

Longley

MAIZE GENETICS COOPERATION

NEWS LETTER

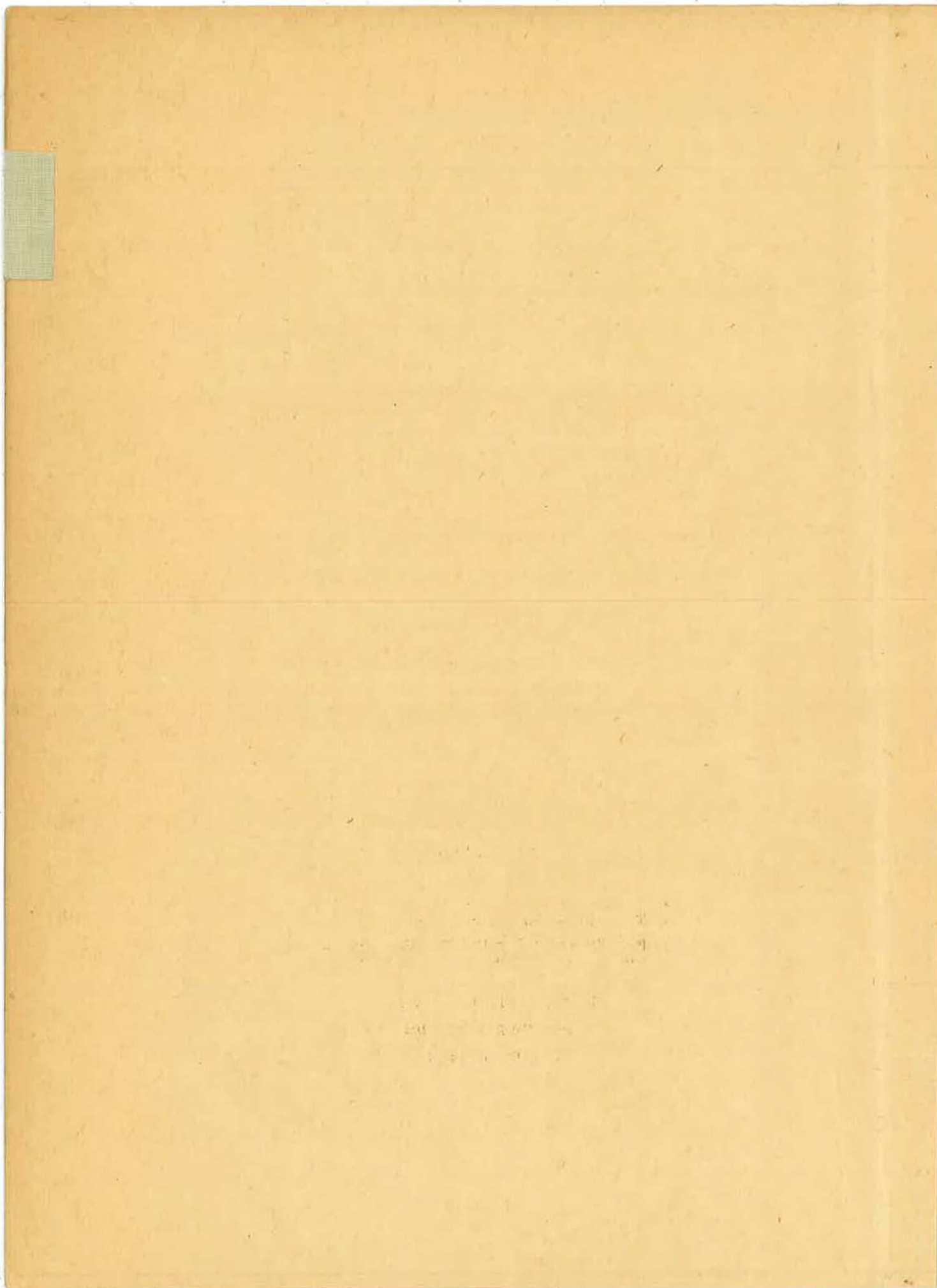
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March 15, 1956

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I. MINUTES OF THE 1955 MEETING OF MAIZE GENETICISTS

Approximately 40 maize geneticists attending the A. I. B. S. meetings at Michigan State University met in conference on September 8, 1955. Dr. James Wright opened the meeting by outlining the agenda to be discussed.

Dr. E. B. Patterson reviewed briefly the transfer of Maize Genetics Cooperation genetic stocks from Cornell University to the University of Illinois, and reported on the present status of the program. The assembly, evaluation, maintenance and distribution of genetic stocks is currently being supported by funds from Research and Marketing, 9B3 (NC-7). Funds for closely-related research activities, including derivation of new tester combinations, linkage determinations of unplaced genes, and the search for new genes are provided by the University of Illinois. In order to improve the vigor and adaptability of the genetic stocks, crosses are being made to selected commercial inbred lines of the corn belt. In response to a question, it was pointed out that the maintenance of a standby collection of genetic stocks at Cornell University has now been discontinued.

Discussion was then directed to a consideration of future plans for preparation of the Maize News Letter. The group was reminded that various members of the Cornell University faculty had expressed a desire to relinquish the responsibility of preparing the MNL in the event some other university were willing to assume the job. It was also pointed out that the Coordination Committee after consideration of this matter had recommended that the MNL be moved to the location of the Maize Cooperation stocks, that is, the University of Illinois, contingent upon the willingness of Dr. M. M. Rhoades to accept the responsibility. Dr. Rhoades agreed to assume the editing task, whereupon it was moved, seconded and passed that beginning with the 1956 issue, the Maize News Letter will be prepared at the University of Illinois. Dr. R. A. Brink moved that the Committee express its gratitude to the University of Illinois for its willingness to assume publication of the News Letter. Seconded and passed.

The point was raised that on various occasions data in the News Letters have been cited without the permission of the authors. Dr. Sherret Chase emphasized that permission to cite should always be obtained, but Dr. Brink remarked that such permission has not always been sought. Dr. Brink further pointed out that journals often object to citing publications such as the Drosophila Information Service and the Maize News Letter because of the informal nature of their communications and the general lack of availability of copies. It was the general sentiment of the group that the chief value of the Newsletter derives from its informal communication of preliminary data and that it might best be continued in its present form, retaining the admonition on the cover against citing included data without express permission.

Dr. E. G. Anderson led a discussion of the placement of genes to chromosomes and emphasized the need for locating and mapping the large number of unplaced genes which have accumulated. He advised that the job be done in two steps, first, the placement of genes to chromosome and, second, their location in linkage groups. For the first of these steps, he suggested the use of a selected series of reciprocal translocations marked with the gene wx as a screening method, and outlined the procedure involved. He suggested that the second step, chromosome mapping, could be carried out most efficiently after a considerable number of traits had been assigned to individual chromosomes. It was his opinion that chromosomal placement of the bulk of the new genes can be accomplished within the next two years. Dr. Anderson offered to make crosses of his translocation stocks with unplaced genes supplied by maize workers, with further testing to be done by the cooperators. Dr. E. R. Leng asked what procedure was proposed in publishing linkage data obtained through such a cooperative arrangement. Dr. Anderson indicated that cooperators using the technique might individually publish the results they obtained.

A discussion of chromosome mapping was directed by Dr. C. R. Burnham, who pointed out that the last attempt (1941) to assign individual responsibility for the mapping of each of the chromosomes met with varied success. Dr. Burnham asked for the views of the group concerning the effectiveness of this procedure. Dr. Anderson offered the opinion that many of the new traits are probably not worth mapping in detail unless they prove to be in poorly marked chromosome regions, but suggested they be kept in stock for the use of persons interested in specific chromosome segments. Dr. Rhoades urged to general approval that only good traits be saved. Dr. Laughnan then asked for a show of hands of those willing to participate by agreeing to map specific chromosomes. The following people volunteered to assume responsibility for individual chromosomes:

Chromosome 1S	Brink;	1L	Galinat
"	2		Burnham
"	3		Laughnan
"	4		Mangelsdorf
"	5		Burnham, Dempsey
"	6		Kramer
"	7		Morris
"	8		Wright
"	9S	Coe;	9L Anderson
"	10		Rhoades

The group agreed with Dr. Laughnan's observation that others should be welcomed and encouraged to help in these mapping studies. Dr. Coe asked what distribution should be made of new traits which were placed to chromosome, and Dr. Anderson suggested that stocks be sent both to the Maize Cooperative and to the person responsible for mapping the particular chromosome.

In regard to future publication arising from linkage studies, Dr. Wright stressed the need for a more complete description of genetic traits. It was proposed by Dr. Brink, and approved by the group, that Dr. Patterson take responsibility for assembling gene descriptions. As a first step, it was suggested that a tentative preliminary listing of genes with descriptions of such features as their expression, viability, and classifiability be circulated among maize geneticists for suggested additions and modifications.

Dr. Wright brought up the question of the membership of the Coordination Committee, and proposed that the current Committee members be continued, with the addition of Dr. Patterson as Secretary, ex officio. Dr. Rhoades moved the approval of these members. Seconded and passed. The Committee members retained are as follows: Dr. Burnham (President), Dr. Laughnan, Dr. Anderson, Dr. Wright, and Dr. Eckhardt.

E. B. Patterson

II. SYMPOSIUM ON GENETICS IN PLANT BREEDING

You may be interested in knowing that the Brookhaven National Laboratory is sponsoring a symposium on Genetics in Plant Breeding from May 21-23 inclusive. The topics listed for discussion are: (I) Uses of Changes in the Chromosome Complement, (II) Applications of Studies in Quantitative Inheritance, (III) Use of Self-Incompatibility and Male Sterility, (IV) Use of Radiation Induced Mutations, and (V) Use of Natural and Induced Variability. Further information concerning this symposium should be sought from H. H. Smith, Brookhaven National Laboratory, Upton, Long Island, New York.

III. REPORTS FROM COOPERATORS

CALIFORNIA INSTITUTE OF TECHNOLOGY
Pasadena 4, Calif.
and
PIONEER HI-BRED CORN COMPANY
Johnston, Iowa

1. Use of translocations to locate fertility restorer genes.

A test cross utilizing translocation 3-9_{F24} has shown a close linkage between the translocation locus and the major fertility restorer (FR) factor of the inbred WG3. (See table 1.) WG3 restores fertility to the T type of cytoplasmic pollen sterility. Test crosses with translocations 1-9c, 1-9, 6-9 and 7-9 showed no apparent linkage.

Table 1. wx WF9^T/wx 3-9 (R4) F-24 ear no. 54-2799-1
WG3 2784-4

Kernel type	Row No.	Number of Plants			Total
		Sterile	Partially Fertile	Fertile	
Non-waxy	222	4	0	19	23
	223	<u>5</u>	<u>3</u>	<u>18</u>	<u>26</u>
	Total	9	3	37	49
Waxy	224	23	1	4	28
	225	<u>17</u>	<u>0</u>	<u>4</u>	<u>21</u>
	Total	40	1	8	49
Grand Total		49	4	45	98

The limited data in table 1 indicate about 11% crossovers between the translocation and the FR locus, after allowing for misclassifications due to crossovers between wx and the translocation locus (about 7.3%), minus about 1% correction due to double crossovers involving translocation, wx and FR loci. Since translocation 3-9_{F24} is near the middle of the long arm of chromosome 3 (3L .46) this would place the FR locus about 11 crossover units either side of that location. It is interesting to note that Snyder (Maize News Letter, 1955) placed a restorer gene for T cytoplasm in about the proximal third of the long arm of chromosome 3. The FR line he tested was a marker stock, Coop 50-32. A test cross for allelism between the FR locus of WG3 and the FR locus of Coop 50-32 is being made (in cooperation with Dr. J. E. Wright, Jr.) and will be grown in 1956.

Additional test crosses utilizing other translocations, including 3-9c which tests a different location on the long arm of chromosome 3, have been made and will be grown in 1956.

E. G. Anderson
Donald M. Duvick

CALIFORNIA INSTITUTE OF TECHNOLOGY
AND UNITED STATES DEPARTMENT OF AGRICULTURE
Pasadena 4, California

1. Cytological observations on translocations preceding the Bikini and Eniwetok series. Revision of list given in 1952 News Letter.

Symbol	Temporary designation	Cytological determination	Symbol	Temporary designation	Cytological determination
1-2b		1S.43 2S.36	1-6a		1L.21 6L.59
c		1S.77 2L.33	c		1S.25 6L.27
d	17	1S.78 2L.56	d	Conn R-28	1L.13 6S.74
e	B-75	1S.61 2L.47	e	A-80	1S.37 6L.21
1-3a		1S.19 3L.14	f	B-92	1L.32 6L.42
c		1S.14 3L.14	g	F-30	1L.16 6L.84
d		1L.67 3S.81	h	X-41-13	1L.03 6L.17
e	A-33	1L.58 3L.45	1-7a		1L.28 7L.13
f	B-2	1L.17 3L.11	b		1L.53 7S.12
g	B-104	1L.17 3L.13	c		1L.39 7L.14
h	C-15	1S.12 3L.11	d		1L.81 7S.44
i	C-43	1L.68 3S.30	e	42	1L.39 7L.11
j	F-10	1L.11 3L.13	f	A-69	(1S.72 7L.80
k	G-3	1S.17 3L.34			(1S.10 7S.50
1-4a		1L.51 4S.69	g	B-49	1S.79 7S.22
b	Conn R-29	1S.55 4L.83	h	B-94	1L.46 7L.19
c	A-57	1L.33 4S.23	i	I-17	1S.31 7L.26
e	B-89	1L.45 4S.27	j	X-55-16	1L.20 7L.61
f	C-46	1L.25 4L.16		A-37	1L.10 7L.56
g	C-49	1L.95 4L.35	1-8a	Conn R-20	1L.41 8S.52
h	X-22-61	1S.94 4L.52	b	B-42	1L.59 8L.82
	K-40	1S.13 4S.42	c	B-49	1L.94 8L.89
1-5a		1L.52 5S.42	1-9a		1S.13 9L.15
b		1S.17 5L.10	b		1L.50 9L.60
c		1L.34 5L.29	c		1S.48 9L.22
e	A-90	1L.03 5L.09	d	I-9	1L.42 9L.25
f	D-5	1L.07 5L.09	1-10a		1L.29 10L.33
g	I-24	1L.58 5S.85	b	Conn R-41	1L.19 10S.39
h	X-1-37	1L.18 5L.53	c	A-50	1L.43 10L.74
i	X-23-2	1S.71 5S.74	d	A-84	1L.50 10L.68

Symbol	Temporary designation	Cytological determination		Symbol	Temporary designation	Cytological determination	
e	B-98	1L.16	10L.31	e	C-40	2L.07	8L.10
f	C-36	1S.04	10L.30	f	C-57	2 near cent.	8 near cent.
g	C-47	1S.80	10L.21				
	B-29	1L.93	10L.26	g	G-2	2L.71	8S.71
2-3b		2L.45	3L.08	h	X-42-32	2L.23	8L.22
c		2S.46	3S.52		84	2L.32	8L.30
d		2L.67	3L.48	2-9a		2S.36	9L.58
e		2S.76	3L.48	b		2S.18	9L.22
f	A-61	2L.35	3S.60	c	C-61	2S.49	9S.33
g	F-35	2L.21	3S.21	d	H-7	2L.83	9L.27
h	K-7	2L.05	3L.08	2-10a	2-8 ²	25-27 2L.16	11-22 10L.55
2-3-6	I-10	2L.19	3S.51	b		2S.50	10L.75
2-4a		2L.30	4L.21	I-3		2L.30	10S.40
b		2L.81	4L.53	A-21		3L.07	4L.85
c		2L.81	4S.09	3-4		3L.28	5L.60
d		2L.17	4L.45	3-5a		3L.61	5L.57
e	Conn R-42	2L.31	4S.47	b		3L.62	5L.27
f	A-29	2L.75	4L.12	c		3S.34	5S.16
g	C-31	2L.13	4S.31	e	A-101	3L.01	5S.73
j	K-10	2S.19	4L.34	g	X-4-108	3L.55	5L.22
k	X-1-1	2L.13	4L.04	h	X-7-38	3L.23	5L.20
l	X-2-64	2L.56	4S.51	B-104		3L.06	6L.30
m	X-47-41	2S.34	4S.47	3-6a		3S.73	6S.82
2-5a		2L.16	5L.18	b		3S.56	6L.54
b		2L.06	5S.09	c	Conn R-34	3L.23	6L.82
c	Conn R-50	2L.16	5S.48	d	A-53	3S.25	7L.18
d	A-74	2L.91	5L.86	3-7a		3S.92	7L.03
e	B-69	2S.19	5L.28	b		3L.46	7L.45
f	K-3	2L.91	5L.10	c		3L.64	7L.81
g	X-14-122	2S.79	5S.24	d	C-75	3L.25	7S.56
	A-16	2L.34	5S.30	e	F-25	3L.41	8L.61
2-6a		2L.28	6L.20	3-8a		3L.16	8L.23
b		2S.69	6L.49	b		3S.23	8L.85
c		2L.32	6L.23	c	Burnham	3S.36	8L.21
d		2L.41	6L.45	e	A-22	3L.08	8L.10
e		2L.18	6L.20	f	A-104	3L.12	8L.19
f	84-2	2L.79	6L.87	g	B-37	3L.53	8S.46
	78	2L.19	6L.29	h	X-23-26	3L.11	9L.16
2-7b		2L.37	7L.12	3-9a		3L.48	9L.53
c		2L.48	7S.50	b		3L.09	9L.12
d	B-108	2L.16	7L.18	c		3L.13	9L.26
e	C-44	2L.82	7L.63	d	A-41	3L.06	9L.26
f	F-29	2L.34	7L.70	e	A-94	3L.63	9S.69
2-8b	A-1	2L.20	8L.18	f	B-103	3L.40	9L.14
c	A-36	2S.15	8S.11	g	F-24	3L.09	9L.33
d	C-24	2L.05	8L.10	h	X-23-158		

