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**L. FOREWORD**

This year it has not been necessary to solicit funds from hybrid corn companies to help defray the publication costs of the 1960 Maize Genetics Cooperation News Letter. Modest grants made by Indiana University and by the National Science Foundation should be sufficient and we are happy that we do not have to pass the hat. For the first time we are using a new method of reproduction which we hope meets with your approval. I wish to acknowledge with gratitude the editorial assistance of Miss Ellen Dempsey, who has been largely responsible for assembling the News Letter.

M. M. Rhoades

## II. REPORTS FROM COOPERATORS

BLANDY EXPERIMENTAL FARM  
University of Virginia  
Charlottesville, Virginia

1. A yellow green mutant from Afghanistan.

A yellow green mutant was isolated from open pollinated seed from Afghanistan. Pollination of this stock by  $yg_2$  gave seedlings that were all green, hence it is not allelic to  $yg_2$ . Seed is available.

W. Ralph Singleton

2. A mutant for indeterminate growth.

In the same open pollinated lot of corn from Afghanistan there arose a mutant for indeterminate growth similar to one reported earlier (Singleton, Jour. Hered. 37:61-64). The plants continue to grow all summer producing very short internodes, and produce tassels and silks only after being moved into the greenhouse. Apparently the short days inhibit floral development.

W. Ralph Singleton

3. Correlation of silk, anther and pericarp color.

Plants segregating for silk, anther, and pericarp color were classified at time of silking for silk and anther color and later classified for the "cherry" pericarp color or absence of it. In one progeny the following counts were obtained:

Genotype	Silk color.	Anther color.	Cherry Pericarp	
			Present	Absent
$R^{mm}$	Deep wine	Red-variegated	49	1
$R^{gg}$	Green	Green	0	27
Total			49	28

Only one exception was noted; this may have been due to faulty classification.

Another progeny produced 31 ears with cherry pericarp from plants with  $R^{mm}$  silk and anthers and 25 ears with no pericarp color from plants with green silks and anthers. No exceptions were noted in this progeny.

One progeny in 1959 was homozygous for the deep cherry pericarp, with the usual red silk and anther color. Apparently this mutant behaves similarly to  $R^{ch}$  although the plant color is believed darker. Does any one have seed of  $R^{ch}$ ?

W. Ralph Singleton

#### 4. Mutations induced in preembryo stage.

In 1959 a stock of  $Yg_2/Yg_2$  was pollinated by  $yg_2/yg_2$ . The first set of plants was placed in the radiation field where they received 33r/hr for 23.5 hours to give a total dose of 775r. Every day thereafter for 10 days a different set of plants was radiated.

No mutations were scored in the material radiated on the first day. However, the ears radiated on the second day produced several seedlings which were yellow green and several which were one-half yellow green. Ears radiated at later stages of development produced seedlings which showed streaks of yellow green. The size of the streaks decreased with the later stages.

The mutations remain to be analyzed. This seems to be a desirable stage for the induction of recoverable mutations in maize, possibly other material as well. Severely damaged cells will be eliminated, thus giving an automatic screening of most harmful changes. Other genes will be tested in 1960.

Alan Caspar

CALIFORNIA INSTITUTE OF TECHNOLOGY  
Pasadena, California

#### 1. Translocations.

The following list of translocations were obtained from irradiation of CC5/L317 and closely related stocks (numbers 8001 to 8864) or from irradiation of a high knob stock (8890 to 9021).

Symbol	Chromosomes	Chromosomal Designation	
8001	1-9	1S. 51	9L. 24
8041	1-5	1L. 80	5L. 15
8004	4-8	4S. 27	8L. 84
8045	2-7	2S. 12	7L. 06
8006	3-7	3L. 88	7L. 90
8048	1-3	1L. 11	3S. 18
8302	1-9	1S. 55	9L. 29
8103	4-7	4S. 81	7L. 76
8104	3-5	3L. 05	5L. 08
8069	4-5	4S. 34	5S. 71
8108	4-5	4S. 37	5S. 72
8249	1-4	1L. 26	4L. 63
8023	3-8	3L. 18	8L. 16
8027	2-4	2L. 15	4L. 43
8143	6-7	6L. 35	7L. 36
8145	3-6	3L. 17	6L. 26
8032	3-9	3S. 26	9L. 96
8219	2-10	2L. 50	10L. 35
8219	5-6	5L. 71	6S. 84 <sup>sat</sup>
8321	2-5	2L. 86	5L. 11
8322	2-7	2L. 76	7L. 74

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Symbol	Chromosomes	Chromosomal Designation	
8339	4-6	4L. 87	6L. 79
8345	5-10	5L. 87	10S. 61
8346	7-8	7S. 49	8S. 30
8347	1-5	1S. 84	5L. 51
8349	3-10	3S variable	10 variable
8350	3-8	3L. 75	8S. 60
8351	3-5	3L. 68	5L. 76
8367	3-8	3S. 28	8S. 52
8368	1-4	1S. 14	4S. 30
8374	4-7	4L. 24	7L. 55
8375	1-10	1L. 69	10L. 64
8376	2-8	2L. 95	8L. 03
8380	4-6	4S. 47	6L. 18
8383	7-9	7 near cent.	9 near cent.
8386	5-9	5L. 87	9S. 13
8388	1-5	1S. 30	5S. 25
8389	1-9	1L. 74	9L. 13
8395	4-5	4L. 63	5L. 82
8397	3-4	3S. 74	4S. 55
8405	1-3	1L. 60	3L. 31
8412	3-10	3S. 39	10S. 36
8415	1-6	1L. 29	6S. 82 <sup>org.</sup>
8420	5-8	5S. 90	8L. 33
8428	4-6	4L. 32	6L. 28
8428	2-8	2L. 16	8L. 10
8439	6-9	6L. 06	9S. 73
8441	2-6	2L. 94	6S. 79 <sup>org.</sup>
8443	3-4	3L. 12	4L. 13
8447	3-9	3S. 44	9L. 14
8452	1-6	1S. 80	6L. 52
8456	4-8	4S. 22	8L. 78
8457	5-9	5L. 78	9S. 83
8460	1-9	1S. 13	9L. 24
8465	3-9	3S. 27	9L. 41
8483	2-3	2L. 14	3L. 12
8491	1-10	1L. 45	10L. 76
8513	5-8	5S. 34	8L. 24
8525	8-9	8L. 06	9S. 63
8536	6-9	6L. 18	9S. 81
8553	2-5	2L. 24	5L. 23
8558	7-9	7S. 22	9L. 16
8562	3-9	3L. 65	9L. 22
8563	1-4	1L. 39	4S. 21
8580	7-8	7 variable	8 variable
8590	5-6	5S. 29	6L. 56
8591	5-9	5S. 09	9L. 25
8602	1-4	1S. 41	4L. 81
8607	4-8	4S. 30	8L. 33
8622	4-5	4L. 30	5L. 52

Symbol	Chromosomes	Chromosomal Designation	
8628	2-3	2L. 54	3L. 44
8630	9-10	9S. 28	10L. 37
8630	5-7	5L. 38	7L. 24
8634	3-4	3S. 71	4L. 75
8637	1-3	1L. 37	3S. 50
8640	1-8	1L. 11	8L. 16
8645	6-10	6L. 21	10L. 28
8651	6-10	6L. 27	10L. 48
8658	1-6	1L. 81	6L. 90
8659	7-9	7S. 55	9S. 55
8662	2-3	2S. 78	3L. 83
8663	1-4	1S. 09	4S. 36
8665	5-6	5L. 58	6L. 25
8666	3-8	3S. 30	8L. 14
8671	5-7	5L. 96	7L. 67
8672	3-6	3L. 44	6L. 87
8679	5-7	5S. 09	7S. 26
8682	2-4	2S. 70	4S. 25
8683	1-8	1L. 11	8L. near cent.
8696	5-6	5L. 89	6S. 80 <sup>org.</sup>
8704	5-9	5L. 35	9L. 85
8746	5-8	5S. 84	8L. 25
8764	4-6	4L. 32	6L. 90
8768	6-9	6L. 89	9S. 61
8770	1-10	1L. 05	10L. 38
8782	1-5	1 near cent.	5 near cent.
8786	2-6	2S. 90	6S. 77
8796	5-8	5L. 76	8L. 11
8806	5-8	5L. 72	8S. 59
8818	5-6	5S. 91	6L. 93
8824	1-9	1S. 06	9L. 83
8854	5-9	5S. 33	9S. 36
8857	2-6	2S. 08	6L. 24
8864	2-10	2S. 10	10L. 76
8890	1-9	1L. 28	9L. 22
8891	4-9	4 near cent.	9 near cent.
8895	5-9	5L. 37	9L. 17
8904	6-10	6L. 51	10L. 83
8906	6-9	6L. 27	9L. 59
9028	4-10	4S. 57	10L. 89
8918	1-9	1S. 21	9L. 20
8919	1-8	1S. 53	8L. 44
8927	4-6	4L. 70	6L. 18
8936	5-9	5L. 43	9L. 80
8963	3-6	3S. 24	6L. 14
8969	3-4	3S. 75	4L. 75
8972	1-5	1S. 56	5S. 29
8987	4-8	4S. 58	8L. 76
8995	1-3	1S. 49	3L. 06

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Symbol	Chromosomes	Chromosomal Designation	
8997	5-8	5L. 16	8L. 08
9002	2-6	2L. 57	6L. 58
9020	8-10	8L. 13	10S. 50
9021	1-9	1L. 26	9L. 83

E. G. Anderson

A. E. Longley

## CLYDE BLACK &amp; SON HYBRID SEED FARMS

Ames, Iowa

and

## MEYERS HYBRID CORN COMPANY

Hillsboro, Ohio

1. Yield, stand and lodging of restored and of male sterile single crosses of maize compared to their regular counterpart single crosses.

Tests were conducted in the summer of 1959 to compare thirteen restorer single crosses and thirty-one male sterile single crosses on T cytoplasm with their regular counterpart single crosses on normal cytoplasm for yield, stand and lodging. All the single crosses in these tests were samples from lots produced by open pollination in isolated fields and represent material available for the production of commercial hybrid seed corn.

All the lines were regular corn belt dents and none of them originally were on T cytoplasm or carried the dominant allele of the full restoring gene designated as the "Rf" gene. However, some of the lines used, namely, M14, Oh41 and K166, carried a gene or genes for heavy partial restoring which made it impossible to follow the "Rf" gene in the conversion process and are therefore designated with the suffix "TRp" or "NRp", depending on whether the line had been converted to T cytoplasm or not. All other lines were non-restorers, unless the dominant allele of the Rf gene had been introduced in the conversion process. All converted lines were on T cytoplasm, whether they carried the full restorer gene, the partial gene or genes or were cytoplasmic male sterile. The suffixes TRf, TRp and Tms were used with the regular line designations to give the pertinent added information concerning the hereditary make-up of these converted counterpart lines.

Four donors for the Rf gene were used in the pollen restorer conversion matings. These had all been tested to determine that the restorer gene which they carried was allelic with the full restorer gene carried by the I153 inbred line. All the converted lines (TRf, TRp and Tms) had been backcrossed five generations or more after the initial outcross to introduce the T cytoplasm and the Rf gene, if also introduced. In addition, the restorer line L317TRf had been selfed twice before the production of the restorer singles in which it was used. The line K166 had not been converted onto T cytoplasm but was known to carry a gene or genes for heavy partial restoring. This line was used as the pollinator in the production of one of the restorer single crosses. All the other restorer (TRf) lines used were in the last backcross generation and the plants shedding pollen in the single-crossing field were therefore heterozygous for the Rf alleles. As seed parents in making up several of the restorer single crosses, some inbred lines on T cytoplasm but without restorer genes, (Tms lines), were used.



All comparisons of these counterpart single crosses on the two cytoplasm were made between paired plots which were adjacent to each other in all locations. The restorer single crosses versus their regular counterparts were grown in three locations: Ames, Iowa, Frankfort, Indiana, and Hillsboro, Ohio, in the summer of 1959. In all locations the test plots were planted by hand and the intended rate of planting was 16,000 seeds per acre. The plantings were made in hills with 40-inch spacings, each having four kernels. The stands were not thinned. The total number of plants in all plots were counted at harvest, as were the number of lodged plants. There were five hills planted in each of two replications at Ames and a full stand would have been forty plants. Eight hills were planted in each of two replications at Frankfort, Indiana, and a full stand would have been sixty-four plants. At Hillsboro, Ohio, ten hills were planted in one series and a full stand would have been forty plants. The plots were harvested by hand at maturity and yields were calculated as bushels per acre of shelled corn corrected to 15.5% moisture.

The male sterile singles versus their regular counterparts were tested at one location, Ames, Iowa, in 1959. The tests for these comparisons were conducted the same as were the restorer comparisons at the same location.

The yields for all the samples in the test of the restorer singles are given in Table 1, and Table 2 shows the differences for the paired comparison when the yield of the regular single cross was subtracted from the yield of the restorer single cross.

TABLE 1

Yield of 13 Restorer Single Crosses on T Cytoplasm Compared with their Counterpart Regular Single Crosses on Normal Cytoplasm.

Pedigrees of restorer single crosses	Yield in b. p. a. 15.5% H <sub>2</sub> O			Pedigrees of regular single crosses	Yield in b. p. a. 15.5% H <sub>2</sub> O		
	Ames Iowa	Frank- fort Ind.	Hills- boro Ohio		Ames Iowa	Frank- fort Ind.	Hills- boro Ohio
M14TRpxB103TRf	108	86	77	: M14xB103	82	81	67
M14TRpxOh51A TRf	101	112	83	: M14xOh51A	124	113	86
M14TRpxOh43TRf	113	79	93	: M14xOh43	121	105	93
M14TRpxB14TRf	131	116	84	: M14xB14	124	115	74
M14TRpxC103TRf	139	134	100	: M14xC103	114	101	102
M14TRpx187-2TRf	106	108	76	: M14x187-2	100	97	88
Oh41TRpxHyTRf	126	115	100	: Oh41xHy	121	123	90
Oh43TmsxC103TRf	140	125	X	: Oh43xC103	133	108	X
C103TmsxB14TRf	117	141	116	: C103xB14	116	119	120
420TmsxHyTRf	114	110	X	: 420xHy	109	98	X
HyTmsxL317TRf	130	132	122	: HyxL317	133	130	96
HyTmsxB14TRf	129	96	107	: HyxB14	115	116	74
L317TRfxK166NRp	127	X	98	: L317xK166	106	X	96

TABLE 2

Differences in Yield Between Restorer Single Crosses on T Cytoplasm Minus Yield of Counterpart Regular Single Crosses on Normal Cytoplasm. Data from Table 1.

Basic Pedigree	Yield in bushels per acre			Av. dif.
	Ames Iowa	Frank- fort Ind.	Hills- boro Ohio	
M14xB103	26	5	10	14
M14xOh51A	-23	- 1	- 3	- 9
M14xOh43	- 8	-26	- 0	-11
M14xB14	7	1	10	6
M14xC103	25	33	- 2	19
M14x187-2	6	11	-12	2
Oh41xHy	5	- 8	10	2
Oh43xC103	7	17	X	12*
C103xB14	1	22	- 4	6
420xHy	5	12	X	8*
HyxL317	- 3	2	26	8
HyxB14	14	-20	33	9
L317xK166	21	X	2	8*
	Total	201		

\* Yields from 2 locations only

Mean difference: Plus 5.6 bushels per acre

$\sigma$  s. dif. = 14.3 b. p. a.

$\sigma$  mean dif. = 2.4 b. p. a.

The yields for the pollen restorer single crosses on T cytoplasm averaged 5.6 bushels per acre higher than the values for the regular single crosses on normal cytoplasm and the standard deviation for this mean difference was 2.4 bushels per acre. From these values it can be assumed that these pollen restorer single crosses on T cytoplasm yielded significantly higher than their counterpart regular single crosses on normal cytoplasm.

The values for the stands of all the cultures in the thirty-six paired comparisons are given in Table 3.

TABLE 3

Stands of 13 Restored Single Crosses on T Cytoplasm Compared with their Counterpart Regular Single Crosses on Normal Cytoplasm.

Basic Pedigree	Number of Plants per Comparison							Total	
	Pollen restorer single crosses on T cytoplasm				:	Regular counterpart single crosses on normal cytoplasm			
	Ames Iowa	Frank- fort Ind.	Hills- boro Ohio	Total	:	Ames Iowa	Frank- fort Ind.		Hills- boro Ohio
M14xB103	39	58	31	128	:	30	55	30	115
M14xOh51A	32	62	34	128	:	39	60	32	131
M14xOh43	35	49	34	118	:	40	61	32	133
M14xB14	39	63	36	138	:	40	58	33	131
M14xC103	36	64	31	131	:	33	51	37	121
M14x187-2	31	63	36	130	:	36	59	35	130
Oh41xHy	38	57	36	131	:	39	61	31	131
Oh43xC103	36	56	X	92*	:	37	55	X	92*
C103xB14	37	63	37	137	:	36	56	33	125
420xHy	36	59	X	95*	:	35	55	X	90*
HyxL317	39	62	28	129	:	35	55	35	125
HyxB14	38	51	33	122	:	39	57	30	126
L317xK166	38	X	37	75*	:	33	X	32	65*
Total				1554					1515

\* Stands from 2 locations only.

Average difference 36 paired comparisons equals 1.1 plant per test more for the restorer single crosses. This difference is not significant in these data.

Table 4 gives the number of lodged plants in each plot of the thirty-six paired comparisons.

TABLE 4

Paired Comparisons for Lodged Plants of Restorer Single Crosses on T Cytoplasm with their Counterpart Regular Single Crosses on Normal Cytoplasm.

Basic Pedigree	Number of Lodged Plants per Comparison								
	Pollen restorer single crosses on T cytoplasm				:	Regular counterpart single crosses on normal cytoplasm			Total
	Ames	fort	Hills-	Total :	Ames	fort	Hills-		
	Iowa	Ind.	Ohio		Iowa	Ind.	Ohio		
M14xB103	0	6	1	7 :	1	3	5	9	
M14xOh51A	0	2	2	4 :	0	10	1	11	
M14xOh43	0	10	0	10 :	0	0	1	1	
M14xB14	0	0	0	0 :	0	3	1	4	
M14xC103	1	16	4	21 :	4	23	6	33	
M14x187-2	0	35	3	38 :	6	34	2	42	
Oh41xHy	1	7	24	32 :	2	29	7	38	
Oh43xC103	0	3	X	3* :	1	5	X	6*	
C103xB14	0	1	0	1 :	0	1	0	1	
420xHy	3	44	X	47* :	4	29	X	33*	
HyxL317	12	28	15	55 :	12	45	25	82	
HyxB14	0	1	0	1 :	0	0	0	0	
L317xK166	8	X	18	26* :	8	X	19	27*	
	Total				245			287	

\* Lodged plants from 2 locations only.

Average differences 36 paired comparisons equals 1.0 plant per paired comparisons more for the regular single crosses on normal cytoplasm. This value is not significant in these data. Significant differences very evidently exist between the values for the varieties and the values for the locations. A study of these differences was not, however, the purpose of this investigation.

The percentages of restored plants were determined in two tests, one at Lantana, Florida, season of 58-59 and one at Hillsboro, Ohio, in the season of 1959 for the 13 pollen restorer lots of seed in these experiments. In the Hillsboro test the percent restoring was determined for the plants in the same plots on which the other determinations were made. At Lantana, Florida, the plants were in a special planting for the determination of the percent restoring. The results are shown in Table 5.

TABLE 5

Percent of Restored Plants for the Restorer Single Crosses on T Cytoplasm in Two Tests.

Pedigree	Florida 58-59			:	Hillsboro 59		
	Total Plants	Restored Plants	% Restored		Total Plants	Restored Plants	% Restored
M14TRpxB103TRf	164	145	88%	:	38	37	97%
M14TRpxOh51A TRf	153	133	87%	:	36	18	50%
M14TRpxOh43TRf	160	132	82%	:	35	22	63%
M14TRpxB14TRf	162	142	88%	:	38	38	100%
M14TRpxC103TRf	105	78	74%	:	35	20	57%
M14TRpx187-2TRf	174	168	96%	:	37	32	86%
Oh41TRpxHyTRf	173	128	74%	:	38	27	71%
Oh43TmsxC103TRf	183	105	57%	:	39	20	51%
C103TmsxB14TRf	173	104	60%	:	40	19	48%
Os420TmsxHyTRf	147	122	83%	:	40	21	52%
HyTmsxL317TRf	X	X	X	:	29	25	86%*
HyTmsxB14TRf	176	84	48%	:	35	23	66%
L317TRfxK166NRp	177	177	100%	:	37	29	78%
Weighted average:	78% restored				68% restored		

\* Not included in weighted average percent restored.

All the TRf inbred lines except L317TRf were heterozygous for the Rf rf alleles. The M14TRp, Oh41TRp, and the K166NRp theoretically should be homozygous or nearly so for the gene or genes for heavy partial restoring. Therefore, in all the single crosses except those with L317TRf 50% of the plants would have been restored by the dominant Rf gene. Any significant increase of restoring in excess of 50% in these single crosses would be assumed to be the result of the dominant gene or genes for partial restoring carried by the M14TRp, Oh41TRp, or the K166NRp as influenced by environmental conditions or by modifying genes carried in either or both inbred lines or random variations of sampling.

The data from the paired comparisons of the 31 cytoplasmic male sterile singles with their regular counterpart singles are given in Table 6.

The yields for the cytoplasmic male sterile single crosses averaged 2.2 b. p. a. less than the values for the regular counterpart singles on normal cytoplasm. The standard deviation for this mean difference was 2.2 b. p. a. This difference is not large and in these data is not statistically significant. The total stands differed by only one plant between the totals for these two groups of single crosses. There was very little lodging in this test as a whole but no significant differences in lodging between the cytoplasmic male sterile cultures and the normal cultures were noted.

The T type of cytoplasm seems destined to replace the original type or types of cytoplasm in more and more of the commercial corn in the United States in the near future, with seed production following the "restored-sterile" method on this cytoplasm. Any, even minor, beneficial or detrimental effects of these two changes in the hereditary make-up of the corn plants becomes of great economic importance, as well as of basic scientific interest.

The results from these tests indicate that the cytoplasmic male sterile cultures tended to yield practically the same or slightly less than their pollen-fertile counterparts on normal cytoplasm, while the cultures with 50% or more restored pollen-fertile plants on T cytoplasm yielded appreciably more than their pollen-fertile counterpart cultures on normal cytoplasm. It would seem, therefore, that the yield of hybrids produced by the "restored-sterile" method on T cytoplasm would tend to yield sub-

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stantially higher than their sterile counterparts on T cytoplasm. This agrees with the results reported by Stringfield, G. H. "Fertility Restoration and Yields in Maize," *Agronomy Journal*, Vol. 50:215-218. 1958. This would indicate that as high a percentage of restored plants as possible should be obtained in seed produced by the "restored-sterile" method when T cytoplasm is involved.

TABLE 6

Yields, Stands and Lodged Plants of 31 Male Sterile Single Crosses Compared with their Counterpart Regular Single Crosses on Normal Cytoplasm. Tested at Ames, Iowa, in 1959.

Cyto- plasmic male sterile	Pedigree		Yield		Stand		Lodged	
	: Cyto- plasmic male sterile	: Cyto- plasmic male sterile	Reg- ular	reg- ular	minus : male sterile	Reg- ular	: male sterile	Reg- ular
Oh51A TmsxB8	: Oh51Ax88	: 91	101	-10	: 33	37	: 0	0
Oh51A TmsxW64A	: Oh51AxW64A	: 116	101	15	: 39	29	: 1	0
RLTmsx182B	: RLx182B	: 111	110	1	: 38	35	: 0	2
RLTmsx162	: RLx162	: 94	103	- 9	: 38	40	: 0	2
RLTmsxOh43	: RLxOh43	: 116	124	- 8	: 39	39	: 0	0
RLTmsx751	: RLx751	: 100	130	-30	: 34	39	: 1	0
RLTmsxOh51A	: RLxOh51A	: 110	112	- 2	: 40	38	: 2	0
W64ATmsxWF9	: W64AxWF9	: 102	82	20	: 37	31	: 0	0
WF9TmsxOh56A	: WF9xOh56A	: 107	115	- 8	: 37	36	: 6	1
WF9TmsxRL-4	: WF9xRL-4	: 102	92	10	: 36	38	: 0	3
WF9TmsxB8	: WF9xB8	: 118	118	0	: 37	33	: 0	0
WF9TmsxOh51A	: WF9xOh51A	: 130	100	30	: 38	35	: 0	1
WF9TmsxOh43	: WF9xOh43	: 112	133	-21	: 33	37	: 0	0
WF9TmsxB21	: WF9xB21	: 134	130	4	: 36	39	: 5	2
WF9TmsxOs420	: WF9xOs420	: 129	132	- 3	: 35	37	: 0	2
WF9TmsxI205	: WF9xI205	: 122	124	- 2	: 37	37	: 0	1
WF9TmsxB6	: WF9xB6	: 134	127	7	: 38	37	: 0	0
WF9TmsxW22	: WF9xW22	: 132	128	4	: 39	33	: 0	0
WF9TmsxB14	: WF9xB14	: 119	122	- 3	: 34	37	: 0	0
WF9TmsxHy	: WF9xHy	: 114	126	-12	: 29	37	: 0	0
WF9TmsxC103	: WF9xC103	: 152	136	16	: 39	35	: 0	1
WF9TmsxN6	: WF9xN6	: 132	125	7	: 39	38	: 0	1
WF9Tmsx751	: WF9x751	: 122	124	- 2	: 38	38	: 0	1
WF9Tmsx187-2	: WF9x187-2	: 118	120	- 2	: 38	37	: 0	2
WF9Tmsx38-11	: WF9x38-11	: 127	134	- 7	: 35	36	: 2	0
WF9Tmsx07	: WF9x07	: 122	134	-12	: 36	39	: 1	1
WF9Tmsx07A	: WF9x07A	: 118	129	-11	: 35	39	: 0	0
WF9TmsxB7	: WF9xB7	: 104	110	- 6	: 40	34	: 2	0
WF9TmsxR61	: WF9xR61	: 112	118	- 6	: 31	34	: 2	2
WF9Tmsx317	: WF9x317	: 108	116	- 8	: 38	35	: 9	5
07Tmsx187-2	: 07x187-2	: 110	131	-21	: 28	36	: 0	0
n = 31		: 3618	3687	-69	: 1124	1125	: 31	27

Mean difference in yield = -2.2 b. p. a.

$\sigma$  s. dif. = 12.4 b. p. a.

$\sigma$  mean dif. = 2.2 b. p. a.

In trying to explain the differences between cultures such as those reported here, at least four main variables must be considered. They are:

1. Differences due to the effects of the cytoplasm themselves
2. Possible pleiotropic effects of the restorer genes on other functions of the plant in addition to the restoration of pollen fertility
3. Changes in the genotypic make-up of the counterpart inbred lines remaining after the conversion processes have been carried out
4. The effect of pollen shedding as such on the other functions of the plants.

The results reported above may be explained as being due to two or more of the factors listed above. One very important problem will be to devise matings and experimental methods which will determine, as far as possible, the effects of each of these variables with the others held constant. Such matings are being made in the Florida 1959-1960 nursery for testing in experiments in the Corn Belt in 1960.

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1. Characterization of sterile cytoplasm.

In addition to the original S and T sources of sterile cytoplasm, we are currently maintaining 12 other sources, each in process of being combined with the genotypes of inbreds WF9 and A158. The detailed origins of 8 of these sources are given in Bulletin 610 of The Connecticut Agricultural Experiment Station, but for convenient reference the origins of the 12 new sources are presented in the table below. It will be noted that three sources, C, D and E, stem from various Vg stocks. Source E was listed in Bull. 610 as having originated from a cross between two Pennsylvania lines, but records kindly furnished by J. E. Wright show clearly that the source of this sterile cytoplasm was Coop stock 49-10, which was segregating Vg. The records also state that earlier Coop notes made by Emerson mention the presence of male sterile plants in this Vg stock (some progenies consisted of all male sterile plants). It is entirely possible that the Vg material originally maintained by the Coop carried sterile cytoplasm and restorer genes. Since the anthers of Vg plants often blast, it is probable that such plants would be used as seed parents in crosses, and in this way the cytoplasm of the Vg stock would be transmitted along with the Vg gene. Continued backcrossing would eliminate the restorer genes. This could account for the origin of cytoplasmic male steriles from Vg stocks.

A preliminary genetic test has been conducted on nine of the sources to determine whether each is S, T or a different type. The A158 and WF9 series of steriles, with from two to seven generations of backcrosses, were crossed by the inbreds NY16 and Ky21, both of which restore S and T. However, Buchert's findings (MNL, 1959) on the behavior of S restorer genes makes it possible to distinguish between S and T type restored steriles, provided the restorer genes are in heterozygous condition. In heterozygous restored S steriles, pollen grains with the non-restoring allele abort; thus, restoration is only 50 per cent. Heterozygous restored T steriles, on the other hand, approach 100 per cent restoration, since T restorers behave as though sporophytic in action.

The last two columns in the table show the results of the crosses sterile x NY16, and sterile x Ky21. The degree of restoration was estimated on the basis of pollen examinations in the field with a pocket magnifier, and on microscopic examinations of pollen stained with IKI. Exact counts of normal and aborted pollen grains were not made, but the difference between approximately 50 per cent and approximately 100 per cent normal pollen grains is readily apparent. The nine sources A through I were 50 per cent restored by NY16 and Ky21 in both the A158 and WF9 series of steriles. This indicates that all nine sources of cytoplasm are S type.

One cannot, of course, be certain that the restoration in all cases is effected by the conventional S restorer genes known to be present in NY16 and Ky21, since these inbreds could possess other restorer genes. It is apparent, nevertheless, that the restoration of cytoplasm A - I is similar to that characteristic of S type restoration. If the A - I restored sterile plants do have S type cytoplasm and typical S restorer genes, these plants should give all fertile offspring when crossed as pollen parents to S steriles. These crosses plus additional tests involving known S and T restorer lines have been made with all sources of sterile cytoplasm, and the results should provide more critical evidence on the nature of these cytoplasm.

Cytoplasmic Designation	Origin of cytoplasm	Source of Seed	Restoration (100% or 50%)	
			NY16	Ky21
T			100%	100%
S			50%	50%
A	Turkish Flint	PI 171 892	"	"
B	Brazilian Flint	F. G. Brieger	"	"
C	segregating progeny of Vg. sy. j. v <sub>16</sub>	G. F. Sprague	"	"
D	B9 Vg su stock	W. C. Galinat	"	"
E	Coop 49-40: seg. Vg	J. E. Wright	"	"
F	iojap induced	M. M. Rhoades	"	"
G	3 way cross (Q63MxC115)F5E	C. C. Wernham	"	"
H	Ind. 33-16	L. M. Josephson	"	"
I	New England Flint (Vt.)	R. M. Bailey	"	"
J	Bolivian variety	P. C. Mangelsdorf	-	-
K	Turkish Flint	PI 204 830 B	-	-
L	Turkish Flint	PI 204 830 A	-	-

Harry T. Stinson, Jr.

## 2. Comments on the comparison of sources of sterile cytoplasm.

If, as the evidence above indicates, all nine sources of sterile cytoplasm are S type, there are several interesting implications. First, this would mean that the sterile cytoplasm in our collection so far fall into either the S or T classification on the basis of the restorer tests. However, as reported in the 1959 MNL (p. 22), chromatographic analyses of mature anthers of nine sources of sterile cytoplasm (in various stages of backcrossing by WF9) revealed differences among them, especially in the presence of UV light fluorescent spots. On this basis of classification the nine sources of cytoplasm were tentatively put into 5 groups, as follows: 1) T; 2) S; 3) E; 4) B and F; 5) A, D, G, H. All steriles were chromatographically different from normal WF9. These results suggest that the chromatographic technique may disclose cytoplasmic differences not detected by the restorer tests. These findings may mean that while the sterile cytoplasm are restored by S restorer genes, perhaps even by the same S restorers, the cytoplasm are not absolutely identical in their action, that is, in the metabolic disturbances leading to pollen abortion. There is the possibility that subcategories of S cytoplasm



exist. It is recognized that chromatographic analyses need to be repeated after further generations of backcrossing, so that the genotypes in the various cytoplasm are more nearly alike. But this may not be as essential as appears, for in our extensive investigations of T cytoplasm it was found that the chromatographic pattern of ninhydrin-positive spots in the early backcross generations was identical with the pattern of the later generations.

A second noteworthy feature of the results of the restorer tests concerns cytoplasmic sources F and H. According to the notation accompanying the original seed, the male sterility of source F was iojap induced by introducing the *ij* gene into the cytoplasm of a normal, fertile line. If this is correct, then S type cytoplasm can arise from the action of the *ij* gene. Alternatively, it may be suggested that S cytoplasm and S restorers were present in the original female parents, and that as a result of the crosses with iojap the restorer genes were lost, thereby allowing expression of male sterility. In this connection a peculiar feature of the S type sterility system should be pointed out. Since in plants with S cytoplasm the non-restoring allele is eliminated in the pollen, and all functional pollen carries the restorer allele, there is no way, in the normal course of events, whereby sterile plants can arise in a population with S cytoplasm, so long as selfs and intercrosses are confined within the population. The presence of sterile cytoplasm would not be suspected unless outcrosses were made to pollen parents which possessed non-restoring alleles associated with normal (or T) cytoplasm.

The second cytoplasm of interest, source H, is derived from Ind. 33-16. The finding that this is S type cytoplasm means that the peculiar behavior of Ind. 33-16 described by Josephson and Jenkins apparently lies with nuclear factors rather than with the cytoplasm.

Harry T. Stinson, Jr.

### 3. Chlorophyll variegation in normal and sterile WF9 lines.

In the 1959 MNL the mode of inheritance of a chlorophyll variegation in a WF9 stock was reported. The results were interpreted to indicate that the chlorophyll abnormality, characterized by streaks of pale to yellow-green leaf tissue, was cytoplasmically inherited. Additional crosses grown in 1959 support this interpretation. Three families of the third backcross generation of WF9 streaked ♀ x WF9 normal ♂ again produced all streaked plants. In contrast, the reciprocal backcross, WF9 normal ♀ x WF9 streaked ♂, now in the second generation, gave all green offspring. Also mentioned in last year's report was the fact that it had not been possible to eliminate the chlorophyll abnormality by selecting, from earlier generations, what appeared to be green plants. This statement still holds. Selfs of the greenest plants again produced some obviously streaked offspring, as did the second generation backcrosses of WF9 "green" ♀ x normal WF9 ♂. The intensity of streaking is, however, somewhat less severe in families of the "green" plants than in families of the obviously streaked plants. As previously mentioned, the families in which this chlorophyll abnormality appeared were derived from two WF9 plants which carried S type cytoplasm, but which had undergone a change from male sterility to male fertility. The event leading to the alteration in pollen behavior presumably occurred in the cytoplasm. As yet there is no indication of any causal connection between the chlorophyll aberration and the alteration in fertility.

In 1959 other WF9 lines were examined for signs of the chlorophyll disturbance. These lines included several normal WF9 stocks as well as cytoplasmic male sterile lines in various stages of conversion to a WF9 genotype. In an attempt to evaluate the chlorophyll variegation on a slightly more objective basis, the top 8 leaves of the plants in each family were scored for the extent (number and size of streaks) of yellow or pale green streaking on a scale from 0 to 5. By adding the values for the 8 leaves it is possible to get numerical expressions for the intensity of variegation for each streaked plant, and from these an average value for the family can be calculated. In scoring, relatively small

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streaks that probably would not be noticed in a more superficial inspection were counted and given a value of 0.5. Thus, some plants tabulated as variegated would probably have been considered green in previous years. The results are summarized in the table below.

Family	Pedigree	No. Plts.	No. Variegated	% Variegated	Avg. intensity of variegation
1	WF9 normal	19	4	21%	0.75
2	" "	16	5	31%	0.60
3	" "	20	7	35%	0.57
4	" "	18	9	50%	0.72
5	" "	17	4	24%	2.60
6	" "	20	4	20%	1.60
7	" "	20	4	20%	2.00
8	" "	17	5	29%	1.40
Totals		147	42	Avg. 29%	1.29

Family	Pedigree	No. Plts.	No. Variegated	% Variegated	Avg. intensity of variegation
9	WF9 A5	22	19	86%	11.3
10	" B7	17	17	100%	1.9
11	" C4	17	11	65%	1.2
12	" D4	18	12	72%	2.1
13	" E5	14	14	100%	2.1
14	" F4	17	17	100%	2.3
15	" G3	17	13	76%	1.7
16	" H6	16	11	69%	11.5
17	" S12	17	10	59%	2.2
Totals		155	125	Avg. 81%	4.03
18	WF9 T11	32	0	0	0

Streaked plants appeared in all 8 families of normal WF9. In 4 of these families, as seen from the values in the last column of the table, (Nos. 1 - 4), the variegated plants were only slightly variegated, with only 1 or 2 leaves showing a small non-green streak. Such plants are essentially green, and these 4 families may be considered to be virtually free of variegated plants. Although the proportion of streaked plants is no greater, the values expressing the average degree of variegation are higher in the remaining 4 WF9 normal families (Nos. 5-8). In each family this is the result of the presence of one plant with fairly extensive streaking, i. e. families 5-8 contained one obviously streaked plant in addition to some slightly streaked plants like those in families 1-4.

The various sterile versions of WF9 with cytoplasmic sources A through H, and with type S, also contained streaked plants. In all families the proportion of streaked plants was greater than in any of the normal WF9 lines. The average intensity of variegation observed in all sterile WF9 lines was also relatively high, none of the values reaching the low readings obtained in 4 of the normal WF9 families.

The best comparison in this sense is between the sterile WF9 lines and family 1 of the normal WF9 stocks, which was the recurrent parent used for the conversion of all sterile lines.

These results tend to suggest that the chlorophyll abnormality occurs with a higher frequency and with greater severity in the WF9 sterile families. Since in terms of pollen abortion, cytoplasmic sources A through H are of the S type (see preceding page), the readings for the 9 sterile families have been pooled for comparison with the pooled data from the 8 WF9 normal families. It will be noted that approximately 3 times more plants were streaked in the sterile families, and also that the intensity of streaking was about 3 times greater in the sterile families. However, it is apparent that not all sterile families were identical with respect to intensity of variegation, for the plants in WF9 A5 and WF9 H6 were clearly more severely streaked.

No streaked plants were observed in a single family of WF9 T sterile. We have, however, noted in past years an occasional streaked individual among WF9T plants, and Brown and Duvick have also reported chlorophyll streaking in their WF9 T material. Variegation in WF9T stocks probably occurs with about the same frequency as in WF9 normal.

Although the precise explanation of the origin and inheritance of the chlorophyll abnormality in WF9 is perhaps uncertain, there are some features about the phenomenon that seem fairly well established from our own studies and from those of other investigations (see Brown and Duvick, MNL 1958, p. 120). The chlorophyll abnormality appears sporadically and "spontaneously" in WF9 stocks, and few lines of the inbred seem to escape entirely the production of an occasional streaked plant. Whatever its mode of origin, the character, once initiated, is then maternally inherited. Rarely, however, a streaked plant may appear in the progeny from a cross of the type normal WF9♀ x streaked WF9♂. While this might indicate male transmission of the character, it is difficult to be certain of this interpretation, since the streaked phenotype also occurs in selfs of normal WF9 and in crosses between normal lines.

One possible interpretation of the variegation phenomenon would be that the WF9 genotype from time to time induces alterations in the cytoplasm or plastids, the altered cytoplasmic constituents subsequently being maternally transmitted and remaining in the altered condition throughout sexual generations in the absence of the specific WF9 genotype which produced the alteration. On this view the abnormal chlorophyll condition in WF9 is analogous to the variegation brought about by the *iojap* gene, except that homozygous *ij/ij* plants are regularly variegated, whereas only an occasional WF9 plant is variegated. This explanation focuses attention on the WF9 genotype as the primary cause of the abnormal plastid condition.

As an alternative explanation which does not involve the WF9 genotype, it could be suggested that the plastid alterations arise directly from mutations in the plastids, or other cytoplasmic elements capable of self-duplication. On this interpretation, there is apparently an unstable condition specifically characteristic of certain cytoplasm (including the cytoplasm in many WF9 stocks), but not characteristic of other cytoplasm. There are reasons for considering this second explanation less likely. First, the variegation which was so frequent in the WF9 S, and A through H stocks, has not appeared in a similar series of these same cytoplasm with an A158 genotype. Second, variegation in WF9 plants has been observed by investigators working with various selected and reworked lines of WF9. It seems questionable that all of these lines would have the same source of cytoplasm. With available evidence, there is thus reason for believing that the WF9 genotype is somehow intimately associated with the origin of the chlorophyll variegation, although this genotype may not be required for maintenance of the condition.

If the WF9 genotype has the property of inducing or allowing the expression of cytoplasmic alterations affecting the chloroplasts, the results reported above may indicate an additional basis for dis-

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tinguishing among cytoplasm. If it is true that variegation is more frequent in the WF9 S steriles, this would mean that the normal and sterile cytoplasm differ not only in their effects on pollen viability, but also in the cytoplasmic factors whose response to a WF9 nucleus produces the chlorophyll abnormality. Also, there is some indication of differences in the response of cytoplasm A - H. In short, it is suggested that the relative frequency with which cytoplasmically inherited plastid alterations occur in the presence of a WF9 genotype may be used as a criterion for characterizing different cytoplasm. This is only a speculation, and further investigation is needed to establish the validity of this approach.

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#### 4. The origin of cytoplasmic sterility in maize.

So far all of the many different sources of cytoplasmic male sterility or pollen abortion fall into two distinct groups which we have designated S and T. These two plasmatypes together with the usual cytoplasm, which may be called the M type, found in most of the cultivated maize varieties commonly grown throughout the world, form three distinct classes of cytoplasmic differences. Their classification is based on their interaction with fertility restoring genes. It is possible that these cytoplasm originated in the different species that are considered to have had a part in the development of cultivated maize. These are the primitive pod corn or pro-maize described by Mangelsdorf, *Tripsacum* (gama grass) and *Euchlaena* (teosinte). Mazoti has shown that chlorophyll genes that are aberrant in maize cytoplasm are normal in teosinte cytoplasm. This is evidence that teosinte cytoplasm is different from that of *Zea mays*.

If this conjecture should be borne out by more complete evidence it would show that cytoplasmic differences are permanent over very long periods of time and that they are more important in the origin and separation of species than is generally realized.

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#### 5. The performance of restored-sterile hybrids.

Many double crossed hybrids made on sterile seed parents with various non-restoring and restoring pollinators have been compared in yield, time of maturity, and stalk quality. The results are given in our annual corn report (Conn. A. E. S. Progress Report G1, 1960). Where natural restoring inbreds are used with either normal fertile or sterile inbreds as pollinator single crosses, the final double crosses are equal in performance in all characters measured. The actual ratio of fertile and sterile plants in percent is 56:44 where the pollinator is fertile  $\times$  restorer and 58:42 where the pollinator is sterile  $\times$  restorer. The excess of fertile plants in both cases is probably due to minor modifying factors.

Twelve different double crosses were made with restoring pollinators nearly alike in genotype but differing in plasmatype. One series is a normal fertile inbred  $\times$  a restored sterile inbred. The other series is the sterile version of the same inbred by the same restored sterile inbred. In both series the segregation of fertile and sterile plants is practically the same; 47:53 in the normal  $\times$  restored sterile, and 46:54 in the sterile  $\times$  restored sterile. In both series there is a slight excess of sterile plants. The excess of steriles in this series and an excess of fertiles in the other is probably due to residual gene differences in the different inbreds used for the sterile seed parents and restoring pollinators. For practical purposes the differences are not important since adequate pollen production is supplied in both series.

It is important to note that in all of these experiments where a heterozygous T restoring gene is acting in either T cytoplasm or in M cytoplasm there is no selective action determining the survival of either the dominant or recessive gamete as in the case with S restorers in S cytoplasm.

In another series of double crossed hybrids three types of pollen parent single crosses were compared, all crossed on the same sterile seed parents. One group was made with the original non-restoring inbreds with no restoration. In another group one inbred was sterile and the other a restored sterile version of the same inbred as used in the first group, giving approximately 50 percent of the plants shedding pollen. In the third group both of the inbreds had been converted to restored sterile versions. This group gave all plants shedding pollen normally. The restored sterile inbreds had been backcrossed four times and then selfed three times.

