlings

(a) Inheritance of electrophoretic variants. Glucosidase bands in starch gels (pH7.8 Tris-citrate) were developed using a 6 bromo-2 naphthyl β-D glucoside and Fast Garnet GBC salt. Most inbred lines contain a single isozyme band, but in 2 of the 40 lines assayed (P10 and P11) a faster band was observed. Hybrids between variants have 3 isozyme bands, the additional band being a hybrid isozyme of intermediate migration. The segregation of the isozyme variants in F_2 and BC progeny is consistent with the hypothesis that the isozymes are determined by alleles (Table 1). We propose to call this gene glucosidase and the alleles Glu-A and Glu-C. A third variant, Glu-B, has recently been observed.

Table 1. Inheritance of glucosidase isozyme variants. C and A represent lines breeding true for the isozyme variants. χ^2 was calculated on the Null hypothesis that C and A are determined by alleles.

	Number of Progeny					
Cross	C	C/A	A	Σ	χ^2	P
C/A self	5	10	6	21	.04	>.05
C/A x C	9	10	-	19	.05	>.05
C/A x A	-	9	8	17	.05	>.05

(b) Null mutants at the Glu locus. Glucosidase activity has been implicated in the mechanism of plant disease resistance by mediation of the release of pathogen-toxic materials from inactive glycosidic precursors (Pridham, J. B., 1960, Phenolics in Plants in Health and Disease, Pergamon Press, New York). For the glucosidase determined by the gene Glu this supposed role can be tested by determining whether resistance is still expressed in a plant homozygous for a null mutation of the Glu gene.

Mutants were obtained by EMS treatment of seed homozygous for Glu-A, Gdh-F and Adh-S. During the latter half of the study seedling roots were immersed in water for 12 hours prior to electrophoresis to induce the Adh2 gene and allow scoring at this locus. By using electrophoretically recognizable pollen (Glu-C Gdh-N Adh-F) we should have been able to recognize a variety of mutant types at the 4 loci. However, only one class of apparent mutation was observed (Table 2). These ears carried sectors of seed containing only the pollen parent isozyme for glucosidase C. Plants from 17 of the 33 apparent mutants were selfed. In all cases the F_2 progeny segregated, having either the pollen parent isozyme or no glucosidase activity (Table 3), and in most cases where numbers were sufficient the segregation ratio did not differ significantly from a 3:1 ratio. Thus, absence of the female parent isozyme segregates as an allele of the glucosidase gene. Similarly in crosses Glu-A/Glu-C x Glu-C/mutant, progeny occurred in the ratio 1A:1AC:2C. The homozygous nulls obtained from the F_2 progeny breed true.

Table 2. Summary of ears screened for EMS mutants.

Expt. 1*	Glu	Gdh	Adh	Adh-2
Total No. Ears	38	34	33	16
Ears Mutant	5	0	0	0
%	13			
Expt. 2*				
Total No. Ears	149	143	155	83
Ears Mutant	28	0	0	0
%	19			

*EMS Concentration: Experiment 1, 0.16 M
Experiment 2, 0.08 M

Table 3. Segregation of glucosidase isozymes in selfed progeny of plants from 'mutant' sectors.

Mutant No.	C	Null	Σ
G1	12	5	17
G2	18	4	22
G3	12	4	16
G5	11	4	15
G6	16	6	22
G8	12	5	17
G9	10	6	16
G10	15	7	22
G12	11	3	14
G13	14	7	21
G15	9	6	15
G18	4	2	6
G24	9	5	14
G25	14	5	19
G28	9	8	17
G31	3	5	8
G33	8	5	13

Complementation studies between the different nulls are in progress, and in several F_1s so far examined there was no evidence of activity. Thus, by all criteria the null mutants behave as true alleles of the glucosidase gene. However, the high frequency with which they occurred (18% of tested ears) and the absence of other mutant types at this or the other three loci tested leave open some important questions. Further work is aimed at determining the true nature and origin of these nulls.

Tony Pryor

A genetic test for the involvement of catechol oxidase in hypersensitive resistance to rust

Phenolic compounds and polyphenol oxidases have been implicated frequently in plant resistance mechanisms (Kosuge, T., 1969, Ann. Rev. Phytopath. 7:195). In previous work, we also suggested (Pryor and Schwartz, 1973, Genetics 75:75) that a specific phenol oxidase, catechol oxidase (CX), functioned in the resistance mechanism. We have now been able to demonstrate that this enzyme activity is not involved in the resistance of corn to its rust Puccinia sorghi Sch. Nor does the level of endogenous CX substrate appear to affect the expression of resistance.

The experimental method was to construct a line which carries the gene for resistance and is homozygous for a null mutant of CX (Cx-N). Two different null lines were used, P3 and P4, having respectively high and low levels of endogenous CX substrate. The expression of resistance in these plants will then allow us to determine the involvement of CX activity and endogenous substrate in the hypersensitivity mechanism.

Table 1. Segregation of monogenic resistance to Puccinia sorghi in testcrosses also segregating for a null allele of catechol oxidase.

Gene	Backcross*	Susceptible	Resistant	Total	χ^2(1:1)
Rp-d	3 x 68.3	18	28	46	2.2
	68.3 x 3	27	23	50	0.32
	4 x 68.4	-	-	-	-
	68.4 x 4	26	18	44	1.45
Rp-f	3 x 70.3	22	24	46	0.09
	70.3 x 3	28	22	50	0.72
	4 x 70.4	-	-	-	-
	70.4 x 4	16	17	33	0.03
Rp-d(2)	3 x 77.3	20	25	45	0.56
	77.3 x 3	25	29	54	0.30
	4 x 77.4	-	-	-	-
	77.4 x 4	24	19	43	0.58
Rp-g	3 x 78.3	-	-	-	-
	78.3 x 3	20	25	45	0.56
	4 x 78.4	30	19	49	2.47
	78.4 x 4	62	77	139	1.62
Rp4-a	3 x 85.3	-	-	-	-
	85.4 x 3	24	19	43	0.58
	4 x 85.4	-	-	-	-
	85.4 x 4	25	20	45	0.56
Rp5	3 x 87.3	-	-	-	-
	87.3 x 3	19	26	45	1.09
	4 x 87.4	22	24	46	0.35
	87.4 x 4	16	15	31	0.03

*68, 70, 77, 78, 85 and 87 are our family numbers given to the monogenic resistant lines carrying the resistance genes listed in column one. Lines 3 and 4 are susceptible, and homozygous for Cx-N.

The resistance genes were derived from samples of the International Rust Monogenic lines developed by Hooker and supplied by Dr. K. S. McWhirter. All lines carrying a gene for resistance were homozygous for the Cx-F allele of catechol oxidase. Six of those lines showing resistance to the local rust strain were crossed and backcrossed reciprocally to the two null lines, P3 and P4. If CX activity is a necessary component of the resistance mechanism then only 25% of the backcross progeny will carry the gene for resistance with an active CX and will show resistance. Conversely, if CX is not involved, 50% of the progeny will be resistant and 50% susceptible. The results are presented in Table 1 and indicate 50% resistant progeny for all alleles and the three loci tested. This result indicates that CX is not involved with the expression of resistance with one reservation. This would arise if the genes for resistance and CX were tightly linked. Rp, Rp5 and Cx are on chromosome 10 but should be some 33 recombination units apart (Rp is at position 0 and Cx is very close (<0.2% recombination) to dull endosperm (du) at position 33). Rp4 is unlinked on chromosome 4. For reasons mentioned previously (Pryor and Schwartz 1973) it was not possible to assay unambiguously for resistance and catechol oxidase in the same plants. Thus, seedlings from the backcross involving the Rp-g gene were grown to maturity and the selfed progeny were scored for Cx genotype:

rp Cx-N	rp Cx-F	Rp-g Cx-N	Rp-g Cx-F	Total
9	3	6	8	26

Recombination between Rp and Cx is estimated at 34%. But, more significantly, 6 of 14 resistant plants were also homozygous for the null gene (Cx-N) for catechol oxidase.

Conclusion: Catechol oxidase activity is not required for the expression of genes for resistance to rust.

Tony Pryor

CORNELL UNIVERSITY
Department of Plant Breeding and Biometry,
Ithaca, New York and
UNIVERSITY OF DELAWARE
Department of Crop Science,
Newark, Delaware

Genetics of fertility restoration for male sterile cytoplasms

Crosses were made between homozygous male sterile (rf rf) and homozygous restored (Rf Rf) plants to produce a series of plants heterozygous for the pollen-restoring genes (Rf rf) for each of 26 different sources of cytoplasmic male sterility. These heterozygous F_1 plants were crossed onto their respective cytoplasmic male sterile parent; Table 1 presents the data on the number of fertile versus sterile plants in each backcross. All of the cms-S type cytoplasms and cms-K, -L, -B, and -D (which are similar to cms-S but have shown some fertility restoration differences) gave no sterile plants. Therefore, all of the cms-S type cytoplasms exhibited gametophytic restoration in which the recessive (rf) fertility restoration alleles produced by the Rf rf parent were not functional. The cms-T cytoplasms gave the 1:1 ratio between fertile and sterile plants expected of the sporophytic type of fertility restoration in which both rf as well as Rf pollen grains are functional. The cms-C type cytoplasms also follow the sporophytic pattern of restoration.

Table 1. Ratio of fertile and male sterile plants from the backcross of heterozygous (Rf rf) F_1s to homozygous (rf rf) parental cytoplasmic male sterile lines.

Cytoplasm	Reaction Type	Fertile	Male Sterile
T	sporophytic	20	23
P	"	17	25
RS	"	22	16
Q	"	21	19
HA	"	21	25
C	"	23	24
RB	"	14	11
S	gametophytic	38	0
G	"	38	0
I	"	32	0
J	"	36	0
M	"	35	0
R	"	23	0
ML	"	50	0
VG	"	36	0
H	"	30	0
EK	"	36	0
IA	"	36	1
MY	"	38	0
PS	"	37	0
SD	"	40	0
TA	"	25	0
K	"	37	0
L	"	45	0
B	"	33	0
D	"	35	0

Although all of the cms-S group of cytoplasms show the gametophytic type of restoration and exhibit similar patterns of fertility restoration reactions, we have observed a number of exceptional reactions within the cms-S group (Gracen and Grogan, Agron. J. 66:654, 1974), which seem to be due to the involvement of genes other than Rf3. Studies are underway to determine whether other alleles are involved in cms-S restoration or whether the exceptional reactions observed result from the differential action of modifying genes which control the degree of fertility restoration (full versus partial) of cms-S cytoplasms in different environments.

V. E. Gracen and S. L. Sullivan

CORNNUTS, INC.
Plant Breeding Department, Salinas, California

Conversions for earliness in maize inbreds

Numerous studies have shown earliness to be a completely inherited quantitative trait when a large range of difference in parents is considered. However, such studies do not usually address the ordinary problems which confront the practical plant breeder, since he is more often concerned with smaller differences, which if brought under precise control, can have large economic significance. If, among all the factors controlling earliness, there are a few major genes, each of which produces a recognizable phenotypic effect when heterozygous, then the backcrossing procedure itself becomes an efficient means to both detect and transfer such major genes if these exist. The plant breeder could then make discreet conversions for this quantitative trait, in the same manner as many other conversions are handled in plant breeding.

In 1956, the inbred parents of hybrid U. S. 13 were selected (Wf9, Hy2, Oh41 and 38-11, hereafter designated 9, Hy, 41 and 38 respectively), and crossed to the very early variety, "Gaspe Flint." Then, ten uninterrupted backcrosses were made to each of the four inbreds. In each backcross recovery progeny, the sole selection criterion of fewest days to anthesis was used to select 4 to 6 plants for further backcrossing from a minimum population of 64. After completion of the 10 straight backcrosses, 2 generations of sibbing, then two of selfing were completed. After the last selfing generation, a single ear progeny was selected as the final modified version of each inbred, and these $BC_{10}S_4$ recoveries were designated "9E," "HyE," "41E" and "38E." In the summer of 1971 all possible inbred and parental single cross combinations were grown out in 5 rep. experiments; the data collected are in Table 1. Total leaf numbers were determined by marking the 5th leaf while the first leaf was still present, and by marking the 10th leaf while the 5th was still present.

Little difficulty was encountered during the 10 backcrosses in identifying markedly earlier segregates, indicating that major earliness genes were being "dragged" (controlled). The completed early recoveries appear to be precise recoveries of the original lines, indicating that the major Gaspe genes are not linked to any easily recognizable phenotypic trait.

Days to Anthesis was markedly shortened in the 4 inbred lines, by 12.6, 6.84, 2.0, and 6.56 days in 9, Hy, 41 and 38, respectively. Factors producing this modification are partially dominant as seen by the fact that the crosses between original and modified "E" versions are earlier by 8.68, 6.20, -2.00 and 4.98 days respectively. (The exceptional result for inb. 41 will be discussed later). The degree of modification produced by E versions of inbreds when used in single crosses is proportional to the degree in which the inbred itself is modified. For example, inbred 9 was most modified by the earliness conversion, and 9E is more prepotent in single cross combination than any other E version. This indicates that different major Gaspe genes have about the same degree of dominance. Since there was never any visual evidence in backcross progenies that the earliest class of plants among the 4 inbreds (except for inb. 41) was more numerous in one than another, it is believed that the same number of loci was being transferred in each line, but that these differed from line to line, presumably because a given inbred may already have been isogenic for a given Gaspe gene, while another inbred may have been isogenic for another. If this is so, then the differing degrees of earliness modification among the 4 lines are due to the differing potencies of the Gaspe genes to which a given line was susceptible to modification.

Table 1. Inbreds, early recoveries, and their F_1s.

Pedigree	Days to Anthesis	Total Leaf No.	Height Top Ligule	Height EPN*	Ear Length	Kernel Row No.	Tillers Per Plant	Ears Per Plant	Grams Per Kernel	Yield lb/A
9	95.18	20.00	58.0	24.4	6.27	16.27	.000	0.967	.239	3,588
9E	82.58	15.50	39.9	12.9	5.99	13.87	.017	1.000	.235	2,377
9 x 9E	86.50	17.76	52.5	21.1	6.50	15.60	.000	1.000	.261	4,273
Hy	94.06	18.90	47.6	24.4	5.07	14.93	.017	.983	.223	2,256
HyE	87.22	15.72	37.0	15.6	5.13	16.43	.018	1.018	.160	2,008
Hy x HyE	87.86	17.48	43.4	20.4	6.21	16.27	.078	.961	.173	2,318
41	101.20	19.32	55.5	26.7	7.04	12.27	.180	1.016	.189	2,513
41E	99.20	18.98	52.0	24.9	6.42	12.13	.133	0.967	.213	2,665
41 x 41E	103.20	19.70	56.0	27.0	6.88	12.27	.098	0.984	.221	2,976
38	103.10	20.96	65.6	35.0	7.65	15.34	.180	1.000	.213	3,018
38E	96.54	19.20	60.2	26.8	7.71	13.63	.491	1.018	.238	2,985
38 x 38E	98.12	19.76	64.3	32.5	8.24	14.43	.441	1.017	.235	3,842
9 x Hy	86.07	20.11	74.8	40.7	7.24	18.40	.580	0.992	.255	7,301
9E x Hy	83.48	18.09	66.8	33.6	6.78	17.53	.680	1.000	.282	6,948
9 x HyE	84.17	18.52	67.6	30.7	6.83	18.69	.538	1.000	.251	6,696
9E x HyE	81.01	16.62	58.5	24.1	6.46	18.20	.683	1.008	.267	6,386
41 x 38	94.55	20.51	78.9	47.2	8.16	13.67	1.442	1.033	.286	6,810
41E x 38	92.73	19.88	75.2	42.9	8.18	13.93	1.303	.992	.268	6,510
41 x 38E	91.38	19.85	76.7	43.3	8.23	13.54	1.467	1.025	.318	7,220
41E x 38E	89.56	19.17	74.2	40.6	8.42	13.50	1.393	1.016	.246	6,955

*Ear Placement Node

Leaf number was reduced in the early conversions by 4.50, 3.18, 0.34 and 1.76 leaves respectively, in proportion to the degree of chronological modifications. Plant height to the top ligule and height of the ear placement node were reduced in proportion, and these relationships are carried into the single cross hybrids.

Effects upon ear length, kernel row number, tillers and ears per plant, and individual kernel weight were inconsistent.

Yielding ability of inbred lines was generally reduced by the earliness conversion, but the cross between a line and its "E" counterpart always showed heterosis for yield, presumably because of heterozygosity for the transferred chromosome segments. An increase in yield for these extremely close sister crosses of an average of 508 pounds per acre is rather surprising, and tells why the seed industry is rapidly abandoning the marginally economic pure single cross hybrid in favor of modified singles. In spite of their superior yielding ability, these sister crosses looked identical, except for traits directly related to earliness, to their unmodified counterparts. Heterosis in these narrow sister crosses was accompanied by increased ear length, so this study agrees with the general finding that ear length is the yield component most clearly associated with heterosis.

Yielding ability of 9 x Hy single crosses was reduced by insertion of E line conversions into the pedigree. It is difficult to say how real this reduction is, since only one population was used, and it can be expected that the smaller plants of the E versions would yield relatively better at higher populations. On the other hand, if the reduction is real, it is explainable on the basis that if conversion of both 9 and Hy "dragged" the same Gaspe locus, then their single cross hybrid would be homozygous for this segment and therefore less heterotic.

Yielding ability of the 41 x 38 single crosses was not altered by the insertion of E versions, and it is worth noting that leaf number and plant stature was least altered also. The several ways in which the 41 derivatives behaved differently seem unexplainable. The 41E line is earlier than 41 and has fewer leaves, but is prepotent for lateness and greater leaf number when combined with inb. 41; these data are consistent throughout the 50 individual data of 5 reps. In combination with inb. 38, it is prepotent for earliness and reduced leaf number. During the extended backcrosses by which 41E was derived, there seemed to be only 2 classes of plants, half the population being only slightly earlier than the other half, in marked contrast to the usual situation where each generation presents a very few plants really much earlier than the general population. Nevertheless, we are unable to devise a plausible genetic model to explain the erratic Oh41 data.

The finding in this research that earliness is always associated with a reduction in leaf number (and plant stature) is consistent with the generally accepted idea that earliness is determined by a signal which "tells" the apical meristem when to stop cutting off leaves, and when to produce the apical inflorescence (tassel). Our transferred loci from Gaspe always worked their effects by this means. Since the backcrossing process was just as effective when conducted during the very short days of wintertime in Hawaii, it is clear that the loci are independent of day-length effects, and operate to control the number of plastichrons to be completed by the apical meristem. Since ear placement is also always lower in early-converted entities, it is apparent that control is exercised by the transferred loci during the whole period of morphogenesis, since the ear inflorescence, as well as the tassel, was cut off after fewer plastichrons. The clarity of the relationship between earliness and leaf number makes it tempting to suppose that leaf number is the primary (or only) criterion of earliness. The data in Table 2 were derived from those in Table 1 by dividing days to anthesis by leaf number plus one (to account for the tassel) and are intended to show the time required by each genotype to complete one unit (plastichron) of development.

Table 2. Plastichron indices (time to anthesis divided by leaf number plus one).

Non-heterotic		Heterotic	
Pedigree	Index	Pedigree	Index
9	4.53	9 x Hy	4.08
9E	5.00	9E x Hy	4.37
9 x 9E	4.61	9 x HyE	4.31
Hy	4.73	9E x HyE	4.60
HyE	5.22	41 x 38	4.40
Hy x HyE	4.75	41E x 38	4.44
41	4.98	41 x 38E	4.38
41E	4.96	41E x 38E	4.44
41 x 41E	4.99		
38	4.69		
38E	4.78		
38 x 38E	4.73		
Overall Mean	4.83	Overall mean	4.38
Mean of normals	4.73	Mean of normal x normal	4.24
Mean of earlies	4.99	Mean of normal x early	4.39
Mean of normal x early	4.77	Mean of early x early	4.52

Data in Table 2 show a remarkable consistency in overall number of days required per plastichron in all genotypes, but it is notable that heterotic entities (even the very narrow sister crosses) are always a little faster, and hence leaf number, while an overwhelmingly important factor, is not the sole determiner of earliness.

Very surprising is the fact that in both heterotic and non heterotic pedigrees, the "E" conversions in every case required more time to complete a plastichron than did normal counterparts. This strengthens the role played by leaf number in earliness, and indeed the transferred loci produced earliness solely by this means, even having to swamp the delay of a slower plastichron cycle to do so.

Since doing the original work on the U. S. 12 inbreds reported here, we have made earliness conversions of numerous other inbred lines. No other cases of anomalous behavior besides Oh41 have been observed, although the degree to which individual inbred lines are susceptible to earliness modification does vary. Often the recurrent parent is switched to a related line, or a finished "E" conversion is used as a source of major earliness loci, rather than Gaspe itself. In some cases our material is removed from Gaspe by 15 straight backcrosses, and it is still perfectly easy to "control" the earliness genes. As in the classical Nilsson-Ehle experiment, repeated attempts to quantitate numbers of genes controlling earliness in our experiments by scoring individual plants in the backcross progenies and then erecting frequency distributions result only in normal-appearing population curves. Nevertheless, the ease with which we continue to control transferred loci for extended backcrosses using only relatively small populations leads us to suggest that we are controlling only two major loci, or at most three.

The practical significance of earliness conversions is vast: A valuable inbred line can be moved widely across maturity zones without losing the attributes from which its value derives. A "pure" singlecross hybrid can be made to have an extended pollen/silking period by the insertion of, say, B73 x B73E as one parent. Field crosses can be made which would otherwise require split planting. Availability of germ plasm for a given maturity zone can be greatly expanded. Late exotics can be made amenable to maintenance in temperate zone breeding stations.

Attempts have been made to extend the oligometric approach outlined here to modify other quantitative traits such as shuck number, shuck texture, shank length, ear number, kernel row number, and internode length. All these endeavors have been successful, although not with the ease associated with the earliness conversion.

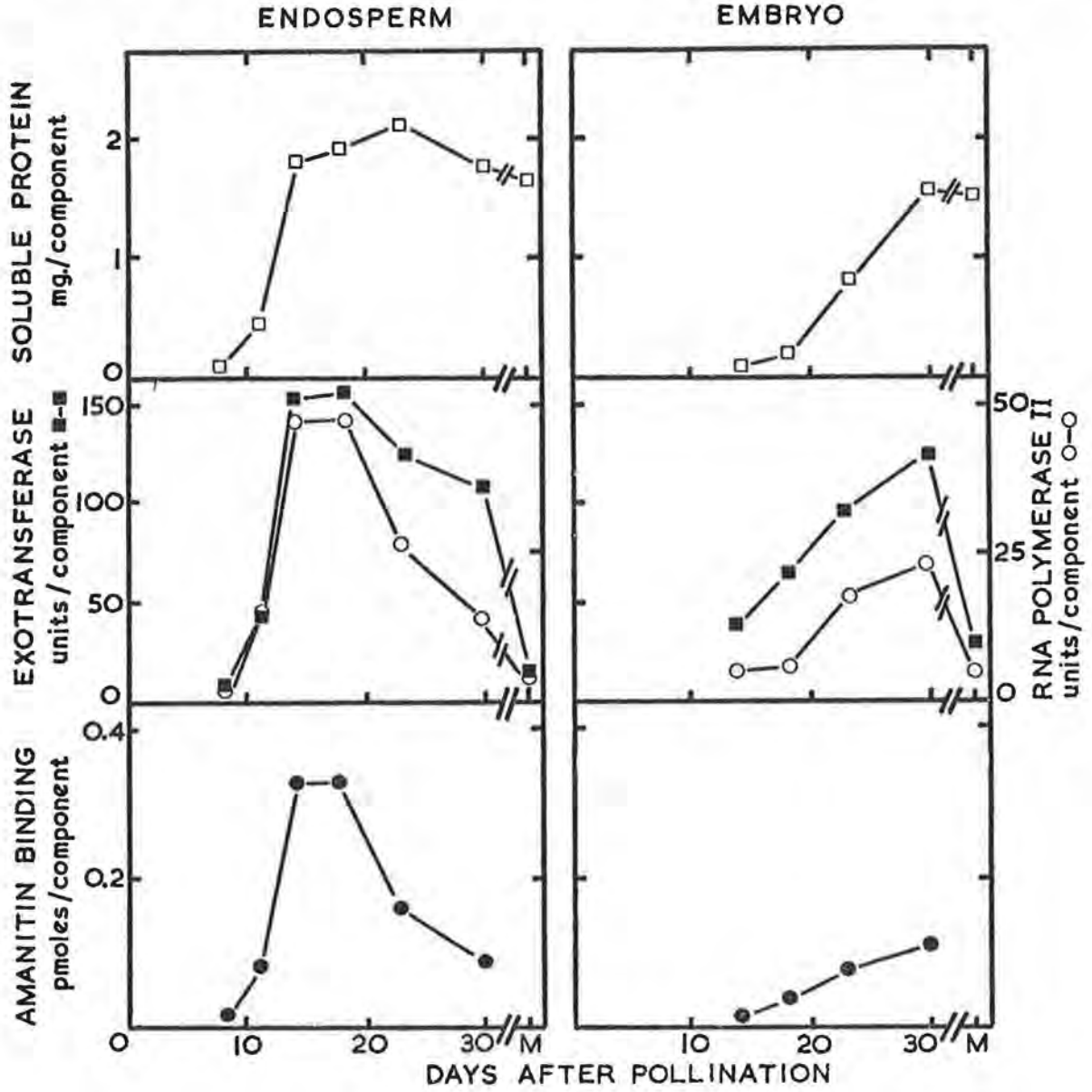
The research pursuant to this paper was conducted at the University of Illinois, at Indiana University, at Brookhaven National Laboratory, and at Cornnuts Research Department. More detailed data and statistical treatments are available on request.

D. L. Shaver

UNIVERSITY OF FLORIDA
Department of Biochemistry, Gainesville, Florida

Levels of RNA polymerase II and polynucleotide adenylyltransferase in maturing maize kernels

Post-transcriptional modification of messenger RNA may regulate the expression of information derived from the chromosome. Most mRNAs are modified at the 3'-hydroxyl terminus by the addition of a poly (A) sequence. The ubiquity of this sequence and of enzymes capable of its synthesis suggest it plays a fundamental role in the expression of genetic information. Such a role could be direct as in the termination of transcription or indirect as in the processing of HnRNA or even more remotely as in the maintenance of mRNA function during translation. By examining tissues in different physiologic stages of maturation, we hope to find times when processing may be dissociated from transcription. As a first step we are determining if mRNA and poly (A) synthesis are directly coupled by following the two enzymic activities involved, namely RNA polymerase II and polynucleotide



adenylyltransferase (exotransferase) during differentiation and development. The maize kernel was examined since it consists predominantly of two tissues: the endosperm, where mRNA synthesis may be specifically enhanced for the accumulation of starch synthesizing enzymes and storage protein, and the embryo, where the mRNA spectrum is likely to be more diverse among the many cell types differentiating during kernel development. Our approach has been to develop specific assays for these enzymes (Walter and Mans, 1975, Plant Physiol. in press). RNA polymerase II was determined as the α-amanitin sensitive incorporation of [^{14}C] UTP (1 enzyme unit is the incorporation of 1 mole UMP/min) or by a radioactive binding assay using [^{3}H] α-amanitin (Cochet-Meilhac and Chambon, 1974, Biochim. Biophys. Acta 353:160), a specific inhibitor of this enzyme. Exotransferase was assayed by the incorporation of [^{14}C] ATP into poly (A) (1 enzyme unit is the incorporation of 1 pmole AMP/min). Endosperms and embryos were dissected from maturing ears of corn (WF9 x Bear 38, waxy) beginning at 8 days after controlled self-pollination. Partially purified extracts were prepared by high speed centrifugation to remove cellular particulates, including DNA and ribosomes, and gel filtration to remove inhibitory low molecular weight components. Control experiments established that activity was not lost on dissection and that the sum of the observed activities in the isolated components corresponded quantitatively to the total activity in whole kernels.

Endosperms isolated at 8 days showed little activity (see figure), but a rapid increase in both activities was observed up to 14 days concomitant with the rapid proliferation of this tissue in the kernel. RNA polymerase II activity declined in the endosperm between 18 and 30 days. However, the loss of exotransferase activity was delayed and high levels of this enzymic activity were still present in the endosperm when the tissue was undergoing desiccation. The changes in RNA polymerase II were observed if the enzyme was assayed by in vitro RNA synthesis and by the binding of the specific inhibitor α-amanitin, indicating that levels of enzymic protein changed during maturation. Under our growth conditions, invertase activity (Tsai et al., 1970, Plant Physiol. 46:299) peaked at 14 days and ADP:glucose pyrophosphorylase (Ozbun et al., 1973, Plant Physiol. 51:1) reached almost maximal activity at 14 days in the endosperm. The coincidence of the increase in RNA polymerase and exotransferase activities with those of invertase and ADP:glucose pyrophosphorylase is consistent with the former's postulated role in providing mRNAs for the latter prior to the accumulation of starch and storage protein. Unlike the endosperm, the rise in embryo exotransferase preceded RNA polymerase activity and was proportionately higher during the 14 to 30 day period.

The changes in activities of the enzymes catalyzing RNA synthesis and polyadenylation of RNA differed in the two metabolically distinct tissues: (i) in the time of increased activities, (ii) in the relative level of activities attained and (iii) in the decay rates of the two activities and precludes a coupled relationship between them. A less direct and perhaps regulatory role for the exotransferase in processing transcripts is suggested.

Trevor J. Walter and Rusty J. Mans

In vitro studies on the initiation of transcription by maize RNA polymerase II

The control of transcription in higher organisms is of primary importance in the regulation of gene expression. We have previously reported (Am. Soc. Agron. Abstr. 1975, p. 52) the construction of a model system for the study of transcription in maize. The in vitro system contains RNA polymerase II purified from maize seedlings as the transcriptive enzyme, while the allomorphic forms of bacteriophage φX174 provide homogeneous and genetically defined DNA templates. In our previous report, we demonstrated that circular, single-stranded DNA was

transcribed by the maize RNA polymerase without nicking the template, while linear strands of the same DNA (generated by DNAase treatment) were transcribed with the same efficiency. We concluded that transcription was initiated on internal sequences of the DNA molecule and not at nicks or ends.

In studies on mammalian RNA polymerases, it has been shown that nicking of double-stranded DNA (which facilitates local denaturation of the template) stimulated initiation by RNA polymerase (Meilhac and Chambon, 1973, Eur. J. Biochem. 35:454-463), while nicking of superhelical DNA (which removes the loosely base-paired regions of the superhelix) blocked initiation (Mendel and Chambon, 1974, Eur. J. Biochem. 41:367-378). In light of our findings with the maize enzyme, we suggest that *in vitro* initiation sites for eukaryotic RNA polymerases are always denatured or loosely base-paired regions of the DNA template and not nicks or ends of molecules.

Recently, we have found that the double-stranded, circular, superhelical DNA of ϕX174 replicative form I (RF 1) is a good template for transcription by maize RNA polymerase II, while intact, double-stranded DNAs that are not superhelical, such as phage T4 DNA, are poor templates. Similar observations have been made with mammalian RNA polymerases. Circular, superhelical DNAs are known to exist in chloroplasts, mitochondria, and nucleoli, and a significant proportion of chromosomal DNA may be superhelical as well. Perhaps DNAs must be superhelical in order to be transcribed *in vivo* and the loosely base-paired regions of the superhelix are the *in vivo* sites of RNA chain initiation.

Charles O. Gardner, Jr. and Rusty J. Mans

UNIVERSITY OF FLORIDA
Department of Vegetable Crops, Gainesville, Florida

Further characterization of embryo ADP-glucose pyrophosphorylase

Endosperm adenosine diphosphoglucose pyrophosphorylase is of genetic and physiological interest because it is reduced in *sh2* and *bt2* mutants and it is an important and possibly regulatory enzyme in starch biosynthesis. Recent observations have suggested that the embryo and endosperm contain different forms of this enzyme. Preiss et al. (Pl. Physiol. 47:104, 1971) reported that the embryo enzyme differs from the endosperm enzyme in sensitivity to phosphate inhibition and extent of heat denaturation. It is not affected severely by mutants of *sh2* and *bt2* (Dickinson and Preiss, Pl. Physiol. 44:1058, 1969). These genetic and biochemical observations are, in general, reproducible (Hannah and Nelson, Pl. Physiol. 55:297, 1975). To further investigate the question of whether these tissues do contain different forms of this enzyme, a comparison of electrophoretic mobility was made.

Frozen 22-day-old kernels of the F_2 of W64A x 182E were dissected and the tissues were ground in phosphate buffer, passed through cheese cloth, centrifuged and the supernatant used as the enzyme source. Electrophoresis was done on 3.5% acrylamide-agarose gels as described in detail elsewhere (Hannah and Nelson, submitted to Biochemical Genetics). The gels permit rapid movement of pyrophosphorylase. It was found that the mobilities of the two enzymes were the same. This experiment was repeated approximately 10 times and in no case was a difference in mobility observed. Furthermore, Warren Bryce in Oliver Nelson's laboratory has obtained the same results. These results suggest that these tissues may contain the same form of pyrophosphorylase.

In cooperation with Drs. Trevor Walter and Rusty Mans, a more critical comparison, using highly purified preparations, of these two enzymatic activities is

being conducted. It has been found that embryo preparations, purified as in previous experiments, contain a heat sensitive enzymatic activity which destroys a component of the reaction mixture, probably glucose-1-P. Thus, attention is now focused on the removal of this latter enzyme from the embryo pyrophosphorylase preparation in order to compare, in a definitive way, the pyrophosphorylases from the two tissues.

L. Curtis Hannah

Characterization of a gametophyte factor-like system on chromosome 5

A genetic system which leads to preferential fertilization by male gametes which contain bt-A on chromosome 5 has been discovered and is now being characterized. Given below is a summary of some features of this system. Seen initially in Dr. Oliver Nelson's laboratory, this system has several features in common with gametophyte factors and, because of this, the gene located on chromosome 5 will be given the symbol Ga. Because appropriate allelism tests with other known ga loci on chromosome 5 have not been completed, the allele carried on the chromosome favored in fertilization will be denoted Ga*-7001; the contrasting allele is termed ga*-7001. Initially, it was found that plants of the genotype Bt/bt-A gave rise to excess bt kernels when self-pollinated or when used as male parents in crosses with bt-A/bt-A plants. The reciprocal cross yielded the expected 50% frequency of bt kernels.

Furthermore, this system appears to select male gametes which carry Ga*-7001 for fertilization but not at the complete exclusion of ga*-7001 gametes. This is suggested from the following lines of evidence. First, among 43 F_2 families from the original F_2 progeny, 42 contained bt kernels at a frequency significantly greater than 25%. An average frequency of 39.5% was calculated from 17,570 kernels. If selection is complete for Ga*-7001, this gene must be approximately 21 map units from the bt locus. It follows then that 32% of the resulting F_2 Bt/bt-A kernels should be also Ga*-7001/Ga*-7001 and should give rise to 25% bt in the F_3 generation. Among 26 Bt/bt-A plants selected from 4 F_2 progenies, only one gave, upon self-pollination, a frequency not significantly greater than 25%. Again, 32%, or a total of 8, would be expected were the genetic distance equal to 21 map units. These latter results suggest, then, that Ga*-7001 and bt-A are much closer than 21 map units and this would suggest that some ga*-7001 pollen also effect fertilization. Secondly, there appears to be genetic modification of the extent of Ga*-7001 selection. This is from the following evidence.

Two F_2 families contained bt kernels at frequencies of 29.5% and 29.1%. These values are significantly greater than 25% but much lower than the overall average of 39.5%. Four Bt kernels, selected from each of these families and which proved to be Bt/bt-A, gave rise, upon self-pollination, to bt kernels at average frequencies of 27.8% and 30.8% respectively. Similarly, Bt/bt-A kernels selected from four other F_2 progenies which had bt frequencies of 53.8%, 39.5%, 49.5% and 40.7% produced F_3 progenies in which the average percent bt was 39.6%, 34.7%, 43.0% and 42.5%. The simplest explanation is that there exists a genetic system in which Ga*-7001 gametes are favored in fertilization but that the extent of Ga*-7001 selection is susceptible to genetic modification. Genetic heterogeneity for this modification existed in the original F_1 progeny.

In analogy with other ga systems, the simplest model to account for the observations thus far is that there exist two alleles of this locus; the allele Ga*-7001, when carried in the female, favors fertilization by pollen also carrying Ga*-7001. Data presented in Table 1 show, however, that this model cannot account for all the observations. It can be seen that plants heterozygous for other alleles of bt yield, upon self-pollination, the expected results. However, when these plants are used as males onto Bt/bt-A heterozygotes, an excess of bt kernels is observed.

Table 1. The percentage of brittle kernels resulting from self-pollinations and crosses of various bt heterozygotes.

Plant	Genotype	% bt kernels Selfs	% bt kernels Onto Bt/bt-A
16-1	Bt/bt-D	23.2	35.9
16-3	Bt/bt-D	29.8	40.3
15-14	Bt/bt-D	22.2	35.9
6554-6	Bt/bt-C	28.2	44.9
6556-6	Bt/bt-D	25.7	40.2
6556-13	Bt/bt-D	28.9	41.0
6558-5	Bt/bt-E	24.2	46.8
6560-6	Bt/bt-F	22.2	31.8

Clearly, the one locus-two allele system is ruled out. At the next level of complexity are the following two models.

First, there may exist three alleles of this locus; the two alleles carried, for example, by plant 16-1 (Table 1) would lack female action (could not condition the ability to detect, in the incoming male gametes, the heterogeneity conditioned by this locus), but would have male action (Ga*-7001 in the female can differentiate between them). Secondly, there may be two loci involved. In its simplest form, this model would be the following. One gene would act in the male gametes to condition the differences detected and a second, independently acting, gene would condition in the female the ability to detect differences in the male gametes.

To distinguish between these possibilities, the following crosses were analyzed. Plant 8780-11, shown to be Bt ga*-7001/bt-A Ga*-7001 from appropriate crosses and, from pedigree analysis, homozygous for the presumed second gene, was crossed as female by plant 8777 (bt bv/bt bv). The resulting bt kernels were grown, self-pollinated and the resulting Bv progeny were tested for their ability to select Ga*-7001 pollen. Since bt and bv are 5 map units apart, and thus the maximum distance between Ga*-7001 and Bv is 26 units, a minimum of 85% of Bv plants would also carry Ga*-7001. Among 23 plants tested for female action, only 10 could select male gametes that contained Ga*-7001. Again, 20 of the 23 should have shown positive female action if Ga*-7001 alone can select Ga*-7001 pollen. Thus, the first alternative hypothesis appears unlikely. However, a second test, outlined below, suggests that Ga*-7001, or a recessive gene linked to it, is involved in selection. The Bt kernels from the 8780-11 x 8777 cross would lack Ga*-7001. These kernels were grown, self-pollinated, and the Bt progeny were tested for female action. Of 17 plants tested, only one gave rise to excess bt kernels in the cross. This would suggest that Ga*-7001 or a recessive gene linked to it is needed for female action. Future work will be directed at obtaining more definitive data concerning the proper mechanism.

L. Curtis Hannah

FUNK SEEDS INTERNATIONAL
Bloomington, Illinois

Attempts to induce cytoplasmic male sterility with chemical agents

During this past summer male sterile material that had been crossed with various inbreds (MNL 49:35) was grown to determine if any of the plants were

cytoplasmically male sterile. To date no sterile individuals have been obtained that can be considered to be the result of an induced cytoplasmic mutation.

It was proposed by the author (MNL 47:35-37) that nuclear fertility restorer genes in the material that was treated with the mutagen may disguise an induced cytoplasmic male sterile, i.e., a sterile cytoplasm may be induced with a mutagen but still produce fertile plants due to the presence of nuclear restorer genes. In previously reported research the inbred A632 was used; according to Gracen and Grogan (MNL 48:20-23) and Gracen (personal communication), this inbred has restorer genes for many different sterile cytoplasms. If this inbred carries restorer genes for many of the known sterile cytoplasms, it might also carry restorer genes for sterile cytoplasms that might be induced with chemical agents. To examine this idea, an inbred that does not restore many sterile cytoplasms should be chosen; the inbred W59M was suggested by Gracen.

In an effort to continue this research and examine these theories, during the past summer the inbred W59M was treated with streptomycin and ethidium bromide according to procedures previously published (MNL 47:35-37).

Robert W. Briggs

Use of a genetic marker to make self- and cross-pollinations on the same ear

A procedure which makes it possible to make self- and cross-pollinations on the same ear by using purple aleurone markers was employed to carry out a form of full-sib reciprocal recurrent selection. Full-sib reciprocal recurrent selection is a breeding procedure in which the second ears from individual plants in two populations are self-pollinated, and reciprocal crosses are made on the top ears of the paired plants. At least one member of each crossed pair must be prolific so that crossed seed and selfed seed of both parent plants is obtained. Procedures for sull-sib reciprocal recurrent selection have been described by Hallauer (Crop Sci. 7:192, 1967), Hallauer (Egypt. J. Genet. Cytol. 2:84, 1973) and Lonnquist and Williams (Crop Sci. 7:369, 1967).

Full-sib reciprocal recurrent selection is an excellent breeding procedure but it requires that at least one parent be prolific; and many maize populations are not strongly prolific. A procedure has been developed this past summer which allows this breeding technique to be applied to nonprolific strains of maize. The procedure basically consists of self-pollinating a number of plants in each population, crossing these same shoots with an aleurone marker stock and then reciprocally crossing the plants from the two populations. The first silks available develop from the basal end of the female inflorescence. Thus, the self-pollinated seeds would be at the base of the ear, the purple aleurone kernels in the middle of the ear, and the cross pollinated kernels at the tip of the ear; the purple aleurone kernels would separate the selfed and crossed kernels on each ear. The plant is self-pollinated before it is cross-pollinated since maize is basically protandrous, and in many cases viable pollen would not be present for self-pollinations if the cross-pollinations were made first.

In the field the plants were self-pollinated as soon as silks were present; on the next day the self-pollinated ears were crossed with A C R-nj pollen. Two more days elapsed before plants from the two populations were crossed reciprocally.

Only a small amount of selfed seed is required to recombine selections in order to initiate another cycle of selection. However, relatively large amounts of crossed seed are needed to perform replicated yield trials. The amount of seed needed depends on the number of kernels in one replication and the number of replications tested. The number of crossed seeds and the frequency of ears by number class were:

Number	Frequency
50-75	3
76-100	10
101-125	6
126-150	20
151-175	8
176-200	11
201-225	7
226-250	5
251-275	5
276-300	9
301-325	1
326-350	
351-375	
376-400	
401-425	1
Total	86

The amount of seed on the crossed portion of the ear ranged from 54-401 kernels; a total of 86 ears were obtained in which both selfed and crossed seed were available. The seed from the reciprocally crossed plants was bulked.

Approximately 500 plants in each population were available to make the reciprocal full sibs. The two populations were the F_2 generation from single crosses which differed in average pollen date by 4.6 days and in silk date by 3.2 days. Populations that produced pollen and silks closer together undoubtedly would have increased the success of this scheme. At the suggestion of Dr. J. H. Lonnquist only every other row was planted in order to reduce the population stress as much as possible and to encourage development of a large ear; after germination the seedlings were thinned to one plant every 18 inches (45 cm). When shoot bagging and pollinating was carried out, no leaves were removed in an attempt to facilitate maximum ear development. Just before the reciprocal crosses were made, the silks were trimmed with a scissors to a uniform length in an attempt to expose fresh silks and in hopes of obtaining a distinct line between the purple aleurone kernels and the crossed seeds.

A C R-nj pollen was used because it was available at the time the marker pollen was needed; regular A C R pollen would be satisfactory. Furthermore, A B Pl markers may facilitate the separation of any seed mixture in the next generation.

Long-eared strains would certainly facilitate the success of this modified reciprocal recurrent full-sib scheme, even more than would strains with a high kernel row number. One of the biggest problems other than a lack of cross-pollinated seed was that the selfed kernels at the base of the ear were often mixed with the purple aleurone kernels. When this occurred, the yellow kernels at the base of the ear were hand-shelled and saved as the self-pollinated kernels; in most cases, however, the crossed seed was nicely separated by a distinct line from the purple aleurone kernels. The main problem was that the self-pollinated kernels and purple aleurone kernels comprised too much of the total length of the ear.

Robert W. Briggs

UNIVERSITY OF GEORGIA
Department of Agronomy, Athens, Georgia

Cytoplasmic effects on chloroplast and mitochondrial development in a maize inbred

The nuclear genotype of inbred CI 21 (Athens) was transferred to the cytoplasm of inbred GA 199 through a backcross program. This cytoplasm/genotype combination was then compared under a Siemens 101 electron microscope with that of inbred CI 21 (Athens) in its own cytoplasm.

Leaves of five-day-old seedlings from each of the two sources of cytoplasm were fixed in Chang's cocktail solution and embedded in blocks of epon, araldite resin at 50 C. The blocks were sectioned on a Reichert microtome.

The cells of CI 21 (Athens) with its own genotype showed matured plastids at 11,000 X, whereas cells of the CI 21 (Athens) genotype in GA 199 cytoplasm did not exhibit any plastids in the five-day-old seedlings. Mitochondria were present in both cytoplasms.

A. P. Rao and A. A. Fleming

Differential preferences of raccoons for maize cultivars

Fourteen maize hybrids, classified as early-season maturity at Athens, Georgia, were evaluated for palatability by raccoons from the surrounding woods. Evaluations were made at the "roasting ear" stage on August 10 by counting the number of plants damaged by the raccoons.

The raccoons selected in "cafeteria style" certain entries upon which to feed; they clearly preferred one entry. The average number of damaged plants/plot for this entry was 16.6 (64%) compared to the next most preferred entry, which had 2.7 damaged plants/plot (10%). Five entries had no damage. The 14 entries in the experiment were placed into three groups of significant differences based on Duncan's Multiple Range Test at the 5% level.

The yield of dry corn was greatly reduced for the entry having the most damage. The yield was only 46% of the overall average yield of all entries in the experiment.

A. A. Fleming and C. E. Simmons, Jr.

UNIVERSITY OF HAWAII
Department of Horticulture, Honolulu, Hawaii

The genetics of resistance to the corn leaf aphid, Rhopalosiphum maidis (Fitch)

We continue to work on the genetics of resistance to the corn leaf aphid, Rhopalosiphum maidis (Fitch) (see MGNL 48:37-38). To achieve greater control of the aphid predators and parasites of Hawaii, most experiments are now conducted in greenhouses. The plants are grown in 6" pots and rated during development; plants on which the uppermost leaves and tassel are not infested or are very lightly infested are scored as resistant, while those that are moderately to severely infested are considered susceptible.

Materials worked on in this report were lines from our segregating AA8sh2 population. A cross between resistant line 3660 and susceptible line 3655, its backcrosses, the F_2 and the two parental lines were grown and rated at tassling. The results are summarized in Table 1.

The F_1 was susceptible, demonstrating the recessive nature of the resistance. Backcross data point to monogenic inheritance, though three plants in the susceptible-parent BC were classified as resistant where there should have been none; these were attributed to 'escapes.' Chi-square for the F_2 generation was 0.0919, which was not significant, indicating a good fit to 3:1 ratio.

Table 1. Results of ratings of aphid reactions in the AA8sh2 population.