Symbol	Temporary designation	Cytological determination	Symbol	Temporary designation	Cytological determination
3-10a		3L.16 10L.22	5-8a		5L.49 8S.58
b		3L.61 10S.25	b	84	5S.23 8L.23
c		3L.22 10L.30	c	B-10	5S.24 8L.20
4-5a		4L.19 5S.29	d	B-18	5S.55 8L.12
b		4L.76 5L.68	f	C-52	5L.02 8S.08
c		4S.34 5L.27	g	X-27-87	5L.28 8S.44
d		4S.21 5L.22		A-50	5S.07 8L.11
e	Conn R-18	4S.41 5S.32	5-9a		5L.59 9S.17
g	Conn R-32	(4L.27 5S.70)	b	X-7-39	5L.68 9L.44
h	B-2	(4S.48.5) 5L.30	c	X-10-6	5S.07 9L.10
i	B-74	4L.13 5L.08	d	X-11-73	5L.34 9L.10
j	X-6-77	4L.20 5S.15	e	X-14-111	5L.46 9L.74
k	X-19-5	4L.21 5L.36		B-94	5S.17 9L.27
4-6a		4S.06 5L.13		B-91	5L.23 9L.21
b		4L.37 6L.43	5-10a	A-49	5L.14 10S.54
c		4S.80 6L.16	b	B-70	5L.09 10S.25
d	Conn R-43	4S.33 6S.83		X-57-16	5S.42 10L.42
e	X-57-31	4L.49 6L.53	6-7	X-1-31	6L.73 7L.68
4-7a		4S.62 6L.56	6-8a		6L.41 8L.80
4-8a		4S.32 7L.07	b	B-83	6L.79 8S.76
b	X-17-108	4S.59 8L.19	c	C-59	6L.27 8L.50
4-9a		4S.18 8L.16	d	D-1	6L.51 8L.77
b		4L.18 9L.50.58	6-9a		6S.79 9L.40
c	bp	4L.90 9L.29	b		6L.10 9S.37
d	A-26	4L.82 9L.29	c	A-66	6L.15 9L.29
e	A-52	4L.12 9L.17	d	C-23	6S.73 9L.82
f	D-25	4S.53 9L.26	e	X-25-78	6L.18 9L.24
g	F-22	4L.55 9L.18	6-10a		6L.75 10L.15
4-10b		4S.27 9L.27	b		6L.12 10L.29
c	B-45	4L.15 10L.60	c	A-23	6L.51 10S.36
d	G-1	4S.64 10L.18	d	C-27	6L.16 10L.29
e	K-17	4S.36 10L.36	e	D-13	6L.14 10S.43
f	X-12-57	4L.14 10L.13.14	f	I-22	6S.92 10S.28
5-6a		4L.94 10L.14	g	X-17-15	6L.85 10L.20
b		5L.35 6L.43	h	X-46-13	6L.47 10L.87
c		5L.72 6L.21	7-9a	A-76	7L.63 9S.07
d	A-75	5S.81 6L.08	b	F-11	7S.76 9S.19
e	A-77	5S.54 6S.91.87	c	X-56-86	7L.14 9L.22
f	X-23-41	5L.11 6L.60	7-10a	D-36	7L.23 10L.06
5-7a		5S.37 6S.76	8-9a		8L.13 9L.38
b		5L.78 7L.72	b		8S.67 9L.75
c		5L.18 7S.36	c	C-12	(8L.14 9L.16)
d		5L.42 7L.72	d	X-22-92	(8S.38.4) 9S.26
e	B-21	5S.63 7S.33	e	X-26-8	8L.09 9S.16
f	X-27-44	5S.40 7S.18			8S.32 9L.25
		5L.80 7L.85			

Symbol	Temporary designation	Cytological determination	Symbol	Temporary designation	Cytological determination
8-10a		8L.48 10S.5	9-10a		9L.14 10L.92 ✓
b		8 cent 10 cent	b		9S.13 10S.10 .40
c		8L.41 10S.56	A-75		9L.28 10L.34 .30
d	F-1	8L.39 10L.16			
e	F-33	8L.84 10S.37			
	K-7	8L.07 10S.22			

E. G. Anderson
Albert E. Longley

2. Glossy

- gl₉ - Stock of gl₉ from Sprague showed a very good glossy. Chromosome tests place it in chromosome 7. Allele tests with gl₁ will be needed to determine if this is gl₉ or if gl₁ has crept in during the building up of our stock.
- gl₁ Stadler 3 - Stock from Burnham. Chromosome 5. An allele test with gl₈ gave only normals so should be non-allelic.
- gl₁₀ - Stock from Sprague. Tests indicate chromosome 5. As gl₈, gl₈₋₃, and gl₁₀ are all good glossies, adequate allele tests are needed.
- gl₁₆ - Tests indicate chromosome 4.
- gl₇ - Tests indicate chromosome 4. Since gl₃ and gl₄ are both established in chromosome 4, it is essential that any possible allelism be checked.

E. G. Anderson

3. Dwarfs

Chromosome 1

Three dwarf mutants from radiation material have been placed in chromosome 1. These are tentatively listed as midget 8043, tiny 8446 and dwarf 4963.

Midget 8043 in the seedling stage has a blunt first leaf and a broad pointed second leaf. Both leaves are about 1/2 normal size with undulant margins. When fully grown, midget 8043 is up to 2 ft. tall, is contorted in appearance but produces pollen and small ears.

Both tiny 8446 and dwarf 4963 in the seedling stage are much smaller than dwarfs 1, 2 or 3. In the seedling stage, tiny, the smallest of all dwarfs grown here, has narrow sharp-pointed leaves, whereas dwarf 4963's leaves are short and blunt. They both grow at most a few inches tall. We have not, as yet, succeeded in growing these 2 mutants to maturity.

Chromosome 2

Dwarf 5232 resembles the original dwarfs 1, 2 and 3. It first appeared in Bikini material and was placed in chromosome 2 by translocation tests as reported in the 1955 News Letter.

During the past season linkage tests were carried out with Dwarf 5232 and B. A testcross of B d gave a total of 48 crossovers out of 306 plants or 15.7% crossovers. ⁺This is close to the expectation for the B - d₅ linkage from the recorded information of Emerson, Beadle and Fraser. If no stocks of d₅ are in existence, this may well be substituted for d₅.

Note 1

The dwarfs tested by Dr. B. O. Phinney of U.C.L.A. (See this News Letter) for response to gibberellic acid were:

Dwarf 1, An 1 and Dwarf 5232 showing positive response.
Dwarf 4963 showing no growth response.

Note 2

We would be glad to receive seed of Dwarfs 4, 5 and 7 if any is in existence.

Fred D. Pettem

4. Mutants with altered carotenoid synthesis.

Linkage data has been accumulated on the mutants having an altered carotenoid composition in endosperm (white to pale yellow) and seedling (albino).

	Parental Classes	Recombination Classes			Total	% Recombination	
		Region	Region	Region		Region	Region
		1	2	1&2		1	2
<u>vp</u> ₂ - <u>gl</u> ₈	150	67	--	--	217	30.9	--
<u>vp</u> ₂ - <u>A</u> ₂	161	13	--	--	174	7.5	--
<u>ps</u> - <u>gl</u> ₈	69	12	--	--	81	14.8	--
<u>wx</u> - T5-9a - <u>ps</u>	104	5	42	0	151	3.3	27.8
<u>su</u> - T2-4c - <u>w</u> ₃	350	16	4	2	372	4.8	1.6

	Parental Classes	Recombination Classes			Total	% Recombination	
		Region	Region	Region		Region	Region
		1	2	1&2		1	2
$\underline{ts}_1 - \underline{v}_4 - \underline{w}_3$	37	14	17	4	72	25.1	29.2
$\underline{B} - \underline{v}_4 - \underline{w}_3$	57	36	25	6	124	33.9	25.0
$\underline{su} - T1-4a - \underline{lw}_1$	194	0	51	0	245	0	20.8
$\underline{wx} - T1-9a - \underline{lw}_1$	14	2	15	0	31	6.5	48.4
$\underline{Kn} - \underline{lw}_1$	28	0	--	--	28	0	--
$\underline{wx} - T5-9c - \underline{lw}_2$	44	2	3	1	50	6.0	8.0
$\underline{gl}_8 - \underline{lw}_2$	208	0	--	--	208	0	--
$\underline{wx} - T3-9c - \underline{cl}_1$	373	5	20	0	398	1.3	5.0
$\underline{A}_1 - \underline{cl}_1$	125	108	--	--	233	46.4	--
$\underline{lg}_2 - \underline{cl}_1$	127	31	--	--	158	19.6	--
$\underline{ra}_2 - \underline{cl}_1$	16	3	--	--	19	15.8	--

Our mutant 7748 has been placed on chromosome three. A mutant with pale endosperm and pale green seedling (8549) has proved to be allelic to \underline{y}_1 .

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1. Dwarf mutants in maize and their growth response to a new plant hormone, gibberellic acid.

Gibberellic acid as well as a mixture of gibberellic acid and gibberellin A was applied to the leaves of a number of genetically different dwarfs. Results show that some mutants will respond by normal growth while others respond only slightly or not at all. Mutants will respond to as little as .01 micrograms of gibberellic acid per plant. With this amount normal seedlings give no growth response. With 10 micrograms of gibberellic acid per mutant, elongation is evident within 24 hours following treatment. This growth response is apparently confined to tissues that have not reached final differentiation. A continuous supply of gibberellic acid is necessary to maintain normal growth of the mutants. For the mutant, dwarf-1, treated plants reach a mature height very close to that of treated and non-treated normals, with leaf size and shape, leaf color, and internode length of treated mutants being very similar to

normals. While normals show a growth response with higher amounts of gibberellic acid, treated mutants reach a height very near to that of treated normals.

Table I. Growth response of mutant seedlings to a single application of 10 micrograms of gibberellic acid per plant. Treatments given at the time of emergence of the first leaf from the coleoptile. Response recorded 10 days following treatment. Response (+) if mutants reach the same height as treated normals, (\pm) if mutants show a response but do not reach the height of treated normals, and (-) if mutants show no response or only a very slight response.

<u>Mutant*</u>	<u>Linkage group</u>	<u>Response</u>
anther ear-1	I	+
dwarf (7281)	I	+
dwarf (4963)	I	-
dwarf (5232)	II	+
dwarf-1	III	+
nana-1	III	\pm ?
dwarf (8201)	IX	+
tiny (8446)	I	-
Dominant Dwarf	unknown	-

*Dominant Dwarf was obtained from Dr. R. R. Seaney, the mutant having originally been found by Dr. G. H. Stringfield. All other stocks were provided by Dr. E. G. Anderson and Dr. F. D. Pettem, who have also provided the linkage information. See also the linkage data reported by Dr. Pettem on page 10.

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1. Further study of the a_1^{m-1} - Spm system.

A general outline of the system of control of gene action at a_1^{m-1} was given last year in this News Letter, and transpositions of the controlling element, Spm, were mentioned. To determine Spm constitutions in the cells of different parts of a plant, several ears of a single plant were utilized in test crosses. From 101 plants, tests of two ears per plant were obtained. In 95 plants, the number of Spm elements was the same in the cells that produced each ear (63 with 1 Spm; 26 with 2 Spm; 6 with 3 Spm). In 6 plants, the Spm constitution was not the same in the cells that gave rise to each ear (1 case of 1 Spm in one ear

and no Spm in the other; 3 cases of 1 Spm in one ear and 2 Spm in the second; 2 cases of 1 Spm in one ear, the second ear having a sector with no Spm). From 12 other plants, tests of three ears per plant were obtained and correspondence in number of Spm elements was evident in each of the 3 ears of 11 of them (6 with 1 Spm; 4 with 2 Spm; 1 with 3 Spm). In one plant, the cells that gave rise to two ears contained 1 Spm element but 2 Spm elements were present in the cells that gave rise to the third ear.

Tests were made of Spm constitutions in the progeny of plants in which 1, 2, or 3 Spm elements were known to be present. One test of 238 individuals derived from plants having 1 Spm element will illustrate the nature of the results obtained. The parent plants carrying Spm had been crossed by plants homozygous for a_1^{m-1} but having no Spm. Kernels on the resulting ears that showed the presence of Spm in the endosperm were selected and the plants grown from them were again crossed by plants homozygous for a_1^{m-1} but carrying no Spm. On the ear produced by 7 of these plants, no kernels having Spm appeared. One Spm element was present in 205 plants, 2 Spm elements were present in 20 plants and in 6 plants, 3 Spm elements were present. Also, tests were conducted to determine the position of Spm in the progeny of plants in which the location of Spm was known. In the majority of such tests, the Spm element occupied the same position in the chromosome complement as it had in the parent plant, with some exceptions, however, that were to be expected. In one such test, 103 individuals in the progeny of plants carrying Spm in chromosome 6 and showing approximately 35% recombination with Y, were examined. In 92 of these plants, 1 Spm was present and it showed the same linkage with Y as it had shown in the parent plants. Two plants had 2 Spm elements, one of which was linked with Y. Five plants had 1 Spm but it showed no linkage with Y, and 1 plant had 3 Spm elements whose linkage relationships could not be detected because of the high number of Spm elements that were present. In another test of 22 individuals in the progeny of a plant carrying Spm in chromosome 6 but showing, in this case, closer linkage with Y, 19 plants proved to have 1 Spm element and its location was similar to that in the parent plant. In two plants, 2 Spm elements were present and one of them was linked with Y. In the remaining plant of this culture, 1 Spm was present but it showed no linkage with Y. The table below will illustrate the nature of the tests conducted and the results obtained from them for this progeny of 22 plants.

$a_1^{m-1}/a_1^{m-1};$
 or Y/y ♀ x $a_1^{m-1}/a_1^{m-1}; y/y;$ No Spm ♂
 $a_1^{m-1}/a_1;$

Plant No.	Pale aleurone (No Spm)		Colorless aleurone with spots of A_1 (Spm present)		Totals	Germinal Mutations
	<u>Y</u>	<u>y</u>	<u>Y</u>	<u>y</u>		
A. One Spm, linked with Y						
1	38	132	114	44	328	1
2	27	161	144	27	359	
3	31	172	154	17	374	3
4	28	186	150	18	382	
5	48	125	130	32	335	
6	40	234	222	54	550	
7	30	196	151	34	411	
8	51	238	230	46	565	
9	37	174	174	53	438	
10	32	157	149	25	363	
11	43	113	125	40	321	
12	41	153	155	32	381	
13	34	164	199	51	448	
14	45	161	155	38	399	
15	20	156	139	24	339	
16	23	136	154	34	347	
17	35	192	164	44	435	
18	28	142	153	31	354	
19	52	172	171	40	435	1
Totals for						
A	683	3164	3033	684	7564	5
B. Two Spm elements, one linked with Y						
20	9	17	63	29	118	
21	30	101	252	152	535	
Totals for						
B	39	118	315	181	653	
C. One Spm, not linked with Y						
22	117	112	101	100	430	2

Similar results were obtained from tests of progeny of plants carrying Spm in chromosome 5 and showing linkage with Pr. However, in one other test of a small progeny of only 5 plants, quite aberrant results were obtained. In the parent plant, 1 Spm element was present and from the ratio of kernel types on the ear it produced, there was no evidence of linkage of Spm with alleles of Y, Pr, or Wx which were also segregating. In one of the 5 plants in this progeny, 2 Spm elements were present and one of them was loosely linked with Y. In each of the remaining 4 plants, 1 Spm element was present. It was very closely linked with Y in one plant. In another, it showed 35% recombination with Pr. In the third plant, it gave 33% recombination with Wx, and in the fourth plant, no linkage of Spm with any of these markers was noted. It is suspected that many transpositions of Spm occurred in the parent plant and at a time that was late in the development of its sporogenous cells.