In all cases the three groups were closely alike in days to silking and in percent of moisture in the grain at harvest. However, in yield of grain and percent of plants erect at harvest the 50 percent restored version of the same hybrids were significantly lower. From this evidence it appears that four generations of backcrossing are not enough to change an inbred to pollen restoration without altering performance in other characters. Yield of grain was reduced less than erectness of stalk. This may be due to the source of the restoring gene which was Ky21. This inbred has good yielding ability but poor stalk quality. Evidently some of the linked genes determining stalk breakage have not been eliminated in the backcrossed plants.

In this experiment where the same hybrids were restored to 100 percent pollen fertility (both pollinator inbreds converted to pollen restoration) yield of grain was the same in one and above in two of the combinations. In these cases the other restored inbred evidently brought in additional genes for yielding ability. But in all three of these fully restored hybrids stalk quality was reduced.

Donald F. Jones

#### 6. Recurrent selection for pollen restoration and yield performance.

In three widely used inbreds a program of selection in test crosses is underway for pollen restoration and ability to yield with proper maturity and equal or better stalk quality. The procedure is to cross the T sterile version of the inbred by a good restorer source and then backcross on to the sterile inbred for enough generations to recover the inbred type and then self for several generations to obtain homozygosity for the necessary pollen restoring genes as shown by progenies that are all normal in pollen production. During this process selection is also made for the desired maturity, stalk quality, disease and insect resistance, and other agronomic characters.

As soon as the lines are reasonably well converted to type and appear to be suitable for use as pollinators they are then further selected by test crossing. In some cases selections are made while the lines are still segregating for pollen restoration. Selected individual plants in each progeny are self-pollinated and crossed on to a suitable sterile single cross seed parent. These 3-way test crosses are then grown and scored for pollen fertility, time of flowering, stalk quality, grain quality and yield. The selfed inbreds giving both good fertility and superior performance are then composited, either by intercrossing by hand pollination or by bulking and growing in an isolated plot. Further selections from these composites are again tested. The inbreds being selected in this way at the present time are C103, Hy and Kr.

Donald F. Jones

## 7. Identification of plasmatypes.

Restored sterile inbreds that are maintained in S or T types of cytoplasm must be correctly identified and used only with the corresponding S or T sterile seed parents. Failure to do this has led to much confusion and unsatisfactory pollen restoration. Many of the sources of pollen restoration carry genes for both S and T restoration. When maintained in one type the restoring genes for the other type are unselected for and tend to be lost although the inbreds themselves may be fully fertile. Fertile inbreds cannot be tested for their plasmatype by crossing on to S or T steriles since they may be carrying re-storing genes for both types. If they are segregating for sterile plants these sterile plants can be tested by being pollinated by suitable testers. If not segregating they can be crossed by non-restoring inbreds. The segregating sterile plants in later generations can then be tested.

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### 1. Mutational Behavior of $R^f$ Jana

Previous studies have shown that the action of the standard  $R^f$  allele (Cornell) is due to two closely linked genes which are separable by crossing over. The  $R^f$ :Cornell allele mutates both to  $r^b$  and  $r^f$  but only rarely to  $r^b$ . Earlier, Stadler had observed the same type of mutational sequence in stocks possessing the following  $R^f$  alleles:  $R^f$ :Boone, Quapaw, Ponca, and Black. Stadler concluded that in the case of these 5 alleles the action of the  $R$  segment is due to separate genes rather than to the action of a single gene.

Later, Stadler found that this stepwise course of spontaneous mutation is not characteristic of all  $R^f$  alleles. He reported that two  $R^f$  alleles with dilute pigmentation mutate directly to  $r^b$  and not to  $r^f$ . In the case of these two alleles, he proposed that both plant and seed color are dependent upon a single component.

Recently a third type of  $R^f$  allele has been analyzed which mutates regularly to  $r^b$  and less frequently to  $r^f$ . In contrast to  $R^f$ :Catspaw and Winnebago, this allele, which is known as  $R^f$ :Jana, is identified by strong plant color both in the seedling and the flowering stages.

The seed mutation data from the cross of ♀♀  $g R^f$ :Jana  $K/G R^f$ :Jana  $k$  x ♂♂  $g r^b k/g r^b k$  are summarized in Table 1. The stocks of homozygous  $R^f$ :Jana were marked on either side of the  $R$  complex with  $g$  and  $K$ .

Out of a total population of 245,515 female gametes tested, 24 colorless seed mutants were analyzed and of these all but two were  $r^b$ ; none of these cases exhibited defective pollen. Of the 22  $r^b$  mutants produced, 13 were  $g r^b K$ , 7 were  $G r^b k$ , and 2 were  $G r^b K$  in constitution. The simplest explanation of the origin of these cases is that the plant and seed color determiners of  $R^f$ :Jana mutated simultaneously to the double recessive or to  $r^b$ . On this assumption the  $g r^b K$  mutants would be attributed to mutations in the  $g R^f K$  chromosome, and the  $G r^b k$  mutants to mutations in the  $G R^f k$  chromosome. The origin of the two  $G r^b K$  cases in which a crossover occurred may be ascribed to mutations in the  $g R^f K$  chromosome with a coincidental crossover between  $g$  and  $k$ , for the number of crossovers expected by coincidence is about 3.

Table 1 The frequencies and types of seed color mutants observed in progenies from homozygous R<sup>F</sup>: Jana.  
 ♀♀ gR<sup>F</sup>K/GR<sup>F</sup>k x ♂♂ gr<sup>8</sup>k/gr<sup>8</sup>k.

<u>Culture</u>	<u>Number of seeds examined</u>	<u>Number of colorless seeds</u>	<u>Mutant fraction determined</u>	<u>Phenotype of mutant individuals</u>			
				<u>gr<sup>F</sup>k</u>	<u>gr<sup>8</sup>k</u>	<u>Gr<sup>8</sup>K</u>	<u>Gr<sup>8</sup>k</u>
56: 825	75, 525	6	4/6	1	3	0	0
826	66, 970	9	7/9	0	4	0	3
827	23, 460	5	3/5	0	2	1	0
828	26, 480	1	1/1	0	0	0	1
829	31, 135	6	5/6	1	2	1	1
830	21, 200	3	3/3	0	1	0	2
58F 3245	745	1	1/1	0	1	0	0
<b>Total</b>	<b>245, 515*</b>	<b>31</b>	<b>24/31</b>	<b>2</b>	<b>13</b>	<b>2</b>	<b>7</b>

\* Adjusted mutation frequency 24/31 x 245, 515 = 24/190, 076.

It will be seen in Table 1 that homozygous  $\underline{R}^f$ :Jana also produced two seed color mutants of type  $\underline{g} \underline{r}^f \underline{K}$ . These are mutants that would be expected if the plant and seed color effects of the  $\underline{R}^f$  segment were independent components. On this basis the origin of the two  $\underline{g} \underline{r}^f \underline{K}$  mutants would be ascribed to mutations of the seed color determiner  $\underline{R}$  to  $\underline{r}$  in the  $\underline{g} \underline{R}^f \underline{K}$  chromosome, since the mutant chromosomes are of the same  $\underline{g}$  and  $\underline{K}$  constitution as the  $\underline{g} \underline{R}^f \underline{K}$  chromosome.

In general it is evident that  $\underline{R}^f$ :Jana mutated more frequently to  $\underline{r}^g$  (rate =  $1.16 \times 10^{-4}$ ) than to  $\underline{r}^f$  (rate =  $0.11 \times 10^{-4}$ ), and that the mutations were chiefly the result of non-crossover alterations. It also appears evident that a large proportion of the seed color mutants from  $\underline{R}^f$ :Jana were of the type that would be expected if (P) and (S) were a single entity with two kinds of action. Whether, however, the  $\underline{R}$  segment of  $\underline{R}^f$ :Jana actually consists of a single element cannot be definitely concluded on the basis of the present results, since a small proportion of the mutants were of the type expected from the action of two independent genes. For the moment, the significance of this finding still remains unclear. Although it is possible that the seed color factor of  $\underline{R}^f$ :Jana mutated independently of the plant color element, it is also conceivable that the origin of the  $\underline{r}^f$  mutants may be attributed to some other mechanism which is not apparent at the present time. It is also puzzling, in view of the high frequency of oblique crossing over in stocks of  $\underline{R}^f$ :Cornell, to find so few oblique crossovers in the progeny of  $\underline{R}^f$ :Jana. It may be that the structure of  $\underline{R}^f$ :Jana is a complex of two spatially segregated parts so oriented as to be nearly incapable of separation by crossing over. One may suggest from these results that the origin of the  $\underline{r}^g$  mutants is due to a suppressive type of mechanism, inhibiting both plant and seed color. However, there is no evidence that indicates such a mutator system present in the stock. The seeds of each of the  $\underline{r}^g$  mutants were closely examined for dominant mutations, but no spots or sectors of colored aleurone were found. A similar examination was made of the plant tissues.

M. H. Emmerling

## 2. New abnormal chromosomes 10.

A number of altered abnormal chromosomes 10 arose as a result of crossing over in abnormal 10/duplicated abnormal 10 heterozygotes. The effect of these altered chromosomes 10 on preferential segregation was studied in backcrossed ears produced by pollinating female plants of  $\underline{R}$  altered  $\underline{K}/\underline{r} \underline{k}$  constitution by  $\underline{r} \underline{k}/\underline{r} \underline{k}$ . The results to date are summarized below.

Culture	Type of chr. 10	Numbers of		Percent Altered
		Altered K	Unchanged k	
58:243-3	new knob <sup>o</sup> (2) *	1416	1365	51
-7	Trisomic-K10, k10, new knob <sup>o</sup> (3) *	565	536	51
-9	new knob <sup>o</sup> (4) *	161	133	54
-10	interstitial K10	1480	1456	50
-20	Trisomic-K10, k10, interstitial K10	1177	1181	48
-23	Trisomic-K10, k10, interstitial K10	1459	1282	53
-24	altered abnormal 10 with 2 knobs on 10L	1231	1184	50
-27	Trisomic-ring-10, k10, new knob <sup>s</sup> (2) **	1457	1417	51
-28	Trisomic-ring-10, K10, k10	834	862	49



Culture	Type of chr. 10	Numbers of		Percent Altered
		Altered K	Unchanged k	
-36	interstitial K10	1024	1027	50
-39	Trisomic-ring-10, K10, k10	687	656	51
-44	new knob <sup>o</sup> (5) *			
-49	new knob <sup>s</sup> (3) **	3195	2590	55
-51	ring-10			
-57	Trisomic-K10, k10 ring-10	755	865	47
-59	new altered chr. with the 3 prominent chromomeres and 4 <sup>+</sup> distal chromomeres; shorter than K <sup>o</sup> .	1263	1003	53

\* altered abnormal 10 without the heterochromatic segment; similar to knob <sup>o</sup> (1).

\*\* altered abnormal 10 lacking about one-half of the heterochromatic segment; similar to knob <sup>s</sup> (1).

M. H. Emmerling

3. Further analysis of the R<sup>g</sup> non-crossovers.

A number of additional seed color mutants were analyzed to supplement the data of the R<sup>g</sup> non-crossovers reported in 1958 C. S. H. S. This was considered necessary because of the possibility that the frequency of the critical crossover class may have been exceedingly rare. The retests were made using the same R<sup>g</sup> non-crossovers as in the original experiment. The results to date are summarized below.

Culture	Non-crossovers		Crossovers	
	r <sup>+</sup> K	r <sup>g</sup> k	r <sup>+</sup> k	r <sup>g</sup> K
<b>R<sup>g</sup>nco-2</b>				
1958 data	28	6	13	0
1959 data	1	0	3	0
Total	29	6	16	0
<b>R<sup>g</sup>nco-3</b>				
1958 data	10	5	24	1
1959 data	2	3	13	0
Total	12	8	37	1
<b>R<sup>g</sup>nco-4</b>				
1958 data	24	11	17	1
1959 data	7	0	1	1
Total	31	11	18	2

These results support the previous conclusion that (p) is deficient in non-crossovers 2, 3, and 4.

#### 4. Studies of chlorophyll suppressors.

Several nonallelic pleiotropic genes have been described which result in light endosperm and albino seedling phenotypes. Segregating stocks of four such genes,  $\underline{Lw}_1 \underline{lw}_1$ ,  $\underline{Lw}_2 \underline{lw}_2$ ,  $\underline{W}_3 \underline{w}_3$ , and  $\underline{Ps} \underline{ps}$  were supplied by Dr. D. Robertson and added to a fifth type  $\underline{Cl}_1 \underline{cl}_1$ . In 1956 the five stocks were outcrossed to the open pollinated heterogeneous varieties Cornell 11 (C11) and Minnesota 13 (M13). In the summer of 1957, these crosses were selfed and, at maturity, ears segregating for kernel color were selected and stored.

The dark and light kernels were hand separated, counted, and  $X^2$  values for 3:1 segregations determined. Light colored kernels were grown in germinators to determine seedling characteristics. Green seedlings were classified as (a) misclassification, (b) heterofertilization, (c) suppressor gene mutant.

Stocks with presumed suppressor genes were increased last summer and the following new suppressors have now been isolated:

<u>Pleiotropic gene</u>	<u>Suppressor designation</u>	<u>Amount of Chlorophyll</u>
$\underline{Lw}_2 \underline{lw}_2$	S $\underline{lw}_2$	Partial
$\underline{Cl}_1 \underline{cl}_1$	S $\underline{cl}_1$ . (Possibly allelic to $\underline{Cl}_3$ )	Partial
$\underline{Ps} \underline{ps}$	S $\underline{ps}$	Complete

In 1958, crosses were made between the five major gene stocks and the suppressors  $\underline{Cl}_3$  and  $\underline{S} \underline{ps}$ . Segregating trihybrid progenies have been observed.

B. S. Sidhu  
H. L. Everett

#### 5. Suppressor action in controlled environments.

The several suppressor stocks were germinated under day light white (wave length 650-410), blue (545-420), and red (620-580) light tubes.  $\underline{S} \underline{lw}_2$  showed an interesting difference in apparent quantities of chlorophyll present when compared to the normal  $\underline{Lw}_2$ .

Thus: $\underline{Lw}_2$ -	Amount of Chlorophyll	$\underline{S} \underline{lw}_2$ -	Amount of Chlorophyll
White Light	Red Light > Blue Light	Blue Light	White Light > Red Light

The differences appeared to be quantitative rather than qualitative. The  $\underline{S} \underline{lw}_2$  absorption spectra (measured in a Beckman spectrophotometer) rather closely approximated the  $\underline{Lw}_2$  - curve in blue light, however,  $\underline{S} \underline{lw}_2$  had much less chlorophyll than the  $\underline{Lw}_2$  - in the other light chambers.

B. S. Sidhu  
H. L. Everett

## 6. Cytomorphology of chloroplasts.

Microscopic observation of plastid morphology for the five major gene types in the normal green, albino, and suppressor stocks has been made. Chloroplast size and shape have been measured. The expression of green color in the leaves is not based solely on the number of chloroplasts per cell, but is related to the quantity of pigmentation in plastids as well. There appeared to be no significant difference in the shape or size of chloroplasts among these stocks. The most common shape is circular (2-3  $\mu$ ) but ovoid forms are not infrequent. Partial suppressors showed a wide range of pigmentation in the chloroplasts of even a single cell. The maximum size of chloroplast was attained within a week in the growth chambers, and represented a simple enlargement of a proplastid in a majority of cases.

B. S. Sidhu  
H. L. Everett

## 7. Hornlike coleoptile (hc).

A heritable and unrelated variation was observed in seedlings of one of the chlorophyll mutant stocks. These seedlings show hornlike projections on the coleoptile tip. A comparable case has been reported by Sass and Sprague where a green leaf-bladelike outgrowth occurred on the maize coleoptile. Sprague (1959 personal communication) indicated that this character is controlled by a single recessive gene ac. Recently, Bianchi (1960 personal communication via Galinat) found a single ear segregating for "bikeeled" outgrowths borne either on the coleoptile or on the first true leaf apex. These mutants appear to be quite distinct from the hornlike coleoptile mutant (suggested symbol hc). In the dark growth chamber, this mutant has a blunt, rough coleoptilar apex. Eventually hornlike growths occur which often reach a length of 2.5 - 3.0 cms. over a two week period. The outgrowths may be equal or unequal and are associated with the vascular strands. Often, the outgrowths show a marked curvature and less frequently horns were seen to be fused. The apical tip of the first leaf is rolled and compressed. At the time this leaf opens to form a spatula or spoon-shaped tip, the hornlike structures cease growth.

In five segregating ear progeny there was a good fit for a 3:1 ratio. Four abnormal seedlings were selfed under the greenhouse conditions. All selfs bred true for hornlike coleoptile. Subsequent crosses between homozygous mutants hc hc and heterozygous normals Hc hc showed 1:1 segregation ratios. Critical crosses with the ac stock and the mutant discovered by Bianchi have yet to be made. Based on the data at hand "hornlike coleoptile," hc, is proposed as a new simple Mendelian recessive gene. Linkage studies are being carried out.

B. S. Sidhu  
H. L. Everett

## 8. Anatomy of hornlike coleoptile (hc).

Mesocotyl anatomy of normal corn seedlings has been considered by Tucker (1957). The normal coleoptile (Hc) is characterized by two lateral vascular bundles. Both of these bundles run parallel and approach the anterior end of the tapering coleoptile apex. In the hc mutant, each of the two hornlike outgrowths possess one vascular strand which appears to be a continuation of one of the two main vascular strands. There is, however, considerable variation in expressivity of the hc gene. It is worth mention that Bianchi's material seems to possess a regular tendency toward equal sized accessory bundles in the bikeeled coleoptiles. Only two of them are present when the spurs are present at the

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B. S. Sidhu  
H. L. Everett

9. Nature of the grass coleoptile and the ac, hc, and "bikeel" genes.

Studies on hc gene expression and information gathered on the ac and bikeel mutants suggest the construction of hypothetical stepwise stages involved in the evolution of the coleoptile from one or two leaves in Zea mays.

Thus ac action allows a green leaf blade like expression on one side of the coleoptile due to marginal meristematic activity while a spur-like outgrowth on the first true leaf of the bikeel mutant represents an intermediate stage. Bikeeled and hornlike coleoptiles represent still another stage toward the normal coleoptile. A single outgrowth may be considered as equivalent to an underdeveloped leaf blade. It may be underdeveloped because of altered position and reduced growth activity of the basal meristem regularly present at the base of the normal leaf blade above the collar region.

Thus, the coleoptile is proposed to be an incompletely developed leaf which has evolved via fusion and modification to undertake a protective function. The question remains as to the number of leaves which go to make up the coleoptile. At present, it may be suggested that there are two leaves fused along marginal sheath regions. Such a suggestion is supported by (1) the presence of a leaf blade in ac stocks along margins on one side, (2) the frequent occurrence of two hornlike leaf blade rudiments in hc stocks, and (3) the presence of more than two regular vascular strands in the "bikeel" plants from Bianchi.

B. S. Sidhu  
H. L. Everett

DE KALB AGRICULTURAL ASSOCIATION, INC.  
DeKalb, Illinois

1. Comparison of normal vs. restored commercial hybrids.

Data below compares the performance of normal vs. restored (R) version of commercial hybrids for yield, moisture, and stalk quality (the lower the number the better the quality). These results are from 7x7 latin squares in which each entry appeared seven times. Each latin square was replicated four (three \*) times. These figures, therefore, are the average of twenty-eight (twenty-one \*) 2x5, four kernel per hill plots.

<u>Hybrid</u>	<u>Maturity</u>	<u>Yield bu/acre</u>	<u>Moist. %</u>	<u>Stalk Qual. Rating</u>
# 1	400	95.0	26.4	15.8
# 1 R		100.3	27.3	15.6
# 2	400	96.7	24.8	9.7
# 2 R		103.8	25.7	10.3
# 3	400	95.7	28.8	9.7
# 3 R		105.7	27.7	9.1
# 4 *	400	98.2	23.6	9.9
# 4 R *		97.0	21.9	10.0

<u>Hybrid</u>	<u>Maturity</u>	<u>Yield bu/acre</u>	<u>Moist. %</u>	<u>Stalk Qual. Rating</u>
# 5 *	400	99.4	23.7	8.8
# 5 R *		99.8	23.5	7.9
# 6 *	400	103.4	22.8	5.8
# 6 R *		107.3	22.7	6.0
# 7	600	108.2	22.1	23.2
# 7 R		102.6	23.9	21.9
# 8	600	116.1	22.0	25.3
# 8 R		112.2	22.6	23.7
# 9	600	109.0	22.5	23.8
# 9 R		105.7	23.1	22.6
# 10	600	114.7	19.2	8.1
# 10 R		117.1	19.5	8.2
# 11	600	106.9	21.7	3.0
# 11 R		110.6	20.6	3.2
# 12	600	119.2	21.0	4.9
# 12 R		120.8	20.9	6.3
# 13	800	90.0	22.2	5.7
# 13 R		88.9	21.8	4.0
# 14	800	86.1	22.8	3.8
# 14 R		88.2	22.3	5.2
# 15	800	99.9	22.5	3.6
# 15 R		97.0	23.4	5.5
# 16	800	76.0	18.7	3.7
# 16 R		80.8	18.4	3.3
# 17	800	84.2	19.4	5.0
# 17 R		82.9	19.5	7.8
# 18	800	85.7	18.7	4.6
# 18 R		83.5	19.9	6.8

Some significant differences at the 5% level were found between hybrids within individual 7x7 latin squares. In the yield category, nine significant differences were in favor of the restored version, two in favor of the normal. For moisture %, five significant differences were in favor of the restored, four were significant for the normal version. With respect to stalk quality, no significant differences favored restorer versions, whereas, five favored the normal versions.

All of the experimental, restored versions of the commercial hybrids above have one restorer line in the pollinator side. Hybrids # 8, 9, and 10 are 3-way crosses. In all of the hybrids included in these Please Note: Notes submitted to the Maize Genetics Cooperation Newsletter may be cited only with consent of authors.

7x7 tests the restorer inbred line had at least five backcross generations.

The data indicate that although general performance is quite comparable between normal and restored versions, more than five or six backcross generations are needed for adequate conversion to the recurrent parent.

Details on fertility restoration of commercial hybrids under different environmental conditions will appear in later editions of M. G. C. N. L.

Loring M. Jones

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1. Chromosome knob frequency distribution and frequencies of B-chromosomes in races of maize in Peru.

Progress has been made during the past year on these studies which are almost completed at this time. They will be reported in detail elsewhere.

Table 1 gives a summarized account of the studies on knob frequency distribution and ranges of B-chromosomes in the several races. Additional information is available on size, relative position, and on homo- or heterozygosity of knobs. These data represent an average of three plant samples of pollen mother cells, over a number of collections ranging from 2 to 17 per race.

Two distinct groups of coastal races are obtained on the basis of chromosome knob frequencies: those with high knob numbers, ranging from 4 to 14 knobs per 10 chromosome pairs, such as Alazán, Perla, Jora, Arizona, and Rienda, which can be shown to be either exotic introductions or introgressed with exotic fore-races, and those with low knob numbers: Chancayano, Huachano, Pagaladroga, Mochero, Chaparrefío, Arequípeño, which are likely to be races, whose precursors descended from the Peruvian highlands.

The position of the knobs is primarily on chromosome 7, and secondarily in races with high knob numbers, on chromosomes 9, 8, 6, 4, 3, 2, 1, 5, in that order. Race Jora exhibits an extraordinary high frequency of abnormal-10 chromosomes.

The highland races are all low in knob numbers, ranging from 0 to 3 per ten chromosome pairs. Chromosome 7 had a small sub-terminal knob on its long arm in almost all of the plants of this group of races, that were studied. Some definitely lacked it. The second most common position was that of a small sub-terminal knob on the long arm of chromosome 6.

Consistent with previous reports, is the observation reported here that in races with high knob number the frequency of B-chromosomes tends to be low, while the reverse situation of high number per plant cell, and high frequency of B-chromosomes in races with low average knob number, is also true, regardless of geographical altitude distribution range.

The results of these studies suggest that high or low chromosome knob numbers in maize are not associated with respective low or high geographical altitude distributions, as is implied in previous reports. Races of the coastal region derived from highland races, and which have been prevented from

TABLE 1. Summary of data on frequencies of chromosome knobs and B-chromosomes of races of maize in Peru.

Race	Range in knob No.	Frequency of chromosomes with knobs (percent)										Range in No. of B chromosomes per 10 ps.
		1	2	3	4	5	6	7	8	9	10	
<b>A. Coastal</b>												
1. Alazán	9-14	57	35	57	57	43	64	64	35	64	0	0-1
2. Perla	6-13	35	50	45	60	25	75	80	65	80	5	0
3. Jora	4-10	20	60	60	60	0	60	100	100	80	40	0
4. Arizona	6-8	43	43	14	71	29	86	86	29	86	0	0
5. Rienda	6-?	25	25	25	50	25	50	50	50	75	0	0
6. Chancayano Bl.	1-3	0	0	0	0	0	50	50	50	50	0	0-4
7. Chancayano Pn.	1-2	0	0	0	50	0	0	100	0	0	0	0
8. Huachano	0-2	2	0	0	0	0	0	33	0	50	0	0-2
9. Pardo	0-2	0	0	0	0	22	0	89	0	0	0	0
10. Pagaladroga	0-1	0	0	0	0	0	0	67	0	0	0	0
11. Mochero	0-3	0	0	0	12	0	0	66	0	18	0	0-1
12. Chaparreño	0-2	0	0	0	0	0	0	67	0	0	0	0-2
13. Arequipeño	0-1	0	0	0	0	0	0	25	0	25	0	0-2
<b>B. Highland (Sierra)</b>												
14. Cuzco	0-2	0	0	29	0	0	0	43	0	0	0	0-1
15. Cuzc. Crist. Am.	-	0	0	0	0	0	0	50	0	50	0	-
16. Ancashino	0-3	0	0	0	0	0	22	77	0	0	0	0-4
17. Huayleño	1-2	0	0	0	0	0	14	72	0	0	0	0-2
18. Paro	0-1	0	0	0	0	0	0	57	0	0	0	0-3
19. Confite Puntiaq.	0-2	0	0	0	25	0	8	50	8	8	0	0-2
20. Confite Morocho	1-2	0	0	0	0	0	50	100	0	0	0	0

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TABLE 1. (Continued)

Race	Range in knob No.	Frequency of chromosomes with knobs (percent)										Range in No. of B chromosomes per 10 ps.
		1	2	3	4	5	6	7	8	9	10	
<b>B. <u>Highland (Sierra)</u> (continued)</b>												
21. Morocho	0-2	0	0	0	17	0	0	58	0	0	0	0-4
22. Chullpi	0-2	0	0	0	0	0	22	55	0	0	0	0
23. Kculli	1-2	0	0	0	13	0	13	87	0	0	0	0-5
24. Granada	1-2	0	0	0	0	0	13	87	0	0	0	0-2
25. Sarco	1	0	0	0	0	0	0	100	0	0	0	0
26. Shajatu	1-2	0	0	0	0	0	12	100	0	0	0	0-3
27. Rabo de Zorro	1-3	0	0	0	0	0	29	71	0	0	0	0-4
28. Marañón	0-2	0	0	22	0	0	0	55	0	0	0	0-2
<b>C. <u>Jungle</u></b>												
29. Chuncho	5-11	33	33	33	33	0	44	55	44	22	0	0
30. Piricinco	0-2	0	14	0	29	0	0	71	14	14	0	0-2

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outcrossing to high-knob lowland races by both human and natural selective mechanisms, have retained the characteristics of both low knob numbers and relatively high frequencies of B-chromosomes.

Piricinco, one of the most widely distributed races in the Amazonian basin, although showing considerable tripsacoid influence is low in knob number. This situation is easily explained if it is accepted that the tripsacoid influence in Piricinco originates with knobless Tripsacum australe, whose southern, northern, and eastern distribution ranges overlap those of Piricinco.

Chuncho, another jungle lowland race, but with high knob number, can be shown to have originated in an area where high knob numbers are prevalent among the regional races.

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1. Identification of independent isolations of cytoplasmic male sterility.

A number of independent isolations of cytoplasmic male sterility have been checked for similarity to  $[ms_2]$  -type male sterility.

The following symbolism is being used for discussing genetic work with cytoplasmic male sterility.

$[ms]$  - Cytoplasmic male sterile factor

$[ms_1]$  - T or Texas type

$[ms_2]$  - S or U. S. D. A. type

$[ms_x]$  - other type (A-letter is used until it has been definitely shown to be different from other known types; i. e., at present,  $[ms_1]$  and  $[ms_2]$ .)

$Rf^1$  - restorer for  $[ms_1]$

$Rf^2$  - restorer for  $[ms_2]$

A genotype includes the residual chromotype. The superscript to the residual chromotype designates the number of backcrosses to that chromotype since the last "outcross."

Missing symbols in a genotype infer "wild" or "normal" for that "gene" (plasmagene or chromogene).

The sources checked were:

$[ms_A]$  - A yellow flint dent from Turkey.

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- [ms<sub>B</sub>] - Isolated by Brieger in Brazil.  
 [ms<sub>C</sub>] - From a Vg stock. G. F. Sprague, Iowa.  
 [ms<sub>D</sub>] - From a Vg stock. Galinat, Wisc.  
 [ms<sub>E</sub>] - Isolated by James E. Wright, Pa.  
 [ms<sub>F</sub>] - From Iojap stock. Marcus M. Rhoades, Ill.  
 [ms<sub>G</sub>] - Isolated by C. Wernham, Pa.  
 [ms<sub>H</sub>] - Ky. A. E. S., Ky27 sterile (from 33-16)  
 [ms<sub>I</sub>] - From Hubbard flint. R. E. Bailey, Me.

Each of the above was pollinated by, and backcrossed to, the inbred A158 by D. F. Jones. The genotypes of the stocks received from him were: [ms<sub>A</sub>] A158<sup>6</sup>; [ms<sub>B</sub>] A158<sup>8</sup>; [ms<sub>C</sub>] A158<sup>5</sup>; [ms<sub>D</sub>] A158<sup>1</sup>; [ms<sub>E</sub>] A158<sup>4</sup>; [ms<sub>F</sub>] A158<sup>3</sup>; [ms<sub>G</sub>] A158<sup>0</sup>; [ms<sub>H</sub>] A158<sup>0</sup>; [ms<sub>I</sub>] A158<sup>0</sup>.

Each of these was again crossed by A158. Since none of the backcross progenies contained fertile plants it can be concluded that the A158 chromotype cannot restore any of the types of sterility.

Each was then crossed with plants of the genotype either [ms<sub>2</sub>] Rf<sup>2</sup> rf<sup>2</sup> Rf<sup>1</sup> rf<sup>1</sup> A158<sup>5</sup> or [ms<sub>2</sub>] Rf<sup>2</sup> rf<sup>2</sup> rf<sup>1</sup> rf<sup>1</sup> A158<sup>5</sup> (the male family may or may not have been segregating for Rf<sup>1</sup>). Because Rf<sup>2</sup> is selected-for (rf<sup>2</sup> pollen grains abort) when with [ms<sub>2</sub>] (see M. N. L. 33: 17-19) all offspring would be expected to be fertile if [ms<sub>x</sub>] were [ms<sub>2</sub>]. If [ms<sub>x</sub>] were [ms<sub>1</sub>] either one-half would be fertile or all would be sterile (Rf<sup>2</sup> and Rf<sup>1</sup> have shown no linkage).

The crosses gave the following results:

	X A158	X [ <u>ms</u> <sub>2</sub> ] <u>Rf</u> <sup>2</sup> <u>rf</u> <sup>2</sup> <u>rf</u> <sup>1</sup> A158 <sup>5</sup>	% Aborted Pollen
[ <u>ms</u> <sub>A</sub> ] A158 <sup>6</sup>	all 14 sterile	all 12 fertile	55
[ <u>ms</u> <sub>B</sub> ] A158 <sup>8</sup>	" 9 "	" 10 "	50
[ <u>ms</u> <sub>C</sub> ] A158 <sup>5</sup>	" 14 "	" 13 "	55
[ <u>ms</u> <sub>D</sub> ] A158 <sup>1</sup>	" 12 "	" 14 "	55
[ <u>ms</u> <sub>E</sub> ] A158 <sup>4</sup>	" 14 "	" 9 "	55
[ <u>ms</u> <sub>F</sub> ] A158 <sup>3</sup>	" 14 "	" 7 "	50
[ <u>ms</u> <sub>G</sub> ] A158 <sup>0</sup>	" 14 "	" 8 "	50
[ <u>ms</u> <sub>H</sub> ] A158 <sup>0</sup>	" 13 "	" 11 "	50
[ <u>ms</u> <sub>I</sub> ] A158 <sup>0</sup>	" 15 "	" 15 "	50

Seeing that in each case all offspring of the cross  $[\underline{ms}_x]A158^n \times [\underline{ms}_2]Rf^2rf^2\_rf^1$  were fertile we needn't concern ourselves about  $Rf^1$ . It appears then that each sterile tested has behaved as  $[\underline{ms}_2]$ .

Before concluding that each  $[\underline{ms}]$  was  $[\underline{ms}_2]$ , let us consider other alternatives. Since the genetic material from A158 did not bring about the fertility, the chromogene involved must have been either  $Rf^2$  or another gene so closely linked with  $Rf^2$  that out of ninety-nine progeny observed no cross-overs occurred.

A further check was made. It is known that the time of  $Rf^2$  gene action is shortly after the quartet is formed. This means that when it is with  $[\underline{ms}_2]$ , pollen grains carrying  $rf^2$  abort (see M. N. L. 33: 18-19). Therefore, if the fertile offspring of the cross  $[\underline{ms}_x]A158^n \times [\underline{ms}_2]Rf^2rf^2\_rf^1$  A158<sup>5</sup> had the  $[\underline{ms}_2]$  plasmatype and the restorer involved was  $Rf^2$ , fifty percent of the pollen of these plants would be expected to abort. All of the plants were checked with a hand microscope (60X) and found to have about fifty percent aborted pollen. Differences (as shown in the above table) could have been due to environmental conditions, since the inbred A158 may vary somewhat from day to day. This means that if another gene, closely linked with  $Rf^2$ , was responsible for the restoration its time of action would also have had to be shortly after quartet formation. Although this may seem unreasonable, more plants resulting from the same crosses will be grown this spring in an effort to observe any cross-overs.

Even if  $Rf^2$  is responsible for the restoration it cannot be absolutely concluded that all these plasmatypes are identical with  $[\underline{ms}_2]$  (though they could justifiably be called  $[\underline{ms}_2]$ ), for the plasmagenes can only be differentiated in terms of the restoring genes. It may be possible for one chromogene to compensate for more than one type of cytoplasmic "error." This should be borne in mind when considering that Khoo and Stinson (M. N. L. 33: 22) found chromatographic differences between these same types of cytoplasmic male sterility.

Janson G. Buchert

FLORIDA AGRICULTURAL EXPERIMENT STATION  
Gainesville, Florida

1. Inhibition of geotropism in corn seedling shoots by gamma radiation.

US-13 yellow dent hybrid seedlings four days old (1-3 cm. high) were irradiated in the coleoptile stage or in other experiments were irradiated as dry seed. Fourteen doses from 20 to 640 Kr were administered at ca. 4 Kr per minute to seedlings within the relatively uniform flux center of a hollow cylinder type cobalt-60 irradiator. All plants were handled in individual one ounce square glass bottles containing vermiculite. One hour after irradiation they were "presented" to gravity by turning the bottles on their sides. Time lapse photographs were taken of the geotropic response of the shoots every twenty minutes for forty-eight hours. Geotropic bending and growth were measured on the projected film images. Radiation inhibited both geotropism and growth. Statistical analysis revealed that the primary component in the relation between dose and inhibition of geotropism was linear with significant higher order effects.

Irradiation of dry corn seed with subsequent germination and determination of geotropic response and growth gave a different picture. The inhibiting effect of radiation on geotropism increased to 120 Kr, then decreased, so that at 360 Kr the seedlings responded geotropically almost as well as unirradiated controls. A similar but much less pronounced effect on growth was obtained as had been reported

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previously for corn seed.

Preliminary experiments attempting to reverse 480 Kr inhibition of geotropism and growth with indoleacetic acid and naphthaleneacetic acid were unsuccessful.

H. Teas  
T. Holmsen

2. Physiological study of lazy.

The Coop stock of la, which grew very poorly in Florida, was outcrossed to Florida adapted lines and reisolated. Also, it was separated from su. The breaking strength of lazy and normal sib plant stalks was determined. The weights required to break a six inch span of basal stalk were variable, but the means were not very different. In this stock at least, stalk weakness does not seem to be the basis for the ultimate prostrate growth habit. Although it had been reported by Shafer that lazy plants became ageotropic at an age of ca. 4-7 days, according to temperature, no reference was made to the coleoptile. It was found that shoots of lazy seedlings in the coleoptile stage are normally geotropic, but after breaking through the coleoptile the leaves become ageotropic.

T. Holmsen  
H. Teas

3. The red pigment formed in corn seedling extracts with anthranilic acid.

The red pigment formed in breis of corn seedling leaves (News Letter 28: 22, 1954) has been further studied. Anthranilic acid disappears as the red material is formed. Paper chromatography and other evidence indicate that the substance in leaf extracts is yellow; crystalline; soluble in ether, acetone, and water but not ligroin; is slightly acidic; gives Craven's test for quinone; and the chromatographed 2, 4-dinitro-phenylhydrazone color suggests a benzoquinone.

The red pigment formed from anthranilic acid is acidic, has no free diazotizable amine, and is decolorized by bisulfite. Tentatively it is suggested that the material which combines with anthranilic acid to form the red pigment may be a partially substituted benzoquinone which would make the red pigment an aminoquinone, specifically an anthranilylquinone. It may be that material, which is almost absent in corn embryos and older plants but which is abundant in young plants, has a function in electron transport like Coenzyme Q, or conceivably is a precursor of Coenzyme Q.

H. Teas

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Department of Plant Pathology and Plant Breeding

1. A method for keeping maize plants alive in the tasseling stage after removal from the nursery.

A simple method was developed for transporting and keeping corn plants alive for demonstrations. A mature corn plant undergoing anthesis was dug from the nursery with a shovel. The roots, in a clump

of soil approximately 10-12 inches in diameter, were enclosed in a plastic fertilizer bag 19 inches wide and 28 inches deep. The inside of the plastic bag and the soil were sprinkled with water before tying the bag securely with a string.

Five plants treated in this manner were transported in the trunk of an automobile 202 miles to Douglas, Georgia, and placed in the hot July sun during a demonstration at a corn clinic. Holes were dug in the soil at the site of the meeting for placing the bags and roots underneath the soil. Consequently, the bags were not visible to the audience.

The plants were still alive and in good condition for the demonstration, although one of the plants was dug two days prior to the meeting and the other four plants one day prior to the meeting. Three of the plants were transported back to Athens and placed in a grove of trees on the University campus. Water was sprinkled occasionally into the plastic bags. Two of the three plants lived until 17 days later. The third plant was still alive 22 days after the meeting but not in an entirely satisfactory condition for demonstrational use.

In addition to demonstrations, this method apparently has other possibilities such as transferring plants from greenhouse to the field and vice versa, and crossing plants from different locations.

A. A. Fleming

## 2. Effect of stand on yield and other agronomic characters in double-cross corn performance tests.

Genes controlling some characters in double crosses were affected more by variations in stand than genes controlling other characters. Under the conditions of this experiment, plant height, ear height, root lodging, and stalk lodging were not affected as greatly by deficiencies in stand as maturity, yield per plant, number of ears per plant, and size of ear.

When allowed the same amount of additional space in which to develop, plants of a two-eared hybrid had a greater increase in yield than plants of a one-eared hybrid.

Julian W. Crews

A. A. Fleming

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## 1. The blotching system involving the C locus.

In last year's News Letter it was concluded that the blotching system which causes blotches of color to develop in the aleurone in A c R genotypes involves at least four genes. This conclusion was based in part on the fact that the inbred strain, Oh45, which is not itself blotched, proved in test crosses to be homozygous for the Bh factors on chromosomes 4, 6, and 9. This suggested that there must be at least one additional factor in the system and that this factor is absent in Oh45. Ratios in crosses of Oh45 with testers for the known Bh genes also indicated that an additional factor is involved.

Test crosses made in 1959 show that this additional gene is A<sub>2</sub> rather than a gene specific for blotching. Oh45 has the genotype a<sub>2</sub> a<sub>2</sub>. Our present conclusion is that three different Bh genes on chromo-

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somes 4, 6, and 9 act upon the genotype  $\underline{A}_1 \underline{A}_2 \underline{c} \underline{R}$  to produce blotches of color.

P. C. Mangelsdorf

## 2. The blotching system involving the R locus.

The previous data have indicated that there might be as many as six loci in this blotching system. Test crosses made in 1959 show that the 81:175 ratios repeatedly encountered involved segregation for both  $\underline{A}_2$  and  $\underline{C}$  as well as for two blotching genes. Ratios suggesting segregation for five or more loci are now known, from studies made in 1959, to involve preferential segregation. Thus only two  $\underline{Bh}$  factors are now identified for this system. One of these is known from data previously reported to be located on chromosome 4; the other appears to be on chromosome 2. Previous data had shown linkage between  $\underline{Bh}$  and floury endosperm; recent data show that the floury endosperm gene involved is that on chromosome 2. The data available, since they involve an  $F_2$ , are not satisfactory for determining a linear sequence but, since  $\underline{Bh}$  appears to be strongly linked with  $\underline{Fl}$  and  $\underline{V}_4$  and only weakly linked with  $\underline{Lg}$ ,  $\underline{Gl}_2$ , and  $\underline{B}$ , it is tentatively assumed that this  $\underline{Bh}$  lies between  $\underline{Fl}$  and  $\underline{V}_4$ .

P. C. Mangelsdorf

## 3. The gene for tunicate a compound locus?

Because the allele,  $\underline{tu}^h$  which originated in our cultures as a mutant of  $\underline{Tu}$ , has almost exactly half of the effect on various characters which  $\underline{Tu}$  exhibits, we have for some years suspected that the  $\underline{Tu}$  locus may be a compound one, similar to bar eye in *Drosophila*, resulting from the duplication through unequal crossing over of a more simple locus. We have for some years been developing stocks to test this possibility. A uniform inbred strain of the genotype  $\underline{Su} \underline{Tu} \underline{Gl}$  was crossed with a uniform inbred strain of the genotype  $\underline{su} \underline{tu} \underline{gl}_3$ . The  $F_1$  was backcrossed on a second uniform inbred of the genotype  $\underline{su} \underline{tu} \underline{gl}_3$ . In the population resulting from this backcross, approximately half of the plants should be  $\underline{Tu} \underline{tu}$ . Mutations to  $\underline{tu}^h$  in the previous generation would result in plants of the genotype  $\underline{tu}^h \underline{tu}$  which should be distinguishable from  $\underline{Tu} \underline{tu}$ . In a population of 8134 plants, 4129 were tunicate. Of these two appeared phenotypically to be heterozygous half tunicate ( $\underline{tu}^h \underline{tu}$ ). Both of these are crossovers between  $\underline{Su}$  and  $\underline{Gl}$ : one being the genotype  $\underline{Su} \underline{gl}$ , the other  $\underline{su} \underline{Gl}$ .

Progeny tests to determine whether these plants are mutants or phenocopies are being made in the Florida winter planting. If these prove to be mutants and are identical then it is possible that the  $\underline{Tu}$  locus is a compound one which has originated during domestication. But if the mutants are different it is probable that the compound locus is an ancient one characteristic of the genotype of wild corn.

P. C. Mangelsdorf  
W. C. Galinat

## 4. Linkage relations of an unstable gametophyte mutant.

The position on chromosome 4 of an unstable mutant originating in a maize-teosinte cross and affecting preferential segregation with respect to the  $\underline{Su}$ - $\underline{su}$  locus has now been determined by a three-point test. The data from the back cross  $\underline{ga} \underline{su} \underline{gl}_3 \times \underline{Ga} \underline{Su} \underline{Gl}_3$  follows:

$\underline{ga} \underline{su} \underline{gl}_3 \quad \underline{ga} \underline{su} \underline{gl}_3$

Plant No.	Su $Gl_3$	Su $gl_3$	su $Gl_3$	su $gl_3$	Totals	% Su	% $Gl_3$	% C. O. Su $Gl_3$
211-4	76	39	79	136	330	34.8	47.0	35.8
5	39	33	63	95	230	31.3	44.3	41.7
7	106	39	59	147	351	41.3	47.0	27.9
11	38	28	40	69	175	37.7	44.6	38.9
12	77	53	75	103	308	42.2	49.4	41.6
Totals	336	192	316	550	1394	37.9	46.8	36.4

Previous experiments have indicated that this  $G_a$  is not transmitted through the pollen. If this is true then the percentage of  $Su$  and  $Gl_3$  represent respectively the percentages of crossing over between  $G_a$  and  $Su$  and between  $G_a$  and  $Gl_3$ . On this basis the linear sequence must be  $G_a$   $Su$   $Gl_3$  and  $G_a$  must be on the short arm of chromosome 4, perhaps fairly near the terminal end.