Entry	Generation	Total Rated	Observed Res.	Observed Susc.	Expected Ratio Res:Susc
Resistant 3660	P_1	10	10	0	All resistant
Susceptible 3655	P_2	10	0	10	All susceptible
3660 x 3655	F_1	10	0	10	All susceptible
(3660x3655) x 3660	B_1	20	9	11	1 : 1
(3660x3655) x 3655	B_2	20	3	17	All susceptible
(3660x3655) selfed	F_2	58	16	42	1: 3

This and other evidence has confirmed our previous report that the genetics of resistance to the corn leaf aphid in the AA8sh2 population is monogenic and recessive. In accordance with our previously designated symbol aph, the genotype for resistant line 3660 is aph/aph and that of the susceptible line 3655 is Aph/Aph.

Siew-Hoong Chang and James L. Brewbaker

Benzoxazolinones in teosinte and Tripsacum

The occurrence of the benzoxazolinones in corn is well known. Three known analogs, 2(3)-benzoxazolinone (BOA), 6-methoxy-2(3)-benzoxazolinone (MBOA) and 6,7-dimethoxy-2(3)-benzoxazolinone (dimethoxy-BOA), are present in corn. These compounds and their precursor hydroxamic acids, notably 2,4-hydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA), have been reported as insect and disease resistance factors in corn and wheat.

Using the highly specific gas-liquid chromatography procedure for the detection of benzoxazolinones developed in our laboratory (Tang et al., Phytochem., 1975), some analogs of this group of unique compounds were found in all three races of teosinte (Zea mexicana(Schrader) Kuntze) and three species of Tripsacum tested. Except in one case, only 0.1-0.2 gm fresh weight of shoots of 14- to 20-day-old seedlings were used in each determination; the mature leaves of Tripsacum laxum were assayed, as seedlings were not available. MBOA and dimethoxy-BOA were detected in the teosinte races from Balsas, Chalco and Jutiapa. However, BOA was not detected. MBOA was found in Tripsacum dactyloides(2N), T. dactyloides(4N), T. floridanum and T. laxum. A closer examination of T. dactyloides(2N) showed that all the three analogs, BOA, MBOA and dimethoxy-BOA, were present.

Based on the results of these samples, it appears that the benzoxazolinones are well distributed in teosinte and in the Tripsacum complexes. This finding strengthens past evidence of the close taxonomic relationships of corn, teosinte and Tripsacum. Studies of the distribution and concentration of the analogs in appropriate interspecific crosses may help further our understanding of the origins of corn.

Siew-Hoong Chang, James L. Brewbaker and Chung-Shih Tang

ILLINOIS STATE UNIVERSITY
Department of Biological Sciences, Normal, Illinois

Screening for genetic control of intragenic recombination by monosomic analysis

I recently determined that intergenic recombination in the sh-wx region of chromosome 9 is consistently, significantly lower in monosomic 4 plants (11.2% ± 0.8%) and monosomic 8 plants (17.1% ± 0.9%) than in diploid control plants (23.0% ± 0.8%) (Weber, submitted for publication). It appears to be unchanged in monosomic 7 plants (21.8% ± 1.8%), thus, monosomy per se does not alter intergenic recombination. Since consistent, significant alterations in intergenic recombination were found to occur in specific monosomic types, I have initiated a study to determine if intragenic recombination can also be altered by monosomy of specific maize chromosomes. Initial results of this study are presented in this paper.

To study intragenic recombination, one must analyze large populations because the recombinational frequencies are very low. These large populations can be readily analyzed using the elegant system developed by Nelson (1959, Science 130:794). This system uses the waxy (wx) locus on chromosome 9 of maize. Since the phenotype of a pollen grain is determined by its genotype and because massive numbers of pollen grains are available from a single plant, the populations necessary for such a study can be efficiently analyzed using relatively simple procedures.

The r-X1 deficiency in maize induces chromosomal nondisjunction during the megagametophyte divisions after meiosis, producing large numbers of monosomes, trisomes, double monosomes, double trisomes, and even triple monosomes (Weber, 1973, Theor. Appl. Genet. 43:167). R/r-X1 plants (from Satyanarayana) were backcrossed as female parents by plants homozygous for the wx-90 allele (from O. Nelson) of the wx locus for six backcrosses to establish an inbred line carrying both the r-X1 deficiency and the wx-90 allele.

These r-X1; wx-90 plants were crossed as females by a second inbred, Mangelsdorf's multiple chromosome tester (from Satyanarayana), which bears a recessive gene on each chromosome (bm2; lg; a; su; pr; y; gl; j; wx; g). As the r-X1; wx-90 line carries a dominant gene corresponding to each recessive marker in Mangelsdorf's tester except for wx, the appearance of a recessive phenotype in the F_1 indicates the loss of a chromosome carrying the corresponding allele from the maternal parent. Such a plant would be monosomic for that chromosome. For a more detailed description of the production of monosomics with the r-X1 deficiency, see Weber, 1973, Theor. Appl. Genet. 43:167.

The wx allele in Mangelsdorf's tester is presumably the standard recessive allele of the wx locus designated wx-C, for Cornell (Nelson, 1968, Genetics 60: 507), therefore this allele will be designated wx-(C). All F_1 progeny from the above cross (r-x1; wx-90×Mangelsdorf's tester) are very highly isogenic except for aneuploidy because they are the result of a cross between two inbred lines. All F_1 progeny also carry the wx-90 allele on one chromosome 9 and wx-(C) on its homolog.

F_1 progeny from the above cross were planted in the field and specific monosomic types were selected. Plants monosomic for chromosomes 2, 7 and 10, as well as diploid plants, have been recovered and analyzed to date. Tassel samples from monosomic and diploid plants were fixed in 70% ethanol. Twenty-four anthers were placed into a Virtis microhomogenizer stainless steel cup, cut apart with a scissors, and homogenized for 1 min in 0.5 ml of I_2-KI solution as described by Nelson (1968). The homogenate was then strained through two layers of cheesecloth onto the surface of an 80 x 100 mm slide. A 45 x 50 mm coverglass was placed on the preparation.

The population of normal pollen grains on each slide was estimated by counting twenty 1 mm^2 areas on each slide and multiplying this value by a constant. Only plump pollen filled grains were counted. Each slide was then scanned, and each Wx pollen grain was counted. The Wx frequencies in the two inbred lines were 1.8×10^{-5} for wx-(C) and 0.8×10^{-5} for wx-90. These values are in the range of those reported by Nelson (1968). The mean of these values was subtracted from the frequency of Wx pollen grains from monosomic and diploid plants to compensate for back mutation and suppressor mutation. The corrected values are presented in Table 1.

Table 1. Corrected frequencies of Wx pollen from diploid and monosomic plants.

Plant type	Estimated No. of gametes	Wx X 10^{-5}	$\bar{X} \pm$ SE
Diploid (3 plants)	115,540	66	
	93,260	89	
	172,800	84	79.7 ± 6.99
Monosomic 7 (4 plants)	72,375	86	
	84,380	66	
	120,710	51	
	83,250	64	66.8 ± 8.31
Monosomic 2	73,130	34	
Monosomic 10	124,760	88	

The corrected freguency of Wx pollen in diploid control plants is similar to the value (102×10^{-5}) reported by Nelson (1962, Genetics 47:737) for recombination between wx-C and wx-90; therefore, the wx-(C) allele in the Mangelsdorf's tester stock and wx-C are a similar distance from wx-90. It is likely that wx-C amd wx-(C) are the same allele.

Estimates of corrected Wx frequencies within the diploid and monosomic 7 classes were found to be homogeneous by means of a χ^2 test for homogeneity of binomial proportions, and a pooled frequency was calculated for each class. Neither the frequency in the monosomic 10 plant nor the pooled frequency in the monosomic 7 plants was significantly different from the pooled frequency in diploids. Thus, monosomy per se does not alter intragenic recombination between these two alleles.

However, the corrected Wx frequency from the monosomic 2 plant was highly significantly different from that of the diploids ($p<.0001$). More data are obviously needed, but this indicates that intragenic recombination in this monosomic 2 plant was sharply reduced from that which occurred in the controls or the other monosomic types analyzed. It will be extremely interesting to determine if a comparable reduction will be found in intergenic recombination in monosomic 2 plants, or an increase in trisomic 2 plants.

We would like to express our appreciation to Funk's Seeds International for generously providing summer nursery space in Shirley, Illinois, and winter nursery space in Molokai, Hawaii, in which material utilized in these studies was grown.

David F. Weber

Effect of trisomy 4 on intergenic recombination in chromosome 9 of maize

We are using monosomic analysis as a probe to analyze the maize genome. In a monosomic of a diploid species, an entire chromosome is present in the hemizygous condition. By comparing a plant monosomic for a specific chromosome with its disomic siblings, one compares one and two copies of all genes on an entire chromosome simultaneously. If a gene that exhibits dosage effects is present on the monosomic chromosome then a difference will be found between these two plant types for the experimental parameter being measured. In this way, one screens simultaneously all gene loci on a given chromosome by gene dosage comparisons. With this new method of analyzing the genome, one analyzes each gene locus on a given chromosome without inducing gene mutations. We are currently screening the maize genome with this approach to detect factors affecting genetic recombination.

I recently found (Weber, submitted for publication) that intergenic recombination in the sh-wx region of chromosome 9 in monosomic-4 plants testcrossed as males (11.2 ± 0.8%) is less than half of that found in comparable crosses with diploid control plants (23.0 ± 0.8%). A significant but smaller reduction in recombination was also found in monosomic-8 plants (17.1 ± 0.9%) but not in monosomic 7 plants (21.8 ± 1.8%). Therefore, monosomy per se does not cause a reduction in recombination in the sh-wx region.

To further explore the recombinational alteration detected in monosomic 4 plants, I initiated a series of experiments to compare the amount of recombination in this same region (sh-wx) of chromosome 9 in trisomic 4 plants with that occurring in diploid sibling plants. A trisomic 4 stock (from G. Doyle) was planted, and a trisomic 4 plant from this stock was crossed as a female parent with the same sh wx inbred that was used in the monosomic study described above. This sh wx stock was originally obtained from M. M. Rhoades.

Trisomic and diploid sibling plants from this cross were identified from somatic chromosome counts of root tips. The trisomics and diploids were each test-crossed both as male and female parents. The results are given in Tables 1 and 2.

Table 1. Recombinational frequency in the sh-wx region of chromosome 9 where heterozygous trisomic 4 and diploid sibling plants were testcrossed as male parents.

Plant	Plant type	No. kernels scored	% recombination in sh-wx region	$\bar{X}$ ± SE
75-603-1	Trisomic 4	530	22.6	
75-603-6	Trisomic 4	256	28.1	
75-603-12	Trisomic 4	230	26.1	25.6 ± 1.6
75-602-9	Diploid	805	21.6	
75-602-13	Diploid	504	23.6	
75-602-6	Diploid	712	22.1	22.4 ± .6

Recombinational frequencies in the four classes (trisomics crossed as males, trisomics crossed as females, diploids crossed as males, and diploids crossed as females) were each found to be homogeneous by means of a Chi square test for homogeneity of binomial proportions, and a pooled frequency was calculated for each class.

Table 2. Recombination frequency in the sh-wx region of chromosome 9 where heterozygous trisomic 4 and diploid sibling plants were testcrossed as female parents.

Plant	Plant type	No. kernels scored	% recombination in sh-wx region	$\bar{X} \pm$ SE
75-603-1	Trisomic 4	141	21.3	
75-603-11	Trisomic 4	207	22.2	
75-603-12	Trisomic 4	288	19.1	20.9 ± .9
75-602-6	Diploid	478	19.5	
75-602-13	Diploid	456	19.5	
75-603-9	Diploid	426	17.6	18.9 ± .6

A highly significant ($p<.005$) increase in recombination in the sh-wx region occurred in males (pooled trisomics and diploids) over that which took place in females (pooled trisomics and diploids). Numerous other investigators have also found that recombination in male maize flowers is higher than in female flowers (reviewed by Phillips 1969, Genetics 61:117, and Ghidoni 1975, Genetics 81:253).

When all diploid crosses (both as male and female parents) are compared with all trisomic crosses (both as male and female parents), the data are nearly significantly different ($p=.06$). Therefore, recombination appears to be higher in trisomic 4 plants than in diploid plants. Although the recombinational frequency in male flowers of trisomic 4 plants (25.6 ± 1.6%) is higher than that in their sibling diploids (22.4 ± .6%), the increase was not statistically significant ($p=.12$). The increase in recombination in the female flowers induced by the addition of an extra chromosome 4 (from 18.9 ± .6% to 20.9 ± 9%) was smaller ($p=.37$). Ghidoni (1975, Genetics 81:253) found that trisomy of chromosome 6 increased recombination in the sh-wx region in both sexes of maize by approximately the same amount.

As noted before, I testcrossed heterozygous monosomic 4 and control diploid maize plants as males to determine if monosomy could alter recombination in the sh-wx region. Monosomic 4 plants had only 11.2 ± .8% whereas diploid control plants had 23.0 ± 0.8%. Therefore, monosomic 4 plants had only approximately half the amount of recombination found in their diploid controls. If the amount of recombination in the sh-wx region in chromosome 9 was proportional to the number of chromosomes 4, then a recombinational frequency in the trisomic 4 plants male flowers would be expected to be 1-1/2 times that found in the diploid siblings (or 1.5 x 22.24% = 33.36%). This obviously was not the case because the recombination frequency increased to only 25.61%. It therefore appears that a plateau in recombinational alteration is being reached. These data indicate that monosomic-diploid comparisons are a far more sensitive system for measuring this continuously variable quantitative trait, and presumably other quantitative traits, than disomic-trisomic comparisons.

David F. Weber

The homeostatic nature of the acid extractable amino acids (free amino acid pool) in leaves

Since the acid extractable amino acid pool (free amino acid pool) is an intermediate, and not an end-product of a series of reactions involved in protein

synthesis, it would seem reasonable to believe that it should be a highly sensitive parameter to examine, one that would reflect in a very efficient way any changes in amino acid synthetic activity or utilization in the plant. In the present study, we determined the relative proportions of the different acidic and neutral acid extractable amino acids at three different developmental stages in the same maize plants to determine what, if any, changes would occur during development in the leaves. The basic amino acids could not be analyzed because of technical problems with the amino acid analyzer.

All plants analyzed were from a cross between W22 inbred line and inbred Mangelsdorf's Multiple chromosome tester. Both lines were obtained from K. Satyanarayana. Each of two sets of two diploid sibling plants were sampled separately at each of three different developmental stages: seedling stage, sporocyte stage, and anthesis. The seedling stage was approximately two weeks after germination when the plants had 5-6 leaves. The sporocyte stage was approximately six weeks after germination when the plants had 10-12 leaves. This is when microsporocyte samples would be taken from the plant for meiotic analysis. Anthesis is the time of pollen shed. Three-gram leaf samples were excised from the uppermost leaves of the same plants at each of the three developmental stages. All leaf samples were from plants grown under field conditions. The samples were taken at the same time of day (7-8 A.M.) to reduce environmental variations. All samples were placed on ice and transported back to the laboratory for immediate preparation and analysis.

Amino acid extracts were prepared from leaf samples as follows. Three g of leaf tissue was placed in a Virtis homogenizing cup with 9 ml of water. Each sample was homogenized in a Virtis "45" homogenizer at a setting of 60 for 10 min and placed over a boiling water bath for 1 min. One ml of 30% sulfosalicylic acid was then added as a deproteinizing agent and the homogenate was then reheated for 1 additional min and rehomogenized for 10 min. The homogenate was centrifuged in a clinical centrifuge (International Model CL) for two ten min periods at 2900 rpm to remove all unwanted plant material. The supernatant (the amino acid extract) was then adjusted to a pH of 2.0-2.3. No glutathion was present in the samples so the standard oxidation procedure involving 2M $NaSO_3$ solution was unnecessary. The samples were maintained at -22 C until used. A JEOL model JLC-6 AH fully automatic Amino Acid Analyzer was used to analyze the samples.

The data obtained from this approach are summarized in Table 1. The amount of each amino acid is expressed as the percent of that amino acid in the total of all neutral and acidic amino acids from that sample. This was calculated by adding the μm/ml values of all the amino acids sampled to obtain a grand total. The proportion of each amino acid was then computed as a percentage of this total. The mean and standard errors were calculated for each amino acid fraction at each of the three developmental stages. By examining the means and standard errors for each amino acid during the three developmental stages, it appears that no major differences took place during development. To determine if this is true, the data were tested using a two way analysis of variance with replication over a developmental time period, and between full sibling families. The significance levels (0.05 and 0.01) for each amino acid are listed in Table 2. The F scores indicate that the percent of each amino acid does not change through development. Since none of the F values are significant at the 1% significance level, and all but one of the values are not significant at the 5% significance level, this indicates that the acid extractable acidic and neutral amino acids are an extremely stable component in the plant throughout development. Since the acidic and neutral amino acids are stable through development, it is not unreasonable to assume the remaining basic amino acids are just as stable. The F values between full family siblings are significant in many cases. These data show that

Table 1. RELATIVE PERCENTAGES OF ACIDIC AND NEUTRAL AMINO ACIDS IN THE FREE AMINO ACID POOL IN LEAVES OF FOUR Zea mays PLANTS AT THREE DEVELOPMENTAL STAGES.

Amino Acid	Seedling Stage					Sporocyte Stage					Anthesis				
	Family A Plant #		Family B Plant #		$\bar{X} \pm$ SE	Family A Plant #		Family B Plant #		$\bar{X} \pm$ SE	Family A Plant #		Family B Plant #		$\bar{X} \pm$ SE
	1*	2*	1	2		1	2	1	2		1	2	1	2	
Phosphoserine	8.05	8.10	6.32	6.81	7.32± 0.44	7.92	8.00	6.20	6.57	7.17± 0.46	8.11	8.07	6.44	6.78	7.35± 0.43
Aspartic Acid	9.91	12.53	9.57	11.01	10.75± 0.66	10.03	11.93	9.76	10.88	10.65± 0.48	10.13	11.69	9.60	11.18	10.65± 0.47
Threonine	3.04	3.11	2.07	2.32	2.63± 0.25	3.27	3.07	2.01	2.34	2.67± 0.29	3.21	3.15	2.12	2.41	2.72± 0.27
Serine	7.88	7.17	6.20	5.91	6.79± 0.45	7.56	7.25	6.32	5.89	6.75± 0.39	7.82	7.00	6.11	5.77	6.67± 0.46
Asparagine	1.93	2.40	3.63	2.15	2.52± 0.37	1.85	2.13	3.51	2.07	2.39± 0.37	2.04	2.32	3.59	2.11	2.51± 0.36
Glutamic Acid	9.79	11.76	11.03	12.47	11.26± 0.57	10.11	11.55	11.33	12.32	11.32± 0.45	9.96	11.51	10.93	12.37	11.19± 0.50
Glutamine	4.17	5.98	3.40	3.84	4.34± 0.56	4.22	5.28	3.78	3.96	4.31± 0.33	4.37	4.69	3.33	3.72	4.02± 0.30
Glycine	0.98	0.79	1.29	1.98	1.26± 0.26	1.10	0.96	1.38	1.76	1.30± 0.17	1.16	1.03	1.39	1.99	1.39± 0.21
Alanine	27.60	29.38	27.37	30.97	28.83± 0.84	27.00	22.69	26.56	29.55	26.45± 1.41	26.70	22.13	27.52	28.74	26.27± 1.44
Valine	4.00	4.57	2.77	3.29	3.65± 0.39	3.93	3.23	2.89	3.49	3.36± 0.19	4.12	4.02	2.85	3.36	3.58± 0.29
Cystine	1.48	1.60	1.34	1.48	1.47± 0.05	1.58	1.56	1.46	1.55	1.53± 0.02	1.67	1.68	1.41	1.52	1.57± 0.06
Methionine	0.45	0.41	0.50	0.38	0.43± 0.02	0.57	0.39	0.48	0.40	0.46± 0.04	0.49	0.39	0.47	0.36	0.42± 0.03
Isoleucine	0.76	0.77	0.67	0.46	0.66± 0.07	0.77	0.72	0.65	0.41	0.63± 0.07	0.85	0.78	0.75	0.52	0.72± 0.06
Leucine	1.18	1.07	0.83	0.69	0.94± 0.11	1.09	1.26	0.78	0.73	0.96± 0.12	1.23	1.14	0.85	0.71	0.98± 0.12
Tyrosine	0.63	0.89	1.06	1.17	0.93± 0.11	0.61	0.94	1.01	1.26	0.95± 0.13	0.66	0.91	0.99	1.20	0.94± 0.11
Phenylalanine	0.33	0.57	0.47	0.50	0.46± 0.05	0.47	0.55	0.42	0.47	0.47± 0.02	0.44	0.52	0.50	0.53	0.49± 0.02
B-Alanine	2.16	2.83	2.79	1.39	2.29± 0.33	2.23	2.49	2.69	1.44	2.21± 0.27	2.39	2.38	2.84	1.94	2.38± 0.18
Proline	1.59	3.11	1.67	0.82	1.79± 0.47	1.48	2.87	1.50	1.17	1.75± 0.37	1.38	2.56	1.54	1.20	1.67± 0.30
Hydroxyproline	13.96	15.39	16.93	12.26	14.63± 1.00	14.21	13.11	17.37	13.74	14.60± 0.94	13.27	14.03	16.77	13.59	14.41± 0.80

*Represents sibling plants 1 and 2 under representative family.

Table 2. F values as determined by variance analysis.

AMINO ACID	Significance of F values at 5% and 1% error								
	TIME	5%	1%	FAMILY	5%	1%	TIME X FAMILY	5%	1%
Phosphoserine	15.69	ns.	ns.	3020.17	*	*	0.05	ns.	ns.
Aspartic Acid	00.34	ns.	ns.	34.19	*	ns.	0.03	ns.	ns.
Threonine	2.20	ns.	ns.	741.34	*	*	0.14	ns.	ns.
Serine	1.00	ns.	ns.	599.00	*	*	0.01	ns.	ns.
Asparagine	5.50	ns.	ns.	382.38	*	*	0.00	ns.	ns.
Glutamic Acid	10.70	ns.	ns.	1632.00	*	*	0.00	ns	ns.
Glutamine	1.33	ns.	ns.	40.64	*	ns.	0.22	ns.	ns.
Glycine	1.57	ns.	ns.	100.37	*	*	0.13	ns.	ns.
Alanine	3.08	ns.	ns.	7.29	ns.	ns.	0.48	ns.	ns.
Valine	0.41	ns.	ns.	11.72	ns.	ns.	1.36	ns.	ns.
Cystine	1.79	ns.	ns.	10.52	ns.	ns.	1.15	ns.	ns.
Methionine	1.83	ns.	ns.	1.66	ns.	ns.	0.09	ns.	ns.
Isoleucine	26.66	*	ns.	393.33	*	*	0.02	ns.	ns.
Leucine	0.19	ns.	ns.	55.53	*	ns.	1.13	ns.	ns.
Tyrosine	0.43	ns.	ns.	500.28	*	*	0.02	ns.	ns.
Phenylalanine	0.27	ns.	ns.	0.00	ns.	ns.	0.54	ns.	ns.
B-Alanine	0.68	ns.	ns.	3.57	ns.	ns.	0.11	ns.	ns.
Proline	0.26	ns.	ns.	33.84	*	ns.	0.12	ns.	ns.
Hydroxyproline	0.05	ns.	ns.	3.38	ns.	ns.	0.27	ns.	ns.

*means number is significantly different statistically; ns. means number is not significantly different.

phosphoserine, threonine, serine, asparagine, glutamic acid, glycine, isoleucine and tyrosine proportions differed significantly between these two families. The remaining amino acids did not exhibit family differences. This conclusion is difficult to explain because all progeny were F1 hybrids between the same two inbred lines, thus genetic differences should be small. The most reasonable explanation is that environmental factors experienced by each different family during its growth and development in the field were responsible for the differences. Possible influencing factors could be: temperature, moisture, light levels, leaching, insect damage, disease, or levels of nitrogen in the soil. No significant differences were found between families over a period of time. Similar comparisons are being made for specific monosomic types through their development.

These data establish that the relative amounts of the different neutral and acidic amino acids in the amino acid pool in maize leaves are remarkably stable during the development of the plant. Thus, the stage of maturity at which a sample would be taken from a plant is relatively unimportant. The free amino acid pool must be under a very stringent genetic regulatory mechanism, one that deserves further analysis.

James W. Cook and David F. Weber

Monosomic analysis of the acid extractable amino acids (free amino acid pool) in leaves

Monosomics generated by the r-X1 deficiency are being used to study the free amino acid pool in Zea mays leaves. In the previous paper in this Newsletter, we demonstrated that the acid extractable amino acids (free amino acid pool) remain remarkably stable throughout development from the seedling stage to anthesis. Therefore, the stage at which leaf samples are taken from the plant appears to make no difference in a study of the relative proportions of the different acid extractable amino acids in the maize leaves. This remarkable constancy of the acid soluble amino acid proportions is extremely helpful in a comparison of a specific monosomic type with its diploid (disomic) siblings because monosomics mature at a much slower rate than their diploid siblings (monosomics reach anthesis two to three weeks later than their diploid siblings). Thus, even though monosomics and disomics may be sampled at the same time they are at a different stage of maturity. If they are sampled at the same stage of maturity, they are of a different chronological age. However, since differences in the amino acid pool are not found as the plant matures, the above considerations are unimportant.

The acid extractable amino acids in specific monosomic types are being compared with those in their diploid sibling control in an attempt to learn more about the control of amino acids in the amino acid pool. If a gene expressing dosage effects, affecting the amino acid pool, is located on a specific chromosome, then the amino acid pool of a plant monosomic for that chromosome will be different from that found in its diploid sibling control. In this way we are comparing one vs. two copies of all genes on a given chromosome. In this paper, we describe the differences that have been found in monosomic 6 plants.

The experimental procedures are the same as those described in the previous paper. All plants used in this study were from field plantings. The diploid control plants used in this study were the same plants analyzed throughout development in the previous study. R/r-X1 plants of the W22 genetic background were crossed as females by a second inbred, Mangelsdorf's multiple chromosome tester. Monosomics are generated at a frequency in excess of 11% from this cross.

Monosomic 6 plants were detected by their distinctive plant morphology. They have darker foliage and leaves that point more upward (almost liguleless in phenotype) than their disomic siblings.

The results at the seedling stage are presented in Table 1. The amino acids analyzed in this study are the neutral and acidic amino acids. The basic amino acids could not be analyzed due to mechanical problems with the amino acid analyzer. Means and standard errors were computed for the percent of each amino acid in monosomic 6 plants and in disomic controls. The means and standard errors for the controls were based on four individual plants. The means and standard errors for the monosomic 6 class were derived from three plants. The data were tested for significant differences with a t test. The extremely high levels of hydroxyproline found in all samples is unexplained. It is unusual for plant tissue to contain high levels of hydroxyproline. Therefore, the compound absorbing in the same position as hydroxyproline is either hydroxyproline, or a similar 5 carbon imino ring compound resembling hydroxyproline. The most striking difference found in the monosomic 6 plants was the massive reduction in the aspartic acid levels in the acid-soluble amino acids. Monosomic 6 plants have only 29.1% of the aspartic acid found in their diploid controls. It is interesting to note that threonine levels drop significantly, and methionine levels are also slightly reduced, but not significantly, in the

Table 1. Relative percentages of neutral and acidic amino acids in the free amino acid pool in monosomic and diploid maize leaves.

	Diploid Controls Mean ± SE	Monosomic 6 Mean ± SE	Percent of diploid value
Phosphoserine	7.32 ± 0.44	5.68 ± 0.38	77.5
Aspartic Acid	10.75 ± 0.66	3.13 ± 0.05**	29.1
Threonine	2.63 ± 0.25	1.60 ± 0.02*	60.8
Serine	6.79 ± 0.45	5.78 ± 0.11	85.1
Asparagine	2.52 ± 0.37	1.90 ± 0.12	75.4
Glutamic Acid	11.26 ± 0.57	13.13 ± 0.50*	116.6
Glutamine	4.34 ± 0.56	2.25 ± 0.05*	51.8
Glycine	1.26 ± 0.26	1.28 ± 0.08	101.6
Alanine	28.83 ± 0.84	29.93 ± 0.46	103.8
Valine	3.65 ± 0.39	4.26 ± 0.26	116.7
Cystine	1.47 ± 0.05	3.23 ± 0.19**	219.7
Methionine	0.43 ± 0.02	0.37 ± 0.01	86.0
Isoleucine	0.66 ± 0.07	0.61 ± 0.02	92.4
Leucine	0.94 ± 0.11	1.22 ± 0.10	129.8
Tyrosine	0.93 ± 0.11	2.92 ± 0.20**	314.0
Phenylalanine	0.46 ± 0.05	0.60 ± 0.08	130.4
B-Alanine	2.29 ± 0.33	2.28 ± 0.11	99.6
Proline	1.79 ± 0.47	1.57 ± 0.03	87.7
Hydroxyproline	14.63 ± 1.00	18.21 ± 0.18*	124.5

*indicates number is significantly different at 0.05 significance level
**indicates number is significantly different at 0.01 level

monosomic 6 plants. Since these two amino acids are synthesized directly from aspartic acid in other plants (Dougall and Fulton, 1967, Plant Physiol. 42: 941), they presumably follow the same pathway in maize. We speculate, therefore, that a genetic factor controlling the amount of aspartic acid is located on chromosome 6. This gene could be a structural gene directly involved in the biosynthesis of aspartic acid or a regulatory gene. The reduction in the amount of threonine and possibly methionine are presumably due to the lack of aspartic acid as a substrate for further reactions.

Another interesting observation in the monosomic 6 plants is the significant decrease in glutamine (51.8% of the diploid level) accompanied by a significant increase in glutamic acid (116.6% of the diploid level). Glutamine is believed to be derived from glutamic acid in plants (Davies, 1964, Plant Biochemistry). We speculate, therefore, that a factor located on chromosome 6 is controlling the conversion of glutamic acid into glutamine. This factor could also be regulatory or structural in nature. The buildup of hydroxyproline levels, or a similar compound, in the monosomic 6 plants could also be related to the increased levels of glutamic acid, because hydroxyproline is also indirectly derived from glutamic acid.

The aromatic amino acid tyrosine is also sharply increased in monosomic 6 plants. The pathway for tyrosine and phenylalanine in animal and bacterial systems involves a branched pathway from a common precursor, prephenic acid (Horecker and Stadtman, 1971, Current Topics in Cellular Regulation). It is also known that tyrosine is synthesized by the direct hydroxylation of

phenylalanine in animals and bacteria. The same branched biosynthetic pathway from prephenic acid that occurs for bacteria and animals also occurs in plants (Miflin, 1973, in Milborrow, Biosynthesis and Its Control in Plants); little evidence is available on the plant's ability to hydroxylate phenylalanine directly to tyrosine. The fact that tyrosine is strikingly affected when phenylalanine remains essentially constant indicates an alteration has occurred in the biosynthetic pathway between prephenic acid and the formation of tyrosine. A possible explanation for this buildup of tyrosine could be the lack of genetic regulation within this segment of the biosynthetic pathway.

Another difference in the monosomic 6 plants is the significant increase in cystine (219.7%). This difference is not understood.

The same monosomic 6 plants were examined at the sporocyting stage and at anthesis. The data are presented in Table 2. The same changes observed at the seedling stage (Table 1) are also seen at these two subsequent developmental stages. Thus, those changes persist throughout development.

Table 2. Relative percentages of neutral and acidic amino acids in the free amino acid pool in monosomic 6 plants through development

	Seedling Stage Mean±SE	% of Diploid Value	Sporocyte Stage Mean±SE	% of Diploid Value	Anthesis Stage Mean±SE	% of Diploid Value
Phosphoserine	5.68±0.38	77.5	5.86±1.02	81.7	6.85±0.34	93.1
Aspartic Acid	3.13±0.05	29.1	3.62±0.24	33.9	3.39±0.08	31.8
Threonine	1.60±0.02	60.8	1.97±0.48	73.7	1.89±0.23	69.4
Serine	5.78±0.11	85.1	6.62±0.73	98.0	7.66±1.99	114.8
Asparagine	1.90±0.12	75.4	2.56±0.32	107.1	3.17±0.57	126.2
Glutamic Acid	13.13±0.50	116.6	13.04±0.35	115.1	12.06±0.47	107.7
Glutamine	2.25±0.05	51.8	2.49±0.49	57.7	2.47±0.27	61.4
Glycine	1.28±0.08	101.6	1.48±0.10	113.8	1.00±0.17	71.0
Alanine	29.93±0.46	103.8	29.60±1.18	111.9	29.10±1.61	110.7
Valine	4.26±0.26	116.7	3.85±0.57	114.5	4.67±0.40	130.4
Cystine	3.23±0.19	219.7	3.13±0.57	204.5	2.63±0.42	167.5
Methionine	0.37±0.01	86.0	0.37±0.02	80.4	0.40±0.03	95.2
Isoleucine	0.61±0.02	92.4	0.43±0.01	68.2	0.64±0.11	88.8
Leucine	1.22±0.10	129.8	1.05±0.19	109.3	1.18±0.06	120.4
Tyrosine	2.92±0.20	314.0	3.38±1.21	355.7	2.14±0.23	227.6
Phenylalanine	0.60±0.08	130.4	0.80±0.08	170.2	0.69±0.05	140.8
B-Alanine	2.28±0.11	99.6	0.87±0.24	64.2	0.82±0.08	37.4
Proline	1.57±0.03	87.7	1.42±0.17	81.1	1.20±0.24	71.8
Hydroxyproline	18.21±0.18	124.5	17.32±1.86	118.6	17.87±2.14	124.0

Although this study is in its early stages, this study might allow us to ascribe genetic control of certain amino acids to specific chromosomes. In addition, the amino acid biosynthetic pathways are poorly known in plants. If a coordinate increase or decrease is found for two or more amino acids in the same putative pathway (as for aspartic acid, threonine, and methionine) it would support that pathway. Also, if an increased concentration of a putative precursor and a concomitant decrease in its end product are found, this would also lend support for that pathway. In this case, a block would be present between the precursor and the end product.

James W. Cook and David F. Weber

An ultrastructural investigation of monosomic maize

Satyanarayana (unpublished) observed that the r-X1 deficiency produced a large number of monosomic and trisomic plants. The r-X1 deficiency includes the R locus on chromosome 10 of maize and was originally induced with X-ray irradiation by L. J. Stadler. Using this system, Weber (1973, Genetics 74:S292) has been able to produce plants monosomic for nine, and possibly all ten, of the maize chromosomes. This is the first time that a series of this type has been produced in any diploid organism.

A comparison of a monosomic with its diploid siblings is a comparison between one and two copies of all genes on the monosomic chromosome. If a gene expressing dosage effects is located on the monosomic chromosome, then a difference will be found between the monosomic and its diploid siblings in the phenotypic expression of that gene. In this way, one can simultaneously screen all the genes on the monosomic chromosome without using mutations. It has been shown that monosomic-diploid comparisons can be used to locate genes expressing dosage effects (Plewa and Weber, 1973, Can. J. Genet. Cytol. 15:313; 1975, Genetics 81:277).

The purpose of this study was to compare the ultrastructure of monosomic and diploid sibling plants to determine if genes located on specific chromosomes, expressing a dosage effect, have an influence on the ultrastructure of selected maize cells.

In this study, monosomics for chromosome 2, 6, 7, 8 and 10 were used. Leaves from different monosomic plants and normal diploid plants were sampled for electron microscopic investigation at three different stages: seedling stage (two weeks after germination), sporocyte stage (6 weeks after germination), and during anthesis (10 weeks after germination). All leaf samples were taken from the middle part of the first leaf of plants at each different stage. Root tips from the apical meristematic region from different monosomic plants and normal diploid plants were also sampled for electron microscopy. However, in all cases root tips were taken only from seedling stage growing in clay pots in the greenhouse.

Although no obvious morphological differences between monosomic plants and their diploid siblings were detected in leaf mesophyll cells or root-tip meristematic cells, there appear to be certain differences at the ultrastructural level, such as the number of thylakoids per granum in chloroplasts. These differences will be the basis of a future discussion. (Supported in part by ERDA Contract No. E(11-1)-2121).

Tau-San Chou, Mathew J. Nadakavukaren and David F. Weber

UNIVERSITY OF ILLINOIS
Department of Agronomy, Urbana, Illinois

Linkage of y3 and al

I have assumed that y3 and al were different pleiotropic manifestations of a single allele. Apparent crossovers were rare and could be accounted for by either misclassification of endosperm color or through hetero-fertilization, known to be high in these stocks. In the winter season of 1974-75 sizable F_2 progenies from the cross Y3 A1/y3 al were classified and grown in the sand bench. A random sample of the apparent crossovers, y3 A1, were transplanted and grown to maturity. Without adjustment the apparent percentage of crossing over between y3 and al was 3.5. Selfed progeny of the presumed crossovers indicated that approximately half were not crossovers and the assigned y3 A1 phenotype was due either to misclassification or heterofertilization. If the total number of presumed crossovers is adjusted on the basis of the tested sub-sample, the percentage crossing over is reduced to 2.0. Stocks of y3 A1 are now available, the genotypic constitution having been verified by appropriate testcrosses in 1975.

G. F. Sprague

UNIVERSITY OF ILLINOIS
Department of Agronomy, Urbana, Illinois, and
YALE UNIVERSITY
Department of Human Genetics, New Haven, Connecticut

Plant activation of herbicides into environmental mutagens: the waxy reversion bioassay

Recently we reported (MNL 49:40-43; Mutation Res. 31:317) that maize seedlings exposed to atrazine (2-chloro-4-ethylamino-6-isopropylamino-s-triazine) contain a potent mutagen and that it is absent in untreated control plants. Atrazine alone is not mutagenic. To evaluate the mutagen-inducing capabilities of field-applied atrazine, we developed a bioassay in which the reversion frequency at the waxy locus in maize pollen grains is used. This bioassay is especially suited for detecting environmental mutagens because (i) reversion at a specific locus can be studied and the genetic effect of a chemical upon the germ cells of a higher eukaryote can be determined, (ii) great numbers of pollen grains can be easily and rapidly scored, and (iii) the mutagen tests can be conducted under field conditions common in agriculture.

An isolation plot was planted with inbred W22 homozygous for the wx-C allele. Field grade atrazine (Aatrex-80W, Ciba Geigy) was applied before emergence at rates of 1, 3, 5, 10, 20, 30 and 50 equivalent lbs/acre (1.12, 3.37, 5.61, 11.22, 22.44, 33.66 and 56.10 equivalent kg/ha) on seven sub-plots. One sub-plot was not treated. Additional control plants were grown for us by G. W. Beadle in his herbicide-free nursery at the University of Chicago. After the plants reached anthesis the tassels were harvested, fixed, and stored in 70% ethanol. Anthers were dissected from unopened florets, the pollen isolated, and scored for Wx or wx according to the method outlined by Nelson (Am. Naturalist 91:331-332).

Data from five sub-plots have been collected (Table 1). The data clearly indicate an increase of over an order of magnitude in the reversion frequency at the wx locus in pollen grains from atrazine treated plants as compared to the control reversion frequency.

Table 1. The Wx reversion frequency of homoallelic inbred W22 exposed to various concentrations of field-applied atrazine.

Concentration of atrazine (equivalent lbs/acre)	Estimated number of gametes	Reversion frequency of Wx (X 10^{-5})
0 Control	514,530	3.11
1	1,017,920	6.19
3	570,710	26.28
5	878,400	29.71
10	993,760	38.74

We believe that these preliminary findings along with previously reported data strongly indicate that a plant-mediated metabolite of atrazine is a potent mutagen to eukaryotes. Also we contend that this bioassay can be easily incorporated with other mutagen test systems for the evaluation of pesticides used in the production of corn. (Partially funded by a D. F. Jones Fellowship, Research Corporation, New York).

Michael J. Plewa and James M. Gentile

UNIVERSITY OF ILLINOIS
Department of Genetics and Development, Urbana, Illinois

Allelism of the cms-S restorers carried by different inbred lines

The gene that restores fertility to S-type male-sterile cytoplasm (cms-S) is designated Rf3 (Duvick, Advan. Genet. 13:1-56, 1965). Its mode of action is gametophytic (Buchert, P.N.A.S. 47:1436-1440, 1961), the phenotype being determined by the genotype of the pollen grain and not of the sporophyte. Our investigations of newly arisen restorers of cms-S (Laughnan and Gabay, In: Genetics and the Biogenesis of Cell Organelles, pp. 330-352, 1975) and attempts to assign them to chromosome have led to a renewed interest in Rf3.

Six of the ten newly arisen restorer genes have been tested for allelism with Rf3, carried by inbred line CE1, and none is allelic. Unpublished studies indicate that the Rf3 gene carried by inbred line CE1 is located in chromosome 2, probably in the long arm. The four newly arisen restorers not tested for allelism with the CE1 restorer have been assigned to chromosomes other than chromosome 2 through use of the waxy translocation series (Gabay and Laughnan, MGCNL 48:44-45, 1974). It is known, therefore, that none of our new restorers is allelic to the standard Rf3 carried by CE1. The question then arises whether the natural restorers found in different maize strains are allelic with the Rf3 of CE1, or do they also represent genes at different loci?

Duvick (MGCNL 31:114, 1957) made all possible crosses between inbred lines CE1, Ky21, BH2, JG3 and JG5, each of which carries the ability to restore fertility to cms-S plants. The resulting F_1 plants were then crossed with cms-S plants of inbred line WF9. Each of the ten F_1 combinations gave testcross progenies that were all fertile, indicating that the restorers carried by the five lines are allelic.

We recently tested the restorer genes carried by the five inbred lines CE1, Ky21, Tr, C103 and CI21E for allelism. The cms-S restorer version of one of the lines to be tested was crossed as female parent with a second line and pollen samples from F_1 offspring were examined for the frequency of aborted pollen grains. If the restorer genes in the tested lines are not allelic, the F_1 pollen sample should contain approximately 25% aborted pollen grains. If, on the other hand, the restorer genes are allelic, all or nearly all of the pollen grains of the F_1 sample should be normal. Eight of the ten possible F_1 combinations were tested in this way, and all five inbred lines were involved in one or more of these combinations. In each case, the F_1 plants produced all, or nearly all normal pollen, indicating that the restorer genes carried in the five lines are allelic. These results are being confirmed by testcrosses. Since two of these lines, CE1 and Ky21, were among those analyzed by Duvick, it may be concluded that the eight lines involved carry the same restorer gene, though it is possible that closely linked restorer loci are involved.

We are currently conducting a search among open pollinated varieties of maize for naturally occurring restorers of cms-S, and having identified numbers of these will determine whether or not the restorers in these strains are allelic to the Rf3 of CE1. In addition, the restorer genes carried by other inbred lines known to restore cms-S are being tested for allelism with Rf3. In this connection, we would appreciate receiving small samples of strains that others have identified as cms-S restorers.

J. R. Laughnan and S. J. Gabay

Chromosomal location of Rf3

Preliminary evidence (Singh, Ph.D. thesis, Univ. of Illinois, 1969) suggested that the cms-S restorer carried by inbred line CE1 is located in either chromosome 2 or 3, probably the former. Unpublished studies (S. W. Noble, personal communication) involving use of translocation testers indicate that the cms-S restorer of inbred line CE1 is located in chromosome 2, probably in the long arm.

Our recent studies confirm the assignment of cms-S restorers carried in a number of inbred strains to the chromosome 2 linkage group. One of these involves an inbred strain carrying Inversion 2a (breakpoints = 2S.75-2L.80), the plant color allele B, and, as it turned out, a natural cms-S restorer not previously identified. cms-S plants heterozygous for the inversion, for B and for the restorer allele, when testcrossed as females gave a total of 335 offspring in 10 families. The data indicate that the restorer factor is closely linked with both B and In2a, recombination values being 5.7 and 3.0, respectively.

The cms-S restorer carried in the In2a stock has been shown independently to be allelic with the restorer carried by inbred line Tr, thus indicating that the latter is also located in chromosome 2. And since Tr is one of the eight restoring lines for which allelism is indicated in an accompanying report in this volume, it appears that all these restorers are assignable to the chromosome 2 linkage group.

Independent evidence for the assignment of the cms-S restorer to chromosome 2 comes from linkage studies involving chromosome 2 translocation heterozygotes. The restorers involved are those carried by inbred lines CE1 and Tr, as well as one carried by the Vg (vestigial glume) strain in which cms-Vg, a member of the S group of sterile cytoplasms, was identified. There is a loose linkage between each of these restorers and the T2-9b interchange point, which is located at 0.2 in the short arm of chromosome 2. These studies also indicate linkage between the restorer carried by the two inbred lines CE1 and Tr, and three translocations with breakpoints well out in the long arm of chromosome 2. Since there is other evidence that the restorer carried by CE1 segregates independently of the ws3, lg and gl2 markers, which lie beyond B in the short arm, the combined information on linkage and recombination from both inversion and translocation heterozygotes suggests that Rf3 is located in 2L, most likely in its proximal region.

J. R. Laughnan and S. J. Gabay

Linkage relations of newly arisen cms-S restorers

Using a new method (Gabay and Laughnan, MGCNL 48:44-45, 1974) involving analysis of pollen samples from waxy translocation heterozygotes, six of the ten new cms-S restorers of spontaneous origin (Laughnan and Gabay, MGCNL 48:38-42, 1974) have been located to chromosome. The pollen data indicate that restorers I and VIII are located in chromosome 8, restorers IV and VII in chromosome 3, and restorers IX and X in chromosome 1. These assignments have been confirmed by test cross data that are now available for all but restorer VII. The data do not rule out the possibility that restorers IX and X may be located at the same site in chromosome 1, but they do suggest that restorers I and VIII, and restorers IV and VII, are at different locations in chromosomes 8 and 3, respectively. Restorers II, III, V and VI have not yet been assigned to chromosomes but tests for allelism indicate that these new restorers are neither allelic with each other nor with the standard restorer Rf3 carried by inbred line CE1. These and other findings support the notion that the spontaneous changes from male-sterile to male-fertile phenotype occurring at the nuclear level involve the integration of a fertility element F, with episomal characteristics, into one or another of the maize chromosomes, rather than mutation at pre-existing restorer or suppressor loci.

S. J. Gabay and J. R. Laughnan

Additional male-sterile sources

Among plantings of varieties of maize obtained from the North Central Regional Plant Introduction Station, Ames, Iowa, a number of sources were observed to segregate male-sterile plants. These sterile plants were crossed by inbred lines WF9 or Oh51A, which are nonrestoring for the three major cytoplasmic male-sterile groups: cms-C, cms-T and cms-S. Since these inbred lines do not exhibit segregation for male sterility they should carry the normal versions of all nuclear ms alleles.

If the F_1 test cross progeny were fertile, the source of sterility was presumed to be genic, though it could represent a new type of sterile cytoplasm that is restored by WF9 or Oh51A. If the F_1 progeny were sterile, the source of sterility was considered to be cytoplasmic. In this case, the F_1 male-sterile plants were crossed with inbred lines that permit diagnosis of the cms group involved. According to a shorthand notation we have used to indicate restoring capabilities of these inbred lines, + indicates restoration, - indicates non-restoration, and the cms types are considered in the order C, T and S. An inbred line that restores cms-C but not cms-T or cms-S is designated (+ - -); a line restoring cms-C and cms-T but not cms-S is designated (+ + -), and so on. On this basis both WF9 and Oh51A are designated (- - -). Using inbred lines N6 (+ - -) or W23 (+ - -), K55 (+ + -) or M14 (+ + -), and Tr (- - +) or C103 (- - +), it is possible to assign a cms strain to one of the three groups. We find that two or three backcrosses with the recurrent diagnostic inbred line are sufficient for this assignment. Moreover, field analysis of pollen samples of restored plants is a reliable criterion on which to distinguish between cms-C and cms-T on the one hand, and cms-S on the other, since restoration is sporophytic in the former cases, and gametophytic in the latter.