On test ears, such as those described above, an occasional kernel may appear showing a markedly altered pattern of mutation. Some of them arise from a change in state of the a_1^{m-1} locus. Others, however, arise from modifications of another type. Several examples of the latter type of modification have received some study. One type appears relatively frequently and the evidence suggests that it may arise from a change in the Spm element itself. In the presence of the modified element and in the absence of Spm, plant tissues show pigmentation but the aleurone layer is almost totally colorless, only a few specks or dots of color appearing in it. When both the modified element and Spm are present in the same plant, the action of Spm is dominant to that of the modified element and clear-cut segregations of these two different controlling elements are observed. Like Spm, the modified element may occupy different positions within the chromosome complement. Other types of modifiers have also arisen and in the same general manner. Their presence results in altered distributions of pigmentation in the plant tissues and in the aleurone layer of the kernels and also in an altered time and frequency of occurrence of mutations at the locus of a_1^{m-1} in these tissues.

2. Further study of Ac control of mutation at the bronze locus in chromosome 9.

In last year's News Letter, a case was described of control by Ac of gene action at the bronze locus in chromosome 9. This case has been further examined and evidence was obtained suggesting a relationship between an apparent direct Ac control of gene action and indirect control of this action, such as that exhibited by the Ds - Ac two element system where the Ds element directly controls types of modification in gene action but does so through the influence that Ac exerts on it. As mentioned last year, the recessive bz in this case was capable of mutating to higher alleles of Bz as well as to stable recessives, and control of this process was found to be associated with the presence of Ac at the locus. The relatively simple types of change in gene action are those that give rise to stable dominants or to stable recessives. Altogether, 14 independent mutations to a stable dominant were examined. In all 14 cases, mutation to Bz was associated with removal of Ac from

the bronze locus. In 6 cases, it was not present in the gamete that carried the Bz mutant. In the remaining 8 cases, Ac was present in the gamete but its location was altered. In 4 of these 8 cases, the Ac element showed no linkage with markers in the short arm of chromosome 9. In the 4 other cases, Ac was linked to these markers. In 3 of them, it was located several crossover units to the right of Bz and in one case it was located very close to Wx.

Twenty-four cases of mutation to a stable recessive were examined. In 9 of these cases, Ac was absent in the gamete that carried the stable recessive. In 5 cases, one Ac was present but it showed no linkage with markers in the short arm of chromosome 9. In 9 cases, one Ac was present and it showed linkage with markers in the short arm of chromosome 9. In 2 of these 9 cases, Ac was located close to Wx, and in one case, it was located very close to sh. In the remaining 6 of these 9 cases, its exact location was not determined; it was linked with Wx and showed from 20 to 30% recombination with it. In the remaining case, two Ac elements were present, one located close to but to the right of bz, the other showing no linkage with markers in the short arm of chromosome 9.

Two cases were found in which control of mutation at bz had changed from apparent direct Ac control to indirect control by this element. In all essential respects, the system of control of mutation in these two cases is the same as that exhibited by the Ds - Ac two element system. Ac is not present at the locus of bz but its presence in the chromosome complement is necessary for mutations to occur there, and the time of their occurrence reflects the Ac dose in the cells.

In addition to the mutant types mentioned above, two cases of mutation to an unstable dominant, Bz, were examined. In both of them, Ac was present and located at or close to Bz. Examination of a number of derivatives of one of them was made and the types of modification found are listed below:

1. Change to a stable dominant associated with removal of Ac from the Bz locus,--apparently a frequent occurrence but only 3 cases examined in detail.
2. Change to a mutable recessive, bz. 8 cases examined. All had Ac at the bz locus. Mutations controlled by Ac. Marked change in Ac dose action was exhibited by 4 of these cases.
3. A change in state of the Bz locus recognized by a very high rate of mutation from Bz to bz. Ac present at or close to the Bz locus and the mutation process controlled by it.
4. Appearance of a high rate of Ds-type chromosome breaks at a position a few crossover units to the right of Bz. The Bz phenotype is stable. Ac occupies the locus where the Ds-type breaks are occurring. Twelve derivatives of this particular modification that showed no breaks

or a reduced frequency of them were examined. In 2 cases, Ac was not present in the plant. In 6 cases, the location of Ac was apparently unchanged but Ds-type breaks were very much reduced in frequency or did not occur. In the remaining 4 cases, 2 Ac elements were present, one at or close to the former location and one located elsewhere (the second Ac element was close to wx in two cases and not linked to markers in the short arm of chromosome 9 in one case.).

5. Appearance of an intermediate allele giving a weak Bz expression. Ac no longer present at the locus. However, if Ac is present somewhere in the chromosome complement, mutations occur at this locus to give alleles expressing higher or lower levels of the Bz phenotype. This intermediate allele is stable in the absence of Ac.

6. Mutability of a component of the Bz locus detected in kernels that are C sh bz wx ds/C sh bz wx ds/I Sh BzAc Wx Ds in constitution. Breaks at Ds in the I Sh BzAc Wx Ds chromosome during development of the endosperm produce areas that are C sh bz wx in phenotype. When the normal Bz locus is present, such areas have rims showing the Bz phenotype due to diffusion of a substance produced in the surrounding I Sh Bz Wx cells in response to the presence in them of Bz. In the case here considered, only short, interrupted streaks of the Bz phenotype appear in the boundary rims of the C sh bz wx areas. In kernels that are I Sh BzAc Wx Ds/I Sh BzAc Wx Ds/C sh bz wx ds in constitution, the majority of C sh bz wx areas show either no Bz streaks in the rim cells or only an occasional very small streak. However, in kernels that are C BzAc/C bz/C bz in constitution and in the plants derived from them, full Bz color appears. This suggests a possible dual activity of the genic materials at the Bz locus and, in this case, mutability is being expressed by only one of these components.

3. Degree of spread of mutation along the chromosome induced by Ds.

When Ds is located immediately to the left of Sh in chromosome 9 it induces, in the presence of Ac, changes in action of genic materials located to either side of it. Ds is retained following such an event and it is unaltered in its location. A number of mutations of Sh and simultaneous mutations of both Sh and Bz have been examined in the past, as well as those changes that affect the genic materials located to its left and extending into the I locus. In order to expand the study of spread of mutational change along the chromosome, plants having Ds-induced modifications of gene action in the segment which extends to its left and includes the I locus were used in crosses in order to isolate from these plants some cases in which Sh or both Sh and Bz, located to the right of Ds, were subsequently modified. Three cases of modification of Sh expression but not that of Bz were isolated and examined. In two other examined cases, both Sh and Bz were modified in their expression to give the recessives, sh and bz. In none of these 5 cases was the position of Ds detectably altered as a consequence of the modifications

in gene action it induced, nor was the previously modified action of genetic materials, located to its left, altered by these events. Cytological examination of plants carrying these 5 modifications gave no detectible evidence of alteration of chromosome components within the affected segment. These cases indicate that Ds-induced change in gene action can spread along the chromosome to include a segment of chromosome extending from the locus of Bz to and including that of I.

4. Studies of instability of chromosome behavior of components of a modified chromosome 9.

A preliminary study was made of a modification affecting the organization of chromosome 9. This modified chromosome is composed of two independent segments. One segment includes the distal third of the short arm and will be called the fragment chromosome. The other segment is composed of the proximal two-thirds of the short arm and all of the long arm and will be called the deficient chromosome. The distal end of the fragment terminates in a knob and its proximal end is composed of a centromere from which a short piece of very deep-staining chromatin extends. These two independent segments carry the full genic complement of chromosome 9. The locus of C is carried in the fragment chromosome. That of Sh is very close to the end of the short arm of the deficient chromosome. The deficient chromosome is transmitted through the female gametophyte but its transmission through the pollen occurs only when the fragment chromosome is also present in the tube nucleus. Study of this modification was undertaken because the fragment chromosome undergoes many changes in constitution in somatic cells: "misdivision" of its centromere leading to loss or non-disjunction of the fragment; loss of the deep-staining component adjacent to the centromere or duplications of this component; ring chromosome formation; deletion of segments of chromatin composing the fragment; attachment of the fragment at its centromere region to the end of another chromosome, its own centromere being lost in the process; attachment of its centromere to that of another chromosome resulting in loss of an arm of the other chromosome; etc. These events affecting the fragment chromosome appear to be regulated in a manner somewhat similar to that which controls mutation at a "mutable locus." This is made evident in some isolates by the patterns produced by patches of colorless aleurone in a colored background that appear in kernels having one or two normal chromosomes 9 carrying c and a fragment chromosome carrying C. The colorless patches represent those areas in which C has been lost from the cells. The broken end of the deficient chromosome also initiates modifications that affect its own organization and also that of other chromosomes of the complement but the frequency of occurrence of such events appears to be lower.

In structural heterozygotes, crossing over occurs between the locus of C and the centromere of the fragment chromosome and isolates having c in the fragment chromosome have been obtained as well as isolates in which the C from the fragment has been introduced into a normal chromosome 9. Several sets of data suggest that a segment carrying sh and bz

may be included in the fragment. If so, the constitution of this modification includes a duplication of the segment that carries the loci of sh and bz for both Sh and Bz are present in the deficient chromosome. Plants carrying Bz both in the normal chromosome 9 and in the deficient chromosome and also a fragment chromosome, when crossed to plants homozygous for bz have produced ears on which kernels showing the bz phenotype have appeared in constant proportions. This is made evident in B of the following table:

A. ♀ C sh bz wx/C sh bz wx x ♂ sh Bz wx; normal chromosome,
Sh Bz Wx; deficient chromosome
 No Fragment.

B. ♀ " " x ♂ Same as A but fragment present.

Phenotype of kernel	A.	B. Plants 1 to 5					Totals for B
		1	2	3	4	5	
Sh Bz Wx	0	81	141	147	169	249	787
Sh Bz wx	0	4	15	12	27	33	91
sh Bz Wx	71	65	81	95	147	154	542 = 19.5% of sh Bz class
sh Bz wx	367	357	335	454	480	602	2229
sh bz Wx	0	2	1	1	3	2	9 = 21.9% of sh bz class
sh bz wx	0	5	3	6	6	12	32
Totals	438	514	576	716	832	1052	3690
% bz among sh class	0	1.6	0.95	1.2	1.4	1.8	1.4

Substantiating evidence of inclusion of sh and bz in the fragment chromosome was obtained from crosses of several plants having a normal chromosome 9 carrying c sh Bz wx, a fragment chromosome 9 carrying C, and a deficient chromosome 9 carrying Sh Bz Wx. When crossed by plants homozygous for c, sh, bz, and wx, the following phenotypes appeared among the kernels on the ears of these plants: 84 C Sh Bz Wx, 4 C Sh Bz wx, 53 c Sh Wx, 12 c Sh wx, 1 C sh Bz Wx, 35 C sh Bz wx, 5 C sh bz wx, 18 c sh Wx and 294 c sh wx. Among the 41 sh kernels in which C, originally carried in the fragment chromosome, was present, 5 were bz in phenotype. The duplicated region must be very short for cytological evidence of it has been difficult to substantiate. Also, mutation at the locus of Bz in the normal chromosome 9 from some event at meiosis associated with synapsis of the fragment chromosome with its homologous segment in the normal chromosome cannot be excluded, for it is known

from other studies of this modification that changes in expression of C, of Sh, and of Bz that cannot be accounted for by normal crossover processes, have occurred.

Barbara McClintock

The following publications by McClintock were not included in the list of recent maize publications given at the end of the News Letter:

McClintock, B. Intranuclear systems controlling gene action and mutation. Brookhaven Symposium in Biology 8: 58-74. 1955.

_____. Controlled mutation in maize. Carnegie Institution of Washington Year Book No. 54: 245-255. 1955.

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1. Preliminary results of tests designed to detect non-allelic gene interaction (Epistasis) in maize.

A definite answer to what type or types of gene action are involved in heterosis and quantitative inheritance has proved elusive. Experiments designed to obtain estimates of gene number, and degree of dominance have, in many cases, assumed that non-allelic gene interaction or epistasis was not involved. Epistasis would contribute to the non-additive portion of the genetic variance. These tests would be somewhat in error if epistasis were involved.

The proposed test to determine the presence of epistatic gene action involves crossing two inbred lines and the single cross between the two inbreds onto an unrelated tester as shown in the following example.

		<u>Expectation based on</u>		
		<u>Over-</u>		
		Dominance	Dominance	Epistasis
WF9	x Tester	90	90	90
38-11	x Tester	100	100	100
(WF9 x 38-11)	x Tester	95	95	100

Based on theoretical expectation, with any degree of dominance or over-dominance, the single cross x tester cross will always equal

the mean of the two inbred x tester crosses. However, if the performance of the single cross x tester cross deviated significantly from the mean of the two inbred x tester crosses, non-allelic gene interaction or epistasis must be involved.

This test determines the amount of epistasis that exists in the single cross, however the epistatic effect is reduced by one-half because of segregation. For example, if the single cross x tester cross differs from the mean of the two inbred x tester crosses by five bushels, then ten bushels of the yield of the single cross itself might be ascribed to epistatic gene action.

The test provides a minimum estimate of epistasis since the tester genotype may mask or cover up some epistatic alleles in the single cross. However, regardless of the tester genotype, if a significant deviation is detected between the single cross x tester and the mean of the two inbred x tester crosses, some sort of non-allelic gene interaction must be involved.

Some tests of this type were conducted in 1954, but were not harvested because of extreme drouth. The table below gives results of the 1955 tests conducted in replicated plots at two locations with the exception of group IV which was tested at one location.

Group	Pedigree	Yield	Epistatic Deviation ^{1/}	Ear Height	Epistatic Deviation ^{1/}
		Bu.		In.	
I	(B10 x C103)WF9	81.4		31.3	
	B10 x WF9	70.9	+4.9	26.9	+3.1**
	C103 x WF9	82.2		29.5	
	L.S.D. 5%	5.3		1.8	
II	(WF9 x 38-11)Hy2	77.6		25.9	
	WF9 x Hy2	73.4	+1.6	26.7	-1.5**
	38-11 x Hy2	78.6		28.2	
	L.S.D. 5%	N.S.		1.1	
III	(Hy x Oh41)WF9	81.0		31.5	
	Hy x WF9	77.1	+3.3	27.2	+3.1**
	Oh41 x WF9	78.3		29.7	
	L.S.D. 5%	N.S.		1.2	

**Significant at .01 level.

^{1/} Indicates amount the single cross x tester deviates from the mean of the inbred x tester crosses.

(Table continued on next page)

Group	Pedigree	Yield	Epistatic Deviation ^{1/}	Ear Height	Epistatic ^{1/} Deviation ^{1/}
		Bu.		In.	
IV	(L578 x GT112)F44	77.3		51.1	
	L578 x F44	71.1	+3.8	52.4	+3.7**
	GT112 x F44	76.0		42.5	
	L.S.D. 5%	5.4		1.4	
V	(WF9 x C103)Hy2	72.1		21.1	
	WF9 x Hy2	74.3	-5.7	21.4	- .3
	C103 x Hy2	81.3		21.5	
	L.S.D.	N.S.		N.S.	

Four of the five groups tested gave significant evidence of epistasis for ear height. None of the five groups gave significant deviations for yield. However, under a more favorable and less variable testing environment I feel significant results may have been obtained for yield.

It may be noted that group II showed "negative" epistasis for ear height. It is possible to have negative epistasis deviation and still the effect in the cross would show positive or plus heterosis for the character concerned.

Loyal F. Bauman

2. Inheritance studies on the "Kys" male sterility.

As originally reported by Schwartz (Genetics 36: 676-696. 1951) male sterile plants of the "Kys" sterile have (1) sterile cytoplasm, (2) dominant Ms_{21} gene, and (3) recessive suppressor gene s^{ga} . The alternative condition of any one of these factors would give normal fertile plants. Upon further testing it appears that a "specific" cytoplasmic factor is not involved or is not necessary for the expression of male sterility (Agronomy Journal 47: 189-191. 1955).

Schwartz also reported that the suppressor gene ($s^{ga}s^{ga}$) exhibited male gametophyte competition, i.e., recessive s^{ga} pollen could not compete with dominant S^{ga} pollen. The writer (Abstract paper 1953 Agronomy meetings) found that plants with the Ms gene and heterozygous for $s^{ga}s^{ga}$ could be identified by the presence of 50% of the pollen being partially filled with starch. The partially filled pollen grains (s^{ga}) abort and do not germinate.

Further tests revealed that apparently pollen of msms s^{ga}s^{ga} plants was normal and crosses showed transmission of recessive s^{ga} through the pollen to be regular. Therefore, it was only in the presence of dominant Ms that s^{ga} pollen was partially filled with starch and failed to germinate. The expression of partially filled pollen was not affected by different cytoplasm. Since a male gametophyte factor was not involved in the accepted sense, the ga superscript may possibly be eliminated.

Segregation of both genes is normal on the female side. The recessive s is not transmitted through the pollen in plants having Msms Ss genotype. Several examples of the results obtained and the theoretical pollen classification of the resulting plants are given below. Pollen classification of the parent plants is given in parentheses below the genotype.