P. C. Mangelsdorf  
S. M. Sehgal

#### 5. The mutagenic effects of homozygous and heterozygous teosinte chromosomes in an isogenic stock.

There has been some indication from previous studies that the mutagenic effects of teosinte chromosomes incorporated into an inbred strain (A158) are greater when the introduced teosinte chromosomes are heterozygous than when they are homozygous. To test this possibility further we conducted the following experiment: Eight different modified strains of A158 each containing one or more introduced teosinte chromosomes in the homozygous condition were scored for seed and seedling abnormalities. These same eight strains were crossed with the original A158 and the  $F_2$  ears were scored for seed and seedling abnormalities. The results are shown in the following table:

Stock	No. ears Scored	Percent with Abnormalities		
		Seed	Seedling	Total
Control, pure A158	100	0.0	0.0	0.0
A158 with homozygous teosinte chromosomes	876	10.0	6.6	16.6
A158 with heterozygous teosinte chromosomes	658	15.2	19.4	34.6

It is probable that some of the abnormalities found are phenocopies rather than inherited mutations. However the fact that the frequency of abnormalities is more than twice as great when the teosinte chromosomes are heterozygous than when they are homozygous is highly significant. It suggests that crossing over between maize and teosinte chromosomes may be involved in the production of abnormalities. Since maize and teosinte chromosomes are probably not completely homologous, crossing over between them may often be unequal. This could result in deficiencies and duplications.

W. C. Galinat

#### 6. Genetic control of phytomer development.

Although different regions of the plant differ greatly in final form, despite their common genom, their initial repetitious design, the so-called "phytomer," is identical. The role of specific genes in modifying development of the phytomeric parts, an internode with attached leaf and an axillary bud with associated prophyll for specialized functions, is revealed by certain genetic variants. In the central region along the plant the leaves are greatly enlarged and widely separated by elongated internodes

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an arrangement which ensures maximum photosynthetic activity (loci: narrow-leaf, brachytic, etc.). Maximum fecundity in the floral region requires many abrupt modifications although the shift to inflorescence development becomes gradual in the presence of either the Corn-grass or Teopod genes. The natural protection and dissemination of the grain and protection of the young anthers from sun-burning requires a very precise accommodation in leaf (glume) shape, size, and texture (loci: Tunicate, Vestigial glume, Papyrescent) although the ideal natural form may not correspond to the ideal domestic form. Where floral leaves would be useless or harmful to fecundity, such as in rachis phytomers, they are completely inhibited or reduced to glume cushions (loci: Corn-grass, Teopod). The genes at four loci control the production of phytomers by various axes of the inflorescence (loci: ramosa 1 and 2, branched-silkless, and polytypic).

W. C. Galinat

#### 7. Evolution of a low glume/rachis ratio in the American Maydeae.

The introduction of the tunicate (or half-tunicate) gene from maize into teosinte transforms the cupulate fruit case into another type of fruit case with a quite different glume-rachis relationship. This synthetic form has long glumes and slender rachis segments in a combination which except for the increased size of the parts resembles Elyonurus tripsacoides in the closely related tribe Andropogoneae. Such an equal enlargement of parts may only reflect increased vigor while, on the other hand, differential development would have taxonomic significance. In modern maize and its relatives, the ordinary-sized pistillate glumes in combination with thick rachises produce low glume/rachis ratios. Since the tunicate gene can reverse this condition in at least maize and teosinte (and probably in Tripsacum) by producing a high glume/rachis ratio of a type typical for the Andropogoneae, this gene or its locus may well have been involved in the evolutionary divergence of the American Maydeae from the Andropogoneae.

W. C. Galinat

#### 8. Intra-plant ear competition in Argentine popcorn.

The many-eared characteristic of Argentine popcorn tends to provide a series of forms intergrading between tassel branches at the top of the plant and tillers at the base of the plant. The progressive changes involved may reflect those which occurred during the evolution of a large centrally-located ear enclosed in many husks from a tiny sub-tassel ear enclosed by only a few husks (Mangelsdorf, 1958). That a central position along the stalk is a more favorable one for development of a larger, more productive ear is supported by the following data:

Ear Character	Position at Various Nodes Below the Tassel				
	1	2	3	4	5
Kernel Rows	8	10	12	14	14
Total No. Kernels	64	190	220	350	336
Weight ear (gms.)	3.2*	10.0	11.3	14.4	12.5
Length Shank (cm.)	2.4	2.7	4.4	5.4	6.3
No. husks	4	5	6	7	8

\* including 0.5 gms. in a staminate tip



The data indicate that ears borne below an optimum position may be reduced in size probably because of competition with longer shanks and more numerous husks.

W. C. Galinat

9. Clustered spikes, an extreme feature of teosinte, present in maize-Tripsacum hybrid.

Since the clustering of spikes is unique to teosinte among the American Maydeae, this character seems at first to oppose the theory that teosinte is derived from a maize-Tripsacum hybrid. But the presence of clustered spikes in an  $F_1$  hybrid between multiple-tester maize and Tripsacum dactyloides, which is currently under study, demonstrates that this feature is merely a hybrid product of combining two other characters from maize and Tripsacum. When the many-noded shank (peduncle) of maize, which has a lateral bud at each node, is combined with the small two-ranked spike of Tripsacum there is a development of the lateral buds into clusters of spikes.

W. C. Galinat

10. Cytological studies of  $F_1$  hybrids between maize and teosinte.

A. Chalco teosinte - maize hybrids. Two  $F_1$  plants of the cross of an inbred maize strain of Wilbur's Flint x Chalco teosinte and its reciprocal were cytologically investigated. A practically terminal inversion was found at pachytene in the short arm of chromosome 8 in both of these plants. This inversion, like In 8 in other varieties of teosinte, formed loop-shaped, ring-shaped and asynaptic configurations. The length of this In 8 and the percentage of the short arm which it occupies are shown in Table I.

Table I. Length of In 8 in Chalco teosinte

Cell No.	Length in microns		Percent of Short arm
	Short arm	Inversion	
1	16.0	13.6	85.0
2	14.0	9.2	65.7
3	12.8	9.6	75.0
4	14.2	10.7	75.3
5	13.4	9.6	71.6
Average	14.0	10.5	74.5

The chromosomes in these  $F_1$  plants were well spread and easily identifiable. There was one knob on the long arm of chromosome 1, and one on each arm of chromosome 2. The long arm of chromosome 3 had a medium-sized knob. A small subterminal knob was present on the short arm of chromosome 4, and a relatively large knob occurred on the long arm. A large knob occurred on the short arm of chromosome 5. Two knobs were found on the long arm of chromosome 6, and a small terminal knob or a large chromomere on the short arm of the same chromosome. A large knob was also present on the

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long arm of both chromosomes 7 and 8. The short arm of chromosome 9 had a large terminal knob. Chromosome 10 in these hybrids was knobless. Since the inbred strain of Wilbur's Flint was previously found to have only large chromomeres and no chromosome inversions, the knobs and In 8 in the hybrids were definitely contributed by the Chalco teosinte parent.

In a total of 626 randomly chosen sporocytes, 9.4 per cent had two univalents at diakinesis, the remainder having all of their 20 chromosomes associated into ten different bivalents. Sporocytes having more than two univalents were not observed. The low percentage of sporocytes having univalent chromosomes at diakinesis indicates that the chromosomes of Chalco teosinte and of the inbred strain of Wilbur's Flint have a high degree of homology.

**B. Florida teosinte - maize hybrids.** Four  $F_1$  plants of the cross of Wilbur's Flint x Florida teosinte and one  $F_1$  plant of the reciprocal cross were cytologically examined. At pachytene the chromosomes in all of the plants appeared sticky and highly heterochromatic. A heterochromatic segment attached to the end of an unknown chromosome seemed larger than that attached to the distal end of the abnormal chromosome 10, previously described (Chromosoma, 1958). It was very difficult to identify the chromosomes and their irregularities. However, a practically terminal inversion in the short arm of chromosome 9 was definitely identified. On the basis of three separate measurements, it was concluded that the average length of this inversion was 19.1  $\mu$  which was about equivalent to 81.9 per cent of the length of the short arm. There were probably two other paracentric inversions, but due to their stickiness the chromosomes involved were not definitely known, although they seemed to occur on chromosomes 3, 4, or 5.

At diakinesis of 448 randomly chosen sporocytes studied, 297 or 66 per cent had all of the ten chromosomes paired as bivalents; 115 or 26 per cent had two univalents; 34 or seven per cent had four univalents and two cells or less than one per cent, had six univalents.

At anaphases I and II, bridges and fragments in various combinations were frequently found. The results are shown in Table II on the following page.

Lagging chromosomes were also frequently present at anaphase I. Most of these laggards were individual chromosomes showing no association even when two occurred in the same cell. The number of laggards varied from one to five. The frequency of each number is shown in Table III.

Table III. Laggards found at anaphase I of  $F_1$  plants of maize and Florida teosinte

	Number of Laggards					
	0	1	2	3	4	5
Frequency	360	55	49	4	7	2
Per cent of total	75.3	11.5	10.3	0.8	1.4	0.4

Y. C. Ting

Table II. Frequency of dicentric bridges (B) and acentric fragments (F) at anaphases I and II of F<sub>1</sub> plants of maize and Florida teosinte.

	Anaphase I										Anaphase II Based on single Cell Counts	
	0 B	1 B	2 Bs	1 B	0 B	1 B	1 B	2 Bs	1 B	0 B	0 B	1 B
	0 F	1 Free F	2 Free Fs	0 F	1 F	1 attached F	3 Free Fs	1 Free F	2 Free Fs	2 Free Fs	0 F	0 F
Frequency	362	58	2	2	40	2	1	1	1	3	325	8
% of total	76.6	12.0	0.4	0.4	8.5	0.4	0.2	0.2	0.2	0.6	97.5	2.4

11. Cytological observations on the first backcrossed progenies of maize - teosinte hybrids

F<sub>1</sub> plants of Huixta teosinte x Wilbur's Flint were crossed back by their maize parent. Inflorescences from 22 plants of these backcrossed progenies were studied with the following results:

A. Sticky versus well-spread pachytene chromosomes. Among 22 plants studied, 13 had well-spread pachytene chromosomes. Centromeres, knobs and other characteristics of the chromosomes in these were readily identifiable. In the remaining nine plants, with sticky chromosomes, the characteristics were difficult to recognize. Since pachytene chromosomes in the F<sub>1</sub> plant used and those of the Huixta teosinte parent were well spread, while those in the maize parent were not, it seems that the character of well-spread pachytene chromosomes in Huixta teosinte is controlled by one or two genes which are dominant over those for stickiness.

B. Changes in knob morphology. In one plant, 58-795-18, a heterozygous knob on the short arm of chromosome 2 appeared larger at pachytene than that in the F<sub>1</sub> plant at the same stage. The maize parent had no knob at this position. In a group of seven plants having a heterozygous knob on the long arm of chromosome 5, this knob was found frequently split into two parts in six of those seven plants. The separation between the two parts was often very clear. A split knob did not occur in either the F<sub>1</sub> plants or the recurrent maize parent.

C. Triploid plants. Two of the 22 plants studied were found to be triploid. These two plants had 30 chromosomes instead of 20, which were normally present in their sibs. The behavior of the chromosomes in these plants has been reported elsewhere.

Y. C. Ting

12. On heterochromatin repulsion.

The meiotic behavior of abnormal chromosome 10, was studied in a plant which was homozygous for this abnormal chromosome described by Longley. At the pachytene stage, a total of 126 microsporocytes was selected at random. Fifty-six percent, or 71 of them, were observed to have the extra pieces of heterochromatin attached to chromosome 10 in a repulsion configuration. Starting at the joints of attachment, the extra pieces of heterochromatin were spread widely apart as if they had no homology between them. The remaining 51 cells were found to have the heterochromatic homologues closely paired. Four cells or three per cent, were found to have the heterochromatic homologues only partially associated while their distal halves were in an asynaptic configuration. It appears that the degree of homology between two heterochromatin segments in maize can not be measured only by the frequency of primary associations between them at pachytene stage.

Y. C. Ting

13. Extra element in microsporocytes.

During 1958 and 1959 an extra element in maize microsporocytes at pachytene was found in three different cultures fixed in the standard way. Its shape varied: ring-, spiral- and rod-shaped configurations all being observed. The staining of this element was sometimes as dark as that of the chromosomes. Granules or chromomere-like structures were clearly shown along the main strand of this element. Its location was not confined to any particular part of the cell; at one time it was found in the nucleolus, and at another in the cell periphery. Affinity with other elements in the cell did not seem

to occur. As division advanced, this element persisted. But at anaphase I, it failed to divide. Hence it is expected to appear in only one of the two daughter cells after the first division. Its genetic significance and the manner by which it is transmitted from one generation to the other are under investigation.

Y. C. Ting

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### 1. Induction of monoploidy.

From field observations in the nursery it has been found that Coe's "Mexican Flour High Haploid Strain" (hereafter abbreviated as CMHH) yields monoploid plants with a frequency running as high as 4-5% on selfing. The derivation of a monoploid inducing strain based on the properties exhibited by CMHH, and carrying the seedling color markers as used by Chase, would depend for its ease on the number and type of factors involved in the high incidence of monoploidy in CMHH, and for its usefulness on the manner in which the high incidence of monoploidy is induced, i. e. (1) whether the male or female gamete is the one which is transmitted, and (2), whether factors carried by the transmitted gamete affect the frequency with which it develops into a monoploid plant.

F<sub>1</sub>'s from the cross CMHH ( $A_1 \underline{b} \underline{pl} R^{\underline{g}} Lg_2/A_1 \underline{b} \underline{pl} R^{\underline{g}} Lg_2$ ) X  $a_1 B Pl R^f lg_2/a_1 B Pl R^f lg_2$  were grown, and populations derived from them observed, as listed in the table below. Monoploids were scored on the basis of phenotypic appearance in the field, and checked several times during the growing season.

Population	No. of families grown	Total no. of plants	Total no. of mono-ploids	Total no. of $lg_2$ mono-ploids	No. of families with the following percentage of monoploids (to the nearest per cent)				
					0	1	2	3	4
1. F <sub>2</sub>	7	880	5	0	5	0	1	1	0
2. (CMHH X F <sub>1</sub> ) ⊗	3	259	6	1	0	2	0	1	0
3. CMHH X F <sub>1</sub> ♂	4	300	4	0	0	2	2	0	0
4. CMHH X F <sub>1</sub> ♀	7	560	13	5	2	0	3	1	1

Diploid liguleless plants were segregating in the expected manner, and none were found in the last two populations listed. Liguleless monoploids appeared in two of the three populations where the female parent was heterozygous for the locus, and in one of these, the male parent did not carry  $lg_2$  at all. From this last cross it may be concluded that only the female complement is transmitted in the monoploids derived from the CMHH strain.

If it were simply a matter of the male gametes carrying a certain factor the presence of which results in the failure of double fertilization with a certain frequency, then the frequencies observed in lines (1) and (3) of the table should check more closely. Cytoplasmic differences between the female parents should not exist here, since the cytoplasm of the F<sub>1</sub> came from CMHH. On the other hand, when CMHH was used as the male parent, the frequency of monoploidy was strikingly higher.

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The small size of the individual families does not permit speculation on whether the high incidence of monoploidy observed is due mainly to the effects of one gene in the male gamete.

Tests are now underway to score the efficiency of monoploid induction by the derivatives of the above populations on unrelated material.

Wolf Prensky

2. Wanted:

Seedling character mutants (liguleless, glossy, dwarf, midribless) found in highly inbred lines.

Wolf Prensky

UNIVERSITY OF ILLINOIS  
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Department of Botany

1. Noncrossover derivatives from serial duplications.

The available evidence indicates that noncrossover alpha derivatives from the beta: alpha  $A^b$  complex in maize are the result of an intrachromosomal event. Critical evidence that the homologue is not involved is the occurrence of noncrossover alphas from hemizygotes deficient for the  $a_1$  region. Since there is evidence that the members of the  $A^b$  complex are serial duplications, it seemed appropriate to determine whether similar derivatives occur from other serial duplications.

The Bar duplication in *Drosophila melanogaster* provides an opportunity for such a test, and offers the possibility of cytological analysis of any derivatives obtained. Deficiency  $B^{263-20}$  was used for the *Drosophila* tests in heterozygotes with Bar marked with forked and fused.  $B^{263-20}$  includes the forked locus, thus permitting no crossovers between  $f$  and  $B$ . Unfortunately, however, band 7 of the Bar region is not included in the deficient piece and may allow for pairing of the Bar segments to give crossover wild type derivatives.

Heterozygous females  $Df + \underline{fu}/f \underline{B} \underline{fu}$  were crossed with males from a number of stocks carrying different autosomal markers to produce progenies for analysis. As the deficient chromosome is lethal in males, only  $f \underline{B} (\underline{fu})$  males are expected.

However, among approximately 70,000 males scored, 17  $f +^B$  individuals were found. Of the 15 which thus far have been analyzed genetically, all have segregated the autosomal marker introduced by their father, and 14 have transmitted  $f +^B$  to their grandsons. Of these 14, four are noncrossovers for the  $\underline{fu}$  marker and ten are recombinants for  $\underline{fu}$ .

Stocks of the four noncrossover derivatives and of the crossovers are now being grown for cytological study.

Two other experiments with Bar are now being set up. First, we are attempting to obtain with X-rays a deficiency which includes all of the Bar duplication bands, so that crossover derivatives, and particularly close-distance multiple crossovers can, as in the case of  $A^b$  in maize, be positively ruled

out. The other experiment involves the use of CIB/f B odsy heterozygotes with + B + / f B odsy sibs. Our interest in using the CIB inversion stems from the fact that Inversion 3a heterozygotes in maize produce a high rate of alpha derivatives from A<sup>b</sup>.

H. M. Peterson

J. R. Laughnan

## 2. Pairing of normal and inversion chromosomes in trisomic-3 individuals.

The occurrence in the 1957 nursery of a trisomic-3 individual, whose chromosomes 3 were differentially marked at the a<sub>1</sub> and sh<sub>2</sub> loci, one carrying Inversion 3a, provided an opportunity to determine whether this inversion has an effect on frequency of synapsis in a nucleus which also carries two normal chromosomes.

This trisomic individual, having the constitution A<sup>b</sup> sh/a sh/Inv. 3a: a Sh, was pollinated by a a sh/a sh tester plant, and colored non-shrunken kernels were planted for test in 1959. Pollen of twelve of these plants, whose constitution was again that of the parent trisomic, was used on a a sh/a sh tester plants to produce ears for the data presented below:

Trisomic plants used as pollen parents	Number of ears scored	Phenotypic Classes				Total kernels scored
		I Colorless, non-shrunken	II Purple, shrunken	III Colorless, shrunken	IV Purple, non-shrunken	
59-466-1	5	217	455	438	23	1,133
-2	2	100	197	177	2	476
-3	5	281	547	491	9	1,328
-4	4	149	418	386	9	962
-5	5	228	453	460	20	1,161
-6	4	303	505	488	7	1,303
-7	6	307	606	608	20	1,541
-8	5	184	405	364	13	966
-9	5	290	583	579	8	1,460
-10	2	70	232	206	5	513
-11	4	183	464	455	9	1,111
-12	5	337	630	563	11	1,541
Total	52	2,649	5,495	5,215	136	13,495
Per cent		19.6	40.7	38.6	1.0	99.9

Three main classes of kernels were obtained: about 20% colorless non-shrunken, representing primarily those receiving Inv. 3a: a Sh gametes; about 40% purple shrunken (A<sup>b</sup> sh); and about 40% colorless shrunken (a sh). The fourth class (to be tested in 1960) may represent the rare functioning of disomic pollen carrying A<sup>b</sup> sh and Inv. 3a: a Sh to give trisomic embryos; trisomics Inv. 3a: a Sh/a sh/a sh may be included in class I and A<sup>b</sup> sh/a sh/a sh in class II. This may explain the highly significant difference between classes II and III.

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In a trisomic, any one of the three chromosomes would be expected to pair at the centromere region in 67% of the cells, disjoin normally from its partner, and transmit in 33% of the balanced gametophytes. The 20% transmission found here for the inversion-carrying chromosome indicates that its pairing in the centromere region is greatly reduced.

That the inversion chromosome does not carry an aberration reducing transmission in pollen was checked by counting colorless (Inversion 3a) and purple (normal 3) kernels on diploid selfed ears. On ten such ears 2,463 purple kernels (74.2%) and 858 (25.8%) colorless kernels occurred. Trisomic plants carrying two Inversion 3a chromosomes and one normal one are available for test next summer.

The data reported here are in agreement with the results of a similar study reported by G. G. Doyle in the 1959 issue of M. G. C. N. L.

J. R. Laughnan  
H. M. Peterson



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1. Genes for resistance to rust, Puccinia sorghi, Schw.

Six major genes which condition resistance to Puccinia sorghi have been located by means of inheritance studies involving rust-resistant inbreds and rust-susceptible inbreds and F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub>, and backcross progenies derived from them. These studies have been referred to in previous News Letters. The genes are in an allelic series. Their designation and the corn strains in which they were located are indicated in the following table:

Gene	Corn strain in which located	Additional corn strains which probably contain this gene
Rp <sup>1</sup>	GG208R	Golden Glow O.P., Golden King O.P., P. I. 213777
Rp <sup>2</sup>	B38	B216, B217, Burr White O.P.
Rp <sup>3</sup>	K148	Synthetic A
Rp <sup>4</sup>	Cuzco	
Rp <sup>5</sup>	B49	
Rp <sup>6</sup>	P. I. 172332	

The gene Rp<sup>1</sup> is believed to be identical to the gene previously identified as Rp discovered by Mains and located in chromosome 10 by Rhoades. This is supported by the data in the following article.

-- A. L. Hooker

2. Translocation studies involving GG208R.

To check on the location of the resistance gene (Rp<sup>1</sup>) in GG208R, semi-sterility due to a heterozygous translocation was used as a marker. Two populations of (susceptible translocation x resistant GG208R) x susceptible B14 were classified; one involved T5-10 wherein the break in #10 is at 0.54 on the short arm and the second involved T8-10a with the break in #10 at 0.48 in the short arm. The segregations showed 6.4 per cent crossing over between semi-sterility and susceptibility in T5-10 and 10.3 per cent in T8-10a. These data indicate that the gene for resistance to P. sorghi in GG208R is probably the same as reported earlier by Rhoades.

-- W. A. Russell

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1. Further studies of nucleic acids and allied compounds in relation to suppression of meiosis in ameiotic maize.

The preliminary biochemical studies on the action of the ameiotic gene controlling meiosis in maize (MNL 33) have been extended, and some results of further analysis have been briefly reported (Science, 1959). The present status of the findings will be summarized under four categories: (1) acid soluble precursors of nucleic acids, (2) ribonucleic acid or RNA, (3) deoxyribonucleic acid or DNA and (4) "histones." All investigations, so far, are limited to young ears and 3mm long root tips.

(1) Acid soluble precursors of nucleic acids

a) In young ears: As revealed by spectrophotometric analysis of the cold acid extracts from delipidated materials, there is an accumulation of precursors of nucleic acids in the ameiotic ears at all stages of development except at a very early stage much prior to megasporogenesis. In the materials from normal plants the concentration of the precursors is found to be low. This is probably due to a more rapid utilization of the precursors in the synthesis of nucleic acids in the ears of normal plants.

On further analysis the accumulating material is found to be some ribonucleosides. Chromatographic separation has indicated the presence of at least four different compounds in this acid soluble fraction. These have been tentatively identified as adenosine, guanosine, uridine and xanthosine. Uridine is in maximum concentration and xanthosine is in minimum.

b) In root tips: Precursors of nucleic acids have not been found in the extracts of root tips of ameiotic plants. It appears that the synthesis of the precursors is more rapid at the time of meiosis than at mitosis.

(2) Ribonucleic acid (RNA)

a) In young ears: Following a modified Ogur-Rosen and Schmidt-Thannhauser procedure an attempt has been made to fractionate different types of RNA (differing in their solubility behaviour and probably metabolically different). The fraction extractable with very dilute cold Perchloric acid will be called RNA -1 (may be polyribonucleotide of low molecular weight or SRNA of Hoagland); the fraction extracted with cold but stronger Perchloric acid will be referred to as RNA -2; and the acid resistant but alkali soluble RNA will be designated as RNA -3. It is found that there is an excess of RNA -1 in the ameiotic ears as compared with the normal ones. The quantity of RNA -2 is also greater in ameiotic ears, though the difference is not as big as in the case of RNA -1. Inference regarding RNA -3 has to be deferred.

b) In root tips: Difficulty of obtaining sufficient material has hampered an elaborate fractionation of RNA from root-tips. It has been, however, observed that the root tips of ameiotic plants contain more of acid soluble RNA (Ogur-Rosen and equivalent to the sum of RNA -1 and RNA -2; there may not be any RNA -3) than those of normal plants.

(3) Deoxyribonucleic acid or DNA:

a) In young ears: The DNA extracted by the Ogur-Rosen method is found to be contaminated with some RNA (RNA-3), because of the incomplete extraction of RNA from the ear material. After necessary correction for this RNA, the total amount of DNA expressed per unit fresh or dry weight of tissue is found to be the same for both normal and ameiotic material.

The earlier finding (MNL 33; Science, 1959) of a possible difference in the so-called apurinic DNA fraction obtained after a brief hydrolysis with dilute hydrochloric acid is being further analyzed in this light. Since the difference was indicated in the base composition of this fraction, an analysis of the base composition of RNA has appeared necessary.

The ratio of RNA/DNA is higher in the ameiotic plants than in their normal sibs.

b) In root tips: In the root material, however, the DNA extracted by the Ogur-Rosen method is found to be free from any contaminating RNA indicating thereby an absence of the acid resistant RNA (RNA-3) in root tips. The estimated values for DNA are found to be the same in the ameiotic plants and their normal sibs.

(4) "Histones" and other proteins:

a) In young ears: The estimation of proteins extractable by the Daly-Mirsky method for histone determination has given much higher values for ameiotic material. If this is a true measure of histones, then the histone/DNA ratio is about twice as high in the ameiotic ears. Besides "histones", there are indications for a higher level of other proteins in the ameiotic material and further analysis is in progress.

Values obtained for "histones" in the root tips are too low to be given any weight. These are to be redetermined.

These results permit attempting a tentative and unified scheme to explain the suppression of meiosis in ameiotic maize so as to guide the course of further work towards an understanding of the physiology of meiosis and the delicate balance between meiosis and mitosis. It appears that the gene partially blocks some step(s) in the conversion of ribonucleosides into deoxy compounds, thereby preventing their rapid incorporation into DNA and leading to their accumulation in the ameiotic ears. An increase in the concentration of these precursors would favour an increased synthesis of RNA, which in its turn would cause greater synthesis of proteins. Excess of RNA even in the absence of any accumulation of precursors as in ameiotic root tips and in the extremely early stage of ameiotic ears perhaps points to a second possibility, that the pathway for RNA synthesis is more active at all stages of development of the ameiotic plants, which may or may not be associated with a partial block of DNA synthesis.

For normal meiosis a critical balance between 1) DNA and RNA, 2) DNA and histones as well as other proteins, and 3) two different types of RNA (one metabolically more active than the other) appears essential. A high RNA/DNA, histone/DNA, and RNA-1/total RNA appears to favour mitosis and suppress meiosis.

-- S. K. Sinha

2. A preliminary biochemical study of the action of the 'asynaptic' gene in maize.

Encouraged by the results obtained from the biochemical studies of the "ameiotic" gene (MNL 33; Science, 1959), an attempt has been made to see if the gene "asynaptic" affects nucleic acid metabolism in some way. Only three young ears of asynaptic plants and three of their normal sibs have been

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analyzed as a preliminary trial. Analyses have been made with material fixed in Carnoy's fluid, following the Ogur-Rosen procedure for nucleic acid extraction and estimation.

Acid soluble RNA per unit weight of fixed tissue is significantly greater in asynaptic plants than in the normal sibs. The "apparent" DNA (probably containing some acid resistant RNA) is found to be in equal amounts in both normal and asynaptic material. The amount of "histones" (Daly and Mirsky) is only slightly higher in the asynaptic material.

Besides the possible effect of histones (Ansley's finding), an excess of RNA appears detrimental to meiotic pairing in asynaptic maize plants. In view of a similar situation in ameiotic maize, it appears interesting and necessary to examine in detail as to how the situation in asynaptic plants differs from that in the ameiotic ones. Further work will be undertaken with regard to this and other biochemical aspects.

-- S. K. Sinha

### 3. Chemically induced chromosomal asynapsis in maize.

Paper chromatographic studies have indicated the presence of some phenolic compounds in ameiotic maize plants and their virtual absence in the normal sibs (MNL 33). In the ameiotic plants meiosis is found to be replaced by a type of mitotic division. The possibility of converting meiosis to mitosis experimentally by the administration of several phenols has been investigated.

The compounds tested were: 1) phenol, 2) resorcinol, 3) hydroquinone, 4) catechol, 5) pyrogallol. Solutions of these compounds in two different concentrations, viz. 0.01M and 0.1M, were fed into the plants through cut stems for 24 hours about a week before the initiation of meiosis in the tassels. A few plants were similarly fed with distilled water to serve as controls. All plants were heterozygous for Inversion-4a against a KYS background. Two replicate plants were taken for each concentration of a particular compound. Pollen mother cells were examined 9 days after treatment.

At the higher concentration all compounds prevented an appreciable percentage of meiocytes from undergoing any division. The nuclei appeared pycnotic. However, no mitotically dividing meiocytes were observed. On the other hand, various degrees of asynapsis of chromosomes were noted. Since no asynapsis was observed in the control plants fed with distilled water, the effect was evidently due to phenols. A maximum degree of asynapsis was found in plants treated with 0.1M phenol. Other compounds produced less extreme effects at this concentration, and still less at the lower concentration. In most cells, where asynapsis was less drastic, at least one chromosome was found to be more severely affected than the rest. In some cells this could be identified as the chromosome heterozygous for the inverted segment. Thus the synapsis of the segment heterozygous for an inversion appears more readily affected. A second feature noted in the mildly affected cells was that the segments containing knobs were more frequently asynapsed than the other regions.

However, more thorough examination is necessary before ruling out the possibility of involvement of some phenolic compounds in suppression of meiosis or its conversion to mitosis.

-- S. K. Sinha

### 4. Effect of RNA on meiosis in maize.

The finding that there is an excess of RNA in ameiotic plants suggested the possibility of converting meiosis to mitosis by treatment with RNA. Treatments were made as above along with necessary controls. No mitotically dividing meiocytes could be observed. However, several other interesting

effects were noted in anthers of RNA-treated plants, but not in the control ones. These were: 1) fusion of meiocytes forming plasmodial masses of varying sizes; 2) polyploid metaphase plates; 3) single cells with both hypoploid and hyperploid metaphase plates; 4) elongation of spindle; 5) precocious anaphase separation of some chromosomes, etc. These effects are similar to those found by Morgan (J. of Hered., 1956) in a monosomic plant (a member of two monozygotic twins). In both cases there might be a common basis in disturbed nucleic acid balance.

Further studies on the effect of variously induced nucleic acid imbalance on meiosis are in progress with a view to testing the hypothesis of a critical nucleic acid balance in the interconversion of meiosis and mitosis.

-- S. K. Sinha

#### 5. Preferential pairing in trisomes, triploids, and tetraploids which are heterozygous for inversion 3a.

In the Maize News Letters (1958 and 1959) preliminary data were presented which indicated that preferential pairing was active in chromosome 3 trisomes and in tetraploids which were heterozygous for inversion 3a (3L.4 -.95). Rhoades (MNL 1957) has presented data which showed the presence of preferential pairing in triploids which were heterozygous for In 3a and In 3b. These data concerned the effect of preferential pairing on gene segregation (Rhoades 1957, Doyle 1958 and 1959) and on chromatid bridge frequency (1959). More extensive data have been collected and will be reported here. In addition, another method of detecting preferential pairing based on the trivalent frequency in control and inversion heterozygote trisomes will be discussed and data obtained by use of this method will be analyzed.

#### A. Gene segregation in inversion heterozygotes and corresponding controls.

CROSS	PROGENY					
	CONTROL			INVERSION HETEROZYGOTE		
TRISOME	Ash	aSh	ash	ASh	aSh	ash
ASh*/aSh/ash X ash/ash	1868 47.1%	1322 33.3%	777 19.6%	2473 44.2%	1654 29.6%	1462 26.2%
ash/ash X ASh*/aSh/ash	116 33.6%	119 34.5%	110 31.9%	847 21.7%	1530 39.4%	1518 38.9%
a/a X A*/a/a	A 1843 33.6%	a 3644 66.4%	A : a 1 : 1.98	A 1481 22.1%	a 5234 77.9%	A : a 1 : 3.53
a/a X A*/A*/a	7473 66.8%	3722 33.2%	2.01 : 1	3092 78.6%	840 21.4%	3.68 : 1
A*/A*/a X a/a	2592 79.5%	667 20.5%	3.84 : 1	1355 90.7%	139 9.3%	9.75 : 1

CROSS	PROGENY					
	CONTROL		A : a	INVERSION HETEROZYGOTE		
TRIPLOID	A	a		A	a	A : a
A/A/a* X a/a	944 79.3%	246 20.7%	3.84 : 1	5647 84.1%	1068 15.9%	5.29 : 1
TETRAPLOID						
A*/a/a/a X 4n a	446 45.4%	537 54.6%	1 : 1.20	434 47.1%	488 52.9%	1 : 1.12
4n a X A*/a/a/a	1385 48.2%	1488 51.8%	1 : 1.07	763 48.8%	802 51.2%	1 : 1.05
4n a X A*/A*/A*/a	2227 97.5%	57 2.5%	39.1 : 1	440 98.7%	6 1.3%	73.3 : 1
A*/A*/a/a X 4n a	3498 79.3%	915 20.7%	3.82 : 1	2468 88.9%	309 11.1%	7.99 : 1
A/A/a*/a* X 4n a				5124 87.6%	727 12.4%	7.05 : 1
4n a X A*/A*/a/a	6674 80.2%	1647 19.8%	4.05 : 1	3802 86.7%	581 13.3%	6.54 : 1
4n a X A/A/a*/a*				8177 86.2%	1308 13.8%	6.26 : 1

\* indicates that the gene so marked is included in the inverted chromosome in the inversion heterozygote.

The differences between the gametic ratios of the various types of inversion heterozygotes and their corresponding controls are all highly significant, except in the cases of the simplex and triplex tetraploids. When three chromosomes are of one type and one is of another type there is no chance for preferential pairing to be expressed, since the odd chromosome must pair with an unlike chromosome. When the simplex tetraploid is used as the female parent the chi-square is .55 ( $p > .40$ ); when it is used as the male parent the chi-square is .11 ( $p > .70$ ). The chi-square for the triplexes is 2.2 ( $p > .10$ ). However, it is believed that with sufficient data it could be shown that the ratios in the progeny of these plants are significantly different. The frequency of double reduction should be less in polyploid inversion heterozygotes because of the presence of the inversion which decreases crossing over.

A detailed discussion of the theoretical effect of preferential pairing on gene segregation would be too lengthy to include in this report. However, the general principles may be stated briefly.

In a trisome or a triploid when a bivalent and a univalent are formed, the pairing may be homosynaptic or heterosynaptic. The random frequencies of homosynapsis and heterosynapsis are  $1/3$  and  $2/3$ , respectively. When preferential pairing is active, these frequencies become  $1/3 + p$  and  $2/3 - p$ . The factor "p" may be defined as the frequency with which homosynapsis occurs over the random amount.

It may be seen that the frequency of a gametes in the progeny of a duplex (AAa) trisomes and duplex triploids used as the female parent would be  $1/4(2/3 - p)$  if only bivalents and univalents were formed. When a trisome is used as the pollen parent the frequency of a gametes would be about  $1/2(2/3 - p)$  since disomic pollen rarely functions.

Since In 3a includes only about 37% of the length of the chromosome three, the other parts of the chromosome may pair at random. Preferential pairing probably only takes place in the region of the inversion. Thus it is possible to have homosynaptic or heterosynaptic trivalents, depending on the way the inverted region is paired. The expected gametic ratios depend on the way these trivalents disjoin and on the frequency with which the chromosomes acquire the equational constitution (AA-Aa-Aa). Assuming that the disjunction of the trivalent is at random, it may be theorized that an excess in the frequency of homosynaptic trivalents should increase the A : a ratio. Random segregation from the reductional mode gives a  $5\bar{A} : 1\bar{a}$  ratio, while random segregation from the equational mode (AA-Aa-Aa) gives a ratio of  $3.8\bar{A} : 1\bar{a}$ . Homosynaptic trivalents may be expected to contribute less to the equational mode than the heterosynaptic trivalents do. For a homosynaptic trivalent to form equational chromosomes an exchange of pairing partners and crossing over must take place in the region between the centromere and the proximal break point of the inversion. This is probably a rare event.

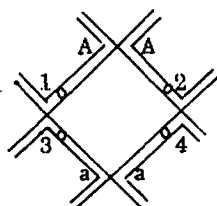
An additional factor to be considered is the loss of one of the chromosomes during meiosis, which will give a proportion of monosomic to disomic gametes of greater than one. A further complication is the effect of the formation of dup-def. and def. chromosomes (arising from breakage of chromatid bridges) on the gametic ratios.

It should be noted that triploid and trisomic inversion heterozygotes do not give the same ratio. This may be the result of a higher trivalent frequency in the triploid than in the trisome.

On the tetraploid level the situation is analogous. The frequency of homosynaptic bivalents and heterosynaptic bivalents is  $(1/3 + p)$  and  $(2/3 - p)$  respectively. If only bivalents were formed the expected frequency of aa gametes should be  $1/4(2/3 - p)$ . The p value for the tetraploid inversion heterozygotes would not be expected to be the same as the p value for the trisomes and triploids.

When a quadrivalent is formed, it may be either homosynaptic or heterosynaptic. An excess over random of homosynaptic quadrivalents should increase the A : a ratio, since double reduction may be expected to detract less from the Aa class of gametes than in the control. A further decrease in double reduction would be caused by a decrease in the quadrivalent frequency in the duplex inversion heterozygote.

If the chromosomes of a quadrivalent do not disjoin at random, preferential pairing will modify the gametic ratios. The random frequency with which two chromosomes of a quadrivalent go to the same pole is  $1/3$ . If two chromosomes which had their marker genes paired go to the same pole, this is called genetic non-disjunction and its frequency is designated by Mather as "a". Thus the frequency of aa gametes arising from a homosynaptic quadrivalent is  $1/2 a$ . See diagram below.



		AA	Aa	aa
(a) genetic non-disjunction	1, 2/3, 4	1/2	0	1/2
(1-a) genetic disjunction	1, 3/2, 4	0	1	0
	1, 4/2, 3			

There is some suggestive evidence that the value of "a" is less than 1/3. If only ring quadrivalents were formed the frequency of genetic non-disjunction would be half the frequency of adjacent disjunction assuming that the two types of adjacent disjunction (1,2/3,4) and (1,3/2,4) are of equal frequency. In translocation heterozygotes where a somewhat analogous situation is present adjacent disjunction is around 50%. There is only a small reduction (12%) in the chromatid bridge frequency of the simplex inversion heterozygote from that of the diploid inversion heterozygote. Since genetic non-disjunction would prevent the resolution of a chromatid bridge at the first division in a heterosynaptic quadrivalent, the reduction in the frequency of first division bridges in the simplex is related to the frequency of genetic non-disjunction. The frequency of crossing over is assumed to be about the same on the tetraploid and diploid levels. Half of the unresolved first division bridges should be resolved at the second division. It may be seen that the frequency of second division bridges is not much greater in a simplex than that found in the diploid inversion heterozygote where 2nd division chromatid bridges are derived solely from certain types of double exchanges (3 strand doubles, one in the loop and one in the proximal segment.) The frequency of regular second division bridges in the simplex tetraploid and the diploid is probably not the same, because of the possible exchange of pairing partners in tetraploids in the region proximal to the inversion which prevents 3 strand doubles of the type which give 2nd division bridges.

#### B. Chromatid bridge frequency in inversion heterozygotes.

##### CHROMATID BRIDGE FREQUENCY

INVERSION HETEROZYGOTE	FIRST DIVISION			SECOND DIVISION		
	No Bridge	Single Bridge	Double Bridge	No Bridge	Bridge	
DIPLOID (In/N)	667 61.8%	394 36.5%	18 1.7%	1940 93.9%	126 6.1%	
TRISOME (In/N/N)	935 85.4%	156 14.2%	4 0.4%	1365 97.4%	37 2.6%	
TETRAPLOID SIMPLEX (In/N/N/N)	656 66.3%	324 32.7%	9 0.9%	Two Bridges 885 93.4%	63 6.6%	
DUPLEX (In/In/N/N)	754 86.1%	103 11.8%	6 0.7%	13 1.5%	460 95.0%	24 5.0%

Since a chromatid bridge is formed after crossing over in a paired inverted and standard segment, it follows that the frequency of chromatid bridges is a function of the frequency of heterosynapsis. If there were no preferential pairing, the chromatid bridge frequency of the trisomes should be about 2/3 of that of the diploid heterozygote. Two difficulties arise; crossing over may not take place with the same frequency in a diploid and a trisome and secondly, some of the bridges formed will not be resolved at the first division because two chromosomes of a trivalent with a potential bridge may go to the same pole. Half of the unresolved first division bridges should be resolved at the second division. Unfortunately, these bridges cannot be distinguished from the ordinary second division bridges which arise following a 3 strand double exchange with one crossover in the loop and one in the proximal segment. The frequency of this event would probably be lower in the trisomic inversion heterozygote, because of the exchange of pairing partners in the segment proximal to the inversion loop. However,



the low chromatid bridge frequency of the trisomics (14.6%) provides qualitative evidence for presence of preferential pairing since the expected frequency of chromatid bridges,  $2/3$  the chromatid bridge frequency of the diploid heterozygote, is 25.5%.

However, by comparing the chromatid bridge frequency of simplex (In/N/N/N) and duplex (In/In/N/N) tetraploid inversion heterozygotes, an estimate of the magnitude of preferential pairing can be made. The simplex tetraploid provides a fairly good control for the expected frequency of bridge formation following crossing over in a paired inverted and standard segment as the frequency of crossing over in a simplex and duplex tetraploid should be the same. Also the frequency of unresolved bridges, resulting when two chromosomes of a quadrivalent with a potential bridge pass to the same pole, should be about the same.

If there were no preferential pairing, then the chromatid bridge frequency of the duplex should be twice that of the simplex times  $2/3$  -- since by chance alone the two inverted segments should pair together  $1/3$  of the time. Since  $(2 \times .336 \times 2/3) \neq .154$ , the frequency of heterosynapsis is not the random value  $2/3$  but is reduced by the preferential pairing factor "p". Thus by inserting the term  $2/3 - p$ , the equation may be balanced and the factor "p" may be solved for.

$$2 \times .336 \times (2/3 - p) = .154$$

$$p = .438$$

This means that the frequency of homosynapsis is 77% ( $1/3 + p$ ) in the duplex tetraploid.

C. Trivalent frequency in control and inversion heterozygote trisomes.

Another cytological manifestation of preferential pairing is the frequency of trivalent formation in trisomic plants. When there are three chromosomes capable of pairing together, two of which have greater pairing affinity for each other than toward a third chromosome, there will be a tendency for them to form a bivalent leaving the unlike chromosome represented as a univalent. This, of course, is true for the triploid as well as the trisome and there should be an analogous effect at the tetraploid level on the quadrivalent vs. two bivalent ratio for chromosome three. However, since chromosome three is not distinguishable from the other chromosomes at diakinesis, it is impossible to obtain a good estimate of the disturbance in the type of pairing configuration in the triploid and tetraploid. Such data can be obtained in trisomic plants, however, and the frequencies of chromosome 3 trivalents as opposed to univalent plus bivalent configurations are given below.