Table 1. Characterization of 17 new male-sterile sources.

P. I. No.	Source	Cultivar	Type sterility
186208	South Africa	Bozeman yellow dent	Genic
213703	Iowa	Yellow dent	cms-S
213717	Iowa	Krug yellow dent	cms-S
213726	Iowa	Miller yellow dent	cms-S
213779	North Dakota	Blue flour	Genic
214199*	Canada	Rainbow flint	cms-S
214287	Iowa	Cassel white	Genic
214296	Iowa	Rainbow flint	cms-S
218131	New Mexico	Cochiti	cms-C
218179	Arizona	San Xavier	cms-C
218187	Arizona	Mojave tribe	cms-C or genic
222313	Nebraska	Mid-season composite	cms-S
279032	Spain	Fino	Genic
279034	Spain	Millo de Regadio	Genic
311236	Virginia	Imprv. Leaming (Ohio)	cms-T
311237	Virginia	Hickory King	cms-S
311244	Virginia	Golden dent	cms-S

*This source has previously been found to carry an S type cytoplasm designated cms-CA (Beckett, Crop Science 11: 724-727, 1971).

The foregoing criteria have allowed placement of 16 new male-sterile sources and tentative placement of a 17th. The uncertainty in the latter case is due to the fact that the only diagnostic line thus far crossed with this source is N6, which produced fertile F_1 progeny. Further testing will allow placement of this source. The results of analyses of the 17 new sterile strains are presented in Table 1.

S. J. Gabay, C. E. Hall and J. R. Laughnan

INDIAN AGRICULTURAL RESEARCH INSTITUTE
Division of Genetics, New Delhi-110012, India

Unusual occurrence of phlobaphenes: the non-anthocyanic co-pigments in maize embryo

Investigations on a number of R alleles have shown that the R-nj allele conditions pigmented crown and embryo (plumule). Chemico-genetical studies on the unusual presence of the pigments in the embryo could help in studying gene action. During characterization of these reddish-purple pigments it was found that, apart from anthocyanins, some other water-insoluble co-pigments of non-anthocyanic nature were also present and could be isolated from embryo tissue in ethyl acetate. The solubility of these reddish-purple pigments is ethyl acetate and their degradation during acidic hydrolysis indicate them to be non-anthocyanic. Unlike anthocyanins and anthocyanidins, the absorbance of the pigments does not decrease on standing in the unacidified solvents even after several weeks, and hence they do not undergo pseudo-base transformation. Upon exposure to ammonia vapours, the new pigments darken but do not turn blue; they are insoluble in alkali, and addition of acid results in green colour. Paper chromatographic analysis in Forestal (acetic acid-conc. HCl-water, 30:3:10 V/V) and BAW (butanol-acetic acid-water, 4:1:5 V/V, upper phase) solvent systems gave one spot near the solvent front.

Some colourless hydroxyflavans such as hydroxyflavan-3-ols and hydroxyflavan-3:4-diols are known to occur in nature. On treatment with dilute acids they are easily converted into insoluble phlobaphenes. Dehydrogenative polymerisation of polyhydroxyflavans occurs with formation of brown or red insoluble phlobaphenes, and in nature self-condensation of polyhydroxyflavans proceeds without the assistance of enzymes (non-enzymically). Also, since phlobaphenes of the 3:4-diol series may form considerable amounts of anthocyanidin under acidic conditions, their possible involvement in anthocyanin biosynthesis through 'interconversions' cannot be ruled out unless they play some sole key role in meeting other metabolic demands.

J. M. S. Mathur and N. D. Sharma

Biosynthesis of anthocyanins in maize: action spectra and role of phytochromes

Physiological studies on anthocyanin biosynthesis 'in laboratorium' were carried out to study action spectra and phytochrome reversibility for several alleles of the R locus (R-g:Canada, R-r:Em, R-r:Standard and r-r) using red and far-red filters of predetermined absorption maxima. When exposed for a period of two days with light of restricted wavelengths in the red and far-red regions, maximum anthocyanin synthesis (determined spectrophotometrically) was found at 730 nm. Thus, wavelength dependence for anthocyanin biosynthesis in seedlings given prolonged exposures to light of approximately equal energy shows a main peak at 730 nm and a minor peak at 660 nm. These results indicate complexity of photo-control of anthocyanin synthesis, and that it is controlled by

two light steps: R-1, with an active band from about 700-780 nm and probably including some action throughout the red region; and R-2, a phytochrome mediated reaction requiring the presence of only a small amount of phytochrome in the far-red form (pfr).

The studies on action spectra suggest that light activates a flavo-protein (butyryl coenzyme A-dehydrogenase), which shows that the A ring of the flavonoid molecule is formed from 'acetate units.' It is found that increased sugar in the absence of light allows some anthocyanin formation and that leuco-anthocyanin synthesis is not light dependent. The quality of light plays an indirect role. Hence, if the leuco-anthocyanin synthesis is not light dependent and they differ from anthocyanins only in the middle (oxygenated) ring, then the light influences in some way the aliphatic chain (C-3 group) of the B-ring precursor, probably prior to cyclization. There may or may not be competition between anthocyanins and other classes of flavonoids.

J. M. S. Mathur and N. D. Sharma

Inheritance of carotenoids in maize

Investigations on the inheritance of carotenoids, the yellow pigments of maize kernels, were carried out using Parent I, orange kernels (P-I, 2904A.31) and Parent II, colorless kernels (P-II, 2360P-8) colorgraded as 18 and 1 respectively, depending upon visual intensity of pigmentation. The two parents and F_1 and F_2 populations (similarly colorgraded between 18 and 1) were analyzed for total carotenoids as well as individual component carotenoids, the latter because of the fact that dark yellow/orange color may mask the presence of light colored components and so also the dilute colored components may show diluting effect on the darker pigments.

About 25 gm of whole kernels were extracted with ether to remove any wax coating from pericarps, 20 gm dried and powdered kernels (40 mesh) extracted twice with ca. 200 ml portions of hexane-acetone-water, 15:75:10 V/V, and the slurry allowed to stand overnight. The supernatant was centrifuged at 2000 xg for 15 min, passed through a column of anhydrous sodium sulphate and exhaustively extracted with n-hexane. The extract was evaporated under vacuum in a thin-film flash evaporator (bath temp. 40 C) and made up to known volume (50 ml) using n-hexane. Absorbance was measured in a 10 ml aliquot at 435 nm and 450 nm and compared with a standard β-carotene calibration curve, and total carotenoids were expressed as β-carotene (ppm).

The individual carotenoids in a 40 ml aliquot of the above extract were separated chromatographically on a magnesia column. The first fraction (polyenes) was eluted with 5% acetone in hexane followed by elution of different fractions using hexane-acetone-ethanol V/V in the proportions of 90:10:0 for zeinoxanthin, 90:10:0 for cryptoxanthin, 89:10:1 for lutein, 88:10:2 for zeaxanthin and 80:10:10 for polyoxy pigments. After diluting the different fractions, the absorbance values were determined at the appropriate wavelength: phytoene (85), phytofluene (98), β-carotene (228), zeinoxanthin (268), cryptoxanthin (216), lutein (256), and zeaxanthin and polyoxy pigments (248). To estimate major components of the polyene fraction, the values used were: phytoene (285), phytofluene (330), β-carotene (480) and total polyene fraction (425).

Total carotenoids in the colorless parent were found to be 0.4 ppm, in the orange one as high as 68.5 ppm, and in the F_1 59 ppm. In the F_2 the total pigments were in between and in varying proportions. In the F_1 all those pigments present in the parents were detected. However, the proportions of zeaxanthin, lutein, carotenes and cryptoxanthin were less than those of zeinoxanthin and polyoxy pigments. Total carotenes were found to be more in colorless (42 ppm) than in colored (6 ppm) kernels of the parents, and in the F_1 only 5.8 ppm.

J. M. S. Mathur and N. D. Sharma

Biosynthesis of anthocyanins in maize: presence and role of o-diphenolase and monophenolase enzymes and their isoenzyme polymorphism

During the course of chemico-genetical investigations on anthocyanin biosynthesis in maize, the cut ends of silks in many lines were found to turn brownish within a few minutes, developing a melanin type of pigment. Interest in polyphenol oxidases arises from their role in phenolic biosynthesis, oxidation of phenols and formation of dark colored pigment. By screening the genetic background of these lines it may be possible to ascertain the role of polyphenols. Polyphenols are also known to aid in pollen germination and tube growth in vitro and thus their presence in silks may have a more definite role in aiding pollen germination rather than in the synthesis of anthocyanins.

With this view in mind, silks from some 97 lines of different genetic background were studied for the activity of polyphenol oxidases and their isoenzyme polymorphism.

The enzyme was extracted by homogenizing 5 gm silks with 15 ml prechilled (-15 C) 0.05 M phosphate buffer (pH 6.6) and centrifuging at 20,000 xg for 20 min at 5 C. The supernatant extract was assayed immediately for polyphenol oxidase activity using catechol (10 mg/ml) and L-tyrosine (1.0 mg/ml) as substrates. The reaction mixture consisted of 2 ml catechol, 0.1 ml of enzyme preparation and 0.05 M phosphate buffer (pH 6.6) to bring the total volume to 5 ml. The mixture was incubated at 37 C for 3 min before addition of enzyme. Absorbancy was measured at 430 nm at intervals of 15 seconds. For measuring the monophenolase, 2 ml of L-tyrosine (1.0 mg/ml) solution and 0.5 ml of crude enzyme extract were used. After oxygenating the substrate for a few minutes, absorbancy was measured at 430 nm after 3 hr of incubation at 37 C. Controls consisted of everything else except substrates.

Isoenzyme studies were carried out by electrophoresis in 7.5% polyacrylamide, using tris-glycine buffer (pH 8.3). The gels were stained with L-tyrosine (1.0 mg/ml in 80% ethanol), destained and stored in 30% alcohol.

In about 10 lines no o-diphenolase activity and only negligible monophenolase activity were recorded. These lines showed no browning of cut ends of silks. In the rest of the lines definite polyphenol oxidase activity was observed, mainly the activity of o-diphenolase. The latter was also found to give 5-7 isoenzyme bands of similar nature. Unlike o-diphenolase, no multiple forms were observed for the monophenolase enzyme.

J. M. S. Mathur

Biosynthesis of anthocyanins in maize: in vitro tissue culture

Tissue culture of certain critical plant parts affected by each allelic form might prove useful in studies on gene action. It was found indispensable to standarize a suitable nutrient medium for culturing maize kernels in vitro from the early stages after anthesis, to trace the anthocyanin biosynthetic pathway based on enzyme activities and specificities. Moreover, it is possible to incorporate enzyme inhibitors or inducers in the culture medium in order to induce or inhibit the synthesis of anthocyanins.

Attempts were made to develop such a medium, and a basal nutrient medium has been standarized which gives profuse growth of maize kernels inoculated the 10th day after pollination. The medium consists of White's major elements and vitamin mixture, Nitsch's trace elements, 2% sucrose, 0.8% agar and 0.5% yeast extract (pH 6.1 - 7.0), and can be used to culture whole kernels, endosperm or embryo alone. Microscopic examination of transverse sections of kernels developed in vitro 20 days after inoculation revealed tissue differentiation--i.e., formation of a distinct aleurone layer.

By culturing the kernels at 10 days post-pollination, studies were carried out in vitro on the role of Spm and Spf in causing patched aleurone patterns (a-ml and R-rEm) and also on the 'Anthocyanin Decolorizing Enzyme Complex.' The results confirm our findings from studies in vivo.

J. M. S. Mathur and N. D. Sharma

Biosynthesis of anthocyanins in maize: Presence and role of an 'Anthocyanin Decolorizing Enzyme Complex'

During in vivo and in vitro studies on the role of the regulatory systems Spm and Spf in causing spotted aleurone patterns (a-ml and R-rEm), the presence of an 'Anthocyanin Decolorizing Enzyme Complex' has been demonstrated in maize for the first time. The object was to ascertain whether anthocyanins in colorless patches are not synthesized at all or are decolorized in localized areas only after synthesis, leading to spotted patterns.

The crude enzyme complex was isolated from endosperm of R-rEm, R-sd2 and a-ml; pericarp of R-rEm, R-sd2 and a-ml; and aleurone (colorless portions) of R-sd2 and a-ml by homogenizing about 1 gm tissue in cold (-15 C) acetone. The homogenate was vacuum filtered in a Buchner funnel, and the residue was suspended in cold 0.05 M phosphate buffer (pH 6.6) and centrifuged at 2000xg for 15 min at 4 C. The supernatant was used immediately for assaying activity with substrates prepared from aleurone of R-rEm and pigmented portions of aleurone of a-ml and R-sd2. For preparation of substrates the tissues were extracted with cold 1% methanolic HCl, evaporated to dryness and dissolved in enough dilute HCl to get a solution with maximum 5% transmittance at 515 nm.

The assay mixture consisted of 4 ml of freshly prepared substrate, 2.5 ml of enzyme preparation in 0.05 M phosphate buffer (pH 6.6) and water to bring the total volume to 8 ml. The anthocyanin decolorizing capacity of the enzyme complex was measured spectrophotometrically by observing changes in transmittance at 515 nm after intervals of 45 min, 2 hr, 4½ hr and 24 hr.

The results given in Table 1 indicate that the enzyme complex from aleurone tissue of a-ml dilutes R-rEm colored aleurone substrate, enzyme complex from peri-

Table 1. Activity of 'Anthocyanin Decolorizing Enzyme Complex.'

Source of enzyme complex	Substrate*	% Transmittance				
		0 hr	45 min	2 hr	4½ hr	24 hr
R-rEm endosperm	A	58	60	63	69	49
	C	63	68	60	56	59
R-sd2 endosperm	C	66	50	44	46	38
a-ml endosperm	A	48	52	52	50	44
	B	65	64	69	61	62
	C	60	64	68	68	-
R-rEm pericarp	A	60	65	67	68	68
	C	52	56	56	56	51
R-sd2 pericarp	C	66	71	74	67	70
a-ml pericarp	A	48	48	56	46	42
	B	65	71	68	70	72
	C	62	49	48	52	-
R-sd2 aleurone (colorless portion)	B	80	82	-	-	87
	C	86	89	88	-	85
a-ml aleurone (colorless portion)	A	66	72	73	76	78

*Key for substrates: A = R-rEm aleurone; B = a-ml aleurone (pigmented portion); C = R-sd2 aleurone (pigmented portion)

carp and endosperm of R-rEm and a-ml mildly decolorizes the aleurone anthocyanins in R-rEm as well as hand-dissected pigmented patches of aleurone from R-rEm with Spf. However, the enzyme complex from colorless portions of spotted aleurone, both in R-rEm with Spf and a-ml with Spm, show very significant diluting capacity for the substrates prepared from pigmented patches of their own aleurone as well as between them.

These results suggest the possibility of increased accumulation and activity of this enzyme complex in colorless portions of aleurone of spotted kernels, which may be genetically related to Spm or Spf or presence of some concomitant pigment promotor such as catechol. The role of Spm and Spf may also be related to breakdown of membrane integrity permitting the mixing of enzyme and vacuolar substrate at certain points, resulting in dilution and causing patched appearance.

J. M. S. Mathur and N. D. Sharma

Biosynthesis of anthocyanins in maize: Presence and role of phenyl-alanine ammonia-lyase enzyme

Phenolic acids play a key role in biosynthesis of the B- ring of the anthocyanidin molecule. Tracer and enzymic studies have shown that cinnamic acid derivatives in higher plants are synthesized from aromatic amino acids via the shikimic-prephenic acid pathway. Phenylalanine is effectively utilized in biosynthesis of the anthocyanin skeleton, forming trans-cinnamic acid by deamination through the agency of the enzyme phenylalanine ammonia-lyase. Demonstration of the presence or accumulation of a particular intermediate would mean the presence of active enzymes synthesizing it.

In B pl plants anthocyanins are synthesized only in sun-exposed parts. Studies were undertaken to decipher whether anthocyanins are not synthesized at all in colorless (unexposed) portions or if the biosynthetic pathway leading to formation of anthocyanins is blocked at any particular stage, and whether the effect is genetic or physiological.

Free phenolic acids were extracted from cob, silk, kernels, anthocyanin-bearing sun-exposed parts and colorless parts of leaves by refluxing with 80% ethanol for 3 hr. The extract was evaporated and the residue was dissolved in distilled water and filtered. The filtrate was adjusted to pH 4 with 6 N HCl, extracted with ether and washed with 25% aq. sodium carbonate solution followed by re-extraction with ether. The ether was again evaporated and the residue moistened with 50% alcohol. Identification was done by two-dimensional descending paper chromatography using benzene-acetic acid-water, 6:7:1 V/V (upper phase) and sodium formate-formic acid-water, 10:1:200 V/V, followed by spraying specific chromogenic reagents and viewing under U.V. light for locating the spots.

For the preparation of enzyme, phenylalanine deaminase, the tissues were ground with 20 ml prechilled (-15 C) acetone. The homogenate was filtered in a Buchner funnel and the residue was washed with cold acetone and dried at room temperature. The dried powder was suspended in 10 ml cold 0.1 M borate buffer at 8.8 and the mixture was stirred for 15 min in an ice bath. The extract was clarified by centrifuging in the cold at 2000xg for 10 min. The crude extract is not stable and was assayed immediately.

The enzyme-catalyzed deamination of phenylalanine was followed by measuring spectrophotometrically the increase in absorption at 290 nm at 20 min intervals for 3 hr. The diluted enzyme contributes negligible absorption at this wave-length. The reaction mixture consisted of 50 μ moles of L-phenylalanine, 200 μ moles of borate buffer (pH 8.8), 1 ml of enzyme extract (200-250 mg of protein) and water to bring the volume to 6 ml. The reaction was carried out at room temperature. No increase in absorption occurs when enzyme or phenylalanine is omitted. Controls consisted of everything else except phenylalanine.

In the sun-exposed pigment-bearing tissues, four substituted cinnamic acids have been identified in addition to trans-cinnamic acid, which was predominant. These acids are 3-methoxy-4-hydroxy cinnamic acid (ferulic); 3,5-dimethoxy, 4-hydroxy

cinnamic acid (sinapic); 3,4-dihydroxy cinnamic acid (caffeic); and p-hydroxy cinnamic acid (p-coumaric), showing, thereby, the presence and activity of phenylalanine deaminase. The activity of this enzyme seems to be photocontrolled and is induced by phytochromes, resulting in absence of cinnamic acid in unexposed parts and an accumulation of aromatic amino-acids which could otherwise enter the anthocyanin biosynthetic pathway. The biosynthesis of anthocyanins in unexposed portions does not start even though phenylalanine is not lacking and the enzyme is also present, but the latter, being wavelength dependent, is activated only in the presence of light. This is further confirmed by the fact that the enzyme isolated from unexposed parts does not convert phenylalanine to trans-cinnamic acid during assay.

J. M. S. Mathur

Biosynthesis of anthocyanins in maize: Presence and role of transcinnamic acid-4-hydroxylase enzyme

The second step in biosynthesis of anthocyanins in maize is brought about through the agency of an enzyme, trans-cinnamic acid-4-hydroxylase, which catalyzes the formation of coumaric acid from trans-cinnamic acid.

The crude enzyme has been isolated by homogenizing 5 gm tissue with prechilled (-15 C) acetone, filtering in a Buchner funnel and suspending the acetone powder in cold 0.05 M phosphate buffer (pH 6.6), followed by centrifuging at 10,000xg for 30 min at 4C. The supernatant was used for assay and the activity was followed spectrophotometrically.

All the sun-exposed pigment-bearing portions of B pl plants show its presence in active form, accompanied by accumulation of substantial quantities of coumaric acid. The activity of this enzyme and presence of coumaric acid have not been observed in B pl x C-I hybrids, neither in vivo nor in vitro, although activity of phenylalanine ammonia lyase and presence of trans-cinnamic acids have been demonstrated.

These results further support the view that the dominant inhibitor C-I influences only the second step of biosynthesis in B pl plants and is incapable of blocking the first step of the biosynthetic pathway.

J. M. S. Mathur

Biosynthesis of anthocyanins in maize: Role of dominant inhibitor C-I

Since the dominant inhibitor C-I totally inhibits formation of anthocyanin in the aleurone layer, it was found to be excellent material to study gene action. By studying B pl and C-I (homozygous) and B pl x C-I hybrids (different tissues at different stages of development) both in vitro and in vivo, it was ascertained how C-I inhibits the biosynthesis of anthocyanins and at what stage this blockage occurs. The colored and colorless portions of B pl plants were examined for precursors (phenolic acids) in cob, silk, kernels, stem and colorless portions of leaves and so also in C-I plants. B pl plants showed the presence of the first compound of anthocyanin biosynthesis, cinnamic acid. The phenylalanine ammonia-lyase enzyme is present in all plant parts, and this converts the aromatic amino acid, phenylalanine, into trans-cinnamic acid; thus, biosynthesis of anthocyanins can proceed beyond the first step. However, we have found that the activity of this enzyme is wavelength dependent. This induction of biosynthesis through phytochromes results in formation of anthocyanins only in sun-exposed portions, and unexposed parts do not synthesize anthocyanins even though there is phenylalanine accumulation and enzyme is present. This is because the latter is in an inactive form. This is further confirmed by the fact that we have not been able to demonstrate the presence of trans-cinnamic acid in colorless unexposed portions.

In none of the plant parts from C-I have we been able to identify cinnamic acid or the activity of the enzyme, not even in the presence of light or at any devel-

opmental stage. In kernels of B pl x C-I hybrids, phenylalanine deaminase activity as well as the presence of the first precursor, trans-cinnamic acid, have been shown but no coumaric acid or trans-cinnamic acid-4-hydroxylase activity. Also, 10-day-old kernels of B pl x C-I hybrids cultured in vitro did not show coumaric acid or activity of the trans-cinnamic acid-4-hydroxylase enzyme, but cinnamic acid and phenylalanine deaminase activity have been demonstrated just after inoculation.

These results show that dominant inhibitor C-I inhibits the second step of biosynthesis of anthocyanins--i.e., conversion of trans-cinnamic acid into coumaric acid--but is incapable of blocking the first step--i.e., conversion of phenylalanine into trans-cinnamic acid.

J. M. S. Mathur

INSTITUTE OF CYTOLOGY AND GENETICS
Novosibirsk, U.S.S.R.

A rapid method of seeking frequency of alleles controlling multimeric enzymes in plant populations

When analyzing the allele frequency controlling the synthesis of multimeric enzymes one can, rather than analyze single plants from the population, carry out electrophoresis of total extract from sampled plants. Accuracy of the definition increases with the enlargement of sampling size.

The basis of the method is the relation between the relative quantity of the enzyme in the band on the electrophoretogram and the frequency of the corresponding allele in the population. For an equilibrium population of diploid plants with two alleles and for an enzyme with multimery equal to k this relation may be expressed by:

$$p = C_1 + 1/2 \sum_{i=2}^{k} C_i \; ; \quad q = C_{k+1} + 1/2 \sum_{i=2}^{k} C_i ; \qquad (1)$$

where p and q are the frequencies of two alleles controlling the synthesis of two types of subunits aggregating to form enzyme molecules with different electrophoretic mobility; C_1 and C_{k+1} are the relative quantity of homomultimeric molecules; and C_i is the relative quantity of heteromultimeric molecules (where i=2,...k).

For instance, for the dimeric enzyme (alcohol dehydrogenase, ADH) with two alleles, F and S in the population; the relation between the allele frequency and the relative enzyme quantity on the electrophoretogram is expressed by:

$$p = C_1 + 1/2\, C_2 \; , \; q = C_3 + 1/2\, C_2 \; ; \qquad (2)$$

where p is allele frequency F and q is allele frequency S, while C_1 and C_3 are the relative quantities of homodimeric molecules and C_2 is the relative quantity of heterodimeric molecules.

With the electrophoretogram data one can define the frequency of homozygous genotypes (p^2 and q^2) as well as heterozygous ones (2pq) in plants:

$$p^2 = C_1 - \frac{1}{2^k - 2} \cdot \sum_{i=2}^{k} C_i \; ; \; q^2 = C_{k+1} - \frac{1}{2^k - 2} \cdot \sum_{i=2}^{k} C_i ;$$

$$2pq = \frac{2^k}{2^k - 2} \cdot \sum_{i=2}^{k} C_i \qquad (3)$$

--the conventional signs in formula (3) and formula (1) are the same.

For the concrete enzymes the use of the method is limited by the possibility of clear electrophoretic division, by the method of staining and by the accuracy of the scanning apparatus.

The model experiments carried out by us on the ADH of maize have shown that one can identify one grain of F F genotype among 100 S S homozygotes; that is, the accuracy of this method for ADH is rather high. In particular, for the dimeric enzyme the relative frequency of F F (p^2), S S (q^2) and F S (2pq) genotypes will be defined by:

$$p^2 = C_1 - 1/2\ C_2;\ q^2 = C_3 - 1/2\ C_2;\ 2\ pq = 2C_2; \qquad (4)$$

The theoretically expected relation between p and q, p^2:2pq:q^2, and the relative quantity of protein in bands for dimeric enzymes are cited in Table 1. It is supposed that there is equal activity of alleles and equal specific activity of isoenzymes.

Table 1. Theoretically expected relationships between the allele frequency and genotype in the population and relative quantity of the homo- and heterodimeric isoenzyme.

Allele frequency		Theoretically expected frequency of genotypes in equilibrium population			Theoretically expected relative quantity of homo- and heterodimeric molecules on electrophoretogram		
P(F)	q(S)	p^2(F F)	2pq(F S)	q^2(S S)	C_1(F F)	C_2(F S)	C_3(S S)
0.5	0.5	0.25	0.50	0.25	0.375	0.250	0.375
0.6	0.4	0.36	0.48	0.16	0.480	0.240	0.280
0.7	0.3	0.49	0.42	0.09	0.595	0.210	0.195
0.8	0.2	0.64	0.32	0.04	0.720	0.160	0.120
0.9	0.1	0.81	0.18	0.01	0.855	0.090	0.055

A. N. Shenderov, S. I. Maletzky and E. V. Levites

Minimization of time of search for strains of maize with changed electrophoretic mobility of the enzyme

In searches for inbred strains having rare electrophoretic variants of enzymes, usually each separate strain is analyzed. However, this search may be accelerated if one mixes extracts from many strains and determines whether there are, among many normal strains, some mutants in the mixture. The number of the strains analyzed in one extract mixture depends on the possiblity of distinquishing the weakly stained zone of the mutant enzyme close to the bright wide band of the normal enzyme on the electrophoretogram. The experiments carried out by us on alcohol dehydrogenase (ADH) demonstrated that on an electrophoretogram it is possible to pick out the zone of ADH-F molecules when one seed of Adh-F Adh-F genotype is mixed with 30, 50 and even 100 seeds of Adh-S Adh-S genotype. Thus, the mixing procedure allows us to reduce significantly the time for finding one mutant strain among many normal ones. Which exact strain is mutant may be determined by means of sequential dichotomic division of the sample containing the mutant, with subsequent analysis of each half. The mutant strain can also be quickly isolated by means of an algorhythm whose principle is given in Table 1.

Table 1. Algorhythm* of search for one mutant strain among 62 normal ones.

** / ***	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
I	+						+	+	+	+	+									
II		+					+					+	+	+	+					
III			+					+				+				+	+	+		
IV				+					+				+			+			+	+
V					+					+				+			+		+	
VI						+					+				+			+		+

** / ***	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
I		+	+	+	+	+	+	+	+	+	+						
II		+	+	+	+							+	+	+	+	+	+
III		+				+	+	+				+	+	+			
IV			+			+			+	+		+			+	+	
V	+			+			+		+		+		+		+		+
VI	+				+			+		+	+			+		+	+

** / ***	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
I					+	+	+	+	+	+	+	+	+	+			
II					+	+	+	+	+	+					+	+	+
III	+	+	+		+	+	+				+	+	+		+	+	+
IV	+	+		+	+			+	+		+	+		+	+	+	
V	+		+	+		+		+		+	+		+	+	+		+
VI		+	+	+			+		+	+		+	+	+		+	+

** / ***	55	56	57	58	59	60	61	62	63
I			+	+	+	+	+		+
II	+		+	+	+	+		+	+
III		+	+	+	+		+	+	+
IV	+	+	+	+		+	+	+	+
V	+	+	+		+	+	+	+	+
VI	+	+		+	+	+	+	+	+

*From strains 1 to 6, one seed from each strain is taken and added to one of the mixtures. From strains 7-21, two seeds from each strain are taken and each seed is added to a different mixture; for each strain of this group, there exists a definite combination of two mixtures. From strains 22-41, three seeds from each strain are taken and each seed is added to one mixture; for each strain of this group there exists a definite combination of three mixtures, etc.

**Line corresponds to the number of the strain.

***Column corresponds to the number of the mixture.

+Means that the seed from the respective strain is added to the respective mixture.

If, after an electrophoretic analysis of the mixtures formed according to this principle, it turns out that in some mixtures there are mutant enzymes, then, by the algorhythm of formation of mixtures, one can determine the number of the strain whose seeds are contained only in these mixtures. Thus, the number of the strain with the changed electrophoretic variant of the enzyme is determined.

Our model experiments demonstrated that the algorhythm described works well. We took 62 ears of Adh-S Adh-S genotype, and one of Adh-F Adh-F genotype. Having numbered them randomly, we made mixtures of seeds from these ears according to the algorhythm. An electrophoretic analysis of the mixtures showed that Adh-F isozyme was present in mixtures III, IV and VI, which points to the fact that the ear of genotype Adh-F Adh-F had the number 39. In this way, the time of determination of the number of the ear is reduced by the factor of 10.

A. N. Shenderoph and E. V. Levites

Analysis of peroxidase isozyme patterns in internodes in haploid and diploid maize

This study was carried out on line W155 and corresponding haploids obtained from W155 by means of "Chase tester" pollination proposed by Chase (Chase, 1947). Haploid plants were exposed by the absence of coloring in embryos at the seed stage, with subsequent cytological control at the seedling stage. The plants were studied at the stage of the formation of the fifth internode, when the growing internode was about half as long as the internode which has developed before it. Isozyme patterns of peroxidase were investigated in small underdeveloped, growing, and mature internodes. The staining of peroxidase isozymes after starch gel electrophoresis was carried out with benzidine. Internode growth in both diploid and haploid plants is associated with definite change in pattern of peroxidase isozymes. Isozyme patterns in diploid and haploid plants were not different. However, haploid plants differed from diploid ones in relative intensity of some individual bands in peroxidase isozyme patterns.

E. V. Levites and R. S. Chukalina

INSTITUTO FITOTECNICO DE SANTA CATALINA
Llavallol F.N.G.R., Argentina

Further studies about heritable plastid variations produced by nuclear genes

This letter brings some data and an hypothesis based on molecular genetics that would confirm an already discovered phenomenon (Mazoti, L. B. , Cienc. e Invest. 5:387, 1949; Caryologia 6 Suppl.: 1231, 1954). This phenomenon consists in the restoration or normalization of "deficient" extrachromosomal heritable units (proplastids that are incapable of developing and synthesizing chlorophyll) by the action of a simple gene.

The induction of "deficient" heritable variations in the plastids by gene action has been demonstrated in corn (Rhoades, M. M., Proc. Nat. Acad. Sci. Wash. 29:327, 1943; Mazoti, L. B., Rev. Arg. Agr. 12:174, 1945; Stroup, D., J. Hered. 61:139, 1970). Rhoades and Stroup consider that these variations are irreversible. However, the irreversible character of this variation is only true when the R gene is not present, because when these "deficient" proplastids are in the presence of the R-r or the R-g gene they will be normalized (Mazoti, 1954). There follows a summary of the experimental data gathered to the present that would confirm this phenomenon. The material used has been "tester" lines from Cornell University, introduced in Argentina in 1934 and maintained since that date by inbreeding. 1. The line of the ij/ij gl/gl r/r genotype produced in inbreeding 8,624 variegated plants and 408 white seedlings (4.7%). 2. In the cross ij/ij gl/gl r/r x +/+ +/+ r-r/r-r (or r-g/r-g) there were obtained 6,513 normal plants (all green) and 173 lethal white seedlings. This proves heritable plastid variation, because there were "deficient" plastids in the normal nuclear genotype: ij/+. 3. In the cross of ij/ij gl/gl r/r x +/+ +/+ R-r/R-r (or R-g/R-g), using as parents lines that carried R-r or R-g in different "backgrounds," there were obtained progenies that summed up to more than 15,000 individuals. All of them were normal (green chlorophyll), with the exception of chlorophyll variations caused by chromosomal abnormalities, detected by the gl gene used as a marker. The one per thousand of these chlorophyll variations was due to haploid seedlings (Mazoti, L. B., and C. E. Mühlenberg, Rev. Arg. Agr. 25:171, 1958).

In the segregations that were obtained from the cross ij/ij gl/gl r/r x +/+ +/+ R/r, 4,250 colored grains (r/r/R) did not give any white seedlings, and 4,509 individuals of colorless (r/r/r) aleurone gave 40 white seedlings, a result that confirms the specificness of the R gene in the reversion of the "deficient" proplastids.

These studies would confirm that the "deficient" plastids of the mother plant have reverted to normality in the following generation because of a structural change, induced by the R gene, or because of the complementary action produced by a metabolite synthesized by the the R gene that would compensate for the plastid structural deficiency induced by the ij gene, with the plastids continuing to be structurally deficient (irreversible condition).

In order to determine which of the alternatives considered above is the valid one, we have to situate the "deficient" plastids in the genotypes in which we know that their deficiency will be shown. To this aim, we cross this F_1 of the gl/+ ij/+ r/R genotype with the +/+ +/+ r/r genotype, and we should expect that 4.7% of the progenies would consist of individuals with mutant plastids (structurally modified) or individuals with plastids structurally reverted to their normal state by the action of the R gene. Specifically 25% of the individuals of those progenies would be of +/ij r/r genotype, in which we know that the "deficient" plastids would be seen if there would not exist a plastid structural reversion to normality.

In order to apply tests of statistical significance, we have to compare the ratio of normal individuals vs. albinos, resulting from the cross ij/ij r/r x +/+ r/r, with the normal progenies vs. segregating progenies resulting from the cross (ij/ij r/r x +/+ R/R) x +/+ r/r (Table 1).

Table 1. Heritable variations of the plastids in relation to genotype.

Cross	Normal Seedling	White Seedling
ij/*ij* *r*/*r* x +/+ *r*/*r*	6,513	173
	Normal progenies	Segregating progenies
(*ij*/*ij* *r*/*r* x +/+ *R*/*R*) x +/+ *r*/*r*	417	0

$X^2 = 11$; $P < 0.001$

Applying to the above results a test of significance by means of a 2 x 2 contingency table we obtain that the heritable variation of the plastids induced by the *ij* gene appears to be reversible to normality by the action of the *R-r* or *R-g* gene, by means of a structural change of the plastids that would normalize them hereditarily.

The interpretation of this phenomenon of the heritable variations of the plastids (mutation and reversion) produced by genes can be the following one if we base our opinion in the knowledge of molecular genetics.

Mazoti (M.N.L. 40:62, 1966; 41:87, 1967; 49:66, 1975; Publ. No. 88 Inst. Fitotec., 1975.) formulated hypotheses based on free replication of DNA to interpret cases of inheritance in corn that deviate from the Mendelian mechanism. The same hypothesis based on free replication of DNA will be useful to us to elaborate our hypothesis on the action of the *ij* gene over the plastids. Thus, if the *ij* gene produces its replica, this replica would have the quality of hybridizing with the plastid DNA, in a specific segment; and it will produce heritable variations in the plastids if it acts as an episome. The "mutational" frequency of all the plastids of a cell will depend on the number of free DNA replicas and on the degree of affinity with the plastid DNA.

If we consider that the *R* gene would also produce its replica, this hypothesis would also interpret the reversion of plastid mutations by the *R* gene. This replica would be, at least in part, homologous with the *ij* segment in its nucleotide sequence, and it would produce a segmental trisomy of DNA: *R*/*ij*/plastid. Stability of this synaptic state in a small chromosomal segment is rather improbable, because the synapsis of homologous chromosomes in trivalents is partial; and when the pairing of two chromosomes is produced in one segment, the homologous segment of the third one tends to get free. By means of the mechanism mentioned before, plastid reversion to normality would be produced because of the *ij* replica becoming free from the association.

L. B. Mazoti

IOWA STATE UNIVERSITY
Department of Agronomy, Ames, Iowa

A dominant color allele, A-m(r), responsive to a specific En (Spm)

In the course of investigations of the *Fcu* controlling element system (Abstracts 1975 International Maize Symposium) two ears segregating an unexpected class of spotted kernels resulting from the cross of *a-m(r)*/*a-dt sh2* plants by an *a2 bt*/*a2 bt* tester stock were found. The progeny included 75% solid colored and 25% spotted kernels, leading to the initial interpretation that perhaps a change in state had occurred in the components (*r-cu* or *Fcu* or both) responsible for the aleurone color variegation in kernels from the Cuna tribal maize from Colombia (MGNL 48:66-68). Test crosses of the spotted progeny by an *r*/*r* tester invalidated the initial

interpretation of an r change since these plants were homozygous for a dominant R allele.

Crosses by a-dt sh2/a-dt sh2, however, gave a strong indication that the spotting behavior was due to an En responsive A allele. This is based on results of the following series of crosses (Table 1). It is evident that one of the ear cultures (4 1140-1) segregated colorless shrunken (a-dt sh/a-dt sh) kernels which had

Table 1. Percent progeny segregation of plants from spotted kernels crossed by an a-dt sh2/a-dt sh2 tester stock.

Cross	Round			Shrunken	Genotype
	Colored	Spotted	Colorless	Colorless	
'4 1140-1/1167	24.68	25.22	0	50.10	A/a-dt sh2
-2/1167	27.68	47.00	25.32	0	A/a-m(r)*
-3/3623	20.93	51.86	27.21	0	A/a-m(r)
-4/1170	24.97	52.06	22.97	0	A/a-m(r)
-5/1202	25.55	45.74	28.71	0	A/a-m(r)

*a-m(r) is an allele known to respond to En. In the absence of En a colorless phenotype is produced but in its presence spots appear on a colorless background.

absolutely no dots, indicating that the cause of the spotting was not a Dt-like element. This ear showed 25% spotted kernels. The remaining 4 ears segregated approximately 25% colored, 50% spotted and 25% colorless round kernels, with the spotted ones showing two different patterns: fine, very high, clear (f, v.hi, cl = small spots with a very high frequency on a clear background) and fine, medium, pale (f, m, pale - small spots with a medium frequency on a pale to dark background). It is hypothesized that the spotting is due to an En (Spm) element to which both a-m(r) and a particular A allele (originating from the a2 bt/a2 bt tester stock) are responsive.

The involvement of En in this spotting behavior was confirmed by the following crosses, utilizing a-m(r) --a specific tester for En. Plants from colorless-round kernels isolated from 4 1140-2/1167 when crossed by numbered a-dt sh2/a-dt sh2 plants from 4 1140-1/1167, which were tested for En presence with a standard En tester, a-m(r)/a-m(r), showed that each case of confirmed En activity was associated with spotted kernels. Conversely, when En was absent no spotted progeny were obtained.

From the cross initially segregating spotted progeny (a-m(r)/a-dt sh, A2/A2 x A/A, a2 bt/a2 bt) two classes of kernel pattern types observed among the spotted class were tested for a allele content by crossing by a-dt sh2/a-dt sh2. In all cases, those with the very high spot frequency were A/a-m(r) whereas those with the medium frequency were A/a-dt sh2, indicating a differential expression resulting from the two genotypes.

This En-responsive A allele is designated A-m(r) and the En is designated En-A-m(r). In the absence of En-A-m(r) the phenotype of A-m(r) is full-color, but in its presence the level of action of A-m(r) is reduced to a pale background. When a mutational event occurs full A expression results, producing a phenotype consisting of full-colored spots on a pale to dark background.

The origin of the En element was initially believed to be the Fcu-containing Colombia Cuna maize population known to possess a very weak En (small and very infrequent spots with standard a-m(r)) but which occasionally changes in activity resulting in a very high frequency of spots with a-m(r). However, this interpretation seems invalid for the following reason. When spotted progeny from the crosses listed in Table 1 are crossed by the a2 bt/a2 bt tester from which A-m(r) was extracted, spotted kernels are again isolated. When these spotted progeny are testcrossed by a-dt sh2/a-dt sh2, ears segregating what appears to be homozygous En are obtained. No such behavior is observed when only a-dt sh2/a-dt sh2 is

recurrently used. It appears, therefore, that this particular a2 bt/a2 bt stock is not only the donor of A-m(r) but also of the En. This is presently being tested.

A-m(r) is not responsive to all En elements as revealed by the negative results with a different En source, nor are all A alleles responsive to En-A-m(r). Thus, A-m(r)-En-A-m(r) represents a quasi-specific interaction.

Jaime Gonella and Peter A. Peterson

R-mo(cu), a new allele of the Fcu controlling-element system

In the course of investigations of the Fcu controlling-element system (Abstracts 1975 International Maize Symposium) a new allele at the R locus was uncovered. Of three crosses of the type C/c sh wx, R/r-cu x r/r, wx/wx (where the R allele in the female parent came from a previous cross by a c sh wx/c sh wx tester stock) one ear showed an unusual phenotypic segregation consisting of the following three kernel types: colorless, a variously expressed dilute, and mottled kernels. The first two classes were expected based on the variable expression of r-cu, which produces a continuous range of phenotypes from colorless to seemingly fully colored (MGNL 48:66-68 and the 4th section of this report). The mottled class, however, was not expected.

The three phenotypic classes from the unusual phenotypic segregation were used to test the basis for the allele conditioning the mottled behavior. The colorless progeny were testcrossed by r/r, wx/wx producing 14 progeny ears: 6 segregated dilute and colorless kernels (ear genotype r-cu/r); the other 8 showed mottled and colorless phenotypes (ear genotype R-mo(cu)/r). The test crosses of the dilute sibs gave only dilute and colorless kernels. The segregation of the mottled sibs is given in Table 1.

Table 1. Phenotypic segregation from testcrosses of mottled progeny, R-mo(cu)/r x r/r, wx/wx.

Cross		Colorless	Mottled	Total
'4	1037-1/1235	209 (78.28)	58 (21.72)	267
	-2/36A36	309 (77.64)	89 (22.36)	398
	-3/1235	421 (82.87)	87 (17.13)	508
	-4/1238	330 (79.90)	83 (20.10)	413
	-5/1235	245 (53.73)	211 (46.27)	456
	-6/36A34	368 (67.28)	179 (32.72)	547
	-7/1236	239 (64.77)	130 (35.23)	309
	-8/1239	216 (70.36)	91 (29.64)	307

It can be observed from the table that no consistent segregations were obtained when the mottled class of kernels was tested. It was suspected, however, that the cause of the erratic behavior might be the particular r tester used. Accordingly, mottled progeny were selected and crossed by either W22 r-g/r-g or the r/r, wx/wx tester with the resulting data in Table 2. None of the crosses by W22 r-g/r-g gave a Chi-square value significant at the 0.05 level for a 1 mottled:1 colorless segregation. However, the deviations from 1:1 were very highly significant when the r/r, wx/wx tester was used. This R allele conditioning a mottled phenotype will be designated R-mo(cu), where mo identifies the mottled behavior and cu indicates that it responds to Fcu. Proof for this is now presented.

The possibility that R-mo(cu) responds to Fcu signals was tested by crossing mottled progeny (R-mo(cu)/r) by plants identified for the presence or absence of Fcu (determined with an Fcu tester stock - r-cu/r). The findings are presented in Table 3. The results show that the presence of Fcu in the male parent is associated with variegation and conversely, no variegation occurs when the male parent lacks Fcu. It is concluded that R-mo(cu) is an allele of the Fcu controlling-

Table 2. Phenotypic segregation from testcrosses of mottled progeny by two different r testers, R-mo(cu)/r x r-g/r-g or r/r, wx/wx.

Cross		Colorless	Mottled	Total	χ^2(a)	(b)
'5 4550-1/4651		197 (47.70)	216 (52.30)	413	0.87	ns
-2/2102		200 (47.39)	222 (52.61)	422	1.15	ns
-3/2106		138 (47.75)	151 (52.25)	289	0.58	ns
-4/2105		198 (53.51)	172 (46.49)	370	1.83	ns
-5/2105		116 (44.62)	144 (55.38)	260	3.02	ns
-6/2109		217 (50.00)	217 (50.00)	434	0.00	ns
-7/2102		182 (45.27)	220 (54.73)	402	3.59	ns
-8/2105		185 (46.84)	210 (53.16)	395	1.58	ns
'5 4552-1/4651		174 (53.21)	153 (46.79)	327	1.35	ns
-2/4651		155 (46.55)	178 (53.45)	333	1.59	ns
-3/4652		200 (53.91)	171 (46.09)	371	2.27	ns
† -6/4722		256 (76.42)	79 (23.58)	335	93.52	*
† -7/4721		267 (78.99)	71 (21.01)	338	113.66	*
† -8/4722		232 (72.50)	88 (27.50)	320	64.80	*
† -9/4722		370 (82.41)	79 (17.59)	449	188.60	*

(a) Chi-square value for a segregation of 1 mottled:1 colorless
(b) ns = χ^2 not significant at the 5% level of probability; * = probability of a greater χ^2 is < 0.005
† = indicates crosses by the r wx/r wx tester

element system and that the element present in r-cu which makes this allele responsive to Fcu must also be present in the R-mo(cu) allele.

Table 3. Results of testing the responsiveness of R-mo(cu) to the variegation inducing Factor Fcu (*). R-mo(cu)/r x Fcu line.

Cross	Presence of variegation	Presence of Fcu in male
'5 4553-1/4625-3	+	+
-2/4625-3	+	+
-3/4625-9	+	+
-4/4625-10	-	-
-5/4626-1	-	-
-6/4626-1	-	-
-7/4626-3	+	+
-8/4626-6	+	+
-9/4626-6	+	+
-10/4626-7	+	+
-11/4627-3	+	+
-12/4626-9	-	-

*All ears segregated colorless and mottled kernels

As far as can be determined from pedigree analysis and utilizing crosses by an r/r tester, the c sh wx/c sh wx stock from which the R-mo(cu) allele originated was R/R, indicating that R-mo(cu) most probably originated in the plant where its characteristic mottled phenotype was originally observed. Despite extensive test

crosses of R/r-cu genotypes no R-mottled type allele or any other unusual R allele has been found.

Jaime Gonella and Peter A. Peterson

Comparison of the Fcu controlling element system to the spotted-dilute R system: The relationship between Fcu and Spf

The spotted-dilute R system was originally described by Sastry and Kurmi (MGNL 44:101-105). They explained the aleurone spotting behavior of unstable R alleles designated as spotted-dilute (R-sd) based on two dominant factors, Dil (diluting factor) and Spf (spotting factor). In the presence of Dil alone the R allele of R-sd isolates conditions a dilute phenotype with no spots whereas Spf by itself results in spots on a colorless background. In further studies, Singh et al. (MGNL 49:45) showed that when both Dil and Spf are present spots appear on a dilute background, indicating that the two factors are autonomous and their effects superimposable.

The r-cu allele of the Fcu controlling element system has a variable expression in aleurone color ranging from completely colorless to dark dilutes and apparently fully colored phenotypes (MGNL 48:66-68 and the following section of this report).

The question was asked whether Fcu could substitute for Spf in inducing spots on ears that would be segregating dilute (R-r Dil) kernels from R-sd Dil Spf/r-r ⊗ and from R-r/r-r Dil/+ x r/r by crossing by plants of an Fcu line (stock segregating Fcu) whose Fcu content was determined with the Fcu tester r-cu/r. The results are shown in Table 1. The data indicate that when Fcu is present in the

Table 1. Results of tests of the relationship between Fcu and Spf.