Pedigree		Resulting Plants	
<u>Msms</u> <u>Ss</u> ♀ (Partial)	x <u>msms</u> <u>Ss</u> (Normal)	<u>Msms</u> <u>ss</u> <u>Msms</u> <u>Ss</u> <u>Msms</u> <u>SS</u> <u>mm</u> <u>SS</u> <u>mm</u> <u>Ss</u> <u>mm</u> <u>ss</u>	1 male sterile 2 partial pollen* 1) 1) 2) 5 normal pollen 1)
<u>Msms</u> <u>ss</u> ♀ (Male sterile)	x <u>msms</u> <u>Ss</u> (Normal)	<u>Msms</u> <u>ss</u> <u>Msms</u> <u>Ss</u> <u>msms</u> <u>Ss</u> <u>msms</u> <u>ss</u>	1 male sterile 1 partial pollen*) 2 normal pollen
<u>Msms</u> <u>Ss</u> ♀ (Partial)	x <u>msms</u> <u>ss</u> (Normal)	<u>Msms</u> <u>ss</u> <u>Msms</u> <u>Ss</u> <u>msms</u> <u>Ss</u> <u>msms</u> <u>ss</u>	1 male sterile 1 partial pollen*) 2 normal pollen
<u>MsMs</u> <u>SS</u> ♀ (Normal)	x <u>msms</u> <u>Ss</u> (Normal)	<u>Msms</u> <u>SS</u> <u>Msms</u> <u>Ss</u>	normal pollen partial pollen*
<u>MsMs</u> <u>SS</u> ♀ (Normal)	x <u>Msms</u> <u>Ss</u> (Partial)	<u>MsMs</u> <u>SS</u> <u>Msms</u> <u>SS</u>)) Normal pollen
<u>Msms</u> <u>Ss</u> (x) (Partial)		<u>MsMs</u> <u>Ss</u> <u>Msms</u> <u>Ss</u> <u>MsMs</u> <u>SS</u> <u>Msms</u> <u>SS</u> <u>msms</u> <u>SS</u> <u>msms</u> <u>Ss</u>	1) 2) 3 partial pollen* 1) 2) 1) 5 normal pollen 1)

*50% pollen partially filled

This last cross, giving an expected 5:3 ratio or 37.85% partially filled pollen plants in the F_2 , would explain the results from Nebraska in the 1955 Newsletter in which case they reported 31% of the F_2 plants had partially filled pollen.

Apparently some inbreds carry modifiers affecting the expression of the Kys sterile. Classification of partially filled pollen plants was difficult in some crosses. Crosses involving inbred M14 were irregular, but since these stocks were left at Illinois I have not been able to verify its behavior.

In summary, (1) the Kys sterile is apparently not dependent on a "specific" sterile cytoplasm, (2) Msms ss or MsMs ss plants are male sterile, (3) recessive s is not transmitted through the pollen in Msms Ss or MsMs Ss plants, (4) in segregating populations, Msms Ss or MsMs Ss plants can be identified, with a reasonable degree of accuracy, by the presence of 50% of the pollen grains partially filled with starch, and (5) pollen production and transmission of s is normal in msms Ss or msms ss plants.

Loyal F. Bauman

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1. Pollen restoration.

All sources of inbred I153 (from Iowa, Indiana, Minnesota, Wisconsin, Connecticut) restore pollen production to all T sterile inbreds and single crosses tested; 10 different single cross progenies and 12 different 3-way combinations were grown. In time of shedding in relation to silking, in sequence of anther dehiscence on the tassel, and in amount of pollen produced, restoration seemed to be completely normal on all plants grown. WF9T sterile restored by various sources of I153 were used as pollinators on several different sterile single crosses. Five progenies were grown and produced 39 completely fertile and 28 completely sterile plants indicating that I153 has one dominant gene capable of complete pollen restoration for the T type of cytoplasmic sterility.

When these same I153 lines were crossed on the S type of sterility, in single cross and 3-way combinations, all of the progenies were sterile. Either no anthers were produced or a few plants produced some anthers that were almost entirely devoid of well filled pollen grains. Therefore I153 is a good inbred to differentiate between S and T sources of cytoplasmic pollen abortion.

The three single cross combinations of Ky21, Txl27C and NC77 were used as pollinators on standard WF9T sterile single cross seed parents. In a total of 143 plants in 10 progenies all were normal in pollen production except four plants in one progeny which were completely sterile. These could be outcrosses. All three inbreds apparently have the same pollen restoring gene in common. Two of these same inbreds in combination with Oh41 produced 32 fertile and 25 sterile plants, and with A71 32 fertile and 35 sterile plants. Both Oh41 and A71 in combination with Ky21 and Txl27C add little or nothing to the pollen restoring ability of these good restorers.

Oh29, Oh41, A71, and M14 alone or in combination show partial restoration of the T type of sterility. The results are highly variable in combinations with different inbreds but the same combinations perform about the same when grown in widely different places throughout the northern corn growing regions from the Atlantic seaboard to the Missouri Valley.

Oh41 is a better restorer for the S than the T type of pollen sterility. Oh29 and A71 have not been tested on S adequately. M14 has no ability to restore the S type.

Good restorers when crossed on to T sterile inbreds show a wide range of segregation in F_2 selfed generation progenies varying from 3.75 to .50 fertile to 1 sterile plant. Oh41 on T sterile likewise segregates in F_2 selfed progenies varying from 1.50 to .25 fertile to 1 sterile. This indicates either variable number of complementary genes or variable potency.

An S sterile inbred (A158S) converted to fertility by outcrossing by Ky21 and backcrossing on the original S sterile inbred (A158SF4) has good restoring ability on other S sterile inbreds. Seven different progenies were grown. When tested on T sterile inbreds in seven combinations, six were completely sterile. One showed 11 fertile and 8 sterile plants. Therefore backcrossing four times on S sterile plants eliminated all of the T restoring genes in six out of seven backcrossed progenies and S and T restoration must be due to different genes.

D. F. Jones

CROW'S HYBRID CORN COMPANY
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1. Mutations affecting carotenoid synthesis in the endosperm and seedling.

In 1951, in a lot of approximately 1000 selfed ears of Inbred ML4, a single ear was found that segregated in a 3:1 ratio for white seeds. There were no intermediate yellow seeds, such as would have been the case if the parent seed had been outcrossed with white pollen. When the white seeds were planted, they all produced albino seedlings that soon died. By selfing ears produced from the yellow seeds, we continue to get ears that segregate for white.

In 1954, in a lot of about 800 selfed ears of Ohio 7, one ear segregated for light yellow seeds. When the light yellow seeds were planted, they all produced albino seedlings.

Neither mutation seems to have any tendency to be viviparous. The seeds are normal in size and germinate readily.

Seeds of these strains are being sent to California for testing with similar mutants that are being compared there.

2. Semi-dwarf.

In 1952, among some crosses that Dr. I. E. Melhus had brought us from Guatemala, two crosses segregated for a plant type that we have called semi-dwarf. These dwarfs are about five feet tall and are quite uniform. We have crossed them with a number of our inbred lines, and we will be growing the F₂ generation of these crosses this year. We think this mutant has some promise for producing short hybrids.

3. Twin shoots.

In 1950, my son, Robert Mumm, became interested in an inbred Guatemalan strain that occasionally produced twin shoots. When these shoots were selfed, they produced two very good ears at the same node. Considerable variation with respect to the character appeared in the next generation. Selection has continued for the most uniform twin ears, and now in the S₅ generation, about 60% of the population is twin-eared.

The twin ears develop independently of each other from separate ear buds. The stalk has a double ear groove at the node where the twin shoots appear.

This type of corn could be useful in studies where it would be desirable to produce selfed and crossed seed on the same plant at the same time.

W. J. Munn

ESCUELA NACIONAL DE AGRICULTURA
Lima, Peru

1. Races of maize in Peru.

The study of some 1,200 collections of Peruvian maize has been continued during the past year, aiming at the accumulation of biometrical, cytological, morphological, genetical and agronomical data.

Most parts of the country are rather well represented in these collections, except small specific areas in which more collecting has to be done.

As in other countries of Latin America, the races fall into two more or less distinct groups: those of the highlands and those of the lowlands. The latter, in turn, comprise two distinct subgroups, one representing the maize of the western coastal lowlands and the other the maize of the eastern lowlands.

There appear to be approximately thirty more or less distinct races of maize in Peru, and the majority of these are indigenous. There is little evidence here, as there is in Mexico and Central America, of the introduction of races of maize from other parts of the hemisphere. If corn did not originate in Peru, it has at least had a long history of independent evolution here.

Peru, like Mexico, has ancient indigenous races, of which there are three, or possibly four. All of these are popcorn, and are grown at high altitudes. One of these races, Confite Morocho, has a very slender, flexible cob and small, flinty grains which are sometimes round, sometimes pointed. Many ears have staminate tips. Some of the ears of this race have brown pericarp, in a rather pale form. This race could conceivably be the ancestor of the four ancient indigenous races of Mexico: Nal-Tel, Chapalote, Palomero Toluqueño, and Arrocillo Amarillo.

Another popcorn - Confite Puneño - with small, slightly fasciated ears, seems to have originated a group of races with grenade-type ears in the Andean highlands.

Peru appears to be the home of pericarp colors in maize. In one department, Ancash, there occur all the pericarp colors, described by

Emerson, Beadle, and Frazer. These colors are the product of three alleles at the A locus interacting with seven alleles at the P locus. In Ancash, brown is the predominating pericarp color.

There is an abundance of archaeological material in Peru, not only actual specimens of ears, tassels, and plants, but also numerous representations in ceramics, and stone. We have received permission to study and describe all of the specimens at the National Archaeological Museum in Lima, and will have the opportunity to see and photograph specimens in other museums.

Data and observations already accumulated in the studies of corn of the Paracas and Nazca Coastal cultures (800 - B.C. and 400 - A.D. respectively), indicate that two or possibly three races of pop-corn were grown in the coast of Peru long before the Spaniards arrived. Brown and red pericarp colors were universally present, although some cherry specimens have also been found. These two pop-corns are now found only in the highlands in living form, while the earliest distinctive coastal corn appears to be the product of hybridization accompanied by heterosis between these two highland races.

A form of pod corn, either the half-tunicate described by Mangelsdorf or the "semivestidos" reported by Andres, is quite common in some coastal varieties of Peru. We have picked up what appears to be an ear of true pod corn at the ruins of Pachacamac near Lima. A representation of a tiny ear which might well be pod corn is on display at the Museum in Cuzco. However, although present in Bolivia, modern true pod-corn, has not been found in any of our collections in Peru.

A tentative classification of the races of maize of Peru follows:

I. Ancient Indigenous races (Highland).-

1. Confite puntiagudo, short plants, often tillering; leaves with the highest venation index, 3.26
Condensed tassels, with few ramifications; ears usually with no pericarp color, pointed kernels.
2. Confite morocho, short plants, ears with slightly pointed or round kernels, flexible cob, pale brown pericarp color.
3. Confite puneño, very short plants, ears with round kernels, fasciated, elliptically (grenade-like) shaped, pericarp and aleurone color often present.

II. Highland races

4. Huayleño, related to Confite Puneno.

5. Paro, related to Confite Puneño; prominent characteristic is pointed kernels, floury, spreading spikelets.
6. Chullpi, sweet corn, related to Confite Puneño.
7. Morocho, has ears similar to Confite Morocho, enlarged in size. Is related to Sabanero of Colombia and Northern Peru.
8. Cuzco, ears distinctly 8-rowed, floury or flinty kernels, with a large number of sub-races, of which Cuzco gigante is an extreme type as to size of kernel.
9. Kculli, ears with 8 rows of pointed, cherry colored kernels.
10. Huancavelicano, with ears-8-rowed, pointed; related to Kculli.
11. Ancashino, ears longer in size than any other highland race, except Cuzco gigante, conically shaped, kernels round, and frequently with brown pericarp color.
12. Shajatu, related to Ancashino. Ears smaller than the latter, with purple aleurone color.
13. Sabanero, found in Northern Peru and in Colombia.

III. Intermediate races

14. Arequipeño, an intermediate in altitude and type between highland flour and coastal types. Found in Southern Peru.

IV. Coastal races.

15. Pagaladroga, with slender ears, red pericarp, similar to pre-historical coastal.
16. Perla, group of tall, tropical flint corn, probably related to Pagaladroga and Chocoseño from Colombia.
17. Alazán, floury- corn, red pericarp, drought resistant.
18. Pardo, ears with 8 rows of large, floury, kernels, similar to Tabloncillo of Mexico, and related to Cuzco.
19. Huachano, related to Pardo.
20. Chanceyano, floury corn, has highland and coastal influence.
21. Jora, floury corn; shows highland and coastal influence.

22. Rienda, characterized by long, flexible ears, similar to jungle corn.
23. Coruca, found in southern Peru only, with resemblances to Pardo.
24. Mochero, early flour - corn with highland and coastal influence.
25. Arizona, introduced race similar to Tuxpeño, well established in the northern coast.

V. Jungle races. -

26. Alemán, dent corn introduced nearly 100 years ago.
27. Piricincó, floury, long - eared, highly colored corn related to Coroico of Bolivia.
28. Chuncho, large yellow and white dent corn, with big butt - ears, similar to Salpor of Guatemala.
29. Chimlos, similar to Colombian Clavo and Caribbean Chandelle corn.

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1. The blotching system involving the c locus.

New data obtained during the past year require a revision of several statements made in the 1955 News Letter. Blotching is not the product of crossing maize and teosinte derivatives, since it is also produced when the original strain A158, involved in all of our teosinte derivatives, is crossed with a multiple gene linkage tester. There is also some doubt, as shown below, that it represents a mutagenic system.

Data presented last year showed that at least four loci, in addition to R, are involved in this blotching system which causes blotches of color to develop in the aleurone in the presence of recessive c. This has been verified by isolating tester stocks which are homozygous dominant for three of the four loci and homozygous recessive for the fourth. When two stocks differing in their recessive loci, both colorless, are crossed, blotching appears in the F₁ seeds. Three

such stocks have now been isolated. It is hoped to pick up the fourth in the Florida winter crop.

The existence of several loci in this system has been further verified by linkage tests which show that one gene for blotching is associated with Y on chromosome 6, another is linked with Su on chromosome 4, and a third is independent of these two chromosomes.

The data on linkage of Y and one of the Bh loci are in close agreement with those reported by Rhoades (M.N.L. 1948) which showed 30.2 percent of crossing over between Y and Bh. Rhoades also showed that a Bh gene is closely linked to Pl with 0.8 percent of recombination.

The doubt that this is a mutagenic system arises from the fact that the blotches are highly irregular, not at all like the mutant spots in the Dt or Ac-Ds system. Furthermore, not all of the aleurone cells in the blotches become completely colored; some are only slightly colored. These several facts suggest that we are dealing, not with somatic mutations, but with threshold effects. The blotching system acts to produce a substance which causes part of the c genes to elaborate color when normally only their dominant allele is capable of doing this.

Rhoades' experiment (M.N.L. 1945), in which he found less blotching when c was partially absent because of a deficiency, does not necessarily show that c is mutating. His results are susceptible to the threshold interpretation given above.

Paul C. Mangelsdorf

2. The blotching system affecting the r locus.

A similar system affecting the r locus causing blotches of color in the aleurone in the presence of recessive r was reported last year to involve at least two loci. It now appears that it involves at least seven loci, one of which has an allele which acts as a complete inhibitor to the system.

When stocks segregating 9:7 for blotching were crossed with Indiana P39, Mendelian ratios approaching 3:1, 9:7, 27:37, 81:175, 243:781 were obtained, indicating segregation for 1, 2, 3, 4, and 5 loci, respectively.

When similar stocks were crossed with a white P39, being developed by Pearson and still heterozygous, ratios approaching 243:781, 729:3367, and 2187:14,197, corresponding to segregation at 5, 6, and 7 loci, respectively, were obtained. These ratios are still to be verified by backcrosses and progeny tests; but, since evidence for at least four loci has already been obtained in the c blotching system, it is not unlikely that the wider ratios in the r system will prove to involve a greater number of loci.

When similar plants were crossed to Connecticut P39, the F_1 seeds were all non-colored, indicating the presence in this strain of P39 of a dominant inhibitor. The F_2 results verify this; however, the expected ratio of 3:13 was modified to 1:3, indicating that the inhibitor is an allele of one of the Bh genes. Percentage of blotched seeds varies from 25 to 7.5 percent. The ratios correspond to those obtained in the crosses with Indiana P39, except that, because of the presence of the inhibitor, only one-fourth as many seeds are blotched.

Tester stocks, recessive for one of the genes in this system and homozygous dominant for all the others, are being isolated. A cross of one of the testers for the c system with one of those for the r system has produced blotching. This suggests that the two systems may have loci in common but is not proof since individual Bh genes for both systems occur widely in various stocks of corn.