			TYPES OF					
No. of Plants			1 <sup>I</sup> 1 <sup>II</sup>	1 <sup>III</sup>		1 <sup>III</sup>	---	---
TRISOMIC CONTROLS	4	No.	184	407	125	208	74	0
		%	31.1	68.9	30.7	51.1	18.2	0
TRISOMIC INVERSION HETEROZYGOTES	7	No.	185	242	62	97	57	26
		%	43.3	56.7	25.6	40.1	23.6	10.7

The trivalent frequency is significantly lower in the trisomic inversion heterozygotes than in the controls. The  $\chi^2$  is 29.5, which has a "p" value of  $< .005$ . It should be noted that one type of trivalent was observed in the inversion heterozygotes and not in the control, the type shown diagrammati-

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cally on the far right of the table. This type of trivalent arises probably when pairing takes place between an inverted chromosome and the normal chromosome when they are oriented in opposite directions, in which case the homology of the two chromosomes for the inverted region is the same.

-- G. G. Doyle

#### 6. Further evidence on the relationship between maize and teosinte.

The relative phylogenies of maize and teosinte have long been a matter of disagreement. Diploid hybrids between maize and teosinte made by Emerson and Beadle (*Zeit. f. Ind. Abstammgs. u. Vererbungslehre* 62:305-315, 1932) and Arnason (*Genetics* 21:40-60, 1936) showed essentially normal rates of crossing over in marked regions. Cytological observation has shown chromosome pairing in 2N hybrids to be normal, and only small differences in length have been found. Cases of observed major failures in pairing and modification of crossing over in 2N hybrids can be traced to the presence of relatively inverted segments in some strains of teosinte. It must be concluded that study of 2N hybrids has failed to show significant differences between the genomes of maize and teosinte.

The next logical step in determining degree of relationship is the tetraploid hybrid test. Since there are two teosinte and two maize chromosomes present for each member of the set of 10 chromosomes, an opportunity for preference in pairing at meiosis is allowed. Therefore the tetraploid test should be a more sensitive test in determining degrees of chromosome homology. If pairing were strictly preferential, only bivalents would be formed, and recessive alleles introduced by the maize parent would not be expressed in the backcross progeny. Such a plant would be a stable amphidiploid. If pairing were random in the 4N hybrid, the frequency of recovery of recessives would be the same as in similarly marked autotetraploid maize controls. Therefore, preferential gene segregation from 4N "intergeneric" hybrid plants gives a measure of preference in chromosome pairing, and a measure of the degree of chromosome homology between maize and teosinte.

Seven sets of hybrids were made, using the tetraploid perennial form of teosinte and different tetraploid maize genetic stocks. F<sub>1</sub> hybrid plants used in backcrosses were determined from root tips to have 40 chromosomes, and from meiotic study to be balanced euploids. The backcross results are given in table 1.

TABLE 1. Percent of Recessives in Backcross Progenies of the 4N Hybrid of Maize and Perennial Teosinte, and of Corresponding Autotetraploid Maize Controls.

Gene Marker	4N Intergeneric Hybrid		Autotetraploid Maize	
	No.	Percent Recessive	No.	Percent Recessive
B	1952	6.4	2134	18.7
lg <sub>1</sub>	1952	7.8	2134	21.6
lg <sub>2</sub>	1640	9.9		
a <sub>1</sub>	1640	11.6	4413 <sup>1</sup>	20.7 <sup>1</sup>
su <sub>1</sub>	4213	4.9	2268	16.5
gl <sub>3</sub>	4213	7.8	2268	21.9
Y	2021	2.8	2555	17.2
Pl	2021	4.4	2555	19.3
wx	9140	4.4	9008	16.5
sh <sub>1</sub>	3019	4.6	4199	17.2
C	2317	3.3	4809	17.7
YB <sub>2</sub>	2610	3.0	2391	22.9

1. Unpublished data kindly supplied by G. G. Doyle.

In all cases, significant preference in pairing was found. Markers close to the centromere were recovered less frequently than those more distant, indicating that some "intergeneric" crossing over takes place. Genes on some chromosomes were recovered much more frequently than those on other chromosomes, indicating that the degree of homology between maize and teosinte differs from one chromosome to another.

Morphological characteristics which have been chosen as "differentiating" between Zea and teosinte can be considered suspect, since nearly all of them are characters which would come under strong selection pressure during the domestication of maize. A fresh approach to the problem of relationship could be had by simply comparing preferential segregation and chromosome behavior in doubled maize-teosinte hybrids with that in doubled hybrids between species and genera in other plants whose phylogenies are not in dispute.

Intergeneric hybrids in other plants as a rule cannot be made. Of those which yield successful seedlings, most fail to flower. In those which reach maturity, sterility is usually complete. In the maize-Tripsacum intergeneric hybrid, offspring are rarely produced, and then only by apomixis. When intergeneric hybrids are doubled, even here most are infertile. Notable fertile exceptions are Raphanus - Brassica hybrids, and hybrids of Triticum with related genera. Preference in pairing, however, in these few physiologically normal intergeneric hybrids has been found to be perfect, or nearly so.

Clearly, the polysomic test indicates that maize and teosinte are much more closely related than other forms considered to be in separate genera.

Doubled interspecific hybrids have been studied within the genera Gilia, Gossypium, Nicotiana, Primula, and Rubus (Grant, 1954, El Aliso 3:19-34; Beasley, 1942, Genetics 27:25-54; Gerstel & Phillips, 1958, C.S.H.S.Q.B. 23:225-237; Clausen & Goodspeed, 1925, Genetics 10:278-284; Upcott, 1939, Genetics 39:79-100; Crane and Darlington, 1927, Genetica 9:241-274). In every genus, at least most of the doubled interspecific hybrids showed more preference in chromosome pairing and gene segregation than the maize-teosinte hybrid of the present study.

Clearly, the polysomic test indicates that the degree of chromosome affinity between maize and teosinte is intermediate to the degree of chromosome affinity between species within 5 other genera.

The present work provides support for the argument that the relationship between maize and teosinte is co-generic.

-- Donald L. Shaver

#### 7. A simple method of measuring linkage in tetraploids.

Because of double reduction and numerical non-disjunction, calculation of linkage in autotetraploids is exceedingly difficult. No satisfactory method of calculating linkage in duplex tetraploid hybrids has yet been proposed. Mather (Jour. Gen. 32:287-314, 1936) has concluded that linkage calculations in duplexes are meaningless unless the two gene markers are within 15 units of each other, and the centromere distance is known. Even if these qualifications are met, his formula does not consider numerical non-disjunction. Fisher (Phil. Trans. Roy. Soc. London 233:55-88, 1947) has developed formulae for determining linkage, but has concluded that both repulsion and coupling data must be obtained, and that each member of the backcross progeny must be progeny-tested. Because these procedures are impossible in many cases and always require great expenditure of land resources, it seems desirable to propose a practical method for estimating linkage.

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The theoretical backcross ratio from a duplex autotetraploid is 5:1. Double reduction and numerical non-disjunction modify this ratio to a different degree for each gene. In diploid studies, crossover values are based upon the frequency of recombinant strands for a given region. In autotetraploids, only one assumption is needed to simply estimate this parameter from backcross data, namely, that the consummation of a crossover in the region under study does not affect the frequency of double reduction for the region. Because of the possibility, however remote, that this factor could bias tetraploid values and therefore tetraploid values made not strictly comparable to diploid values, the tetraploid statistic is given the designation  $\beta$ , the coefficient of tetraploid linkage.

For coupling, the formula is:

$$\beta = 1 - \frac{Xy + xY}{(a \times B) + (A \times b)}$$

For repulsion, the formula becomes:

$$\beta = 1 - \frac{xy}{a \times b}$$

where a = freq. of gametes phenotypically x,

where A = freq. of gametes phenotypically X,

where b = freq. of gametes phenotypically y,

where B = freq. of gametes phenotypically Y, and where, for example, the combination xy represents the frequency of gametes phenotypically xy. Both formulae simply relate the observed frequency of crossover gametes to expected frequency based on independence of genes x and y.

If linkage is complete,  $\beta$  takes a value of unity, and if linkage is absent,  $\beta$  becomes zero. Intermediate values are linear if the assumption for the formulae is true.

TABLE 2. Comparison of Diploid Recombination Values of Tetraploid  $\beta$  Values.

Region	Usual Diploid Recomb. Value	Tetraploid $\beta$ Value	Progeny Size
B - lg <sub>1</sub>	34	.119	2134
su <sub>1</sub> - gl <sub>3</sub>	34	.184	2268
Y - Pl	28	.505	2555
wx - C	26	.567	2602
wx - sh <sub>1</sub>	21	.547	4199
wx - yg <sub>2</sub>	41	.347	2391

$\beta$  values are not always of magnitudes predictable from diploid data, but a moment's reflection upon the differences between tetraploid and diploid meiosis shows that a host of unknown must be experimentally resolved before one can say whether this predictability should obtain.

At present, it seems best to treat tetraploid genetics as a subject by itself with parameters which have not been compromised by attempts to make values comparable between diploids and tetraploids.

-- Donald L. Shaver

### 8. Linkage in tetraploid hybrids of maize and perennial teosinte.

Because preferential pairing and gene segregation in the 4N hybrid of maize and teosinte affect the frequency of recovery of recessives in the backcross, linkage in the hybrid cannot be compared with that in the autotetraploid control simply by examination of frequencies of crossover-type progeny. However, if the assumption is made that all bivalents in the 4N hybrid are homosynaptic (maize with maize, and teosinte with teosinte), the  $\beta$  coefficient can be used to compare the relative amount of crossing over in the 4N hybrid with that in the autotetraploid maize control during heterosynaptic (quadrivalent) associations. (Limited data indicate that bivalents in the 4N "intergeneric" hybrid are rarely or never heterosynaptic. Conversely, all heterosynaptic associations are in quadrivalents.)

TABLE 3.  $\beta$  Coefficients of Tetraploid Linkage in 4N Duplex Hybrids of Maize and Perennial Teosinte, and in Autotetraploid Maize Controls.

Segment	"Intergenic" Hybrid	Autotetraploid Control
B - lg <sub>1</sub>	.600	.119
su <sub>1</sub> - gl <sub>3</sub>	.542	.184
Y - Pl	.392	.505
wx - C	.023	.567
wx - sh <sub>1</sub>	1.000	.547
wx - yg <sub>2</sub>	1.000	.347

It should be remembered that the above values measure degrees of linkage only during heterosynaptic events. In the B - lg<sub>1</sub> and su<sub>1</sub> - gl<sub>3</sub> regions, crossing over is less in the hybrid, as expected from cytological observations indicating a general reduction in chiasma frequency in the hybrid.

Crossing over in the Y - Pl region was apparently increased in the hybrid. Cytological data for the chromosome involved (6) show that although quadrivalent frequency was less than one-half the average value for other chromosomes, the frequency of quadrivalents with effective partner exchanges was more than twice as great. (An effective partner exchange is defined as the occurrence of chiasmata on both sides of the point of pairing partner exchange within a chromosome arm.) Since an effective partner exchange specifies that one exchange must be heterosynaptic, the explanation for the apparent increase in crossing over per quadrivalent in the hybrid may lie in the special nature of chromosome 6 quadrivalents.

The data from the wx - C, wx - sh<sub>1</sub>, and wx - yg<sub>2</sub> segments of the short arm of chromosome 9 are clearly incongruous. In the wx - C region, linkage was virtually absent, while in the overlapping wx - sh<sub>1</sub> and wx - yg<sub>2</sub> regions, linkage was complete. For reasons given below, it is assumed that the wx - C data are anomalous, and that actual crossovers in the short arm of nine are never or rarely consummated. It seems likely that *E. perennis* carries an inversion in the short arm of chromosome 9, like Florida, Durango, and Nobogame teosintes.

It is interesting to note that Emerson and Beadle (Zeit. f. Induk. Abstammgs. u. Vererbungslehre 62:305-315, 1932) also found apparent crossovers in the wx - C region of triploid hybrids of maize and perennial teosinte. Since the results of the present study are in agreement with theirs, it seems likely that the present results must be considered real, and therefore require a non-conventional explanation.

-- Donald L. Shaver

### 9. Chromosome numbers in the progeny of randomly intercrossing tetraploid maize.

Randolph (Jour. Agr. Res. 50:591-605, 1935), Kadam (Ind. Jour. Gen. & Plt. Breeding 4:8-22, 1944), and Catcheside (Heredity 10:205-218, 1956) have shown that the progeny of 40 chromosome maize plants varies in chromosome number from 36 to 43, with only about 60% having the euploid number of 40.

If 4N maize were to become agronomically important, it is of more vital interest to determine the range of chromosome number in the offspring of a population of randomly intercrossing "tetraploid" maize plants. Such a randomly intercrossing population of both euploids and aneuploids closely approximates potential agronomic populations.

In the present study, chromosome numbers were determined in the progeny of 92 randomly selected and intercrossed tetraploid maize plants. The results are given in table 4.

TABLE 4. Chromosome Numbers of the Progeny of a Randomly Intercrossed Autotetraploid Population, and of the Progeny of 40-Chromosome Plants.

<u>Chromosome<sup>1</sup> Number</u>	<u>Progeny of Random<sup>2</sup> 4N Population</u>	<u>Progeny of 40- Chromosome Plants<sup>3</sup></u>
36	3	4
37	4	2
38	31	42
39	51	57
40	168	338
41	48	98
42	17	13
43	<u>3</u>	<u>3</u>
	325	557

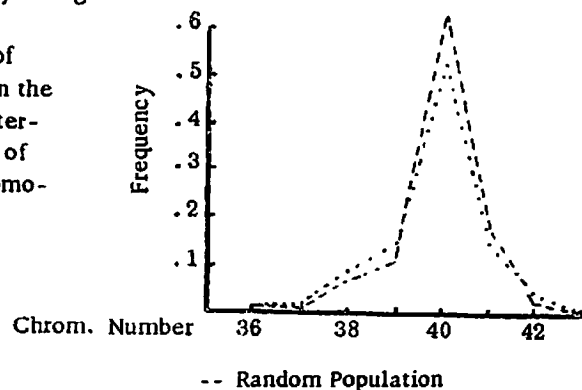
<sup>1</sup> Three plants are not shown in the table. One had 21 chromosomes, and was considered to be a parthenote. The other two had 30 and 31 chromosomes respectively, and were considered to be contaminants.

<sup>2</sup> Figures in both columns are the number of plants having the indicated number of chromosomes.

<sup>3</sup> Pooled data of Randolph (1935), Kadam (1944), and Catcheside (1956).

These data are presented graphically in Figure 1.

FIGURE 1. Frequency Distribution of Chromosome Numbers in the Progeny of Randomly Intercrossing 4N Maize, and of The Progeny of 40-Chromosome Maize.



The difference between the two populations is significant by the F test. These data do, however, support the contention that autotetraploid maize populations should remain stable within the range of 36 to 43 chromosomes.

-- Donald L. Shaver

10. Note on the problem of disjunction from autotetraploid quadrivalents.

In tracing the events giving rise to double reduction in autotetraploids, Mather (Jour. Gen. 32:287-314, 1936) has likened segregation from the tetraploid quadrivalent to segregation from the ring quadrivalent typical of diploid translocation heterozygotes. Mather's model has been widely followed, notably by Little (Bot. Rev. 11:60-85), Catcheside (Heredity 10:205-218, 1956), and others.

However, the two types of quadrivalents are basically different. In the translocation heterozygote, no chromosome region is present more than twice. In the tetraploid, each region is present in quadruplicate.

As a consequence of this basic difference, there are 10 ways for a tetraploid quadrivalent to be ordered at diakinesis. In maize, 8 of these types were found in scoring only 220 sets of homologues (Shaver, unpublished Ph.D. thesis). More than 2/3 of the arrangements were in some configuration other than rings or chains. Since any possible arrangement except rings and chains requires effective partner exchange within arms (see definition above), the concept of alternate vs. adjacent disjunction cannot be applied. Therefore the scoring of alternate vs. adjacent orientation of rings, as Venkateswarlu (cited by Catcheside, 1956) has done, does not provide an adequate basis for genetic inference, since rings are actually a minority class.

In the absence of information as to how the placement of chiasmata in a quadrivalent affects the mode of disjunction, it may be best at present to assume that disjunction from tetraploid quadrivalents is largely random. It is interesting to note that if Catcheside (1956) had assumed randomness, instead of drawing inference from the cytological data of Venkateswarlu, his calculated value for double reduction at the  $su_1$  locus would have agreed closely with his experimental value. Instead the calculation was in disagreement by a factor of about 2.

-- Donald L. Shaver

11. Evidence for homosynapsis of bivalents in 4n hybrids of maize and perennial teosinte.

In article (8) above, it was argued that if all heterosynaptic associations in an allotetraploid were in quadrivalents, then the same  $\beta$  could be used to compare strength of linkage in auto and allotetraploids during heterosynaptic events.

Chromosome 6 was followed cytologically in 242 cells of the "intergeneric" hybrid. It was found to form 2 bivalents at a frequency of .837, to form trivalent-plus-univalent at a frequency of .006, and to form a quadrivalent at a frequency of only .157.

Assuming random disjunction of quadrivalents and trivalents for reasons given in article (10) above, the expected frequency of recessive  $y$  progeny in a backcross population would be .026 (from quadrivalent disjunction) plus .001 (from numerical non-disjunction), plus about .001 (from trivalent-plus-univalents), or a total frequency of .028. The experimentally obtained frequency of  $y$  was .028, in perfect agreement with expectations from cytological data.

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Since random disjunction from multivalents alone accounts for all of the recessive backcross progeny, it is logical to conclude that bivalents in the "intergeneric" hybrid are rarely or never heterosynaptic.

-- Donald L. Shaver

12. The possible significance of a modified type of autotetraploid meiosis in perennial teosinte.

Meiosis was studied in a clonal derivative of the original collection of *E. perennis* made by Collins and Kempton in 1922. It was found that at pachynema, pairing was largely multivalent, as in autotetraploid maize. Many exchanges of pairing partners could be found in single cells.

However, a study of the diakinesis stage in 114 completely analysed cells revealed that quadrivalents were formed at a frequency of only .499, while two bivalents were formed at a frequency of .496. In autotetraploid maize, on the other hand, the quadrivalent frequency was .871, and the bivalent frequency was only .106. Since disjunction from bivalents is always regular, *E. perennis* may be expected to show much greater chromosome stability than autotetraploid maize.

Even more surprising was the fact that the quadrivalents of perennial teosinte were almost always restricted to two of the ten possible types, namely rings and chains of four, which are non-effective pairing (within arms) partner exchange types. Thus, in spite of the fact that exchange of pairing partners is very frequent at pachynema, some mechanism prevents these exchanges from being effective at diakinesis.

Possibly the simplest explanation for such a restriction in chiasma placement would be that the maximal chiasma number per arm in *E. perennis* is one (Chiasma interference is 100%). If this assumption is allowed, then at diakinesis, all of the chiasmata present can be detected. From cytological data from 110 cells (Shaver, unpublished Ph. D. thesis), it was calculated that the average frequency of chiasma per arm was .89. On the assumption of 100% chiasma interference, then, each chromosome arm takes part in a chiasma at a frequency of .89, and fails to do so at a frequency of .11.

The hypothesis of 100% chiasma interference within arms may be tested to see if it can satisfy the data. The hypothesis predicts ring-of-four formation at a frequency of  $.89^4 \times 2/3 = .419$ . The observed value was .410. The frequency of arms not taking part in a chiasma would be predicted as .110, while the observed frequency was .119. Hence, for two values, the hypothesis holds very well.

If the secondary hypothesis is made, that failures of chiasma formation are randomly distributed, further predictions can be made.<sup>1</sup> The predicted frequency of chains-of-four is .207 (observed was .067). Trivalent-plus-univalent is predicted at a frequency of .011 (observed was .003). Bivalent-plus-two-univalents is predicted at a frequency of .011 (observed was .001). Two bivalents are predicted at a frequency of .328 (observed was .494). Obviously the secondary hypothesis does not hold, and it seems likely that distribution of chiasma failure is not at random, but rather is directed to give an excess of bivalents at the expense of univalent formation. This localization can be explained by the hypothesis that the apparently strong chiasma interference within chromosome arms extends, to some degree, across the centromere.

It is therefore possible to explain all of the observed differences in meiotic behavior between perennial teosinte and 4N maize by the single hypothesis that chiasma interference is greatly increased in *E. perennis*, to 100% within arms, and to a lesser extent between arms. This apparently single

<sup>1</sup> The writer is indebted to G. G. Doyle for the method of calculation used here.



change brings a great increase in bivalent formation, and eliminates formation of the more complex types of quadrivalents.

If this change in *E. perennis* can be considered to be evolutionary in nature, it may be deduced that *E. perennis* is intermediate along the road from autotetraploidy to functional diploidy. If the goal is merely the attainment of 100% chiasma interference for whole chromosomes, it seems likely that the end result could be an individual whose chromosomes pair randomly at pachynema, but which has only bivalents at diakinesis. Such a quadridiploid would show the 5:1 backcross ratios typical of autotetraploids, but would have perfect chromosome stability.

The finding of a probable inversion in the short arm of chromosome 9 in perennial teosinte (article 8 above) indicates that *E. perennis* is a recent autotetraploid. The modification in chiasma frequency may therefore relate to a more or less simple genetic system. If simple, it may be amenable to use in improving the fertility of tetraploid maize.

-- Donald L. Shaver

### 13. Pollen physiology and biochemistry.

A study of pollen biochemistry is in progress. Preliminary results (see MNL 33:23, 1959) suggest that the pollen grain can be considered as a metabolically rich entity, analogous to a microorganism. Relatively small samples of pollen can be used for micro-qualitative and quantitative chemical determinations, as well as for physiological observations. From a knowledge of pollen biochemistry, it may be possible to judiciously employ specific chemical tests to elicit a colored test-reaction, thus affording the possibility of describing pollen phenotypes.

To deal with individual pollen grains, the autonomy of the grains and their contents is required in the test system. This requirement can be met favorably by "plating" pollen on agar-type surfaces. Pollen grains will absorb some chemical test materials from 1-5% agar (Difco certified Bacto-agar), yielding the color test. The use of petri dishes for plating is particularly adapted to rapid counting by using the standard equipment of the bacteriologist. Although aliquots of only dried, non-viable pollen samples have been studied thus far, samples of viable pollen will be tested as the pollen becomes available.

-- D. B. Walden

### 14. Effect of the abnormal chromosome 10 on chiasma formation and metaphase orientation in T6-9b heterozygotes.

Cytological observations at diakinesis, metaphase I, and quartet stage were made on two T6-9b heterozygotes, sib plants which differed in that one was N 10/N 10 and the other was N 10/abn 10. The break in 9S is proximal to the *Wx* locus and the break in 6L is between *Y* and the centromere. A large knob was present on chromosome 9 while the 6<sup>9</sup> chromosome was knobless. The results are tabulated below:

Stage	Configuration	N 10/N 10	N 10/abn 10
Dk	rings of 4 . . . . .	14.9%	75.8%
	chains lacking a chiasma in 9S* . . . . .	81.9	20.8
	other . . . . .	3.2	3.4
		(502 cells)	(149 cells)
MI	alt. ring . . . . .	0	5.9%
	adj. ring . . . . .	3.4%	50.9
	alt. chain of 4 . . . . .	16.5	23.0
	adj. chain of 4 . . . . .	21.3	18.5
	triv. & uni. . . . .	58.8	1.8
		(437 cells)	(222 cells)
Quartets	1   1 (alt. adj-1, triv. & uni.)	65.1%	74.8%
	1   1		
	2   2 (adj-2, triv. & uni.)	29.8	23.3
	0   0		
	1   2 (triv. & uni.)	5.1	1.9
	1   0	(1205 quartets)	(873 quartets)

\* includes chains of 3 in which a chiasma was lacking in 9S and 6S.

The frequencies observed at Dk may not be very accurate since many cells were discarded because of superimposed chromosomes in the region of the nucleolus. However, it is obvious that a much higher chiasma frequency in 9S is found in plants carrying the abnormal chromosome 10. As a result, ring formation is higher at MI and the trivalent plus univalent class, in which chiasmata are missing in 9S and 6S, is very rare. The observed frequencies of quartet types can be derived from the observed MI frequencies for both N 10/N 10 and N 10/abn 10 plants if the following assumptions are made:

- 1) no interstitial crossing over
- 2) no loss of the univalent in the cytoplasm
- 3) equal adj-1 and adj-2 disjunction from the open ring
- 4) mainly adj-1 disjunction from chains of 4

The great majority of chains of 4 at Dk lack a chiasma in 9S. At MI these chains are oriented so that the terminal members go to the same pole.

Unfortunately pollen abortion counts were not made on these 2 plants. The predicted abortion is 54% for the N 10/N 10 plants and 70% for the N 10/abn 10 plants. It is interesting to compare the ovule abortion on sib ears with and without abnormal 10 in the same and in related families.

<u>N 10/N 10 plants</u>	<u>No. ovules</u>	<u>% abortion</u>
22708-A	508	53.1
B	477	41.3
2	458	43.4
6	230	45.6
22703-10	485	50.7
19	556	60.6
A	376	50.5
B	328	51.2
22708-8	527	57.3
9	443	54.9
18	462	65.4
21	428	63.4
M	484	61.4
22703-1	349	70.8
22704-1	400	66.7
	N 10/N 10	N 10/abn 10
average % abortion	50.1	63.0

The lower seed set on ears from plants with abnormal 10 is presumably due to a higher frequency of open rings at metaphase I. These would lead to adjacent disjunction and aborted ovules. The almost complete absence of zigzag rings at metaphase I must be a consequence of the extreme shortness of the two arms, 6S and 9S, which makes it difficult for the necessary twist to occur.

It is evident that the abnormal chromosome 10 causes a striking increase in chiasma frequency which, in turn, alters the types of MI configurations. This is in agreement with the increase in genetic crossing over observed by Rhoades and Kikudome and also noted in these translocation heterozygotes. The fact that zigzag rings are more frequent in plants carrying abnormal 10 may indicate that the effect of this chromosome is to cause a greater flexibility of the chromonemata permitting the occurrence of more chiasmata, as well as zigzag rings.

-- Ellen Dempsey

15. A test for pseudoallelism at the A<sub>2</sub> locus.

A mutant a<sub>2</sub> allele (a<sub>2</sub><sup>BlMex</sup>) which was found by Rhoades in Black Mexican sweet corn is being tested for pseudoallelism with the standard a<sub>2</sub> allele (a<sub>2</sub><sup>St</sup>). A cross of  $\frac{Gl\ 17\ a_2^{BlMex}\ Bm}{gl\ 17\ a_2^{St}\ bm} \times \frac{gl\ 17\ a_2^{St}\ bt}{gl\ 17\ a_2^{St}\ bt} \delta$  gave 10 A<sub>2</sub> seeds in an estimated population of 20,900. These plants were selfed and 8 proved to be contaminants while 2 arose by hetero-fertilization and had a<sub>2</sub> embryos. A second cross was made in which markers to the right and left of a<sub>2</sub> were available:

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$$\frac{Gl_{17} a_2^{B1Mex} Bt V_2 \quad y \quad y \quad X}{g_{17} a_2^{St} \quad bt V_2} \quad \frac{g_{17} a_2^{St} \quad bt Pr v_2 \quad y \quad \delta}{}$$

The egg parents were detasselled and a block of tetraploid corn decreased chances of contaminating pollen grains on one side. Nine colored seeds were obtained (1  $\underline{A_2 Bt Y}$ , 5  $\underline{A_2 Bt y}$ , and 3  $\underline{A_2 bt y}$ ) in a total population of 179,500. These plants will be tested next summer.

-- Ellen Dempsey

16. The occurrence of  $pg_{11}$  and  $pg_{12}$  in various lines.

The lines listed below were crossed with a  $pg_{11} pg_{12} y wx$  stock and the  $F_1$ 's were selfed to test for the presence of one or the other of the duplicate factors. Five of the 8 lines are homozygous for one of the  $pg$  genes, four of them possessing  $pg_{11}$  on chromosome 6 and one having  $pg_{12}$  on chromosome 9. Apparently homozygosity for one member of the duplicate factor pair is common.

	Ratio in $F_2$	Homozygous for
Black Mexican . . . . .	15:1	
$a_2$ bt pr tester . . . . .	15:1	
M14 . . . . .	3:1	$pg_{11}$
Iowa B14 . . . . .	3:1	$pg_{11}$
Oh45 . . . . .	3:1	$pg_{11}$
$a_1$ sh <sub>2</sub> tester . . . . .	15:1	
Oh43 . . . . .	3:1	$pg_{11}$
KYS . . . . .	3:1	$pg_{12}$

-- Ellen Dempsey

17. A case of normal functioning of hyperploid pollen.

In previous work with plants carrying a normal 9 and a 9 with a piece of 3L transposed into the short arm between the Sh and Wx loci, the pollen grains with a normal 9 had a marked superiority in achieving fertilization over the grains with the transposed piece of 3L which were hyperploid for this segment when a normal chromosome 3 was present. The advantage of the euploid pollen varied in different crosses but there was always a marked difference in the percentage of functioning pollen between the two types of pollen. This past summer a different result was obtained when plants heterozygous for N9 Dp 9 and the C Sh Wx loci were used as the male parent on a c sh wx  $g_{15}$  tester. When sister Dp9 N9 Df3 N3 and Dp9 N9 N3 N3 plants (see 1959 News Letter for description of this aberration) were used as the female parent in test crosses the results were in close agreement with those found in extensive previous experiments -- namely, a marked reduction in crossing over and an approximate 2:1 ratio of Dp9:N9 ovules from the Dp9 N9 Df3 N3 class and a 1:1 ratio of Dp9:N9 ovules from the Dp9 N9 N3 N3 plants. It is clear that the Dp9 chromosome was present. Wholly unexpected results were found in the reciprocal crosses where Dp9 N3 pollen was just as effective in fertilization as N9 N3 grains. It should be noted that the present experiment involved a tester strain which had not been used before and it is possible that the genotype of the female parent plays a significant role in pollen competition. A somewhat similar situation was reported by Singleton (1940 P.N.A.S.) who found that sp pollen from Sp sp heterozygotes functioned with a much higher percentage on certain female tester lines than on others. This summer a duplicate planting will be made and pollen from individual plants will be applied to a number of tester strains in order to ascertain if the nature of the egg parent influenced

pollen functioning. Another unexpected feature of the data is the relatively high frequency of crossing over in the C Sh region found among the male gametes in both the Dp9 N9 Df3 N3 and Dp9 N9 N3 N3 backcrosses. Again in former studies we found a striking reduction in crossing over throughout the short arm of 9 and this was true for the C Sh interval.

	(0)	(2)	(1-2)	(1)	(1)	(1-2)	(2)	(0)	
	C	C	C	C	c	c	c	c	
	Sh	Sh	sh	sh	Sh	Sh	sh	sh	%
	Wx	wx	Wx	wx	Wx	wx	Wx	wx	Recomb.
<hr/>									
Dp9 <u>C Sh Dp Wx</u> Df3 N3									
N 9 <u>c sh N wx</u>	1299	9	0	4	5	0	9	654	C-Sh 0.45
as female in B. C.									Sh -Wx 0.91
<hr/>									
Dp 9 <u>C Sh Dp Wx</u> Df3 N3									
N 9 <u>c sh N wx</u>	1005	15	0	6	27	0	18	512	C-Sh 2.1
as male in B. C.									Sh -Wx 2.1
<hr/>									
Dp 9 <u>C Sh Dp Wx</u> N3 N3									
N 9 <u>c sh N wx</u>	1422	13	0	1	3	0	14	1541	C-Sh 0.13
as female in B. C.									Sh -Wx 0.90
<hr/>									
Dp 9 <u>C Sh Dp Wx</u> N3 N3									
N 9 <u>c sh N wx</u>	541	9	0	8	9	0	11	539	C-Sh 1.5
as male in B. C.									Sh -Wx 1.8

-- M. M. Rhoades

18. Crossing over in homozygous Dp 9 plants.

Plants homozygous for the piece of 3L inserted into 9S between the Sh and Wx genes should have a marked increase in recombination values for the Sh-Wx region since the size of the chromatin segment lying between these loci would be increased by the length of the inserted 3L segment. However, when Dp 9 Dp 9 plants heterozygous for yg<sub>2</sub> C wx, and in some cases for C wx or sh wx, were backcrossed there was no increase observed in the C-wx or the sh-wx interval. Indeed the amount of recombination averaged about 17% for C-wx, a value which is significantly less than the standard frequency. So far as I can tell this is the first experiment of the kind conducted in maize and possibly in any organism. The only comparable case I am aware of is the work on the pale translocation in *Drosophila* where Hamlett (Biol. Bull. 1926) presumably studied crossing over in females homozygous for a small duplicated (inserted) piece and found that crossing over in flies homozygous for the duplication was reduced as much as in heterozygous individuals. Kossikov and Muller (J. Heredity 1935), however, have criticized the design of the experiment and believe it unlikely that Hamlett's flies were actually homozygous for the duplication.

One might reasonably assume that the longer the chromosome segment the greater would be the frequency of exchanges within the segment. This obviously is not true for the homozygous Dp. Apparently the insertion of foreign chromatin (piece of 3L) into 9S has modified in some way the mechanism of crossing over within 9S. The data could be interpreted as indicating that corn chromosomes have a certain autonomy in crossing over and that the system is disturbed by the insertion of chromatin from a non-homologous chromosome.

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1. Popcorn fertility restorer.

The popcorn inbred line W41 previously reported as a fertility restorer (Maize Newsletter 1957, pp. 95-96) with "T" sterile cytoplasm has also been tested on "S" sterile cytoplasm. Fertility Restoration was complete in 1958 and 1959. In addition, "S" sterile cytoplasm was completely restored in 1959 in crosses involving the male single cross Ky21 x W41.

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1. Relationship between the two components of a mutable system.

In the mutable pg system it is hypothesized that I, the inhibitor, is located at the pg locus and is removed by En the Enhancer. The interaction of these two components results in the mutation of pale green to green.

There is some suggestion that I and En are more closely related than previously supposed. This is inferred from the observation of individual stripes and sectors of mutability in stable (Pgl) plants. These mutable sectors in stable seedlings indicate that mutability has been induced at the otherwise stable locus. Such a possibility is strengthened by the isolation in stable stocks of a newly arisen mutable allele. In tests, this new mutable was found to be of the autonomous type (PglEn). It follows, therefore, that in this case, En arose at the locus. Perhaps the En factor arises from the I factor that is associated with the pg allele.

New m-type  $F_2$  progenies have also originated in outcrosses of pg<sup>m</sup> stocks containing independent En. Four m-type  $F_2$  progenies were observed in such outcrosses. It is proposed that En arose from I material at the pg locus.

Other evidence supporting the relationship between I and En is seen in the interaction effect of both pg<sup>s</sup> and En upon pg<sup>mo</sup>. In the hybrid, pg<sup>mo</sup>/pg<sup>s</sup>, the seedlings are stable. The characteristic pg<sup>mo</sup> expression is inhibited. Likewise, the independent Enhancer (En) causes pg<sup>mo</sup> to appear stable. Thus the I element at the pg<sup>s</sup> locus and independent En act in a similar manner upon the pg<sup>mo</sup> allele.

I and En therefore appear to be related although they differ in activity. I inhibits the expression of the normal allele (Pg) whereas En inactivates or causes the removal of I. Whether the difference in activity of the two elements is a question of position or chemical composition can only be conjectured.

-- Peter A. Peterson

## 2. a<sub>1</sub>-mutable.

It has now been confirmed that a<sup>m</sup> found originally in pg<sup>m</sup> stocks, has the same components (I and En) as the pg mutable system. Direction of mutation, pattern types, rate of appearance and types of stables, and the relationship of particular patterns to specific stables have been studied.

The direction of mutation: Many kernel patterns have been described. They vary from a very dense pigmentation type to small, infrequently spotted types. (The former result from early, the latter from late mutations.) Each of the distinct pattern types can give rise to other pattern types and each of these derivatives has been tested and found to be heritable. The events that lead to changed patterns occur at the a<sup>m</sup> locus or result from the mutation of the autonomous controller of mutability to the independent type.

Rate of appearance and types of stables: The rate of occurrence of stables varies with the particular pattern. The higher rates are associated with the dense type mutable patterns. Although stables are phenotypically alike, some mutate in the presence of En, others do not. Thus the response to En is a means of distinguishing among the "stables." Particular patterns give rise to a designated type of stable. This is relevant to the analysis of the genetic events that accompany changes in pattern phenotype.

Factor causing dense kernels: In the last newsletter, it was reported that in the presence of a factor "D", a specific fine pattern allele becomes dense (appears full colored), and in its absence, the pattern remains fine. It has now been confirmed that this factor is En. The stable derivatives from the dense phenotype may contain En but do not respond to it.

-- Peter A. Peterson

## 3. Some thoughts on the white-albino mutants.

For the past ten years I have been accumulating albino mutants. Most of these have white (or pale yellow) endosperm and chalky-white, albino seedlings when germinated in the light. I have called these mutants white-albino, although other terms have been used to describe them such as lemon-white, viviparous, (because of the tendency of some to germinate prematurely), white, etc.

The pleiotropic effects of these genes are of some interest and several explanations have been suggested for these effects. Biochemical studies which have been made here (see below) suggest that the basic block is in the carotenoid synthesis of these mutants. The lack of chlorophyll might be due to a lack of phytol which most likely is synthesized via the carotenoid pathway. However, J. H. C. Smith (Stanford) and I. C. Anderson (Iowa State) have shown that some of these mutants synthesize chlorophyllide in the dark and also have sufficient phytol available to form chlorophyll, which suggests that the lack of chlorophyll in the light-grown seedlings might be due to a secondary factor such as the photodestruction of chlorophyll in the presence of oxygen when carotenoids are absent (see below).

The simultaneous involvement of pigment synthesis in the endosperm and seedling of these mutants is most easily explained by assuming that the mutated gene blocks carotenoid synthesis wherever it occurs. However, mutants are known where carotenoid synthesis of only one or the other of these tissues is involved, such as  $\underline{y}$ -1, where only the endosperm and not the seedling is affected. The reciprocal class of mutants, with yellow seeds and albino seedlings, is also found in corn. To further complicate the picture we have pastel (pale-green) mutants which have the white endosperm but produce pale-green instead of albino seedlings. A summary of the different classes of mutants with defective pigment production in endosperm and seedling which we have been studying is given in table 1. Some of the mutants which do not have the typical white-albino phenotype nevertheless have been found to be allelic to them. For example, there has been found an allele for a white-albino mutant in which the endosperm is yellow and an allele to another in which the seedling is pale-green. An allele of this latter type has been found for  $\underline{y}$ -1. A summary of the phenotypes of known alleles is given in table 2.

Table I. A summary of the different classes of pigment deficient mutants that have been studied at Iowa State.

Class of mutant	Phenotype of Endosperm	Phenotype of Plant
1	White	Albino
2	White	Green
3	White	Pale Green (pastel)
4	Yellow	Albino

Table II. A summary of alleles found for the white-albino mutants.

Genes involved in allelic series (included between lines)	Mutant classes of the alleles (see Table I.)
$\underline{w}$ -3	1
$\underline{pas}$ -8686	3
$\underline{y}$ -1	2
$\underline{pas}$ -8549	3
$\underline{cl}$ -1	1
( $\underline{pas}$ )-pioneer	2 or 3*
** $\underline{vp}$ -9	1
** $\underline{pas}$ -4889	3
** $\underline{w}$ -8657	4

\* Actual phenotype of (pastel)-pioneer is somewhat uncertain at the present time. These two mutants are definitely alleles on the basis of endosperm phenotype. However, the homozygous (pastel)-pioneer plants will have to be grown in the field next year before a definite plant phenotype can be established.

\*\* This last summer there was obtained one segregating  $F_1$  ear between  $\underline{vp}$ -9 and pastel-4889 and one segregating  $F_1$  ear between pastel-4889 and  $\underline{w}$ -8657. These results will have to be confirmed next year and the  $F_1$  between  $\underline{vp}$ -9 and  $\underline{w}$ -8657 obtained before this series can be established as certain.



The information summarized in tables 1 & 2 would suggest that the endosperm and seedling phenotypes can be modified independently. Dr. Everett has shown a similar independent modification of seedling and endosperm by the use of suppressor genes on the cl-1 and other loci.

In order to explain the independent modification of endosperm and seedling in these mutants it can be assumed that we are dealing with two closely linked loci, one concerned with pigment production in the endosperm and the other with pigment production in the seedling (plant). However, the fact that many (20 or more counting alleles) of these white-albino mutants have occurred spontaneously or were induced by irradiation, would suggest that this was not so. It is extremely unlikely that the two closely linked loci would mutate simultaneously in all of these instances. Another possibility is that we are dealing with complex gene loci that consist of at least two parts. One portion is involved in the synthesis of pigment in the endosperm and the other in the seedling. Allele tests would suggest that the different portions of the complex gene could mutate simultaneously or independently and also, that the plant portion is capable of mutating in two ways: 1) complete inactivation resulting in no pigment formation or 2) partial inactivation, resulting in pale-green plants. The latter could be accomplished by a change in a portion of the plant part of the complex (suggesting a further subdivision of the locus) or by a more subtle rearrangement of the plant unit as a whole. See figure 1 for a summary of the possible alleles.

There are several lines of evidence that can be used to determine if the white-albino mutants are indeed complex loci. Two of these are circumstantial and have been mentioned above. One is by finding suppressor genes (such as Dr. Everett and colleagues have been doing) that suppress the mutant phenotype in one or the other of the tissues. The other line of evidence that has been mentioned is the finding of allelic series of genes with different endosperm and seedling phenotypes. A third line of evidence would be to separate the two portions of the complex by crossing over. We are concentrating on the latter two lines of evidence here.

Such complex loci could be similar in structure to the R locus as revealed by Stadler and Emmerling, where it has been possible to demonstrate seed and plant sub-units. However, the white-albinos differ in one important regard from the R-locus alleles in that mutation can proceed from yellow endosperm-green plant (equivalent to R<sup>1</sup>) to white endosperm-albino plant (equivalent to r<sup>2</sup>) in one step.






The presence of a seed and plant unit at the R locus and the possibility of a similar compound structure for these many white-albino mutants suggest that a compound structure might be characteristic of some of the other genes that have obvious phenotypic effects in seed and plant, such as A-1 (compound structure has already been demonstrated by Laughnan but not divided along the lines indicated above) and A-2.

We would like to solicit the help of other corn workers in finding alleles of the types described above to these white-albino mutants.






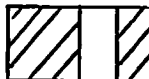
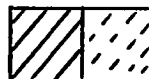


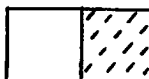


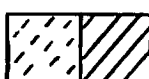
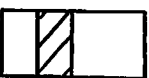
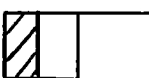






We would particularly be interested in finding white endosperm mutants with green plants (other than y-1), white endosperm pale-green mutants, and yellow endosperm chalky-white albinos. Additional white-albino mutants would also be welcome.

-- Donald S. Robertson

Figure 1. Possible Types of Subunits Composing White-Albino Loci.

		<u>Seed Phenotype</u>	<u>Seedling Phenotype</u>
	- Functional unit	yellow	green
	- Inactivated unit	white	albino
 or  or 	- Partially inactivated unit	pale yellow	pale green (pastel)

## Types of Alleles

		yellow	green
		white	green
		yellow	albino
		white	albino
 or  or 		white	pale-green
 or  or 		yellow	pale-green
 or  or 		pale-yellow	albino
 or  or 		pale-yellow	green
 or  or 		pale-yellow	pale-green
 or 			

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4. Temperature sensitive alleles of the Y-1 locus.

Two mutants which are allelic to Y-1 were found at the California Institute of Technology by Dr. E. G. Anderson. One of these, pastel-8549, originated in the progeny of a seed exposed to a gamma ray dose of 40,000 r units. This allele has white endosperm but when germinated at high temperatures produces a pale green (pastel) seedling. The second allele, white-mutable, arose as a spontaneous mutant in one of Dr. Anderson's stocks and is similar to pastel-8549. However, it is unstable and regularly back mutates to normal in both endosperm and plant tissue. As a result, white-mutable seeds have a white endosperm with spots of normal yellow tissue. Grown under high temperature the seedlings are pale green with streaks of normal green tissue. Grown in the field both pastel-8549 and white-mutable plants are considerably paler than normal plants and have a distinct zebra phenotype, and white sheaths and leaf midribs. In addition white mutable plants have the streaks of dark green tissue. Only an occasional pastel-8549 plant can be grown to maturity, and these are extremely weak. In contrast, many white-mutable plants have been grown to maturity and some are strong enough to produce ears and set seed. The white-mutable plants are very similar to a mutant described by Dr. Dolinger (MGCNL 31 & 33), which he has shown to be allelic to y-1 and pb-1.