Cross	Presence of spotted kernels	Presence of Fcu in male
'5 4607-1/4625-9	+	+
-2/4626-2	-	-
-7/4626-4	-	-
-8/4626-6	+	+
-9/4626-7	+	+
-11/4628-9	+	+
-13/4628-10	+	+
'5 4605-1/4626-7	+	+
-2/4628-5	+	+
-3/4628-9	+	+
-4/4628-10	+	+
-6/4625-10	-	-
-7/4625-6	-	-

male parent spotted kernels are produced in the crosses. Conversely, spotted kernels are absent if the male tester does not contain Fcu. It can be concluded that the factor at the R locus associated with the spotting behavior of R-sd isolates (i.e., responds to Spf) is also responsive to signals from Fcu. Based on this relationship one might also expect that r-cu should respond to signals from Spf. Tests of the type presented in Table 1 gave negative results, however.

When R alleles from R-sd isolates are separated by segregation from the factors Dil and Spf a full color phenotype appears and the associated R allele no longer responds to either factor. This differs from the Fcu system, from which no colored derivatives have been isolated, as will be shown in the following section.

Jaime Gonella and Peter A. Peterson

Tests of seemingly colored derivatives of r-cu

What appear to be fully colored kernels are observed in plants segregating for r-cu. From a cross of the type r-cu/r-r, Fcu/+ x r-g/r-g fully colored kernels were collected and the plants tested with a W22 r-g/r-g stock. Twelve ears were obtained, all of which showed the presence of r-cu as revealed by its variable expression (MGNL 48:66-68). Furthermore, five of the ears segregated variegated kernels, indicating the presence of Fcu. No mottled kernels were observed in reciprocal crosses, a characteristic of r-cu.

Tests of 29 other apparently colored derivatives from crosses with another r tester (r/r, wx/wx) showed that the behavior of r-cu was unchanged, producing a continuous range of phenotypes from near colorless to dark dilutes and again what seem to be fully colored derivatives.

These apparent full-color derivatives arising in r-cu crosses are, therefore, a phenotypic extreme of the widely ranging expressiveness of r-cu.

Jaime Gonella and Peter A. Peterson

The nature of En-induced germinal derivatives of mutable alleles in maize: Characterization of colored, pale and colorless derivatives of a2-m

Controlling element systems in maize such as Ac-Ds and En-I initiate mutation events at diverse loci. The resultant phenotypic changes include widely diverse levels of genic expression from completely null (non-functional) to fully functional alleles. These are induced by the initial insertion of regulatory elements such as Ac or En (or Spm) at the designated locus or their respective controlling element Ds or I. Within the En controlling-element system there are a large number of independently induced mutable alleles at the A, A2 and C loci, each originating from the dominant fully functional allele. Some of these alleles, in turn, give rise to several phenotypically diverse derivatives. A wide assortment of such derivatives with varied phenotypic expression (from null to full colored aleurone) arose at several mutable a2 loci under the control of En system. The present study reports the characterization of colored, pale and colorless derivatives of four different a2 mutable alleles: a2-m78018, a2-m68144, a2-m68140 and a2-m11511.

Isolation of derivatives: The colored derivatives of a2-m78018 (coarse type mutability) were originally isolated from the following testcross of a mutable allele: a2-m(coarse) Bt/a2-m(pale) Bt x a2 bt/a2 bt. In a typical set of nine testcrosses, the frequencies varied from 1 to 9% of total Bt kernels. Plants grown from these were crossed by a2-m(r) Bt/a2-m(r) Bt, an En tester, to identify the En content. All the colored derivatives were found to contain one or more En, indicating that these are non-responsive types (nr). All these derivatives are maintained in a uniform genetic background: W22-Colored converted, homozygous for all anthocyanin controlling genes, C, C2, R, A, A2, Bz, Bz2 and pr (hereafter identified as W22-Col).

Pale derivatives of a2-m68144 (pattern type: very fine, clear dots with medium high frequency) were originally isolated from the following type of testcrosses: a2-m(v.v.f.cl.m.hi) Bt/a2 bt x a2 bt/a2 bt. Several plants were grown from these pale kernels and recurrently crossed for two generations to W22-Col. Pale kernels were finally selected from the selfed ears, W22-Col/pale ⊗. The isolation and characterization of pales of a2-m11511 were described previously (Peterson, Genetics, 1966; Fowler and Peterson, Genetics, 1974). Quantitative determination of anthocyanin content: Replicate samples of kernels of the desired genotype were collected from segregating ears and their relative anthocyanin content was determined by quantitative analysis (Table 1).

Several possible conclusions can be drawn from the statistical analysis of the data: 1) significant differences exist between colored derivatives in terms of the anthocyanin content of the aleurone; 2) there can be significant differences between colored derivatives arising from the same source, indicating that the original allele does not represent a predetermined potential; 3) colored derivatives

Table 1. Quantitative determination of anthocyanin pigments from colored, pale and colorless derivatives of different a2 mutable alleles.

Pedigree	Phenotype	Mean O.D.	% control	Origin
B 2561/sib	Colored	0.588	100.00	W22-Col (control)
4 4409-4/2335	Colored	0.375	67.24	a2-m78018
4 4409-1/2335	Colored	0.493	84.40	a2-m78018
4 4409-1/2335	Colorless	0.005	0.85	a2-m78018
4 4415-1/2340	Colored	0.373	63.79	a2-m78018
4 4415-1/2340	Colorless	0.005	0.85	a2-m78018
4 4474-4/2347	Colored	0.478	82.75	a2-m78018
4 4417-4/2347	Colorless	0.005	0.85	a2-m78018
308-78-7A (x)	Pale	0.0715	12.00	a2-m68144
4 3048 (x)	Pale	0.0445	6.80	a2-m68140
4 3048 (x)	Colored	0.435	74.13	a2-m68140
4 3036 (x)	Pale	0.0265	5.17	a2-m68140
4 3049 (x)	Colored	0.403	68.96	a2-m68140
8 3825 (x)	Pale	0.075	11.20	a2-m11511

arising from one source allele can be significantly different from the derivatives of other alleles, indicating that the processes involved in the origin of such derivatives may not be identical; 4) every colored derivative included in this study is significantly different from pale, colorless and colored control; thus, it can be concluded that all these colored derivatives represent a differential impairment of anthocyanin synthesis in the aleurone of kernels.

Similarly the pales, which are distinctly different from the colored and colorless types, also show significant differences in anthocyanin content. Also, significant differences exist between pales originating from the same source as well as pales originating from different sources. All the tested pales are significantly different from colorless and colored types. Again, these intermediate allelic types represent a higher degree of impairment of anthocyanin production, since these accumulate relatively low quantities of anthocyanins in the aleurone tissue (as little as 6 to 13% of control). Absolutely no anthocyanin pigments were present in the aleurone of colorless derivatives.

Qualitative analysis: Qualitative differences among the colored, pale and colorless types have been investigated by thin layer chromatography and spectroscopic techniques. The results suggest that there are no qualitative differences in terms of anthocyanin pigments between colored, pale and colored control. All of them accumulate the same anthocyanin pigments, namely cyanidin-3-glucoside and pelargonidin-3-glucoside in appropriate proportions depending on Pr and pr constitution.

Arjula R. Reddy and Peter A. Peterson

Pattern differentiation of mutable c alleles; a second factor conditioning pattern type

In the En controlling-element system, there are a large number of independently originated mutable c alleles with widely varied spotting patterns of aleurone, ranging from coarse to very finely spotted type. Some of these mutable alleles, for example, c-m55301, c-m55398, c-m55453 and c-m55351, express two distinct patterns: (a) coarse and (b) fine type in testcrosses (c-m Sh Wx/c sh wx x c sh wx/c sh wx).

Each of the pattern types was tested. When the plants grown from the coarse kernels of the above cross were testcrossed (c-m sh wx/c sh wx x c sh wx/c sh wx) only coarse types appeared in the progeny (Table 1). In tests of fine type kernels (c-m Sh Wx/c sh wx x c sh wx/c sh wx) both coarse and fine kernels were

Table 1. Segregation of second factor; pattern differentiation. Test crosses of coarse and fine plants. c-m Sh Wx/c sh wx x c sh wx/c sh wx.

Cross	♀♀ Genotype	♀♀ Phenotype	Mutable allele	Sh Fine(%)	Sh Coarse	Sh Colorless	sh Fine	sh Coarse	sh Colorless	Total
8 3103-1/3314	c-m Sh Wx/c sh wx	fine	c-m55301	73(4.48)	74	16	3	2	118	402
8 3116-1/2903	c-m Sh Wx/c sh wx	fine	c-m55301	85(38.29)	104	33	3	8	226	459
8 3102-1/3322	c-m Sh Wx/c sh wx	coarse	c-m55301	0 -	72	88	0	0	147	307
8 3118-1/3330	c-m Sh Wx/c sh wx	coarse	c-m55301	0 -	49	37	0	0	75	151
8 3106-1/3314	c-m Sh Wx/c sh wx	fine	c-m55351	136(46.74)	125	30	0	0	214	505
8 3106-2/3314	c-m Sh Wx/c sh wx	fine	c-m55351	70(28.46)	108	68	1	1	142	390
8 3107-1/3324	c-m Sh Wx/c sh wx	coarse	c-m55351	0 -	203	27	0	6	150	386
8 3107-2/3324	c-m Sh Wx/c sh wx	coarse	c-m55351	0 -	167	30	0	2	140	339
8 3108-1/3317	c-m Sh Wx/c sh wx	fine	c-m55398	90(35.29)	114	51	6	8	242	511
8 3109-2/3320	c-m Sh Wx/c sh wx	fine	c-m55398	74(30.0)	69	97	0	1	250	491
8 3110-1/3322	c-m Sh Wx/c sh wx	coarse	c-m55398	4 -	52	123	1	2	140	322
8 3119-1/2904	c-m Sh Wx/c sh wx	fine	c-m55453	68(40.96)	74	24	1	1	130	298
8 3120-1/3302	c-m Sh Wx/c sh wx	coarse	c-m55453	0 -	189	59	0	10	231	509

Table 2. The determination of segregation of coarse and fine kernels in the sib cross progeny of c-m Sh Wx/c sh wx x c sh wx/c sh wx En (in each case, En was identified in the male parent).

Cross	♀♀ Phenotype	♀♀ Genotype	Mutable allele	Total number tested	Number of ears segregating coarse and fine
5 1719/1720	coarse	c-m Sh Wx/c sh wx	c-m55301	9	7
5 1721/1722	coarse	c-m Sh Wx/c sh wx	c-m55301	4	0
5 1723/1724	coarse	c-m Sh Wx/c sh wx	c-m55301	1	1
5 1725/1726	coarse	c-m Sh Wx/c sh wx	c-m55301	3	1
5 1727/1728	coarse	c-m Sh Wx/c sh wx	c-m55301	7	2
5 1729/1730	coarse	c-m Sh Wx/c sh wx	c-m55351	4	4
5 1731/1732	coarse	c-m Sh Wx/c sh wx	c-m55351	4	1
5 1733/1734	coarse	c-m Sh Wx/c sh wx	c-m55398	4	2
5 1735/1736	coarse	c-m Sh Wx/c sh wx	c-m55398	6	3
5 1737/1738	coarse	c-m Sh Wx/c sh wx	c-m55398	7	3
5 1739/1740	coarse	c-m Sh Wx/c sh wx	c-m55398	4	2

segregating in the progeny in approximately a 1:1 ratio. In the light of these results, it is assumed that the c-m allele expresses a coarse pattern that is modified by a second factor resulting in a fine pattern. However, the nature of this second factor remains unknown.

Attempts have been made to determine if the second factor is En itself. Plants grown from the coarse kernels of the original testcross of fine plants (c-m Sh Wx/c sh wx x c sh wx/c sh wx) were sibcrossed by colorless shrunken sibs known to contain En (c sh wx/c sh wx En). The results are given in Table 2. Among the 53 tested, 26 showed segregation of coarse and fine patterns. In view of the absence of segregation for coarse and fine types in all of the progenies, even in the presence of En, there is a strong indication that the second factor modifying the coarse pattern is not En. Further tests to characterize the second factor are in progress.

Arjula R. Reddy and Peter A. Peterson

Initiation and maintenance of callus cultures of the En-Spm controlled allele, wx-m8

We are presently developing callus and cell cultures of homozygous recessive wx-m8 endosperm and scutellar tissue. Endosperm cultures were obtained by the following procedure. Immature ears were harvested (7 to 10 days post-pollination) and immediately processed for culture on solid media. The young ears were cut into small pieces and surface sterilized for 10 minutes in 0.5% Clorox solution. After rinsing three times in sterile distilled water, the tops of the kernels were cut off with a fine scalpel and the endosperm squeezed with a spatula onto the medium. The basal medium used consisted of the major and minor salts of revised Murashige and Skoog (1962): 0.5 mg of thiamine per litre of medium; 0.5 mg/L of pyridoxin HCl; 0.5 mg/L of niacin; 8 mg/L of glutamine; 2 gm/L of asparagin; 30 gm/L of sucrose; 8 mg/L of agar; 500 mg/L of yeast extract and 2 mg/L of 2,4-dichlorophenoxyacetic acid; pH 5.8 to 6; dark incubation 80 F. The callus was transferred to fresh medium every 21 days.

Callus induction was not successful either with (a) White's basal medium plus Nitsch's trace elements, 2% sucrose, 2 gm/L of asparagine; 9 gm/L of agar; and 2 gm/L of yeast extract or, (b) Linsmaier and Skoog medium: 0.4 mg/L of thiamine HCl; 100 mg/L of i-inositol; 2 mg/L of NAA; 2 mg/L of IAA; 30 gm/L of sucrose; 10 gm/L agar and 150 ml/L of coconut milk. In both of these cases, no callus growth was observed even after transferring to fresh medium.

Arjula R. Reddy and Peter A. Peterson

IOWA STATE UNIVERSITY
Department of Genetics, Ames, Iowa

Further data on the location of the modifier gene of the cl locus

In the 1972 News Letter (M.G.C.N.L. 46:93-95, 1972) and the 1973 News Letter (M.G.C.N.L. 47:79-81, 1973) F_2 data were presented that indicated the modifier of cl (Clm) was linked to the breakpoint of T8-9(6673) in chromosome 8. The Clm locus has a series of alleles that partially or completely suppress the albino phenotype of cl seedlings. The pale yellow or white endosperm phenotype of this mutant is not suppressed. In the 1972 report, it was indicated that there were two modifiers of cl in the inbred M14. One was responsible for green seedlings (Clm-M14 gr) and the other for pale green or pastel seedlings (Clm-M14 pas). Allele tests had confirmed that Clm-M14 gr was allelic to the other modifier genes of cl. However, the Clm-M14 pas, which was involved in the 1972 linkage tests with T8-9(6673), had not actually been shown to be allelic to the other modifiers. In 1973 allele tests between Clm-3 and Clm-M14 pas were made by self-pollinating plants from the cross of cl cl Clm-3 Clm-3 X Cl cl-7716 Clm-M14 pas Clm-M14 pas.

These selfed plants were either Cl cl Clm-3 Clm-14 pas or cl cl-7716 Clm-3 Clm-14 pas. All of the pale yellow seeds from these selfs were seedling tested. If Clm-3 and Clm-M14 pas are allelic, no white seedlings should be observed in the F_2 seedlings from the pale yellow seeds. This turned out to be the situation. No albino seedlings were observed out of 10,588 seedlings scored. Thus the linkage tests in 1972 involved the Clm locus and placed it on chromosome 8.

Observations of seedlings with Clm-M14 grown under controlled temperature conditions revealed that the inbred M14 did not have two different modifiers (i.e., Clm-M14 gr and Clm-M14 pas). The tests demonstrated that the Clm-M14 allele is actually temperature sensitive. At high temperature (95 F) the seedlings with Clm-M14 are pale green or pastel while at low temperatures they are green.

In the 1973 report the same indication of linkage was obtained with T8-9(6673) in crosses involving the Clm-3 modifier.

Last summer testcross progeny were grown of a cross between + clm T8-9(6673)/ cl Clm-3 + plants and plants of the inbred OH43 (lacks any dominant modifiers). The testcross progeny were scored for sterility and the plants self-pollinated. All the pale yellow seeds from the selfed ears that segregated for cl were grown and scored for the presence or absence of green seedlings:

Parental		Crossovers			
clm T	Clm-3 +	Clm-3 T	clm +	Total	% C.O.
97	93	40	33	263	27.8

The Clm modifier undergoes 27.8% recombination with the T8-9(6673) breakpoint in chromosome 8. Since the breakpoint is at 8L.35 it is impossible to determine the chromosome arm in which this locus is located.

Donald S. Robertson

Additional studies of a mutator locus on chromosome 10

Previous reports (M.G.C.N.L. 45:81-87, 1971 and 49:73-79, 1975) have indicated that a factor at or near the y9 locus is responsible for an increased spontaneous mutation rate. In these reports, it was noted that a given outcross family would frequently have several plants that segregated for mutants which were quite similar in phenotype. Such mutants were assumed to have arisen by individual somatic events resulting in tassel sectors. Results of a series of allele tests (Table 1) on mutants of similar phenotype within families indicate that most mutants arise by a very late somatic or a meiotic mutation, since in most cases the mutants are not allelic. In only 2 out of 11 families were positive tests observed. In family 72-3120, 2 phenotypes were noted, luteus (l) and albino (w). All allele tests for the luteus mutants were positive except that of 18(l) x 20(l). Since both 18(l) and 20(l) were allelic to 6(l), the negative results observed in the 18(l) x 20(l) cross are unexpected. These crosses will be repeated next summer. Until further data are obtained all luteus mutants of family 72-3120 are assumed to be allelic. The two albino mutants from this family also proved to be allelic. It is conceivable, since these mutants are in a heterogeneous background, that the luteus and albino mutants of family 72-3120 may be allelic. Further tests of allelism within this family are required but until such tests are performed the albino will be assumed to be different from the luteus mutants. In family 72-3125 both allelic and nonallelic mutants were observed. Thus in 2 out of 11 families, allelic mutants were observed while in 10 out of 11 families nonallelic mutants with similar phenotype were recovered. It is assumed that allelic mutants are of somatic origin while nonallelic mutants may be meiotic or the result of two independent somatic mutations which occurred late in development, resulting in very small tassel sectors.

These results indicate that in about 90% of the families tested, with two or more mutants of similar phenotype, there is evidence that mutation takes place very

Table 1. Allele tests of mutants with similar phenotypes within individual mutator outcross families.

Family No.	Plant numbers and (phenotypes)*	Number of crosses involving one heterozygous parent	Number of positive tests	Probability of allelism
72-3108	18(l) x 23(py)	11	0	< .01
72-3112	13(l) x 23(l)	13	0	< .01
72-3113	27(pg) x 33(pg)	13	0	< .01
72-3114	3(l) x 48(py)	22	0	< .01
72-3120	6(l) x 18(l)	20	10	1
	6(l) x 20(l)	16	4	1
	6(l) x 46(l)	10	6	1
	18(l) x 20(l)	30	0	0**
	18(l) x 46(l)	21	12	1
72-3120	22(w) x 35(w)	16	6	1
72-3124	5(l) x 14(l)	15	0	< .01
	5(l) x 19(l)	14	0	< .01
	14(l) x 19(l)	11	0	< .01
72-3125	18(l) x 20(l)	9	1	1
	18(l) x 23(l)	8	0	< .01
	18(l) x 24(l)	6	0	< .01
	20(l) x 23(l)	10	0	< .01
	20(l) x 24(l)	17	0	< .01
	20(l) x 29(l)	9	3	1
	24(l) x 29(l)	9	0	< .01
72-3126	11(l) x 27(l)	9	0	< .01
	11(l) x 40(l)	14	0	< .01
	27(l) x 40(l)	13	0	< .01
72-3132	13(l) x 30(l)	9	0	< .01
72-3225	43(l) x 31(l)	13	0	< .01
72-3232	12(l) x 20(l)	8	0	< .01

*phenotypes: l-luteus, py-pale yellow, pg-pale green, w-albino.

**4 female parents known to be heterozygous. These results are inconsistent with other crosses from this family. Further tests will be made.

late in development or during meiosis. Two other lines of evidence support such a conclusion. In 1974 and again in 1975 the mutator lines heterozygous for the genes for purple aleurone were crossed to a homozygous c sh bz wx stock. If somatic mutations involving these loci were occurring throughout development, seeds showing sectoring for these genes should be observed. So far in 20 such outcross ears (most of which were segregating in a 1:1 ratio for purple and nonpurple seeds) only two seeds with purple and colorless sectors were observed. No sectoring was observed for sh, bz or wx. Also, the mutator line was crossed to homozygous yg2 plants. Out of 1071 seedlings tested three had yellow-green sectors and two were entirely yellow-green. Similar crosses to yg2 plants with standard lines gave 796 seedlings of which one had a yellow-green sector and one was entirely yellow-green. These crosses do not indicate that the mutator line is consistently inducing early somatic mutations at the yg2 locus. To test for later mutations at this locus, plants of these crosses were grown to maturity. No yg2 sectors were observed at any stage in development for 302 plants of the mutator progeny or 251 plants of the standard progeny. The presence of two yg2 seedlings in the mutator cross may indicate that meiotic mutations had occurred. However, the occurrence of a yg2 seedling in the control cross would indicate that these yg2 seedlings are probably the result of contamination. The stocks involved in these crosses did not carry contamination markers.

In summary, the allele tests indicate that in the mutator line most mutations occur very late in development or during meiosis. Early mutations that give rise to sizable mutant tassel sectors can occur, however, at low frequency. Tests involving the c sh bz wx stock and yg2 gave no evidence for somatic mutants for any of the loci involved.

If most mutations are very late somatic or meiotic in origin the estimated mutation rates reported in 1975 are much too low. Instead of an average 31.5-fold increase in mutation rate it would be closer to a 50-60 fold increase.

Donald S. Robertson and Peter Mascia

Chromosome segregation in hyperploid female plants carrying compound A-B translocations

In 1967 Robertson (Genetics 55:433-449, 1967) tested the transmission of chromosomes from hyperploid TB-9b plants of the genotype 9(c sh wx) 9^{B}(Wx) B^{9}(C Sh) B^{9}(C Sh). The evidence suggested that approximately 96% of the time the two B^{9} chromosomes separated from each other and went to daughter poles. Occasional nondisjunction of the B^{9} element would result in recessive c sh wx seeds. In one test 3.44% of the progeny were c. Included in this 3.44% are those seed that are c due to nondisjunction (2.34%) and those that are c as a result of crossing over (1.10%).

In 1974 hyperploid female plants of compound A-B translocations involving the long arm of chromosome 4 of the genotype 4(c2) B^{4}(C2) B^{4}(C2) were pollinated by c2 c2 plants. Table 1 lists the translocations studied and the pertinent cytological information. The results of the hyperploid tests are given in Table 2.

Table 1. Compound A-B translocations studied in the hyperploid tests.

Compound A-B Translocation	Old A-B Transl.	Reciprocal A Transl.	A segments in new compound B^{A}	Length of A segments of new B^{A}
TB-1La-4L4692	TB-1a	T1-4(4692)	1L.20-.46, 4L.15 to end	125.0
TB-7Lb-4L4698	TB-7b	T4-9(4698)	7L.30-.74, 4L.08 to end	144.3
TB-9Sb-4L6222	TB-9b	T4-9(6222)	9S.40-.68, 4L.03 to end	116.6
TB-9Sb-4L6504	TB-9b	T4-9(6504)	9S.40-.83, 4L.09 to end	116.2

Table 2. Results of crossing hyperploid female plants of the constitution 4(c2) B^{4}(C2) B^{4}(C2) with c2 c2 male plants.

Translocation	No. of C2 seeds	No. of c2 seeds	Total	% C2	% c2
TB-1La-4L4692	1185	167	1352	87.6	12.4
TB-7Lb-4L4698	2239	317	2556	87.6	12.4
TB-9Sb-4L6222	2288	261	2549	89.8	10.2
TB-9Sb-4L6504	3027	319	3346	90.5	9.5

The low percentage of c2 seeds indicates that the hyperploid compound B^{A} elements regularly separate from each other, ending up in daughter cells. The small percentage of c2 seeds is due to either nondisjunction of the B^{A} elements or crossing over, as were the small percentage of c seeds in the TB-9b crosses. In the latter crosses, only 3.44% c seeds were observed while in the crosses in Table 2 c2 seeds occur in a considerably higher frequency (9.5 - 12.4%). The higher percentage of recessive seeds in the TB-4 crosses could be due to a higher rate of nondisjunction in the TB-4L translocations than in TB-9b. However, in the TB-4L translocation the segments attached to the B centromere are considerably longer (unit lengths 116.2 - 144.3) compared to that of the B^{9} element (unit

length 24.4). The longer segments involved in the TB-4L translocations may result in more effective pairing (in spite of the complex configuration) and thus allow for more crossing over than is possible in the TB-9b translocation. Higher crossing over would result in a higher percentage of recessive c2 seeds.

In the crosses of each of the TB-4L translocations one or two ears with off ratios were observed. These were not included in Table 2 but are listed in Table 3.

Table 3. Off ratio types from the cross of compound TB-4L translocations.

Translocation	No. of C2 seeds	No. of c2 seeds	Total	% C2	% c2
TB-1La-4L4692	84	75	159	52.8	47.2
TB-1La-4L4692	63	27	90	70.0	30.0
TB-7Lb-4L4698	125	95	220	56.8	43.2
TB-9Sb-4L6222	110	74	184	59.8	40.2
TB-9Sb-4L6504	93	62	155	60.0	40.0
TB-9Sb-4L6504	165	129	294	56.1	43.9
Total	640	462	1102	58.1	41.9

The 41.9% c2 seed is very close to the 41.8% c seeds observed when euploid heterozygous female TB-9b plants (9c $9^{B}B^{9}c$) are pollinated by c c plants (Robertson, Genetics 55:433-449, 1967). Thus, it is possible that the TB-4L plants that gave off ratios were not hyperploid for the translocation but euploid. An analysis of the TB-9b euploid ratios indicated that the B^{A} element moved at random with respect to the 9 and 9^{B} chromosomes. If the off ratios are from euploid TB-4L plants they would suggest that the compound B^{A} elements in these translocations also are moving at random with respect to the other elements.

Donald S. Robertson

The cytological localization of bm on the short arm of chromosome 5

Last year I reported (M.G.C.N.L. 49:79-81, 1975) on the production of the new compound translocation TB-1La-5S8041. This translocation had 90% of the short arm of chromosome 5 attached to a proximal portion of B^{1} segment of TB-1a. In 1974 plants carrying this translocation (genotype a2 1^{B} $B^{5,1}$A2 $B^{5,1}$A2 5^{1}) were crossed to a homozygous a2 bm bt stock. Last summer I grew out large purple seeds and large yellow seeds from this cross and obtained the following plants:

Large purple seeds			Large yellow seeds		
Tall Plants	Small green midrib plants	Very small, brown midrib	Tall plants	Small green midrib plants	Very small, brown midrib
10	1	5	18	5	0

Two classes of small plants were observed in this cross. In one, the plants were about 3 feet tall and had green midribs and in the other the plants were about 2 feet tall and had brown midribs. The taller of these small plants were similar to deficient TB-1a plants and are probably produced following crossing over that reconstituted the original B^{1} chromosome. The smaller brown midrib plants probably represent those that are deficient for the new compound translocation. Because of the genotype of the cross, these small brown midrib deficient plants would only be expected from purple seeds while the B^{1} deficient plants could occur from both purple and yellow seeds. Five small brown midrib plants were observed from the purple seeds and none from the yellow seeds while the taller small green midrib

plants were produced by both classes of seeds. These results would place bm distal to 5S.10, the breakpoint of T1-5(8041) in chromosome 5.

Donald S. Robertson

UNIVERSITY OF MASSACHUSETTS
Suburban Experiment Station, Waltham, Massachusetts and
HARVARD UNIVERSITY
Bussey Institution, Cambridge, Massachusetts

Genetic systems for the production of hybrid corn seed without detasseling

True genetic systems to eliminate detasseling (in contrast to cytogenetic systems that require translocations and deficiencies for gamete selection) are possible if man takes a physical part in selection for certain seed or plant characters associated with male sterility. Two such systems are described here.

A y ms system based on the close linkage of yellow-white endosperm and the male sterile gene on chromosome 6 was described by Singleton and Jones in 1930. The system was never put to use because the problem of contamination by the five percent of recombinant plants was not resolved. A modification in this system by applying the electronic eye seed sorters can make it practical. The y ms kernels that give male sterile plants are electronically sorted from a sib to heterozygous yellow endosperm, male fertile (Y y Ms ms) counterparts. When these white kernels are planted as the female in a crossing field with a normal yellow male, damage from selfing and sibbing by the five percent fertile recombinants appears as white kernels. Here again the electronic seed sorters are used but this second time to remove the white seed. Thus, the result is 100% hybrid bicolor seed. The farmer's crop will segregate ca. 25% white kernels on each ear.

A ts2 sk system is based on the female development of the tassel and its modifying genes. The ts2 gene raises the level of femaleness, resulting in tassel seed as well as ears with irregular rows from the development of both florets. But when the ts2 gene is combined with the silkless (sk) gene on chromosome 2, the tassels become at least partially male fertile, depending on the environment and other modifying genes. In contrast to the ts2 gene, the sk gene raises the level of maleness, resulting in stamens developing in both tassels and ears. Thus, when both the ts2 and sk genes are combined in the double recessive some sort of a male-female balance is once again established. A line cross between plants that are homozygous for ts2 and Sk with plants that are homozygous for ts2 and sk yields a progeny that is 100% tassel seed male sterile (ts2 ts2 Sk sk) because the recessive silkless gene is heterozygous. When this line cross is used as the female in crossing fields, detasseling is unnecessary. The ts2 ts2 Sk sk parent of this line cross must be maintained by the backcross-sib technique. In producing the line cross, the normal segregants may be cut out of the female rows long before pollen shedding. The tassel silks on the plants to remain in the field appear in the plant-whorl stage two weeks or more before the plant elongates and exposes ear silks.

Walton C. Galinat

Further notes on the use of Tr7 in the production of bisweet hybrids

In last year's MNL we mentioned that Tripsacum chromosome 7 (Tr7), which carries the Su locus also found on corn chromosome 4, may facilitate the practical production of bisweet hybrids. When the double recessive of sugary-shrunken-2 with an extra pair (20+2) of Tr7 chromosomes is line-crossed to su sh2 without the extra pair, the 20+2 condition is reduced to the 20+1 state. Then if the sh2 gene is also covered in the final crossing field involving a normal sugary seed parent, the hybrid seed crop is normal sugary with about 10% starchy kernels from Tr7. These starchy kernels may be eliminated from hybrid seed by the proper combination of

electronic eye sorting and/or gravity - shaker table sorting. The final consumer bite-off is a flavor blend of 25 percent sugary-shrunken on a sugary background. Credit for the suggestion of a physical separation of the ca 10% starchy kernels goes to my son David W. Galinat.

Walton C. Galinat

The practical production of trisweet hybrids

A type of sweet corn hybrid segregating two extra endosperm types on a sugary background is practical from a cross in which both pollen and seed parents carry a different endosperm recessive in combination with sugary. For example, if the pollen parent was su sh2 and the seed parent was su bt2 then the hybrid seed would be all standard su su with both sh2 and bt2 covered by their dominant alleles from the other parent. But the crop ear would be about 7/16 or 44% super-sweet on a sugary background rather than just 25% as in the case of the bisweet types.

Walton C. Galinat

Comparative cytology of certain Maydeae and Andropogoneae

The inclusion of several Oriental and American genera in a single tribe, the Maydeae, has been considered by some as an artificial assemblage of monoecious grasses from the tribe Andropogoneae (Weatherwax, 1954), while others have considered the Maydeae as a valid taxonomic offshoot from the Andropogoneae (Hitchcock and Chase, 1950; Anderson, 1945; Stebbins, 1956a - as reviewed by Chandravadana and Galinat, in press).

Since the floral morphology of the Maydeae is most similar to that of the subtribe Rottboelliinae of the Andropogoneae, it seems possible that studies of comparative chromosome morphology of the subtribe could help to identify the most probable connecting link between the American Maydeae and the Andropogoneae. If the closest possible hybrid between these tribes were produced experimentally, then subsequent studies of its chromosome homeology may serve to elucidate their evolutionary divergence.

In the present study, a comparative analysis is made of the chromosome morphology of the genera Elyonurus, Manisuris and Coelorachis of the tribe Andropogoneae. The individual chromosomes of these genera have been identified at pachytene and tabulated. The morphological details of the pachytene chromosomes have been reported earlier (MNL 44, 1970; MNL 45, 1971; and MNL 46, 1972).

An attempt to compare the morphological details of the chromosomes at pachytene of these genera with those of maize, Tripsacum and Coix, the first two of American Maydeae and the third of Oriental Maydeae, has revealed some interesting correspondences.

It appears that Manisuris and Coelorachis share many cytological features. Out of the 18 chromosomes of Coelorachis, 9 are comparable to the 9 chromosomes of Manisuris. Since no meiotic irregularities were noticed in Coelorachis at any stage, the similarities of nine of the Manisuris chromosomes with the nine of Coelorachis at pachytene, including the nucleolar chromosome, suggests a hybrid origin of Coelorachis. The two collections of Elyonurus tripsacoides from Veracruz and Mexico are distinct both morphologically and cytologically. The chromosomes of these three genera resemble maize chromosomes to a greater extent than they do those of Tripsacum. However, a comparison of maize chromosomes with the other Maydeae like Coix would reveal that they also share some features. They have the same lengths and both have internal and terminal knobs, the nucleolar chromosome of maize is more similar to that of the members of Andropogoneae studied than to that of either Tripsacum or Coix. In the light of the above cytological findings it seems that certain maize (Zea) chromosomes have more in common with certain members of Andropogoneae than with those of the other Maydeae (Coix and Tripsacum). This seems to support the earlier suggestions that Maydeae is an artificial assemblage and might be an offshoot of the Andropogoneae. The close relation of both maize

and teosinte to Tripsacum cannot be denied, however, as is well known from their crossability and cross-mapping studies. Chromosome differentiation in this case seems to be more important in the tactics of immediate divergence than in the ultimate strategy of wider speciation.

P. Chandravadana and W. C. Galinat

UNIVERSITY OF MILAN
Institute of Genetics, Milan, Italy

A second case of transposed duplication in chromosome 10

We have presented evidence that a nonparental strand isolated from heterozygous R-sk/r-r K10 plants carries a chromosome segment in duplicate, one segment in normal position and one transposed to a new position on the same chromosome (G. Gavazzi and G. Galli, MNL 48:106-112; Gavazzi, Heredity in press). The data to be presented refer to another strand, referred to as case 1 strand, isolated from R-st K10/r-r parents as a presumed intralocus recombinant carrying the P component of r-r linked to R-st. The parental genotype expressed in terms of the P and S components of the R locus is symbolized p S-st/P s, where the lower case letters p and s do not distinguish between presence of a recessive allele and absence of the gene component.

The transmission of case 1 strand as determined in heterozygotes with a normal strand is significantly lower than the expected 50%, amounting to about 17% and 43% in the male and female germ line respectively (Table 1). Furthermore, stippled kernels with BFB cycles are frequently observed in testcrosses of

Table 1. Observed segregation on ears obtained by reciprocal crosses of heterozygous P S-st/p s plants to a p s line.

Entering parent	Colorless	Stippled	Light stip.	BFB	Total seeds	Case 1 strand transmission
female	7583	5537	26	95	13241	42.73%
male	3074	622	-	16	3712	17.19%

P S-st/p s plants, while they are not observed when S-st is on a normal strand. The frequent occurrence of the cycles is suggestive of chromosome instability.

The P to S-st recombination value as determined in testcrosses of P S-st/p s females is much higher than expected, suggesting that P of case 1 strand is dislocated to a new position either distal or proximal to the R locus:

Gametes tested	Presumed strand constitution				% nonparental strands	
	P S-st	p s	p S-st	P s	S-st	s
7240	3623	3445	116	56	3.10 (2.33)*	1.60 (1.86)*

*Recombination values corrected for differential transmission of strands with the duplication.

Case 1 strand carries Mst distal to S-st. Its loss through crossing over leads to a light stippled phenotype. Accordingly if this strand carries P distal to R then the light stippled recombinants yielded by testcrosses of P S-st/p s females (see Table 1) should not carry P but they would still carry it if the latter is proximal to R.

Out of 18 presumed light stippled progeny tested, nine bred true. Eight of them lost P, while one retained it. This is the result expected if the gene

sequence of the strand is S-st - Mst - P. The putative light stippled originally isolated were 26 out of 5658. Their frequency, estimated on the basis of the result of their progeny test, amounts to 0.23%, a value much lower than the expected 5.7%, suggesting that crossing over in this chromosomal segment is hampered, possibly by the presence of a structural heterozygosity.

As to the three point testcross data of G S-st P/g p s females the following distribution of the g marker was observed:

Parentals				Recombinants				
S-st P		p s		S-st		p s P		n
G	g	G	g	G	g	G	g	
2374	5	105	3210	62	19	49	0	5814

The recombination value in the g - R region, as determined in our stocks, is about 19%. The results obtained with case 1 strand are unexpected. Among parentals, in fact, g recombinants are almost null in S-st P and only 3.16% in p s strands while among recombinants the frequency of S-st and s strands carrying g is about 23 and 0% respectively. These data are consistent with a model that depicts case 1 strand as a chromosome carrying a chromosomal region 20 or more units long, including the G and P markers, in duplicate--one region in normal position and one translocated distally to R.

The fact that none of the p s P recombinants carries the g marker suggests that the transposed duplication is inverted, as indicated below:

G S-st Mst P G

Evidence for the presence of a duplicated region in case 1 strand: Evidence in favor of the presence of the duplicated region was sought among the light stippled recombinants isolated in testcrosses of G S-st P/g p s females (see Table 1). If the duplicated segment of case 1 strand is distal to R then the light stippled recombinants should have a normal strand without the transposed duplication and they would thus show normal values of recombination in the G - R region. The results reported in Table 2 confirm this expectation.

Table 2. Recombination frequency for g - S-st as determined in testcrosses of stippled and light stippled plants to g p s males.

Aleurone phenotype	Recombination frequency (%)	No. seedlings	Inferred strand constitution
stippled	5.0	100	o// G S-st Mst P G
"	1.6	126	"
"	2.8	106	"
"	0.8	147	"
"	2.9	5814	"
light st.	26.1	199	o// G S-st mst
"	22.8	271	"
"	14.2	183	"
"	15.3	150	"
"	19.2	151	"
"	31.7	328	"
"	4.4	455	o// G S-st mst P G

Further data in favor of the hypothesis come from the analysis of a sample of plants derived from stippled kernels with BFB cycle in their endosperm. These kernels, derived from testcrosses of G S-st P/g p s plants, proved upon germination to have lost P in 8 out of 16 cases. Accordingly they have been used in testcrosses to g p s plants to see whether loss of P of case 1 strand is associated with re-establishment of normal transmission and g - R recombination values:

Case 1 strand	Stippled phenotype	Crossing over % g to S-st	Case 1 strand transmission ♀♀	Case 1 strand transmission ♂♂	Inferred strand constitution
standard*	standard	1.98	44.6	20.6	G S-st P G
deriv. -1	dark	15.10	50.5	51.1	G S-st
deriv. -2	dark	2.07	40.6	38.0	G S-st G
deriv. -3	standard	0.62	44.0	--	G S-st G
deriv. - 4	very dark	1.51	47.6	51.0	G S-st G

*standard refers to a strand carrying P; the four derivatives lost it.

The data indicate that only one of the four derivative strands lost a major portion of the entire translocated duplication while the remaining three retained a portion marked with G. The apparent association of loss of the duplication or part of it with an altered stippled expression remains, at present, unexplained. More data are necessary to confirm it and to understand what might be the relationship between the two events.

G. Gavazzi and Graziella Anzani

Postzygotic lethals as a genetic tool for the analysis of embryogenesis

Embryogenesis in higher plants is a complex process involving many steps whose identification and temporal sequence might be analyzed by means of gene mutations affecting embryo and endosperm morphology. Different mutants of this kind are known in corn. They are also easily inducible with chemical mutagens. The frequency of selfed M2 ears segregating for such mutants following a 0.1% EMS treatment to seeds amounts to about 25% (C. Colella and G. Gavazzi, MNL 47:111). The induced mutants are either viable or lethal. The former consist of etched, collapsed endosperm and small seeds while the latter include the same types as well as aborted seeds, germless and defective endosperm type. Post-zygotic lethals are expected to be mutants of genes whose activity is required in embryogenesis, in the metabolism of the resting seed, or in catabolic reactions of the germination process. They would also include nutritional mutants with blocks in essential metabolites not diffusible from maternal tissues or required by the embryo at a late differentiation stage when the vascular flow originating in the mother plant is interrupted. These mutants are often recognizable at an early stage of seed development. Immature embryos can thus be excised and forced to germinate on enriched media.

Growth on such media should allow survival of some mutants with a nutritional block or with lethality confined to late stages of embryogenesis that are bypassed by inducing precocious germination. Other mutants that might be rescued are those whose endosperm development is genetically blocked, like those with defective endosperm.

We isolated more than 70 postzygotic lethals and began their analysis by excising immature mutant embryos, 1-2 mm long, on M2 and M3 ears, and transferring them on both mineral and enriched media (Gavazzi et al., Z. Pflanzenphysiol. 75:381-391). The results so far obtained on a group of 11 mutants can be summarized as follows:

- five of them do not have a structure identifiable with an embryo.
- three others do not show any growth after excision and transfer to the culture media.
- two others grow very slowly, showing after 10 weeks a small shoot but no roots.
- one mutant grows as much as the wild type on both mineral and enriched media, yielding an albino seedling with green leaf tips; preliminary results seem to indicate that subtraction of sucrose from the medium enhances its chlorophyll content.

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G. Gavazzi, M. Motta and M. Nava-Racchi

Variation of pollen fertilization ability in relation to the genotype of the stylar tissue

It has been ascertained that in maize there is a wide range of genetic variability with respect to pollen grain fertilization ability. The fitness of the male gametophyte is attributable to different factors, among which the tube growth rate has been shown to be particularly important in determining differences of competetive ability. This character may be affected not only by the pollen grain genotype, but also by the genotype of the stylar tissues where the tube grows.

In order to study the effect of the female plant genotype on the competitive ability of inbred lines of maize, four lines (Wf9, B37, C123, M14), differentiated with regard to this character (M. Sari Gorla, E. Ottaviano and D. Faini, Theor. Appl. Genetics 46, 1975), were compared two by two in all possible combinations. Mixtures composed of equal quantities of pollen from different genetic sources, marked for the presence of the normal or mutant allele of the opaque-2 gene, were used to pollinate two different hybrid female plants, homozygous o2 o2, (OH43/B14 and Rosman/RVa36). Thus, the experiment comprised four controls (opaque and normal versions of the same line) and six comparisons (each in two reciprocal combinations), repeated on two genetically different female plants.

The character studied--pollen competitive ability--was measured as the increase of the relative frequency of one of the two kernel types from the apex to the base of the ear resulting from mixed pollination. The ears of the two female plants were divided transversely into five segments of the same dimensions (number of kernels on row). In the absence of competition, no differences in the frequency of normal and opaque kernels in the different segments are to be expected, whereas greater fertilization ability of one of the two pollen types will be revealed by an increase of the frequency of that type from the apex to the base of the ear, where the styles are longest.

The results with regard to the control combinations are shown in Table 1. Here the opaque kernel frequencies in the five segments of the ear following mixed pollination with pollen from the two versions of the same line are reported. In these cases, the frequency of the two kernel types is not statistically different from the first to the fifth segment, irrespective of the female plant used; this is to be expected when the two pollen types in the mixture have the same growth rate.

Table 2 shows the results of the competition between lines. For each comparison, the proportion of kernels of one of the two lines (the one which revealed greater competitive ability) obtained from the two reciprocal combinations is indicated. For example, in the WF9-C123 comparison, the frequencies reported were obtained by adding the opaque kernels from the pollen mixture WF9o2-C123O2 to the normal kernels from the WF9O2-C123o2 mixture. Here a significant increase of the relative frequencies of the kernels of one genotype from the first to the fifth segment is revealed. The lines reveal different competitive abilities: WF9 has the greatest competitive ability, followed by C123, M14 and finally B37. Some of the comparisons, made last year, confirm the line characteristics previously observed. In each line pair, the relative frequency trend had the same direction in both females. But the slope of the trend, that is, the extent of the increase from one segment to

TABLE 1. Opaque kernel frequencies from mixture of o2 and O2 pollen of the same line.

Segment	WF9		B37		C123		M14	
	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$
1	50	51	53	45	46	49	60	51
2	53	51	52	49	41	52	63	52
3	56	50	52	48	39	46	63	53
4	54	49	57	51	41	57	62	53
5	52	54	53	53	43	47	58	53
Total n. of kernels	1182	625	1532	782	2267	217	2931	2544
Significance of $X^2_{[1]}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Significance of $X^2_{[3]}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

TABLE 2. Competition between lines.

Segment	WF9-C123 % WF9 kern.		WF9-B37 % WF9 kern.		WF9-M14 % WF9 ker.		C123-B37 % C123 kern.		C123-M14 %C123 kern.		M14-B37 % M14 kern.	
	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$	$♀_{+1}$	$♀_{+2}$
1	61	56	53	65	39	36	49	39	32	26	55	55
2	61	59	60	70	45	41	53	43	35	30	60	62
3	65	59	68	69	51	41	54	42	37	34	62	62
4	65	63	74	71	57	41	61	46	44	34	69	65
5	74	68	76	79	67	44	70	53	50	34	75	69
Total n.of kernels	3401	4421	3879	3881	5843	4658	5151	3798	5323	6150	5406	4947
Significance of $X^2_{[1]}$	**	**	**	**	**	**	**	**	**	**	**	**
Significance of $X^2_{[3]}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.
b (x100)	2.60	3.01	1.69	6.86	2.67	6.07	2.19	4.46	2.99	4.75	2.88	4.71
$s.e._b$ (x100)	0.55	0.66	0.53	0.49	0.60	0.58	0.44	0.51	0.57	0.54	0.51	0.50

$♀_{+1}$: OH43/B14 o2o2, $♀_{+2}$: Rosman/RVa36 o2o2

$X^2_{[1]}$ tests linear trend, $X^2_{[3]}$ tests deviation from linearity.
b and $s.e._b$ were computed by means of Armitage method (1955).

the next, was generally different: b computed from the data concerning the first female is different from b computed from the data concerning the second female.

It is thus possible to draw the conclusion that the female plant genotype plays a part in determining the pollen fertilization ability: this is a characteristic of the male gametophyte, but it may be greater or less according to the stylar tissues where it grows.

M. Sari Gorla and R. Bellintani

UNIVERSITY OF MINNESOTA
Department of Agronomy and Plant Genetics, St. Paul, Minnesota

Transmission of nucleolus organizer region deficiencies

In animals, gametes deficient for most chromosomal segments are transmissible and the resultant hypoploid zygote either survives or dies. In plants, the gametophytic screen usually prevents the transmission of gametes deficient for most chromosomal segments. However, maize gametes deficient for the chromosomal segment distal to the nucleolus organizer region (NOR) of chromosome 6, the satellite, are readily transmissible at least through the egg (Phillips, et al., 1971, Crop Sci. 11:525-528; Phillips 1975, MGCNL 49:118-119; and Phillips, unpublished). The question is: How much of the NOR is essential for the normal development of the gametophyte and subsequent gametic transmission?