Paul C. Mangelsdorf

3. Cytological studies of the c blotching system.

To determine whether blotching is associated with any kind of irregular chromosome behavior or with differences in heterochromatin, a comparison was made of the plants grown from blotched and non-blotched seeds from fourteen different ears, each segregating in a 3:1 ratio. Pachytene smears of some ninety different plants were studied. Special attention was given to the size, shape, location, and number of knobs, the characteristics of prominent chromomeres, and any irregularities of the chromosomes. No consistent differences were found between the plants grown from blotched and unblotched kernels in any of the fourteen progenies. The c blotching system apparently involves genes rather than heterochromatin or chromosome irregularities of any kind.

Yu-Chen Ting

4. Defective endosperm mutants from maize-teosinte derivatives.

At least twenty-eight defective endosperm mutants have been recorded in our maize-teosinte derivatives. To indicate their origin, they are designated as de^{t1}, de^{t2}, etc. Tests to determine how many different loci are involved and to identify cases of allelism have not yet been completed, but the data so far obtained suggest that the majority of the mutants are genetically different.

One of the common features of these mutants is a characteristic heterogeneity in their segregation. The number of recessives on a segregating ear may, on the average, approach the expected twenty-five percent, but individual ears vary greatly. Chi-square tests for heterogeneity are summarized in Table I.

Table I. Heterogeneity in segregation of defective endosperm mutants.

de ^t factor	no. ears	no. kernels	average percent de	heterogeneity chi-square	p. value
de ^{t1}	38	9682	24.3	106.7	<.001
de ^{t2}	55	13243	19.8	276.9	<.001
de ^{t5}	10	2960	21.1	93.6	<.01
de ^{t13}	8	2342	24.5	62.0	<.01
de ^{t17}	7	1650	28.1	37.1	<.01
de ^{t20}	6	1468	26.3	1.0	.96
de ^{t21}	5	1569	25.2	13.5	<.01
de ^{t22}	7	2598	23.1	12.0	.05-.10

This marked heterogeneity may be due to one or more of the following causes. The mutant genes are themselves mutable and highly unstable. This is known to be true of de^{t5}, which Mangelsdorf is studying extensively, and on which he is reporting elsewhere in this News Letter. Genetic background may result in poor "penetrance." De^{t1}, for example, segregates poorly in the selfed strain but gives good ratios in hybrids. Differential fertilization, due either to gametophyte factors or to the de^t genes themselves, may be involved. In the case of de^{t9}, the upper part of the ear shows higher frequencies of defective than the lower.

Data have been obtained on weights and germination of the normal and defective seeds on the same ears. Weights, expressed in percent of the normal seed, range from 4.0 - 7.9 percent for de^{t12}, de^{t21}, de^{t13} to 62 - 72 percent for de^{t19}, de^{t20}. Germination varies from 0 - 1 percent for the more defective mutants to 91 - 98 percent for de^{t14} and de^{t19}. Germination does not seem to be a simple function of the weight of the defective kernels; also there is an interaction between some of the defective seed types and su.

The linkage relations for de^{t1}, de^{t2}, and de^{t3} are shown in Table II.

Table II. Crossing over values for de^t genes on the 4th chromosome.

factors couple	linkage phase	number of individuals				recombination
		XY	Xy	xY	xy	
$de^{t1}-su_1$	RS	2009	942	771	89	31.0 ± 1.0
$de^{t1}-su_3$	CS	4203	893	813	663	$32.2 \pm .5$
$de^{t2}-su_1$	RS	2384	943	484	67	$35.4 \pm .9$
$de^{t2}-su_1$	CS	1924	529	296	274	$33.9 \pm .7$
$de^{t3}-su_1$	RS	778	276	142	32	43.5 ± 1.6
$de^{t3}-su_1$	CS	349	81	68	61	32.2 ± 1.7
$de^{t2}-gl_3$	RS*	522	613	67	39	29.9 ± 3.2

*glossy:non-glossy segregating 9:7 for gl_1 and gl_3 .

The data suggest that de^{t2} and de^{t3} may be alleles. They indicate that de^{t2} is on the short arm of chromosome 4. Crosses of de^{t1} and de^{t2} show about 33 percent of crossing over, but the figure is undoubtedly high because of a deficiency in both of the defective classes.

Linkage relationships between fourteen other de^t genes and marker genes for chromosomes 2, 4, 5, 6, 7, and 9 have been tested. Omitting the cases in which significant deviations do not indicate linkage and for which gametophyte factors probably should be postulated, Table III shows the crosses in which significant deviations indicate the possibility of linkage.

Table III. Linkage between de^t genes and marker genes

factors couple	linkage phase	number of individuals				heterogeneity chi-square for linkage	probability	recombination percent - pr. error
		XY	Xy	xY	xy			
$De^{t11}-lg_1$	RS	1164	500	91	26	8.77	<.01	44.3 ± 1.3
$De^{t20}-su_1$	RS	1224	465	167	39	6.05	~.01	43.1 ± 1.3
$De^{t20}-gl_3$	RS	501	188	55	16	1.05	~.30	46.5 ± 1.9
$De^{t23}-gl_1$	RS	1291	515	104	35	3.58	~.05	48.7 ± 1.2

factors couple	linkage phase	number of individuals				heterogeneity chi-square for linkage	probability	recombination percent - pr. error
		XY	Xy	xY	xy			
De ^{t26} -Pr	CS	143	41	41	20	2.67	~.10	42.6 ± 2.9
De ^{t28} -y ₁	CS	224	64	31	46	4.02	~.02	29.0 ± 2.0

Cytological studies do not reveal any chromosome aberrations regularly associated with the defective mutants. If the defective seeds are a result of small deficiencies, these are too minute to be seen under the microscope.

Angelo Bianchi

5. An unstable locus for size of endosperm.

A study has been made of the inheritance of de^{t5} , one of the defective seed mutants resulting from the hybridization of maize and teosinte. This defective proved to be unstable in its inheritance. When defective seeds are grown, the ears which they produce bear seeds which vary greatly in size and weight, ranging from complete defectives to normal seeds. The weights of seeds on the same ear vary from approximately 5 to approximately 275 mg. The frequency distribution of seed weights is always multimodal. Some of the modes are undoubtedly no more than random fluctuations, but the fact that the frequency curves are always multimodal is probably significant.

When the data on seed weights from fifteen different ears were pooled to eliminate random fluctuations, a frequency curve with five distinct modes resulted, indicating that five different phenotypes are involved.

The most simple explanation of this situation is that we are dealing with a series of three alleles or "states", all mutable, of which the highest, De^{t5} , is completely dominant and the other two interact with various degrees of dominance of the first over the second, producing various degrees of defectiveness, as the result of dosage relations in the triploid endosperm.

If this explanation is correct, then there are six different embryo genotypes and there should be six different kinds of frequency distributions with respect to seed weight in the progeny of any ear of this stock. This appears to be the case. The frequency curves for seed weights of the seventeen ears so far analyzed fall into six distinct groups with respect to their pattern.

It is assumed that none of the "alleles" breed true, each mutating to the two alternative states. The rates of mutation of each state to the other two has not yet been determined; and, since the different endosperm genotypes are not completely distinguishable, it may not be possible to do so.

This defective seed mutant is of interest in representing an unstable locus, affecting size and development rather than a simple qualitative character like color.

Paul C. Mangelsdorf

6. Cytological studies of maize-teosinte derivatives.

An intensive study was begun during the year of the maize-teosinte derivatives developed by Mangelsdorf. All of these are the product of crossing varieties of teosinte with the inbred Al58, followed by three or more generations of backcrossing to Al58 and several generations of selfing. The derivatives, therefore, represent uniform inbred strains of maize in which entire chromosomes or parts of chromosomes from teosinte have been substituted for the corresponding chromosomes or parts of chromosomes from maize.

Before beginning the cytological studies, the derivatives were crossed with an inbred strain of Wilbur's Flint which has knobless chromosomes and which imparts excellent spreading qualities to pachytene smears. In such F_1 hybrids, the individual chromosomes can be much more readily identified than in ordinary F_1 maize-teosinte hybrids.

A cross of Al58 with the knobless inbred served as a control. This hybrid is heterozygous for one knob on chromosome 7, contributed by Al58. Any knobs other than this or any chromosome irregularities in the hybrids involving the teosinte derivatives can be attributed to teosinte chromosomes.

Knobs. Studies so far completed show that knobs have been introduced into Al58 from chromosomes 1, 3, and 9 of Durango teosinte and from chromosome 4 of Nobogame teosinte.

Inversions. Three different inversions were found. One of these, on chromosome 9 of Durango teosinte, has been previously reported. The other two involve chromosome 8 of Durango and chromosome 10 of Nobogame.

The inversion of chromosome 8 is terminal and involves about two-thirds of the short arm of this chromosome. Various configurations formed as a result of this inversion are (a) the two chromosomes forming a loop; (b) one chromosome stretching out, the other folding back to pair with its homologous part in the other member of the pair; (c) one chromosome stretching out, the other folding back on itself in non-homologous pairing.

In 1084 cells studied, the inversion could be detected in only 82 or 7.6 percent, although it was presumably present in all of them.

The inversion in chromosome 10 is equivalent to about one-fourth of its total length and includes the centromere.

Non-homologous pairing. In addition to the cases involving inversion, non-homologous pairing was observed between chromosome 4 of Nobogame and chromosome 2 of maize. The segment involved was equivalent to the distance between the knob position on chromosome 4 and the distal end. In another cross, chromosome 4 of Florida teosinte was observed to pair with an unidentified chromosome. The length of the segment involved in this association was from the distal end of the long arm to about two chromomeres beyond the knob. A third case of non-homologous pairing, between chromosomes 9 and 10 and involving approximately one-fifth of the long arm, of 10, occurred in another teosinte derivative which had been outcrossed to a multiple-gene linkage tester.

Asynaptic figures were found in a number of hybrids involving teosinte derivatives. These were sometimes terminal, forming V-shaped configurations and sometimes interstitial, forming loops. The asynaptic segments usually involved not more than three chromomeres. These configurations have involved chromosomes 1, 2, 4, and 7 of Durango teosinte, and chromosomes 1, 3, 7, and 9 of Florida and 1, 4, and 7 of Nobogame.

Summary. The cytological studies so far completed on maize-teosinte derivatives show that chromosomes of teosinte can be transferred to maize, introducing into maize not only knobs, but also inversions, non-homologous pairing, and asynapsis. The chromosomes of teosinte are by no means as completely homologous to those of maize as earlier studies had suggested.

Yu-Chen Ting

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1. Further evidence for crossing-over between non-homologous chromosomes during megasporogenesis of haploids.

In the 1954 Maize Genetics Coop News Letter we briefly reported work that strongly suggested crossing-over had occurred between non-homologs during megasporogenesis of haploid maize plants. This supposition was based upon two facts, first, that "bridge-like" configurations appeared with regularity at anaphase I of haploid microsporogenesis, and second, that semi-sterile progeny were found in the progeny of haploid females x normal males.

Since this report, progenies have been grown from the three semi-sterile individuals found in the population derived from crossing haploid females with normal males. One plant carried a reciprocal translocation involving chromosomes six and seven. Segregation for semi-sterility clearly indicated that the second plant was heterozygous for a reciprocal translocation, although the chromosomes involved in the translocation have not been identified.

Several hundred seeds have been produced by outcrossing haploid females with normal males. Plants arising from these seeds are to be classified for pollen abortion, and the semi-steriles selfed and outcrossed to normal strains. Subsequent cytological studies on these progeny should indicate whether the translocations occur randomly between chromosomes within the genome, or whether they occur only between certain members. Should it be found that exchanges occur only between certain chromosomes, and further, that they occur only within certain segments of those chromosomes, then this would strongly indicate that genetic duplication exists within the genome.

D. E. Alexander

2. The relationship of pollen abortion and seed set in tetraploid maize.

Forty-three open-pollinated plants from an isolated block of tetraploid maize, produced by the "elongate" method, were classified for amount of pollen abortion and seed set. A very low correlation coefficient (0.09) between percentage of good pollen and percentage seed set was found in plants ranging from 4.5 percent to 75.5 percent seed set. Such a low degree of association indicates that pollen classification cannot effectively be used as a basis of selection for high seed set.

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1. Genic control of chromosomal behavior.

Two new recessive genes affecting chromosomal behavior are under investigation. One of these is a gene for ameiosis. Both the male and female inflorescences are affected; the plants are completely male sterile and highly female sterile. The very infrequently occurring kernels have with one exception given rise to $3N$ plants. This exception was a diploid homozygous for ameiotic and arose by parthenogenesis. Cytological studies have been confined to the male inflorescence where

it was found that the sporogenous cells underwent normal mitoses up to the time when PMC should be differentiated but the onset of meiosis fails to occur and the sporogenous cells degenerate. Presumably a similar behavior is present in the ovules since a vast majority of the ovules do not develop a functional embryo sac.

The second gene, designated as elongate, has been more extensively studied. The following effects have been observed during microsporogenesis: (a) the chromonemata are uncoiled at MI, AI, MII and AII giving "elongated" chromosomes but disjunction is normal and only haploid spores have been observed; (b) misdivision of the centromere sometimes takes place at the 2nd meiotic division; and (c) neocentric regions are occasionally formed at MII. Plants homozygous for el are not copious pollen shedders. Some el plants have a considerable amount of aborted pollen but this is so variable that pollen abortion cannot be used to separate el from normal sibs. Ears borne on el plants have plump and shriveled kernels as well as aborted ovules. The relative frequencies of these vary greatly in different families and are evidently affected by modifying genes but, with the exception of one B.C. family, no difficulty was found in classifying for normal and el plants on the basis of ovule sterility and the formation of shriveled kernels. Although many of the shriveled kernels do not germinate, root tip counts of the chromosome number of plants from shriveled kernels have been made for 825 individuals. These data are as follows:

Chromosome No.	Frequency
25	1
26	1
27	2
28	17
29	71
30	676
31	46
32	10
33	1
	<hr/> 825

From these data it is evident that the el gene produces many functional eggs with an unreduced number of chromosomes as well as some with aneuploid numbers. The plump kernels gave rise to only diploid plants; to date no trisomes have been obtained from plump kernels.

The unreduced eggs could arise in the following ways: (a) somatic doubling in nucellar tissue thus forming $4N$ meiocytes; (b) doubling in the gametophyte generation; (c) doubling by a failure of the 1st meiotic division; and (d) doubling at the 2nd meiotic division. Genetic and cytological studies permit discrimination between these various hypotheses. Since observations of megasporogenesis have disclosed only 10 pairs of chromosomes at Dk and MI, it seems clear that nucellar doubling is not responsible for the diploid eggs. In support of this

conclusion is the fact that the ratio of dominant to recessive phenotypes found in diploid eggs from heterozygous plants is not the 5:1 expected from tetravalents with two dominant and two recessive alleles.

The genetic studies are involved but illuminating. Diploid plants homozygous for e1 and heterozygous for the lg₂ and a₁ loci in coupling, both lying in the long arm of chromosome 3 with lg nearest the centromere, were crossed by pollen from recessive plants. Shriveled kernels found on these B.C. ears were germinated and the ensuing seedlings transplanted to the field. The chromosome number of each plant was determined; all were at the triploid level. These plants were scored phenotypically for the lg and a characteristics; the genotypic constitution of the diploid eggs was determined by testcrosses using the triploids as both egg and pollen parents.

A total of 204 triploid plants were successfully tested for their genotypic constitution. In terms of the constitution of their diploid eggs derived from the e1 parent the following classes with their frequencies were obtained:

Lg A/Lg A = 9	Lg A/lg A = 21
lg a/lg a = 4	Lg a/lg a = 16
Lg A/lg a = 66	lg A/Lg a = 22
Lg A/Lg a = 26	lg A/lg A = 3
lg A/lg a = 37	

A similar experiment was run where e1 plants heterozygous for the Sh and Wx loci in coupling were crossed by sh wx pollen. These two loci lie in the short arm of chromosome 9 with Wx nearest the centromere. The genotypic constitution of 156 triploids was determined. The constitutions of the diploid eggs contributed by the e1 parent and their frequencies are as follows:

Sh Wx/Sh Wx = 24	Sh Wx/Sh wx = 4
sh wx/sh wx = 28	sh wx/sh Wx = 2
Sh Wx/sh wx = 30	
Sh Wx/sh Wx = 35	
sh wx/Sh wx = 33	

In both the lg a and sh wx experiments many of the diploid eggs were heterozygous for one or both of the marked loci. Obviously such heterozygous diploid eggs could not have arisen by doubling in the gametophyte generation because, on such a mechanism, both homologues would carry the same alleles. Therefore hypothesis (b) is not the mechanism operating in e1 plants.

The essential difference between the remaining two hypotheses is that on (c) the doubling results from a failure of the 1st meiotic division followed by a normal 2nd division while in (d) the 1st meiotic

division is normal but an aberrant 2nd division produces a diploid megaspore. The genotypic constitution of the diploid eggs will not be the same on hypothesis (c) as with (d).