In seedling tests of the white-mutable and pastel-8549 mutants, it was frequently difficult to distinguish between normal and mutant seedlings. Since most of the difficulties in classification were encountered in winter and the best classifications were made in spring or early summer, it was felt that the lower temperature in the greenhouse during winter months might be responsible for the difficulty in classification.

To test the effect of temperature upon these mutants, seedlings were grown in a constant temperature box at 37° C and 19° C (+ 2 1/2° C). Mutant and normal seedlings grown at 37° C could be readily distinguished while those grown at 19° C were difficult to separate consistently.

The pigments of normal and mutant seedlings grown at the two temperatures were extracted and total chlorophyll determined. Table I summarizes the results of these determinations for pastel-8549 seedlings.

Table I Summary of chlorophyll analyses of normal and pastel-8549 seedlings grown at 37° C and 19° C.

	37° C		19° C		Calc. Mut 19° C	
	Average Pigment Concentration mg/gm f. w.	Mutant Normal	Average Pigment Concentration mg/gm f. w.	Mutant Normal	(mut 37° / (Nor. 37° ÷ Nor. 19°))	obs. Mut 19° C / Calc. Mut. 19° C
Normal	.74		.090	73.3%	.009	7.3
Pastel-8549	.076	10.3%	.066			

At 37° C the mutants have about 10% the chlorophyll content of the normals, while at 19° C the chlorophyll content of the mutants is about 73% that of the normals. If one takes the behavior of normal seedlings as standard, a marked temperature effect is observed upon the concentration of chlorophyll. In normal seedlings the chlorophyll level at 37° C is 8.2 times the level at 19° C. If temperature had

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the same effect on the mutant, a chlorophyll concentration of .009 mg/gm f.w. would be expected (Table I, column 6) at 19° C. The value of .066 mg/gm f.w. observed for the mutant at this temperature is seven times higher than expected.

A similar temperature effect upon the content of the yellow pigments of mutant seedlings also has been demonstrated although the exact quantitative relationships have not been worked out as yet.

-- Donald S. Robertson and I. C. Anderson

5. The use of w-3 to study the role of carotenoids in the protection of chlorophyll from photodestruction.

The studies of Cohen-Bazire and Stainer, (Nature 181:250-252. 1959), and Fuller and Anderson (Nature 181:252-254. 1958), have shown that colored carotenoids are required for the protection of bacteriochlorophyll from photodestruction in the photosynthetic bacteria. It has been proposed that this is a unique role of carotenoids in all phototrophs. The white-albino mutant, w-3, provides a tool for determining if carotenoids might serve such a protective function in higher plants. This mutant is a chalky-white albino when grown in the light. However, when grown in the dark it produces protochlorophyll which is converted to chlorophyll on short exposure to light, but upon continued illumination the chlorophyll is bleached.

To determine the carotenoid content of white-3 and normal seedlings, plants grown in the greenhouse seedling bench were ground in a mixture of acetone and hexane. The hexane fractions containing carotene and colorless precursors of carotene were isolated and their spectra were made with a Beckman DU spectrophotometer. The visible and ultraviolet spectra of white-3 seedlings did not show any absorption typical of carotenoid as was found for the extract of normal seedlings. Instead, the w-3 extracts had large amounts of a substance which absorbed light in the ultraviolet region with peaks at 275, 285, and 297 m $\mu$ . These peaks are similar to those reported for the carotenoid precursor, phytoene. Extracts of normal seedlings showed no absorption at these wave lengths.

Koski and Smith (Arch. Biochem. Biophys. 34:189-195. 1951) reported that dark grown white-3 seedlings contained as much and usually more protochlorophyll than did normal seedlings and that the protochlorophyll of both normal and mutants was readily converted to chlorophyll upon exposure of the seedlings to light. To determine if oxygen was necessary for the photodestruction of chlorophyll observed in white-3 seedlings, one group of normal and mutant dark-grown plants was exposed to light in an atmosphere of air and another group of normal and mutant dark-grown seedlings was exposed to light under anaerobic conditions. When normal seedlings were exposed to light in the anaerobic environment, the chlorophyll level diminished slightly for the first twenty minutes, after which stabilization was observed, followed by an eventual increase in chlorophyll content. The chlorophyll level of dark-grown normal seedlings, exposed to light in an anaerobic environment, remained essentially constant for the 100 minutes of the experiment. The chlorophyll of dark-grown white-3 seedlings was completely destroyed after a twenty minutes exposure to light under aerobic conditions. However, upon exposure to light under anaerobic conditions the chlorophyll level of dark-grown white-3 seedlings remained stable.

The chlorophyll content of white-3 seedlings grown in dim-light (less than 0.5 foot candle) increased over a two-week period. Visual observations of chloroplasts from sectioned leaves of such mutant material reveal that they are as numerous and of the same size as those of normal seedlings. Free chloroplasts obtained from grinding mutant leaves in sand and 0.35 Na Cl and centrifuging were a little more opalescent but otherwise they appear to be normal.

These results would suggest that the albino phenotype of w-3 when grown in the light is not due to the inability of the plants to synthesize chlorophyll or to their lack of chloroplasts. The rapid destruction of chlorophyll in this carotenoidless mutant when exposed to light under aerobic conditions would suggest that the colored carotenoids of higher plants have a role in the protection of chlorophyll from auto-photodestruction in the presence of oxygen.

-- I. C. Anderson and Donald S. Robertson

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1. Defective endosperm factors from maize teosinte derivatives.

Additional data have been obtained on the defective endosperm types detected in the derivatives of controlled teosinte introgression into the inbred A158. So far, allelism has been established for the following two series:

A. (de<sup>t2</sup>), de<sup>t3</sup>, de<sup>t4</sup>, de<sup>t5</sup>, de<sup>t10</sup>, de<sup>t11</sup>, de<sup>t14</sup>, de<sup>t15</sup>, de<sup>t17</sup>, de<sup>t18</sup>, de<sup>t19</sup>, de<sup>t20</sup>, de<sup>t23</sup>,  
and de<sup>t24</sup>.

Allelism seems also established for the series:

B. de<sup>t13</sup>, de<sup>t22</sup>, de<sup>t26</sup>, de<sup>t27</sup>, and de<sup>t29</sup>.

As described in previous M N L issues, each series appears to have a characteristic behaviour. When defective kernels of the A-series type, apparently homozygous, give rise to adult plants, these can be self-pollinated and produce ears showing all the kinds of kernels from extreme defective to normal ones. When, on the other hand, apparent homozygotes of the B-type produce adult plants, these, after self-pollination, produce ears showing a 3:1 ratio of normal to defective kernels. Such behaviour seems to hold also for de<sup>t28</sup>. Both de<sup>t28</sup> and the B-series have in common the condition of a clear cut distinction between the defective and the normal phenotype, which is not the case, as known, for the A-series. Moreover, although allelism tests have not yet been conducted, de<sup>t28</sup> and the B-series seem located at different "loci." In fact, there is some evidence that the de<sup>t22</sup> is linked with su, and de<sup>t28</sup> with y, as suggested by the data presented in Table I. However, this point needs confirmation, in view of the peculiarity of this hereditary behaviour.

Extensive data, on the contrary, are now available on the behaviour of the B-series factors, when kept in heterozygous condition. As reported in MNL 33, normal kernels from ears segregating extreme (de<sup>t29</sup>) or intermediate (de<sup>t22</sup>) defective give rise, following self-pollination, to ears which show no defectives in 1/3 of the cases and in 2/3 of the cases to ears segregating defectives, among which the extreme or intermediate defective, according to the parental condition, represented 9/10 of the defectives and 1/10 were of the alternative type. Moreover, the stocks segregating both types of defectives produce ears in which a unique type is present or both; in the latter case the percentage of defective may exceed greatly the expected 25%.

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Table I. F<sub>2</sub> segregation data for de<sup>t22</sup> and de<sup>t28</sup> and the markers su and y.

Row and Ear No.	Factors and supposed linkage phase involved		No. of Individuals				Percent of recombination + P.E. (Immer tables)
			XY	Xy	xY	xy	
56-482-3	Y <sub>1</sub> De <sub>28</sub>	R	95	50	50	10	36.5 ± 3.96
-11		C	167	40	44	21	40.5 ± 2.73
58-505-2		R	142	57	61	17	45.0 ± 3.20
-1		R	79	30	30	6	41.0 ± 4.60
59-105-9		R	45	24	14	4	41.5 ± 5.92
-106-12		C	158	31	3	6	21.0 ± 2.24
-11		R	92	36	27	4	36.5 ± 4.57
-10		C	77	24	16	10	40.5 ± 3.97
-3		R	54	19	28	5	40.5 ± 5.41
-108-3		C	150	50	32	37	33.0 ± 2.45
-6		R	83	34	32	5	36.5 ± 4.65
-5		R	149	73	47	5	30.0 ± 3.66
-8		R	132	62	26	6	40.0 ± 3.72
56-459-14	Su <sub>1</sub> De <sub>22</sub>	C	185	48	19	11	39.0 ± 2.72
498-4		R	269	101	78	14	40.0 ± 2.22
498-14		R	182	86	38	7	37.5 ± 2.44
58-500-5		R	109	45	34	9	44.0 ± 3.36
-7		C	217	62	47	16	47.5 ± 2.66
501-1		R	224	77	70	16	48.0 ± 2.51
-3		C	200	67	40	24	42.0 ± 2.52
-5		R	164	63	52	11	41.5 ± 2.68

Table II. Results in self-pollinated ears produced by plants originated from normal seeds of ears segregating extreme defectives for two successive generations.

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears ears segregating no de
	extreme type	intermediate type		
153				2
154				6
-2	21	0	107	
-3	11	1	179	

Table III. Results in self-pollinated ears produced by plants originated from normal seeds of ears that segregated extreme defective in 1957 and extreme plus intermediate defectives in 1958 (58-578-10 and 61)

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears ears segregating no de
	extreme type	intermediate type		
155				1
-4	11	24	68	
-7	15	5	185	
-8	10	20	226	
156				1

Table IV. Results in self-pollinated ears produced by plants originated from normal seeds of ears segregating intermediate defectives for two successive generations.

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears ears segregating no de
	extreme type	intermediate type		
145				3
-1	10	27	286	
-3	12	12	257	
-7	8	25	182	
-9	10	27	292	
-10	8	20	305	
146				4
-3	2	15	58	
-5	6	25	219	
-7	2	18	133	
-8	8	21	159	
-9	12	26	173	
147				3
-1	16	24	222	
-3	3	22	109	
-6	35	14	54	
-7	25	6	33	
148				1
-1	3	42	178	
-3	1	27	140	
-4	4	31	54	
-6	1	19	108	
-7	1	25	237	
-8	6	19	227	
149				5
-1	10	22	271	
-5	6	18	116	
-6	1	24	102	

Table V. Results in self-pollinated ears produced by plants originating from normal seeds of ears that segregated intermediate defective in 1957 and a mixture of extreme plus intermediate defectives in 1958 (58-577-9,11, 23)

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears segregating no de
	extreme type	intermediate type		
150				4
-1	1	28	203	
-2	11	27	218	
-4	2	13	185	
-7	5	21	149	
151				2
-4	6	23	257	
152				1
-1	2	29	165	
-2	2	36	282	
-3	1	22	254	
-4	1	19	231	
-6	1	23	181	

Table VIII. Results in self-pollinated ears produced by plants originating from normal seeds of ears that segregated both kind of defective in 1957 and only the intermediate type in 1958 (58-579-4, 23, 37)

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears segregating no de
	extreme type	intermediate type		
166				1
-5	1	29	192	
-10	8	33	166	
167				4
-3	7	21	194	
-5	4	25	185	
-7	5	25	185	
-9	1	24	339	
-15	5	20	168	

Table IX. Results in self-pollinated ears produced by plants originating from normal seeds of ears that segregated defective in 1957, but were completely free of defective in 1958.

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears segregating no de
	extreme type	intermediate type		
		1957 : intermediate de		
169				7
-2	4	2	136	
-3	10	21	149	
170				5
171				4
-2	1	5	216	
-3	20	0	304	
-5	5	9	339	
172 & 173				9
174				9
-1	20	17	343	
175				8
-3	2	4	303	
176				7
-6	5	10	313	
		1957 : extreme de		
177 to 182				38
		1957 : extreme and intermediate de		
183 & 184				11

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Table VI. Results in self-pollinated ears produced by plants originating from normal seeds of ears that segregated extreme and intermediate defectives for two successive generations.

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears segregating no de
	extreme type	intermediate type		
157				2
-6	3	32	138	
-7	26	23	309	
-8	24	25	217	
-9	11	18	266	
158				2
-3	16	1	322	
-4	11	21	136	
-5	3	24	331	
-6	19	23	68	
-7	3	5	81	
159				1
-1	27	16	256	
160				1
-2	36	23	59	
-3	25	18	319	
-4	23	21	326	
-5	6	25	180	
-6	24	18	186	
161				1
-1	32	15	149	
-3	14	17	173	
-5	32	1	111	
-6	28	33	136	
-7	35	9	134	
-10	1	35	183	

Table VII. Results in self-pollinated ears produced by plants originating from normal seeds of ears that segregated both kind of defective in 1957 and only the extreme type in 1958 (58-579-3, 10, 22, 28)

Row and ear No.	Approximate percentage of defectives		Total number of seeds	No. of ears segregating no de
	extreme type	intermediate type		
162				1
-4	33	0	92	
-6	25	2	59	
-7	15	2	143	
-10	21	0	186	
163				4
-1	28	0	229	
-2	27	1	183	
-6	28	3	69	
-8	1	6	205	
-9	28	7	228	
-10	17	7	271	
164				1
-2	48	5	87	
-7	21	0	99	
-8	27	6	131	
-10	22	13	287	
-11	16	11	97	
165				2
-6	25	26	173	
-7	26	1	329	
-10	19	3	294	
-11	17	11	76	

Last summer progenies of about 10 plants each were grown from the normal seeds on most of the ears that in 1958 segregated extreme defective, intermediate defective, both defectives, or no defective, and a total of about 300 ears was obtained, as presented in Tables II-IX. (The percentages appearing in such tables have been obtained from diagrams constructed on the basis of the actual weights of the individual kernels.)

An inspection of Tables II-VIII confirms what has been described previously, and reported above.

Table IX shows that the non-segregating ears, sibs of those segregating defectives, breed true, in the sense that in successive generations they do not give defective seeds. However, there are some remarkable exceptions: these occur in the progeny of De De ears that were derived in the previous generation from sibs of individuals segregating the intermediate type of defective endosperm. Tentative conclusions can be drawn as follows:

a) the intermediate type of defective seed that is observable in certain derivatives of teosinte introgression is highly unstable;

b) the genetic factors conditioning such a defective may be brought to what can be considered a homozygous condition by selfing heterozygous plants; however, the 25% defective kernels supposed to be homozygotes give rise to plants which appear heterozygous; the progeny of the normal sibs of such homozygotes seems to behave in a relatively normal way (30 proved to be segregating; 16 non-segregating);

c) normal individuals, sibs of homozygous intermediate defectives, in about 2/3 of the cases again segregate defectives; however, the percentage often exceeds significantly the expected 25%, and, besides the intermediate type, the extreme type is found with a consistent proportion; the other 1/3 supposed to be of De De genotype occurring in the progeny of ears segregating the extreme de behave in a more orthodox way;

d) the preceding facts seem understandable if an extragenic element, or a controlling element in the sense of McClintock, is postulated, which would interact chiefly with the intermediate type of defective, and to a minor degree with both the extreme one and with the "normal" condition.

-- Angelo Bianchi

-- Annamaria Morandi

## 2. Mendelian characters in Italian maize varieties.

To detect genetic mutants in Italian varieties, self-pollination has been carried out in a few plants grown from many seed samples of populations grown throughout Italy. The selfed ears were examined and scored first for kernel characters. Subsequently 50 kernels from every ear were germinated in the greenhouse and classified for seedling mutants.

With the exception of color characters (A C R P1 system) the segregation was often 3:1; in other cases the ratio was close to 15:1.

The following mutants have been obtained in a total of 347 selfed-ears belonging to 128 different open-pollinated varieties:

Character	No. of ears in which found a ratio of	
	3:1	15:1
Defective seeds . . . . .	12	
Opaque endosperm . . . . .	2	1
Lemon endosperm . . . . .	1	
White endosperm . . . . .	1	
Oily spot seedling . . . . .	3	
Albino seedling . . . . .	22	1
Dwarf seedling . . . . .	8	
Booster color . . . . .	4	3
Luteus seedling . . . . .	22	2
Yellow-green seedling . . . . .	13	1
Pale-green seedling . . . . .	17	3
Fine stripe seedling . . . . .	73	10
Glossy seedling . . . . .	19	8
Abnormal growth . . . . .	6	3
Liguleless plant . . . . .	6	
Virescent . . . . .	14	5
Abnormal leaves . . . . .		1
Yellow stripe . . . . .	9	
Albescens . . . . .	1	
Horn-like coleoptile . . . . .	1	

-- Angelo Bianchi  
 -- Marisa Pozzi

3. Knobs in open-pollinated maize populations in Italy.

Additional cytological data have been obtained from samples of open-pollinated maize populations, collected throughout Italy.

Some populations have been studied with the following results (to be added to those which appeared in M N L, 1958, p. 13):

Origin	No. of Knobs						Total	B chromosomes
	0	1	2	3	4	5		
Northern Italy . . . . .	7	17	20	35	11	6	96	0
Middle Italy . . . . .	5	6	7	1	2	0	21	0
Southern Italy . . . . .	1	6	4	6	3	1	21	4
Italy . . . . .	13	29	31	42	16	7	138	

As reported for the samples studied previously (M N L, 1958) the knob frequency is low, and B chromosomes are practically absent.

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The identification of specific knobs has been possible in most cases. The following table summarizes the results for the samples where all the knobs have been identified.

Origin	Position of knobs										Total samples
	1S2	3L1	4L1	5L1	6L1	6L2	7L1	7Lit.	8L1	9S1	
Northern It.	2	12	48	39	9	2	44	23	70	43	292
Middle It.	0	2	8	6	3	0	6	3	12	14	54
Southern It.	0	7	5	9	1	0	8	2	14	8	54
Italy	2	21	61	54	13	2	58	28	96	65	400

The indication 7 L It. refers to a characteristic knob structure which is frequent in Italian maize (Genetics 44 : 500).

-- Angelo Bianchi

#### 4. Cytoplasmic sterility restoration in Italian populations.

Crosses have been made on cytoplasmic male sterile types of plants of open pollinated Italian populations. A progeny of 20 individuals has been carefully scrutinized during the flowering time for every single cross. Although the number of crosses for the various populations was low, Table 1 shows that the Italian populations consist chiefly of the genotypes  $Rf\ rf$  and  $rf\ rf$ . Homozygosity for the restoration factors seems rather rare. This situation is of meaning in the maize breeding program.

Table 1. Results of crossing types of Italian open-pollinated populations on cytoplasmic male steriles.

Populations denomination	Seed parent type											
	A 158 T			WF9 T			W 22 T			C106S X A158		
	No. of Plants			No. of Plants			No. of Plants			No. of Plants		
	RfRf	Rfrf	rfrf	RfRf	Rfrf	rfrf	RfRf	Rfrf	rfrf	Rfrf	Rfrf	rfrf
V. L. Matera											2	7
V. L. Arezzo												4
Bianco Perla		3				4						
Marano	1	3	5			1						
Scagliolo 23A		1	2		1	1						
V. O. Coll. bol.		1							2			
Bianco veron.									2			
Var. Brianza		1	1									
Tisica			2									
Cinquantino			2									
Pallot. bianca	1	1										
Ottofile			2									
Spadona					2							
Ambrogio				2								

-- Angelo Bianchi

-- Giuseppe Marchesi

5. Liquid retention on the surface of the glossy mutant.

As is known, when sprinkled with water, normal seedlings shed it almost completely, while glossy mutants retain drops on the surface of the leaves. A quantitative demonstration of such a differential behaviour has been obtained by weighing the first leaves of G1, gl<sup>H</sup>, gl<sup>1</sup><sub>1</sub>, gl<sup>1</sup><sub>2</sub> and gl<sup>1</sup><sub>3</sub> types before and after sinking them in water; the weight difference has been related to the calculated leaf surface. As shown in Table 1, gl<sup>1</sup><sub>1</sub>, gl<sup>1</sup><sub>2</sub> and gl<sup>1</sup><sub>3</sub> are expressed throughout all the leaves while gl<sup>H</sup> differentiates from the 4th leaf onward.

Since the practice of providing the plants with nutrient elements through the leaves is now spreading, and because insecticide treatments to the plants are likely to be more efficient as long as the active solutions adhere to the leaf surface, the above mentioned types have been sprinkled with the following solutions:

1% Foliar K (chemical mixture containing N<sub>2</sub> 14%, P<sub>2</sub>O<sub>5</sub> 13%, K<sub>2</sub>O 20%, minor elements, phytohormones, tension-active, especially suited for leaf nutrition);

3% Cytosol PB 50 (DDT 50%) plus Irol (adhesive liquid);

5% Foliar (chemical mixture containing N<sub>2</sub> 15%, P<sub>2</sub>O<sub>5</sub> 15%, K<sub>2</sub>O 16%, minor elements, phytohormones, tension-active, especially suited for leaf nutrition).

It is apparent from Table X that the solutions provided with tension-active chemicals, especially suited for the normal type, greatly reduce or eliminate completely the difference between the G1 and gl phenotypes. Although more extensive data are needed, it seems that, with the solutions used, there is no special advantage in substituting the G1 factor with gl in the inbred lines and eventually in their hybrids in order to improve their properties for some field practices.

-- Angelo Bianchi  
-- Giuseppe Marchesi

Table X. Liquid retention on the leaf surface of normal and gl mutants (average values expressed as mg of the specified liquid per cm<sup>2</sup>).

Genotype	Leaf No.					
	1	2	3	4	5	6
Distilled water						
<u>G1</u> . . . . .	6.7	5.1	4.0	1.8	1.2	5.0
<u>gl<sup>H</sup></u> . . . . .	4.8	5.5	5.4	5.0	4.4	13.7
<u>gl<sup>1</sup><sub>1</sub></u> . . . . .	9.1	9.2	8.0	5.5	4.8	15.7
<u>gl<sup>1</sup><sub>2</sub></u> . . . . .	15.2	10.2	8.6	8.3	7.3	7.9
<u>gl<sup>1</sup><sub>3</sub></u> . . . . .	12.2	12.1	8.0	9.7	6.6	5.8
Foliar K, 1%						
<u>G1</u> . . . . .	10.8	10.1	8.5	9.3	12.2	
<u>gl<sup>H</sup></u> . . . . .	9.4	4.2	10.5	3.1	8.3	
<u>gl<sup>1</sup><sub>1</sub></u> . . . . .	20.5	11.6	8.8	7.4	12.4	
<u>gl<sup>1</sup><sub>2</sub></u> . . . . .	9.5	8.5	6.9	9.2	10.4	
<u>gl<sup>1</sup><sub>3</sub></u> . . . . .				2.8	6.1	

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Genotype	Leaf No.					
	1	2	3	4	5	6
Citrox PB 50, 3% plus Irol						
G1	16.3	5.6	8.2	9.0	15.7	
g <sup>1H</sup>	14.6	7.9	10.5	5.2	11.9	
g <sup>1</sup> <sub>1</sub>	18.9	12.7	7.2	5.6	9.7	
g <sup>1</sup> <sub>2</sub>	11.5	6.6	8.7	7.7	7.8	
g <sup>1</sup> <sub>3</sub>	13.1	7.5	10.0	10.0	12.5	
Foliar, 5%						
G1	9.0	10.2	7.1			
g <sup>1H</sup>	11.5	10.6	8.2			
g <sup>1</sup> <sub>1</sub>	9.0	8.7	6.5			
g <sup>1</sup> <sub>2</sub>	9.8	11.2	6.3			
g <sup>1</sup> <sub>3</sub>	9.7	8.0	6.0			

6. Crossing-over in the C-sh-bz-wx region, in male and female flowers.

The F<sub>1</sub> Yg I Sh Bz Wx Ds/yg C sh wx (ds) has been crossed by and on the multiple recessive tester yg C sh bz wx (ds). The data obtained are summarized below.

From the totals of the Table XI, the following percents of crossing over may be calculated  $\pm$  P.E., according to Immer's Tables:

	I-Sh	Sh-Bz	Bz-Wx
F <sub>1</sub> X multiple recessive	5.8 $\pm$ 1.5	3.3 $\pm$ 1.0	20.0 $\pm$ 2.5
Multiple recessive X F <sub>1</sub>	5.1 $\pm$ 1.7	3.7 $\pm$ 1.4	18.2 $\pm$ 3.0

The discrepancy between the two series of values is clearly not significant.

It may be noted, however, that the regions I-Sh and Sh-Bz appear larger than the standard ones; the contrary is true for the region Bz-Wx (the Yg-Sh distance is being investigated).

Table XI. Actual frequency in the classes of the indicated kernel phenotype.

Number of examined ears	I Sh Bz Wx+	I Sh bz Wx	C Sh Bz Wx	C Sh bz Wx	I sh Bz Wx+	I sh bz Wx	C sh Bz Wx	C sh bz Wx	I Sh Bz wx+	I Sh bz wx	C Sh Bz wx	C Sh bz wx	I sh Bz wx+	I sh bz wx	C sh Bz wx	C sh bz wx
	F <sub>1</sub> X multiple recessive															
47	4456	268	30	25	132	1131	1287	20	48	311	4	4320				
Multiple recessive X F <sub>1</sub>																
38	2793	148	15	13	101	582	831	7	12	188	3	2920				

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-- Maria Luisa Contin

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1. Expanded glumes.

Previous tests for linkage using interchanges had indicated that this gene is in the long arm of chromosome 5 (M.N.L. 32:93). Tests in F<sub>2</sub> with bm ys yg and bm v<sub>2</sub> indicate about 32% recombination with v<sub>2</sub> and with yg. Limited data suggest the order is bm ys yg -- expanded. If true, crossing over must be high in the distal segment of 5. There was some variability of expression of the expanded character in F<sub>2</sub>. Backcross tests are planned.

2. Linkage studies in multiple interchange heterozygotes.

Studies of the effect of a  $\Theta$  8 (1-5-6-7) and a  $\Theta$  10 (1-5-6-7-8) on crossing over in genetically marked chromosomes in the rings are in progress. In the regions measured thus far there is little if any difference between the two stocks. The use of genetic markers in chromosomes 5 and 7 should make it possible to check the products of crossing over in the differential segment in 5 and those from c.o. in the differential segment in 7. From the former, T1-5 and T5-6-7 are predicted; from the latter T6-7 and T1-5-7 (M.N.L. 27:64).

3. Progress in producing multiple interchange stocks.

A stock homozygous for 1-7-5-9 has been established (a combination of 1-7 (4405), 5-7 (5179), and 1-9b interchanges). This stock was isolated from the cross of 1-7-5 x 1-7-9 (2 rings of 4). Other combinations for rings of 8 made up in a similar manner are being tested. Various problems dealing with the use of multiple interchange stocks in studies of the inheritance of quantitative characters are being studied, e.g., frequencies of crossing over in differential segments, methods of making com-

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parisons, types of crosses to use. It should be possible to compare the effects of various groupings of the multiple factors responsible for a given character, by using rings of 6 or rings of 8 made up in various chromosome combinations.

Crossovers were selected which should produce the following rings of 6: 2-9-10, 3-9-5, 3-9-10, 6-5-8 and 7-5-9, and 2-5-6.

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#### 4. Studies of chromosome pairing in maize by using interchanges involving the same two chromosomes.

Interchanges between chromosome 2 and 6, 3 and 6, and 6 and 9 were used. Four intercrossovers belonged to type 1a (breaks in both chromosomes in opposite arms), eight to type 1b (breaks in one chromosome in opposite arms and in the same arm in the other chromosome), and five to type 2 (the breaks in both chromosomes in the same arm).

At pachytene in type 1a and type 2 intercrossovers, homologous end segments of the chromosomes usually showed complete homologous pairing whether in an association of four chromosomes or in "pairs." The intercalary segments showed extensive non-homologous association or asynapsis. Likewise in type 1b intercrossovers, the ends were associated in the  $\Theta$  4 configurations. In none did the centromeres play a significant role in the initiation of pairing. Usually in these intercrossovers pairing begins at the ends, although it may start occasionally at other points. Genetic linkage tests and microspore quartet analyses show reduced or no crossing over in regions showing asynapsis or non-homologous pairing. Unusually high frequencies of adjacent-2 segregation from the associations of four chromosomes were found in two type 1a intercrossovers. It is difficult to account for these values. In type 1a intercrossovers, a new viable set of chromosomes should arise by simultaneous crossing-over in the two 'between-breaks' segments in the complex of four chromosomes. In this set the centromere-bearing 'between breaks' segments of the two non-homologues would have exchanged positions.

The diakinesis configurations observed in the three types of intercrossovers may be summarized as follows:

<u>Type of intercross</u>	<u>No. of crosses</u>	<u>Av. % Assoc. of 4</u>	<u>% of "pairs"</u>	<u>Range in % of "pairs"</u>
Type 1a (see paragraph 1)	3	32.6	67.4	55.9-75.9
Type 1a	1	100.0	0	
Type 1b (see paragraph 1)	5	98.3	1.7	0.0-6.6
Type 2 (see paragraph 1)	8	10.0	90.0	73.0-100.0



In type 1b intercrosses "pairs" were rarely observed. In the exceptional type 1a intercross that showed no pairs one break in one parental interchange was in the satellite, and hence it regularly forms chains when heterozygous.

Those with the highest percentages of "pairs" are group 2 in which both breaks in both chromosomes are in the same arm. In those with the breaks in both chromosomes in opposite arms, the percentage of pairs is intermediate. There is some overlapping between type 1a and type 2. These results indicate that high frequencies of "pairs" do not necessarily indicate that both breaks are in the same arm in both chromosomes, an assumption that has been made by Hagberg (*Der Zuchter* 28:32-36, 1958) in barley interchanges.

-- M. Tabata

#### 5. Cytological studies of asynaptic maize.

Rhoades and Dempsey (MNL 23) reported higher than normal single crossovers and much greater than normal double crossovers in the c-sh-wx and ws-1g-gl regions in both diploid and haploid eggs of asynaptic maize. Dempsey (MNL 33) later showed that on a basis of total ovules rather than seed set single crossovers in the same two regions are reduced in haploid gametes to about half the normal value but that double crossovers still remain higher in asynaptic plants. The increase in crossing over when based on number of seed set was interpreted as due to functional gametes being derived primarily from EMC's with more frequent chiasmata and therefore more regular chromosome behavior than occurred in aborting gametes. It should be pointed out, however, that if similar increases could be demonstrated for all genetic regions of maize chromosomes, EMC's giving rise to functional gametes in asynaptic plants would have had a higher chiasma frequency per EMC than occurs in normal maize, an event which would be highly unlikely in view of the chiasma frequencies demonstrated in as plants even if the counts are limited to cells with 10 bivalents present at MI. Although diploid as eggs containing crossover chromatids at first were presumed to come from EMC's with few or no chiasmata (Rhoades, *Genetics* 32), Dempsey (MNL 32) has presented evidence that such eggs contain both sister and non-sister centromeres and suggested that diploid gametes might arise by precocious dyad centromere separation and failure of Div II following a Div I in which both bivalents and univalents had divided. The studies reported here have been confined to microsporogenesis and pollen formation but are considered pertinent with respect to crossing over and the possible origin of diploid gametes in as plants.

(1) Origin of diploid gametes. Fourteen asynaptic plants were examined from diakinesis through the quartet or 1st microspore mitosis stage. Mean number of bivalents at MI ranged from 0 to 9.95 in separate plants. Pre-meiotic fusion giving rise to polyploid PMC's occurred in six plants with 1% the highest frequency and 8N the highest ploidy observed. Although cells resulting from premeiotic fusion were observed at all meiotic stages, the infrequent occurrence in as plants and the absence of fusion in cytological studies of megasporogenesis in asynaptic mutants of certain other species would seem to rule out syncytes as a source of diploid gametes. Extremely long and curved spindles and infrequently split spindles were observed in many of the plants at MI and AI. In no instance, however, was nuclear restitution observed due to failure of spindle formation or complete failure of chromosome movement toward the poles. Precocious separation of the centromeres of chromosome dyads was noted at AI in only one plant. However, Div II spindles and quartet formation were normal although unequal distribution of monads usually occurred. Complete or partial failure of cytokinesis frequently took place after Div II and less often following Div I in most of the as plants and was independent of degree of asynapsis or year of culture. Nuclear fusion following failure of cell division occurs during the microspore interphase or at the 1st microspore mitosis. In plants showing cytokinesis failure, division figures with 10, 20 and 40 chromosomes were observed at the 1st microspore mitosis. Size of the

proportion was proportional to the number of chromosomes. When placed on the silks of tetraploid maize

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plants, similar mature pollen produced only 4N embryos as determined by root tip counts of four germinating seed. Since failure of cytokinesis during megasporogenesis apparently occurs under genetic control (Lebedeff, *Cytologia* 10), it is probable that both male and female diploid gametes result from nuclear fusion following failure of cytokinesis during the meiotic divisions. The functioning of diploid pollen on 4N females indicates that diploid male gametes can be used in crossing over studies in asynaptic maize. Pollen from the asynaptic plants, however, should be examined for the presence of viable, diploid-sized grains before pollination.

(2) Absence of cytological exchanges in asynapsed chromosomes. Three heterochromatic knobs (K4L, K9S, K10L) were incorporated in heterozygous condition into plants with low asynapsis. PMC's were examined at early diakinesis to determine if knob disjunction was reductional or equational in univalents or rod bivalents with chiasmata in the knobless arms. The respective knobs could be critically identified in almost every cell. The number of cells in which each chromosome was present as univalents or as the proper rod bivalent was 121 for chrom 4, 78 for chrom 9, and 116 for chrom 10. The frequency of rod bivalents with a short arm chiasma was more than twice that of rods with a long arm chiasma for each of the three chromosomes. Equational disjunction of knobs never was observed although genetic data indicate that in normal stocks chiasmata would be expected to occur proximal to the knob in a high percentage of PMC's. The experimental results warrant the conclusion that no cytological crossing over followed by precocious resolution of chiasmata occurs in chromosomes which exhibit asynapsis at diakinesis or MI and supports the cytological observations that diploid gametes do not arise by restitution following failure of chiasmata formation.

(3) Extent and location of pairing during early prophase. Plants with complete, medium or low asynapsis at MI were examined during all successive stages from leptotene to MI. With the possible exception of some centromere pairing, no clearly homologous pairing was observed at any stage in plants with complete asynapsis. The amount of pairing throughout the early prophase stages in plants with medium or low asynapsis was correlated with the degree of asynapsis at MI. It was concluded that chromosome segments unpaired at late pachytene had not been previously paired. The frequency and distribution of unpaired segments in chromosomes 6-10 were ascertained at pachytene in plants with low asynapsis. Chromosome 7 showed partial asynapsis versus apparently normal pairing in 51% of the figures in which 7 was identified, chrom 8 in 35%, chrom 10 in 19%, chrom 6 in 14% and chrom 9 in 4%. With the exception of chromosome 8 which frequently exhibited terminal asynapsis in the short arm, unpaired segments usually were intercalary and were more extensive and more frequent in the long arms. Long arm to short arm ratios often were considerably higher than normal even though no asynapsis or abnormal stretching was evident. A chromatid split never was observed in the unpaired chromosome segments. No matter how extensive the partial asynapsis, the centromere always was paired and terminal regions usually paired, indicating that initial chromosome synapsis probably involves both the centromere and chromosome ends.

The two genetic regions utilized in the studies of crossing over in haploid as gametes are located in short arms. Available inversion and translocation data place the ws - lg - gl region in the distal 1/4 of the short arm of chromosome 2 and the c-sh - wx region in the distal 1/2 of the short arm of chromosome 9. Since most of the partial asynapsis observed in these studies was interstitial and proximal, it is predicted that genetic regions physically closer to the centromere than the two regions so far studied will show a large reduction in crossing over in as plants. The cause of the higher than normal crossing over in these two regions when based on the number of seed on as ears is speculated upon as follows. With the exception of chromosome 8, pairing in asynaptic plants occurs much more often in short than in long arms. When pairing occurs in the short arm the distal half pairs more often than the proximal half. When pairing occurs, tighter than normal torsion coiling (a la Darlington) takes place so that for the segments paired both single and double crossovers are produced at a higher rate than in normal material. Since functional gametes are derived from EMC's with relatively high chiasma frequencies, the distal parts of the short arms, although sometimes unpaired, will

pair and cross over often enough to show a higher frequency of crossing over than that occurring in an equivalent number of normal EMC's. Such an increase may be comparable to the increased crossing over in *Drosophila* when certain heterozygous inversions are present, and it is suggested that the introduction of one or more paracentric (to maintain fertility on female side) inversions which exhibit frequent asynapsis in pachytene figures may increase crossing over in other regions of maize chromosomes. It is hypothesized that the degree of coiling and/or crossing over is dependent on a substance which normally is limited in quantity in meiocytes and is competed for with differential success by all regions of the chromosomes. When the amount available is increased for uninvolved regions either by nonpairing within heterozygous inversions or by partial asynapsis in as plants, tighter torsion coiling and increased crossing over will result.

-- O. L. Miller, Jr.

#### 6. Persistent nucleolus.

The nucleolus in maize is described as disappearing at late diakinesis or prometaphase (Rhoades, J. Heredity 40). Sampayo (MNL 33) reported the persistence of a nucleolar remnant throughout meiosis in PMC's of plants heterozygous for abnormal 10. During a cytological study of asynaptic maize, a similar persistent nucleolus was discovered independently and at first was assumed to be an irregularity due to the as gene. Several normal stocks with and without the abnormal 10 chromosome subsequently were examined, however, and a persistent nucleolus was found in each. The remnant is about the size of a MI univalent of one of the longer chromosomes. It appears to be a passive body and its movement essentially is that described by Sampayo. Separating from the organizer region at prometaphase, it moves through the spindle and lies at or near one of the poles at MI. Further movement along the cell periphery brings it near the cell equator outside of the spindle at AI. The position of the remnant at Telo I and interphase appears to be random. The remnant is present in the cytoplasm of some microspores but its fate after that stage is unknown. It is presumed that with proper staining the persistent nucleolus can be demonstrated in all maize stocks and, if so, must be considered a normal cell component at meiosis. The significance of the remnant in cellular metabolism is obscure. It perhaps is a relatively insoluble waste product of nucleolar activity. Persistence of a remnant in somatic mitoses has not been investigated.

-- O. L. Miller, Jr.

#### 7. A hand scope for pollen examination.

The "Midguard" Pocket Microscope, similar to the Leitz hand scope, is available from the following source for about \$3.00 plus postage and duty. The scope is approximately 2" by 1" and has a magnification of 35X.

Nippon Microscope Works Co.  
35-2 Minami Cho  
Aoyama, Akasaka  
Tokyo, Japan

-- O. L. Miller, Jr.

UNIVERSITY OF MISSOURI  
and  
U. S. DEPARTMENT OF AGRICULTURE  
Columbia, Missouri

1. Subject index -- a clarification.

Several cooperators have requested index references to specific subjects in volumes 4-30, as was hoped. However, because the note in volume 33 was not worded clearly and was misunderstood by some, please accept my apologies and the following: I will be happy to send references on a reasonable number of specific topics (you name them) to any cooperator wishing them. The index presently consists of about 3,000 file cards and is still somewhat disorganized, else it would be put in final form and be re-produced immediately, for full distribution. We have found the index particularly helpful in locating scattered linkage notes (by chromosome) and similar items. An index by gene symbols for linkage, description, interaction, action, distribution, structure, mutation and mutability is also in preparation and presently covers through volume 27.

-- E. H. Coe, Jr.

2. Normal segregation of markers flanking B<sup>1</sup>/B.

From heterozygotes of B<sup>1</sup>/B (weak/intense color), only B<sup>1</sup> individuals are obtained, while B<sup>1</sup>/b (weak/green) yields both B<sup>1</sup> ("converter") and b gametes, as previously reported. The critical test against elimination from transmission of B by B<sup>1</sup>, using flanking markers, has been conducted. Comparisons were made between + B<sup>1</sup> + and + B + (of the same background) over gl B sk, selfed and backcrossed to gl B sk. The progenies were graded for color (0 for glume bar color only; other grades have increasing husk color) and classified for the markers. Selfs gave the following:

Markers	+ +					gl sk					+ sk					gl +					Sum				
Grade	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	0	1		2	3	4	5
B <sup>1</sup> test	34	4	1				2	5	1				1	4					8	1					61
B check		1	5	11	8	4				1	4	1					2	2				4	0	2	45

The backcrosses to gl B sk gave the following:

Markers	+ +					gl sk					+ sk					gl +					Sum					
Grade	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	0	1		2	3	4	5	
B <sup>1</sup> test	4	21	1				3	17	1				0	9	2				2	6					66	
B check				11	21	4				11	14	1					3	4	1				4	2	0	76

Although B (of the gl sk class) and B<sup>1</sup> (of the + + class) do not "segregate" in the normal sense, markers on either side recombine, segregate, and are transmitted normally. It will be noted that some overlapping for grade occurred in the selfs; since grade 2 is much lighter than grade 3 (other grades are less widely separated), these overlaps are assumed to be due to the origin of new B<sup>1</sup> cases in the B check.

-- E. H. Coe, Jr.

3. Effects of "converter" on an intermediate allele and on a variegated allele of B.

The conversion-type phenomenon reported last year considered the effects of  $B^1$  on  $B$  and  $b$  only. Two additional alleles,  $B^V$  (Singleton, Newsletter 23:5), which is  $b$ -like but mutable, and  $B^b$  (an apparent allele, not yet firmly established), which brings about strong pigment production only in the glume bar, have been tested against  $B^1$ .  $B^V$  is tractable, while  $B^b$  is not. For  $B^b$ , comparisons were made between  $+ B^1 +$  and  $+ B +$  over  $gl B^b sk$ , selfed and crossed to  $gl B sk$ . In selfs  $B^b$  and  $B^1$  are indistinguishable, since both elicit strong glume bar color but weak husk and sheath color. The cross to  $gl B sk$  gave the following:

Markers Grade	+ +				gl sk				+ sk				gl +				Sum				
	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0		1	2	3	4
B <sup>1</sup> test	6	7	1						9	6		1	1	1			1	2			35
B check				3	1				1				2						3		10

The  $B^1$  class ( $+ +$ ) was weak (the newly-introduced  $B$  has been affected), while the  $B^b$  class ( $gl sk$ ) was not. In the  $B$  check, though the numbers are small, the grades were all of the intense level, as expected.

For  $B^V$ , comparisons were made between  $+ B^1$  and  $+ B$  over  $gl B^V$ , selfed and crossed to  $gl B$ . In this case segregation for  $Pl-pl$  was present and although the analysis was complicated because of previous inexperience with  $Pl$  in this system, the results were even more striking in  $Pl$  plants. Only the  $Pl$  individuals are presented below, for simplicity. Variegated plants in the selfs were graded according to the color level of sectors, with the following results:

Marker Grade	+				Uniform							gl Varieg.				gl Uniform							Sum
	1	2	6	7	0	1	2	5	6	7	1	2	6	7	0	1	5	6	7				
B <sup>1</sup> test	2	1			16	35	4				8	3			3					73			
B check			2	0				3	6	12		4	1						2	30			

Note that at least two grade levels separate intense and weak individuals in each case. The cross to  $gl B$  gave the following:

Marker Grade	+							gl							Sum		
	0	1	2	3	4	5	6	7	0	1	2	3	4	5		6	7
B <sup>1</sup> test			2	11	7					1	4	12	4				41
B check						1	1	12					1	0	6	2	23

It is interesting that the functionally intermediate allele  $B^b$  is like the null  $b$  in its response to  $B^1$ , while the functionally null allele (except after mutation),  $B^V$ , is affected by  $B^1$  and is thus similar to  $B$ .

-- E. H. Coe, Jr.

4. Effects of  $c_2$

This factor is still unlinked. TB-3 tests (long arm) were negative. In combinations with intensifier,  $c_2$  was found. Selfs of confirmed  $c_2 c_2$  in segregate 3 colorless:1 dilute, while  $c_2$  is affected by  $B^1$  and is thus similar to  $B$ .

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selves of homozygous  $c_2 c_2$  in in give all dilute kernels. Acid tests, even on  $c_2 c_2 c_2$  in in in , are negative on visually colorless types. This is therefore a new example of a 13:3 interaction. Further observations on plant color show that  $c_2$  does affect this character:  $c_2 c_2$  B P1 plants have much reduced pigmentation in the husks and sheaths but intensely-pigmented auricles, glume bars, and similar tissues.