NOR-interchange heterozygotes provide excellent material to test for the dependency of various distal portions of the NOR. Pollen sterility of NOR-interchange heterozygotes would be an expected 25% if one of the duplication-deficiency (Dp-Df) combinations does not abort and adjacent-2 disjunction is rare. None of the NOR-interchange heterozygotes possesses 25% pollen abortion; most are not significantly different from the 50% expectation if both Dp-Df chromosome combinations abort (Table 1). However, a large amount of variability in pollen phenotype percentages appears to exist among plants heterozygous for a particular interchange. Variability also was reported for T6-9a by E. G. Anderson (Amer. Nat. 68:345-350, 1934). In addition, all of the NOR interchange heterozygotes possess some pollen that is smaller than normal and either well-filled or partially-filled with starch, suggesting that certain Dp-Df gametes may be transmissible at least through the egg. Competition effects usually eliminate the pollen transmission of Dp-Df gametes.

A genetic test for transmission of Dp-Df gametes from NOR-interchange heterozygotes was prompted by the observations of variability in pollen sterility and smaller but well-filled or partially-filled pollen phenotypes. The yellow-white endosperm marker (Y y) was used since it is the most convenient marker located near the NOR. Another chromosome 6 marker, sugary-2 (su2), also was employed in these tests. The Y locus is approximately 20 map units from the NOR while su2 is independent, being about 40 map units from Y. Backcross Y:y ratios should be 1:1 if the Dp-Df chromosome combination that is deficient for a portion of the NOR is not transmitted. If Dp-Df gametes deficient for a part of the NOR do function, the ratio should approach 2Y:1y. If the Dp-Df gamete deficient for a portion of the other chromosome involved in the interchange functions, then the ratio would be reversed, approaching 1Y:2y. The results in Table 2 indicate that none of the NOR-interchange heterozygotes regularly transmits a terminal NOR-deficiency through either pollen or ovules. A few heterozygous plants of certain interchanges, particularly T6-7(5181) and T6-9d, appear to transmit NOR-deficiencies but further tests are needed on these exceptions. The occurrence of these exceptions may be related to the variability observed in pollen phenotypes. Among the interchanges with certain plants producing abnormal Y:y ratios, there is no obvious relationship with the position of the break in the NOR.

Interchange T6-10(5519) consistently transmitted through the ovules Dp-Df gametes deficient for the distal portion of 10L and duplicate for the secondary

Table 1. Pollen phenotypes and frequencies of plants heterozygous for various NOR-interchanges.

Interchange	Chromosome 6	Other	No. plants	Pollen Phenotypes‡ Normal %	Devoid %	Well-filled %	Part-filled %	Percent abortion
1-6Li	S.C.* - prox.	1L.81						
1-6(4986)	"	1S.11	6+	68.3 ± 12.9	20.4 ± 2.3	11.0 ± 13.5	0.7 ± 0.8	31.9 ± 13.0
1-6(5495)	"							
1-6(6189)	Het* .10	1S.50	4	54.1 ± 6.1	23.9 ± 3.6	8.5 ± 5.6	13.4 ± 7.9	45.9 ± 6.1
2-6(027-4)	S.C. - prox.	2L.04	4	62.3 ± 6.7	18.6 ± 8.2	11.0 ± 5.1	8.0 ± 7.0	37.7 ± 6.7
2-6(8786)	Het .88	2S.97	4	55.8 ± 4.4	1.7 ± 1.7	26.2 ± 9.0	16.3 ± 7.4	44.2 ± 4.4
2-6(5419)	S.C. - .25	2L.82	6	58.7 ± 6.5	2.9 ± 2.4	16.9 ± 6.6	21.4 ± 3.9	41.2 ± 6.5
3-6(030-8)	S.C. - .25	3S.05	10	64.7 ± 12.1	16.2 ± 6.3	11.5 ± 7.3	7.6 ± 4.0	35.2 ± 12.1
3-6(032-3)	S.C. - midway	3S.34	8	63.5 ± 9.8	11.4 ± 3.9	14.0 ± 8.3	11.1 ± 3.6	35.9 ± 9.3
4-6(4341)	Het .50	4S.36	9	59.6 ± 4.1	21.6 ± 6.7	14.6 ± 4.1	4.2 ± 3.3	40.3 ± 4.2
5-6f	S.C. - midway	5S.23	8	63.8 ± 10.2	23.2 ± 3.2	10.1 ± 6.8	2.8 ± 5.7	36.0 ± 10.3
5-6(8696)	"	5L.79	5	56.8 ± 3.5	5.9 ± 8.5	16.7 ± 6.8	20.5 ± 4.9	43.2 ± 3.5
6-7(4964)	Het .32	7L.67	4	51.6 ± 3.9	13.8 ± 10.1	4.96± 3.7	29.7 ± 5.5	48.5 ± 4.0
6-7(035-3)	S.C. - .25	7L.59	9	62.4 ± 8.2	15.3 ± 7.3	5.9 ± 5.0	16.3 ± 8.4	37.3 ± 8.2
6-7(5181)	Het .71	7L.85	6	64.3 ± 7.3	6.2 ± 2.9	11.8 ± 8.3	17.7 ± 1.1	35.7 ± 7.3
6-9a	Het .67	9L.32	6	62.5 ± 5.0	18.6 ± 1.9	13.5 ± 6.8	5.4 ± 5.8	37.5 ± 5.0
6-9d	Het .46	9L.84	7	60.8 ± 6.7	16.1 ± 10.6	14.3 ± 11.6	8.7 ± 3.3	38.9 ± 6.9
6-10(5519)	S.C. - prox.	10L.10	7	64.4 ± 12.0	11.3 ± 5.6	11.0 ± 5.9	13.3 ± 6.5	35.4 ± 12.2

* S.C. = Secondary Constriction Het. = NOR-heterochromatin

\+ A minimum of 500 pollen grains were classified per plant.

‡ Well-filled = pollen smaller than normal and well-filled with starch by IKI staining.
Part-filled = smaller but partially filled with starch.

Table 2. Transmission tests of NOR-deficiencies from NOR-interchange heterozygotes using a linked marker gene.

Interchange	F_1 used as ♀ Y:y	F_1 used as ♂ Y:y	Number paired reciprocal backcrosses
1-6Li	210:192(2)†	70:70(1)	0
1-6(4986)	267:252(1)	219:232(2)	1
1-6(5495)	150:157(1)	267:251(2)	1
1-6(6189)	101:114(1)	131:115(1)	1
2-6(027-4)‡	126:119(2)	174:187(2)	2
2-6(8786)	210:198(1)	166:179(1)	1
	185:214(1)	43:23*(1)	1
2-6(5419)	114:85*(1)	64:66(1)	1
	119:100(1)	194:193(1)	1
	110:103(1)	71:118**(1)	1
3-6(030-8)	165:150(1)	272:225(2)	1
	87:59*(1)		0
	186:147*(1)		0
3-6(032-3)	231:220(2)	302:312(2)	1
4-6(4341)	213:202(2)	70:53(2)	1
5-6f	264:284(1)		0
5-6(8696)	105:86(1)	182:185(1)	1
	116:103(1)	244:194*(1)	1
		52:32*(1)	0
6-7(4964)	395:375(2)	197:233(2)	1
6-7(035-3)	318:118 F_2(1)	154:153(1)	0
6-7(5181)	1356:1331(11)	363:360(3)	2
	284:184**(1)	28:30(1)	1
	101:109(1)	228:173**(1)	1
	143:97**(1)		0
	131:180**(1)		0
	141:177*(1)		0
6-9a	245:217(3)	226:238(2)	2
6-9d	271:230(2)	176:134(2)	1
	112:119(1)	196:121**(1)	1
		118:85*(1)	0
6-10(5519)	257:420**(3)	534:504(5)	2

* Significant Chi-square test for goodness of fit (.05 level)

** (.01 level)

† Data mostly from backcrosses of F_1 (interchange x marker stock) to recessive marker stock. Ears giving homogeneous data are pooled, others are reported separately. Number of ears pooled are given in parentheses. Both reciprocal crosses are reported separately if one had a Y:y ratio deviating significantly from 1:1. If ears with a Y:y ratio differing significantly from 1:1 also have a significant deviation of Su2:su2, one would expect that the deviation for Y:y is not due to Dp-Df transmission; such ears are not included in the data presented above. Ears included in the table differing significantly from 1Y:1y have Su2:su2 ratios not significantly different from 1:1.

‡ Data for linked chromosome 2 marker virescent-4.

constriction and the satellite. Plants with this chromosome combination may be useful in future NOR studies. Duplicate-deficient plants have been recovered from this interchange by E. B. Patterson (Eucarpia, 1973) and utilized in studies on male sterility.

When crossing plants heterozygous for T2-6(5419) or T4-6(4341), two of the NOR-interchanges, with pollen from plants heterozygous for polymitotic (po), Patterson (MGCNL 33:131, 1959) obtained occasional small seed that gave rise to plants with the polymitotic phenotype. The po locus is assumed to be proximal to the NOR since it maps proximally to ragged (rgd), which is proximal to the midpoint of the NOR-heterochromatin, based on tests with TB-6a (R. G. Palmer and E. Dempsey, 1968, MGCNL 42:75-77). One could speculate that the unexpected po plants are not due to the simple transmission of Dp-Df gametes but are the result of a breakage event after the first postmeiotic division that would generate a chromosome deficient for a terminal portion of 6S including the entire NOR. The mechanism could be similar to that described for Neurospora (D. D. Perkins et al., 1972, Genetics 71:s46) and Aspergillus (Lieber 1973, Univ. of Sheffield, Ph.D. Thesis) where certain chromosomes of duplicate-deficient progeny undergo structural modifications. Data presented in Table 2 give no positive evidence for transmission of Dp-Df gametes from T4-6(4341) and mixed evidence for T2-6(5419). Occasional transmission of Dp-Df gametes could have occurred but not in sufficient frequency to result in an abnormal Y:y ratio. Additional evidence has been gained in cooperation with Dr. E. B. Patterson against the chromosome breakage hypothesis to explain po progeny in crosses of heterozygous interchanges with Po/po as pollen parent. Cytological examination of occasional po progeny in crosses involving T3-6(030-8) and T6-7(5181) revealed a heteromorphic chromosome 6 bivalent as expected in a duplication-deficiency heterozygote. No evidence of chromosome breakage was apparent. The po gene must be in the NOR-secondary constriction or the satellite. Since T3-6(030-8) has a break in the NOR-secondary constriction and T6-7(5181) has one in the NOR-heterochromatin, rare transmissions of NOR-deficiencies apparently occur at least for the distal 29% of the NOR-heterochromatin and the site giving rise to the secondary constriction. Study of progeny of these and other maize NOR-interchanges may provide valuable materials for future NOR investigations.

The conclusion we reach from these studies is that the NOR-heterochromatin and at least a large portion of the site giving rise to the secondary constriction are usually necessary for normal gametophytic development and transmission, although occasional transmissions occur of NOR-deficiencies.

R. L. Phillips

Progress in establishing a true-breeding line that will produce "all male-sterile" progeny when crossed on genetic male-sterile plants

I am now assuming that certain of the ms plants among the progeny of ms ms or Ms ms pollinated by X-rayed pollen from a normal stock may have received a treated chromosome with an inactivated Ms allele. When those male steriles are crossed with pollen of a normal inbred, the progeny which received that chromosome through the female would, when selfed, produce only fertile (non-male sterile) progeny. The progeny which received the normal, untreated chromosome carrying ms would segregate 3 fertile: 1 ms when selfed. There are eight lines that have behaved in this manner, indicating that the inactivated Ms allele was transmitted through the female. Plants in those cultures which did not segregate ms were selfed and test crossed on ms as a test to identify plants that might be homozygous for the inactivated allele and also to test transmissibility through the pollen. For three lines which had normal pollen and normal seed set, the progeny from the test crosses of certain plants included ms plants indicating pollen transmission. For one of the three lines, there were 85 ms in a total of 506 plants (17% male steriles), for another line 4 ms in 139 (3% male-steriles), and in the other line 9 ms in 15 (possibly 1:1). Since in these lines pollen and ovule transmission occurs, one would expect to obtain the homozygote for the inactivated Ms allele. Too few

plants have been tested, but crosses for further tests of these and additional lines will be grown in 1976. The limited data suggest that lines with reasonably good pollen transmission can be selected. However, once the homozygote is established, this should be a problem only when transferring it into desirable inbreds.

Germination was low for many of the crosses made in 1974 because of severe frosts the first week in September. Another problem in 1974 and again in 1975 has been that many of the crosses made on the ms stock had very low or no seed set. This may be an example of cross sterility similar to that reported by M. Demerec (1929, Z.I.A.V. 50:281-291).

Similar tests are in progress for ms2, ms8 and ms10. Only those for ms2 have reached the stage where tests for pollen transmission or homozygosity for the inactivated Ms2 allele will be grown in 1976.

Charles R. Burnham

Other possible methods of producing "all male-sterile" progeny using genetic male sterility

One of the methods proposed for using genetic male steriles in barley for this purpose was an application of the principle involved in the balanced lethal. Plants with two very closely linked recessive male sterile genes in repulsion, when crossed on plants homozygous for both male sterile genes, would produce an "all male-sterile" progeny (Eslick, 1971, Proc. 2nd Internat. Barley Genetics Symp.: 292-297). The cross would be ms(1) ms(1) ms(2) ms(2) x ms(1) +/+ ms(2). With complete linkage the pollen parent could be maintained if grown in isolation.

A modification of this would utilize a chromosomal interchange and two different independent male sterile genes, one closely linked with one of the two breakpoints and present in the interchange chromosome, the other ms gene closely linked with the second breakpoint, but located in the normal chromosome. The cross would be:

ms(1) ms(1) ms(2) ms(2) x

All the progeny would be male sterile, half ms(1) and half ms(2). Only the ms(1) progeny would be interchange heterozygotes. In a species with directed segregation, the degree of sterility would depend on the frequency of crossing over between the centromeres and the interchange breakpoints in both chromosomes.

With complete linkage between each male-sterile gene and the breakpoint, the double heterozygote could be maintained if grown in isolation. One problem remaining would be how to produce progeny all of which would be homozygous for both male sterile genes, which is needed for efficient hybrid seed production. This might be accomplished by using certain types of multiple duplication stocks, one duplication covering one male sterile gene. For one method of producing such multiple duplication stocks, see Burnham, International Maize Symposium, 1975. It is possible that the multiple duplication stock could be used to maintain the heterozygote for both male steriles as well as for producing an all male sterile progeny homozygous for both male steriles. I am presenting this now, hoping that someone can devise workable schemes.

Charles R. Burnham

UNIVERSITY OF MISSOURI
Division of Biological Sciences, Columbia, Missouri

Studies of callus tissue derived from the scutellum of maize

C. E. Green and R. L. Phillips have previously reported on their studies of maize tissue culture (Crop Sci. 14:54-58 and 14:827-830, 1974) and on their success with plant regeneration (Crop Sci. 15:417-427, 1975). The significance of such research is apparent: cell cultures provide the opportunity for *in vitro* study of a higher organism and regeneration provides a link between *in vitro* culture and classical genetic and breeding procedures.

The material employed in this study was inbred A188, obtained from C. E. Green; a genetic stock obtained from M. G. Neuffer; and their reciprocal hybrids. The genetic stock represents the F_1 of M14/W23 by a *p r Y* strain derived from a synthetic involving Longfellow Flint, inbred Kys, and Argentine Pop. Over a thousand immature embryos have been excised following the procedures outlined by Green and Phillips (1975). Excision was performed 12 to 24 days after pollination. The embryos, with their attached scutellum intact, were placed on a solid culture medium with the flat embryonic axis in contact with the medium.

The culture medium used was that of T. Murashige and F. Skoog (Physiol. Plant. 15:473-497, 1962), modified according to Green and Phillips (1975) by replacing the MS organic components with the following: 7.7 mg glycine, 1.98 g L-asparagine, 1.3 mg niacin, 0.25 mg thiamin-HCl, 0.25 mg pyridoxine-HCl and 0.25 mg Ca pantothenate per liter. Sucrose and agar were added at 20 g and 8 g per liter respectively. The plant hormone 2,4-dichlorophenoxyacetic acid (2,4-D) was added at 2 to 4 mg/l. The medium was adjusted to pH 6.0 with NaOH and autoclaved for 20 minutes at 20 psi.

Cultures were incubated at 28 to 30 C with a 16/8 hour photoperiod. Lighting was provided by cool-white fluorescent lamps in combinations to provide intensities ranging from 150 to 15,000 lux. Subculturing was performed every 3 to 4 weeks.

After 24 to 48 hours of incubation, the dome-shaped scutellum showed a characteristic swelling. Within 72 hours of excision, there was evidence of embryonic growth. Except for 6 instances, the embryo flipped over and callus began to form at the first node of the shoot within 2 weeks after excision. The 6 noted exceptions showed a swelling of the scutellum, no embryonic development, and the development of what appeared to be a brown-colored callus on the dome of the scutellum within the same time period. No further growth was apparent in these cases even after subculture.

The sequence of events described above was the same for 14, 16, 18, 20, 22, and 24 day old embryos placed on media containing 2, 3, or 4 mg/l 2,4-D. Twelve-day embryos placed on media containing 2 mg/l 2,4-D showed little or no shoot development. Callus formed only after the scutellum flipped over due to root growth from the area of the embryonic axis.

A compact yellow callus proliferates once the remains of the embryo are removed after the first subculture. A few roots are produced which rapidly increase in number if the callus is left on the same medium without subculture for more than 4 weeks. This is attributed to a rapidly decreasing concentration of 2,4-D.

Quite often areas of the callus begin to green and structures apparently lacking any organization appear in association with these green areas. If these cultures are subcultured to media containing the same concentration of 2,4-D, these structures persist and the callus continues to proliferate. If the cultures are transferred to media containing 0.25 mg/l 2,4-D, the green areas may or may not persist, and roots will begin to differentiate. This response is continued if the culture is then transferred to media lacking any hormone, with a concomitant increase in the number of roots. If cultures containing a plethora of roots are broken up and returned to media containing 2 mg/l 2,4-D, callus may again proliferate but at a much slower rate. Table 1 provides data from the most recent set of excisions.

The only regeneration was from a 24-day embryo from a self of Neuffer's genetic

Table 1. Ability of immature embryos to form callus.

Genotype	Embryo age	Embryo size[1]	Number isolated	Nodal callus[2]	Scutellar callus[3]
(Light intensity 15,000 lux; 2 mg/l 2,4-D)					
A188/"ABPHYLL"	18	6-7	20	20	0
A188/genetic stock	18	6-7	30	30	0
A188/genetic stock	16	5-6	20	20	0
genetic stock/"ABPHYLL"	16	4-5	10	10	0
A188	12	2-3	10	4	0
A188/genetic stock	12	2-3	20	8	0
genetic stock/"ABPHYLL"	12	3	1	0	0
genetic stock	12	1-3	5	2	0
(Light intensity 7500 lux; 2 mg/l 2,4-D)					
genetic stock	18	5-6	20	20	0
A188	18	5-6	10	10	0
A188/"ABPHYLL"	18	5-6	20	20	0
genetic stock/"ABPHYLL"	18	5-6	10	10	0
"ABPHYLL"	18	3-4	5	5	0
(Light intensity 1400-3400 lux; 2 mg/l 2,4-D)					
A188	16	4	2	2	0
"ABPHYLL"	18	3-4	5	5	0
(Light intensity 150 lux; 2 mg/l 2,4-D)					
A188/genetic stock	18	5-6	5	5	0
A188	16	4	2	2	0
"ABPHYLL"	18	3-4	5	5	0

[1]length in millimeters

[2]scutellum flipped over due to embryonic growth, callus formed from first node of epicotyl

[3]scutellum did not flip over, embryonic growth aborted, callus formed from dome of scutellum

stock. The culture was initiated and maintained on 4 mg/l 2,4-D and incubated under a combination of fluorescent and incandescent lamps with a combined intensity in excess of 15,000 lux. The temperature was 28 to 30 C and the photoperiod 16/8 hours. It should be noted that this culture was in a group of cultures that were regularly subcultured late, that is, every 5 to 6 weeks. Consequently, it had been nearly 6 months since the initial excision.

Approximately 5 weeks after the third subculture, the callus had a dull yellow color with several roots and a few white-colored, unorganized structures along with a small, leaf-like structure. The culture was divided in half and the half with the leaf-like structure was placed in media lacking any hormone. The other half was placed in media containing 4 mg/l 2,4-D. The latter exhibited no further organization.

Within 4 weeks, a definite shoot had developed and the culture was transferred to a medium used for the *in vitro* culture of mature embryos. It contained 0.6 g NH_4NO_3, 0.4 g $MgSO_4 \cdot 7H_2O$, 0.4 g $Ca(H_2PO_4)_2 \cdot H_2O$, 0.4 g KH_2PO_4, 0.160 g K_2HPO_4, 6 mg ferric citrate, 10 g sucrose, and 7 g agar per liter. The plantlet was placed in a 4 liter flask containing a liter of this medium and was incubated at 28 to 30 C with a combination of fluorescent and incandescent lamps closely approximating daylight. The photoperiod was 16/8 hours. Growth continued, and after 3½ weeks

the plant was potted in sterilized soil in a 10" pot and returned to the growth chamber. After 3 weeks it was placed in the greenhouse. A month later it was evident that the regenerated plant had a decussate leaf arrangement closely resembling the ABPHYLL syndrome reported by R. I. Greyson and D. B. Walden (Am. J. Bot. 59:466-472, 1972). The plant produced two ears, at opposite nodes, and had fully fertile pollen. There were 27 leaves on the plant compared to 12 to 14 leaves on other plants of the same background. Leaf width ranged from 3.5 to 4.5 cm and leaf length from 20 cm (the short, upper leaves) to 67 cm (the long, lower leaves). The plant, in a 10" pot, was 50 cm tall. It was selfed and also outcrossed to the genetic stock and to A188. The F_1 seed from these crosses produced plants with a distichous leaf arrangement and 12 to 14 leaves. These plants were selfed and the F_2 will be analyzed with a winter greenhouse crop. Chromosome counts of root tips prepared from seedlings grown from the seeds from the self of the regenerated plant revealed no chromosome aberrations or any deviation in ploidy.

Unfortunately, attempts for further successes at regeneration by mimicking the conditions that produced the "ABPHYLL" plant have been in vain. No plants have been regenerated by using the same procedures outlined by Green and Phillips. Experiments are being continued in this area.

William S. Rafaill

UNIVERSITY OF MISSOURI and
AGRICULTURAL RESEARCH SERVICE, U. S. DEPT. OF AGRICULTURE
Columbia, Missouri

Pollen suspending media: A retraction regarding cyclohexane

In 1973 (MNL 47:144) we reported experiments in which cyclohexane appeared to be a promising medium for suspension of pollen if the solvent was volatilized before pollination. Experiments in three subsequent seasons have failed completely; no reasons for the difference between the original and subsequent tests have become apparent, and we have discontinued attempts to exploit this solvent. If anyone has succeeded with cyclohexane (or any other) in obtaining good seed sets following suspension and volatilization, please compare notes.

E. H. Coe, Jr.

Symbolization: Need for a generic form

The common practice in the past of using a to represent generically any or all of a (i.e., a1, a2, etc.,) is precluded by the current rules, since the subscript 1 is no longer used. Ambiguity arises in expressing this generic meaning with a symbol rather than with words or a phrase (e.g., white seedling). A simple solution would be to use the asterisk, already stipulated for new isolates, without the isolation number: a*, w*, etc. In developing symbol listings and indexes, I plan to follow this practice, and would appreciate reactions from cooperators.

E. H. Coe, Jr.

Dating pollinating bags

To date bags rapidly, we have been using in our laboratory a simple binary-number system marked onto the bags with a soft graphite carpenter's crayon. Bags in groups of 50 can be fanned out uniformly in the lengthwise direction with a little practice, then marked in strokes along the stepped upper segments. Identifying five positions across the top of the bag as 16, 8, 4, 2, 1 (left edge, center, center right, right edge), markings in these positions identify 31 dates in typical binary notation: 00001, 00010, 00011, 00100, 00101, etc. The markings are unmistakeable and remain until harvest if applied carefully and firmly.

E. H. Coe, Jr.

A germination procedure for corn seedlings

A procedure has been developed for the germination of large quantities of either etiolated or green corn seedlings. This procedure employs treatment of the seed with the fungicide Captan (N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide), two surface sterilizations in 0.5 sodium hypochlorite and germination in sterile polycarbonate boxes (Econo-cages, Maryland Plastics, Inc., 9 East 37th Street, New York, N.Y. 10016) on 2% bacteriological agar.

Dichloromethane (DCM) was proposed by H. Meyer and A. M. Meyer (1971, Science 171:583-584) as a solvent for introduction of chemicals into dry seed, since treatments for up to 24 hours with this chemical had no effect on germination or oxygen uptake. Seeds (approximately 400 g) were stirred with 2 g Captan per liter DCM for 24 hours. Upon removal, the seeds were allowed to dry thoroughly and were carried through to planting on the same day. Results were satisfactory, however, when they were held in the dried state for a week or more. Captan-treated seeds would germinate as well as seeds treated with DCM alone and slightly better than untreated seeds. In addition, there was far less contamination in the Captan-DCM treated seed.

Each 100-gram batch of Captan-DCM-treated seed was immersed in 200 ml of 0.5% sodium hypochlorite for 15 minutes and rinsed three times with approximately 300 ml per rinse of distilled water. The seeds were then immersed in 300 ml distilled water for 4 hours to induce growth of fungal spores that might have survived the sodium hypochlorite treatment. At the end of this period, the seeds were drained and treated a second time with 200 ml 0.5% sodium hypochlorite for five minutes. This second treatment was followed by three rinses with 200 ml distilled water and holding for 30 to 60 minutes in a final rinse of 200 ml distilled water containing 1% Captan.

Prior to the surface sterilization procedure, 20 grams of agar and 1 liter distilled water were placed in a clean polycarbonate box, which was then covered with aluminum foil, autoclaved at 121 C with 15 psi pressure for 20 minutes, and allowed to cool at least 4 hours prior to use. One 29.2 x 18.4 x 12.7 cm polycarbonate box was prepared for each 100-gram batch of seed.

After surface sterilization, the seeds were drained, spread in a monolayer on the agar, and then covered with approximately 500 ml dry vermiculite. For germination of etiolated seedlings, the polycarbonate boxes were re-covered with aluminum foil and placed in light-proof cardboard freezer boxes. They were subsequently placed in a growth chamber (28-30 C) and harvested 7-9 days after planting. For germination of green seedlings, ethanol-washed polyethylene film may be used to cover the polycarbonate boxes.

P. L. Bolen* and E. H. Coe, Jr.
*Present address: Dept. of Botany, Duke University

Electrophoresis of shoot mitochondrial proteins from diverse cytoplasms

Six inbred lines (Ky21, Hy2, CI21E, N6, Tr and K55) were backcrossed into five cytoplasms (cms-T, cms-S, cms-C, Wn and 249) to produce a diallel consisting of 36 lines (see Table 1). As shown in Table 1, the six inbreds selected differ in their fertility-restoring capabilities for the cms-T, cms-S and cms-C cytoplasms.

Seedling shoot mitochondria were isolated from each of these lines and analyzed with two electrophoretic techniques. One technique employed the detergent sodium dodecyl sulfate (SDS). Proteins solubilized and electrophoresed in the presence of SDS are separated by differences in their molecular weights. The other technique, isoelectric focusing, allows a separation of proteins by their charge differences. In both techniques, slab acrylamide gels were used to facilitate visual comparisons of the banding patterns that resulted.

Four categories of protein bands were found. The first category included bands that were equally present in all 36 patterns and therefore yielded no genetic information. The second category consisted of bands that varied in staining intensity

Table 1. Fertility ratings of Maintainer, sterile and fertile cytoplasms in six inbred backgrounds.

Inbred	Cytoplasm	Backcrosses	Fertility Rating[a]	1975 Rating[b]
Ky21	Maintainer	continuous	-	5
	cms-T	15	4	5
	cms-S	15	4	5
	cms-C	13	4	5
	Wn	>6	-	5
	249	>5	-	5
CI21E	Maintainer	continuous	-	-
	cms-T	14	1	1
	cms-S	5	5	5
	cms-C	11	3	1
	Wn	9	-	5
	249	8	-	5
K55	Maintainer	continuous	-	5
	cms-T	14	5	5
	cms-S	4	1-2	2
	cms-C	11	5	5
	Wn	7	-	5
	249	8	-	5
N6	Maintainer	continuous	-	5
	cms-T	13	1	1
	cms-S	13	1	1-2
	cms-C	13	5	5
	Wn	9	-	5
	249	11	-	5
Hy2	Maintainer	continuous	-	5
	cms-T	>3-(originally	1	1
	cms-S	7 on type)	1-2	1-2
	cms-C	11	1-3	1
	Wn	8	-	5
	249	7	-	5
Tr	Maintainer	continuous	-	5
	cms-T	12	1	1
	cms-S	12	5	5
	cms-C	5	1	2-4
	Wn	9	-	1-4
	249	8	-	5

[a]Fertility Rating (Beckett, J. B., 1971, Crop Sci. 11:724-727): 1-male sterile; 2-sterile anthers exserted; 3-partially fertile; 4-slightly subnormal; 5-fully fertile.

[b]1975 Rating: 1-no anthers; 2-needle-like anthers, no pollen; 3-partially fertile; 4-slightly subnormal; 5-fully fertile.

between different inbred patterns, but not among cytoplasmic sources of the same inbred. This variation was taken as evidence for the involvement of nuclear genes that affect the concentrations of these bands. A third category included bands that were present in one or more, but not all, of the inbred lines. These bands were not found to vary between different cytoplasmic versions of the same inbred line. Therefore, it was concluded that the presence of these bands is determined by nuclear genes. However, none of these category-3 bands could be correlated with

the restoration of fertility for any of the male-sterile cytoplasms and, consequently, do not appear to be the products of nuclear restorer genes. Finally, in a few instances, particular bands were observed to vary in only one cytoplasmic version of one inbred line. These may be the result of specific nuclear-cytoplasmic interactions. Protein bands that consistently varied between the cytoplasmic versions of these inbreds were not observed.

P. L. Bolen and E. H. Coe, Jr.

Electrophoresis of shoot and tassel mitochondrial proteins from diverse cytoplasms

Important considerations for the identification of specific gene action are the tissue and stage of development at which this action would be expected to occur. Rf3, the standard restorer for cms-S cytoplasm, is known to be expressed after the formation of the microspore (Buchert, J. G., Proc. Nat. Acad. Sci. USA 47:1436-1440, 1961). This fact suggests that Rf3 may produce a protein product just after microspore formation that is not present in microspores with rf3.

If mitochondria are the determinants of cytoplasmic male sterility and the Rf3 allele acts to correct this defect, then a consistent difference in mitochondrial isolates from post-meiotic tassels should be detectable between cms-S versions of two inbreds that possess different alleles (Rf3 and rf3) at this locus.

To investigate this hypothesis, mitochondria were isolated from shoot and tassel tissues of maintainer, cms-S, Wn and 249 cytoplasmic versions of K55 (non-restorer of cms-S) and Tr (restorer of cms-S) inbreds. The same two electrophoretic techniques were used to separate the mitochondrial proteins as in the preceding report.

A comparison of the banding patterns from shoot and tassel mitochondria isolated from the same line revealed developmental differences in protein constituents. Protein bands that were present in only shoot mitochondria and, reciprocally, bands that were present in only tassel mitochondria were identified. However, it was apparent that none of these developmental differences were the result of post-meiotic action by the Rf3 gene since a band present in only the tassel patterns of the various cytoplasmic versions of the inbred Tr (restorer of cms-S) was not identified.

P. L. Bolen and E. H. Coe, Jr.

Renaming of B-A translocations

I propose three changes in designation of translocations between B chromosomes and members of the basic set:

1. Call them B-A translocations instead of A-B translocations, since the B is normally listed first (e.g., TB-1a). Listing the A chromosome first (T1-Ba) would tend to obscure the uniqueness of these translocations.

2. Incorporate L or R into the name of each B-A translocation to indicate the A chromosome arm involved. TB-1a would thus become TB-1La; TB-1b would become TB-1Sb. This change should increase convenience in use.

3. Rename the compound translocations of F. A. Rakha and D. S. Robertson (Genetics 65:223) and of Robertson (NL 49:79) to indicate the B-A translocation originally used to develop each. TB-4L, 1L(4692) would thus become TB-1La-4L4692. Since a portion of the long arm of chromosome 1 is uncovered by this compound translocation, it is important to include 1L in the name. And since a portion of 4L is attached to the B^{1L} chromosome, the order should be 1L-4L instead of the reverse. Concurrence of E. H. Coe, Jr., J. L. Kermicle, R. J. Lambert, Bor-yaw Lin, and D. S. Robertson with the changes outlined above has been obtained.

J. B. Beckett

Inheritance of multiple aleurone layering

Aleurone tissue in corn and other cereals has been shown to be high in protein of excellent quality, and similar in nutrition to germ tissue. Any increase in the amount of aleurone tissue in feed grains should enhance their value as food for monogastric animals.

Prior to the results of M. J. Wolf et al. (Crop Sci. 12:440), no strains of corn had been reported with more than one layer of aleurone tissue. They reported the exotic strain Coroico had as many as six layers and the amount of aleurone tissue per kernel could be increased from 2 percent for single layered kernels to 4 percent for multiple layered kernels. In addition, the aleurone tissue from Coroico had a higher concentration of protein than tissue from single aleurone tissue. Lysine content of the two sources was essentially the same. From a limited number of observations they suggested the multiple aleurone character was controlled by a few partially dominant genes. O. E. Nelson and M. T. Chang (Crop Sci. 14:374, 1974), studying the inheritance of multiple aleurone layering, found considerable variation in the F_2 generation. Their results were not conclusive but neither refuted nor confirmed a single dominant gene hypothesis.

We conducted an inheritance study of the multiple aleurone character in two parts with the assumption that it was controlled by a large number of genes or a few genes plus modifiers. Under the second part we assumed the character was controlled by a few dominant genes.

The quantitive inheritance study consisted of the diallel analysis approach involving five multiple aleurone layered lines. The ratio of general combining ability to specific combining ability was 3.5. The relatively high sca value in relation to gca suggested that few genes with dominance control the multiple aleurone character.

The qualitative study involved two inbred line parents, one with multiple aleurone layering and the second with a single aleurone layer. The reciprocal F_1 crosses showed multiple aleurone layering to be dominant over single aleurone layering. The F_2 generation and two of the four backcrosses and reciprocals agreed with the two gene hypothesis (Table 1). We have no explanation why the one set of backcrosses did not conform to the two gene hypothesis.

Table 1. Chi-square test of the hypothesis that multiple aleurone layering is conditioned by two dominant genes with dosage effects that required at least one dominant gene at each locus.

Generation	Ratio tested	Chi-square value	Average number of aleurone layers	
			Obs.	Pred.
F_2				
(B57ma x B57) ⊗[a]	3:1	16.66**	1.59	1.56
(B57ma x B57) ⊗	9:7	3.18	1.59	1.56
Backcrosses				
(B57ma x B57) x B57	1:3	12.91**	1.24	1.25
(B57ma x B57) x B57ma	1:0	8.00**	1.82	2.00
Reciprocal backcross				
B57 x (B57/ma x B57)	1:3	1.31	1.11	1.15
B57ma x (B57ma x B57)	1:0	0.00	2.06	2.25

[a] 200 kernels observed in population.

** Significant at the 1% level.

The results from our study suggest that the multiple aleurone layering character is controlled by a few genes, possibly two with partial dominance where both dominant genes are necessary.

Soontorn Duangploy, M. S. Zuber and B. G. Cumbie

UNIVERSITY OF NEW HAMPSHIRE
Durham, New Hampshire

Relation of hydroxamic acid concentration (DIMBOA) to resistance to the corn leaf aphid

In 1959, the cyclic hydroxamic acid 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) was first reported in maize and has since been directly implicated in resistance to several pathogens and insects. DIMBOA occurs naturally in the glucosidic form and is converted to the toxic aglucone through mycelial penetration or insect injury.

The objective of this study was to correlate DIMBOA concentration with resistance to the corn leaf aphid, Rhopalosiphum maidis (Fitch), through bioassay and field experiments. The bioassay experiment was performed to test toxic effects of DIMBOA on the corn leaf aphid. An artificial diet consisting mainly of a mixture of amino acids and vitamins was prepared for use in the bioassay. To the diet were added various amounts of DIMBOA (0.1, 0.25, and 0.5 mg/g diet) to give concentrations similar to those found in host plant tissue. Control diets contained no DIMBOA. Approximately 15 first instar apterous aphid nymphs were fed the diets through a Parafilm membrane. Mortality counts were recorded every 48 hours for 12 days.

In field trials twelve inbred lines of corn were evaluated for corn leaf aphid resistance under natural infestation. Aphid damage was evaluated at the mid-silking stage using a visual rating scale and an index system. Index values, indicating severity of aphid infestation, were compared to concentrations of DIMBOA found in each line using a colorimetric procedure based upon the reaction of DIMBOA with $FeCl_3$.

Results from the aphid bioassay demonstrated significant effects of DIMBOA on aphid mortality. DIMBOA concentrations of 0.1, 0.25, and 0.5 mg/g diet produced 5.1, 12.8, and 20.5 percent mortality, respectively, using Abbott's formula. Aphid index values from the field data ranged from 15.0 to 65.0, representing mild and severe damage, respectively. DIMBOA concentrations in plants at the fifth to sixth leaf stage ranged from 0.03 to 1.48 mg/g fresh weight. A significant correlation ($r = -0.72$, df. = 34) was obtained between these two traits, indicating that inbred lines containing a high concentration of DIMBOA generally have improved resistance to the corn leaf aphid.

B. J. Long, G. M. Dunn, J. S. Bowman and D. G. Routley

NORTH CAROLINA STATE UNIVERSITY
Department of Genetics, Raleigh, North Carolina

Localization of factors controlling the Texas type of cytoplasmic male sterility

The location of the factors responsible for the Texas type (cms-T) of cytoplasmic male sterility is unknown. Recent studies (e.g., Science 173:67, 1971; Phytopathology 63:1357, 1973) have shown differences in the response of mitochondria from maize with normal and "Texas" cytoplasms when challenged by toxins produced by race T of Helminthosporium maydis Nisikato and Miyake (southern corn leaf blight) and Phyllosticta maydis Arny and Nelson (yellow leaf blight). Since these studies suggest the involvement of mitochondria, mitochondrial DNA (mtDNA) must be considered as a possible site of factors responsible for traits associated with cms-T.

The traditional means of genetic analysis for nuclear genes are generally not available for studying cytoplasmically inherited traits of higher plants. Another approach lies in characterizing the organelle DNA's and attempting to relate them to the cytoplasmically inherited traits. When a homogenous DNA is digested by a site-specific restriction endonuclease, a characteristic set of fragments is generated. If the DNA is of low complexity, fractionation of the restriction fragments by gel electrophoresis results in a characteristic fragment pattern. This pattern can serve as a fingerprint of the original DNA molecule in a manner analogous to the tryptic fingerprints of protein.

We have isolated mtDNA from maize with normal (fertile) and "Texas" male-sterile cytoplasm. When the mtDNA's from the two cytoplasms were subjected to restriction enzyme fragment analysis the patterns were readily distinguishable. This distinction in fragment patterns has been demonstrated consistent by examining mtDNA from normal and "Texas" cytoplasms in different genetic (nuclear) backgrounds. These results establish an association between mtDNA and the "Texas" type male-sterile cytoplasm.

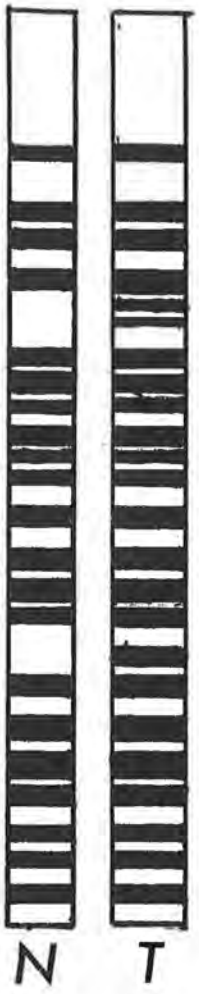
Mitochondria were isolated from etiolated maize coleoptiles and treated with DNase I prior to lysis with 1% Sarkosyl. The DNA from such preparations was centrifuged in CsCl-ethidium bromide gradients and mtDNA was obtained by collecting upper (nicked) or lower (supercoiled) DNA bands. The DNA's were extracted with isopropyl alcohol and dialyzed against restriction buffers. Purified mtDNA's were then digested with R endo·Eco R I or R endo·Hind III, and the resultant DNA fragments were separated by electrophoresis in 0.7 or 1.0% agarose gels. Restriction fragments were visualized by fluorescence after staining with ethidium bromide.

The patterns obtained from the mtDNA digestion with endo R·Hind III revealed about 50 bands, while endo R·Eco R I produced about 40 bands. The agarose gel electrophoretic fragment patterns of endo R·Eco R I (Fig. 1) and of endo R·Hind III (Fig. 2) digestions clearly show that the normal and cms-T fingerprints are different. Although the cleavage patterns from the two restriction endonucleases are not similar, both nucleases generated fragment distinctions between the mtDNA's of normal and "Texas" cytoplasms. We have examined mtDNA from normal cytoplasm of several inbreds or crosses and found all the fragment patterns to be similar when cleaved by the same endonuclease. Similarly mtDNA from several inbreds or crosses in cms-T resulted in indistinguishable patterns when restricted by the same endonuclease. Although the two types of cytoplasm yield readily distinguishable fragment patterns, there is considerable homology in the DNA's as evidenced by the large number of common bands.

Although these experiments were designed to localize the factors responsible for cytoplasmically inherited traits, they also provide unique evidence of uniparental inheritance of the mitochondrial genomes. In our study, we had hybrids in which the male parent contained normal cytoplasm and the female, "Texas." Since the mtDNA's of the two cytoplasms are distinguishable, the parental DNA's are marked. The Hind III digestion pattern of normal mtDNA contains several fragments (Fig. 2) which are not present in the cms T pattern. These fragments effectively mark the male parent, and we have repeatedly been unable to observe these specific fragments in the progeny. The pattern of the mtDNA of the cross was always that of the female parent. The same result was found for cms-T inbred lines, which must be maintained by repeated crossing with male fertile (normal cytoplasm) lines.

The purity of our mtDNA is an important concern. We have examined mtDNA by buoyant density determinations in neutral CsCl. Maize mtDNA is resolved as a single band with a density of 1.706 g/cm^3, which is typical of other higher plant mtDNA's. This density is different from that of maize nuclear or chloroplast DNA's, 1.702 and 1.700 g/cm^3 respectively. Nonetheless, we cannot unequivocally state that our preparations do not contain an alien DNA. The possibility of a DNA-containing virus or virus-like agent in our maize lines is difficult to eliminate.

These results have important implications. To our knowledge this is the first report of restriction endonuclease fragment analysis of any higher plant mtDNA,



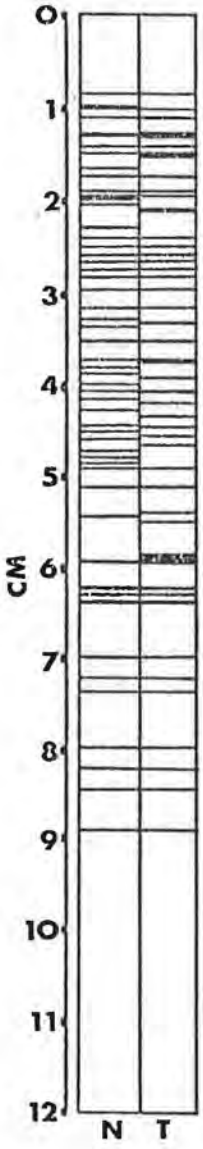


Figure 1 (left). Partial agarose gel electrophoretic patterns of endo R·Eco R I-digested maize mitochondrial DNA's from NC 7 x T204 with normal (N) and Texas (T) cytoplasms. Only the first 5.5 cm of the 12 cm gel is shown; most of the pattern differences occurred in this portion of the gel.

Figure 2 (right). Agarose gel electrophoretic patterns of endo R·Hind III-digested maize mitochondrial DNA's from W64A with normal (N) and Texas (T) cytoplasms.

and we feel it demonstrates the application of a technique which can be used in the analysis of cytoplasmically inherited phenomena. Our results show that a maternally inherited difference in mtDNA is associated with the Texas male-sterile cytoplasm. These observations suggest that the factors conditioning cytoplasmic male sterility and the cytoplasmic inheritance of susceptibility to H. maydis and P. maydis are located on the mitochondrial genome. Although we cannot disregard chloroplasts or other cytoplasmic DNA's as potential carriers of these traits, the preferential effect of the host specific fungal toxins on mitochondria from cms T lines, together with the restriction endonuclease data, constitute strong evidence that the mitochondria are the organelle involved in the inheritance of the traits.

D. R. Pring* and C. S. Levings, III
*Department of Plant Pathology, University of Florida

Conformation and size of mitochondrial DNA of maize

The conformation and size of mitochondrial DNA (mtDNA) were studied for a corn hybrid, NC 7 x T204ms (cms-T), by electron microscopy. Crude mitochondria were obtained from 7-day-old coleoptiles and carried through an additional resuspension and centrifugation cycle. Sarkosyl lysates of this fraction were centrifuged to equilibrium in CsCl-ethidium bromide density gradients. After centrifugation the upper and lower bands were readily visualized with UV light (365 nm). The upper band contained mainly linear and nicked circular mtDNA and contaminating nuclear DNA and was not further studied. The lower band contained covalently closed circular mtDNA. The purity of mtDNA in the lower band was analyzed by CsCl density gradient centrifugation in a model E analytical ultracentrifuge. The mtDNA was found to have a buoyant density of 1.705 g/cm^3, which was in agreement with our previously reported value (Crop Sci. 14:852, 1974). Ethidium bromide in the lower band was removed by extraction with iso-amyl alcohol and the DNA was dialyzed against TES buffer (0.1 M NaCl, 0.05 M Tris, pH 8.0, 0.01 M EDTA) for 24 hours in cold. DNA-protein monolayers for electron microscopy were prepared according to the aqueous technique described by R. W. Davis et al. (Methods in Enzymology, vol. 21, part D, p. 413, 1971). The molecules were photographed at magnifications of either 4,000 or 10,000. Measurements were made at a total magnification of 80,000 or 110,000 respectively. Calibration of magnifications was done with a replica grating (E. Fullam 2160 lines/mm).