Let us consider first the lg a experiment. Region (1) marks the interval from the centromere to lg while region (2) denotes the lg-A interval. Hypothesis (c) assumes that an unreduced restitution nucleus is found at the 1st meiotic division while the 2nd division proceeds normally. If no crossing over occurs in either regions (1) or (2) the diploid egg would possess one lg a and one Lg A chromosome--i.e., no homozygosity for either the lg or a loci. A single crossover in (2) gives rise to four possible kinds of diploid eggs of which one is homozygous for a and one for the A allele but none of the four are homozygous for lg or Lg. A single exchange in (1) produces diploid eggs of lg a/lg a and Lg A/Lg A constitution--i.e., homozygosity for both loci. Of the double exchanges in regions (1) and (2), the 3-strand doubles lead to equal frequencies of homozygosity for lg and a while with both 2- and 4-strand doubles one of the four possible combinations formed at AII is homozygous for lg and none is homozygous for a. Since the frequency of single exchanges in region (2) is between 2 and 3 times the frequency of double exchanges in (1) and (2), it follows that the percentage of homozygosity for the A locus should be greater than that for the Lg locus.

On hypothesis (d), where doubling occurs at the 2nd meiotic division after a normal first division, calculations similar to those made above show that diploid eggs homozygous for the A locus come only from noncrossover tetrads and from those with 2- and 4-strand double exchanges while homozygosity for the Lg locus results from noncrossover tetrads as well as from those with single exchanges in region (2). Therefore on hypothesis (d) the frequency of homozygosity for the more proximally placed locus (lg) should be greater than that of the more distal A locus. Likewise, considering the Sh Wx experiment, the frequency of homozygosity for the Wx locus should be greater than that of the Sh locus. Indeed, if there is no recombination between a locus and the centromere, 50% of the diploid eggs would be homozygous for the recessive allele and 50% homozygous for the dominant allele.

The pertinent data are as follows: In a total of 380 diploid eggs from el el Lg A/lg a plants, 69 (18.2%) were homozygous for the lg allele while only 31 (8.2%) were homozygous for the recessive a allele. (The 204 diploid eggs listed earlier are included in these 380; tests of the genotypic constitutions were incomplete for 176 of them). In the Sh Wx experiment the frequency of homozygosity for the wx allele was 39.1% and only 18.0% for the more distal sh allele. The data from both the Lg A and Sh Wx studies agree in showing that more proximally placed genes have a higher degree of homozygosity in diploid eggs than do more distally located loci. Therefore it may be concluded that hypothesis (c) is invalid and that hypothesis (d) is consistent with the genetic data.

There is a direct relationship between recombination values and the percentage of homozygosis. With no recombination between a marked locus and the centromere 50% of the diploid eggs are homozygous for the recessive allele and 50% for the dominant allele. With 10% recombination, 40% of the diploid eggs would be homozygous for the recessive allele and with 20% recombination, 30% of the eggs would be homozygous recessive, etc. Since 39.1% of the diploid eggs were homozygous wx it would follow that this locus is approximately 11 recombination units from its centromere, a value considerably greater than that reported by Anderson and Randolph from translocation studies. Using the percentage of homozygosis as the measure of recombination, there is 32% recombination between Sh and the centromere. The efficiency of this method for measuring recombination with the centromere can be tested since we know from other studies that the value for the centromere-lg region is about 36%. The observed 18% homozygosis for lg would be expected if there were 32% recombination between this locus and the centromere in el plants. The agreement is good and suggests that this a reliable way of determining recombination with the centromere.

The amounts of recombination found in the diploid eggs from el plants can be calculated from the genotypic determinations. The value of 24% for Sh-wx is within the range normally found in haploid gametes of N plants. The recombination value for the Lg-A region from diploid eggs is 36% which is not far from the average value of 35%.

The el gene has been used to obtain an interesting series of polyploids. Triploids come from the cross of el X N. Crosses of 2N el by 4N gave some plump kernels which were 4N. By self pollination, 4N el stocks were obtained. When these were selfed, 6N plants arose from the union of unreduced 4N eggs with 2N pollen. These 6N plants came from shriveled kernels while the plump kernels on the same ears gave rise to 4N plants. Hexaploid plants homozygous for el have been obtained and self pollinated but no viable seed has yet been produced. If seed were produced, 9N plants should be formed. However plants at the 7N level have arisen from the cross of 4N el X 6N when unreduced 4N eggs were fertilized by 3N pollen. Pentaploids (5N) have come from crosses of 4N el X 6N where reduced 2N eggs were fertilized by 3N pollen. Vigorous plants are obtained up to and including the 5N level but the 6N and 7N plants are runts.

2. Studies with overlapping inversions.

Cytological and genetical studies with In 3a have been presented in a paper published in the Amer. J. Botany (1953). This is a paracentric inversion with both breaks in 3L; the proximal break is at .4 and the distal break at .9. If the long arm is divided into 11 equal segments with segment 1 nearest the centromere and segment 11 representing the distal segment, the proximal break in In 3a lies between segments

4 and 5 and the distal break just to the right of segment 10. Evidence was given that the Lg_2 , A_1 , and Et loci are included in the inverted segment while the Rg locus was in the proximal uninverted region. That both Rg and $G1_6$ lie in the proximal uninverted segment is clear from the following B. C. data from plants homozygous for In 3a.

In gl A Lg / In $G1$ a lg		X	gl lg a	
(0)	gl A Lg 275		(2)	gl A lg 174
(0)	$G1$ a lg 254		(2)	$G1$ a Lg 158
(1)	gl a Lg 71	(1-2)	gl a Lg 27	
(1)	$G1$ A Lg 64	(1-2)	$G1$ A lg 40	

$gl-A$ = 19.0% recombination

$A-Lg$ = 37.5% "

$gl-Lg$ = 43.9% "

The order is gl A lg

In rg a lg / In Rg A Lg		X	rg lg a	
(0)	rg a lg 88		(2)	rg a Lg 58
(0)	Rg A Lg 76		(2)	Rg A lg 71
(1)	rg A Lg 31	(1-2)	rg A lg 24	
(1)	Rg a lg 25	(1-2)	Rg a Lg 24	

$Rg-A$ = 26.2% recombination

$A-Lg$ = 44.6% "

$Rg-Lg$ = 46.6% "

The order is Rg A lg

Since $Rg-G1_6$ shows approximately 5% recombination, it would appear that the normal order is $Rg-G1_6-lg-A-et$ but the vagaries of recombination values are such that this order is highly uncertain and may be $gl-Rg-lg-A-et$. That this latter order may be correct is suggested by the following data obtained from sib plants of the family having 26.2% recombination between Rg and A .

In $G1$ a lg / In gl A Lg		X	gl lg a	
(0)	$G1$ a lg 43		(2)	$G1$ a Lg 33
(0)	gl A Lg 48		(2)	gl A lg 55
(1)	$G1$ A Lg 22	(1-2)	$G1$ A lg 23	
(1)	gl a lg 19	(1-2)	gl a Lg 13	

$G1-A$ = 30.1% recombination

$A-Lg$ = 48.4% "

$G1-Lg$ = 50.4% "

This is a small population but the recombination value for G1-A is greater than that for Rg-A. Three point tests are underway to determine the correct order and they should be completed by this summer.

Another paracentric inversion in 3L is the one found by Longley and designated as In 3b. The proximal break is between segments 2 and 3 and the distal break between segments 8 and 9. In 3a is 1 2 3 4 10 9 8 7 6 5 11 while In 3b is 1 2 8 7 6 5 4 3 9 10 11 so the two have a common inverted segment 8 7 6 5--i.e., they are overlapping inversions. Back-cross data for In 3b heterozygotes are presented below from the cross of:

In	<u>G1</u>	<u>Lg</u>	<u>A</u>	<u>Et</u>	N	<u>gl</u>	<u>lg</u>	<u>a</u>	<u>et</u>	X	N	<u>gl</u>	<u>lg</u>	<u>a</u>	<u>et</u>
<u>G1</u>	<u>Lg</u>	<u>A</u>	<u>Et</u>	1527		<u>G1</u>	<u>Lg</u>	<u>a</u>	<u>Et</u>		6				
<u>gl</u>	<u>lg</u>	<u>a</u>	<u>et</u>	777		<u>gl</u>	<u>lg</u>	<u>A</u>	<u>et</u>		5				
<u>G1</u>	<u>Lg</u>	<u>A</u>	<u>et</u>	184		<u>G1</u>	<u>Lg</u>	<u>a</u>	<u>et</u>		90				
<u>gl</u>	<u>lg</u>	<u>a</u>	<u>Et</u>	358		<u>gl</u>	<u>lg</u>	<u>A</u>	<u>Et</u>		194				
<u>gl</u>	<u>Lg</u>	<u>A</u>	<u>Et</u>	3		<u>G1</u>	<u>lg</u>	<u>A</u>	<u>et</u>		2				
<u>G1</u>	<u>lg</u>	<u>a</u>	<u>et</u>	5		<u>gl</u>	<u>Lg</u>	<u>a</u>	<u>Et</u>		0				
<u>G1</u>	<u>lg</u>	<u>A</u>	<u>Et</u>	3		<u>G1</u>	<u>lg</u>	<u>a</u>	<u>Et</u>		3				
<u>gl</u>	<u>Lg</u>	<u>a</u>	<u>et</u>	2		<u>gl</u>	<u>Lg</u>	<u>A</u>	<u>et</u>		0				

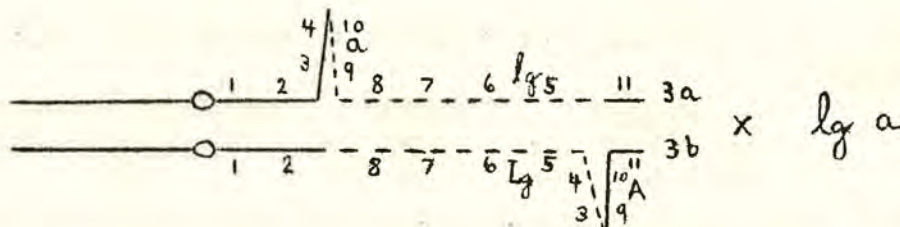
(The marked discrepancy in numbers between the complementary classes is due to the semi-lethal action of the et allele.)

	In/N	Control
<u>G1-Lg</u>	0.57%	29%
<u>G1-A</u>	9.7%	49%
<u>Lg-A</u>	9.6%	36%
<u>A-Et</u>	17.7%	12%

The A₁ locus is not included in In 3b although certainly Lg₂ and probably G1₆ are. If G1₆ is not included, it must lie very close to the proximal break point in terms of recombination units. The increased recombination value for the distal A-Et region in In 3b heterozygotes is in agreement with studies on other inversions which have shown higher than normal crossover values for both proximal and distal uninverted regions in inversion heterozygotes. This finding is contrary to the data obtained from *Drosophila* inversions.

Inasmuch as In 3a and In 3b are overlapping inversions, crosses were made to obtain plants carrying both inversions. Crossing over in the common inverted segment should lead to a chromosome with a known duplication and to one deficient strand. The In 3a chromosome had the

recessive a_1 and lg loci, both of which lie in the inverted region, while the In 3b chromosome carried the dominant alleles but only the Lg locus is in the inversion since A_1 lies distally.



The common inverted segment is 8 7 6 5 with the lg locus lying between 6 and 5. Single crossovers in this segment to the left of lg give a $Lg A$ chromosomes and a complementary lethal combination. These $a Lg A$ crossovers cannot be distinguished without breeding tests from non-crossover $Lg A$ chromosomes but would lead to an excess of A over a gametes. Single crossovers in this common segment to the right of lg produce $a lg A$ chromosomes. These are 1 2 3 4 10 9 8 7 6 5 4 3 9 10 11 in constitution. The complementary crossover class is not recovered. Thus all single exchanges within the common inverted segment lead to viable A -bearing duplication chromosomes; the complementary crossover class is lethal. The excess of A over a kernels is a measure, although obviously not the most precise one, of the frequency of single exchanges in the 8 7 6 5 region. A total of 8529 A : 7466 a kernels were obtained. The difference of 1063 is due to single exchanges producing a chromosome 3 with both the a and A alleles. The total number of crossover chromosomes is 2×1063 or 2126 which gives a frequency of single exchanges in the 8 7 6 5 region of 12.5 percent.

Double crossovers with one exchange to the left of lg and one to the right yield In 3b chromosomes with the lg and A alleles and the complementary crossover class which is In 3a and carries the a and Lg alleles. Both are viable since neither has a deficiency or a duplication.

A portion of the ears included in the above total were planted and gave the following data:

$\frac{A}{Lg}$	$\frac{A}{lg}$	$\frac{a}{Lg}$	$\frac{a}{lg}$	Σ = 6754
3560	92	10	3092	

By taking into consideration the inviable gametes, these data may be converted as follow:

(0)	$\frac{Lg}{A}$	In 3b	3092	viable
(0)	$\frac{a}{lg}$	In 3a	3092	viable
(1)	$\frac{a}{Lg} A$	In Dp	468	viable
(1)	$\frac{Lg}{a}$	In Df	468	inviable

(2)	<u>a</u> <u>lg</u> <u>A</u>	In Dp	82	viable
(2)	<u>Lg</u>	In Df	82	inviable
(1-2)	<u>a</u> <u>Lg</u>	In 3a	10	viable
(1-2)	<u>lg</u> <u>A</u>	In 3b	10	viable

The amount of recombination in the 8 7 6 5 segment may be broken down as follows:

	singles		doubles		recombination value
(1)	12.8%	+	.3%	=	13.1%
(2)	2.2%	+	.3%	=	2.5%

The total frequency of single crossovers in both regions (15.0%) agrees fairly well with the value of 12.5% obtained from the more extensive kernel data. In structurally normal plants this segment would have a map distance of approximately 40 units. It is clear, therefore that the structural dissimilarity to the left and to the right of the 8 7 6 5 segment in In 3a/In 3b heterozygotes markedly reduces crossover values for this segment.

Even though a reduction in crossing over occurs in the 8 7 6 5 segment there is some evidence that the frequency of double crossovers is high when pairing does occur for this region. The expected number of double crossovers with no interference is $(.131) (.025) (7304) = 24$ individuals and the observed number of doubles is 26, giving a coincidence value of 1.1.

The great majority of A lg plants derived from In 3a/In 3b heterozygotes of the constitution diagrammed above should possess the 1 2 3 4 10 9 8 7 6 5 4 3 9 10 11 segments in this order. Nine A lg plants were examined cytologically and eight had the inverted order of In 3a with a duplication of the 4 3 9 10 segments. These came from single crossovers to the right of lg. The remaining A lg plant had the In 3b chromosome and came from a double exchange to the left and right of lg. Four a Lg plants were studied cytologically and all had an In 3a chromosome as expected from a double crossover origin.

The A lg plants coming from single crossovers should carry the recessive a allele in the proximal 10 9 segment, the recessive lg allele in the 6 5 segment and the dominant A allele in the 9 10 segment of the duplication. Chromosomes of this constitution will be referred to as In Dp a lg A. That the recessive a allele is cryptically carried by the a lg A chromosome is evident from the following tests.

Plants homozygous for the In Dp a lg A chromosome have bred true for aleurone color although only limited tests have as yet been made. Crosses were made to obtain heterozygotes for the In Dp a lg A and N Lg A chromosomes. When these heterozygotes were test-crossed by a plants, .2% of the resulting kernels were colorless while 99.8% were colored. These infrequent colorless kernels arise from 2 and 3 strand double

exchanges within the inversion loop producing a chromosome 3 with the a allele. Their rare occurrence would be attributed to a mutational phenomenon of some sort if the structural composition of the chromosomes were not known.

When several plants of In Dp a lg A / N Lg a-x₁ constitution were self-pollinated there were 21 colorless kernels in a population of 493. Homozygous a-x₁ zygotes are lethal so the appearance of a viable a class is due to crossing over following pairing of the uninverted distal 9 10 11 segments of the two homologues thus transferring a-x₁ to the In Dp chromosome and producing a viable a lg a-x₁ chromosome. The colorless kernels should be In Dp a lg a-x₁ / N Lg a-x₁. Plants of In Dp a lg A / In Dp a lg a-x₁ constitution gave a ratio of 1A:1a when used as the pollen parents in test-crosses. The deleterious effect of a-x₁ is thus covered by the presence of the a allele lying in the same chromosome.

In Dp chromosomes are transmitted normally through the megaspores but In Dp pollen is at a disadvantage in competition with N pollen. This is evident in the cross of lg a X In Dp a lg A / N Lg A which produced 2354 colored and 5 colorless kernels. The 2354 colored kernels yielded 1818 Lg and 429 lg (19.1%) seedlings. Most of the lg class came from the functioning of In Dp pollen. Crosses of lg a X In Dp a lg a / N Lg A gave the following phenotypic classes:

<u>A</u> <u>Lg</u>	<u>A</u> <u>lg</u>	<u>a</u> <u>Lg</u>	<u>a</u> <u>lg</u>	{ = 1363
840	58	186	279	
(61.6%)	(4.3%)	(13.6%)	(20.5%)	

Save for very infrequent double exchanges within the inversion loop both the A lg and a lg classes come from In Dp pollen. The A lg class has an a lg A chromosome derived from crossing over in the distal 9 10 11 segments.