-- E. H. Coe, Jr.

5. A sector for brittle stalk-2.

In a progeny segregating for  $bk_2$ , one individual was almost perfectly split into half brittle-half normal. Almost all of the leaves were divided at or near the midrib into brittle and normal and the tassel had very nearly half brittle and half normal branches. Whatever the basis for brittleness it therefore appears to be cell-limited and, since the  $bk_2$  sector was virtually equal in size to the normal,  $bk_2$  must not affect the competitive ability (cell division and growth) of tissues carrying it to any great extent.

-- E. H. Coe, Jr.

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Hiratsuka, Japan

1. Maize races native to the island Kiushiu situated at the southern part of Japan.

The old Japanese corn races have three centers of distribution which occupy upland areas on the mountain sides of Mt. Fuji, Shikoku and Kiushiu and which range from 300 to 1,000 m in altitude. All of the races were shown to belong to a Caribbean type of tropical flint corn. In addition, detailed studies have been carried out from morphological and cytological viewpoints. Some data obtained from the races native to two centers, Mt. Fuji and Shikoku, have already been presented in previous volumes of this News Letter MGCNL 31:105-107, 32:105-107 and 33:84-88. The present study deals with native races from the last center, Kiushiu. In autumn of two years, 1956 and 1958, a large collection of races growing in Kiushiu was made. It was obtained from 200 or more farmers at 65 places and consisted of 300 or more samples. In 1959, 62 of these samples were chosen and grown at three agricultural experiment stations, Iwate, Hiratsuka and Ehime. The same measurements or observations as those mentioned in the previous reports were carried out. Results obtained can be summarized in table 1 on the following page.

(1). For about 300 samples collected, 70 local racial names were encountered. Actually, only 43 distinct races were identified. Of these, 15 races were certainly worth noting from the breeding viewpoint (Table 1). The 43 races were grouped into 11 types (Table 1). Four types were worth considering for breeding purposes. (a) the Oodama type comprises the late races with heavy grain yield, (b) the Shinboso type is superior in grain quality to the other types, and (c) the Kanazuchi and Okuzuru types have a combination of the attributes just mentioned with the former being medium and the latter early in maturity.

(2). The racial differentiation was remarkable in the majority of 68 characters examined. Eighteen attributes were especially useful in identifying any race or type. They consisted of characters concerned with maturity, plant height, stalk diameter, number of stalk nodes, leaf size, ear height,

Table 1. Comparison of 10 attributes of 11 types of the old races native to the island Kiushiu.

Name of type	No. of races	Maturity	Plant height	No. of leaves	Leaf size	Ear height	Kernel rows	Ear weight	Kernel color	Place well-adapted	Race noticed
1. Oodetchi	3	very late	high	many	large	high	14-18	heavy	pale orange	low land in mountain	Tonegawa, Aso No. 1
2. Kanazuchi	5	late	"	"	"	medium	14-16	common	orange	"	Kanazuchi, Mejiro, Torinosu
3. Nakadama	5	"	medium	medium	medium	"	"	"	"	"	-
4. Shinboso	3	"	"	"	"	"	12-14	heavy	dark orange	"	Shinboso, Yamasanga, Yamanguchi
5. Okuzuru	6	very early	"	few	"	somewhat low	8-12	common	"	high land in mountain	Okuzuru, 8-retsu wase, Hattôkibi
6. Hayadama	3	early	low	"	small	low	10-14	light	"	"	Hayadama, Kijiyama
7. 4Ohi-wase	1	"	"	"	"	"	14-16	common	"	"	-
8. Kirishima	4	medium or late	somewhat low	many	medium	medium	14-20	light	yellow	terrace on coastal hill	Nobeoka-zairai
9. Shimabara	2	"	"	"	small	"	14-16	"	"	"	Shimabara-zairai
10. Benkei	8	early or late	"	medium	medium	"	14-24	"	"	all areas	-
11. Pop-like	2	medium or late	low	many	small	high	16-20	"	"	coastal area	-

number of husk leaves, ear exertion, ear length, ear diameter, number of ears, ear weight, number of kernel rows, number of kernels per row, kernel size, kernel weight, tassel length and number of tassel branches. Furthermore, some attributes were remarkably sensitive to the climatic difference in the 3 experimental stations, Iwate, Hiratsuka and Ehime. They were maturity, stalk height, stalk diameter, tillering, prop-rooting, number of green leaves, number of ears, cob diameter, cob weight and kernel weight.

(3). The genetical uniformity of the characters of a race was dependent on the degree of topographic isolation, the diversity of corn cultivation by the farmer, the climatic difference in the growing area and the care of farmers in their seed selection. In accordance with such differences, 65 corn-growing localities could be grouped into 25 areas, Kokonoe, Tsue, Kujū, Asaji, Ogi, Namino, Oguni, Asodani, Shiramizu, Kusakabe, Mamihara, Noziri, Gokasho, Kuwanouchi, Takachiho, Nobeoka, Saigō, Morozuka, Shiiba, Mera, Yuyama, Itsuki, Kirishima, Shibushi and Shimabara. In 8 areas Kokonoe, Tsue, Noziri, Kawanouchi, Morozuka, Shiiba, Nobeoka and Shimabara, there were distinct races with uniform characters, any one of which was rather small in its variability. In 6 other areas, Asaji, Kujū, Ogi, Itsuki, Kirishima and Shibushi, races were more heterogeneous in character. Lastly, the remaining 11 areas were intermediate between the above two cases in their intra-race variability.

(4). The knob analysis of the pachytene chromosomes has been carried out. Data obtained from 67 samples are given in Table 2. The B chromosome was not met with, as seen in the native races in Shikoku. In every race, 5 arms with knobs were always observed: 3L, 5L, 6L, 7L and 8L. Accordingly, it seems that those knob positions should be considered as a fundamental characteristic of the Caribbean flint growing in Japan. In addition, the old races distributed in Kiushiu were characterized by having three marked peculiarities in knob position. As compared with old races native to the other two centers, the races in Kiushiu tended to have a very high occurrence of the knobs on 10L and 2L, giving an average of 0.7 and 0.8 respectively. Another peculiarity was the occasional loss of the second knobs on 6L and 8L, resulting in an average of 1.5 and 1.9 respectively, because the first knobs on 6L and 8L existed in every race. Lastly, the occurrence of knobs on 1L, 4L, 7S and 9S was very low, the frequency varying from 7 to 14 percent. However, their presence or absence was very important in the identification and relationship of the race, in accordance with which the number of knobs varies. The variability of knobs was, however, not as great as that seen in the other two centers. Average number of knobs was computed to be 8.8, ranging from 7 to 12. On the whole, it may be said that a decrease in knob number in a given race should be associated with earliness; the more knobs a race has, the later it becomes. On the other hand, it may also be said that an increase of knob number should be considered as an index of contamination by Japanese old pop corn, because the pop races native to Japan had more knobs than the pure races of Caribbean flint distributed in the same area.

-- T. Sutō

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1. Genetic and genotype x environmental interaction variances in an open-pollinated variety of corn.

This experiment was designed to estimate the magnitude of components of genotype x environmental interaction variance relative to genetic variance. Sixty half-sib families of the Jarvis variety



Table 2. Number and position of the chromosome knobs in 67 races native to the island Kiushiu.

Chromosome		Type of races										Total (67)
		Oodetchi 9	Kanazuchi 7	Nakadama 17	Shinboso 8	Okuzuru 9	Hayadama 11	4Ohi-wase 3	Shimabara 1	Benkei 1	Pop-like 1	
1	S	-	-	-	-	-	-	-	1.0	-	-	-
	L	0.2	0.2	0.2	-	0.1	0.1	-	-	-	-	0.1
2	S	-	-	-	-	-	-	-	-	-	-	-
	L	0.7	0.9	0.8	0.4	1.0	0.8	1.0	1.0	1.0	1.0	0.8
3	S	0.2	0.2	0.1	0.1	-	0.1	-	1.0	-	-	-
	L	1.0	1.0	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
4	S	-	-	-	-	-	-	-	-	-	-	-
	L	1.0	0.7	0.5	0.8	-	0.1	-	-	-	1.0	0.4
5	S	-	-	-	-	-	-	-	-	-	-	-
	L	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
6	S	-	-	-	-	-	-	-	-	-	-	-
	L	1.6	1.6	1.6	1.6	1.2	1.1	1.0	1.0	2.0	1.0	1.5
7	S	0.1	-	0.1	-	-	0.2	-	-	-	1.0	0.1
	L	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
8	S	-	-	-	-	-	-	-	-	-	-	-
	L	2.0	2.0	1.6	2.0	1.9	1.8	2.0	2.0	2.0	2.0	1.9
9	S	0.1	0.2	0.4	-	-	0.2	0.3	-	-	-	-
	L	-	-	-	-	-	-	-	-	-	-	-
10	S	-	-	-	-	-	-	-	-	-	-	-
	L	1.0	0.7	0.7	1.0	0.3	0.4	-	1.0	-	1.0	0.7
M	S	0.4	0.4	0.6	0.1	-	0.5	0.3	2.0	-	1.0	0.3
	L	9.4	9.1	8.6	8.9	7.6	7.3	7.0	8.0	8.0	9.0	8.5
Total		9.9	9.5	9.2	9.0	7.6	7.8	7.3	10.0	8.0	10.0	8.8

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were grown in replicated tests at 5 locations for 5 years. The components of variance estimated from a combined analysis of variance are given in Table 1. The variation attributed to interactions

Table 1. Estimates of Components of Variance in the Jarvis Variety

Variance among half-sib families . . . . .	.0007
Variance due to interaction of families and locations . . . . .	-.0001
Variance due to interaction of families and years . . . . .	-.0001
Variance due to interaction of families and years x locations . . . . .	.0005

between families and locations, and between families and years is very small, whereas the second order interaction involving locations, years and families is of importance. This implies that the important interaction variance is simply due to family x environmental interaction without regard to years and locations. The variance due to families is estimated to be larger than the variance due to interaction of families and environments.

-- R. H. Moll  
-- H. F. Robinson

## 2. Heterosis in crosses of varieties from different geographical regions.

The objective of this study is to determine the relative amounts of heterosis obtained when locally adapted corn varieties were crossed with each other and with varieties from different regions. Geographical separation and isolation leads to genetic diversity through genetic drift and adaptation to different environments. The degree of genetic diversity should be reflected in greater amounts of heterosis in "between region" crosses than for "within region" crosses.

This experiment included two North Carolina varieties, Jarvis and Indian Chief; two midwestern varieties, Krugs and Reids Yellow Dent; and two Puerto Rican varieties, Diente de Cabolla and Mayorbela. These were crossed in all possible combinations. However, one of the crosses, Diente de Cabolla x Krugs, did not produce sufficient seed and was not included in the test. This study was planted in five replicates at two locations for three years.

The average yields for each variety and variety cross are given in Table 1. The highest yielding entry was the cross, Indian Chief x Diente de Cabolla, and the second highest was Indian Chief x Mayorbela. Both of these represent a cross between a locally adapted and an unadapted variety. Table 2 gives the yield of the crosses expressed as per cent of the average of the two parental varieties. The greatest amount of heterosis (as measured from the midparent) occurred in the cross Reids Yellow Dent x Mayorbela. The cross between the two Puerto Rican varieties was less than the midparent. The average heterosis of the "within region" crosses is 3%, and for the "between region" crosses is 25%. The greatest amount of heterosis, on the average, occurred in crosses between midwestern varieties and Puerto Rican varieties. Considering the "between region" crosses, crosses between the North Carolina varieties and the midwestern varieties showed the smallest amount of heterosis, averaging 14% above the mean of the parental varieties.

Table 1. Average Yield of Varieties and Variety Crosses

	Jarvis	Indian Chief	Krugs	Reids Yellow Dent	Diente de Cabolla	Mayorbela
Jarvis . . . . .	.510	.569	.480	.520	.528	.544
Indian Chief . . . . .		.533	.549	.551	.617	.586
Krugs . . . . .			.371	.453	--	.500
Reids Yellow Dent . . . . .				.430	.535	.560
Diente de Cabolla . . . . .					.364	.317
Mayorbela . . . . .						.374

Table 2. Yield of Variety Crosses in Per Cent of Midparent

	Indian Chief	Krugs	Reids Yellow Dent	Diente de Cabolla	Mayorbela
Jarvis . . . . .	109	109	111	121	123
Indian Chief . . . . .		122	114	138	129
Krugs . . . . .			113	---	134
Reids Yellow Dent . . . . .				135	139
Diente de Cabolla . . . . .					86

These results agree, in general, with expectations based on genetic diversity between varieties due to isolation and adaptation to different regions, and further indicate that the maximum yielding crosses may not result from intercrossing the highest yielding parental varieties.

-- R. H. Moll  
 -- W. S. Salhuana  
 -- H. F. Robinson

NORTH DAKOTA AGRICULTURAL COLLEGE  
 Fargo, North Dakota  
 Department of Agronomy

1. Inheritance of resistance to *Diplodea zeae*, *Gibberella zeae* and *Fusarium moniliforme*, stalk rots in corn.

In a preliminary survey, twelve different fungi were isolated (and identified) from diseased stalk tissues of 25 inbred lines of corn grown under normal field conditions at Fargo, North Dakota. No single organism was clearly defined as being predominantly responsible for the stalk rot observed.

In a subsequent detailed study, five inbred lines and their respective F<sub>1</sub> and F<sub>2</sub> progenies were stem-inoculated, after pollination was completed, with pure cultures of *Diplodea zeae* (Schw.) Lev., *Gibberella zeae* (Schw.) Petch and *Fusarium moniliforme* (Sheld.) Snyder and Hansen. The results obtained were as follows:

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D. zeae rot symptoms suggested no dominance for resistance in the  $F_2$  in two crosses and partial dominance in one cross.

G. zeae reaction indicated no dominance for resistance in three crosses.

F. moniliforme reaction indicated no dominance for resistance in three crosses.

Estimations of gene number conditioning reactions to these organisms revealed that only a few factor pairs may be involved. Heritability, in the broad sense, for resistance to the three stalk rot diseases studied was positive and relatively high for eleven out of fourteen estimations as shown in the table below.

#### HERITABILITY OF REACTION TO THREE STALK-ROT DISEASES OF CORN

Disease Organism	Cross	Estimates of Heritability	
		A	B
<u>Diplodia zeae</u> . . . . .	ND-5 x W-22		-137.2
	ND-36 x Oh51-A	47.25	43.93
	ND-230 x Oh51-A	18.83	62.92
<u>Gibberella zeae</u> . . . . .	ND-5 x W-22		10.12
	ND-36 x Oh51-A	77.85	55.70
	ND-230 x Oh51-A	-25.07	92.38
<u>Fusarium moniliforme</u> . . . . .	ND-5 x W-22		71.33
	ND-36 x Oh51-A	32.65	21.09
	ND-230 x Oh51-A	-36.33	29.50

$$(A) \quad H = \frac{V_{F_2} - V_{F_1}}{V_{F_2}} \times 100$$

$$(B) \quad H = \frac{V_{F_2} - V_P}{V_{F_2}} \times 100$$

-- William Wiidakas  
 -- P. C. Sandal  
 -- Houg-Zung Liu

OAK RIDGE NATIONAL LABORATORY<sup>1</sup>  
Oak Ridge, Tennessee  
Biology Division

1. Genetic studies on developing endosperm proteins.

Over the past two years we have been studying protein differences in developing endosperm tissue of mutants which affect starch synthesis and composition. We have used the technique of "substrate electrophoresis" separating the endosperm proteins on starch gel which is substrate for the enzymes involved in starch synthesis and degradation. In this technique, the separation of the proteins depends upon enzyme substrate affinity as well as charge. It is possible to directly test for the enzymes which alter the structure of starch, by staining the gel with iodine following the electrophoretic separation. Those enzymes which reduce the size of the starch polymer by digestion or branching appear as red bands against the blue background of the stained starch gel.

We have found that the  $Sh_1$  gene controls the synthesis of a major protein component which is present in the highest concentration in the immature endosperm. This protein is completely lacking in  $sh_1/sh_1/sh_1$  endosperm. The concentration of this protein (designated  $Sh_1$ ) is dose dependent increasing with increasing doses of the  $Sh_1$  allele. This has been corroborated by immunochemical studies as well as moving boundary electrophoresis. Suppression of  $Sh_1$  by  $Ds$  also results in the complete absence of the  $Sh_1$  protein, however, in the presence of  $Ac$  the  $Sh_1$  protein reappears but in reduced amount as is expected. We have not been able to detect the presence of a new protein band in  $sh_1/sh_1/sh_1$  material; however, the intensity of the band which occupies a position just ahead of the  $Sh_1$  protein is increased in this mutant. This band (designated G) shows a faster migration rate in the  $sh_4$  mutant material and appears to be missing in  $su_1$  and its allele  $su_1^{am}$ ,  $bt_1$  and its allele  $sh_3$ ,  $sh_2$ , and  $du_1$ . That different genes are responsible for the absence of this protein band in these mutants is indicated by the presence of the band in the  $F_1$  hybrid between  $su_1$  and  $sh_2$ , each of which lacks the band. Analysis of double mutant combinations points to gene interaction in the control of the synthesis of this protein.

-- Drew Schwartz

<sup>1</sup> Operated by Union Carbide Corporation for the U. S. Atomic Energy Commission.

UNIVERSITY OF PAVIA  
Pavia, Italy  
Institute of Genetics

1. Investigations on induced polygenic mutability in maize.

An experiment was started in 1957 with the goal of studying polygene mutability in maize. A monoploid stock, HD 73, 1375/11 kindly supplied by Professor G. F. Sprague was used. 8 lines were established in 1957 by selfing as many plants obtained from seed of a single selfed ear. In 1958 three groups of about 5 plants were selfed within each line, one to be treated with 3,000 r applied to the tassel 2 days before using the pollen for self-fertilization, one to be treated with 1,500 r and one receiving no treatment. Treatments were given using an X-ray machine operated at 230 KV, 12 mA,  $\lambda = 0.53$  Angstrom filter. In Winter 1958-1959, the  $R_1$  generation was obtained growing the plants in Somali-

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land, with the cooperation of the Afgoi Agricultural Center, Mogadiscio. From each of the treated and untreated selfed ears obtained in the previous generation, from 5 to 10 plants were selfed establishing sublines.  $R_1$  and  $R_2$  seeds were grown in the same plot in Summer 1959 at the Agricultural Experiment Station in S. Angelo Lodigiano, in the Padana Plain, near Pavia, and observations were made for the following traits:

- 1) flowering time of the tassel determined as the number of days beginning with July 1st; on  $R_1$  and  $R_2$
- 2) number of simple lateral branches of the tassel; on  $R_2$
- 3) number of composite lateral branches of the tassel; on  $R_2$
- 4) total number of lateral branches of the tassel, simple and composite; on  $R_2$
- 5) number of spikelets per mm. of the rachis length in the central axis; on  $R_2$
- 6) number of spikelets per mm. of the rachis length in the upper lateral branch; on  $R_2$ .

It is expected that, as all the plants originated from a single selfed ear of a monoploid stock, any significant increase of variability observed for the treated lines is due to the effect of mutations induced by X-ray treatment, and any significant increase of variability observed for the untreated line in different generations is due to the effect of spontaneous mutations.

As the material used is represented by plants of lines and sublines differentiated by selfing, an increase of variability can be detected:

- a) by comparing the distribution range of variability of lines for the various treatments;
- b) by the analysis of variance within the three treatment groups in order to distinguish the contribution to variability of lines (genetic source), of sublines within lines (genetic source), and within lines (environmental component).

In this preliminary report data for comparison (a) are summarized in the following table, which gives: the mean for lines, their observed range, the estimated variances between lines within treatments and  $X^2$  estimates in the Bartlett test for heterogeneity between treatments.

The P values given in the table show that variances for line means within treatments are significantly heterogeneous for flowering time in  $R_1$  and  $R_2$ , for the number of composite lateral branches of the tassel and probably for the number of spikelets per mm. in the upper lateral branch of the tassel.

-- R. E. Scossiroli

Table 1.

	Means( $\bar{x}$ ), range of line means and estimated variances ( $s^2$ )				$X^2$ of the Bartlett test, 2 d. f.
		control	1,500 r	3,000 r	
1. flowering time, days $R_1$	$\bar{x}$ range $s^2$	20.99 20.65-21.57 0.1022	21.24 20.16-23.36 0.9824	22.13 20.57-23.63 0.8877	<u>9.28</u> <u>P = 0.01</u>
$R_2$	$\bar{x}$ range $s^2$	20.68 19.62-21.49 0.4009	21.16 19.89-22.38 0.5918	21.47 20.75-22.63 0.4194	0.37 P = 0.98-0.99
2. no. simple lateral branches of the tassel, $R_2$	$\bar{x}$ range $s^2$	9.68 8.88-10.44 0.3683	9.59 8.54-10.48 0.4033	10.29 8.92-12.00 0.8644	1.87 P = 0.30-0.50
3. no. composite lateral branches of the tassel, $R_2$	$\bar{x}$ range $s^2$	2.13 2.08-2.20 0.0014	2.10 1.92-2.31 0.0151	2.24 2.09-2.45 0.0195	<u>11.46</u> <u>P = 0.01</u>
4. total no. lateral branches of the tassel, $R_2$	$\bar{x}$ range $s^2$	11.82 10.96-12.63 0.3862	11.70 10.65-12.72 0.4598	12.53 ♦ 11.23-14.25 0.9057	1.71 P = 0.30-0.50
5. no. spikelet/mm, central axis of the tassel, $R_2$	$\bar{x}$ range $s^2$	1.10 1.07-1.15 0.0006	1.11 1.07-1.16 0.0010	1.23 1.09-1.15 0.0005	1.07 P = 0.50-0.70
6. no. spikelet/mm. upper lateral branch of the tassel, $R_2$	$\bar{x}$ range $s^2$	0.26 0.25-0.26 0.00002	0.25 0.24-0.26 0.00012	0.25 0.23-0.27 0.00022	<u>3.65</u> <u>P = 0.10-0.20</u>

PENNSYLVANIA STATE UNIVERSITY  
University Park, Pennsylvania  
Dept. of Botany and Plant Pathology

### 1. Disease resistant synthetics of corn germ plasm.

The administrative policy of this University makes clear that any maize germ plasm in any stage of breeding may be released to the general public provided that said item of germ plasm is not involved in a station hybrid. In the latter situation a policy of delayed release is adhered to.

You may recall that up to the present, six synthetics carrying genes for disease resistance have been available. Three of these were released from this department in 1954 and were arbitrarily designated, Early, Intermediate and Late. Small lots of seed of these are still available from a renewal planting in 1957.

We wish to announce the following additional ones:

- (a) Sweepstakes synthetic; O.P. 2. (open pollinated twice).
- (b) Early synthetic No. 2; O.P. 1.
- (c) South African-American; O.P. 3.
- (d) " " " ; Stiff stalked selection, O.P. 2.
- (e) In many cases the  $S_2$  and  $S_3$  components of these synthetics are available as individual ear selections. (See description notes and policy notes.)

#### Description of Synthetics

In general, these recent synthetics have a broader genetic base than the original three. They have been subjected to more diseases over a longer period of time.

#### Sweepstakes Synthetic

Westbranch Sweepstakes (originated along the West branch of the Susquehanna river) is widely adapted in the northeast, just north of the range of Lancaster Surecrop. It has fairly long ears with flat kernels. The seed has a red pericarp with a yellow or white cap.

About 1000 plants were grown in a mixed planting of the Early, Intermediate and Late Synthetics and detasselled. The whole planting was treated as a disease nursery. The most resistant plants were selected and the seed bulked. Samples were taken of this bulked seed and were planted, in-oculated, selfed and selected for two seasons. The surviving  $S_2$  cultures were reconstituted into a synthetic in an isolation block. To date the Synthetic segregates about two percent yellow ears. It has shown remarkable resistance.

#### Early Synthetic No. 2.

Strains of "Early Butler", "College Whitecap", "Early Sweepstakes", a longfellow flint and an early yellow dent, were detasselled and top crossed at the same time as the Sweepstakes described above. In the disease nursery particular attention was paid to early maturity. The Synthetic was made up of  $S_2$  and  $S_3$  lines, pollinated 7/25 to 8/3 from a May 12 planting. This has been in isolation one season only and the seed is as variable as the lines which comprise it.



S<sub>2</sub> and S<sub>3</sub> components of this Synthetic are available as individual ears. (See note at end of announcement).

### South African-American Synthetic

This Synthetic shows promise as a source of stalk strength as well as disease resistance. It is made up of American breeding material which survived the prolonged drought of 1955 and which remained erect following a subsequent hurricane, crossed with South African inbreds which were selected for their remarkable resistance to Helminthosporium turcicum, the causal agent of Northern leaf blight.

The South African-American Synthetic is somewhat later than the Sweepstakes, which in turn is later than Early Synthetic No. 2.

The stiff stalked selection consists of bulked seed of 94 plants still erect and sturdy Dec. 15, 1959.

Seed of individual ears of these stiff stalked plants is available.

### Note regarding requests for disease resistant early generation inbreds

The corn disease nursery at this station consists of about 1000 10-foot rows of early generation inbreds. We seldom keep anything beyond the S<sub>4</sub> generation at which time, the choice selections are turned over to the Corn breeders in Agronomy for agronomic evaluation. (209 such cultures were given the Agronomists in 1958.) We expect an evaluation report on the combining ability of these cultures, when such information becomes available. In that way, disease resistant inbreds already produced can become available to improve germ plasm at some future date.

We expect and ask for this same type of cooperation from any individual outside this station. We are glad to share our material with you, but our program cannot be nurtured unless we in turn receive credit. We really believe we have something worth while sharing.

Furthermore, I am not interested in packeting small numbers of inbreds of specific maturity dates. Unless you want 50-100 items, why not develop your own from the Synthetics available.

-- C. C. Wernham

PIONEER HI-BRED CORN COMPANY  
Johnston, Iowa  
Department of Plant Breeding

### 1. Parthenogenesis in 2n x 4n crosses.

In crosses between diploid sugary maternal parents and non-sugary tetraploid males, occasional 2n sugary kernels develop. These have been observed in various cultures over the past four years. It was first assumed that such kernels probably arose as a result of fertilization by contaminating sugary pollen. However, in 1958 two ears containing a nearly full set of 2n homozygous sugary seeds were

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found among approximately 150 crosses of 2n sugary x 4n non-sugary. The more than usual care exercised in making the pollinations would seem to render remote the possibility of all seeds on these two ears being contaminants. Plants grown from these seeds were markedly reduced in size when compared with their maternal parents. However, they exhibited considerable variation from plant to plant. Such variation would be expected if the kernels producing these plants arose from reduced eggs followed by subsequent chromosome doubling. Since chromosome doubling of a gamete derived as a product of normal meiosis would impose complete homozygosity, the progenies resulting from selfing such plants should be uniform within individual ear classes. A test for uniformity in this material will be made in 1960. In 1959 pollen from 4n starchy plants was placed on silks of 161 2n sugary ears. Pollinations were delayed approximately one week beyond the time one would normally pollinate for full seed sets. These pollinations resulted in 364 3n starchy kernels, 16 2n sugary kernels. The sixteen diploid sugary kernels were distributed among 10 ears. Additional care was taken in 1959 to reduce the possibility of contamination by stray sugary pollen, i.e. tassels of all sugary plants were removed prior to shedding and no sugary genotypes were grown in the vicinity of the plants being crossed. It would seem not unlikely, therefore, that the 16 diploid sugary kernels arose in the absence of fertilization. If parthenogenesis is involved, the variation between plants from homozygous sugary kernels obtained in 1958 would suggest that reduced eggs, followed by spontaneous chromosome doubling, are functioning as embryos. Although attempts at embryological studies have been made, the infrequent occurrence of possible parthenogenetic kernels renders this a very unattractive approach to this problem.

-- William L. Brown

UNIVERSITY OF PRETORIA  
Pretoria, Union of South Africa

### 1. Resistance to *Helminthosporium turcicum*.

In the South African Journal of Agricultural Science 2:255-259, June 1959, T. van Schaik and P. M. le Roux published on the genetic nature of some sources of resistance to leaf blight in maize caused by *Helminthosporium turcicum*. A maize line, Mex 155 obtained from Dr. E. J. Wellhausen from Mexico with the original number Gto. 57-272-1-7, was found to carry a single dominant gene for almost complete resistance to leaf blight under South African epiphytotic conditions. This inbred line should be extremely useful for incorporation into susceptible maize inbreds which are otherwise desirable and economically important, because in a variety of crosses with other susceptible lines, it gave uniform highly resistant progenies.

The resistance of Mex. 155 was recovered in approximately half of the progeny of the backcross to the susceptible parent and to a large extent, therefore, can be attributed to the action of a single major dominant gene. The variation in grades of susceptibility among the non-resistant segregates may be explained by the influence of some minor modifying genes which are suppressed completely by the dominant resistance gene but show effects in its absence.

-- P. M. le Roux  
Dept. of Plant Pathology

2. Competitive pollen tube growth.

Competitive pollen tube growth studies provided by making use of pollen mixtures from yellow and white sources were reported previously (M. N. L. 1958, 1959). Pollen mixtures in which one or the other component was doubled in amount were studied and the results indicate that where the superiority of say the yellow component was clearly observed when equal amounts of the two components were used, the yellow pollen retained its superiority significantly even though the pollen from the white source was doubled in amount. Hence, it would appear that slight differences which would normally occur when making up pollen mixtures would not affect the results materially, and that the differences observed in such studies must be mainly of a genetic nature.

-- J. D. J. Hofmeyr  
Dept. Genetics

3. Pollen tube growth and combining ability.

As reported in a previous number of the newsletter, our studies on the behavior of maize pollen in pollen mixtures (from plants carrying different endosperm colors) led us to suspect that a correlation existed between combining ability and the capability to produce an excess of progeny over that of other pollen in the mixture. Certain Russian workers reported the same suspicion. This has been tested in a pollen mixture and yield trial experiment with 103 entries. It was found that no such correlation existed between the ratios of kernels produced by the two types of pollen and the ratios of the yields of the pairs of progenies. A significant correlation was found, however, between the ratios of progenies produced on different female parents by the same pollen mixture and the ratios of the progeny yields.

J. M. P. Geerthsen  
Dept. of Genetics

4. Comparison of two methods for estimating additive and dominant components of genetic variance for yield.

In an experiment designed to test five open pollinated South African maize varieties for differences in additive (G) and dominant (D) components of genetic variance for yield, two methods were used. The first method was based on a comparison of intra-class correlations of full sib and half-sib families as proposed by Fisher (1918) as reported in last year's newsletter. The second method used is similar to that of Comstock and Robinson using biparental progenies, analyzed according to the method developed by Comstock and Robinson (Biom. 4:254). The results of both methods are given in table 1.

Table 1. Estimates, derived from two methods, of dominant (D) and additive (G) components of genetic variance for yield in different varieties of maize.

Variety	First method (full sib-half sib comparison)			Second method (biparental progenies)		
	No. of Progenies	D	G	No. of Progenies	D	G
Anveld . . . . .	48	13.00	3.60	60	-2.48	6.84
Teko . . . . .	52	1.20	7.72	116	-0.44	4.96
Sahara . . . . .	48	-5.64	7.92	72	0.20	4.20
Robyn . . . . .	48	0.12	8.20	80	11.16	0.16
American white flint	58	-6.92	4.16	75	-4.88	9.64

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Although the main aim of this experiment, namely the comparison of different varieties with respect to their dominant and additive variance components, was not achieved satisfactorily, the data did allow a comparison of the two methods which seem to be in fair agreement with each other. Estimates of D for individual varieties using either method seem to fluctuate around a positive value quite small when compared to that of G. Differences between varieties are not consistent over different methods but are probably due to sampling errors (as indicated by the negative values which by definition are impossible.)

The high G:D ratio obtained agrees with the results of Robinson et. al. (Genetics 40:45) and the same conclusion may be drawn, *nl.* that true overdominance can hardly explain the amount of hybrid vigour commonly found in maize.

An assumption to which the theory employed in the above studies was subject is the lack of epistasis. Cockerham (Genetics 39:859) indicated that correlations between relatives contain only small proportions of the existing epistasis. Epistasis, therefore is not expected to bias the estimates of D and G much unless the amount of epistasis is considerable. Available data (Comstock, C. S. H. Symp. Quant. Biol 20:93) give little evidence for epistasis. Jinks (Her. 9:223) by means of the diallel method concluded that epistasis was important only in those maize inbreds that showed outstanding combining ability. The use of non-selected material to avoid upward bias of dominance estimates as a result of epistasis seems advisable.

Genotype-environment interaction could very well be an important source of error or bias in the above experiments. An extensive study with local maize variety crosses by van Schaik et. al (S. A. J. Agr. Sci. 1:423) stressed the importance of environmental interaction with heterosis. Rojas and Sprague (Agron. J. 44:462) found a large amount of environmental interaction with the specific combining ability for yield variance in maize.

In conclusion it may safely be stated that in non-selected open pollinated material of the type used in the experiments reported here the assumptions of no effective linkage or epistasis are plausible but that genotype-environmental interaction may have a pronounced effect on the results.

-- T. van Schaik  
Dept. of Genetics

##### 5. Effect of inbreeding on variability of yield.

An extensive experiment was carried out to examine the effect of inbreeding on the variability of yield of five South African open pollinated varieties (Sahara, Teko, Anveld, American white flint and Robyn). Twenty of each of the following strains were developed from each variety:

1. Half-sib matings,  $F = 0.125$
2. Full sib matings,  $F = 0.25$
3.  $S_1$ -full sib mating,  $F = 0.375$
4.  $S_1$ ,  $F = 0.50$
5.  $S_2$ ,  $F = 0.75$ .

The experimental field was subdivided into 20 blocks. One strain taken at random from each of the five different degrees of inbreeding of each of the five varieties was grown in two separated replications within each of the twenty blocks. Two replications of each of the open pollinated ( $S_0$ ) varieties and a single cross ( $F_1$  of the two homozygous strains A 441-5 and A 272) were included in each block as well. The 31 strains within each replication were allotted positions at random (total no. of plots was 1240). Table 1 shows the mean yields per plot of the twenty strains replicated twice for each variety for the different inbreeding coefficients.

Table 1. Mean yields per plot in lbs.

F	Variety				
	Sahara	Teko	Anveld	Am. W. F.	Robyn
0	10.7	8.2	8.1	7.6	7.2
0.125	8.5	8.5	6.1	7.0	7.4
0.25	7.3	7.9	6.6	5.7	6.5
0.375	3.9	5.1	3.3	3.3	5.9
0.50	3.5	4.0	2.2	2.7	3.9
0.75	2.5	3.1	1.4	2.0	4.0

It appears that yield is not exactly proportional to 1-F or the amount of heterozygosis. Four of the varieties show very slight decline in yield until F is 0.25. Then in all five varieties there is a quick decrease in yield until F is 0.50 followed by a slow decrease beyond that.

Variability of yield totals of the twenty strains for each variety and all varieties combined is shown in Tables 2 and 3.

Table 2. Coefficient of variability of strain yields.

F	Variety					Comb. vars.
	Sah.	Teko	Anv.	AWF.	Rob.	
0	9.1	12.4	8.0	9.5	13.5	22.0
.125	18.7	24.3	23.6	15.2	19.9	19.7
.25	19.2	19.2	22.0	16.2	13.5	39.6
.375	41.8	29.0	29.9	38.8	38.6	37.0
.50	42.9	23.0	32.7	38.0	38.3	55.0
.75	72.7	30.3	42.9	58.8	42.1	

Variability estimates at F = 0 represent variability between different random samples taken from a variety plus between block differences. Variability is expressed in terms of coefficient of variability. Variability in four of the varieties shows an irregular but distinctly upward trend with increase in F while the fifth variety, Teko, shows this trend to a slight degree only. Variability between strains was also determined in terms of variance as presented in Table 3.

Table 3. Variances of total strain yields.

F	Variety					Comb. var.
	Sah.	Teko	Anv.	AWF	Rob.	
0	3.80	4.12	1.67	2.06	3.81	10.9
.125	10.10	16.90	8.28	4.51	8.68	7.2
.25	15.47	9.24	8.44	3.32	3.12	11.9
.375	10.65	8.94	3.99	6.78	21.12	5.8
.50	8.79	3.37	2.08	4.36	8.73	8.2
.75		2.53	1.45	5.52	11.39	

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There appears to be no consistent change in variance as  $F$  increases beyond 0.125. Teko and Anveld show some decline while Sahara and Robyn show a slight increase with increasing  $F$ .

Both estimates of variability are subject to certain biases when used for the material concerned. The upward trend shown in Table 2 could be explained in part by the downward trend of the means in Table 1 since the mean is inversely proportional to the coefficient of variability. Van Schaik (Proc. I Cong. S. A. Genet. Soc. 1:66) obtained an overall correlation coefficient of  $-.69$  between coefficient of variability and mean yield for a number of nonsegregating inbred and  $F_1$  strains chosen in such a way that the whole yield range was represented as well as possible. Re-examination of this data gave a highly significant overall positive correlation of  $.51$  between variance and yield. If the factors responsible for this relationship were operative also in the material presented in this paper, which seems likely, a downward trend would be expected in Table 3 unless other factors interfere.

In conclusion it would seem that the truth must be found somewhere between the trends shown in Tables 2 and 3. This would mean that the data indicate an increase in variability between strains with inbreeding. No exact quantitative estimate of this increase can be given, however.

It is interesting to note the contrasting behaviour of the varieties Teko and Sahara. While the former showed hardly any inbreeding effect until  $F = .25$ , the Sahara strains on the average had lost about a third of the yield capacity of the open pollinated variety at this stage of inbreeding. In Table 2 Teko shows little if any increase in variability between strains with inbreeding beyond  $F = 0.125$  while Sahara shows a steep incline in variability. In Table 3 Teko again behaves exceptionally in that it indicates a slight decrease in between strains variance as  $F$  increases from 0.125. Sahara shows a gradual but fairly regular upward trend. It would appear, therefore, that Teko in contrast to Sahara and the other varieties does not show some of the typical effects of inbreeding. This characteristic could be explained by assuming that Teko is more homozygous than the other varieties. As reported in last year's newsletter there was little difference between the number of visible seedling abnormalities segregating from nonselected self-pollinated ears of the two varieties, so this would seem not to be the case. Indeed with continued inbreeding, Teko does lose its vigour to almost the same extent as the other varieties. It also shows more variability from  $F = 0$  to  $F = 0.125$  than the other varieties.

Another prominent feature of the data is the distinct and consistent peaks at  $F = 0.125$  and  $0.375$  in the variability data. No satisfactory explanation can be offered for this phenomenon. Graphs showing the effect of inbreeding on yield were straightened out by the method of least squares and new coefficients of variability were determined but the characteristic peaks remained approximately the same indicating that they have no relation with the irregularities in inbreeding depression.

The surprisingly gradual yield decline at early stages of inbreeding of some varieties is of practical importance. Many inbred strains (up to  $F = 0.375$ ) yielded considerably more than the parental open pollinated variety within the same block. These observations have renewed interest in the possibility of selecting for yield during mild inbreeding.

-- T. van Schaik  
-- M. M. P. Geerthsen  
Dept. of Genetics

#### 6. Maize uniformity trials.

A series of uniformity trials was carried out on the experimental farm of the University of Pretoria to determine the minimum plot size and shape for lattice experiments for the testing of lines in

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the hybrid maize breeding program. It was found that a plot of about 14 square yards gave a coefficient of variation of about 10%. An increase in the size gave no reduction in the coefficient of variation while smaller plots showed a considerably increased C.V. The shape of the plots had no material effect on the coefficient of variation. Thus, under these circumstances where the plants were spaced 3 ft. x 2 ft., one plant per hill, and where the commercial maize variety "Improved Potchefstroom Pearl" was used, a plot of about 14 sq. yds. was found the most efficient size and nothing was gained by using larger plots.

-- J. J. Human  
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1. Linkage studies on chromosome 5 with special reference to ae.

a. v<sub>3</sub> - ae - pr linkage

Five ears of the genotype  $\frac{+ ae +}{v_3 + pr}$  were self-pollinated with the following results:

+++	+ ae +	v <sub>3</sub> ++	v <sub>3</sub> ae +	++ pr	+ ae pr	v <sub>3</sub> + pr	v <sub>3</sub> ae pr
544	290	155	12	175	5	124	0

colorless			
++	v <sub>3</sub> +	ae +	ae v <sub>3</sub>
290	112	102	5

Recombination %

v<sub>3</sub>-ae 22 ± 0.02 (colored or colorless)

ae-pr 14 ± 0.03

v<sub>3</sub>-pr 34 ± 0.02

The gene order is v<sub>3</sub> - ae - pr. The data indicate the map positions to be

10	32	46
<u>v<sub>3</sub></u>	<u>ae</u>	<u>pr</u>

b. bv - ae - pr linkage.

Six ears of the genotype  $\frac{+ ae +}{bv + pr}$  were self-pollinated with the following results:

+++	+ ae +	bv ++	bv ae +	++ pr	+ ae pr	bv + pr	bv ae pr
269	123	41	7	39	4	121	2

colorless			
++	+ ae	bv +	bv ae
394	165	170	11

Recombination %

bv - ae 25 (colored + colorless)

ae - pr 20

bv - pr 16

In general, these data agree with the  $v_3 - \underline{ae} - \underline{pr}$  data presented above. There seems to be a high frequency of associated crossovers in these data. It appears that whenever a cross over occurs between  $\underline{bv}$  and  $\underline{ae}$  there tends also to be one between  $\underline{ae}$  and  $\underline{pr}$ . This would result in a reduced recombination percentage between  $\underline{bv}$  and  $\underline{pr}$  as is shown by the 16% recombination.

These data indicate (1) an increase in the total number of double crossovers, as well as (2) an increase in the number of two-strand double crossovers.

c.  $\underline{bm}_1 - \underline{ae} - \underline{pr}$  linkages.

A cross of  $\frac{+ \underline{ae} +}{\underline{bm}_1 + \underline{pr}} \times \frac{\underline{bm}_1 \underline{ae} \underline{pr}}{\underline{bm}_1 \underline{ae} \underline{pr}}$  gave the following results:

+++	+ ae +	++ pr	+ ae pr	bm ++	bm ae +	bm + pr	bm ae pr
1	124	27	11	16	10	141	3

Recombination %

$\underline{bm}_1 - \underline{ae}$	12.3
$\underline{ae} - \underline{pr}$	9.3
$\underline{bm}_1 - \underline{pr}$	19.2

Individual Gene Segregation

$\underline{Ae}$ 185:	$\underline{ae}$ 148*
$\underline{Bm}_1$ 163:	$\underline{bm}_1$ 170
$\underline{Pr}$ 151:	$\underline{pr}$ 182

\* Significant deviation from 1:1 ratio.

These recombination values appear to be normal in that the  $\underline{bm}_1 - \underline{pr}$  recombination is what one expects from the  $\underline{bm}_1 - \underline{ae}$ ,  $\underline{ae} - \underline{pr}$  recombination observed. However, two things are aberrant in these data: (1) the recombination values are smaller than expected when they are compared with the  $v_3 - \underline{ae} - \underline{pr}$  and  $\underline{bv} - \underline{ae} - \underline{pr}$  data presented above, and (2) the  $\underline{Ae}$  vs  $\underline{ae}$  segregation deviates from a 1:1 ratio.

These data indicate differential transmission of the  $\underline{ae}$  and  $\underline{Ae}$  alleles through the female. A comparison of the reciprocal crossover classes supports differential transmission rather than misclassification of  $\underline{ae}$ .

Differential transmission would reduce the measurable recombination between the genes and could account for the observed differences between these recombination values and those mentioned above for  $v_3 - \underline{ae} - \underline{pr}$  and  $\underline{bv} - \underline{ae} - \underline{pr}$ .

-- J. N. Jenkins

2. A new locus for studying the fine structure of the gene.

A method for studying the fine structure of the  $\underline{ae}$  locus has been developed. By overstaining with an excess of iodine and destaining with 25% alcohol and slight heating, one is able to differentiate  $\underline{wx} \underline{ae}$  from  $\underline{wx} +$  pollen. The  $\underline{wx} \underline{ae}$  pollen stains black and the  $\underline{wx} +$  pollen stains red. This technique allows a study of recombination at the  $\underline{ae}$  locus in a  $\underline{wx}$  background when different sources of  $\underline{ae}$  are crossed and the  $F_1$  pollen is observed.