Electron microscope examination of DNA revealed the presence of circular mtDNA in corn. Figure 1 presents the frequency distribution of the circular mtDNA. It is evident that mtDNA in corn exists as a very heterogeneous population of molecules in the young coleoptile tissue. We have not yet studied the distribution of mtDNA from leaves. The high degree of intermolecular heterogeneity makes it difficult for us to accurately determine the molecular weight of maize mtDNA. The present data suggest that the total genetic information of corn mitochondrial DNA is probably distributed amongst more than one class (based on size) of mtDNA molecules differing in molecular weight. We have arbitrarily divided the mtDNA in six principal classes with average length of 5.3, 8.8, 10.7, 12.7, 15.1 and 17.4 μ. The size distribution also suggests that there are at least two, probably three, oligomeric series of circles which are integral multiples of unit size circles. There seems to be one series of 5.3, 10.7...; a second of 8.8, 17.4...; and a third of 12.7, 24.3 μ.... Further members of these series are also present but they could not be assigned to a particular series because of overlapping that is inherently involved. Our data indicate that mtDNA of corn is different from the mtDNA of other higher plants which have been studied by R. Kolodner and K. K. Tewari (Proc. Nat. Acad. Sci. USA 69:1830, 1972), who have found circles of 30 μ in the mtDNA preparations of pea, spinach, lettuce and beans with no evidence for intermolecular heterogeneity. At present, we have no evidence that intermolecular heterogeneity in corn mtDNA is a reflection of the differential amplification of mtDNA segments despite the fact that there are several species of supercoiled mtDNA present within mitochondria. Such differential amplification of

organelle DNA has been postulated for Euglena chloroplast DNA by J. R. Mielenz and C. L. Hershberger (Biochem. Biophys. Res. Commun. 58:769, 1974), who have identified five species of covalently closed circular chloroplast DNA that differ in buoyant density.

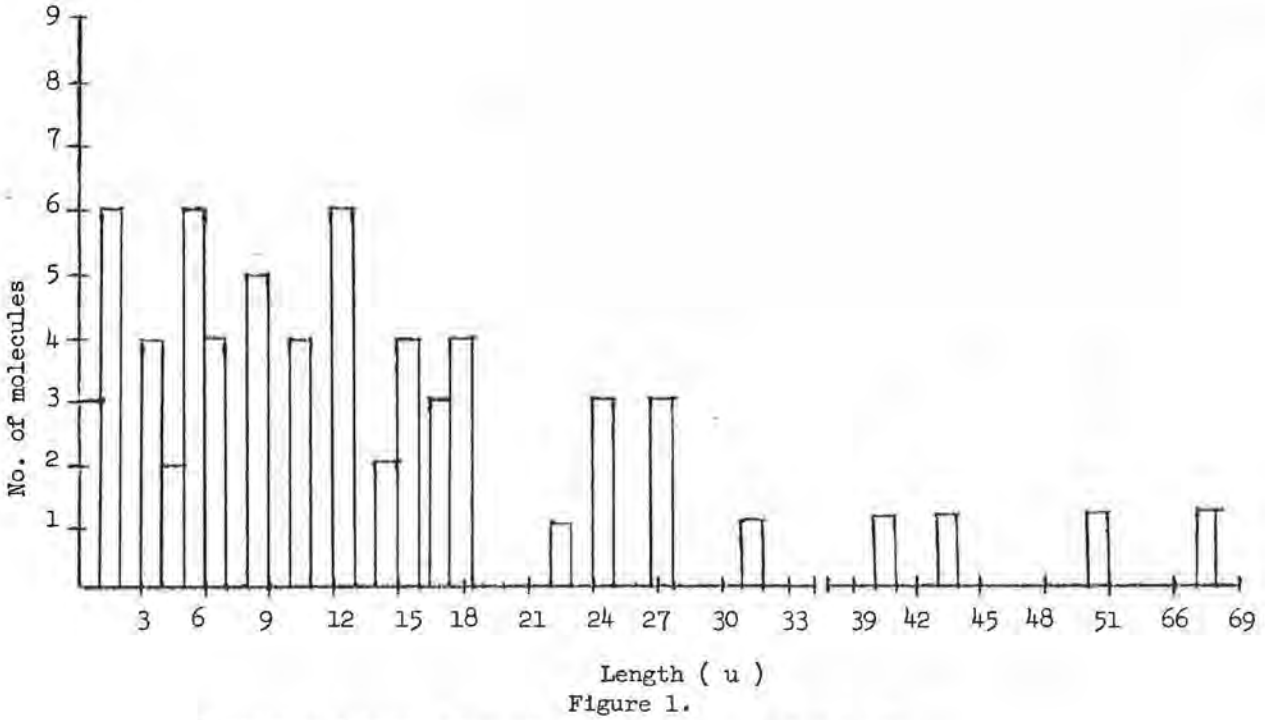


Figure 1.

Frequency distribution of circular mitochondrial DNA.

We have also observed a significant number of mini-circles in our mtDNA preparations with the average molecular lengths of 0.6, 1.7 and 3.6 μ. A fraction of these mini-circles has been found to be resistant to digestion by Eco RI restriction endonuclease. Mini-circles have also been demonstrated in mitochondria of other higher plants. The significance of these mini-circles is presently unknown.

Finally, we have identified circular molecules with attached double-stranded tails (rolling circles). The length of the tail varied from 6.4% to 880% as compared to the length of the attached circle, which varied from 1.7 to 17.9 μ. This suggests that rolling circles are a mechanism for mtDNA replication in corn and also a probable means to provide for amplification of mtDNA.

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

Preliminary genetic analysis of the maize catalase inhibitor

We have previously reported on quantitative variation of catalase inhibitor levels in several inbred lines (MGCNL, Vol. 49). We have presently screened over forty inbreds, and inhibitor levels in all can be categorized into one of three distinct groups having either high, intermediate, or low inhibitor activity. The F_1 hybrids between lines in the low and intermediate categories suggest that the low levels may be dominant to intermediate levels:

	Inhibitor Specific Activity
Line 386	21.7 U/mg
Line 399	9.4 U/mg
386 x 399	11.6 U/mg

Suitable crosses are presently being made to confirm this relationship, to further characterize the genetic relationships of the variants, and to establish any linkage relationships with the two catalase structural loci in maize.

John C. Sorenson and John G. Scandalios

Comparative biochemical properties of maize aminopeptidases

We have investigated some biochemical properties of maize aminopeptidase isozymes for comparative purposes. Maize aminopeptidases ("leucine" aminopeptidase, LAP) are the products of four diallelic loci (Scandalios, 1969, Biochem. Gen. 3:37-79), which are designated A, B, C, and D.

Figure 1 shows the relative heat stabilities of the aminopeptidases which have been separated by starch gel electrophoresis of immature endosperm extracts. The

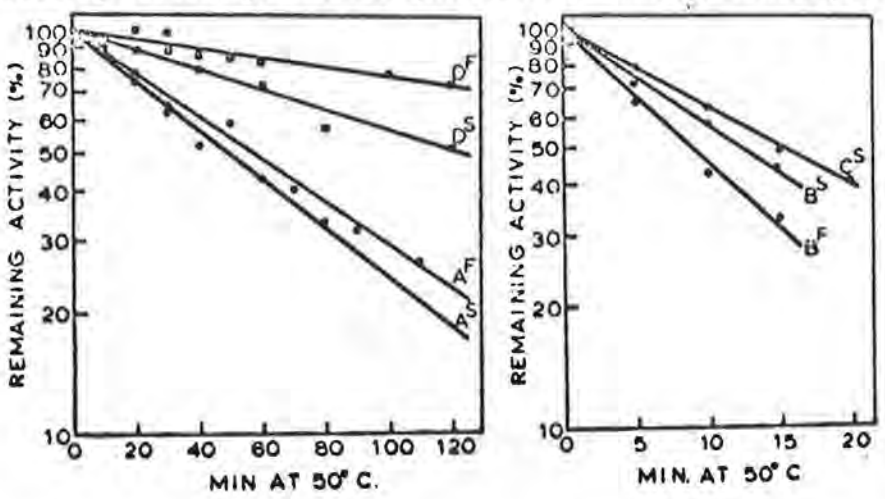


Figure 1. Relative heat stabilities of maize aminopeptidase isozymes at 50 C.

B^F, B^S, and CS forms have half-lives of approximately 9, 12, and 15 minutes at 50 C, respectively. In contrast, the A and D forms are much more heat stable. $T_{½}$ for the A forms is in the range of 55 minutes while the half-lives for the D variants are over 120 minutes at 50 C.

We have previously reported on the substrate specificities and apparent Michaelis constants for the aminopeptidase isozymes with various amino acid-naphthylamide substrates (MNL 49:145, 1975). The molecular weights of the aminopeptidases have been determined utilizing the knowledge of their differential substrate specificities. Immature endosperm extracts were applied to a calibrated G-200 Sephadex column. Ten-drop (0.61 ml) fractions were collected to maximize resolution. Aliquots of the fractions were assayed with three substrates, arginine-, alanine-, and leucine-naphthylamide for aminopeptidase activities and with benzoyl DL-arginine-naphthylamide (BANA) for maize endopeptidase activity.

Figure 2 shows the resolution of the aminopeptidase activities. Based on knowledge of the substrate specificities, the alanine-NA peak represents the D isozyme (the D forms have high activities toward alanine-NA in addition to high activities with arginine-NA). The arginine-NA peak, which coincides with the alanine-NA peak, would be less specific. Its value would be contributed to by both the A and D forms. The B and C isozymes have highest activities with leucine-NA and would constitute this peak. Zymogram patterns of column fractions are consistent with this interpretation. They show that the A isozyme elutes ahead of the B and C forms. Based on this evidence, it is clear that the arginine-NA peak represents both the A and D isozymes, which have molecular weights of 71,500. The B and C forms are 63,500, and the endopeptidase is somewhat smaller, 58,000. While

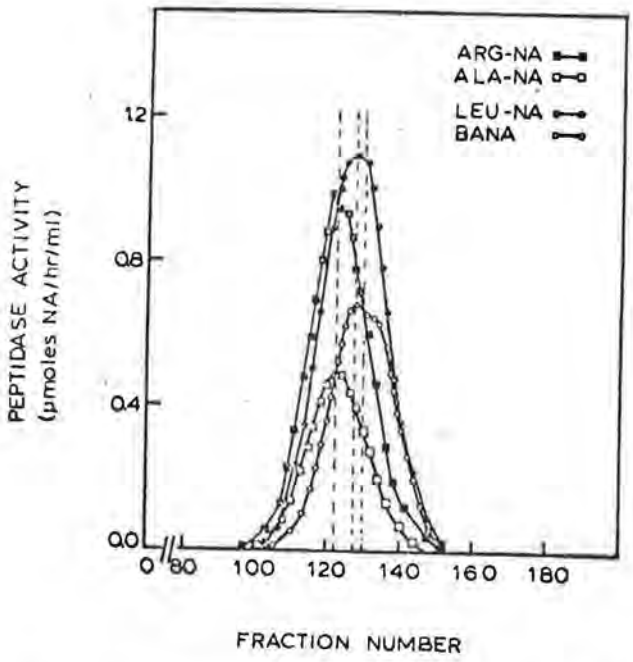


Figure 2. Molecular weight determination for maize endo- and aminopeptidases by elution from G-200 Sephadex. Dotted lines denote the peaks for the indicated activities.

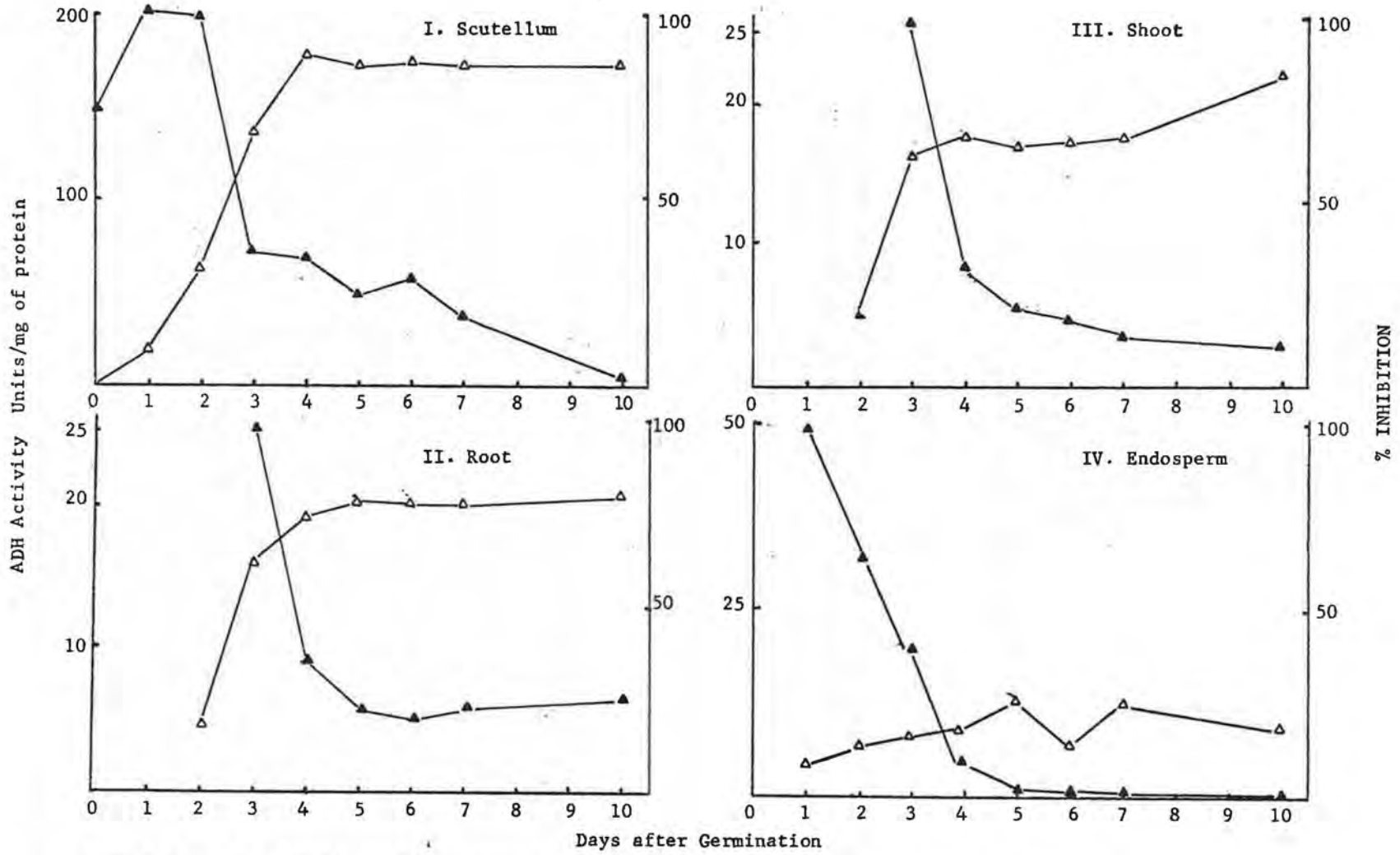
the maize aminopeptidase isozymes do overlap in specificities, they are distinct enough to show the molecular weight differences.

Lila A. Ott and John G. Scandalios

Quantitative expression of alcohol dehydrogenase (ADH) and the ADH-specific inhibitor during germination

Quantitatively, ADH in any given tissue, including the scutellum, the root, the shoot and the endosperm, declines sharply after germination (Fig. 1). Ho and Scandalios demonstrated that the decline of ADH in the scutellum is due to the increase of an endogenous ADH-specific inhibitor (Plant Physiol.56:56, 1975). Further studies suggested the regulation of ADH in the root and in the shoot follow the same scheme: the control of the degenerative process of ADH activity relies on the buildup of a specific inhibitor to the enzyme. The inhibitor activity would then maintain at a certain level after the fourth day of germination (Fig. 1). In contrast, in the endosperm, the inhibitor activity is low and does not increase significantly after germination. Presumably, the inactivation of the enzyme in this tissue preceded the formation of the inhibitor prior to kernel maturation. In fact, the enzyme level in the endosperm of dry seeds is significantly lower than that in the milky endosperm stage. The decrease of ADH activity in the endosperm during kernel development has been reported to be due to inactivation of pre-existing enzyme (D. Fischer, MNL 47:55, 1973). Control of ADH activity after germination does not rely only on the inhibitor; when 6 day-old seedlings were subjected to anaerobic conditions, ADH was found to be increased in the root and the shoot but not in the scutellum and the endosperm. Whether it is due to de novo synthesis or other activating mechanisms for ADH protein molecules is not yet known. Correlations between the anaerobic "induction" and inhibitor levels are being investigated.

Yiu Kay Lai and John G. Scandalios



1 unit = $0.01 \Delta O.D._{340}/min$ (All Enzyme assays and Inhibitor assays are performed as described, Ho and Scandalios, Plant Physiol. 56:56, 1975)

THE PENNSYLVANIA STATE UNIVERSITY
Department of Horticulture, University Park, Pennsylvania

Phenotypic dosage effects of the ae and wx loci on mature kernel phenotype

C. W. Moore and R. G. Creech (MGCNL 43:140) reported that Ae ae ae wx wx wx kernels were tarnished waxy in appearance and smaller than either Ae Ae ae wx wx wx or Ae Ae Ae wx wx wx kernels but distinguishable from partially shrunken ae ae ae wx wx wx kernels. In studies of the interaction of these two loci, we have now observed all 16 endosperm genotypes of the dosage series. The W64A inbred (Ae Ae Wx Wx) and the ae, wx, and ae wx backcross conversions (backcrossed 9, 9 and 4 times respectively) were self-pollinated and crossed in all possible combinations. Phenotypes of the mature kernels are given in Table 1 using the terminology of Garwood and Creech (Crop Sci. 12:119, 1972).

Table 1. Effect of increasing doses of ae and wx upon mature kernel phenotype.

Doses of wx	Doses of ae			
	0	1	2	3
0	Full[a] Translucent	Full[a] Translucent	Full[a] Translucent	Semi-collapsed Tarnished[c]
1	Full[a] Translucent	Full[a] Translucent	Full[a] Translucent	Semi-collapsed Tarnished[c]
2	Full[a] Translucent	Full[a] Translucent	Semi-collapsed Tarnished	Collapsed Tarnished
3	Full[b] Opaque	Full[b] Opaque	Semi-collapsed Tarnished	Shrunken Translucent to glassy

[a]Normal appearing.

[b]Waxy appearing.

[c]Typical ae in appearance

Eight genotypes were normal in appearance as expected. Ae Ae Ae wx wx wx and Ae Ae ae wx wx wx had the typical waxy phenotype. The double mutant kernels were shrunken. We have observed that the phenotypes of these genotypes converted to W64A are often more extreme than observed in other backgrounds. In addition, phenotypes may be more extreme than typically encountered by other researchers due to cooler growing conditions encountered in Pennsylvania compared to other corn growing areas.

Dosage effects were apparent in the Ae ae ae wx wx wx, Ae ae ae Wx wx wx, and ae ae ae Wx wx wx genotypes. Appearance of Ae ae ae wx wx wx agrees with the observations of Moore and Creech. The Ae ae ae Wx wx wx genotype was clearly distinguishable from normal appearing genotypes and approached the ae ae ae Wx Wx Wx phenotype. The ae ae ae Wx wx wx genotype was clearly distinguishable from ae ae ae Wx Wx wx and ae ae ae wx wx wx. Similar dosage effects were observed in physicochemical examination of the starches of these 16 genotypes.

Dosage effects can be seen in material homozygous for either ae or wx; however, such effects are not apparent in material homozygous for Ae or Wx. Our observations coupled with other published studies of dosage effects involving other

endosperm mutants suggest that the majority of maize endosperm mutants considered to be dominant will exhibit dosage effects if observed when appropriately selected endosperm mutants are present as homozygous recessives.

D. L. Garwood, C. D. Boyer and J. C. Shannon

Sweet corn breeding questionnaire summary

Information has been compiled concerning (1) maintenance of publicly released su inbreds, (2) maintenance of publicly released du, sh2, and su2 inbreds in sweet corn backgrounds, (3) open pollinated sweet corn (su) variety maintenance, and (4) mutant genes being incorporated by backcrossing into sweet corn inbreds and varieties. Copies of the summary are available upon request. Information from individuals not previously contacted would be appreciated.

D. L. Garwood

PIONEER HI-BRED INTERNATIONAL, INC.
Mankato, Minnesota

Progress report on lethal leaf spot (lls)

Dr. A. J. Ullstrup and I reported (Phytopathology 57:1282, 1968) a recessive lethal leaf spot whose lesions resemble H. carbonum race 1. The target-shaped lesions (concentric rings) begin on older leaves at the 5 or 6 leaf stage then spread and enlarge to kill the plant just before or shortly after pollen shed. Our efforts at Mankato on the trait since that report are as follows:

1. We have made allelism tests with hm. Because of the similar phenotype, we made tests with the recessive gene for susceptibility to H. carbonum race 1 in the presence of the disease. F_1 plants were normal and the two genes segregated with normal in F_2, indicating they are non-allelic.
2. We have successfully selected for longer living plants. After ten years of selection, all lls plants shed pollen well; some even produce a few silks, but none have set seed. Our goal is to be able to maintain the stock by selfing.
3. We have tested two new sources of lls and found them to be allelic to the original. The first new source was also from Mankato (we do not think it was a contaminant) out of a background involving a cross of Oh43 by a Pioneer synthetic. The other new source (from Dr. D. N. Duvick of our organization) was in two or more stocks that had Confite Puneno (from Bolivia) in common. The Confite Puneno source dies before shedding, the original dies at about time of shed, and the Oh43 source usually sheds before dying. These differences in time of death are presumed to be due to modifiers that may also condition non-lls stocks.
4. We are trying to map lls. Dr. C. R. Burnham graciously provided 22 translocation stocks. Progenies of T1-3(5883) and T1-3(5982) deviated from expected backcross ratios (p=.05-.02), indicating that lls is probably located on the short arm of chromosome one. Dr. R. J. Lambert provided marker stocks for chromosome one. Backcross ratios with bm2 (at the far end of the long arm) did not deviate significantly (p=0.30) from 1:1:1:1. Two attempts to set up a three point test with br and sr have failed; we have not yet produced the double mutant (lls, sr) let alone the triple mutant. Perhaps lls is very close to sr or perhaps they are incompatible. We will keep trying.
5. We have observed other mutants from the Confite Puneno lls source, including: Pale green or yellowish seedlings that become normal colored when 2 or 3 feet tall, governed by a single recessive gene; double tassels due to a branched stem (usually above the ear), inheritance unknown; and a lethal leaf spot stripe occurring on three or four leaves (one stripe per leaf), usually including the ear leaf (the stripes are 1/8 to 1/2" wide, have straight edges, and contain lethal

leaf spots; if not classified early, the leaf splits and the stripe is not noticeable). The pale green seedlings and double tassels have shown up in progenies involving lethal leaf spot stripe, whose inheritance is not yet known.

6. We have sent seedstocks of lls to the Maize Coop.

A. Forrest Troyer

THE UNIVERSITY OF RHODE ISLAND
Department of Botany, Kingston, Rhode Island

Non-Mendelian inheritance of an aleurone pigment inhibitor

In the progeny of a cross between a C Sh bz-x3m Wx/C Sh bz-x3m Wx ear parent and a C sh bz wx tester stock, colorless kernels and kernels variegated for bz-x3m and colorless tissue were produced. The numbers on the main stalk ear were 221 bz-x3m, 84 variegated and 58 colorless, and on a tiller ear, 167 bz-x3m, 81 variegated and 21 colorless.

Among the progeny of the reciprocal cross in which the bz-x3m stock was used as the pollen donor, no variegated or colorless kernels were observed. It was suspected that the factor responsible for the mutant phenotype was cytoplasmic rather than nuclear since it appeared to be transmitted only through the female gametophyte.

Some of the colorless, variegated and bz-x3m sibs were planted this past summer and used in a number of different crosses. Table 1 lists the progeny obtained when these individuals were used as female parents. From the first two crosses it

Table 1. Progeny obtained in self pollinations or out crosses of colorless individuals and their variegated or full color sibs when used as female parents.

Cross	Parental phenotype	Progeny phenotypes		
		Full color	Variegated	Colorless
4322-2 self	colorless	186	*	235
4322-4 self	colorless	141	19	209
4317-3 self	variegated	273	*	120
4318 self	variegated	102	*	237
4316-2 x 4068a	variegated x bronze	312	115	29
4316-3 x 4068a	variegated x bronze	365	*	23
4319-6 x 4068a	bz-x3m x bronze	368	*	176
4320 x 4068a	bz-x3m x bronze	336	140	45
4316-1 x 3991s	variegated x red	299	98	4
4322 x 4068a	colorless x bronze	383	*	20

*On some ears where the full color pigment was bronze, the full color and variegated phenotypes were difficult, if not impossible, to distinguish; in these cases both types are listed under full color.

can be seen that the colorless trait is not true breeding, a pattern which would be expected if the factor responsible were cytoplasmic. Full color and mosaic kernels as well as colorless ones appear in the progeny of self pollinated colorless individuals but in no apparent ratio. Similar results were obtained in self pollinations of the variegated types. In crosses of either the colorless or variegated individuals with a bronze stock, the colorless and mosaic phenotypes segregated but at an apparently low frequency.

When full color bz-x3m sibs of the colorless types are used as female parents in outcrosses to a bronze stock, the colorless and variegated phenotypes appear

among the progeny in varying numbers, sometimes as high as in self pollinations of variegated individuals.

In crosses of colorless or variegated females with red (Bz) males, the colorless and mosaic phenotypes appear but at much lower frequencies than in self pollinations or outcrosses to bronze. One example (4316-1 x 3991s) is included in Table 1. In some cases, no colorless kernels and only a few variegated ones are observed.

In reciprocal crosses using the colorless or variegated individuals as pollen donors, the appearance of colorless or variegated progeny does in fact occur but is dependent upon the stock used as the ear parent. Of three different bronze families used as females in these crosses, one exhibited the colorless character but the other two produced only full color progeny. The one red stock employed as a female parent yielded only the full color phenotype in the offspring.

When transmission of the character through the pollen is observed, it occurs in unpredictable ratios as in the reciprocal crosses. These inheritance patterns indicate that a cytoplasmic factor is apparently not responsible for the colorless trait.

When the mutant phenotype first appeared, it was thought that bz-x3m was somehow involved because of the color/colorless mosaics. Such kernels indicate an instability of some sort. This relationship, however, does not exist since ears have been recovered which segregate for the colorless and variegated phenotypes but which cannot contain bz-x3m or an element derived from it. The same results indicate that transmission of the colorless phenotype does not necessarily involve sexual reproduction. These observations are described below. Among the offspring of plants which were not related to the colorless individuals but which were in the same field, colorless and variegated kernels appeared. These progeny were from self or sib pollinations of several C sh bz wx lines and from crosses of these lines to other full color stocks. The colorless and variegated frequencies were generally not as high as in progeny of mutant individuals and varied substantially from one ear to another. There appeared to be no relationship between the location of a plant in the field with respect to the colorless types and the frequency of colorless or variegated kernels on the ear. In many cases, fertilization by mutant pollen could be thoroughly ruled out since some of these lines flowered after the colorless stocks and their relatives had completely shed their pollen.

It was also noted that colorless kernels were appearing in a number of open pollinated plants which were homozygous for full color genes. Since there were no stocks in the field carrying C-I, it was concluded that the same factor responsible for the colorless trait in the controlled pollinations was producing white kernels in the open pollinated individuals.

The transmission patterns of the colorless trait suggest that a virus may be responsible. If this proves to be the case, there are two mechanisms which could explain the colorless phenotype. Either the virus has the ability to somehow block the metabolic pathway leading to anthocyanin production in the aleurone; or it carries genetic information for pigment inhibition which is becoming incorporated into the maize genome.

Identification of a virus as the agent and distinction between the two possibilities await further data.

John P. Mottinger

UNIVERSIDADE DE SÃO PAULO
Instituto de Genética, São Paulo, Brazil

A preliminary study on chiasmata frequency in two races and two single hybrids of maize

Variability in a maize population is known to be due to many factors, one of the most important of which is the recombination which is basically determined by

chiasmata. There are many studies on chiasmata frequencies in maize, but they are limited to the effects of systems of breeding and the effect of environment (V. Grant, Cold Spring Harbor Symp. Quant. Biol. 23:337, 1958; W. F. Bodmer and P. A. Parsons, Adv. Genet. 11:40, 1962; S. K. Sinha and A. P. Rao, Cytologia 32:343, 1967).

Seeds of two races and two single crosses of maize were planted in December, 1974, at the Instituto de Genética, ESA "LQ". They were Entrelaçado, an indigenous race; Canario de Ocho, an ancient commercial race; IAC-HS-7.777, a single cross from the Tuxpeño race; and IAC-HS-1.227, a single cross from the Cateto race. Anthers from these plants were collected in February, 1975, fixed in acetic alcohol 1:3 and smeared in propionic-carmin; permanent slides were made, and chiasmata were counted in the permanent preparations. Five plants of Entrelaçado, six plants of Canario de Ocho, seven plants of IAC-HS-1.227 and five plants of IAC-HS-7.777 were studied. Fifty cells at diakinesis and twenty cells at metaphase from each plant were examined. Analysis of variance was made according to G. S. Snedecor and W. G. Cochran (Statistical Methods, 6th ed., Ames: Iowa St. Coll. Press, 1967), with the data transformed in square roots.

Races of maize in the area of the Brazilian Germplasm Bank have been studied by F. G. Brieger et al. (Nat. Acad. Sci. Nat. Res. Council Pub. 593, 1958) and classified by Paterniani (Races of Maize in Brazil, unpublished paper, 1975) into four categories: indigenous, ancient commercial, recent commercial and exotic races. He defined indigenous races as corn which has been cultivated only by Indians; presumably, these races have been maintained in approximately the same state as in pre-Columbian times and have not been greatly disturbed by the influence of people who arrived after 1492. To this category belongs one of the races studied, Entrelaçado. Paterniani's second category, ancient commercial, was defined by Paterniani as races of corn that existed in pre-Columbian times but were adopted from the Indians by the early European immigrant farmers; these races are indigenous in their region but presumably have been changed somewhat by their recent large scale cultivation and probably do not represent precisely the population present in pre-Columbian times. To this category belongs the race Canario de Ocho and the single cross IAC-HS-1.227, which was developed at the Instituto Agronômico de Campinas from Cateto germ plasm. Races of maize in Mexico have been classified by E. J. Wellhausen et al. (Razas de maiz en Mexico. Folleto Tecnico nº 5, Secretaria de Agricultura y Ganaderia. Mexico, 1951) in five categories: ancient indigenous, pre-Columbian exotic "Mestice", pre-historic, incipient modern and not well defined races. It has been suggested that the ancient indigenous races originated in Mexico from primitive popcorn and that they developed independently in different places and different environments. The representatives of these races did not hybridize since they came from a common ancestor. Pre-Columbian exotic races were introduced in Mexico from Central and South America in pre-historic times. The pre-historic "Mestizas" race originated from hybridization between ancient indigenous races and pre-Columbian exotic races. The Tuxpeño race belongs to this category, and IAC-HS-7.77 is a single cross from Tuxpeño which was developed at the Instituto Agronômico de Campinas.

The mean of the frequency of chiasmata, standard deviation, mean standard error and coefficient of variability in these different germplasms at diakinesis (50 cells) and metaphase (20 cells) are presented in Table 1; the analysis of variance is shown in Table 2. It can be seen that the differences between the germ plasms and also among the plants within races are significant. These results are in accord with other reports, which show also that the frequency of chiasmata in maize is highly affected by environment as well as by gene factors (Grant, 1958; Sinha and Rao, 1967). The general mean of the frequency of chiasmata in different germplasms at diakinesis and metaphase can be seen in Table 3. A Tukey test was performed at the 5% level; its significance can be noted in Table 4. Entrelaçado differs from IAC-HC-1.227 at both diakinesis and metaphase. What is worthy of mention here is that the two races showed lower frequencies than the single

Table 1. Number of cells counted at diakinesis and metaphase (N), mean ($\bar{x}$), standard error (s), mean standard error ($s_{\bar{x}}$) and coefficient of variability (CV).

Plant		N	$\bar{x}$	s	$s_{\bar{x}}$	CV
			IAC-HC-7.777			
1	Diak	50	16.53	0.97	0.14	5.88
	Meta	20	13.82	0.82	0.17	6.02
2	Diak	50	17.20	0.87	0.12	5.07
	Meta	20	13.15	0.37	0.08	2.84
3	Diak	50	17.22	0.69	0.09	4.03
	Meta	20	13.85	0.36	0.08	2.64
4	Diak	50	17.28	0.44	0.06	2.58
	Meta	20	13.65	0.49	0.11	3.58
5	Diak	50	17.14	0.89	0.12	5.14
	Meta	20	13.50	0.51	0.11	3.79
			IAC-HS-1.227			
1	Diak	50	18.24	0.79	0.11	4.36
	Meta	20	15.15	0.36	0.08	2.58
2	Diak	50	18.44	0.86	0.12	4.69
	Meta	20	14.35	0.48	0.10	3.40
3	Diak	50	18.92	0.72	0.10	3.82
	Meta	20	14.15	0.36	0.08	2.58
4	Diak	50	19.08	0.90	0.13	4.72
	Meta	20	14.15	0.37	0.08	2.59
5	Diak	50	19.50	0.73	0.10	3.77
	Meta	20	12.40	0.50	0.11	4.05
6	Diak	50	17.32	0.76	0.11	4.49
	Meta	20	14.10	0.30	0.04	2.18
7	Diak	50	18.60	0.63	0.09	3.41
	Meta	20	14.15	0.36	0.08	2.58
			ENTRELACADO			
1	Diak	50	13.12	1.10	0.15	8.38
	Meta	20	10.83	0.62	0.14	5.88
2	Diak	50	15.54	0.50	0.07	5.32
	Meta	20	11.89	0.56	0.11	4.76
3	Diak	50	17.42	0.92	0.13	5.32
	Meta	20	12.70	0.47	0.11	3.70
4	Diak	50	17.74	0.66	0.09	3.74
	Meta	20	11.90	0.31	0.07	2.58
5	Diak	50	19.22	0.81	0.11	4.20
	Meta	20	11.95	0.05	0.25	1.87

Table 1.—continued.

Plant		N	$\bar{x}$	s	$s_{\bar{x}}$	CV
			CANARIO DE OCHO			
1	Diak	50	14.25	0.59	0.08	4.17
	Meta	20	13.76	0.43	0.10	3.17
2	Diak	50	15.89	0.77	0.11	4.89
	Meta	20	13.20	0.41	0.09	3.10
3	Diak	50	16.32	0.62	0.09	3.82
	Meta	20	13.15	0.37	0.08	2.84
4	Diak	50	16.45	0.50	0.07	3.03
	Meta	20	13.10	0.30	0.04	2.34
5	Diak	50	16.77	0.42	0.06	2.51
	Meta	20	13.80	0.41	0.09	2.91
6	Diak	50	17.88	1.08	0.15	6.05
	Meta	20	12.05	0.22	0.05	1.85

Table 2. Analysis of variance.

Sources of variation	d.f.	S.S.	M.S.
	Diakinesis		
Among races	3	20.95	6.99**
Among plants/races	19	25.17	1.32**
Among cells/plants/races	1.127	155.27	0.14
Total	1.149	20.39	
	Metaphase		
Among races	3	5.39	1.79**
Among plants/races	19	2.68	0.14**
Among cells/plants/races	437	1.74	0.004
Total	459	9.81	

Table 3. General mean in both phases.

	Number of plants	Diakinesis	Metaphase
(1) IAC-HS-7.777	5	17.13	13.59
(2) IAC-HS-1.277	7	18.56	13.92
(3) Entrelaçado	5	16.61	11.85
(4) Canario de Ocho	6	16.27	13.18

Table 4. A Tukey test among the four germplasms.

	Diakinesis			Metaphase		
	2	3	4	2	3	4
1	NS	NS	NS	NS	NS	NS
2		*	*		*	NS
3			NS			NS

crosses — the mean was 16.61 in Entrelaçado and 16.27 in Canario de Ocho, whereas the means of the two single crosses were 17.13 and 18.56. This fact may be interpreted to mean that evolution has brought together in these primitive races gene combinations that have a particularly high adaptive value in a given situation (G. L. Stebbins, Chromosomal Evolution in Higher Plants, Reading, Massachusetts: Addison Wesley, 1971). Paterniani reported that Entrelaçado has some primitive characteristics which date back to the very early days of domestication, and he considers this race a stable one. Indeed, he states that plantings made in Piracicaba from this race with seeds collected from the Indians have always resulted in plants showing definite signs of lack of adaptation.

In Entrelaçado there is seen also a phenomenon that may support the above mentioned proposal: it is the only race which exhibits a notable difference between the maximum and minimum chiasmata frequencies at diakinesis (19.22/cell in one plant and 13.12/cell in another). Such a wide difference is not seen in other races, and it may be that a buffering system has evolved which maintains adaptability to the environment through the mechanism of chiasmata formation; such a system could persist for a long time, given the genetic isolation of this race. That is, that race has a kind of polymorphism enabling the population to always have individuals with a low or a high frequency of chiasmata formation.

Table 5. Terminalization index.*

Race	Number of cells observed	Index
IAC-HS-7.777	250	1.35
IAC-HS-1.227	250	1.38
Canario de Ocho	250	1.31
Entrelaçado	250	0.98

*According to Darlington, C. D. , Recent Advances in Cytology, 2nd ed., Philadelphia: Blakiston, 1937.

Table 5 shows the terminalization index of the germplasms, calculated on data from the first five plants from each source listed in Table 1. The notably low level (0.98) of terminalization in the Entrelaçado race contrasts with a figure of 1.3 in other races and reveals a high level of homozygozity, a fact that may be explained by the isolation of this race. It is believed that this race exists today with a genetic constitution similar to that which it displayed in pre-Columbian times.

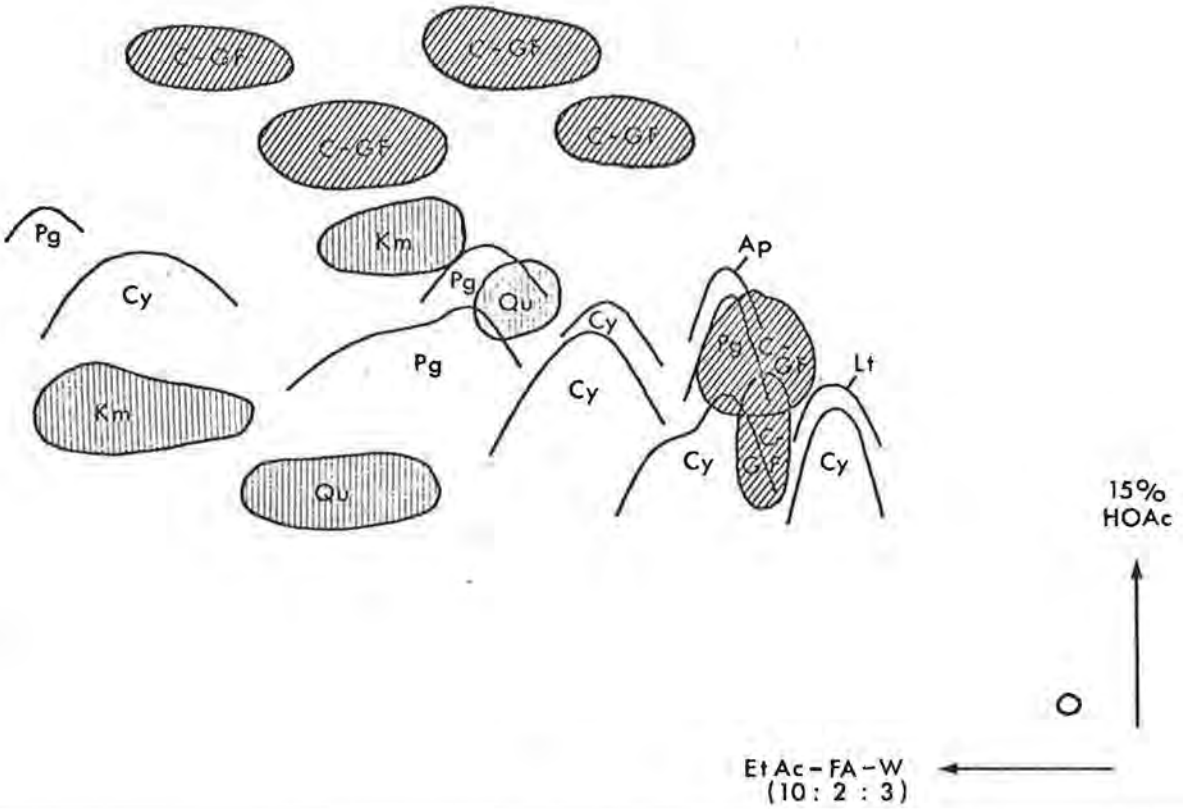
N. M. Nassar* and M. R. Alleoni
*Present address: Universidade Federal de Goiás, Instituto de Ciências Biologicas, Goiania-Goiás

UNIVERSITY OF VICTORIA
Department of Biology, Victoria, B. C., Canada

Flavonoids in maize seedlings

W22 stocks carrying known combinations of pigmentation genes have been characterized by thin-layer chromatography for the presence of flavonoids in seedlings (see figure). We are also screening other lines carrying the same gene combina-

Flavonoids in maize seedlings (two leaf stage). Tissue extracted in 1% HCl in MeOH and the flavonoids separated by two-dimensional thin-layer chromatography. Representative chromatogram of flavonoids in seedlings of genotype A A2 C C2 R-r P Bz Bz2 sm pr In.



CGF: C-Glycosylflavones

Flavonols: Qu = Quercetin glycosides; Km = Kaempferol glycosides

Anthocyanins: Cy= Cyanidin glycosides; Pg= Pelargonidin glycosides
Lt= Luteolinidin glycoside; Ap= Apigeninidin glycoside

tions to be sure we are analyzing for gene-specific compounds. So far, we can report the following:

P: required for presence of C-glycosyl flavones. P-RR seedlings have traces of 3-deoxyanthocyanins; P-WR and P-RW have C-glycosyl flavones only. Some stocks designated P-WW have traces of C-glycosyl flavones in the seedlings, but close examination of the pericarp of such stocks shows some weak pigmentation, indicating that the alleles are not true amorphs. In general, the C-glycosyl flavone concentration in the seedlings is a good indication of P locus potential.

R or B (alleles that give seedling pigment): required for flavonols and 3-hydroxyanthocyanins. Concentrations of these two classes of flavonoids vary together in most stocks, according to the level of R or B action. So far we have found only one stock (of unknown genotype with respect to pigmentation genes) that has anthocyanins but not flavonols in the seedlings.

A: required for all anthocyanins. The intermediate alleles A-d and a-p have reduced amounts of anthocyanins relative to the concentration of flavonols; a stocks have no anthocyanins at all.

A2: required for 3-hydroxyanthocyanins.

Bz: required for flavonols and 3-hydroxyanthocyanins. Traces of leucocyanidin and 3-deoxyanthocyanin (5-glycosylated) are found in bz P-WR seedlings. We have not yet tested a bz P-WW combination to see if the 3-deoxyanthocyanins are formed independently of the P locus action.

Sm: P-WR sm stocks have traces of 3-deoxyanthocyanins, whereas P-WR Sm stocks have none.

c2-Idf: the c2-Idf allele in our W22 stocks prevents the formation of all flavonoids.

Pr: all flavonoids are predominantly 3',4' hydroxylated in Pr stocks, although traces of 4' hydroxylated compounds are usually present also. Seedlings of pr stocks vary as to the relative proportions of 3',4' and 4' compounds, but most have approximately equal amounts of both.

Oldriska Ceska and E. Derek Styles

UNIVERSITY OF WINNIPEG
Biology Department, Winnipeg, Manitoba, Canada

The effect of B chromosomes on chiasmata

Last year I reported on the influence of K10 on the total chiasmata at metaphase I and the distribution of the exchanges. It was indicated that K10 increased the total number of chiasmata and that proximal exchanges increased at the expense of distal exchanges.

The same procedure was used to determine the effect of B chromosomes on chiasma distribution. Sporocytes were taken from a line with mainly 0B and 1B plants, and chiasma counts were made on ten cells in seven plants of each of 0B and 1B groups. A chart was constructed with schematic representations of tetrads having various numbers of proximal and distal exchanges, and a count made of the number of each of the tetrad types; an average was obtained for the number of distal, proximal and total chiasmata for each plant. Statistical analyses were by means of t tests (Table 1).

Table 1. Effect of B's on chiasmata.

	Average chiasmata per cell			Total number of chiasmata		
	distal	proximal	total	distal	proximal	total
0B	9.41	9.54	19.0	659	668	1327
1B	7.50	12.50	20.0	526	873	1399
P	<.01	<.001	<.001			

U. W. Ayonoadu and H. Rees (Genetica 39:75, 1968) were the first to report the enhancement effect of B chromosomes on chiasma frequency in maize. Their results have been repeated here and extended to demonstrate a shift of exchanges from distal to more proximal regions. These observations are not unexpected, as they agree with recombination data. However, only a few regions have been tested genetically, and different responses could occur throughout the genome. The individual tetrads remain unidentified; but, as with the K10 results, it is suggested that all chromosomes are affected by the presence of the B's.

Thus, both B chromosomes and K10 increase chiasma frequency and redistribute chiasmata from distal to more proximal regions.

Ed Ward

UNIVERSITY OF WISCONSIN
Laboratory of Genetics, Madison, Wisconsin

Previously unreported wx heteroalleles

Since the last reported map of the wx locus (Genetics 60:507, 1968), some previously unreported mutations have been mapped. These are the mutations K, L, M, BL2, Stonor and B3. In addition, more extensive data are available for mutations B2, B4, B7, C31 and C34.

The mutations K, L and M occurred as spontaneous mutations in inbred lines of the Bear Hybrid Corn Company of Decatur, Illinois. The BL2 mutation is a presumptive EMS-induced mutation detected by R. W. Briggs, who was then at Brookhaven National Laboratory. The Stonor mutation was found in maize collected in Assam and was received from Edgar Anderson. The B3 mutation, obtained from R. A. Brink, is an autonomous mutable allele that resulted from the association of Mp (Ac) with a functional allele at the wx locus; the rate of germinal reversion is sufficiently

low that its position can be mapped. It cannot be mapped with respect to the Ds-controlled mutations m-1 and m-6, since it induces a high frequency of somatic and germinal reversions to Wx in these mutants; it was this observation which first drew attention to the fact that B3 was carrying Mp (Ac). B3 also induces a high rate of reversion in B4, which was thereby identified as a Ds-controlled mutant.

The frequencies of Wx pollen grains in crosses between wx heteroalleles are given in Table 1. The total population of pollen grains scanned is not given, although the number of plants sampled is noted. There were a minimum of 35,000 and a maximum of about 75,000 pollen grains per slide. A revised map of the wx locus based on these data plus those given in the 1968 Genetics paper is presented in Figure 1; the map is constructed as previously. The knowledge from conventional genetic experiments that the site of C is distal to the site of 90 and proximal to the site of H21 forms the starting point for construction. The pertinent datum for the F_1 between two heteroalleles is whether or not recombination is observed. A Wx frequency of less than 1.5×10^{-5} is interpreted as evidence that two alleles do not recombine. As previously, the map is constructed as a complementation map to emphasize the apparent length of many of the mutants. If the lines depicting the locations of two mutations overlap, the mutations do not recombine; if not, recombination takes place.

The revised map of the locus is not much different than that presented in 1968. It is still not clear whether m-6 is located proximal or distal to C.

The mutations B7 and C34, which appear to cover virtually all other mutations, have now been tested with a number of other mutations. Only B7 and C31 recombine (and at a low frequency); neither B7 nor C34 recombines with any other mutant against which it has been tested.

The paucity of lines in the area of the map subtending C1 may indicate a misplacement of this allele. It shows recombination with every allele with which it has been tested except B7 and C34. It was placed in its present position because such a position best fitted the Wx frequencies observed in heteroallelic combinations with various other wx alleles. It will not be certain that C1 is correctly placed until an allele is found that is non-recombining with both R and C1 or with both C1 and F. If it is correctly placed, there is an interesting discontinuity in this area.

In addition to the controlling element alleles m-1, m-6 and m-8, which were placed on the 1968 map, two more controlling element alleles, B3 and B4, have been placed.