A somewhat similar cross of lg a X In Dp a lg A / N Lg a gave the following phenotypic classes:

<u>A</u> <u>Lg</u>	<u>A</u> <u>lg</u>	<u>a</u> <u>Lg</u>	<u>a</u> <u>lg</u>	{ = 2361
316	525	1425	95	
(13.4%)	(22.2%)	(60.4%)	(4.0%)	

As in the above cross the A lg and a lg classes are derived almost exclusively from the functioning of In Dp pollen. The a lg class has an In Dp a lg a chromosome derived from crossing over in the distal 9 10 11 segment. From the data of the above two crosses the frequency of crossing over between the break point of In 3b and the A locus is 17.7%. This is a significantly higher value than the 9.6% found for the same region in In 3b/N heterozygotes. The greater structural dissimilarity in In Dp/N compounds as compared to In 3b/N leads to more frequent pairing of the uninverted distal 9 10 11 segment and hence to higher recombination values.

3. The effect of temperature on the penetrance of Ragged.

The Ragged phenotype was not expressed in heterozygous plants grown at cool temperatures (60-65 F) in the greenhouse during the winter months of the past three years. Seed produced on these apparently normal plants gave rise to typical Ragged plants when planted in the field the following summers. This observation would seem to be of some interest to those concerned with the physiological action of the Rg gene.

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4. A test for chromosomal interference in crossing over.

Nothing is known in maize about chromosomal interference in crossing over--i. e., are crossovers in the different paired homologues independent events or does a crossover in one chromosome pair decrease or increase the probability of crossing over in another pair. This is a difficult problem to approach experimentally in maize because of the haploid number of ten chromosomes but some information was obtained from a study of the anaphase configurations in plants heterozygous for two paracentric inversions--namely In 3a and In 7a. The acentric fragment produced by crossing over within the inversion loop of In 7a is distinctly larger than the acentric fragment from In 3a crossovers so the PMC can be scored with considerable accuracy for In 7a and In 3a bridges and fragments. The following anaphase I and early telophase data were obtained from plants heterozygous for the two inversions:

3a bridge and fragment	72 PMC	3a and 7a fragments	158
3a fragment	33	3a double and 7a single bridge	17
3a double bridge	2	7a double and 3a single bridge	19
7a bridge and fragment	244	3a double and 7a double bridge	1
7a fragment	72	no bridge or fragment	78
7a double bridge	13	2 bridges and 7a fragment	7
3a and 7a bridge and fragments	276		

In 7a: % single and 3-strand double exchanges = 78.0
 % 4-strand doubles = 3.3

In 3a: % single and 3-strand double exchanges = 57.0
 % 4-strand doubles = 2.0

Simultaneous single or 3-strand double exchanges in both inversion loops:

Expected % $57.0 \times 78.0 = 44.5$
 Observed % = 44.4

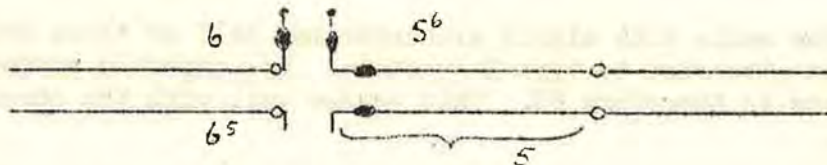
Simultaneous 4-strand double exchanges in both inversion loops:

Expected % $3.3 \times 2.0 = .07\%$
 Observed % = .10%

From the above data it may be concluded that crossing over in chromosome 7 does not influence crossing over in chromosome 3.

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5. Correlation of exchange frequency and crossing over in a translocation heterozygote.



Translocation 5-6c obtained from McClintock was used in the following study. The long interstitial segment indicated by a bracket in the diagram was tested for crossing over cytologically and genetically. The interstitial segment to the left is so short that very little, if any, crossing over occurs in this region.

Exchange frequency in the interstitial segment was determined cytologically from examination of the nucleolar constitution of microspore quartets in two plants heterozygous for the translocation. The types of quartets which occurred with their source and frequency are given in the table below. The values found by Burnham in a more extensive study are also listed.

Type of quartet	Source	Number	Frequency	Burnham data	
				Number	Frequency
1. $\begin{array}{c c} 1 & 1 \\ \hline 1 & 1 \end{array}$	nons + alt seg 2 str d + alt seg 4 str d + adj seg	154	13.7	809	19.3
2. $\begin{array}{c c} 2 & 2 \\ \hline 0 & 0 \end{array}$	nons + adj seg 2 str d + adj seg 4 str d + alt seg	106	9.4	742	17.9
3. $\begin{array}{c c} 1 & 2 \\ \hline 0 & 1 \end{array}$	singles + alt seg singles + adj seg 3 str d + alt seg 3 str d + adj seg	859	76.8	2678	62.8

The genetic data were obtained from sibs of the above 2 plants. Heterozygotes of constitution $\frac{T}{t} \frac{Pr}{pr} \frac{Bt}{bt}$, in which T marks the breakpoint

and Bt marks the centromere, were used as female parents in backcrosses and the frequency of crossing over in the interstitial segment determined. In a progeny of 1337, 11.4% were crossovers between T and Pr, 32.3% were crossovers between Pr and Bt and 2.2% had exchanges in both regions. The following calculation was made to obtain the expected exchange frequency:

$$\begin{aligned} 11.4 - 2.2 &= 9.2 \times 2 = 18.4 \text{ single exchange } \underline{T-Pr} \\ 32.3 - 2.2 &= 30.1 \times 2 = 60.2 \text{ single exchange } \underline{Pr-Bt} \\ &2.2 \times 4 = 8.8 \text{ double exchanges } \underline{T-Pr-Bt} \end{aligned}$$

All of the cells with single exchanges and half of those with double exchanges give rise to type 3 quartets. The expected percent of type 3 quartets is therefore 83. This agrees well with the observed value of 76.8.

Burnham (1950) gives the following frequencies for exchanges in the interstitial region: single exchanges--43% double exchanges--40%. These values are based in part on his quartet data and in part on an assumption of 10% for recovered double crossover strands. Since 2.2% double crossovers were found in the present study, the estimate of 10% seems rather high.

Certain assumptions have been made in calculating the exchange frequency from the genetic data. The double exchanges were considered to occur in a ratio of 1 two strand: 2 three strand: 1 four strand. It was assumed that the ratio of alternate to adjacent-1 types of segregation was not altered by the occurrence of interstitial exchanges and remained 1:1 following both single and double exchanges in this region. (Burnham has shown that no or very little adjacent-2 segregation occurs in plants heterozygous for T 5-6a). The agreement of the observed and calculated values for type 3 quartets seems to indicate the validity of these assumptions although an exactly compensating deviation in both ratios would give the same result.

Because of inadequate marking, double crossovers within the Pr-Bt interval were not detected. They would not be expected to be as frequent as the doubles found for the T-Bt region and therefore the map distance from Pr to Bt would not be lengthened by more than 4.4 units. The maximum value for the calculated exchange frequency would then be 87.4.

In a separate test involving the same translocation, a plant of constitution $\frac{V_2}{V_2} \frac{T}{t}$ was pollinated by a v_2 male parent. V_2 is located

distal to the break in chromosome 5. No v_2 seedlings were found in a progeny of 303 indicating that there is no transmission through the egg of gametes containing the 5^b and 6 chromosomes. These gametes would be deficient for a short terminal segment of 5L and duplicate for most of 6S.

6. Male sterility involving KYS.

In an attempt to obtain better cytological figures, asynaptic plants were crossed as female with KYS pollen parents. The F_1 plants were backcrossed to KYS. The progeny unexpectedly segregated 198 normal plants and 83 male steriles. The latter produced normally filled ears. This ratio approaches the 5 N: 3 MS expected if the male sterile condition is determined by a dominant male sterile gene Ms and a recessive s which permits expression of Ms. When male sterile plants were backcrossed by KYS, a ratio of 79 N: 61 MS was found. A ratio of 1:1 is expected on the above hypothesis. These results resemble those of Schwartz reported in Genetics 1951. He found a male sterile condition which was dependent on a dominant Ms gene, a recessive s and a specific cytoplasm. The dominant S acts as a suppressor of male sterility and is closely associated with a gamete factor so that in plants of S/s constitution, only S pollen functions. As a result no male steriles are recovered in a self pollination of Ms ms S s plants. In the present case one self pollinated plant from the original backcross population gave 53 N: 15 as: 19 MS: 8 MS as. If the S factor is the same as that reported by Schwartz, it has lost its gametophyte effect. Whether or not a "male sterile" cytoplasm is involved is not yet known.

In the 1955 maize Newsletter, Burnham reported an almost identical case in which male steriles were unexpectedly found in a backcross to KYS. The male sterile phenotype showed linkage with a translocation involving chromosomes 6 and 9. Data obtained from the self pollination mentioned above show independence of male sterility and sh on chromosome 9. One of the factors (Ms or s) may be located on chromosome 6.

7. Linkage in tetraploid corn.

Tetraploid plants of varying constitutions for the C and Wx loci were used in backcrosses with homozygous c wx pollen from a tetraploid line. The linkage formulas of Mather were applied to the group involving plants in simplex condition and coupling phase. The recombination between C and Wx is 25.5%, a value very close to that found in diploids. If exchange of pairing partner occurs at random along the length of the chromosome, a reduction in crossing over might be expected in the tetraploid. Since none was found, it may be that there are preferential points of synaptic interchange which permit uninterrupted pairing throughout the C-Wx region.

The expected frequency of the four phenotypic classes has been calculated on the basis of 50% chiasmata between C and Wx and no chiasmata between Wx and the centromere. A second calculation assuming 20% chiasmata between Wx and the centromere was made for the simplex coupling data and since the change in frequencies of the phenotypic classes was slight, only the first method was used to obtain expected frequencies in the other two cases.

			C Wx	C wx	c Wx	c wx
<u>C Wx</u>		obs. no.	2021	522	602	2114
<u>c Wx</u>	X	obs. freq.	38.4%	9.9%	11.4%	40.2%
<u>c wx</u>		exp. freq.	39.6%	8.4%	10.4%	41.6%
<u>c wx</u>		exp. freq. *	39.1%	8.8%	10.3%	42.2%

*based on 50% C-Wx chiasmata and 20% Wx-centromere chiasmata

			C Wx	C wx	c Wx	c wx
<u>C Wx</u>		obs. no.	436	610	666	441
<u>c Wx</u>	X	obs. freq.	20.2%	28.3%	30.9%	20.5%
<u>c wx</u>		exp. freq.	18.6%	30.4%	31.2%	19.4%

			C Wx	C wx	c Wx	c wx
<u>C Wx</u>		obs. no.	937	83	126	161
<u>C wx</u>	X	obs. freq.	71.7%	6.4%	9.6%	12.3%
<u>c Wx</u>		exp. freq.	75.9%	4.9%	7.7%	11.9%

All calculations were based on the assumption that chromosome disjunction is at random and is unaffected by the occurrence of a crossover in the C-Wx region.

Ellen Dempsey

8. Heterotic genes in the long arm of chromosome 3.

Field tests for heterotic genes in the long arm of chromosome 3 were continued in 1955. A homozygous inversion 3a strain carrying the recessive a_1 allele in the inverted segment was crossed to a number of inbred lines with the A_1 allele. F_1 plants, all heterozygous for the inversion and for $A:a$, were backcrossed by the homozygous inversion strain. There was a ratio of 1 colored : 1 colorless kernels on the F_1 backcrossed ears. The colored kernels were heterozygous for the inversion and for $A:a$. The colorless kernels were homozygous for the inversion and for $a:a$. The kernels of the two classes were planted in the replicated plots. Data for ear height, maturity, grain yield, and kernel weight are presented in the following tables. In the cases where a significant difference is found, the heterotic genes were contributed by the inbred lines except possibly for kernel weight. In the latter case, the difference is either due to the heterotic genes from the inbred lines or the 21% of ovule abortion in the class heterozygous for the inversion. There are some discrepancies between the grain yield data obtained in 1955 and in 1954. There were two inbred lines, K 187-2 and M 14, out of fourteen inbred lines tested in 1954, which showed significant differences between the two classes at the 1% level. None of them had such a difference in 1955. This might be due to environmental differences in the two growing seasons.

	Ear height in cms.				Days from planting to half silking			
	No. reps.	Aa	aa	't' value	No. reps.	Aa	aa	't' value
Oh 45	12	115	101	13.15**	12	67.1	65.5	11.00**
Oh 41	12	119	108	9.83**	12	70.0	69.2	3.04**
M 14	12	96	92	2.84**	12	67.7	67.6	0.44
K 4	12	126	112	7.35**	12	73.4	72.8	2.10
I 205	12	116	107	4.84**	12	68.9	68.5	0.85
C 103	12	108	97	7.68**	12	69.8	70.4	1.80
5120 B	12	114	101	8.64**	12	69.5	68.8	2.50*
K 187-2	12	114	93	10.20**	12	68.2	67.2	2.81**
38-11	12	122	111	5.52**	12	69.1	68.3	3.43**
O 7	12	125	99	13.13**	12	69.5	68.6	3.14**
WF 9	12	103	98	2.25*	12	65.7	65.8	0.52
W 26	12	104	92	7.64**	12	67.0	66.3	2.59*
R 59	12	120	110	9.00**	12	69.4	69.0	1.68

**Significant at 1% level

*Significant at 5% level

	Ave. yield per rep. in lbs.				Wt. of 1,000 kernels in gms.			
	No. reps.	Aa	aa	't' value	No. reps.	Aa	aa	't' value
Oh 45	12	3.54	3.60	0.86	6	270	241	2.37
Oh 41	12	3.03	2.96	0.58	6	239	212	4.95**
M 14	12	3.46	3.44	0.20	6	237	205	7.23**
K 4	12	2.72	2.72	0.00	6	248	206	10.87**
I 205	12	3.20	3.02	1.50	6	254	222	3.76**
C 103	12	2.88	2.73	1.55	6	270	263	1.70
5120 B	12	2.43	2.56	1.08	6	252	220	5.30**
K 187-2	12	2.92	2.97	0.38	6	244	211	2.74*
38-11	12	2.95	3.09	0.78	6	248	217	2.83*
O 7	12	2.75	2.84	0.60	6	233	211	4.94**
WF 9	12	3.23	3.24	0.09	6	241	202	7.21**
W 26	12	2.73	2.67	0.63	6	236	209	3.69**
R 59	12	3.54	3.71	1.13	6	256	217	4.61**

**Significant at 1% level

*Significant at 5% level

Chuan-Ying Chao

9. The non-homologous associations of centromeres and knobs of maize chromosomes at meiosis.

It is well known that the centromeres and knobs of the non-homologous chromosomes of maize are stuck together at pachynema and that this association disappears by diakinesis. In her unpublished M. S. thesis at the University of Illinois Sarah R. Peterson reported on the frequency with which centromeres of non-homologous chromosomes were associated in the prophase of the first meiotic division. She also determined the frequency with which knobs of different homologues were associated. Working with the inbred strain KYS she found a total of 86 cases of centromere adhesion and a total of 96 cases where the knobs of different bivalents were stuck together at pachynema. She concluded that the knob and centromere association were non-random. Inasmuch as the total number of cases observed was low a further study of this phenomenon seemed warranted. Only the KYS inbred was involved in this investigation but some plants were normal structurally while others were homozygous for a reciprocal translocation between chromosomes 4 and 10.

After fixing in 95% ethyl alcohol and propionic acid, the PMC were stained with aceto-carmin. Only cells with well spread chromosomes at pachynema were studied. The chromosomes involved in non-homologous association at the centromere regions and at the knobs were identified. Centromere and knob adhesions occurred in 70% and 25% of the cells studied, respectively.

It was deemed necessary to ascertain the pachytene lengths of the 10 maize chromosomes of the KYS inbred since it appeared likely that the non-random association might be a function of the relative length of the different chromosomes. The pachytene lengths given below for the normal strain are the average measurements from 6 good cells at late pachynema where there was no obvious distortion due to stretching while the measurements for the chromosomes of the homozygous translocation strain are from 4 good cells. In general the lengths and arm ratios reported here are in good agreement with those found by Longley but some differences are apparent. The greatest deviation is for chromosome 1 where ratios of long to short arms of 1.1:1 and 1.3:1 were found by us and Longley, respectively.

Table 1. (See next page)

Table 1. Lengths in micra and arm ratios of inbred KYS chromosomes and those of a homozygous 4-10 translocation in comparison with Longley's data.