-- Roy G. Creech



### 3. Effect of $su_2$ on $sh_2$ .

When  $Sh_2 sh_2$  is segregating in ears homozygous for  $su_2 su_2$ , the highly collapsed phenotype typical of  $sh_2 sh_2$  is not obtained. The doubly recessive  $su_2 su_2 sh_2 sh_2$  kernels are similar to  $su^{am} su^{am} du du$  kernels in phenotype. This reaction is similar to the effect of  $ae$  on  $su_1$ .

-- Herbert H. Kramer

### 4. A new "salmon silk."

A salmon silk character which shows good expression in the absence of red pericarp has appeared in progeny from U. V. treated pollen. If allelic to  $sm$ , linkage studies on chromosome 6 should be facilitated.

-- Herbert H. Kramer

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### 1. The $Wx/wx$ locus.

#### A. Segregation in backcross progenies

The frequency of  $\pm^{Wx}$  pollen grains in plants of a backcross progeny  $(90 \times C) \times C$  has been investigated with greater numbers than previously. At the same time the  $F_1$  was grown as a standard. The mean frequency of  $\pm^{Wx}$  pollen grains in the  $F_1$  plants sampled was  $74 \times 10^{-5}$  with the individual plant estimates being 73; 68; 80; 89; 66; 69; 80; 82; 89; 77; 74; 58; 67; 86; 59. These represent single estimates from each of 15 plants. In 1958 the mean frequency of  $\pm^{Wx}$  pollen grains from the same cross was  $88 \times 10^{-5}$ .

Sixty plants from the BC progeny were sampled. Of these 34 plants had a  $\pm^{Wx}$  frequency of less than  $2 \times 10^{-5}$  (or 0 after correction for parental  $\pm^{Wx}$  frequency). For the remaining 26 plants the mean frequency of  $\pm^{Wx}$  was  $89 \times 10^{-5}$  with the individual plant estimates being 98; 103; 75; 65; 107; 138 (125, 151); 57; 93; 87; 65 (51, 78); 89; 63; 74; 108; 87; 75; 63; 103; 115; 92; 68; 99; 114; 138 (143, 132); 70; 78. These figures represent single estimates for each plant with the exception of three which are an average of the estimates enclosed in parentheses. Some of the frequencies estimated for BC plants appear obviously to be outside the range of estimates for the  $F_1$  plants and may represent an effect of genetic background on this recombinational process.

Another backcross progeny  $(C \times H21) \times C$  has also been sampled. Here there were 37 plants of which 18 had a  $\pm^{Wx}$  frequency of less than  $2 \times 10^{-5}$  while 19 plants had high frequencies.

The relative proportions of zero frequency (after correction for parental frequency) plants to high frequency plants in the two backcross progenies are not in disagreement with the ratio of 1 zero frequency plant:1 high frequency plant expected if heterozygosity at the waxy locus were a prerequisite for the production of a high frequency of  $\pm^{Wx}$  pollen grains.

B. Investigation of intragenic recombination by conventional techniques.

With the realization that an  $F_1$  plant of a cross between two independently occurring waxy mutants could have a frequency of  $+^{wx}$  pollen grains averaging  $88 \times 10^{-5}$ , it becomes possible to study recombination in such a high frequency  $F_1$  by seed classification.

The highest frequency  $F_1$  is  $90 \times C$ . The C stock (for Cornell), which was obtained from the Maize Coop in 1951, is marked on only one side as  $c \ sh \ wx^C$ . However, a stock from E. H. Coe which is  $sh \ bz \ wx \ v_1$  behaves in crosses as does  $wxC$  with respect to frequency of  $\pm^{wx}$  pollen in  $F_1$  crosses with other mutants. The allele from Coe's stock and  $wxC$  are probably the same, but for the record it will be referred to as  $wxCoe$ .

The  $F_1$  between  $90$  and  $sh \ bz \ wx^{Coe} \ v_1$  gives a mean frequency of  $90 \ +^{wx} \times 10^{-5}$  pollen grains. An estimated population of  $1.4 \times 10^6$  pollen grains from 26 plants was scanned. These 26 (+ other)  $F_1$  plants were pollinated by  $bz \ wx^{Coe} \ v_1$  pollen, and pollen from them was put on  $bz \ wx^{Coe} \ v_1$  plants. The results are given in Table 1. It is clear that there is a significant difference in the frequency of  $+^{wx}$  kernels between the reciprocal crosses. While the  $+^{wx}$  frequency where the  $F_1$  was the female is in the range which might be expected from the pollen studies (.072% from a relatively small sample of kernels as compared to .090% from the pollen), there is a greatly reduced frequency when the pollination is made in the other direction.

Table 1. Backcrosses of  $(wx^{90} \times wx^{Coe})$  with  $wxCoe$ .

Cross	No. Ears	No. Kernels	No. $+^{wx} k$	% $+^{wx} k$
$\frac{+ \ wx^{90}}{bz \ wx^{Coe} \ v_1} \times \frac{+}{bz \ wx^{Coe} \ v_1}$	68	23591	17	.072
$\frac{+ \ wx^{90}}{bz \ wx^{Coe} \ v_1} \times \frac{+}{bz \ wx^{Coe} \ v_1}$	309	61004	12	.019

Two possibilities suggest themselves as explanations of this reciprocal difference. The first is that some of the pollen grains which are scored as  $+^{wx}$  are not carrying fully functional  $+^{wx}$  alleles but intermediate alleles. In the case of such alleles, gene dosage could be the critical factor in determining whether or not we detect the kernel carrying the recombinant. Some support is given to this idea by the observation that using our standard stain pollen grains from a mutant which gives 5% amylose in the endosperm stain as normals. In any case, it will be relatively simple to determine by chemical analyses of the stocks arising from the  $+^{wx}$  kernels if intermediacy constitutes the basis for the reciprocal differences observed.

A second possibility is that the  $bz \ wx^{Coe} \ v_1$  stock is carrying a gametophyte factor. Then, it may be assumed that the event or events resulting in the formation of the  $+^{wx}$  locus in the  $F_1$  plant usually place this locus in a chromosome not carrying the gametophyte factor. Such gametes will be at a disadvantage in effecting fertilization on the  $bz \ wx^{Coe} \ v_1$  when competing with others carrying the gametophyte factor and this would reduce the frequency of  $+^{wx}$  kernels when the  $F_1$  is used as the male but not as the female parent. We know, however, that in the cross  $\frac{bz \ wx^{Coe} \ v_1 \times + \ wx^{90}}{bz \ wx^{Coe} \ v_1}$  there are no deficiencies of  $bz$  kernels. We are testing now for  $v_1$  so that the possibility of a gametophyte factor can be either excluded or explored further.

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This is the second year in which a reciprocal difference has been found. In 1958, we used the  $F_1$ ,  $90 \times C$ , as both male and female parent in crosses with various  $wx$  stocks. When the cross was made ( $90 \times C$ )  $\times wx$  we found 4  $+wx$  kernels in a total of 4054 (.1%) kernels. For the reciprocal,  $wx \times (90 \times C)$ , there were 2  $+wx$  of 7724 total (.03%). But the numbers are small, and without markers contamination could not be excluded. Thus, it was not thought to be noteworthy until this year's data showed a similar effect.

Since outside markers  $bz$  and  $v_1$  were present in this year's test, it is of interest to note their assortment in the  $+wx$  kernels. There were a total of 29  $+wx$  kernels of which 27 germinated so that they could be scored for both markers. Of the 27, 12 were  $bz +v$ , 7  $bz v$ , 6  $+bz v$ , and 2  $+bz +v$ . The kernels in this last group may represent contaminants. The outside markers are so far from the  $wx$  locus that great reliance should not be put on the data. It seems, however, reasonable to conclude that not all  $+wx$  kernels arise from an orthodox recombinational event in one direction.

### C. Technique

In the past year, it has been found that the greatest possible differentiation between  $wx$  and  $+wx$  pollen grains is found when preparations are made using anthers from the less mature floret (which is distal to the tassel branch) at a time when the proximal or more mature floret is ready to extrude its anthers. Making pollen preparations in this manner will not change the estimate of  $+wx$  frequency, but the preparations are easier to score.

It has not been mentioned, but to work successfully with  $wx^a$  or crosses involving  $wx^a$  it is necessary to reduce the strength of the iodine from the 45 mg./25 ml of the standard stain to 31 mg./25 ml. and to allow somewhat more time for destaining to take place before scoring.

### D. Preliminary tests of nitrogen base analogues as mutagens on maize.

One of the problems in the  $Wx/wx$  locus work is the lack of a number of mutants induced in a common background. As part of the attack on this problem, we tested for mutagenicity an assortment of purine and pyrimidine analogues as well as a few other compounds which have been reported as having mutagenic activity. The advantage of such compounds (where they are effective mutagens) is their propensity to produce point mutations. Specifically with maize we would hope that some of these would be pre-meiotic in time of origin.

The base analogues tested were 2,6,8-trichloropurine; 2,6-di(diethyl-amino) purine; 2-thioxanthine; 5-bromodeoxyuridine; 2-thioadenine; 2-oxypurine; isoguanine; 2,6-diaminopurine; 6-methyl-2-oxypurine; 6-azathymine, 6-oxy-2,8-thiopurine; 2-amino-6-thiopurine; and 5-bromouracil. Acridine and proflavine were also tested. I am indebted to Dr. Seymour Benzer for supplies of the above chemicals.

All the compounds were tested by injecting a solution of the compound into wells bored into the stem of a plant at three-day intervals extending from a time judged to be premeiotic until the first pollen was shed. Multiple injections were made, therefore, into each plant. Because most of the compounds have limited solubilities in water, saturated aqueous solutions were generally used. Even with the wells bored into the plants only .25 to .5 ml could be injected at one time. On each injection day after allowing time for uptake, a second injection was made. There was no effect on growth nor delay in flowering with any compound used.

The treated line was the dent inbred M14 ( $+bz +wx +v_1$ ). Pollinations were made onto a recessive tester stock,  $bz wx v_1$ , and the ears scored for  $bz$  or  $wx$  kernels (kernels which were both  $bz$  and  $wx$  were considered to be the result of accidental self-pollination) and for  $bz$ ,  $wx$

or bz wx sectors. Between 3,000 and 6,500 gametes were sampled per treatment. The sum of apparent gametic mutations plus sectors for most compounds ranged from .03% to .09%. One compound, 2-amino-6-thiopurine, did not produce any mutations nor sectors in 3074 kernels. Two compounds, proflavine and 2-thioadenine, were apparently more effective than the other substances since the sum of mutants plus sectors was .29% for 2-thioadenine (2779 kernels) and .20% for proflavine (4645 kernels). For 5-bromouracil, only 1 pollination was obtained owing to breakage of the injected plant. One apparent mutation to wx was found in 474 kernels. All the mutant kernels are being grown to ascertain whether the embryos are homozygous or heterozygous for bz or wx as the case may be.

Pollen of untreated M14 plants was irradiated for 4 and 6 minutes under an ultraviolet lamp. The sum for the 4-minute treatment was .9%, and for the 6-minute treatment it was 1.1%.

#### E. Attempts to affect inter- and intragenic recombination differentially.

It is still a question as to whether intergenic and intragenic recombination have the same physical basis. If a stimulus could affect markedly one type but not the other, it would suggest a different basis for the two types. Roman has shown in yeast that ultra-violet radiation can greatly increase intragenic recombination without apparently affecting intergenic recombination. We have attempted to do the converse in maize (i. e., use agents which have been reported to increase intergenic recombination and then look for an effect on intragenic recombination). The material used here was the  $F_1$   $\frac{+ + wx^{90}}{sh\ bz\ wx^{Coe}\ v_1}$  which has already been reported on in other con-

nections. Two plants were injected as described for the base analogues with .001 M Versene ( $Na_2$ ) every two days from a premeiotic stage until pollen shed. The usual pollen collections were made, and pollinations were made onto the sh bz wx<sup>Coe</sup> v<sub>1</sub> stock. The frequency of +wx pollen grains in the treated plants was not different from the frequency in control plants. Nor could any increase in the frequency of recombination between sh and bz over the controls be detected in the pollinations made from the treated plants. The same negative results were garnered from 4 plants which were sprayed with .2 M  $MnSO_4$  every five days from the time that they were 10 inches high until the emergence of tassels from the boot.

With the apparent inability of these agents to affect either type of recombination under the conditions of our test, it was not possible to obtain the information originally desired.

-- Oliver E. Nelson

#### 2. The fourth chromosome gametophyte factor in some Central and South American races.

As has been pointed out previously, knowledge of the allelic constitution of a variety for the fourth chromosome gametophyte factor, ga/Ga/Ga<sup>s</sup>, can be an aid in tracing the evolutionary history of that variety. This is so because male gametophytes carrying Ga and Ga<sup>s</sup> exclude or nearly exclude male gametophytes carrying ga when both types are competing to effect fertilization in plants which are ga/Ga, ga/Ga<sup>s</sup>, Ga/Ga<sup>s</sup>, Ga/Ga, or Ga<sup>s</sup>/Ga<sup>s</sup>. The competitive advantage of Ga<sup>s</sup> or Ga alleles over ga in such situations is close to 1. On the other hand, there is no advantage of ga gametophytes over Ga or Ga<sup>s</sup> gametophytes on ga/ga plants. When either Ga or Ga<sup>s</sup> is introduced into a stock by introgressive hybridization or mutation and becomes established, its frequency must increase rapidly until it is equal to 1. It is not possible to derive a variety which is ga/ga from a cross between two other varieties one of which is Ga or Ga<sup>s</sup>. All United States varieties which we have tested here have been ga/ga (except for Papago Indian Corn which is Ga/Ga). This includes southern whites, northern flints, and middle western dents.

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Through the kindness of Dr. E. J. Wellhausen and Dr. Robert Osler of the Rockefeller Foundation in Mexico and Dr. David Timothy of the Rockefeller Foundation in Colombia, we were able to assemble a number of Central and South American races of maize for tests of their constitution with reference to the 4th chromosome gametophyte factor. The details of the test are as follows: all possible plants of the variety under test were pollinated by a ga/ga stock while pollen from each of 4 plants of the variety was used to pollinate 2 plants of a Ga<sup>s</sup>/Ga<sup>s</sup> stock. Three types of results were found: plants of a particular variety did not set seed with ga pollen but were capable of inducing seed set on Ga<sup>s</sup> plants (variety is Ga<sup>s</sup>); plants of the variety set seed with ga pollen and could induce seed set on Ga<sup>s</sup> plants (variety is Ga); plants of the variety set seed with ga pollen but did not induce seed set on Ga<sup>s</sup> plants (variety is ga). If, as is often the case with introduced varieties, it was not possible to obtain ears on the variety and the variety could be scored only for ability to induce seed set in the Ga<sup>s</sup>/Ga<sup>s</sup> stock, it could not be determined whether a variety is Ga or Ga<sup>s</sup> if it was able to fertilize Ga<sup>s</sup>/Ga<sup>s</sup> plants.

Table 2. Tests of Central and South American Varieties for 4th Chromosome Gametophyte Factors

Variety	x ga	on Ga <sup>s</sup>	Probable Allele
Arrocillo Amarillo . . . . .	N.P.	Intermediate (.25-.9 of normal seed set)	?
Nal-Tel . . . . .	N.P.	+	Ga <sup>s</sup> or Ga
Palmero Toluqueño . . . . .	+	0	ga
Harinoso de Ocho . . . . .	+	0	ga
Cacahuacintle . . . . .	+	+	Ga
Reventador . . . . .	0	+	Ga <sup>s</sup>
Maiz Dulce . . . . .	0	+	Ga <sup>s</sup>
Chapalote . . . . .	N.P.	+	Ga <sup>s</sup> or Ga
Olotillo . . . . .	N.P.	+	Ga <sup>s</sup> or Ga
Zapalote Grande . . . . .	+	+	Ga
Zapalote Chico . . . . .	+	+	Ga
Guat. 211H (Nal-Tel, 3300 <sup>1</sup> ) . . . . .	0	+	Ga <sup>s</sup>
Guat. 229H (Nal-Tel, 6700 <sup>1</sup> ) . . . . .	+	+	Ga
Guat. 230H (Nal-Tel, 6700 <sup>1</sup> ) . . . . .	+	0	ga
Guat. 232H (Nal-Tel, 6,600 <sup>1</sup> ) . . . . .	+	0	ga
Guat. 41H (Chimbo, 8,000 <sup>1</sup> ) . . . . .	N.P.	0	ga
Guat. 75H (Quicheño, 9400 <sup>1</sup> ) . . . . .	N.P.	0	Ga <sup>s</sup> or Ga
Guat. 76H (9400 <sup>1</sup> ) . . . . .	N.P.	+	Both ga & Ga <sup>s</sup>
Guat. 78H (8800 <sup>1</sup> ) . . . . .	N.P.	+, 0	Ga
Guat. 122H . . . . .	+	+	Ga <sup>s</sup>
Guat. 139H (3,200 <sup>1</sup> ) . . . . .	0	+	Ga <sup>s</sup> or Ga
Guat. 159H (Nal-Tel, Tropical) . . . . .	N.P.	+	Ga <sup>s</sup> or Ga
Guat. 188H (Koc-Jal) . . . . .	N.P.	+	Ga <sup>s</sup>
Costa Rica 227 . . . . .	0	+	Ga <sup>s</sup>
Costa Rica 379 . . . . .	0	+	Ga <sup>s</sup> or Ga
Costeño Amarillo . . . . .	N.P.	+	Ga <sup>s</sup> or Ga
Costeño Blanco . . . . .	N.P.	+	ga & Ga
Nariño 330-°-xa-° . . . . .	N.P.	+, +, 0, 0	ga
Peru 330-L-°-° . . . . .	N.P.	0	Both Ga & ga
Eto-°-° . . . . .	+	+, +, 0, 0	Ga <sup>s</sup> or Ga
Nariño-330-°-°b-L-°-° . . . . .	N.P.	+, +, +	Ga <sup>s</sup> or Ga
Venezuela 305-°-°-° . . . . .	N.P.	+, +, +, 0	Ga <sup>s</sup> or Ga
Bolita . . . . .	N.P.	(1 plant)	Ga <sup>s</sup> or Ga

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Variety	x ga	on Ga <sup>s</sup>	Probable Allele
Maiz pisankalla . . . . .	0	+	Ga <sup>s</sup>
Pollo amarillo . . . . .	N.P.	0	ga
Pollo blanco . . . . .	N.P.	0	ga
Pira blanco . . . . .	N.P.	0 (but late and poll on tillers)	ga

N.P. = No Pollinations  
 0 = No Seed Set  
 + = Full Seed Set

The results of our tests are summarized in Table 2. For most varieties tested, the results were homogeneous. This is not so, however, for the Guatemalan variety 78H, nor for the South American varieties Nariño 330, Eto, and Venezuela 305. In all these varieties there were both plants identified as Ga<sup>s</sup> (or Ga) and plants identified as ga. Such a situation could result from recent introgression of a Ga<sup>s</sup> variety into a ga variety or the recent establishment of a synthetic variety from varieties one or more of which are Ga<sup>s</sup> (or Ga) and the others ga. In this connection, it should be noted that heterozygotes Ga<sup>s</sup>/ga or Ga/ga can fertilize Ga<sup>s</sup>/Ga<sup>s</sup> plants and hence are scored as Ga<sup>s</sup> or Ga plants. Some of the varieties tested here in 1959 previously have been tested as accessions from other sources. Chapalote and Zapalote Chico from Anderson and Brown's Standard Exotic Collection in tests in 1953 were found to be Ga<sup>s</sup> and Ga respectively. Maiz pisankalla was also previously identified as Ga<sup>s</sup>. Reference to Table 2 show that those races again were similarly identified.

The results of the tests are particularly interesting in several ways. In the first place, the collections of Palmero Toluqueño and Harinoso de Ocho which we tested are clearly ga/ga. Palmero Toluqueño, a popcorn, is classified by Wellhausen et al as an Ancient Indigenous race and Harinoso de Ocho as a Pre-Columbian Exotic race. The considerations already presented as to the great selective advantage of the Ga and Ga<sup>s</sup> alleles plus the knowledge that United States varieties tested are ga/ga demand the existence of primitive races which are ga/ga. It is reassuring to find that they do exist together with the Ancient Indigenous races (Chapalote and Nal-Tel) which are Ga<sup>s</sup>. Secondly, all the other more complex Mexican races tested are either Ga or Ga<sup>s</sup>.

With regard to the Guatemalan collections, several identified as Nal-Tel give divergent results in tests for the Ga factors. All that can be inferred here is that if these actually represent one line of descent the ga races are the original types and the Ga<sup>s</sup> races the result of introgression into them of another race which is Ga<sup>s</sup>. There is a suggestion in the data for these Guatemalan races that the majority of high altitude races may be ga in contrast to the tropical races, but the sample is too small to place much reliance on it.

-- Oliver E. Nelson

SCOTTISH HORTICULTURAL RESEARCH INSTITUTE  
 By Dundee, Scotland

1. Adaptation and problems of growing sweet corn in Scotland.

For the first time trials have been conducted with four varieties of sweet corn that I had shown to be the best in English conditions. The main differences in growing sweet corn in Scotland rather than

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England are that there is a long summer day in Scotland and that owing to the cooler temperature growth is slower; at the same time sowings have to be made later than in England in order to have the soil reasonably warm, either for germinating seedlings or for establishing young plants put out in soil plots. However, in 1959 (which was an exceptionally good year for Scotland) we had a very good harvest of Canada Cross (=Canada Gold x Singleton's C. 13) and North Star (Joseph Harris Inc.) and somewhat later Northern Cross (Joseph Harris Inc.). The first two varieties gave very nice crops. The difficulty which we had not expected was that there were quite heavy attacks by frit fly (*Oscinella frit*). Several growers in Perthshire are growing sweet corn in walled gardens, mostly using the Canada Cross, but their main difficulty seems to be devastation from frit fly. Considering that the plants are being grown in a latitude of 56°N., it is surprising how adaptable maize can be providing the right germplasm is selected: thus, Canada Gold, North Star and Northern Cross all carry Extra Early Bantam in their ancestry, i.e. flint derivatives. Two varieties are thus adaptable 14° North of their seed origin.

-- Gordon Haskell

SERVICE DE LA RECHERCHE AGRONOMIQUE  
ET DE L'ENSEIGNEMENT  
Rabat, Morocco

1. A hereditary case of abortion of the corn embryo.

In a Moroccan selfed line, MR 077, grains with aborted embryos or affected by partial necrosis are observed every year on all the harvested ears in variable numbers. The healthy grains proceeding from selfing, as well as the few partly necrotic grains that germinate again transmit this character in the same way. The proportion of affected grains (with regard to the total number of grains of the ear) varies from 15 to 90 per cent.

From a morphological point of view this character shows numerous gradations and all the intermediaries exist between grains with completely desiccated embryo and healthy grains. The least affected grains show a faint, more or less greyish withering on the periphery of the embryo. In most cases the endosperm appears normal.

Hybridizations between line MR 077 and other lines have allowed the following observations:

1. - Cross-pollination does not prevent the appearance of this character on the ear of line MR 077. Consequently there exist hybrid grains with aborted embryos. Mixed pollinations (Selfing + Hybridization) have shown that the proportion of affected hybrid grains could be equal or inferior (according to the pollen lines) to the proportion of affected grains from selfing.
2. - Reciprocal crossing does not produce grains with aborted embryos on the ears of the lines that were pollinated by MR 077.
3. - On ears of selfed F<sub>1</sub> plants in all cases grains with aborted embryos are observed, but at much lower rates than on ears of the line 077. These percentages of affected grains are more or less important according to the crossed lines (see table below). Hitherto no difference has been observed in these percentages, between reciprocal hybrids.

Hybrid	Number of selfed F <sub>1</sub> plants	Average percentages of affected grains
089 x 077	11	0.46
077 x 359	9	2.48
359 x 077	9	2.50
535 x 077	22	4.63
077 x 520	19	3.50
077 x 368	20	0.38
077 x 686	26	4.68

4. - The study of segregating progenies obtained from F<sub>1</sub> plants by selfing or back-crossing has not revealed any Mendelian disjunction. The rates of necrotic grains on the ears vary in a continuous manner from 0 to 70%.

The study of the distribution of the affected grains on selfed ears of line MR 077 shows that these grains are much more numerous on the basal part or the middle of the ear than on the terminal part. The greatest number of healthy grains is to be found towards the apex of the ear.

Investigations are being continued but at present it would seem that this hereditary "disease" of the embryo may be ascribed to a non-Mendelian "factor", free with regard to the chromosomes, and transmittable by the female gamete and by the male gamete.

-- A. Cornu

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Syracuse, New York

1. Atypical variegated phenotype arising from orange variegated pericarp maize.

Preliminary tests of a very light variegated phenotype, which originated as a somatic mutation on an orange medium variegated ear ( $\underline{p}^{\text{ovov-2}}/\underline{p}^{\text{ww}}$ ), demonstrate that this mutant is not a typical variegated, but rather represents a new phenotype not previously described. This mutant phenotype is due to a P allele and, in heterozygotes with  $\underline{p}^{\text{ww}}$ , exhibits a low frequency of colored stripes in an otherwise colorless pericarp and cob, comparable to very light variegated (Brink 1954). It differs from very light variegated, however, in that the stripes are not a homogeneous red but are sectors of orange variegated phenotype typical of  $\underline{p}^{\text{ovov-2}}$ . This difference is not apparent in most ears because the mutant sectors are usually very narrow. In occasional sectors extending over one-half or more of the abgerminal side of the kernel and one sector that included two entire kernels and a part of a third, the orange variegated phenotype is obvious.

The progenies obtained in large families of this mutant allele are summarized in Table 1. The parent ears, from plants heterozygous for the atypical variegated allele and  $\underline{p}^{\text{ww}}$ , had been backcrossed to the recurrent inbred parent, 4Co63, ( $\underline{p}^{\text{ww}}/\underline{p}^{\text{ww}}$ ), so that one-half of the progeny would be expected to be like the parent plant and one-half, homozygous  $\underline{p}^{\text{ww}}$  (colorless pericarp and cob). Table 2 summarizes the classes of progenies obtained from orange medium variegated ears ( $\underline{p}^{\text{ovov-2}}/\underline{p}^{\text{ww}}$ ) backcrossed to 4Co63.



Table 1

Family number	Parent ear phenotype	Number of progeny					Total
		Colored pericarp and cob				Colorless	
		Lt V	Very lt V	Or med V <sup>1</sup>	Total		
8-47A	Very lt V	1	119		120	134	254
8-47B	Very lt V	1	87	1	89	103	192
Total		2	206	1	209	237	446

<sup>1</sup> Or = orange

Table 2

Family number	Parent ear phenotype	Number of progeny				Total	Colorless	Total
		Colored pericarp and cob						
		Or med V	Or lt V	Red				
8-585	Or med V	51	5	3	59	54	113	
8-847	Or med V	77	2	8	87	84	171	
8-47C	Or med V	90	16	16	122	109	231	
Total		218	23	27	268	247	515	

It should be noted that the atypical very light variegated allele is very stable, with only 3 out of 209 colored progeny (1.4%) differing from the parent phenotype. The one orange medium variegated ear in this group was unexpected and appeared typical of povov-2. The distribution of progenies of the orange medium variegated ears is similar to that obtained from other orange variegateds, with a low frequency of orange light variegateds and a slightly higher frequency of self reds. The higher frequency of colorless progeny in the atypical variegated families (53.1%) than in the orange variegated families (48.0%) may be due to the occurrence of subliminal variegateds which would be classified as colorless.

Tests were conducted to determine whether there was a difference in the time and frequency of Ds-type chromosome breakages induced by these alleles. An Mp-tester stock (McClintock's homozygous A; C Ds; R and lacking Ac) was used as the male parent in crosses with heterozygous atypical variegated/pww and povov-2/pww plants (both homozygous A; c; r). The resulting kernels on the orange medium variegated ears were easily scored and approximated the expected 1 colored (no Ds events) to 1 colored with colorless sectors (Ds events). Only a few kernels on each of several of the atypical variegated ears, however, could be positively classified as colored with colorless sectors. The remainder appeared to be colored. The R-mottle due to the Rrr genotype of the aleurone was not pronounced in these crosses and did not interfere with the classification. Because of the difference in the two groups in this test, a further cross was made to compare the pattern of chromosome breakage at Ds induced by a single dose of the Modulators. Seed from these ears was planted and pollen from the resulting plants was placed on silks of inbred 4Co63 (homozygous A; c; r) and also used for self-pollinating each plant. The kernels produced on the 4Co63 ears were scored, and those from the atypical variegated cross as well as the orange variegated were found to approximate the expected classes: 75% colorless, 16% colored, and 9% colored with colorless sectors (due to independent assortment of Modulator, C Ds, and R loci and 26% crossing over between C and Ds). There was no obvious difference in the frequency of large colorless sectors representing chromosome breaks occurring

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early in the development of the endosperm. Kernels from the atypical variegated cross, however, exhibited a high frequency of very small colorless sectors (6 to 8 aleurone cells each) which was not found in the kernels from the orange medium variegated crosses.

The occurrence of the orange variegated phenotype as pericarp sectors and among the progeny of this mutant atypical very light variegated indicates that the Modulator component of  $\overline{povov}$ ,  $\overline{Mpa}$ , has not changed to a new state (mutant form). The loss of  $\overline{Mpa}$  from  $\overline{povov}$  which results in the orange variegated phenotype, however, is inhibited except for rare somatic and germinal changes which allow the normal expression of this unstable allele. This atypical variegated phenotype could most easily be explained by postulating a second transposable element as a component of this new mutant  $\overline{P}$  allele that suppresses  $\overline{povov}$  until it leaves the  $\overline{P}$  locus by transposition allowing the normal expression of  $\overline{povov}$ . The difference observed in the  $\overline{Ds}$ -type chromosome breakage pattern induced by the atypical very light variegated and by  $\overline{povov}$  could then be attributed to the action of this second element. The action of this second transposable element at  $\overline{P}$  would appear similar to that of the  $\overline{Mp}$  component of  $\overline{PvV}$  as postulated by Brink and Nilan (1952). In this new mutant allele, however, the action of  $\overline{Mpa}$  as well as  $\overline{prf}$  (i. e.  $\overline{povov}$ ) would be suppressed. The present tests do not provide direct evidence for such a second element. Additional tests now in progress may provide information which will clarify the nature of this atypical very light variegated allele.

-- F. A. Valentine

TENNESSEE AGRICULTURAL EXPERIMENT STATION  
and  
UNITED STATES DEPARTMENT OF AGRICULTURE  
Knoxville, Tennessee

1. Fertility restoration in Southern inbreds.

The fertility restoring inbred lines K55, Ky21, T115, Mp307, T210, T216, H-40B, Mp460, A14, E184 and A447 have been used in restored sterile hybrids in Tennessee. The last three are South African lines. All lines were crossed with A14Tcms and E184Tcms and advanced to F<sub>2</sub>. All crosses failed to segregate sterile plants indicating that the restoring factors in all lines are allelic and controlled by a single dominant gene. This fact was also demonstrated by F<sub>2</sub> crosses and backcrosses. It is assumed from the tests that all lines carry the two dominant complementary genes as demonstrated for Ky21 and K55 by other workers and which are lacking in WF9.

-- L. M. Josephson

2. Studies with 33-16 male-sterile cytoplasm.

F<sub>1</sub> hybrids of 33-16 as seed parent and CI.61, CI.43 and H21 have been completely fertile while those with K63, Mo2RF, Ky27, K64 and K6 have been only partially fertile. In backcrosses, plants segregate completely fertile, completely sterile, and into various degrees of partially fertile plants indicating that more than one genetic factor, or at least modifiers, as well as sterile cytoplasm is operating in determining sterility. Some crosses indicate only a single gene for partial fertility is operating while others indicate both a gene for complete fertility and one for partial fertility are operating. Further backcrosses to sterile plants have generally rendered the populations completely sterile. Inbred Ky27 has remained completely sterile through 13 generations of backcrossing. This source has in turn been transferred to several other inbreds and has remained stable.

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Of 18 inbreds which restore Texas sterile cytoplasm, only 9 restore 33-16 sterile cytoplasm. K55, K63, R6, K6, Ky122, E184, A325, E788 and K64 which are good restorers to Texas sterile cytoplasm do not restore 33-16 sterile cytoplasm. Ky39, A310, A328, Tx325, Cl.7 and Ky49 restore 33-16 sterile cytoplasm but have no effect on the Texas type.

Pollen fertility restoration was studied in six inbreds using Ky27 and K55 as sterile cytoplasm sources. The restoring abilities of 33-16, Ky21, A14, R7, Ky39 and R7 were inherited similarly in all crosses. Pooled progeny data for Ky21 and 33-16 are shown for different generations and years.

Generation	Year	Total Plants	Fertility Grades					Expected Ratio	P(.05)
			4	3	2	1	0		
F <sub>2</sub>	1957	60	<u>JcmsKy27xKy21</u>					15:1	.90
	1958	105	39	15	2	3	1	15:1	.37
BC(F <sub>1</sub> xKy27)	1957	113	8	17	30	1	57	1:1	.87
	1958	61	26	6	0	0	29	1:1	.80
	1959	69	18	14	0	3	34	1:1	.60
BC(JcmsKy27xF <sub>1</sub> )	1957	109	33	26	28	2	20	3:1	.28
	1958	44	12	19	10	0	3	3:1	.02
F <sub>2</sub>	1958	74	<u>JcmsKy27x33-16</u>					15:1	.08
	1959	640	53	18	2	1	0	15:1	.19
BC(F <sub>1</sub> xKy27)	1958	19	2	7	0	3	7	1:1	.90
	1959	542	82	166	35	43	216	1:1	.35
F <sub>2</sub>	1958	205	<u>JcmsK55x33-16</u>					15:1	.40
	1959-Ear 1	84	149	27	13	10	6	15:1	.46
	Ear 2	89	45	11	21	4	3	15:1	.56
	Ear 3	90	55	21	6	5	2	15:1	.28
	Ear 4	90	61	21	5	2	1	3:1	.19

The F<sub>1</sub> populations were all completely fertile. With the exception of progeny 4 with Jcms K55x33-16, individual ear progenies segregated similarly so only totals are shown. Grade 1 plants were considered sterile and grades 2 and 3 fertile in developing ratios. Although X<sup>2</sup> values are high, the F<sub>2</sub> data fit a two-gene hypothesis. Even though grade 2 would be considered sterile, there is still a poor fit for a 3:1 ratio. These segregations can be explained by postulating a major dominant gene plus a modifying gene which is necessary for complete fertility, but either one alone being capable of producing partial fertility. On this basis fully fertile and partially fertile plants should segregate in a ratio of 3:2. The segregations for Jcms Ky27xKy21 in 1958 and Jcms K55x33-16 in 1958 deviate from this ratio but all other segregations show good fits. The F<sub>1</sub> crosses pollinated by Ky27 give good fits to a single factor hypothesis. Apparently, if modifying genes are necessary, they do not produce fertility except in the presence of the major gene.

Reciprocal backcrosses were available for classification in the cross Jcms Ky27xKy21. The plants segregated more in line with expectation on the basis of the F<sub>2</sub> data; however, more plants segregated

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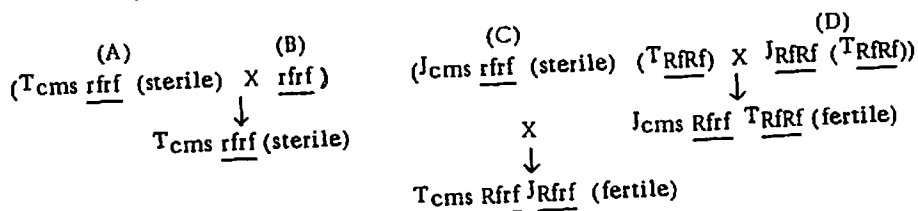
for partial fertility in 1958 than expected on the basis of two factors. Genes operating for partial fertility in F<sub>2</sub> would likewise be expected to operate in the backcrosses. Such is not the case. If the modifying gene is necessary for complete fertility half of the fertile plants in the backcrosses should be only partially fertile. In some populations a higher percentage of fully fertile plants was obtained, while in others more partially fertile plants were obtained.

Progeny tests should reveal whether genes for partial fertility can operate independently from the major gene. Differences in the two types of backcrosses indicate that Ky27 possibly possesses a modifying gene necessary for fertility that functions only when carried in sterile cytoplasm. The different results obtained in the two types of backcrosses suggests a gametic influence. If backcrosses are considered a more accurate determination of the genetic mechanism, then it must be assumed that an excess of fertile or partially fertile plants is expressed in the F<sub>2</sub> populations. This could be caused by differential competitive effects between Rf and rf pollen grains such that genotypes carrying rf genes are eliminated. This would also account for the excess number of fertile plants in the backcrosses made by pollinating the sterile inbred with fertile F<sub>1</sub> pollen.

-- L. M. Josephson

### 3. Hybrids without detasseling.

It is interesting to note that by utilizing both Texas and 33-16 type sterile cytoplasm it will be possible, without detasseling at any stage, to produce double crosses giving only fertile plants in the farmer's fields by the following method:



Texas sterile cytoplasm will be used to produce the seed parent single cross and 33-16 sterile cytoplasm to produce the male parent single cross. Inbred K55 can be utilized in the (C) position since it has been converted to 33-16 sterile cytoplasm and is a natural restorer of Texas sterile cytoplasm. Inbred K64 can be used in the (D) position since a selection which is a full restorer of Texas sterile cytoplasm has been obtained and it in turn is being converted to a restorer of 33-16 sterile cytoplasm. Other lines could similarly be converted.

-- L. M. Josephson

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Madison, Wisconsin

### 1. A presumed stippled-Navajo compound R allele.

A new R allele has been isolated giving an aleurone phenotype resembling the effects of both stippled (R<sup>st</sup>) and Navajo (R<sup>nj</sup>). Pigmentation is restricted mostly to the crown region of the kernel, as in Navajo, but occurs in spots rather than a solid patch, as in stippled. The limited evidence at present available suggests that (i) the new allele reflects the action of R<sup>st</sup> and R<sup>nj</sup> when present in the

same chromosome, (ii) in this relation,  $R^{nj}$  determines the area competent to form pigment and (iii) formation of pigment within this area is dependent upon the action of  $R^{st}$ . (In ordinary  $R^{st}/R^{nj}$  heterozygotes, and also in  $R^{st}/R^{nj}/r\bar{g}$  trisomics, however, the full action of both alleles is expressed. That is, the crown region is solidly colored, and the remainder of the aleurone is spotted).

The new phenotype appeared on the ear of one plant among 138 offspring from an  $R^{st}/R^{nj}/r\bar{g}$  ♀ x  $R^f/R^f$  ♂ mating. The remaining progeny were distributed among the six classes expected from such a trisomic ♀ x disomic ♂ cross. The plant in question was pollinated by  $r\bar{g}r\bar{g}$ . About 1/2 the resulting kernels were self-colored, as expected, and the rest (except 8) showed the new aleurone phenotype ( $R^{st:nj}$ ). Composition of the exceptional individual, therefore, was  $R^f/R^{st:nj}$ . Of 20 plants reared from  $R^{st:nj}/r\bar{g}$  seeds, and then pollinated by  $r\bar{g}r\bar{g}$ , 19 yielded  $R^{st:nj}$  and  $r\bar{g}$  kernels with about equal frequency, and 1 individual gave a 1:1 ratio for typical Navajo and colorless. Five of the 8 exceptional kernels on the original ear showed the Navajo phenotype, but the four plants obtained from these seeds bred as  $R^{st:nj}/r\bar{g}$  individuals. The other 3 exceptional kernels possessed comparatively few spots in the crown region. Progeny data suggest that they are probably the counterparts of "light stippled" which, as Ashman has shown, differs from stippled in a modifying factor normally situated about 6 crossover units distal to  $R$ , and widely distributed in non-stippled strains.

-- R. A. Brink

## 2. Enhancement of $R^f$ action associated with reciprocal translocation T2-10a, involving a break in chromosome 10 proximal to the $R$ locus.

The following report is supplementary to that presented by Dr. Margaret Blackwood and the writer last year (MGC News Letter 33, pages 120-121, 1959).

1. As earlier observed, T2-10a  $R^f$  ( $TR^f$ ) gametes from  $TR^f/R^f$  plants have a lower pigment producing potential, on the average, than  $TR^f$  gametes from  $TR^f/r^f$  sibs. Testcross kernels from  $r\bar{g}r\bar{g}$  ♀ x  $TR^f/R^f$  matings nevertheless tend to give bimodal distributions for aleurone pigmentation. It has now been shown that the darker kernels from the latter mating, when subsequently grown out, yield a preponderance of semisterile, whereas the light kernels give a pronounced excess of fully fertile plants.

2. The effects of T2-10a on  $R^f$  action have been retested using the offspring from the mating  $R_4^B/r^f$  x  $TR^f/r^f$ . The  $R_4^B$  allele is a mutant from standard  $R^f$ , indistinguishable from the latter in aleurone pigment-producing action and in paramutability in heterozygotes with stippled. Employment of the  $R_4^B$  allele, carrying the green seedling marker, made it possible to identify definitively all eight classes of offspring from the  $R_4^B/r^f$  x  $TR^f/r^f$  cross, including the crossovers between T and the  $R$  locus. The results of testcrosses on  $r\bar{g}r\bar{g}$  ♀♀ of these 8 genotypes confirm the conclusions summarized in last year's News Letter. The points of particular interest are:

- (a)  $R^f$  pigment-producing action is enhanced when  $R^f$  is carried in coupling with T2-10a.
- (b) Enhancement of pigment-producing action is retained for one generation at least after  $R^f$  is returned by crossing over from a T to a structurally normal chromosome.
- (c) The pigment-producing action of  $R_4^B$  is not enhanced when in repulsion with T ( $TR^f/R_4^B$ ).
- (d) The pigment-producing potential of  $TR^f$  gametes from  $TR^f/r^f$  plants is significantly higher than that of  $TR^f$  gametes from  $TR^f/R^f$  sibs. Likewise  $R^f$ , following return from a T chromosome to a structurally normal chromosome, has a higher pigment-producing potential in

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$\underline{R}^f/\underline{r}^f$  than in  $\underline{R}^f/\underline{R}^f$  plants, at least in the generation immediately following that in which the crossovers occurred.

3. Additional tests show that the immediately resulting T2-10a  $\underline{R}^f/\underline{r}^f$  (crossover) offspring from  $\underline{T}^f/\underline{R}^f \times \underline{r}^f/\underline{r}^f$  matings, when testcrossed on  $\underline{r}^f/\underline{r}^f$  ♀♀, do not yield  $\underline{R}^f/\underline{r}^f$  kernels exhibiting enhanced aleurone pigmentation, in contrast to  $\underline{T}^f/\underline{r}^f$  plants from stock cultures in which T and  $\underline{R}^f$  have been in coupling for at least two generations. Whatever the basis of the action of the translocation on  $\underline{R}^f$  pigment-producing potential, therefore, there is a lag of at least one generation in expression of the phenomenon after the structural rearrangement is effected.

4. It was shown previously that  $\underline{R}^f$  carried by a T2-10a chromosome (stock culture) is relatively insensitive to paramutation in  $\underline{T}^f/\underline{R}^f$  heterozygotes. More recent experiments establish the additional fact that  $\underline{R}^f$  retains this insensitivity to paramutation in  $\underline{R}^f/\underline{R}^f$  individuals after return by crossing over from a T chromosome to a structurally normal chromosome, at least for one generation.

-- R. A. Brink

3. The effect on  $\underline{R}^f$  action of a reciprocal translocation (T9-10a) involving a break in chromosome 10 distal to the  $\underline{R}$  locus.

Several of the experiments made with T2-10a (and T4-10b) which involve chromosome 10 breaks proximal to the R locus (10L.53 and 10L.57) have recently been carried out with T9-10a also. The break in chromosome 10, according to Longley, is at 10L.92 in the latter case, and thus distal to the R locus (R is probably located at about .7). It is significant that the effects of T9-10a on  $\underline{R}^f$  action are closely parallel to those of T2-10a and T4-10b. In the T9-10a  $\underline{R}^f/\underline{r}^f$  (stock culture) combination,  $\underline{R}^f$ , for example, shows enhanced pigment-producing action, and also is relatively insensitive to paramutation in T9-10a  $\underline{R}^f/\underline{R}^f$  plants.