In an effort to make the map as complete as possible, the mutation BL2 has been placed tentatively on the basis of preliminary crosses. It should be pointed out that BL2 has not been crossed by m-6R. It is known to recombine with B but has not been tested with the other alleles that do not recombine with B. Two other mutants, BL1 and BL3, isolated by Briggs, have also been investigated. BL1 is apparently a slightly leaky mutant (synthesizes some amylose) and produces pollen grains that stain more deeply than the usual waxy pollen. It is therefore difficult to use in pollen analysis and has been set aside. BL3 is non-recombining with B but does recombine with BL2, C, F, R and H21.

M recombines at a low frequency with F, but has not been tested against C or BL2. For this reason its distal terminus is indicated by a dotted line indicating uncertainty.

Table 2 presents data for crosses between heteroalleles that have been made for the second time. Overall the results show generally good agreement, but in two crosses, B x B8 and B6 x B8, it would have been estimated from the original cross that there was a low rate of recombination between the alleles. The second time that these crosses were made and sampled, the results would have indicated no recombination between B8 and either B or B6.

Table 1. The mean Wx frequency (per 10^5) in the pollen of crosses between wx heteroalleles.

Hybrid	Year	Wx frequency ± $s_{\bar{x}}$	Plants No.
K/			
R	68GH	0	4
	68F	0	6
F	68F	5.7 ± 1.5	6
B	68GH	40.0 ± 11.2	5
	68F	31.0 ± 5.8	7
H	69F	0.4 ± 0.8	7
C1	69F	11.0 ± 1.3	6
J	69F	0	6
L	69F	31.0 ± 4.3	7
M	69F	4.3 ± 0.8	6
m-8	70F	0	9
I	70F	0.4 ± 0.2	10
H21	70F	0.5 ± 0.3	8
m-1	70F	19.0 ± 2.1	6
F	70F	25.0 ± 3.9	7
B7/			
C31	69GH	3.0 ± 0.8	5
	69F	1.3 ± 0.5	6
B	69GH	0.3 ± 0.3	6
90	69GH	0	2
B1	69GH	0	4
B6	69GH	0.3 ± 0.3	6
C	69F	0	4
C1	71F	0	9
H21	71F	0.6 ± 0.3	8
B4/			
C2	69F	1.2 ± 0.5	8
C3	69F	5.3 ± 0.9	6
m-8	69F	1.6 ± 0.5	8
M/			
R	68GH	15.0 ± 3.9	6
F	68GH	1.6 ± 1.0	5
	71F	2.2 ± 0.7	7
	72F	2.8 ± 0.9	7
B	68GH	0	4
C1	72F	2.7 ± 1.4	7
B1	69F	0.3 ± 0.3	7
B6	69F	0	7
B8	69F	0.6 ± 0.3	8
90	70F	0	9
m-6R	70F	4.6 ± 1.1	8
	71F	1.4 ± 0.6	7
	72F	2.7 ± 0.9	7
C4	71F	1.8 ± 0.7	5
C31	71F	0	10
m-1	71F	5.1 ± 1.1	7
L/			
R	68GH	20.0 ± 3.4	6
	68F	8.0 ± 2.7	7
F	68GH	1.0 ± 0.7	7
	68F	1.8 ± 0.7	7
B	68GH	0	5
90	69F	0.3 ± 0.3	6
m-6R	69F	4.6 ± 0.8	8
B1	69F	0.5 ± 0.4	6
C1	70F	23.0 ± 1.7	7
B6	70F	1.1 ± 0.3	8
C4	71F	0	3
C	71F	28.0 ± 5.6	8
C31	71F	3.6 ± 1.2	10
B8	71F	6.3 ± 1.3	10
B7	70F	0.5 ± 0.3	8
C31/			
m-6NR	68F	22.0 ± 8.8	7
	69GH	16.0 ± 3.6	6
B	68GH	1.0 ± 0.9	5
	69GH	0.8 ± 0.5	6
90	68GH	1.1 ± 0.7	6
	69GH	0	11
B1	68F	5.7 ± 0.4	7
	71F	5.5 ± 1.3	8
B6	69GH	0	9
B8	68F	2.3 ± 0.6	7
	69GH	2.5 ± 1.2	6
	71F	2.9 ± 0.5	10
C4	71F	20.0 ± 4.2	8
B2/			
J	69F	1.3 ± 0.7	7
H	69F	2.0 ± 1.1	3
B4	69F	10.0 ± 2.4	6
C2	69F	1.3 ± 0.5	8
C3	69F	0	7
m-8	69F	0	8
B3/			
H21	71F	3.9 ± 1.2	8
R	71F	0.9 ± 0.5	9
m-8	71F	1.6 ± 0.5	9
C2	71F	1.6 ± 0.4	7
C3	71F	0.1	10
B2	71F	6.6 ± 2.3	10
H	71F	8.7 ± 2.0	9
	72F	8.0	6
I	71F	1.1 ± 0.4	9

Table 1.--continued

Hybrid	Year	Wx frequency ± $s_{\bar{x}}$	Plants No.	Hybrid	Year	Wx frequency ± $s_{\bar{x}}$	Plants No.
C34/				Stonor/			
B2	68GH	0.3 ± 0.3	6	C31	71F	10.7 ± 1.7	9
	68F	0.9 ± 0.6	7	C34	69GH	0.1 ± 0.1	6
B4	68GH	0.3 ± 0.3	6	C1	69GH	2.9 ± 1.5	5
	68F	0.2 ± 0.2	7		69F	5.1 ± 1.2	6
I	68GH	0.8 ± 0.4	6	90	69GH	6.4 ± 2.1	5
F	68GH	0	5	B	69GH	0.4 ± 0.4	5
	68F	0.2 ± 0.3	7	B1	69GH	10.0 ± 2.9	6
B1	69GH	0.7 ± 0.5	6	B7	69GH	0.2 ± 0.2	6
B6	69GH	0	10	C4	71F	7.0 ± 2.4	5
B8	69GH	0	7	C	71F	0	8
C1	69GH	0.1 ± 0.1	5	m-6R	71F	0.8 ± 0.5	7
90	69GH	0	7				
B7	69GH	0	6	BL2/			
C31	69GH	1.7 ± 0.5	5	BL3	68F	33.0 ± 2.9	6
	69F	0	9		71F	46.0 ± 10.4	5
				C	71F	0	7
BL3/				H21	71F	74.0 ± 12.5	5
H21	71F	39.0 ± 5.5	7	R	71F	29.0 ± 2.6	10
C	71F	38.0 ± 7.3	7	F	72F	2.1 ± 0.9	7
R	71F	18.0 ± 2.7	10	B	72F	22.0 ± 4.1	7
B	71F	0.9 ± 0.4	7				
	72F	0.6 ± 0.4	7				
F	71F	29.0 ± 4.5	9				

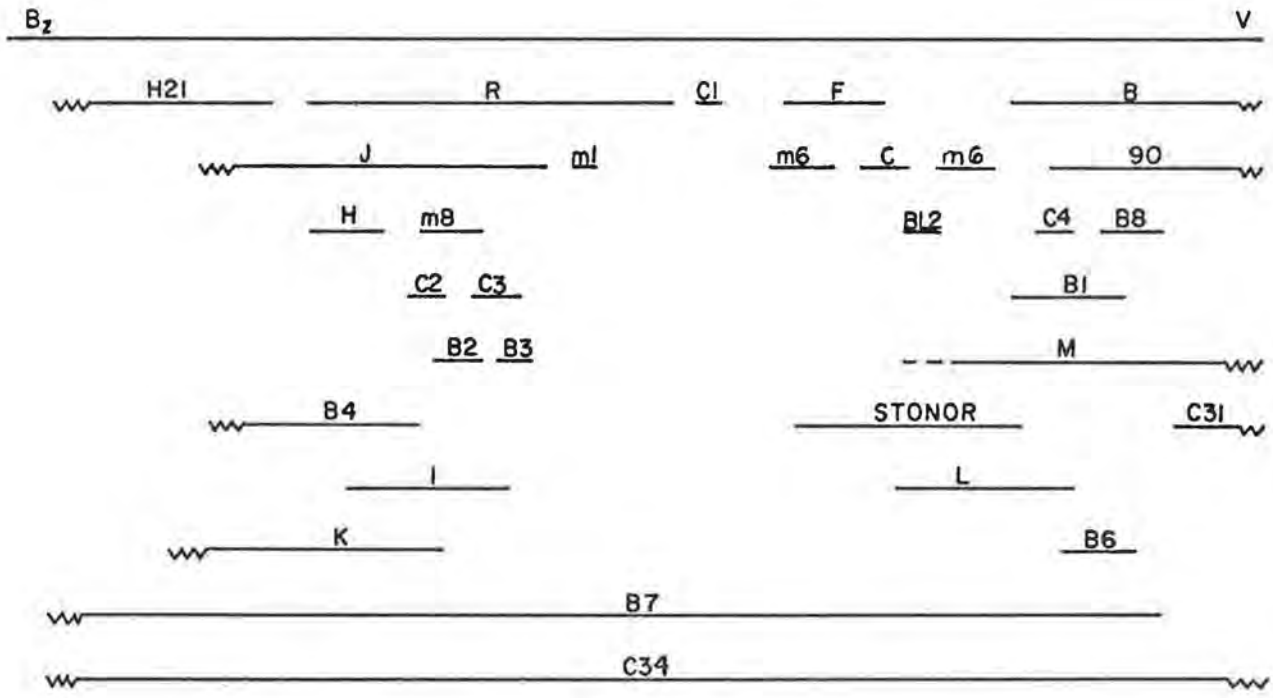


Table 2. The mean Wx frequency (per 10^5) of the pollen of crosses between wx heteroalleles made and sampled for the second time.

Hybrid	Year	Wx frequency ± s_x	Plants No.	Hybrid	Year	Wx frequency ± s_x	Plants No.
m-6R/				B6/			
m-8	Prev.	26.0 ± 2.5	3	B8	Prev.	3.1	3
	69F	13.0 ± 5.2	7		69H	0.8	1
90/				B/			
B	Prev.	1.4	4	B1	Prev.	1.7	2
	69GH	0	6		69GH	0	5
B1	Prev.	0	4	B6	Prev.	1	2
	69GH	0.8 ± 0.4	6		69GH	0	6
B6	Prev.	0	2	B8	Prev.	3.2	2
	69GH	0	6		69GH	0.3 ± 0.3	4
I/				C2/			
J	Prev.	0	3	I	Prev.	0	3
	69F	0	7		69F	1.1 ± 0.5	10
H	Prev.	0.4 ± 0.2	3	C3	Prev.	3.7 ± 1.8	3
	69F	0.4 ± 0.4	7		69F	3.4 ± 1.1	6
B4	Prev.	2.0	1	m-8	Prev.	0.7 ± 0.2	3
	69F	0	6		69F	1.4 ± 0.7	6
C3/				m-8/			
I	Prev.	0	3	I	Prev.	0.4 ± 0.5	3
	69F	1.9 ± 0.7	7		69F	0	6
J	Prev.	0.1 ± 0.1	3	J	Prev.	0	3
	69F	0	7		69F	0	8
m-8	Prev.	1.0 ± 0.5	3	H	Prev.	13.0 ± 1.5	3
	69F	1.3 ± 0.4	6		69F	9.1 ± 1.2	7
B1/				H/			
B6	Prev.	0	2	C2	Prev.	15.0 ± 4.8	4
	69GH	0	3		69F	24.0 ± 1.5	6
B8	Prev.	1.4	2	C3	Prev.	21.0 ± 5.9	3
	69GH	0	3		69F	23.0 ± 2.8	9
J/				B2/			
H	Prev.	0	3	B4	Prev.	21.0	2
	69F	0.5 ± 0.2	7		69F	10.0 ± 2.4	6
B2	Prev.	None	None	C3	Prev.	None	None
	69F	0.8 ± 0.5	7		69F	0.3 ± 0.2	7
B4	Prev.	None	None				
	69F	0	6	B4/			
C2	Prev.	0	3	C3	Prev.	None	None
	69F	0.3 ± 0.4	5		69F	5.3 ± 0.9	6

The location of f13 on chromosome 8

A new floury endosperm mutant originally obtained from Bear Seed Company in 1968 has been designated as floury-3 since two doses of the mutant gene in the endosperm condition a mutant phenotype, as with floury-1 and floury-2. The effect of the mutation on storage proteins and amino acid composition has been reported (Y. Ma and O. E. Nelson, Cereal Chem. 52:412, 1975).

Efforts to locate f13 by crosses with a set of waxy translocation stocks indicated that f13 is located on chromosome 8. Subsequently a f13 stock was used to pollinate plants of the constitution v16 ms8 j/v16 ms8 j. The phenotypically floury seeds in the F_2 progeny, which would be those receiving the f13 gene from the maternal parent, were selected for planting. The results confirm the location of f13 on chromosome 8 and indicate the gene order to be f13 v16 ms8 j:

+ + +	v + +	v ms +	+ ms j	+ + j	+ ms +	v + j	v ms j	Total
196	4	1	20	15	3	0	12	251

v = 6.7% ms = 14.3% j = 18.7%

The percentages of v/v, ms/ms and j/j plants indicate recombination values between f13 and v16 of approximately 14 percent, between f13 and ms8 of 28 percent and between f13 and j of 38 percent, disregarding double crossovers.

The numbers of plants in the phenotypic classes agree reasonably well with the numbers expected if f13 is located 14 crossover units proximal to v16 except for an excess of plants that are male sterile but non-japonica; possibly this arises from difficulties in the classification of japonica. There were also difficulties in the classification of virescent, and the estimate of 14 percent recombination between f13 and v16 should be regarded as a minimal estimate.

Backcross progenies to be grown in the summer of 1976 should permit more accurate estimates of the map distances separating f13 from the other markers on chromosome 8.

Oliver Nelson

b) The growth regulator and gibberellin physiology of sensitive lines should be explored in order to clarify the timing, concentration and methods of application necessary to bring about maximum reversion;

c) A study of the effect of the so-called "anti-gibberellins" upon sterility in normal cultivars should be initiated.

We invite correspondence with researchers who have material they feel would be suitable for inclusion in such a program.

R. I. Greyson and D. B. Walden

ADDENDUM

UNIVERSITY OF WESTERN ONTARIO
Department of Plant Sciences, London, Ontario

The effect of intermittent light on chlorophyll content of selected virescent mutants

Selective accumulation of chlorophyll a in dark-grown seedlings of bean (J. H. Argyroudi-Akoyunoglou and G. Akoyunoglou, 1970, Plant Physiol. 46:247) and pea (C. J. Arntzen, personal communication) subsequently exposed to intermittent light-dark cycles has also been shown in young maize seedlings (Hopkins, unpublished observations). In our laboratory, this phenomenon is being employed to produce chlorophyll b-deficient maize chloroplasts for the purpose of studying functional organization of chloroplast membranes. As an adjunct to this study, selected virescent mutants of maize were surveyed to learn whether these mutants respond in a similar fashion to intermittent light.

Seedlings were grown at 25 C under either 16 hr photoperiods (Controls) or intermittent light-dark cycles consisting of 2 min light and 58 min darkness (ImL); light intensity of approximately 800 ft-c was provided by a combination of cool white fluorescent and incandescent lamps. Seedlings were harvested at ten days and the leaf tissue extracted into 80% acetone. The first leaf was excluded, since earlier experiments had indicated that chl a/chl b ratios were significantly lower in the first leaf than in subsequent leaves. Chlorophyll content was calculated from absorbance values according to Arnon (1949, Plant Physiol. 24:1). The results of the survey are shown in Table 1.

Table 1. Effect of an intermittent light regime on chlorophyll composition of selected virescent mutants.

Genotype	Total Chl (mg/g f.w.)		Chl a/b Ratio		ImL-Cont.
	Controls	ImL	Controls	ImL	Cont.
+/+	1.52	0.17	2.6	9.1	2.5
Group I					
v/v	0.79	0.04	2.8	9.4	2.4
v2/v2	1.55	0.20	3.1	9.3	2.0
v3/v3	1.22	0.06	1.6	7.8	3.9
v4/v4	1.07	0.13	2.7	9.6	2.6
v5/v5	1.18	0.16	2.6	8.9	2.4
v16/v16	0.70	0.07	1.9	6.2	2.3
v17/v17	1.90	0.15	3.0	8.0	1.7
Group II					
v12/v12	0.83	0.12	2.1	3.3	0.6
v18/v18	0.68	0.09	3.4	4.8	0.4

Several observations may be drawn from the data:

1. Under control conditions of low light (ca. 800 ft-c) and 25 C, the virescent character was not strongly expressed. In fact, only v, v12, v16 and v18 showed any signs of virescence, as suggested by the slightly lowered chlorophyll contents. In our experience, pronounced phenotypic expression of the virescent character is obtained only under conditions of high light intensity (>1500 ft-c) and/or lower temperature.
2. In all genotypes surveyed, intermittent light conditions brought about a severe reduction in the total chlorophyll content of the seedlings; these reductions ranged between 85% and 95%.

3. There is evident some variation in the normal chl a/chl b ratios under control conditions, with ratios ranging from a low of 1.6 to a high of 3.1.
4. The virescent stocks may be placed in one of two groups on the basis of their response to intermittent light. In the first group are those in which, like the wild-type, the chl a/chl b ratio increases some 2-3 times under the intermittent light regime. The second group, comprised of only two of the mutants surveyed thus far, is characterized by a minimal enrichment in chlorophyll a content under intermittent light.

This latter observation is perhaps the most interesting. The basis for the absence of any selective accumulation of chlorophyll a in these two genotypes is not known at this time. Previous work in this laboratory has shown that wild-type maize seedlings produced under intermittent light are characterized by mesophyll chloroplasts lacking both grana and a specific chl a-b/protein complex, but possessing fully active photosystems I and II (unpublished observations). Whether either the v12 or v18 mutants will provide further insights into the role of chlorophyll b in the organization of chloroplast membranes remains to be seen.

On the other hand, it becomes increasingly clear that the traditionally vague description of virescence simply according to color and rate of greening belies the complexity of the system(s). The grouping of the virescents into two distinct classes according to their response to intermittent light may prove to be a useful first step toward the eventual biochemical characterization of the phenomenon.

W. G. Hopkins

Possibilities for gibberellin-male sterile relationships in corn--a proposal

Alternatives to cms for breeding programs have been proposed. Two possibilities, not yet fully explored, include nuclear-based male steriles which might be chemically reverted and the chemically induced sterility of normal plants.

In many species, various aspects of stamen growth and pollen production involve giberellin-dependent or -sensitive steps. In some, male sterility can be completely reverted with the application of gibberellins (Can. J. Bot. 51:2473; Euphytica 18:106). In others, it is known that normal stamen development is correlated with high endogenous levels of gibberellin (Plant Cell Physiol. 16:337; J. Am. Soc. Hort. Sci. 97:189 and J. Exp. Bot. 25:1004). The normal growth of filaments involves stamen-produced gibberellin (Amer. J. Bot. 54:971).

In corn, to our knowledge, no study of gibberellin-dependent stamen development has been reported, though the observations of Sladky (Biol. Plantarum 11:208) and Scheverbecke (C. R. Acad. Sci. Paris 260:5085) implicate gibberellins in tassel development and anther extrusion. Two reports (Ann. Mo. Bot. Gard. 46:19; Pl. Physiol. 56 Suppl.:44) of the exogenous application of gibberellin describe an inhibition of stamens of normal plants and therefore suggest a possible alternative interpretation of the role of gibberellin and stamen development.

However, in view of the large number of maize genes which are known to lead to reduced pollen fertility and the clear implication from other species that gibberellins could be involved, we suggest that the fertility of some male-sterile maize mutants might be restored by the administration of a gibberellin. This genetic material, which would respond to an exogenous application, could be a powerful adjunct to the breeder's arsenal for producing hybrid corn.

The opposite approach should also be attempted. Cultivars and procedures should be researched to ascertain if an application of anti-gibberellins could be used to induce male sterility. From a practical standpoint this procedure is less desirable than the first, but might be of value in certain situations.

If one accepts the above line of thought, it follows that:

a) A search for GA sensitive and/or reversible male-sterile mutants in corn should be started as soon as possible;

b) The growth regulator and gibberellin physiology of sensitive lines should be explored in order to clarify the timing, concentration and methods of application necessary to bring about maximum reversion;
c) A study of the effect of the so-called "anti-gibberellins" upon sterility in normal cultivars should be initiated.

We invite correspondence with researchers who have material they feel would be suitable for inclusion in such a program.

R. I. Greyson and D. B. Walden

IV. REPORT ON MAIZE COOPERATION

During 1975 the Maize Genetic Cooperation received 157 requests for maize genetic stocks. There were 121 (77%) domestic and 36 (23%) foreign requests. The distribution of domestic to foreign requests has been rather constant for the past 10 years. The number of requests in 1975 increased 17% over 1974. Requests from geneticists were 54%, physiologists 13%, plant breeders 26%, and educational 7% of the total number of requests received. A total of 1744 seed packets were sent to fill requests; 64% of the total was for domestic and 36% for foreign requests.

Seed stocks of B-A translocations and trisomics along with certain chromosome tester stocks were increased in 1975. In addition, about 50 stocks of reciprocal translocations with low seed viability were increased. Also, allele tests were made with a large number of endosperm mutants that have accumulated in the collection over the past several years.

A list of reciprocal translocation stocks available from the Co-op is published in the Co-op Newsletter report volume 43, 1969, or is available upon request.

Requests for seed and correspondence relative to the stock center 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 zb4 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 ms17 P-WW rs2
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
ms17
ts2 P-RR
ts2 P-WW br bm2
ts2 P-WW bm2
ts2 br f bm2
P-CR
P-RR
P-RW
P-CW
P-MO
P-VV
P-RR as br f an gs bm2
P-RR br f an gs bm2
P-RR 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
P-WW br f bm2
P-WW br f an gs bm2
P-WW br Vg
as
as rs2
rd-Hy
br f
br f Kn

Chromosome 1 (continued)

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
Kn bm2
lw
vp8
gs bm2
Ts6
bm2
id
nec2
ms9
ms12
ms14
mi
D8
TB-1La (1L.20)
TB-1Sb (1S.05)

Chromosome 2

ws3 lg gl2 B
ws3 lg gl2 B sk
ws3 lg gl2 B sk v4
ws3 lg gl2 B sk fl v4
ws3 lg gl2 B ts
ws3 lg gl2 b
ws3 lg gl2 b fl v4
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

Chromosome 2 (continued)

al lg gl2 b sk fl 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 gs2 sk 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 mn v4
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
gl14
gl11
wt
mn
fl
fl v4 Ch
fl Ht v4
fl Ht v4 Ch
fl w3
fl w3 Ch
ts
v4
v4 w3 Ht
v4 Ht Ch
w3
w3 Ht
w3 Ch
Ht (A & B source)
ba2
R2 ; r A A2 C

Chromosome 2 (continued)

Ch
TB-3La-2S6270
Primary Trisomic 2

Chromosome 3

cr
cr d
cr d Lg3
cr pm ts4 lg2
cr ts4 na
d-Tall = d*-6016
d rt Lg3
d Rf lg2
d ys3
d ys3 Rg
d ys3 Rg lg2
d Lg3
d Lg3 ts4 lg2
d Rg ts4 lg2
d pm
d ts4 lg2
d ts4 lg2 a-m ; A2 C R Dt
ra2
ra2 Rg
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 Lg3 gl6
ys3 gl6 lg2 a-m et ; A2 C R Dt
ys3 ts4
ys3 ts4 lg2
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 na
ts4 ba na
ts4 lg2 a-m ; A2 C R Dt
ts4 lg2 gl7

Chromosome 3 (continued)

ts4 na a-m et ; A2 C R Dt
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 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 sh2 et ; A2 C R B Pl Dt
a-p et ; A2 C R dt
a-p et ; A2 C R B Pl Dt
a-xl
a Ga7 ; A2 C R
sh2
vp
Rp3
pgl4
a3
g5
yel*-5787
TB-3La (3L.10)
TB-3Sb (3S.50)
Primary Trisomic 3

Chromosome 4

Rp4
Ga
Ga su

Chromosome 4 (continued)

Ga-S
Ga-S bt2
st
st Ts5
st fl2
st Ts5 su
Ts5
Ts5 fl2
Ts5 su
Ts5 su zb6
Ts5 su zb6 o
Ts5 Tu
la
la su Tu gl3
la su gl3
la su gl3 c2 ; A A2 C R
la su gl3 o
fl2
fl2 su
fl2 bt2
fl2 su bm3
fl2 su gl4 Tu
su
su-am
su bt2 gl4
su bm3
su zb6
su zb6 Tu
su gl4
su gl4 Tu
su gl4 j2
su gl4 o
su gl4 o Tu
su j2
su gl3
su gl3 o
su o
bt2
bm3
gl4
gl4 o
Tu
Tu-1 1st
Tu-1 2nd
Tu-d
Tu-md
Tu gl3
j2
j2 c2 ; A A2 C R
j2 C2 ; A A2 C R
j2 gl3
v8

Chromosome 4 (continued)

gl3
gl3 o
gl3 dp
c2 ; A A2 C R
C2 ; A A2 C R
C2-Idf (Active-1) ; A A2 C R
o
v17
v23
gl7
ra3
Dt4 su ; a-m A2 C R
TB-4Sa (4S.20)
TB-1La-4L4692
Primary Trisomic 4

Chromosome 5

lu
lu sh4
ms13
gl17
gl17 A2 pr ; A C R
gl17 a2 ; A C R
gl17 a2 bt ; A C R
gl17 a2 bt v2 ; A C R
A2 vp7 pr ; A C R
A2 bm bt pr ys ; A C R
A2 bm pr ; A C R
A2 bm pr ys ; A C R
A2 bm pr ys eg ; A C R
A2 bm pr v2 ; A C R
A2 bt v3 pr ; A C R
A2 bt pr ; A C R
A2 bt pr ys ; in A C R
A2 v3 pr ; A C R
A2 pr ; A C R
A2 pr 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

Chromosome 5 (continued)

vp2 pr
vp2 gl8
vp7
bm yg
bt
ms5
v3
td ae
ae
sh4
gl8
na2
lw2
ys
eg
v2
yg
ms13
v12
lw3 lw4
br3
TB-5La
TB-5Lb
Primary Trisomic 5

Chromosome 6

rgd po y
rgd po Y
rgd Y
po = ms6
po y pl
po y Pl
po Y pl
y = pb = w-m
y l10
y l11
y l12
y wl5
y pb4
y pb4 pl
y pb4 Pl
y si
y wi Pl
y Dt2 ; a-m A2 C R
y pgl1 ; Wx pgl2
y pgl1 wi ; wx pgl2
Y pgl1 ; Wx pgl2
y pgl1 ; wx pgl2
Y pgl1 ; wx pgl2
y pl
y Pl

Chromosome 6 (continued)

y Pl Bh ; c sh wx A A2 R
y su2
Y 110
Y 112
Y pb4
Y wi pl
Y wi Pl
Y su2
wi
Pl Dt2 ; a-m A2 C R
pl sm ; P-RR
Pl sm ; P-RR
Pl sm py ; P-RR
Pt
w
w14
ms6
2NOR ; a2 bm pr v2
Primary Trisomic 6

Chromosome 7

Hs o2 v5 ra gl
In-D
In-D gl
o2
o2 v5
o2 v5 ra gl
o2 v5 ra gl sl
o2 v5 ra gl Tp
o2 v5 ra gl ij
o2 v5 gl
o2 v5 ms7
o2 ra gl ij
o2 ra gl sl
o2 gl
o2 gl sl
o2 bd
in ; A2 pr A C R
in gl ; A2 pr A C R
v5
vp9
vp9 gl
ra gl g2
ra gl ij bd
gl
gl-M
gl Tp
gl o5
gl g2
gl mn2
Tp

Chromosome 7 (continued)

ij
ij g2
ms7
ms7 gl Tp
Bn
bd
Pn
o5
g2
va
Dt3 ; a-m A2 C R
v*-8647
yel*-7748
TB-7Lb (7L.30)
Primary Trisomic 7

Chromosome 8

gl18
v16
v16 j
v16 ms8 j
v16 ms8 j nec
v16 ms8 j gl18
ms8
nec
v21
TB-8La (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-I sh bz wx ; A A2 R
C sh bz wx gl15 bm4 ; A A2 R
C sh ; A A2 R
C sh wx ; A A2 R
C wx ar ; A A2 R
C-I sh wx v ; A A2 R
C sh wx K-L9 ; A A2 R

Chromosome 9 (continued)

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
sh wx d3
sh wx pgl2 gl15 ; y pgl1
bp wx ; P-RR
bp wx ; P-RW
bp wx ; P-WW
lo2
wx
wx-a
wl1
wx d3
wx d3 wl1
wx d3 v gl15
wx d3 gl15
Wx pgl2 ; y pgl1
wx pgl2 ; y pgl1

Chromosome 9 (continued)

Wx pgl2 ; Y pgl1
wx pgl2 ; Y pgl1
wx pgl2 bm4 ; y pgl1
wx v
wx bk2
wx bk2 bm4
wx Bf
wx Bf bm4
d3
v
gl15
gl15 Bf
gl15 bm4
bk2 Wc
Wc
bm4
bm4 Bf
16
17
yel*-034-16
w*-4889
w*-8889
w*-8951
w*-8950
w*-9000
TB-9La (9L.40)
TB-9Sb (9S.40)
Primary Trisomic 9

Chromosome 10

oy
oy R ; A A2 C
oy bf2
oy msl1
oy bf2 R ; A A2 C
oy bf2 msl0
oy zn R ; A A2 C
oy du R ; A A2 C R
oy du r ; A A2 C
oy sr2
oy zn
Og
Og du R ; A A2 C
msl1
msl1 bf2
bf2
bf2 zn
bf2 li g r ; A A2 C
bf2 g R sr2 ; A A2 C
bf2 g r sr2 ; A A2 C
bf2 r sr2 ; A A2 C

Chromosome 10 (continued)

nl zn g R ; A A2 C
nl g R ; A A2 C
nl g r ; A A2 C
nl g R sr2 ; A A2 C
y9
li zn g r ; A A2 C
li g R ; A A2 C
li g r ; A A2 C
li g r v18 ; A A2 C
li g R v18 ; A A2 C
ms10
du
du v18
du o7
du g r ; A A2 C
du sr2
zn
zn g
zn g R sr2 ; A A2 C
zn g r ; A A2 C
Tp2 g r ; A A2 C
g R sr2 ; A A2 C
g r ; A A2 C
g r sr2 ; A A2 C
g r sr2 l ; A A2 C
g R-g sr2 ; A A2 C
g R-g sr2 v18 ; A A2 C
g R-g K10 ; A A2 C
g R-g sr2 ; A A2 C
g R-r K10 ; A A2 C
g r-r sr2 ; A A2 C
Ej r-r ; A A2 C
Ej r-r sr2 ; A A2 C
r sr2 l ; A A2 C
R-g ; A A2 C
r-g sr2 ; A A2 C
r K10 ; A A2 C
r-g ; A A2 C
r-r ; A A2 C
R-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
R-st Mst
R-st Mst o7
Lc
w2
w2 l

Chromosome 10 (continued)

o7
o7 ; o2
l
v18
Mst
l yel*-5344
yel*-8721
yel*-8454
yel*-8793
TB-10La (10L.35)
TB-10Sc
Primary Trisomic 10

Unplaced Genes

dv
dy
el
h
l4
Rs
v13
ws ws2
ub
zb
zb2
zb3
zn2
l*-4923
nec*-8376

Multiple Gene Stocks

A A2 C R-g Pr B Pl
A A2 C R-g Pr B pl
A A2 C 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

Multiple Gene Stocks (continued)

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

Tetraploid Stocks (continued)

gl
ij
Y sh wx
sh bz wx
wx
g A A2 C R
A A2 C R B Pl

Cytoplasmic Steriles and Restorers

WF9 - (T)	rf rf2
N6 (S)	
WF9	rf rf2
N6	rf Rf2
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)
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 Inv2a (2S.70; 2L.80)
wx Inv9a (9S.70; 9L.90)

V. RECENT MAIZE PUBLICATIONS

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VI. MAILING LIST*

Aboti, S. S. - Maharashtra Hyb. Seeds LTD., P. O. Box 27, Sardar Patel Road, Jalna (Maharashtra) India
Adeniyi, Gideon I. - Inst. Agric. Research, Ahmadu Bello University, PMB 1044, Zaria, Nigeria
Ainsworth, Tom - Trojan Seed Company, Mason City, Illinois 62664
Akposoe, M. K. - Crops Research Instit., Ghana Acad. Sci. Box 3785, Kumasi, Ghana, West Africa
Aldrich, R. J. - Missouri Agric. Exper. Sta., University of Missouri, Columbia, Missouri 65201
Alexander, D. E. - Dept. of Agronomy, 112 Davenport Hall, University of Illinois, Urbana, Illinois 61801
Ali, S. Mahboob - Maize Research Station, Amberpet, Hyderabad - 13, A. P., India
Alleoni, Maria Ruth - Instituto de Genetica, C. P. 83, Piracicaba, S. Paulo, Brazil
Altschuler, Marsha - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Alvey, David - Farmers Forage Res. Coop., 4112 East State Road 225, West Lafayette, Indiana 47906
Amano, Etsuo - National Inst. of Genetics, Misima, Sizuoka 411, Japan
Anderson, John C. - Purdue Contract, Amer. EMB., Rio de Janeiro/Vicosa, APO, New York 09676
Andrew, R. H. - Dept. of Agronomy, University of Wisconsin, Madison 6, Wisconsin 53706
Arison, John - 1704 Manor Drive, Grinnell, Iowa 50112
Ashman, R. B. - Dept. of Botany, Purdue University, West Lafayette, Indiana 47907
Auerbach, Charlotte - Instit. of Animal Genetics, West Mains Road, Edinburgh 9 Scotland
Avila L., Gonzalo - Centro Eco-Genetico de Pairumani, Casilla 128 Cochabamba, Bolivia
Axtell, J. - Agronomy Dept., Purdue University, West Lafayette, Indiana 47907
Ayers, John - Dept. of Plant Pathology, Pennsylvania State Univ., University Park, Pennsylvania 16802
Baggett, J. R. - Horticulture Dept., Oregon State University, Corvallis, Oregon 97331
Baker, Raymond - Pioneer Hybrid Seed Company, Johnston, Iowa 50131
Baldi, G. - Centro di Ricerche sul Riso, Casella Postale 99, 27036 Mortar (PV) Milano, Italy
Balint, Andor - Agrartudomanyi Egyetem, Mezogazdasagtudomanyi Kar, Novenynemesitestani, Tanszek, Godollo, Hungary
Banerjee, U. C. - Dept. of Biology, Boston Univ., Boston, Massachusetts 02215
Bansal, R. K. - Dept. Sci. Indust. Res., Crop Research Substation, P. O. Box 61-060, Otara, Auckland, New Zealand
Baracco, Nestor P. - Compania Continental, Murphy, Santa Fe, Argentina
Barbosa, Helio M. - ICB-Genetica, Univ. Vicosa, Vicosa, Minas Gerais, Brazil
Barghoorn, E. S. - Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138
Barry, Edward G. - Dept. of Botany, University of North Carolina, Chapel Hill, North Carolina 27514
Bauman, L. F. - Dept. of Botany & Plant Pathology, Purdue University, West Lafayette, Indiana 47907
Beadle, G. W. - 5533 Dorchester Avenue, Chicago, Illinois 60637

*Addresses of libraries and institutes not included.

Bear, Robert P. - Bear Hybrid Corn Co., P. O. Box 628, Decatur, Illinois 62525
Beckett, Jack - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Beil, G. M. - Northeastern Exp. Station, DeKalb Agresearch, Inc., 1440 Okemos Road, Mason, Michigan 48854
Bemis, W. P. - Dept. of Horticulture, University of Arizona, Tucson, Arizona 85721
Bennett, J. H. - Genetics Dept., University of Adelaide, North Terrace, Adelaide, South Australia
Beremand, Marian - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Bergquist, Richard R. - Plant Pathologist, Pfister Hybrid Corn Co., El Paso, Illinois 61738
Berzsenyi-Janosits, L. - Keszthelyi Agr. Foiskola, Kukoricanemesito Csoportja, Keszthely, Deak Ferenc U. 57, Hungary
Bhat, B. K. - Regional Res. Laboratory (CSIR), Srinagar 190005 Kashmir, India
Bianchi, Angelo - Istituto Sperimentale per la Cerealicoltura, Via Cassia, 176, 00191 Rome, Italy
Bingham, E. T. - Dept. of Agronomy, University of Wisconsin, Madison, Wisconsin 53706
Birchler, James - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Bird, Robert McK. - CIMMYT, Apartado Postal 6-641, Mexico 6, D. F. Mexico
Blackwood, Margaret - Botany School, University of Melbourne, Parkville, Victoria 3052, Australia
Blanco, Jose L. - Dept. Inv. Antr. Gen. Cient., U. Barcelona, Av. Jose Antionio, Barcelona 7 Spain
Blanco-Gonzales, Mariano - Estac. Exp. De Aula Dei, Apartado 202, Zaragoza, Spain
Blanco, M. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Blumenschein, Almiro - Instituto de Genetica, Escola "Luiz de Quieroz", Piracicaba S. Paulo, Brazil
Bokde, S. - Maize Section, Est. Exp. Agropecuaria, Pergamina, Buenos Aires, Argentina
Bolen, Paul L. - Botany Dept., Duke University, Durham, North Carolina 27706
Brandolini, Aurelio - Istituto di Ortofloricultura, Minoprio (Como), Italy
Brawn, Robert - Research Dept., Funk Seeds International, Inc., 1300 W. Washington St., Bloomington, Illinois 61701
Brewbaker, James - Dept. of Horticulture, University of Hawaii, 3190 Maile Way, Honolulu, Hawaii 96822
Briggs, Robert W. - Research Dept., Funk Bros. Seed Co., 1300 W. Washington St., Bloomington, Illinois 61701
Brink, R. A. - Dept. of Genetics, University of Wisconsin, Madison, Wisconsin 53706
Brooks, J. S. - Dept. of Agronomy, Oklahoma Agr. Exp. Sta., Stillwater, Oklahoma 74074
Brown, Douglas - Dept. of Biology, Bishop's University, Lennoxville, Quebec, Canada
Brown, John C. - S. W. C., U. S. D. A., Beltsville, Maryland 20705
Brown, Richard P. - Ohio Foundation Seeds, Inc., Croton, Ohio 43013
Brown, William L. - Pioneer HiBred Corn Co., Plant Breeding Dept., Johnston, Iowa 50131
Bryant, James - Pfister Hybrid Corn Co., El Paso, Illinois 61738
Buescher, Patrick - Dept. Agron. & Plant Genetics, Univ. of Minnesota, St. Paul, Minnesota 55108
Burnham, C. R. - Div. of Agronomy & Plant Genetics, University Farm, St. Paul 1, Minnesota 55108
Burr, Benjamin - Biology Div., Oak Ridge Nat. Lab., Oak Ridge, Tennessee 37830

Cabulea, Iancu - Plant Breeding Laboratory, Stat. Exper. Agricola, Str. Agriculturii Nr. 27 Jud, Cluj, Turda, Romania
Camara-Hernandez, Julian - Altolaguirre 1295, Buenos Aires, Argentina
Cameron, James - Citrus Research Center, University of California, Riverside, California 92507
Camp, Lewis M. - O's Gold Research Ctr., P. O. Box 577, 900 Parrot St., Applington, Iowa 50604
Carlson, D. F. - Del Monte Corporation, P. O. Box 89, Rochelle, Illinois 61068
Carlson, Wayne - Botany Department, University of Iowa, Iowa City, Iowa 52240
Caspar, Alan - Blandy Experimental Farm, Boyce, Virginia 22620
Catcheside, David - Res. Sch. Biol. Sci., Australian National Univ., Canberra, A.C.T. 2601, Australia
Chandravadana, P. - Suburban Experiment Station, University of Massachusetts, 240 Beaver Street, Waltham, Massachusetts 02154
Chang, H. S. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Chang, S. H. - Dept. of Horticulture, University of Hawaii, Honolulu, Hawaii 96822
Chao, Chuan-Ying - Dept. of Biology, Chinese University of Hong Kong, Shatin, N. T. Hong Kong
Chao, Eddie Su-En - Bell Facility, P. O. Box U, Station B., Buffalo, New York 14207
Chase, Sherret S. - Dept. of Botany & Phys., State Univ. of New York, College of Arts and Sciences, Oswego, New York 13126
Chen, Chi-Chang - Genetics Laboratory, Taiwan Agric. Research Institut., Taipei, Taiwan, Republic of China
Choke, Ho Choy - School of Biological Sciences, University of Malaya, Kuala Lumpur, Malaya
Chou, Tau-San - Dept. Biol. Sci., Illinois State Univ., Bloomington-Normal, Illinois 61761
Chourey, Prem - Genetics Department, U. of Wisconsin, Madison, Wisconsin 53706
Christie, B. R. - Crop Science Department, University of Guelph, Guelph, Ontario, Canada
Clark, E. M. - Dept. of Botany & Microbiol., Auburn University, Auburn, Alabama 36830
Clark, G. H. - Research Station, Harrow, Ontario, Canada
Coe, E. H. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Colbert, Terry - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Colless, J. M. - Agric. Research Station, Grafton, New South Wales, Australia
Collier, J. W. - Foundation Seed Section, Texas A&M University, College Station, Texas 77843
Commerford, J. E. - Corn Refiners Assoc., Inc., 1001 Connecticut Ave., N. W., Washington, DC 20036
Conger, B. V. - Comparative Animal Res. Lab., 1299 Bethel Valley Rd., Oak Ridge, Tennessee 37830
Cook, James - Dept. Biol. Sci., Illinois State Univ., Bloomington-Normal, Illinois 61761
Cornu, A. - Station D'Amelioration des Plantes, B. V. 1540, 21 Dijon, France
Cortes, Lino - 8605 17th Ave., Bradenton, Florida 33505
Costa-Rodrigues, L. - c/o Semillas Agricolas, J. Garcia - Morato, 4, Madrid - 10 Spain
Cox, Delano K. - College of LA&S, University of Illinois, Urbana, Illinois 61801
Cox, E. L. - Dept. of Horticulture, University of Illinois, Urbana, Illinois 61801
Craig, William F. - Funk Seeds International, 1300 West Washington St., Bloomington, Illinois 61701

Crane, Paul L. - Dept. of Agronomy, Purdue University, West Lafayette, Indiana 47907
Creech, Roy G. - Dept. of Agronomy, Mississippi State Univ., P. O. Box 5248, Mississippi State, Mississippi 39762
Cross, Harold - Dept. of Agronomy, North Dakota State Univ., Fargo, North Dakota 58102
Cuany, Robin L. - Dept. of Agronomy, Colorado State University, Fort Collins, Colorado 80521
Curtis, David L. - DeKalb Shand Seed Co. PTY LMTD, Box 527 P. O., Tamworth 2340, N.S.W., Australia
Cutler, Hugh C. - Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110
Dahmen, Wayne J. - Merck, Sharp & Dohme, Bldg. 33-AG CHEM, Rahway, New Jersey 65070
Dankov, Toma - Instit. of Genetics & Plant Breeding, Sofia 13 Bulgaria
Dawson, G. W. P. - Dept. of Genetics, Trinity College, University of Dublin, Dublin 2, Ireland
Day, Peter R. - Dept. of Genetics, Conn. Agric. Exp. Station, P. O. Box 1106, New Haven, Conn. 06504
De Leon, Carlos - Apartado Postal 6-641, Mexico 6 D. F., Mexico
Dempsey, Ellen, Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Dhawan, N. L. - Ford Foundation, 1, Sharia Osiris, P. O. Box 2344, Garden City, Cairo, U.A.R.
Dicke, F. F. - 1430 Harding Avenue, Ames, Iowa 50010
Dickinson, D. B. - Dept. of Horticulture, University of Illinois, Urbana, Illinois 61801
Dijkhuis, F. J. - P. O. Box 99, Eloff, Transvaal, S. Africa
Dlouhy, Steve - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Doerschug, Earle - Genetics Dept., Iowa State Univ., Ames, Iowa 50010
Dollinger, E. J. - Ohio Agricultural Exp. Station, Wooster, Ohio 44691
Dooner, Hugo K. - Laboratory of Genetics, University of Wisconsin, Madison, Wisconsin 53706
Douglas, G. R. - Dept. of Botany, University of Western Ontario, London, Ontario, Canada
Doyle, G. G. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Drummond, Gladstone A. - Sementes Agroceres S. A., Jacarezinho, PR, Brazil
Duangploy, S. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Duclos, Zachary M. - Rt. 3 Box 132, Leesburg, Georgia 31763
Duesing, John H. - Dept. of Biology, Yale University, New Haven, Connecticut 06520
Dunn, G. M. - Dept. of Plant Sciences, Nesmith Hall, Univ. of New Hampshire, Durham, New Hampshire 03824
Duvick, Donald N. - Pioneer Hi-Bred International Inc., Johnston, Iowa 50131
Efron, Yoel - Dept. of Maize Breeding and Genetics, Newe Ya'ar Experimental Station, P. O. Haifa, Israel
Eisenstark, A. - Tucker Hall, University of Missouri, Columbia, Missouri 65201
Endo, Toru - National Institute of Genetics, Misima 411, Japan
Ericksen, Alvin W. - Great Western Sugar Co., Agricultural Research Center, Sugar Mill Road, Longmont, Colorado 80501
Faberge, A. C. - Dept. of Zoology, University of Texas, Austin, Texas 78711
Fenaroli, Luigi - Stazione Sperimentale Di Maiscoltura I-24100, Bergamo P. O. B. 164 Italy
Fergason, Virgil - Bear Hybrid Corn Co., Box 628, Decatur, Illinois 62525
Feyerabend, W. C. - Asgrow Seed Company, Ames, Iowa 50010
Ficsor, G. - Dept. of Biology, Western Michigan Univ., Kalamazoo, Michigan 49001