-- R. A. Brink

-- N. K. Notani

(Dr. Notani's permanent address is Biological Division, AEET, Indian Cancer Research Center, Bombay 12, India)

4. The paramutagenic action of the marbled aleurone allele ( $\underline{R}^{mb}$ ).

Selection within the uniform W22 inbred line in which marbled was earlier incorporated yielded marbled sub-lines differing in paramutagenic competence. The capacity of  $\underline{R}^{mb}$  to alter standard  $\underline{R}^f$  in  $\underline{R}^f/\underline{R}^{mb}$  heterozygotes can be reduced by first passing the marbled allele through a heterozygote with stippled. Five independent self-colored mutants from marbled, on the other hand, retained the paramutagenicity of the parent  $\underline{R}^{mb}$  allele.

Paramutability of  $\underline{R}^f$  in heterozygotes with  $\underline{R}^{mb}$  was greatly reduced by placing  $\underline{R}^f$  in coupling with a large terminal heterochromatic knob. The return of  $\underline{R}^f$  from the knob-carrying chromosome to a normal chromosome, by crossing over, resulted in an increased sensitivity to paramutation in  $\underline{R}^f/\underline{R}^{mb}$  heterozygotes in the single case tested.

Attempts to change the amount of aleurone spotting in marbled plants by selection within the W22 inbred line resulted in the isolation of marbled families which differed not only in grade of marbling but also in rate of mutation to self-color. Marbled sub-lines which exhibited extensive aleurone pigmentation also showed high frequencies of germinally transmissible mutations to self-color. The

differences between the various sub-lines with regard to aleurone spotting tended to persist in recurrent matings to the W22  $r^1r^1$  inbred strain.

A light marbled family was tested for frequency of mutation to self-color in homozygotes ( $R^1mbR^1mb$ ) and heterozygotes ( $R^1mbR^1$ ). The mutation rates were  $0.0 \times 10^{-4}$  and  $6.8 \times 10^{-4}$ , respectively.

Two W22 marbled sub-lines differing in degree of aleurone spotting and rate of mutation to self-color proved to be indistinguishable in paramutagenic action in  $R^1R^1mb$  heterozygotes.

-- Willem H. Weyers

(The above note, submitted by R. A. Brink, is a slightly paraphrased excerpt from the summary of Dr. Weyer's Ph.D. thesis. Dr. Weyers has recently returned to South Africa. His address is P/B 1021, University of Natal, Pietermaritzburg, Natal, South Africa.)

5. Paramutation of  $R^1g$  mutants from standard  $R^1$ .

A series of mutant genes designated  $R^1g_1$  to  $R^1g_{10}$  were derived from the standard  $R^1$  allele used in previous Wisconsin studies of paramutation. The mutants differ from  $R^1$  in that they produce green, rather than red, seedling and anthers. Comparisons were made of the aleurone phenotypes conditioned by each of the  $R^1g$  genes, relative to that of standard  $R^1$ , and tests were made for paramutability of the mutants.

The following test matings were made: (1) W23  $r^1g_1g_1$  ♀ x W22  $R^1R^1g_1$  ♂, (2) W23  $r^1g_1g_1$  ♀ x W22  $R^1R^1g_1$  ♂.

The aleurone pigmentation of the individual testcross kernels was scored by matching them against a six-kernel standard set selected so as to define seven pigmentation classes. The  $R^1g_1g_1$  and  $R^1r^1g_1g_1$  classes of kernels from testcrosses involving  $R^1R^1g_1$  plants were separated retroactively to scoring by germination and observation of seedling color. The  $R^1g_1g_1$  and  $R^1r^1g_1g_1$  kernels from testcrosses involving  $R^1R^1g_1$  plants were separated visually on the basis of aleurone phenotype, and only  $R^1g_1g_1$  kernels were scored.

A representative sample of the data obtained is shown in table 1.

Table 1. Mean aleurone color scores for  $R^1r^1g_1g_1$  and  $R^1g_1g_1$  kernels from the cross  $r^1g_1g_1$  ♀ x  $R^1R^1g_1$  ♂, and for  $R^1g_1g_1$  kernels from the cross  $r^1g_1g_1$  ♀ x  $R^1R^1g_1$  ♂

Mating	Pedigree	No. of ears	Endosperm genotype	Mean score
$r^1g_1g_1$ ♀ x $R^1R^1g_1$	W23 x J-79	4	$R^1r^1g_1g_1$	5.41
			$R^1g_1g_1$	5.45
$r^1g_1g_1$ ♀ x $R^1R^1g_1$	W23 x J-36	4	$R^1g_1g_1$	2.27

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The complete data show that: (1) the mutant genes are indistinguishable from standard  $\underline{R}^I$  in aleurone pigmentation capacity; and (2) the  $\underline{R}\underline{G}$  gametes produced by  $\underline{R}\underline{G}\underline{R}^{st}$  heterozygotes regularly determine paramutant aleurone phenotypes.

-- Douglas Brown

#### 6. Paramutagenic action of paramutant $\underline{R}^I$ .

Data were collected to test the possibility that paramutant  $\underline{R}^I$  genes have acquired the capacity to promote paramutation in some degree.

$\underline{R}^I\underline{R}\underline{G}$  heterozygotes from matings of the type  $\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$  were used as pollen parents in test crosses to W23  $\underline{r}\underline{G}\underline{r}\underline{G}$  parents. It is expected that paramutagenic action of the paramutant  $\underline{R}^I$  allele, if such exists, would be revealed by reduced pigmentation of  $\underline{R}\underline{G}\underline{r}\underline{G}\underline{r}\underline{G}$  testcross kernels. The controls consisted of  $\underline{R}\underline{G}\underline{r}\underline{G}\underline{r}\underline{G}$  kernels from test matings of  $\underline{R}^I\underline{R}\underline{G}$  heterozygotes derived from  $\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$  crosses. Testcross kernels were scored and identified according to the procedure described in the preceding section.

The results are summarized in table 2.

Table 2. Mean scores for  $\underline{R}\underline{G}\underline{r}\underline{G}\underline{r}\underline{G}$  kernels from testcrosses involving  $\underline{R}^I\underline{R}\underline{G}$  plants derived from  $\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$  and  $\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$  matings

Parentage of $\underline{R}^I\underline{R}\underline{G}$ ♂ testcross parent	No. of testcross ears	Mean score for $\underline{R}\underline{G}\underline{r}\underline{G}\underline{r}\underline{G}$ kernels only
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	4	5.45
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	10	4.36
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	4	5.70
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	10	4.88
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	4	5.53
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	10	4.82
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	4	5.09
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	10	4.11
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	4	5.45
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G}$	10	4.91
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$	4	5.53
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$	10	4.80
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$	4	5.69
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G}\underline{r}\underline{G} \text{♂}$	10	4.55
$\underline{R}^I\underline{R}^I \text{♀} \times \underline{R}\underline{G} \underline{r}\underline{G} \text{♂}$	4	5.38
$\underline{R}^I\underline{R}^{st} \text{♀} \times \underline{R}\underline{G} \underline{r}\underline{G} \text{♂}$	10	5.02



It is evident that  $\underline{R}^f$  extracted from  $\underline{R}^f \underline{R}^{st}$  heterozygotes regularly is paramutagenic, though weakly so when compared with  $\underline{R}^{st}$ .

-- Douglas Brown

#### 7. A test for genetic influence of endosperm on embryo.

Confirmation of Pissarev and Venogradova's claim in which wheat plants of modified characteristics were produced by grafting mature wheat embryos onto rye endosperms has been reported by Muntzing. The alteration was expressed in this case by increased crossability of the "graft hybrid" to rye and was attributed to an incorporation into the embryo of substances from the endosperm upon germination. In a similar experiment with maize, Carangal (M.G.C.N.L.:32) observed no increase in the receptiveness of a dent sterile pop to dent pollen through such embryo-endosperm transplantation. He did note, however, a marked decrease in viability and seedling growth in the heterologous transplant -- pop embryo into dent endosperm -- over the corresponding homologous transplant -- pop embryo into pop endosperm. The question of whether or not there is any permanent, heritable change resulting from the association of the embryo with genetically dissimilar endosperm was the subject of these experiments.

The method of attaining embryo-endosperm dissimilarity for these trials differs from those used previously. The crosses were designed such that cases in which the egg and polar nuclei were fertilized by unlike sperm, i.e. heterofertilized, could be readily detected. In this manner the genetically deviant zygote and fusion nucleus of the endosperm can be juxtaposed at fertilization. Thus exchange of genetic material between the two tissues could occur either in the development of the caryopsis or during germination.

The first of two experiments involved recognition and subsequent study of plants arising from heterofertilized kernels produced by mating  $\underline{r} \underline{g} \underline{r} \underline{g}$  females with  $\underline{R} \underline{g} \underline{r}^f$  male parents. The colorless seeds from this mating were germinated and the seedlings were exposed to light. Those which failed to pigment were selected as the presumed heterofertilized class. The tassels of the resulting plants were examined for red sectors in order to ascertain whether or not the endosperm containing  $\underline{r}^f$  had evoked any change in the  $\underline{R} \underline{g} \underline{r} \underline{g}$  embryo. The possibility that these green plants resulted from  $\underline{r} \underline{g}$  pollen contamination was excluded by verifying the presence of  $\underline{R} \underline{g}$  in the backcross of the mature plants to  $\underline{r} \underline{g} \underline{r} \underline{g}$ . Nine heterofertilized plants ( $\underline{R} \underline{g} \underline{r} \underline{g}$  embryo;  $\underline{r}^f \underline{r} \underline{g} \underline{r} \underline{g}$  endosperm) were positively identified in this manner and all failed to show red tassel sectors.

In the second investigation mixed pollen from  $\underline{R} \underline{r} \underline{R}^f$  and  $\underline{R}^{st} \underline{R}^{st}$  plants was placed on  $\underline{r} \underline{g} \underline{r} \underline{g}$  silks. The  $\underline{R}^{st}$  kernels from this mating were germinated, and the heterofertilized class identified by red seedlings ( $\underline{R}^{st}$  conditions green seedlings and anthers). Seven such plants were testcrossed on  $\underline{r} \underline{g} \underline{r} \underline{g}$  females. The  $\underline{R}^f$  expression in this case was indistinguishable from that resulting from similar testcrosses of plants grown from non-heterofertilized kernels ( $\underline{R} \underline{r} \underline{g} \underline{r} \underline{g}$  embryo;  $\underline{R} \underline{r} \underline{g} \underline{r} \underline{g}$  endosperm). Furthermore the darkly mottled kernels obtained in the above two sets of testcrosses are in sharp contrast to the near colorless, paramutant form of  $\underline{R}^f$  derived from  $\underline{R}^f \underline{R}^{st}$ .

These results support the view of autonomous development of the embryo irrespective of the endosperm genotype. There was no evidence for diffusion of substances bearing genetic potentialities from the endosperm to the embryo. Due to the infrequent occurrence of heterofertilization, the numbers of individuals observed in these studies were small. The need for obtaining a larger population is particularly important if one assumes that incorporation of any single genetic factor from the endosperm (e.g. the red anther component of  $\underline{r}^f$ ) occurs rarely if ever.

An expedient method for regular production of kernels with embryos and endosperms that are not concordant for a specified chromosome region is available in maize, but has not as yet been utilized. This procedure employs the use of A-B interchanges. It is well substantiated that in the case of such translocations the BA segment undergoes non-disjunction at the second microspore division producing non-identical sperm nuclei. One nucleus is hyperploid, the other deficient for the arm of the A chromosome which is attached to the segment of the B possessing the centromere. The fertilization of the egg and polar nuclei by the unlike sperm nuclei would result in the requisite dissimilarity of embryo and endosperm.

-- Jerry Kermicle

#### 8. Genetic composition of twin mutations in medium variegated pericarp maize.

In the initial report of a genetic analysis of red-light variegated twin mutations occurring in medium variegated pericarp, Brink and Nilan (Genetics 1952) demonstrated that the light variegated co-twin differs from medium variegated, not in the  $P^{VV}$  allele present, but in the possession of Modulator ( $Mp$ ) at a locus separate from  $P$ . The Modulator found in the light variegated sector was believed to be the one transposed from the  $P$  locus and lost from the red sector. The postulated absence of  $Mp$  from the red sector was not tested however, since a test, independent of a transposed Modulator ( $tr-Mp$ ) effect on variegation, was not then available. In 1955 Brink (M.G.N.L.), using a " $C - Ds$ " tester stock, reported the results of a test for  $Mp$  in the red sectors of eighteen twin mutations. He found, contrary to the Brink-Nilan hypothesis in its original form, that eleven red co-twins contained a  $tr-Mp$  somewhere in the genome while seven were lacking  $tr-Mp$ .

To date 70 clear cut twin mutations have been tested for the presence of Modulator in the red component using a " $C - Ds$ " tester. Modulator has been found in 52 (74 percent) of the cases. It is thus clear that twin mutations fall into two distinct classes with respect to the presence or absence of  $tr-Mp$  in the red component, and that the class containing  $tr-Mp$  is decidedly more frequent.

In an attempt to explain twin mutations which contain  $tr-Mp$  in the red sector it is postulated that twin mutations result from a single transposition of  $Mp$  during the time of chromosome replication.  $P^{rr}$  and its conjoined  $Mp$  replicates at the  $P$  locus, producing two  $P^{rr}Mp$  complexes, prior to replication of certain other portions of the chromosome. An  $Mp$  from one of the daughter  $P^{rr}Mp$  complexes transposes to such an unreplicated site, and then replicates in phase with the chromosome in that region. The resulting daughter nuclei would then be of two genotypes: 1)  $P^{rr} + tr-Mp$ , conditioning red pericarp, and 2)  $P^{rr}Mp + tr-Mp$ , which gives rise to the light variegated phenotype. From this interpretation it is expected that  $tr-Mp$  would be situated at the same locus in the red and light variegated co-twins.

A three point backcross linkage analysis was employed to test the linkage relations of  $tr-Mp$  in the red and light sectors of a series of twin spots. The markers used were  $tr-Mp$ ,  $P$ , and the breakage point of a reciprocal translocation. The reciprocal translocations utilized marked points both proximal (T1-2b, T1-5b) and distal (T1-7g) to  $P$ . A " $C - Ds$ " tester stock was utilized to disclose the presence of  $tr-Mp$  in the non-variegated offspring resulting from the backcross mating.

Percent recombination between  $P$  and  $tr-Mp$  found in each of the co-twins of thirteen independent twin mutations is presented in table 1. It is seen that the numerical values for the red and light variegated sectors of all but one twin (number 5) correspond well. Statistical analysis of the data ( $X^2$  test of heterogeneity) indicates no greater variability for the values obtained for the linkage of  $P$  and  $tr-Mp$  than for the interval between  $P$  and the breakage point of the reciprocal translocations. The difference in values of  $P - tr-Mp$  found in each of the two sectors of twin number 5 is highly

Table 1. Recombination between P locus and transposed Modulator in thirteen independently arising twin mutations.

Twin number	Position relative to <u>P</u>	Percent recombination <sup>1</sup> ( <u>P</u> and <u>tr-Mp</u> )	
		Red sector	Light variegated sector
1	distal	3.66 (6) <sup>2</sup>	2.21 (4)
2	random	48.94 (4)	46.46 (3)
3	random	46.87 (4)	47.39 (5)
4	distal	8.21 (5)	6.43 (5)
5	- - -	19.19 <sup>3</sup> (3)	50.47 <sup>3</sup> (1)
6	distal	13.87 (2)	9.29 (5)
7	random	48.57 (1)	46.95 (2)
8	random	45.35 (3)	48.85 (2)
9	distal	7.08 (5)	4.13 (1)
10	random	52.81 (2)	46.74 (3)
11	- - -	12.42 (3)	4.39 (3)
12	distal	19.33 (10)	24.13 (6)
13	proximal	29.41 (1)	32.29 (4)

- 1 - Secondary transpositions omitted  
 2 - Number of families scored  
 3 - A highly significant difference

significant. The most plausible explanation of this exception is that a secondary transposition occurred in the single family used to determine the site of tr-Mp in the light variegated component. These results therefore support the proposal that a single transposition of Mp from the P locus underlies a twin mutation and that the position of tr-Mp is the same in each of its two sectors.

There appears to be a single site at which tr-Mp is found within a given twin mutation, whereas the sites are different in the independently occurring twin spots. Of the six twins in which tr-Mp was linked to the P locus, five of the tr-Mp sites were clearly distal to P and one (twin number 13) was proximal to P. The reciprocal translocation in twin 13 was T1-7g (1S.17) marking a site close to the centromere. The site of tr-Mp was found to be 19 units proximal to the breakage point. It is possible that the site taken by tr-Mp in this twin is on the long arm of chromosome 1. The lack of any clear cut proximal positions for tr-Mp on chromosome 1 in this class of twin mutations suggests that a polarity in replication of the chromosome exists and that the distal portion, of this chromosome arm at least, replicates after the proximal portions.

Though no data are currently available, it is interesting to speculate that the class of twin mutations that are void of a Modulator in the red component arise by transposition of Mp from the P locus to a site which has already replicated. Linkage tests of tr-Mp in the light variegated component of such twin spots are now in progress, and should provide evidence for or against this speculation.

-- Irwin M. Greenblatt

#### 9. Reconstitution of the variegated pericarp allele by return of modulator to the P locus.

Certain self-red (prt) mutants from medium variegated (PV) exhibit an instability in the expression of the prt allele in the form of variegated or nearly colorless sectors in the pericarp. A study

was conducted to determine if these sectors result from somatic mutations of  $\underline{P}^{rr}$  to  $\underline{P}^{vv}$ . According to the theory of Brink and Nilan, such mutational events would consist of transpositions which return Modulator to the  $\underline{P}$  locus and thus reconstitute the  $\underline{P}^{vv}$  allele ( $\underline{P}^{rr}\underline{M}p$ ).

Most primary transpositions of Modulator result in relocation of the element at other sites closely linked to the  $\underline{P}$  locus. This fact can be interpreted to mean that, in transposing, Modulator most frequently moves only a short distance along the same chromosome. Based on this premise, and assuming that the observed sectors result from reconstitutions of the  $\underline{P}^{vv}$  allele, it was postulated that the rate of sectoring is a function of the distance of the transposed Modulator ( $\underline{tr-M}p$ ) from the  $\underline{P}$  locus. The present study tests this hypothesis.

One hundred and thirty kernels exhibiting a variegated or nearly colorless pericarp phenotype over part or all of the kernel were selected as possible sporophytic mutants from self-red ears, and grown out in the field for verification. In addition, 23 mutant self-red families were scored for the number of pericarp sectors per 1,000 kernels and the linkage of  $\underline{P}^{rr}$  with  $\underline{tr-M}p$  in an attempt to determine if there is a relationship between the rate of pericarp sectoring and the closeness of the site of  $\underline{tr-M}p$  to the  $\underline{P}$  locus.

In 17 of these families (10 carrying  $\underline{tr-M}p$ , 7 lacking  $\underline{tr-M}p$ ) the pericarp sectoring was associated with the presence in the genome of a transposed Modulator. Among the 10  $\underline{M}p^+$  families, the rate of sectoring was directly related to the linkage of  $\underline{tr-M}p$  to the  $\underline{P}$  locus.

Mutant variegated plants were obtained from sectored kernels in 32 independent cases in which the parent red-eared individual was found to possess a  $\underline{tr-M}p$  linked to  $\underline{P}^{rr}$ . Twenty-four of the variegated mutants were tested for the presence of Modulator, and all proved positive.

These results indicate that the pericarp sectoring observed on self-red ears in these families does indeed, result from transpositions that return  $\underline{M}p$  to the  $\underline{P}$  locus.

In general, the variegated mutants fall into the same phenotypic classes as have been described in other investigations of variegated pericarp. However, the relative frequencies of the mutational events giving rise to the mutants in each class are worthy of consideration. Five (15.63 percent) of the mutational events yielded medium variegated mutants and an equal number gave light variegated mutants. Four (12.50 percent) gave rise to orange medium variegated mutants, and six (18.75 percent) produced orange light variegated mutants. Twelve (37.50 percent) gave rise to mutants with a very light variegated phenotype. Thus, the very light variegated and orange variegated phenotypes were common among the variegated mutants obtained from sectored kernels on  $\underline{M}p^+$ , self-red ears. Brawn (M.G.C.N.L. 32: 142 - 144) has reported that these phenotypes are rare among mutants from medium variegated.

Of the 32 variegated mutants obtained in this study, 23 (71.88 percent) exhibited grades of variegation lighter than that conditioned by the standard  $\underline{P}^{vv}$  allele. The results of a test of the dosage effects of one of the very light variegated mutants on the grade of variegation of standard medium variegated indicate that the phenotypic grade of variegation is not a reliable index of the number of Modulators present in a variegated mutant from self-red. The diversity of phenotypes among the reconstituted variegateds could be due to changes of state of Modulator; to increases in the number of Modulators present; or to different physical associations of Modulator with the  $\underline{P}^{rr}$  allele, either in the position of Modulator within the structural dimensions of the  $\underline{P}$  locus or in the firmness of bonding of Modulator at a particular position.

The pericarp sectoring observed in one group of six closely related families was found to be independent of the presence of  $\underline{tr-M}p$  in the genome. One sporophytic mutant was obtained from a

sectored kernel selected from a self-red ear of one of these families. The phenotype of this mutant was non-variegated. Further study will be conducted in an attempt to determine the cause of the pericarp sectoring observed in this group of families.

-- Elwin R. Orton, Jr. °

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### III. REPORT ON MAIZE COOPERATIVE

Work of the past season was concentrated principally on improving plant vigor and increasing seed supplies of the traits and tester combinations listed in the accompanying catalogue of stocks. Approximately 35,000 plants, comprising 2,200 families, were grown last summer; about 15,000 pollinations were made. Additional plantings were made in greenhouse and Florida generations.

Further crosses were made to derive new tester combinations or to determine chromosome positions of unmapped traits. It is hoped that this work, along with research on newly-acquired traits, may be intensified next season.

As time permits, all stocks are being gradually converted to the inbred lines M14, W23, and Oh51A. As a consequence of this program of developing stocks adapted to the Corn Belt, a considerable amount of effort is required to re-extract tester combinations and to confirm genetic constitutions.

Seed requests have risen sharply during the past few years. Two to three months each year are now required to supply stocks and provide information on the classification, use, and linkage relations of genetic traits.

The following listing of Maize Cooperative stocks includes the more useful combinations now available. Seed requests should be sent to the Botany Department, University of Illinois, Urbana, Illinois.

Chromosome 1ad<sub>1</sub> an<sub>1</sub> bm<sub>2</sub>ad<sub>1</sub> Knan<sub>1</sub> Kn bm<sub>2</sub>

as

Hm

Kn

Kn Ts<sub>6</sub>lw<sub>1</sub>

necrotic 8147-31

pCR

pCW

pMO

PRR ad<sub>1</sub> an<sub>1</sub>PRR ad<sub>1</sub> bm<sub>2</sub>PRR an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>PRR br<sub>1</sub> f<sub>1</sub> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>PRR br<sub>1</sub> f<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>

pVV

pWR bm<sub>2</sub>pWR gs<sub>1</sub> bm<sub>2</sub>pWW br<sub>1</sub> f<sub>1</sub> bm<sub>2</sub>pWW br<sub>1</sub> f<sub>1</sub> an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>sr<sub>1</sub> pWR an<sub>1</sub> bm<sub>2</sub>sr<sub>1</sub> pWR an<sub>1</sub> gs<sub>1</sub> bm<sub>2</sub>sr<sub>1</sub> zb<sub>4</sub> pWWts<sub>2</sub> pWW br<sub>1</sub> bm<sub>2</sub>Ts<sub>3</sub>Ts<sub>6</sub>v<sub>19</sub> bm<sub>2</sub>V<sub>8</sub>V<sub>8</sub> an<sub>1</sub> bm<sub>2</sub>vP<sub>5</sub>vP<sub>8</sub>zb<sub>4</sub> ms<sub>17</sub> pWW

Chromosome 1 (Continued)zb<sub>4</sub> pWW bm<sub>2</sub>zb<sub>4</sub> pWW br<sub>1</sub>zb<sub>4</sub> ts<sub>2</sub> pWWChromosome 2al lg<sub>1</sub>al lg<sub>1</sub> gl<sub>2</sub> B skal lg<sub>1</sub> gl<sub>2</sub> b skba<sub>2</sub>fl<sub>1</sub>lg<sub>1</sub> gl<sub>2</sub> Blg<sub>1</sub> gl<sub>2</sub> blg<sub>1</sub> gl<sub>2</sub> b fl<sub>1</sub> v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b fl<sub>1</sub> v<sub>4</sub> Chlg<sub>1</sub> gl<sub>2</sub> B gs<sub>2</sub>lg<sub>1</sub> gl<sub>2</sub> b gs<sub>2</sub> v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b gs<sub>2</sub> v<sub>4</sub> Chlg<sub>1</sub> gl<sub>2</sub> B sk v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b sk v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b sk fl<sub>1</sub> v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> B v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b v<sub>4</sub>lg<sub>1</sub> gl<sub>2</sub> b v<sub>4</sub> Chlg<sub>1</sub> gs<sub>2</sub> b v<sub>4</sub>ws<sub>3</sub> lg<sub>1</sub> gl<sub>2</sub> Bws<sub>3</sub> lg<sub>1</sub> gl<sub>2</sub> bws<sub>3</sub> lg<sub>1</sub> gl<sub>2</sub> b fl<sub>1</sub> v<sub>4</sub>ws<sub>3</sub> lg<sub>1</sub> gl<sub>2</sub> B skws<sub>3</sub> lg<sub>1</sub> gl<sub>2</sub> b sk

Chromosome 3

A<sub>1</sub> ga<sub>7</sub>; A<sub>2</sub> C R  
 A<sub>1</sub> sh<sub>2</sub>; A<sub>2</sub> C R  
 Ad-31; A<sub>2</sub> C R  
 Ad-31 sh<sub>2</sub>; A<sub>2</sub> C R  
 a<sup>P</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>1</sub>; A<sub>2</sub> C R B Pl dt<sub>1</sub>  
 a<sub>1</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>1</sub> sh<sub>2</sub>; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>1</sub> sh<sub>2</sub>; A<sub>2</sub> C R dt<sub>1</sub>  
 a<sub>1</sub> sh<sub>2</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>1</sub><sup>st</sup> sh<sub>2</sub>; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>1</sub><sup>st</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 a<sub>x</sub>-1; A<sub>2</sub> C R  
 a<sub>x</sub>-3; A<sub>2</sub> C R  
 a<sub>x</sub>-3 et; A<sub>2</sub> C R  
 an<sub>2</sub> = allele of d<sub>1</sub>  
 ba<sub>1</sub>  
 Cg  
 cr<sub>1</sub>  
 d<sub>1</sub>  
 d<sub>1</sub> Cg  
 d<sub>1</sub> gl<sub>6</sub>  
 d<sub>1</sub> gl<sub>6</sub> Lg<sub>3</sub>  
 d<sub>1</sub> lg<sub>2</sub>  
 d<sub>1</sub> Lg<sub>3</sub>  
 d<sub>1</sub> Lg<sub>3</sub> Rg  
 d<sub>1</sub> P<sub>8</sub><sub>2</sub>  
 d<sub>1</sub> Rg  
 d<sub>1</sub> rt  
 d<sub>1</sub> ts<sub>4</sub> lg<sub>2</sub>  
 d<sub>2</sub>  
 gl<sub>6</sub>  
 gl<sub>6</sub> lg<sub>2</sub> a<sub>1</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>  
 gl<sub>6</sub> Lg<sub>3</sub>



Chromosome 3 (Continued)gl<sub>6</sub> Rggl<sub>6</sub> v17gl<sub>6</sub> v17 lg2gl<sub>7</sub>lg2 A<sub>1</sub><sup>b</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>lg2 a<sub>1</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>lg2 a<sub>1</sub> sh<sub>2</sub> et; A<sub>2</sub> C R Dt<sub>1</sub>lg2 a<sub>1</sub><sup>st</sup> et; A<sub>2</sub> C R Dt<sub>1</sub>

lg2 pm

Lg<sub>3</sub>pg<sub>2</sub>

pm

ra<sub>2</sub>ra<sub>2</sub> lg<sub>2</sub> pmra<sub>2</sub> Rg

Rg

rt; A<sub>1</sub> A<sub>2</sub> C Rts<sub>4</sub> na<sub>1</sub>

v17

vp<sub>1</sub>

Primary trisome 3

Chromosome 4bm<sub>3</sub>bt<sub>2</sub>

de (1 or 16?)

Ga<sub>1</sub> Su<sub>1</sub>ga<sub>1</sub> su<sub>1</sub>gl<sub>3</sub>j<sub>2</sub>j<sub>2</sub> gl<sub>3</sub>la su<sub>1</sub> gl<sub>3</sub>

Chromosome 4 (Continued)

lo Su<sub>1</sub>  
 lo su<sub>1</sub>  
 lw<sub>4</sub>; lw<sub>3</sub>  
 o<sub>1</sub>  
 sp<sub>1</sub> su<sub>1</sub>  
 st  
 su<sub>1</sub> bm<sub>3</sub>  
 su<sub>1</sub> gl<sub>3</sub>  
 su<sub>1</sub> gl<sub>4</sub>  
 su<sub>1</sub> j<sub>2</sub> gl<sub>3</sub>  
 su<sub>1</sub> o<sub>1</sub>  
 su<sub>1</sub> ra<sub>3</sub>  
 su<sub>1</sub> Tu  
 su<sub>1</sub> Tu gl<sub>3</sub>  
 su<sub>1</sub> zb<sub>6</sub>  
 su<sub>1</sub> zb<sub>6</sub> gl<sub>3</sub>  
 su<sub>1</sub> zb<sub>6</sub> Tu  
 su<sub>1</sub> am  
 Ts<sub>5</sub>  
 Ts<sub>5</sub> st  
 Ts<sub>5</sub> su<sub>1</sub>  
 Tu gl<sub>3</sub>  
 v<sub>8</sub>

Chromosome 5

a<sub>2</sub>; A<sub>1</sub> C R  
 a<sub>2</sub> bm<sub>1</sub> bt<sub>1</sub> bv<sub>1</sub> pr; A<sub>1</sub> C R  
 a<sub>2</sub> bm<sub>1</sub> pr v<sub>2</sub>; A<sub>1</sub> C R  
 a<sub>2</sub> bm<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> C R  
 a<sub>2</sub> bt<sub>1</sub> pr; A<sub>1</sub> C R  
 a<sub>2</sub> bt<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> C R  
 a<sub>2</sub> pr; A<sub>1</sub> C R  
 ae

Chromosome 5 (Continued)bm<sub>1</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr v<sub>2</sub>; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr ys<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> pr ys<sub>1</sub> v<sub>2</sub>; A<sub>1</sub> A<sub>2</sub> C Rbm<sub>1</sub> yg<sub>1</sub>bt<sub>1</sub> pr; A<sub>1</sub> A<sub>2</sub> C RGa Bt<sub>1</sub>ga bt<sub>1</sub>g<sup>15</sup>g<sup>18</sup>g<sup>17</sup> a<sub>2</sub> bt<sub>1</sub> v<sub>2</sub>; A<sub>1</sub> C Rg<sup>17</sup> v<sub>2</sub>intensifier of pr closely linked to bt<sub>1</sub>lw<sub>2</sub>lw<sub>3</sub>; lw<sub>4</sub>na<sub>2</sub>na<sub>2</sub> prpr; A<sub>1</sub> A<sub>2</sub> C Rpr ys<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C Rshfl = "sh<sub>4</sub>""sh<sub>3</sub>" = allele of bt<sub>1</sub>

tn

v<sub>3</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rv<sub>12</sub>vp<sub>2</sub> g<sup>18</sup>vp<sub>2</sub> pr; A<sub>1</sub> A<sub>2</sub> C Rvp<sub>7</sub>vp<sub>7</sub> pr; A<sub>1</sub> A<sub>2</sub> C RChromosome 6at = allele of si<sub>1</sub>po Y<sub>1</sub> plpo y<sub>1</sub> pl

Please Note: Notes submitted to the Maize Genetics Cooperation Newsletter may be cited only with consent of authors.

Chromosome 6 (Continued)

Pt  
 si<sub>1</sub> Y<sub>1</sub> Pl  
 si<sub>1</sub> Y<sub>1</sub> pl  
 si<sub>1</sub> y<sub>1</sub> pl  
 y<sub>1</sub> l<sub>10</sub>  
 Y<sub>1</sub> ms (1?)  
 y<sub>1</sub> ms (1?)  
 y<sub>1</sub> pb<sub>4</sub> Pl  
 y<sub>1</sub> pb<sub>4</sub> pl  
 Y<sub>1</sub> PG11: wx PG12  
 y<sub>1</sub> PG11: wx PG12  
 y<sub>1</sub> Pl Bh  
 y<sub>1</sub> pl Bh  
 Y<sub>1</sub> Pl sm py; A<sub>1</sub> A<sub>2</sub> b PRR  
 Y<sub>1</sub> pl su<sub>2</sub>  
 y<sub>1</sub> pl su<sub>2</sub>  
 Y<sub>1</sub> Pl; seg w<sub>1</sub>  
 Y<sub>1</sub> pl; seg w<sub>1</sub>  
 y<sub>1</sub> Pl; seg w<sub>1</sub>  
 y<sub>1</sub> pl; seg w<sub>1</sub>  
 "male sterile-silky" = allele of si<sub>1</sub>  
 "orobanche" (seedling)  
 "ragged" (seedling)  
 "white 8522" (seedling)  
 "white 8896" (seedling)

Chromosome 7

bd  
 Bn<sub>1</sub>  
 g<sub>2</sub>  
 gl<sub>1</sub> ij bd  
 gl<sub>1</sub> sl Bn<sub>1</sub>  
 Hs

Chromosome 7 (Continued)

ij  
 in; pr A<sub>1</sub> A<sub>2</sub> C R  
 o<sub>2</sub>  
 o<sub>2</sub> gl<sub>1</sub> sl  
 o<sub>2</sub> gl<sub>1</sub> sl Bn<sub>1</sub>  
 o<sub>2</sub> ra<sub>1</sub> gl<sub>1</sub>  
 o<sub>2</sub> v<sub>5</sub> gl<sub>1</sub>; seg ra<sub>1</sub>  
 o<sub>2</sub> v<sub>5</sub> ra<sub>1</sub> gl<sub>1</sub>  
 o<sub>2</sub> v<sub>5</sub> ra<sub>1</sub> gl<sub>1</sub> Hs  
 ra<sub>1</sub> gl<sub>1</sub>  
 TP<sub>1</sub>  
 v<sub>5</sub> gl<sub>1</sub> TP<sub>1</sub>  
 va<sub>1</sub>  
 vpg gl<sub>1</sub>; wx

Chromosome 8

mn  
 v<sub>16</sub> ms<sub>8</sub> j<sub>1</sub>  
 v<sub>16</sub> ms<sub>8</sub> j<sub>1</sub>; l<sub>1</sub>  
 "necrotic 6697" (seedling)  
 "sienna 7748" (seedling)

Chromosome 9

au<sub>1</sub> au<sub>2</sub>  
 Bf<sub>1</sub>  
 bk<sub>2</sub> ms<sub>20</sub>  
 bk<sub>2</sub> Wc  
 bm<sub>4</sub>  
 C sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 c sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 c sh<sub>1</sub> wx gl<sub>15</sub>; A<sub>1</sub> A<sub>2</sub> R

Chromosome 9 (Continued)

c wx bk<sub>2</sub>; A<sub>1</sub> A<sub>2</sub> R  
 Dt<sub>1</sub> (See Chromosome 3 stocks)  
 I wx; A<sub>1</sub> A<sub>2</sub> R Pr B pl  
 I wx; A<sub>1</sub> A<sub>2</sub> R pr B pl  
 K<sub>9</sub><sup>L</sup> C sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 l<sub>7</sub>  
 ms<sub>2</sub>  
 ms<sub>2</sub> sh<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C R  
 ms<sub>20</sub>  
 sh<sub>1</sub> wx d<sub>3</sub>  
 sh<sub>1</sub> wx l<sub>7</sub>  
 sh<sub>1</sub> wx pg<sub>12</sub>; Y PG<sub>11</sub> pl  
 sh<sub>1</sub> wx v<sub>1</sub>  
 wx ar  
 wx Bf<sub>1</sub>  
 wx bk<sub>2</sub>  
 wx d<sub>3</sub>  
 wx da<sub>1</sub>; A<sub>1</sub> A<sub>2</sub> C R  
 wx g<sub>4</sub>  
 wx l<sub>6</sub>  
 wx pg<sub>12</sub>; Y PG<sub>11</sub>  
 wx pg<sub>12</sub>; Y PG<sub>11</sub>  
 wx<sup>a</sup>  
 yg<sub>2</sub> c sh<sub>1</sub> wx; A<sub>1</sub> A<sub>2</sub> R  
 yg<sub>2</sub> C sh<sub>1</sub> bz wx; A<sub>1</sub> A<sub>2</sub> R  
 Primary trisome 9

Chromosome 10

a<sub>3</sub>  
 bf<sub>2</sub>  
 du<sub>1</sub>  
 g<sub>1</sub>  
 g<sub>1</sub> l<sub>2</sub>

Chromosome 10 (Continued)g<sub>1</sub> r<sup>B</sup>; A<sub>1</sub> A<sub>2</sub> Cg<sub>1</sub> r sr<sub>2</sub>gl<sub>9</sub>l<sub>1</sub>; v<sub>16</sub> ms<sub>8</sub> j<sub>1</sub>li g<sub>1</sub> R; A<sub>1</sub> A<sub>2</sub> Cli g<sub>1</sub> r; A<sub>1</sub> A<sub>2</sub> Cli g<sub>1</sub> r; A<sub>1</sub> A<sub>2</sub> C; carries abnormal 10nl<sub>1</sub> g<sub>1</sub> R; A<sub>1</sub> A<sub>2</sub> COg R; A<sub>1</sub> A<sub>2</sub> C B PlR<sup>B</sup> sr<sub>2</sub>r<sup>r</sup> sr<sub>2</sub>rmb; A<sub>1</sub> A<sub>2</sub> CR<sup>nj</sup>; A<sub>1</sub> A<sub>2</sub> CR<sup>st</sup>; A<sub>1</sub> A<sub>2</sub> Cv<sub>18</sub>w<sub>2</sub>

zn

"oil yellow" (seedling and plant)

Primary trisome 10

Unplaced genes

cl

ct

de<sub>17</sub>

dv

dy

fl<sub>2</sub>gl<sub>11</sub>gl<sub>12</sub>gl<sub>14</sub>gl<sub>16</sub>gl<sub>g</sub>

Unplaced genes (Continued)l<sub>3</sub>ms<sub>5</sub>ms<sub>6</sub>ms<sub>7</sub>ms<sub>9</sub>ms<sub>10</sub>ms<sub>11</sub>ms<sub>12</sub>ms<sub>13</sub>ms<sub>14</sub>

Mt

New starchy

rd

Rs<sub>1</sub>rs<sub>2</sub>"sh<sub>5</sub>"tW<sub>1</sub>tW<sub>2</sub>v<sub>13</sub>va<sub>2</sub>vP<sub>6</sub>

wi

ws<sub>1</sub> ws<sub>2</sub>zb<sub>1</sub>zb<sub>2</sub>zb<sub>3</sub>Multiple gene stocksA<sub>1</sub> A<sub>2</sub> C R<sup>F</sup> Pr B PlA<sub>1</sub> A<sub>2</sub> C R<sup>E</sup> Pr B PlA<sub>1</sub> A<sub>2</sub> C R<sup>E</sup> Pr B pl lg<sub>1</sub> yA<sub>1</sub> A<sub>2</sub> C R PrA<sub>1</sub> A<sub>2</sub> C R Pr wx



Multiple gene stocks (Continued)

A<sub>1</sub> A<sub>2</sub> C R Pr wx gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R Pr wx y  
 A<sub>1</sub> A<sub>2</sub> C R pr  
 A<sub>1</sub> A<sub>2</sub> C R pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R pr su<sub>1</sub> y wx  
 A<sub>1</sub> A<sub>2</sub> C R pr y gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C R pr y wx  
 A<sub>1</sub> A<sub>2</sub> C R pr y wx gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> c R Pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> c R Pr y wx  
 A<sub>1</sub> A<sub>2</sub> c R Pr y sh<sub>1</sub> wx  
 A<sub>1</sub> A<sub>2</sub> C r Pr su<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C r Pr su<sub>1</sub> y gl<sub>1</sub>  
 A<sub>1</sub> A<sub>2</sub> C r Pr y wx  
 A<sub>1</sub> A<sub>2</sub> C r Pr y sh<sub>1</sub> wx  
 bm<sub>2</sub> lg<sub>1</sub> a<sub>1</sub> su<sub>1</sub> pr y<sub>1</sub> gl<sub>1</sub> j<sub>1</sub> wx gl<sub>1</sub>  
 colored scutellum  
 lg<sub>1</sub> su<sub>1</sub> bm<sub>1</sub> y<sub>1</sub> gl<sub>1</sub> j<sub>1</sub>  
 su<sub>1</sub> y<sub>1</sub> wx a<sub>1</sub> A<sub>2</sub> C R<sup>B</sup> pr  
 y<sub>1</sub> su<sub>1</sub> ra<sub>1</sub> gl<sub>1</sub>  
 y<sub>1</sub> wx gl<sub>1</sub>

Popcorns

Amber Pearl  
 Black Beauty  
 Hulless  
 Ladyfinger  
 Ohio Yellow  
 Red  
 South American  
 Supergold  
 White Rice

Exotics and Varieties

Argentine Popcorn

Black Mexican Sweet Corn (with B chromosomes)

Black Mexican Sweet Corn (without B chromosomes)

Gourdseed

Maiz chapolote

Papago Flour Corn

Parker's Flint

Strawberry Popcorn

Tama Flint

Tom Thumb Popcorn

Zapaluta chica

Chromosome rearrangements

The following rearrangements are being maintained primarily for use in determining the chromosome locations of new traits. All are marked with closely-linked endosperm or seedling traits.

The cytological positions of Inv 2a were determined by Dr. Morgan. those of Inv 9a were determined by Dr. Li. The indicated interchange points of the reciprocal translocations are taken from published work of Dr. Longley.

Inversions

lg <sub>1</sub> or gl <sub>2</sub> Inv 2a (also available with Ch)	2S.7; 2L.8
wx Inv 9a	9S.7; 9L.9

Reciprocal translocations

wx 1-9c	1S.48; 9L.22
wx 1-9 4995	1L.19; 9S.20
wx 2-9b	2S.18; 9L.22
wx 3-9c	3L.09; 9L.12
wx 3-9 5775	3L.09; 9S.24
wx 4-9b	4L.90; 9L.29
wx 4-9 5657	4L.33; 9S.25
wx 4-9g	4S.27; 9L.27
wx 5-9a	5L.69; 9S.17
wx 5-9c	5S.07; 9L.10
wx 5-9 4817	5L.06; 9S.07
wx 5-9 5614	5L.09; 9L.06
wx 6-9a	6S.79; 9L.40
wx, y 6-9b	6L.10; 9S.37
wx 6-9 4505	6L.13; 9 cent
wx 6-9 4778	6S.80; 9L.30
wx 7-9a	7L.63; 9S.07
wx or gl <sub>1</sub> 7-9 4363	7 cent; 9 cent
wx 8-9d	8L.09; 9S.16
wx 8-9 6673	8L.35; 9S.31
wx 9-10b	9S.13; 10S.40
su 1-4a (also available with pRR)	1L.51; 4S.69
su 1-4d (also available with pRR)	1L.27; 4L.30
su 4-5j	4L.21; 5L.36
su, y 4-6a	4L.37; 6L.43
su 4-8a	4S.59; 8L.19
su, R 4-10b	4L.15; 10L.60
y 1-6c (also available with pRR)	1S.25; 6L.27
gl <sub>2</sub> 2-3c	2S.46; 3S.52
gl <sub>2</sub> 2-3 5304	2S.62; 3L.29
gl <sub>2</sub> 2-6b	2S.69; 6L.49
gl <sub>2</sub> , R 2-10b	2S.50; 10L.75
gl <sub>1</sub> 6-7 4545	6L.25; 7S.73

Stocks of A-B chromosome translocations

B-1a	1L. 2	Proximal to <u>Hm</u>
B-1b	1S. 05	
B-3a	3L. 1	
B-4a	4S. 25	Proximal to <u>su</u> <sub>1</sub>
B-7b	7L. 3	Proximal to <u>ta</u> <sub>1</sub>
B-9a	9L. 5	
B-9b	9S. 4	Between <u>C</u> and <u>wx</u> ; close to <u>wx</u>
B-10a	10L. 35	Proximal to <u>g</u> <sub>1</sub>

-- Earl B. Patterson

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