Filion, W. G. - Erindale Coll. Univ. of Toronto, 3359 Mississauga Road, Mississauga, Ontario, Canada
Findley, William R. - Agronomy Dept., Ohio Agri. Res. & Dev. Center, Wooster, Ohio 44691
Fitzgerald, P. J. - North Central Region, Agric. Res. Service, U.S.D.A., 2000 W. Pioneer Pkwy., Peoria, Illinois 61614
Fleming, A. A. - Miller Plant Science Bldg., Dept. of Agronomy, University of Georgia, Athens, Georgia 30602
Foard, Donald - Biology Division, Oak Ridge Natl. Laboratory, Oak Ridge, Tennessee 37830
Forster, Michael J. - 405 Bradfield Hall, Cornell University, Ithaca, New York 14850
Fowler, Robert G. - Biology Department, Princeton University, Princeton, New Jersey 05840
Fox, Walter - Dept. Biol. Sci., Illinois State Univ., Bloomington-Normal, Illinois 61761
Freeling, Michael - Dept. of Genetics, U. of California, Berkeley, California 94720
Gabay, S. - Dept. Genetics and Devel., Univ. of Illinois, Urbana, Illinois 61801
Galeev, G. S. - c/o W.I. Safonov, Timiriazev Inst. Pl. Phys., Leninsky Prospekt 33, Moscow B-71, U.S.S.R.
Galinat, Walton C. - Suburban Experiment Station, Univ. of Massachusetts, 240 Beaver Street, Waltham, Massachusetts 02154
Gamble, Edwin E. - Dept. of Crop Science, Ontario Agricultural College, University of Guelph, Guelph, Ontario, Canada
Garber, E. D. - Dept. of Biology, University of Chicago, Chicago, Illinois 60637
Gardner, C. O. - Dept. of Agronomy, Univ. of Nebraska, Lincoln, Nebraska 68503
Gavazzi, Giuseppe - Universita Di Milano, Istituto Di Genetica, Via Celoria 10, Milan, Italy
Geadelmann, J. L. - Dept. Agron. & Pl. Gen., Univ. of Minnesota, St. Paul, Minnesota 55108
Gebauer, Juan - Dept. Agron. & Pl. Gen., Univ. of Minn., St. Paul, Minnesota 55108
Geerthsen, J. M. P. - Dept. of Genetics, Univ. of Pretoria, Pretoria, South Africa
Gengenbach, B. G. - Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul, Minnesota 55108
Georgiev, Trifon - Agr. Res. Institute, Obraztsov Chiflik, Rousse, Bulgaria
Gerrish, Everett E. - Box 359, Grinnell, Iowa 50112
Gettys, Richard E. - Coker's Pedigreed Seed Company, Hartsville, South Carolina 29550
Ghidoni, Achille, Istituto Di Genetica, Universita Di Milano, Via Celoria 10, Milano, Italy
Ghobrial, Helmy - Ministry of Agriculture, Plant Breeding Section, University Avenue, Cairo, United Arab Republic
Gibbon, Edward L. - P. O. Box 3572 F.S.S., Radford, Virginia 24141
Giesbrecht, John - Research Station, Canada Agriculture, Morden, Manitoba, Canada
Gillies, Christopher - School of Biological Sciences, Botany Bldg. A12, University of Sydney, Sydney N.S.W. 2006 Australia
Givens, Jean - Dept. Agronomy & Plant Genetics, U. of Minnesota, St. Paul, Minnesota 55108
Glover, David V. - Dept. of Agronomy, Purdue University, Lafayette, Indiana 47907
Goenaga, Laura Larre De - Estacion Experimental Regional Agropecuaria, INTA-C.C. 31 Pergamino, BS.AS., Argentina
Goertzen, Kenneth L. - Goertzen Seed Res. Inc., R. R. #2, Box 48, Scott City, Kansas 67871
Goldman, Stephen - Dept. of Biology, University of Toledo, Toledo, Ohio 43606

Goodman, Major M. - Dept. of Experimental Statistics, School of Phy. Sci. & App. Math, North Carolina State Univ., Raleigh, North Carolina 27607
Gracen, V. E. - Dept. Plant Breeding, Cornell Univ., Ithaca, New York 14850
Graham, K. M. - Faculty of Agriculture, University of Malaya, Kuala Lumpur, Malaysia
Green, C. E. - Agron. and Plant Genetics, Univ. of Minnesota, St. Paul, Minnesota 55108
Green, M. M. - Dept. of Genetics, University of California, Davis, California 95616
Greenblatt, I. M. - Genetics & Cell Biology, Univ. of Connecticut, Storrs, Connecticut 06268
Grobman, Alexander - Northrup, King & Co., Avenida Arequipa 340, Oficina 601, Lima, Peru
Grogan, C. O. - Dept. of Plant Breeding, Cornell University, Ithaca, New York 14850
Grogan, P. W. - Queensland Agricultural College, Lawes, Queensland, Australia
Groszmann, Americo - Divisao de Genetica, Cenpro Pesquisa, 45.600-1 Tabuna - Bahia Brasil
Gunn, C. L. - DeKalb Agricultural Assoc., Inc., Sycamore Road, DeKalb, Illinois 60115
Gunn, Ralph - DeKalb Agricultural Assoc., Inc., Box 378, Redwood Falls, Minnesota 56283
Gupta, D. - "Chhaya" Shradhanad Marg, Panipat 132103, India
Guthrie, Myron - Technical Service Director, Corn States Hybrid Service Inc., P.O. Box 2706, Des Moines, Iowa 50315
Haapala, Bernard - Dassel, Minnesota 55325
Hadjinov, M. I. - Krasnodar Agric. Res. Inst., Krasnodar-12, U.S.S.R.
Hagan, William - Del Monte Corp., 850 Thornton Street, P. O. Box 36, San Leandro, California 94577
Hair, J. B. - Botany Division, D.S.I.R., Private Bag, Christchurch, New Zealand
Hallauer, Arnel R. - Agronomy Building, Iowa State University, Ames, Iowa 50010
Ham, Young Soo - Crop Experiment Station, Suwon, Korea
Hamilton, R. H. - Buckhout Laboratory, Pennsylvania State University, University Park, Pennsylvania 16802
Hannah, L. C. - Veg. Crops Dept., Univ. of Florida, IFAS, Gainesville, Florida 32611
Hansel, William - PAG Seeds, Box 2, Carrollton, Mo. 64633
Hansen, Dale J. - Agric. Research Dept., Monsanto Commercial Prod. Co., 800 N. Lindbergh Blvd., St. Louis, Missouri 63166
Hanson, George - Dept. of Arboreta & Botanic Gardens, 301 North Baldwin Ave., Arcadia, California 91006
Hanson, W. D. - Dept. of Genetics, North Carolina State Univ., Raleigh, North Carolina 27607
Harris, John W. - Dept. of Biology, Tennessee Tech. Univ., Cookeville, Tennessee 38501
Harris, Robert M. - Committee on Genetics, University of Arizona, Tucson, Arizona 85721
Hartman, Carl J. - Chester Inc., Seed Dept., Boone Grove, Indiana 46302
Harvey, P. H. - NPS - Agricultural Res. Service, U. S. Dept. of Agriculture, Beltsville, Maryland 20705
Haskins, F. A. - Dept. of Agronomy, Univ. of Nebraska, Lincoln, Nebraska 68503
Hayden, D. B. - Dept. of Botany, U. of Western Ontario, London, Ontario, Canada
Heathman, Charles - Pride Company Inc., Glen Haven, Wisconsin 53810
Heidrich-Sobrinho, Edmundo - Departamento De Genetica IB UFRGS, Caixa Postal, 1953, Porto Alegre RS, Brasil

Helgason, S. B. - Dept. of Plant Science, Univ. of Manitoba, Winnipeg 19, Manitoba, Canada
Helm, James L. - McNair Seed Co., P. O. Box 706, Laurinburg, North Carolina 28352
Henderson, Clarion B. - Illinois Foundation Seeds, Inc., P. O. Box 722, Champaign, Illinois 61820
Hendriksen, A. J. Th. - B. J. Van Der Have, Kapelle-Biezelinge, Netherlands
Hoegemeyer, Thomas C. - Hoegemeyer Hybrids Inc., Rt. 2, Hooper, Nebraska 68031
Hofmeyr, J. D. J. - P. O. Box 1222, Pietersburg, South Africa
Holland, R. F. - DeKalb Agresearch, Inc., Sycamore Road, DeKalb, Illinois 60115
Hooker, A. L. - Dept. of Plant Pathology, Univ. of Illinois, Urbana, Illinois 61801
Horn, J. D. - Dept. of Botany, U. of Western Ontario, London, Ontario, Canada
Hu, Wilma Wei-Lin - Dept. of Crop Science, North Carolina State Univ., Raleigh, North Carolina 27607
Hunter, R. B. - Dept. of Crop Science, University of Guelph, Ontario Agricultural College, Guelph, Ontario, Canada
Iltis, Hugh H. - Dept. of Botany, U. of Wisconsin, Madison, Wisconsin 53706
Jackson, R. C. - Biology Department, Texas Tech. Univ., Lubbock, Texas 79409
Jacobs, Michel - 6 Drive De La Grappe, B-1190 Bruxelles, Belgium
Jauhar, Prem P. - No. PPJ/16254, Division of Genetics, Indian Agric. Res. Institute, New Delhi, 12, India
Jellum, Milton D. - Georgia Agr. Exp. Station, Experiment, Georgia 30212
Jenkins, M. T. - Farmers Forage Research Coop., 4112 East State Road 225, W. Lafayette, Indiana 47906
Jennings, Paul H. - Dept. of Plant and Soil Sciences, U. of Massachusetts, Amherst, Massachusetts 01002
Jensen, C. J. - St. Valbyvej Aagerup, Roskilde, Denmark, 4000
Johnson, E. C. - CIMMYT, Apartado Postal 6-641, Mexico 6, D.F. Mexico
Johnson, Elizabeth - Box 371, Kaunakakai, Hawaii 96748
Johnson, Melvin - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Johnson, M. W. - Dept. of Agronomy, Pennsylvania State University, University Park, Pennsylvania 16802
Johnston, Gordon S. - Nasson College, Springvale, Maine 04083
Jones, J. K. - Dept. of Agricultural Botany, The University, Reading, Berks. England
Josephson, L. M. - Agricultural Expt. Station, Knoxville, Tennessee 27916
Jugenheimer, R. W. - Dept. of Agronomy, University of Illinois, Urbana, Illinois 61801
Kaneko, Koji - Tropical Agr. Res. Center, Yatabe-cho, Tsukuba-gun, Ibaraki-ken, Japan
Kang, Manjit S. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Kato Y., Takeo A. - Rama de Genetica, Colegio de Postgraduados, Esc. Nac. de Agric., Chapingo, Mexico, Mexico
Keltgen, Keith - Trojan Seed Co., Olivia, Minnesota 56277
Kermicle, Jerry - Dept. of Genetics, University of Wisconsin, Madison, Wisconsin 53706
Keskar, Pramod - Nimbkar Seeds, Phaltan, Dist. Satara, Maharashtra, India
Kiehl, E. R. - Missouri Agric. Exper. Sta., University of Missouri, Columbia, Missouri 65201
Kikudome, Gary Y. - Tucker Hall, University of Missouri, Columbia, Missouri 65201
Kinugawa, Kenjiro - Lab of Genetics & Plant Breeding, Faculty of Agriculture, Univ. of Osaka Prefecture, Sakai, Osaka, Japan
Kiss, M. Charles - Mais Angevin "Hodee", 49-La Menitre, France

Kleese, Roger - Northrup, King & Co., Stanton, Minnesota 55081
Kohashi, Josue - Dept. of Botany, Escuela Nac. de Agricultura, Chapingo, Mexico
Konzak, Calvin F. - Dept. of Agronomy & Soils, Washington State University, Pullman, Washington 99163
Kovacs, Istvan - Agriculture Research Instit., Hungarian Acad. of Sciences, 2462 Martonvasar, Hungary
Kowles, Richard V. - Biology Dept., St. Mary's College, Winona, Minnesota 55987
Kozelnicky, George M. - Dept. of Plant Pathology, University of Georgia, Athens, Georgia 30601
Krapovickas, Antonio - Univ. Nac. Nordeste, Fac. Agron. Y Vet., Corrientes, Argentina
Kratochvil, D. E. - Sokota Hybrid Producers, Brookings, South Dakota 57006
Kumar, D. - 114 NRL Building, Indian Agr. Res. Inst., New Delhi 110012, India
Kundu, B. C. - Bose Research Instit., Calcutta - 9, India
Lachman, W. H. - Dept. of Plant & Soil Sci., Bowditch Hall, University of Massachusetts, Amherst, Massachusetts 01002
Laible, Charles A. - Research Dept., Funk Seeds International, Inc., Bloomington, Illinois 61701
Lambert, R. J. - Dept. of Agronomy, University of Illinois, Urbana, Illinois 61801
Larson, Russell L. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Laubscher, F. X. - University of Stellenbosch, Stellenbosch, South Africa
Laughnan, John R. - Dept. of Genetics and Development, 515 Morrill Hall, University of Illinois, Urbana, Illinois 61801
Laughner, Bill - Dept. of Biology, Hiram College, Hiram, Ohio 44234
Lehmann, Louis C. - Ram-Bar Corporation, 2303 S. Val Vista Dr., Mesa, Arizona 85204
Leng, Earl - 112 Mumford Hall, University of Illinois, Urbana, Illinois 61801
Leonard, Kurt - USDA - ARS, Box 5397 State Coll. Station, Raleigh, North Carolina 27607
LeRoux, P. M. - Ben Pienaarstraat 26, Baillie Park, Potchefstroom, Republic of South Africa
Leto, Kenneth - Tucker Hall, University of Missouri, Columbia, Missouri 65201
Levings, C. S. - Dept. of Genetics, North Carolina State, Raleigh, North Carolina 27607
Lewis, Herman - Genetic Biology, National Science Foundation, Washington, D. C. 20550
Li, H. W. - Institute of Botany, Academia Sinica, Taipei, Taiwan Rep. of China
Liang, George H. - Dept. of Agronomy, Kansas State University, Manhattan, Kansas 66502
Lin, Bor-Yaw - Laboratory of Genetics, University of Wisconsin, Madison, Wisconsin 53706
Lindsey, M. F. - DeKalb Agresearch Inc., Sycamore Road, DeKalb, Illinois 60115
Littlewood, R. K. - Lab. of Molecular Biol., 1525 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706
Liu, Edwin H. - Dept. of Biology, U. of South Carolina, Columbia, South Carolina 29208
Llorente, Carlos F. - Asgrow Argentina S.A.I.C., Buenos Aires, Argentina
Locy, Robert - Dept. of Horticulture, Purdue University, West Lafayette, Indiana 47907
Loden, H. D. - Acco Seed, Belmond, Iowa 50421
Loeffel, Frank A. - Northrup, King and Co., Research Center, Stanton, Minnesota 55081
Loesch, P. J. Jr. - Agronomy Dept., Iowa State University, Ames, Iowa 50010
Longley, A. E. - Curtis Hall, University of Missouri, Columbia, Missouri 65201

Lonnquist, J. H. - Dept. of Agronomy, 141 Moore Hall, University of Wisconsin, Madison, Wisconsin 53706
Lorenzoni, C. - Istituto de Genetica Vegetale, Universita Cattolica, Piacenza, Italy
Lorenzo-Andreu, A. - Estacion Exper. Aula Dei, Apartado 202, Zaragoza, Spain
Lund, H. R. - Agronomy Dept., North Dakota State Univ., Fargo, North Dakota 58102
Ma, Te-Hsiu - Dept. Biol. Sciences, Western Illinois Univ., Macomb, Illinois 61455
MacDonald, Timothy - Dept. of Biol. Sciences, Lowell Techn. Instit., Lowell, Massachusetts 01854
Maggini, Fabio - Istituto di Genetica della Univ., Via G. Amedola, 165/A, 70126 Bari, Italy
Maguire, Marjorie - Genetics Foundation, University of Texas, Austin, Texas 78712
Majumder, B. - Istituto di Genetica, Via Celoria 10, Milano, Italy
Maletsky, S. I. - Tereshkova St., House 6, Flat-49, Novosibirsk 630090, U.S.S.R.
Mangelsdorf, P. C. - Dept. of Botany, University of North Carolina, Chapel Hill, North Carolina 27514
Manrique, Antonio - Universidad Agraria Progr. Coop Inv. Maiz, La Molina Apt. 456 Lima, Peru
Mans, Rusty J. - Dept. of Biochemistry, J. Hillis Miller Health Center, U. of Florida, Gainesville, Florida 32610
Manwiller, Alfred - Pee Dee Experiment Station, Clemson Agricultural College, Florence, South Carolina 29501
Mariani, Giuseppe - Istituto Sperimentale per la Cerealicoltura, Via Cassis 176, Roma 00191, Italy
Martin, I. F. - Research Station, Kairi, North Queensland, Australia
Mathur, J. M. S. - Division of Genetics, Indian Agricultural Res. Instit., New Delhi - 12, India
Matthews, David L. - Agway Inc., Box 1333, Syracuse, New York 13201
Mazoti, Luis B. - Instituto Fitotecnico de Santa Catalina, Llavallol F.N.G.R., Buenos Aires, Argentina
McClintock, Barbara - Carnegie Institution, Dept. of Genetics, Cold Spring Harbor, New York 11724
McCormick, Sheila - Curtis Hall, University of Missouri, Columbia, Missouri 65201
McKinley, Carolyn - Dept. of Biology, Univ. of Toledo, Toledo, Ohio 43606
McWhirter, K. S. - Dept. of Agricultural Botany, University of Sydney, Sydney, N. S. W., Australia
Mello-Sampayo, Tristao - Centro di Biologia, Instituto Gulbenkian de Ciancia, Oeiras, Portugal
Mertens, Thomas R. - Dept. of Biology, Ball State University, Muncie, Indiana 47306
Metzger, Robert - Farm Crops, Oregon State College, Corvallis, Oregon 97331
Michel, Kenneth - Dept. of Biology, Slippery Rock State Coll., Slippery Rock, Pennsylvania 16057
Mikula, Bernard C. - Defiance College, Defiance, Ohio 43512
Miles, Donald - Tucker Hall, University of Missouri, Columbia, Missouri 65201
Millham, Betty Jo - 1511 Fisk, Pullman, Washington 99163
De Miranda, Luiz Torres - Seccao de Cereais, Instituto Agronomico, Campinas, S. Paulo, Brasil
Mock, James J. - 111 Agronomy, Iowa State University, Ames, Iowa 50010
Mohamed, A. H. - Dept. of Biology, University of Missouri, Kansas City, Missouri 64110
Moll, Robert H. - 2623 Gardner Hall, Dept. of Genetics, North Carolina State Univ., Raleigh, North Carolina 27607
Monaco, Lourival Carmo - Instituto Agronomico cx.P.28, Secao de Genetica, Campinas, Sao Paulo, Brasil

Montgomery, Ilene - 4616 15 Mile Road, Apt. 110, Sterling Heights, Michigan 48088
Moore, Carol W. - Dept. of Biology, U. of Rochester, Rochester, New York 14627
Morgan, D. T. - Dept. of Botany, University of Maryland, College Park, Maryland 20742
Morris, Rosalind - Dept. of Agronomy, University of Nebraska, Lincoln, Nebraska 68503
Mottinger, John - Dept. of Botany, University of Rhode Island, Kingston, Rhode Island 02881
Mukherjee, B. K. - Cummings Lab., Indian Agr. Res. Inst., New Delhi 110012, India
Mulcahy, David - Botany Dept., University of Massachusetts, Amherst, Massachusetts 01002
Mumm, W. J. - Box 306, Milford, Illinois 60953
Murphy, Tim - Dept. Agron. & Pl. Genetics, Univ. of Minnesota, St. Paul, Minnesota 55108
Murray, M. D. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Myers, Oval, Jr. - Dept. of Botany, Southern Illinois University, Carbondale, Illinois 62901
Nagel, C. M. - Dept. of Plant Pathology, South Dakota State College, Brookings, South Dakota 57006
Nakano, Hiroyuki - Tokachi Agr. Exp. Station, Memuro-Cho, Kasai-Gun, Hokkaido, Japan
Nanda, Dave - Trojan Seed Co., Windfall, Indiana 46076

Neely, J. Winston - Coker's Pedigreed Seed Co., Hartsville, South Carolina 29550
Nel, P. M. - Botany Dept., Univ. of the Witwatersrand, Johannesburg, Republic of South Africa
Nelson, O. E., Jr. - Dept. of Genetics, University of Wisconsin, Madison, Wisconsin 63706
Nelson, S. W. - Salisbury Research Station, P. O. Box 8100, Causeway, Salisbury, Rhodesia
Nemeth, J. - Cereal Research Institute, Gabonatermesztesi Kutato Intezet, Szeged, Also Kikotosor 5 Hungary
Neuffer, M. G. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Nickerson, N. H. - Dept. of Botany, Tufts University, Medford, Massachusetts 02115
Nider, Fabio - DeKalb Argentina Saciai, Int. Ruta Prov. No. 31, Y Accesso A. I. Indart, Salto Bs. As. Argentina
Nilan, R. A. - Dept. of Agronomy and Soils, Washington State Univ., Pullman, Washington 99163
Noble, Stephen W., Jr. - Dept. of Corn Breeding, Pioneer Hi-Bred Internat. Inc., Johnston, Iowa 50131
Northrup, Richard N. - Delta College, University Center, Michigan 47810
Notani, N. K. - Bhabha Atomic Research Centre, Biology Division, Modular Laboratories, Trombay, Bombay 74 India
Oaks, Ann - Biology Dept., McMaster University, Hamilton, Ontario, Canada
Odom, W. H. - M.F.A. Seed Division, Missouri Farmers Association, Marshall, Missouri 65340
Ogle, Charles W. - R.R. # 1, Box 145, Sugar Grove, Illinois 60554
Ohta, Y. - Kihara Inst. Biol. Res., Yata-Ohara, Misima, Sizuoka-ken, 411 Japan
Okabe, Takashi - Hokkaido Nat. Agr. Exp. Sta., Hitsujigaoka, Sapporo, Japan
Orton, Elwin R., Jr. - Dept. of Horticulture, Rutgers University, New Brunswick, New Jersey 08903
Osler, R. D. - CIMMYT, Apartado Postal 6-641, Mexico 6, D. F. Mexico
Osterman, John - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401

Ottaviano, E. - Istituto di Genetica, Universita di Milano, Milano, Italy
Paez, Alix V. - Dept. of Corn Breeding, P. O. Box 85, Pioneer Hybrid Intern. Inc., Johnston, Iowa 50131
Palenzona, D. L. - Istituto di Genetica, Universita di Bologna, Via F. Selmi, 3, 40126 Bologna, Italy
Palmer, Reid - Agronomy Dept., Iowa State University, Ames, Iowa 50010
Pande, Mohan Chandra - Birla Institute of Sci. Res., P. O. Amlai Paper Mills, Distt. Shahdol (M.P.), India
Pap, A. - Hurst, Gunson, Cooper, Taber Seed Co., Wiltham, Essex, England
Paterniani, Ernesto - Universidade de Sao Paulo, Escola Superior de Agricul., "Luiz de Queiroz", Piracicaba, Brazil
Patterson, Earl - Agronomy Dept., University of Illinois, Urbana, Illinois 61801
Peacock, W. J. - Dept. of Genetics, C.S.I.R.O., Canberra A.C.T., Australia
Pelham, John - Inst. of Forestry Research, Dept. For. Nat. Res., The University, Mayfield Rd., Edinburgh 9, Scotland
Penny, Lowell - Northern Grain Insects Res. Lab, Agric. Research Service - U.S.D.A., Brookings, South Dakota 57007
Perkins, K. W. - Carolina Biol. Supply Co., Burlington, North Carolina 27215
Peterson, Peter A. - Dept. of Agronomy, Iowa State University, Ames, Iowa 50010
Pfister, Walter - Pfister Hybrid Corn Co., El Paso, Illinois 61738
Phillips, Ronald - Dept. of Agronomy & Plant Gen., University of Minnesota, St. Paul, Minnesota 55108
Phinney, Bernard O. - Division of Botany, University of California, Los Angeles, 24, California 90024
Piovarci, A. - Vyskumny Ustav Kukurice, 91752 Trnava, Trstinska 13, Czechoslovakia
Platt, Margaret Walsh - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Plewa, Michael - Dept. of Agronomy, University of Illinois, Urbana, Illinois 61801
Pollmer, W. G. - Universitat Hohenheim (LH), 7000 Stuttgart 70 (Hohenheim), Postfach 106, Garbenstrasse 9, Germany
Poneleit, Charles G. - Dept. of Agronomy, Agric. Science Center, University of Kentucky, Lexington, Kentucky 40506
Popenoe, John - Fairchild Tropical Garden, 10901 Old Cutler Road, Miami, Florida 33156
Popow, G. - Swiss Experiment Station for Agriculture, 8050 Zurich, Switzerland
Pradhan, K. - West Bengal Haringhata Farm, P.O. Mohanpur, Dist. Nadia, West Bengal, India
Prensky, Wolf - Sloan-Kettering Institute for Cancer Research, 444 East 68th Street, New York, New York 10021
Pryor, A. J. - Div. of Plant Industry, C.S.I.R.O., P. O. Box 109, Canberra City, A.C.T. 2601, Australia
Pujals, Enrique A. - M. Ugarte 1151, Pergamino, B. A., Argentina
Purdy, J. L. - Green Giant Co., LeSueur, Minnesota 56058
Rafaill, W. S. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Rakha, Farouk A. - Dept. of Genetics, Faculty of Agriculture, Alexandria University, Alexandria, Egypt. U.A.R.
Ramaiah, K. V. - ICRISAT, 1-11-256 Begumpet, Hyderabad - 500016, India
Ramaley, Annette - 1606 N. Weber Street, Colorado Springs, Colorado 80907
Ramirez, S. A. - Div. Allied Health & Life Sci., Univ. of Texas at San Antonio, San Antonio, Texas 78285
Randolph, L. F. - Dept. of Botany, Cornell University, Ithaca, New York 14850
Rao, B. G. S. - Dept. of Botany, Andhra University, Waltair, India
Rao, G. R. - Dept. of Botany, S. V. University, Tirupati (A.P.), India
Rao, M. Krishna - Dept. of Botany, Andhra University, Post Graduate Center, Guntur-5, Andhra Pradesh India

Rao, Panuganti N. - Dept. of Botany, Andhra University, Waltair, Andhra Pradesh, India
Rautou, S. - Maitre de Recherches, Sta. Amel. Plantes, Ecol. Nat. Super. Agron., 34 Montpellier France
Raveed, Dan - C. F. Kettering Res. Lab., 150 East South College St., Yellow Springs, Ohio 45387
Reddy, G. M. - Dept. of Genetics, Osmania University, Hyderabad-7, A. P., India
Reddy, P. S. C. - 94 Sorauren Ave., Toronto, Ont. M6R2E2, Canada
Rees, Hubert - Agricultural Botany Dept., Univ. College of Wales, Aberystwyth, Wales
Reid, Wm. R. - P-A-G Seeds, P. O. Box 470, Aurora, Illinois 60507
Remley, Frank M. - 1433 Cargill Bldg., Seed Dept., Minneapolis, Minnesota 55402
Reynolds, Jim - Holden's Foundation Seeds, Inc., Box 299, Williamsburg, Iowa 52361
Rhoades, M. M. - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Rhodes, A. M. - Dept. of Horticulture, University of Illinois, Urbana, Illinois 61801
Riba, Lewis - Northrup King & Co., 13055 Research Road, Eden Prairie, Minnesota 55343
Riccelli, Mauricio - Productora de Semillas C. A., (Proseca), Flor Amarillo, Valencia, Venezuela
Richardson, Dewayne L. - Div. of Tropical Research, Tela Railroad, La Lima, Honduras
Rieffel, Larry D. - 598 East 2nd Street, El Paso, Illinois 61738
Riman, Ludek - Institute of Plant Prod., Dept. of Maize Genetics and Selection, Piest'any, Bratislavska Ul, Czechoslovakia
Rinehart, Karl - 19W 240 Winwood Way, Downers Grove, Illinois 60515
Rinke, E. H. - Northrup King and Co., Minneapolis, Minnesota 55455
Robbelen, G. - Inst. fur Pflanzenbau, 34 Gottingen, Von-Siebold-Strasse 8, Germany
Robbertse, Pieter J. - University of Pretoria, Pretoria, South Africa
Robertson, Donald S. - Dept. of Genetics, Iowa State University, Ames, Iowa 50010
Robinson, H. F. - Purdue University, Lafayette, Indiana 47907
Roderick, T. - Div. Biol. and Medicine, U. S. Atomic Energy Commission, Washington, DC 20545
Roper, J. A. - Dept. of Genetics, The University, Sheffield 10, England
Ross, W. M. - Keim Hall, East Campus, University of Nebraska, Lincoln, Nebraska 68503
Rossman, E. C. - Dept. of Crop & Soil Sci., Michigan State University, East Lansing, Michigan 48823
Roussineau, Jean - France Canada Semences, Avenue de Vendome, 41000 Blois, France
Rubenstein, Irwin - Dept. Genetics & Cell Biol., Univ. of Minnesota, St. Paul, Minnesota 55108
Runge, E. C. A. - Mumford Hall, University of Missouri, Columbia, Missouri 65201
Runge, Richard - Dept. of Biology, Lake Forest College, Lake Forest, Illinois 60045
Russell, W. A. - Dept. of Agronomy, Iowa State University, Ames, Iowa 50010
Ryan, G. S. - Dept. de Genetica, INTA, Casilla de correo 25, Castelar, Argentina
Ryan, Rita M. - Dept. of Biology, Boston College, Chestnut Hill, Massachusetts 02167
Sachan, J. K. S. - Bot. Inst. Fac. Sci., Hiroshima University, 1-1-89 Higashi Sendamachi, Hiroshima City 7 30, Japan
Safonov, W. I. - K. A. Timiriazev Instit. of Plant Physiology, Leninsky Prospekt 33 Moscow, B-71, U.S.S.R.
Sager, Ruth - Sidney Farber Cancer Ctr., 35 Binney St., Boston, Massachusetts 02115

Sahara, Roy - Genetics Greenhouse, Oxford Research Unit, Univ. of California, Berkeley, California 94720
Salama, Salama Ibrahim - Dept. of Agriculture, Giza-Orman, United Arab Republic
Salamini, Francesco - Ist. Sper. Cerealicoltura, 9 Via Stezzano 24, Bergamo, Italy
Sanchez, F. M. - Colegio de Postgraduados, Escuela Nacional de Agric., Chapingo, Mexico
Saric, Tomislav - UL Save Kovasevica 11/I Stan 4, 21000 Novi Sad, Yugoslavia
Sarkar, K. R. - Room 114, Nuclear Res. Lab., Indian Agric. Res. Inst., New Delhi-12, India
Sarkissian, Igor V. - Institt. of Life Science, Texas A & M University, College Station, Texas 77343
Sarma, M. S. - c/o Indian Jute Industries, Research Assoc., 17 Taratala Road, Calcutta 53, India
Sartori, Lorraine - Dept. of Biology, Boston College, Chestnut Hill, Massachusetts 02167
Sastry, G. R. K. - Dept. of Genetics, University of Leeds, Leeds-2, United Kingdom
Saura, Fulgencio - Corrientes 617, piso 10, Buenos Aires, Argentina
Sawtelle, Kathleen - Dept. of Botany, U. of Rhode Island, Kingston, Rhode Island 02881
Saxena, K. M. S. - Dept. of Biology, Grambling State University, Grambling, Louisiana 71245
Sayed, Sayed Galal - P. O. Box 953, Cairo, Egypt
Scandalios, John G. - Dept. of Genetics, N. C. State University, Raleigh, North Carolina 27607
Schaeffer, Jurgen R. - Dept. of Plant & Soil Sci., Montana State College, Bozeman, Montana 59715
van Schaik, N. - Dept. Genetics, Univ. of the Witwatersrand, Johannesburg 2000, Rep. of South Africa
Scheifele, Gordon L.- Dept. of Plant Pathology, Pennsylvania State Univ., University Park, Pennsylvania 16802
Schlick, R. W. - Earl May Seed Co., Shenandoah, Iowa 51603
Schnell, F. W. - Universitat Hohenheim (LH), 7000 Stuttgart 70 (Hohenheim), Postfach 106, Garbenstrasse 9, Germany
Schwartz, Drew - Dept. of Plant Sciences, Indiana University, Bloomington, Indiana 47401
Scossiroli, R. E. - Ist. di Genetica della Univ., Via F. Selmi, 3, 40126 Bologna, Italy
Sehgal, S. M. - Pioneer Hibred Int'l., Inc., 1206 Mulberry St., Des Moines, Iowa 50308
Selley, H. N. G. - P. O. Box 553, Kitale, Kenya, East Africa
Sevilla, Ricardo - Prog. Coop. Inv. En Maiz, Univ. Nac. Agraria-La Molina, Apartado 456, Lima, Peru
Shafer, John - 3031 N. Roselawn Drive, Logansport, Indiana 46947
Shank, D. B. - Dept. of Plant Science, South Dakota State Univ., Brookings, South Dakota 57006
Shaver, Donald - 1143 East John St., Salinas, California 93905
Sheridan, Karen A. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
Sheridan, W. F. - Biol. Dept., Univ. of North Dakota, Grand Forks, North Dakota 58201
Shiga, Toshio - Div. Genet., Nat. Inst. Agr. Sci., Oh-Hara 1-24, Hiratsuka, Kanagawa, 254, Japan
Shih, Katherine Lu - Dept. of Genetics, Stanford University, School of Medicine, Stanford, California 94305
Shoemaker, Russell, L. - Botanical Laboratories, University of Arizona, Tucson, Arizona 85721

Shortess, David K. - Dept. of Biology, New Mexico Inst. of Mining and Technology, Socorro, New Mexico 87801
Silva, Jairo - Embrapa/C. P. 1316, 70.000 - Brasilia, D. F., Brasil
Simchen, G. - Lab. of Genetics, Hebrew University, Jerusalem, Israel
Simmonds, N. W. - Scottish Plant Breeding Sta., Pentlandfield, Roslin, Midlothian, Scotland
Sinclair, John - Zoology Dept., Indiana University, Bloomington, Indiana 47401
Singh, Joginder - Cereal Research Lab., Indian Agricultural Res. Inst., New Delhi, 12, India
Singh, K. B. - Dept. of Plant Breeding, Punjab Agric. University, Ludhiana, India
Singh, Rameshwar - Agric. Research Instit., P. O. Dholi (Muzaffarpur), Behar, India
Singleton, Katerina I. - 5853 Houston Road, West Lafayette, Indiana 47906
Singleton, W. R. - 1841 University Circle, Charlottesville, Virginia 22903
Sinha, S. K. - Dept. of Botany, Orissa Univ. of Agric. & Tech., Bhubaneswar, India
Skepasts, A. V. - New Liskeard College of Agricultural Techn., New Liskeard, Ontario, Canada
Smeltzer, Dale - The Rockefeller Foundation, GPO Box 2453, Bangkok, Thialand
Smirnov, Victor - 7/9 Universitetskaja Embank, Leningrad University, Dept. of Genetics and Selection, Leningrad U.S.S.R.
Smith, Clyde F. - Dept. of Botany, University of Maryland, College Park, Maryland 20742
Smith, George E. - R. 1, Monticello Road, Champaign, Illinois 61820
Smith, H. H. - Dept. of Biology, Brookhaven National Lab., Upton, Long Island, New York 11973
Smith, James D. - Genetics Section, Plant Sciences, Texas A&M University, College Station, Texas 77843
Smith-White, S. - Dept. of Genetics, School of Biological Sci., University of Sydney, Sydney NSW 2006, Australia
Snope, Andrew - Div. of Science & Math, Essex Community College, Essex, Maryland 21237
Snyder, John R. - Agronomic Research Center, Sycamore Road, DeKalb, Illinois 60115
Splitter, Melvin V. - Kathmandu (ID), Dept. of State, Washington, D. C. 20521
Sprague, G. F. - Dept. of Agronomy, University of Illinois, Urbana, Illinois 61801
Springer, Warren D. - Genetics, Cornell Univ., Ithaca, New York 14850
Steele, Leon - Funk Seeds Intern. Inc., 1300 West Washington St., Bloomington, Illinois 61701
Steffensen, Dale - Botany Dept., University of Illinois, Urbana, Illinois 61801
Stein, Otto L. - Dept. of Botany, Univ. of Massachusetts, Amherst, Massachusetts 01002
Stern, Herbert - Dept. of Biology, Univ. of California - San Diego, La Jolla, California 92037
Sternbach, John M. - Ranger Hall, Univ. of Rhode Island, Kingston, Rhode Island 02882
Stevens, Barbara J. - Biologie Cellulaire 4, Batiment 444, Faculte des Sciences, 91 Orsay, France
Stinson, Harry - Dept. of Plant Breeding, Cornell University, Ithaca, New York 14850
Stout, John T. - Genetics Bldg., Univ. of Wisconsin, Madison, Wisconsin 53706
Stringam, Gary R. - Forage Crops Section, Canadian Dept. of Agric., University of Saskatchewan, Saskatoon, Canada
Stringfield, G. H. - 212 Knollwood Drive, DeKalb, Illinois 60115
Stroup, Dorothy - 3743 Jocelyn St. NW, Washington, D. C. 20015

Stuber, Charles W. - Dept. of Genetics, North Carolina State Univ., Raleigh, North Carolina 27607
Stucker, Robert - Dept. of Agron. & Pl. Gen., University of Minnesota, St. Paul, Minnesota 55108
Styles, D. - Dept. of Biology, University of Victoria, Victoria, British Columbia, Canada
Sullivan, Sue Lynn - Dept. Plant. Br. Biom., Cornell University, 252 Emerson Hall, Ithaca, New York 14850
Swaminathan, M. S. - Indian Agricultural Research Institute, New Delhi - 12, India
Tantravahi, R. V. - Suburban Exper. Sta., University of Massachusetts, 240 Beaver Street, Waltham, Massachusetts 02154
Tatum, Loyd A. - 379 Crown Point, Columbia, Missouri 65201
Tavcar, A. - Dept. of Plant Breeding and Genetics, University of Zagreb, Zagreb, Yugoslavia
Taylor, A. D. - Robson Seed Farms Corp., P. O. Box 265, Hall, New York 14463
Thomas, John P. - 739 North Lake Drive, Marshall, Missouri 65340
Thomas, W. I. - Agric. Exper. Sta., 229 Agric. Admin. Bldg., University Park, Pennsylvania 16802
Thompson, D. L. - Crop Science Dept., North Carolina State Col., Raleigh, North Carolina 27607
Thompson, Jack C. - Southern States Co-op, 2600 Durham St., Richmond, Virginia 23220
Thompson, M. E. - Dept. of Biology, Brookhaven National Lab., Upton, Long Island, New York 11973
Timothy, D. H. - Dept. of Crop Science, North Carolina State Univ., Raleigh, North Carolina 27607
Ting, Yu-Chen - Dept. of Biology, Boston College, Chestnut Hill 67, Boston, Massachusetts 02167
Tomov, Nicola - Institute for Maize, Kneja, Bulgaria
Trambusti, Paolo - Asgrow Seed Co., Internat., P. O. Box 725, Orange, Connecticut 06477
Troyer, A. F. - Pioneer Hi-Bred Corn Co., Mankato, Minnesota 56001
Tsotsis, Basil - DeKalb Agresearch, Inc., Sycamore Road, DeKalb, Illinois 60115
Tsuchiya, T. - Dept. of Agronomy, Colorado State University, Fort Collins, Colorado 80521
Tulpule, S. H. - University of Poona, Dept. of Botany, Poona - 7, India
Uchimiya, Hirofumi - Inst. for Agric. Research, Tohoku University, Sendai, Japan
Ullstrup, A. J. - Dept. of Botany & Pl. Path., Purdue University, Lafayette, Indiana 47907
Umali, D. L. - College of Agriculture, University of the Phillippines, College, Laguna, Phillippines
Uzuno, Takumi - The Ford Foundation, G.P.O. Box 668, Lahore, Pakistan
Valentine, Fredrick - Dept. of Botany, SUNY Coll. Envir. Sci. and Forestry, Syracuse, New York 13210
Van Der Walt, W. J. - c/o Asgrow South Africa, Box 2054, Pretoria, South Africa
Van Eijnatten, C. L. - University of Nairobi, P.M.B. 30197, Nairobi, Kenya East Africa
Vasal, S. K. - CIMMYT, Londres 40, Mexico 6, D.F., Apdo. Postal 6-641, Mexico
Vega, Pedro C. - Instituto de Genetica, Univ. Central de Venezuela, Maracay, Venezuela
Venkateswarlu, J. - Botany Dept., Andhra University, Waltair, India
Verma, Ram S. - Dept. of Pediatrics, JFK Center, 4200 E. 9th Ave., Denver, Colorado 80220
Vetturini, Mario - c/o Roffi S.S.A.S., Via di Galliera 27/3, 40013 Castelmaggiore, Bologna, Italy

Viegas, G. P. - Cargill Agricola S/A, Rua Jose Vilagelin Jr. 81, Campinas, Est. S. Paulo Brazil
Vineyard, Marvin L. - Moews Seed Co., Granville, Illinois 61326
Violic M., Alejandro - Estacion Experimental, "La Platina", Casilla 5427, Correo 3, Santiago, Chile
Voris, Merle - Box 457, Windfall, Indiana 46076
Vosa, Ganio G. - Botany School, Oxford University, Oxford, England
Waines, J. Giles - Dept. of Plant Sciences, U. of California, Riverside, California 92502
Walbot, V. - Dept. of Biology, Washington Univ., St. Louis, Missouri 63130
Walden, D. B. - Dept. of Botany, University of Western Ontario, London, Canada
Walles, Bjorn - Royal College of Forestry, Dept. of Genetics, Stockholm 50, Sweden
Wang, Andrew - Dept. of Agron. & Pl. Genetics, University of Minnesota, St. Paul, Minnesota 55108
Ward, Edward - Dept. of Biology, Univ. of Winnipeg, Winnipeg 2, Canada
Watanabe, Y. - Div. of Genetics, Nat. Inst. Agric. Sci., Hiratsuka, Kanagawa, 254, Japan
Weber, David - Dept. of Biological Sci., Illinois State University, Normal, Illinois 61761
Welch, James E. - Dept. of Vegetable Crops, University of California, Davis, California 95616
Wellwood, A. A. - Biology Dept., Waterloo Lutheran Univ., Waterloo, Ontario, Canada
von Wettstein, D. - Institute of Genetics, Oster Farimagsgade 2A, Copenhagen K., Denmark
Whalen, R. H. - Dept. of Biology, South Dakota State University, Brookings, South Dakota 57006
Whitehead, Wayne - PAG Seeds, P. O. Box 467, Monticello, Illinois 61856
Widholm, J. M. - Dept. of Agronomy, University of Illinois, Urbana, Illinois 61801
Widstrom, Neil W. - U.S.D.A., Georgia Coastal Plain Experiment Station, Tifton, Georgia 31794
Wilcox, Wesley C. - Funk Seeds Internat., Inc., 1300 West Washington St., Bloomington, Illinois 61701
Wilkes, H. Garrison - Biology - College II, University of Mass./Boston, Boston, Massachusetts 02125
Williams, Absalom F. - R. R. 1, Mitchell, Indiana 47446
Williams, Robert E. - Columbiana Seed Co., Eldred, Illinois 62027
Williams, W. M. - Grassland Division, DSIR Private Bag, Palmerston North, New Zealand
Wilmarth, Charles E. - Acco Seed Research Dept., Belmond, Iowa 50421
Wright, James E. Jr. - Dept. of Botany, The Pennsylvania State Univ., University Park, Pennsylvania 16802
Yabuno, T. - 238 Yamanouchi-Cho, Sumiyashi-Ko, Osaka, Japan
Yoder, O. C. - Dept. Plant Path., Cornell Univ., Ithaca, New York 14850
Yohe, John M. - Amcongen-Recife, DNPEA Project, Apo, New York, New York 09676
Yong, H. S. - Gen. Div. Sch. Biol. Sci., University of Malaya, Pantai Valley, Kuala Lumpur, Malaysia
Yu, Ming H. - Agricultural Research Service, P. O. Box 5098, Salinas, California 93901
Zainal-Abidin, Md. I. - Curtis Hall, University of Missouri, Columbia, Missouri 65201
de Zerpa, Dora M. - Instituto de Genetica, Univ. Central de Venezuela, Maracay, Venezuela
Zimmering, Stanley, Dept. of Biol., Brown Univ., Providence 12, Rhode Island 02912
Zobel, Richard W. - Monsanto Co., 800 No. Lindbergh, St. Louis, Missouri 63166
Zuber, M. S. - Curtis Hall, University of Missouri, Columbia, Missouri 65201

VII. AUTHOR AND NAME INDEX

Corrigenda for the 1970 Index, volumes 3 through 43

Page	Name	Corrected line
4	Ashman, R. B.	41:171,199 42:155,156
6	Bellini, G.	37:185 39:200 40:81
14	Duvick, D. N.	26:34 27:82
20	Hanson, G. P.	31:91 35:62 36:35
23	Jimenez, T. J.	Jimenez T., J. 36:89 37:139
25	Knott, D. R.	24:66 30:138,140
26	Langham, D. G.	21:55 25:52 29:51
26	Laughnan, J. R.	34:45,46 35:49 36:29,116,117
35	Peterson, P. A.	43:71,238
40	Saramori, H.	Sasamori, H. 34:154
42	Sharma, D.	42:157
45	Stoner, C. R.	Stonor, C. R. 24:44,78 38:69
45	Styles, E. D.	41:38,39,231,232 42:196
45	Tantravahi, J. S.	Tantravahi, U. S. 38:54
49	Weber, D.	42:56,59,207 43:241
50	Wright, J. E.	delete 33:102
50	Wright, S.	15:49 33:102 41:155

Dr. G. P. Redei, organizer of the STADLER GENETICS SYMPOSIA, calls attention to the 8th Symposium, to be held April 9-10, 1976, at Columbia, Missouri:

D. Apirion: Genetic approaches to a cellular organelle, the ribosome.
J. E. Carrel: Aphrodisiacs and antiaphrodisiacs: better loving through chemistry.
A. Cerami: The development of new drugs for genetic diseases.
A. L. Demain: Genetic regulation of fermentation organisms.
J. W. Drake: Mutagenic mechanisms in bacteriophage T4.
A. Loeblich III: Dinoflagellates: genetics and DNA characterization.
D. E. Pettijohn: Tertiary structure of the bacterial nucleoid.
D. Schwartz: Regulation of alcohol dehydrogenase genes in maize.
O. P. Sehgal: RNA:protein and protein:protein interactions in the virions of Southern Bean Mosaic Virus.

The detailed program can be obtained from Conferences and Short Courses, University of Missouri, 347 Hearnes Bldg., Columbia, Missouri 65201, USA. Dr. Redei can be reached by telephone at (314)882-6434.

Proceedings of this and of previous Symposia can be ordered from Stadler Genetics Symposia, 117 Curtis Hall, Univ. of Missouri, Columbia, Missouri 65201. Price is $5.00 per volume plus 50¢ per order for postage and handling.

An announcement from Dr. Mike Shelby:

The Environmental Mutagen Information Center is producing an indexed bibliography entitled Chemical Mutagenesis in Plants. This publication will contain nearly 3,000 references, most published since 1969, and will cite reports of original research, reviews, abstracts, symposia and book chapters. References were selected from several hundred journals covering a large part of the world's literature and encompass two main areas of research--the use of plant systems in detecting chemical mutagenicity and the use of chemical mutagens in mutation breeding. Indexes of authors, organisms, chemicals and assay systems will refer the user to pertinent references in the bibliography. A separate section will contain an indexed bibliography of literature dealing with the mutagenicity of compounds synthesized by plants. As used in this publication "Plants" includes all divisions of the plant kingdom except the fungi. Questions concerning availability should be sent to Dr. Mike Shelby, Environmental Mutagen Information Center, Oak Ridge Nat. Lab., P. O. Box Y, Bldg. 9224, Oak Ridge, Tennessee 37830.

From Dr. Kenton L. Chambers:

The American Society of Plant Taxonomists announces the formation of a new journal, SYSTEMATIC BOTANY, which will begin publication in 1976. It is intended that a minimum of 400 pages per yearly volume will be published, the issues to appear quarterly. The editor will be Dr. William Louis Culberson, Department of Botany, Duke University, Durham, North Carolina 27706, USA. Membership in the ASPT is welcomed from all persons interested in biological systematics, reproductive and evolutionary biology, biogeography, chemotaxonomy, numerical taxonomy, or paleontology. Members of the Society will receive a subscription to the new journal and have the privilege of submitting papers for publication. Any person who would like to join the ASPT should write to the Society's Treasurer, Dr. L. C. Anderson, Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306, USA, and include payment of the yearly dues--$16.00 for a regular membership, $20.00 for a family membership (one copy of the journal), or $8.00 for a student membership. Instructions for the preparation of manuscripts can be obtained from Dr. Culberson. The purpose of SYSTEMATIC BOTANY is to publish both original research reports and interpretive and review articles on all aspects of the systematics of cryptogamic and phanerogamic plants.