Normal KYS					Homozygous 4-10 translocation					Chromosome Atlas (after Longley)		
Chrom.	S	L	Total Length	Arm Ratio	Chrom.	S	L	Total Length	Arm Ratio	Chrom.	Total Length	Arm Ratio
1	40.17	45.73	85.90	1.1:1	1	40.58	45.90	84.48	1.1:1	1	82.40	1.3:1
2	31.52	34.46	67.98	1.2:1	2	31.06	39.66	70.72	1.3:1	2	66.50	1.25:1
3	20.39	40.17	60.56	2.0:1	3	21.08	41.82	62.90	2.0:1	3	62.00	2.0:1
4	22.25	35.23	57.48	1.6:1	4 ¹⁰	12.24	22.10*	34.34	1.8:1	4	58.78	1.6:1
5	29.05	31.52	60.57	1.1:1	5	27.08	33.54	60.62	1.2:1	5	59.82	1.1:1
6	11.74	36.46	48.20	3.1:1	6	11.78	34.68	46.46	2.9:1	6	48.73	3.1:1
7	11.12	33.37	44.49	3.0:1	7	13.14	32.86	46.00	2.5:1	7	46.78	2.8:1
8	11.12	35.23	46.35	3.2:1	8	10.66	34.00	44.66	3.2:1	8	47.48	3.2:1
9	14.21	27.19	41.40	1.9:1	9	12.46	25.16	37.62	2.0:1	9	43.24	1.8:1
10	9.27	25.96	35.23	2.8:1	10 ⁴	11.44	45.78	57.22	4.0:1	10	36.93	2.8:1
Σ	200.84	347.32	548.16	---	Σ	191.52	355.50	547.02	---	Σ	552.66	---

(*) It should be noted that the long arm of the 4¹⁰ chromosome is the short arm of chromosome 4.

The number of times the centromere of each bivalent is found stuck to the centromere of another pair is recorded in Table 2. In order to perform an analysis of the observed frequencies of associations, the expected frequency for each class was calculated on the basis of the total length of the 10 chromosomes at the pachytene stage. The chi-square test indicates a non-random distribution of the centromere adhesion for the total of the 10 chromosomes, but a closer inspection of Table 2 shows that the only significant individual chi-square value is for chromosome 5; for all others the value is not significant. If one excludes chromosome 5, the remaining 9 classes give a total chi-square of 14.56 which is not significant. One can conclude that the association of centromere regions of non-homologous chromosomes in corn is a random affair, according to the relative lengths of the chromosomes, with the exception of chromosome 5.

Table 2. Comparisons of the observed frequencies of centromere adhesions with the expected frequencies calculated on basis of chromosome length.

Normal KYS				Homozygous 4-10 translocation			
Chrom.	ob.	exp.	χ^2	Chrom.	ob.	exp.	χ^2
1	87	105.3	3.18	1	81	96.2	2.37
2	69	83.3	2.45	2	64	78.6	2.71
3	71	74.3	0.15	3	59	69.9	1.70
4	75	70.5	0.29	4 ¹⁰	44	38.2	0.88
5	112	74.3	19.13	5	100	67.4	15.77
6	50	59.1	1.40	6	45	51.6	0.84
7	67	54.5	2.87	7	56	51.1	0.50
8	63	56.7	0.68	8	52	49.6	0.12
9	43	50.8	1.98	9	37	41.8	0.55
10	35	43.2	1.56	10 ⁴	70	63.6	0.64
Σ	672	672.0	33.69	Σ	608	608.0	26.08

In order to check the hypothesis that the frequency of centromere adhesion of non-homologous chromosomes is proportional to chromosome length, the author planned to analyze several homozygous translocations where the length of certain chromosomes is drastically changed. At present adequate data are available only for a homozygous 4-10 translocation. In this translocation the breakage points are near the centromere in 4L and in the middle of the long arm of chromosome 10 (for the length and arm ratio, see Table 1). The 4¹⁰ chromosome with a centromere from chromosome 4 is now the shortest member of the complement while the 10⁴ with a 10 centromere is the second longest chromosome. If the frequency of centromere adhesions is a function of relative chromosome length then the 4¹⁰ chromosome should have a reduced frequency

while that of 10^4 should be increased. This is precisely what was found. Again it should be noted that chromosome 5 is involved more often than expected on the basis of its relative length. The chi-squares are given in the second part of Table 2. The chi-square for the total is significant, but chromosome 5 is responsible for this. If this value is eliminated, the remaining total chi-square is not significant.

In conclusion, it was shown that the number of centromere adhesions is a function of relative chromosome length for all the chromosomes with the exception of chromosome 5, which is more frequently involved than expected.

Table 3. Combinations of bivalents involved in non-homologous knob associations and their frequencies.

Normal KYS			Homozyg. 4-10 transl.		
Knob combin.	No. of adhesions	% of adhesions	Knob combin.	No. of adhesions	% of adhesions
5-6	8	11.3	5-6	4	10.0
5-7	32	45.0	5-7	15	37.5
5-9	15	21.1	5-9	10	25.0
6-7	3	4.2	6-7	2	5.0
6-9	0	0.0	6-9	1	2.5
7-9	13	18.4	7-9	8	20.0
Σ	71	100.0	Σ	40	100.0

In considering knob adhesions, it must be remembered that KYS has a large knob on chromosome 5 and 7, a small one in 6L and a small terminal knob on 9S. Table 3 gives the frequencies and percentages of the six possible types of knob association for the 4 knobs in the normal KYS and in the homozygous 4-10 translocation strains. If knob adhesion occurs at random, one would expect to find that each combination would occur in $1/6$ of the total number of knob fusions. The data in Table 3 show that the frequencies of different knob associations deviate markedly from a random association. The larger knobs on chromosomes 5 and 7 are most frequently involved and the smaller knobs on 6 and 9 are less frequently involved. Although the knobs on 6 and 9 are of the same approximate size the terminal knob on 9 is more frequently involved in knob adhesion than is the interstitial knob in 6L. Our data on knob adhesions are in close agreement with those of Peterson.

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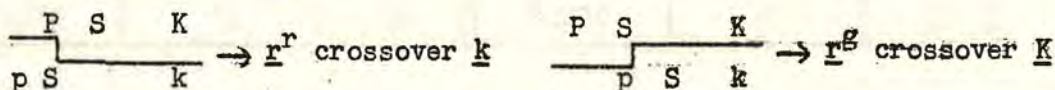
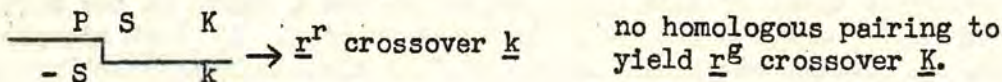
10. Comparison of a non-crossover R^G mutant with a crossover R^G mutant.*

Accumulating evidence suggests that mutations at the R^r locus yield non-crossover R^G mutants of constitution (pS) as well as crossover R^G mutants. A previous paper (Genetics 1956) presents data indicating that an R^G allele, designated R^G-14 , is deficient for element (p). This type is expected to arise as the result of the occurrence of unequal crossing-over in the parent allele. However, R^G-14 was derived from a stock without genetic marking to the left or right of the R^r locus, and thus it could not be proved to be due to unequal crossing-over.

A more critical study to investigate the possibility of these two types of plant-color mutants is now being conducted with several R^G alleles of known crossover and non-crossover origin. This report summarizes the data from R^G non-crossover-1 (designated R^G nco-1) and R^G crossover-1 (designated R^G co-1).

In the case of the compound R^G nco-1 $\underline{k/R^r K}$, the expected types of unequal crossovers (seed-color) would include the apparent mutants $\underline{r^r k}$ and $\underline{r^G K}$, assuming that R^G nco-1 is (pS). The R^G co-1 $\underline{k/R^r K}$ compound, on the other hand, should yield only $\underline{r^r k}$ unequal crossovers, if it lacks the (p) element.

These expected types of unequal crossovers are illustrated in the following diagrams:

A. Non-crossover Mutant (pS)B. Crossover Mutant (- S)

The data from the non-crossover R^G mutant come from two cultures in which the knob-10 linkage is different. In the case of the R^G nco-1 $\underline{k/R^r K}$ compound, the expected types of unequal crossovers would be $\underline{r^r k}$ and $\underline{r^G K}$. The R^G nco-1 $\underline{K/R^r k}$ culture, which is the less desirable one since the $\underline{r^G}$ crossovers would be knobless and thus uncommon, should

* This report represents work done jointly by the late L. J. Stadler and myself.

produce $\underline{r^r} \underline{K}$ and $\underline{r^g} \underline{k}$ crossovers. The results are as follows:

Culture	Pop.	Mutants	$\underline{r^g} \text{ co } K$	$\underline{r^r} \text{ co } k$	$\underline{r^g} \text{ nco } k$	$\underline{r^r} \text{ nco } K$	Deficiency
A. $\underline{R^g} \text{ nco-1 } k/\underline{R^r} \underline{K}$	89,550	24	10	5	4	3	2
			$\underline{r^g} \text{ co } k$	$\underline{r^r} \text{ co } K$	$\underline{r^g} \text{ nco } K$	$\underline{r^r} \text{ nco } k$	
B. $\underline{R^g} \text{ nco-1 } K/\underline{R^r} \underline{k}$	86,217	15	3	4	4	4	0

In culture A, with $\underline{R^g} \text{ nco-1 } \underline{k}$, 24 colorless seeds were found, and of these 15 were unequal crossovers, 7 were non-crossovers, and 2 were \underline{R} deficiencies. Of the 15 crossovers identified, 10 were of type $\underline{r^g} \underline{K}$, the critical class which carries (p), and 5 were of type $\underline{r^r} \underline{k}$.

In culture B, the $\underline{R^g} \text{ nco-1 } \underline{K}/\underline{R^r} \underline{k}$ compound yielded 7 unequal crossovers and 8 non-crossovers. Of the 7 crossovers produced, 3 were $\underline{r^g} \underline{k}$ and 4 were $\underline{r^r} \underline{K}$. The non-crossovers included 4 $\underline{r^g} \underline{K}$ and 4 $\underline{r^r} \underline{k}$.

Thus the occurrence of 13 $\underline{r^g}$ crossovers indicates that change of $\underline{R^r}$ to $\underline{R^g}$ occurred by a recessive mutation of element (P) rather than by a physical loss of this element.

The results of the type and frequency of unequal crossovers produced in cultures heterozygous for $\underline{R^g} \text{ co-1}$ are summarized in the following table:

Culture	Pop.	Mutants	$\underline{r^g} \text{ co } K$	$\underline{r^r} \text{ co } k$	$\underline{r^g} \text{ nco } k$	$\underline{r^r} \text{ nco } K$	Deficiency
$\underline{R^g} \text{ co-1 } k/\underline{R^r} \underline{K}$	102,020	46	0	24	5	13	4

A striking difference appeared in the type of unequal crossovers produced from $\underline{R^g} \text{ co-1 } \underline{k}/\underline{R^r} \underline{K}$ as compared to those from $\underline{R^g} \text{ nco-1}$. Out of 24 crossovers found, all were of the $\underline{r^r} \underline{k}$ class with none of the $\underline{r^g} \underline{K}$ crossover type. Approximately 17 of these 24 crossovers should have been $\underline{r^g} \underline{K}$, assuming a 70% selective advantage of the knob bearing chromosome. In addition, 18 non-crossovers were recovered, of which 13 were $\underline{r^r} \underline{K}$ and 5 were $\underline{r^g} \underline{k}$.

These results indicate that the apparent mutation of $\underline{R^r}$ to $\underline{R^g}$ involved the loss of element (p).

It is also of interest to note that the frequency of unequal crossovers in the R^g co-1 heterozygote, resulting only from proximal displacement of (S), is greater than the frequency of unequal crossovers in R^g nco-1/ R^g from both proximal and distal displacement of (S). Out of 37 seed-color mutants analyzed from R^g nco-1 (two mutants were excluded since they are deficiencies), 22, or 59%, were unequal crossovers. In the case of R^g co-1, 24 of the 42 mutants, or 57%, were crossovers. Previous evidence from R^g -14, which is presumably (-S) in constitution, also showed this increased frequency of unequal crossing-over. If this difference proves to be regular among known crossover R^g alleles, it may be used as another criterion to distinguish crossovers from non-crossover R^g mutants.

11. Further analysis of R^g -14.*

Previous results have provided evidence on absence of (p) element in R^g -14. Another test of determining the existence of (p) may be possible by a comparative analysis of unequal crossing-over in plants homozygous for non-crossover and crossover R^g mutants.

If R^g crossovers lack the (p) element, the homozygote (-S/-S) should yield only r^g non-crossover mutants. The occurrence of unequal crossing-over should be inhibited if this phenomenon requires synapsis of (p) and (S) components. In the case of the R^g non-crossover (pS/pS), however, r^g crossovers should occur, since (p) is presumably present. Also r^g crossovers of one class are expected from the heterozygote (-S/pS). These relations are illustrated in the following diagrams:

	<u>Crossover/Crossover</u>	<u>Non-crossover/Non-crossover</u>	<u>Non-crossover/Crossover</u>
A.	- S absence of - S unequal co.	$\frac{p \quad S}{p \quad S} \rightarrow r^g$ crossover	$\frac{p \quad S}{- \quad S} \rightarrow r^g$ crossover
B.	- S absence of - S unequal co.	$\frac{p \quad S}{p \quad S} \rightarrow r^g$ crossover	class absent

At the present time data are available from an R^g crossover. The seed-color mutants analyzed were produced from plants homozygous for R^g -14 and heterozygous for g and K . Two different compounds were employed in the experiment: (1) g R^g -14 K/G R^g -14 k and (2) G R^g -14 K/g R^g -14 k . In the case of the compound g R^g -14 K/G R^g -14 k , the expected types of unequal crossovers are G r^g K and g r^g k . The unequal crossovers expected from the compound G R^g -14 K/g R^g -14 k are g r^g K and G r^g k . In addition, these same classes of unequal crossovers are expected in 15% of the seed-color mutants regardless of any relation of mutation to unequal crossing-

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over, since the standard crossover frequency for the $\underline{R-K}$ interval is 1% and for the $\underline{R-G}$ interval, 14%.

The compound $\underline{g} \underline{R^G-14} \underline{K/G} \underline{R^G-14} \underline{k}$ produced 8 seed-color mutants, of which 5 were $\underline{g} \underline{r^G} \underline{K}$ non-crossovers and 3 were $\underline{G} \underline{r^G} \underline{k}$ non-crossovers. The total population included a test of 37,037 female gametes.

Out of 21,862 gametes tested in the compound $\underline{G} \underline{R^G-14} \underline{K/g} \underline{R^G-14} \underline{k}$, 5 colorless seeds were found, and of these 2 were of the $\underline{G} \underline{r^G} \underline{K}$ non-crossover type and 3 of the $\underline{g} \underline{r^G} \underline{k}$ non-crossover type.

The occurrence of 13 non-crossovers among the 13 seed-color mutants examined is significant evidence that unequal crossing-over is not involved in the mutations, for if unequal crossing-over had been as frequent in homozygous $\underline{R^G-14}$ as in heterozygous $\underline{R^G-14}$, approximately 6.5 unequal crossovers would be expected in addition to 2 due to coincident crossing-over between \underline{g} and \underline{K} . The number of unequal crossovers expected is based on the relative proportion of unequal crossovers and non-crossovers observed in $\underline{R^G-14}$ and $\underline{R^G}$ co-1 heterozygotes. These results showed that approximately 50% of the mutants identified were unequal crossovers.

Thus the absence of $\underline{r^G}$ crossovers from homozygous $\underline{R^G-14}$ supports the view that this allele is deficient for element (p).

12. Intermediate aleurone-colored alleles of R.*

In the course of the unequal crossing-over analysis several \underline{R} mutants of intermediate seed-color phenotype have been found including mutants of dilute aleurone-color and distinguishable pattern types. These mutants are listed in the following table with their phenotype, unequal crossover origin, and colorless-seed mutation frequency.

(Table on following page)

The occurrence of intermediate alleles of dilute phenotype suggests a qualitative change of a single (S) element. On this basis, these mutants are expected to originate as the result of gene mutation, or non-crossover mutation, and not involve unequal crossing-over. At the present time, four of the dilute mutants that were marked for the determination of unequal-crossing-over were all of the non-crossover type, but the number of mutants analyzed is too small to be statistically significant. Each of these non-crossover mutants was derived from $\underline{R^r}$ Cornell.

* This report represents work done jointly by the late L. J. Stadler and myself.

Mutant Aleurone Color	Parent	Colorless seed Mut. Freq.	Mutant Genotype	Unequal Crossover Origin
Spots on a dilute background	G R ^g McB k/g R ^r K	5/28,728	* g (R) ^r K	non-crossover
Spots on a dilute background	G R ^g McB k/g R ^r K	----	g (R) ^r K	non-crossover
Spots on a dilute background	g R ^g Queens K/ G r ^{ch} k	----	G (R) ^g K	non-crossover (coinci- dent co for g)
Spots on a dilute background	g R ^g nco-1 K/G R ^r k	2/14,228	g (R) ^g K	non-crossover
Spots on a dilute background	g R ^g co-1 k/G R ^r K ₀ **	3/5,429	G (R) ^r K ₀ ?	delayed cytology
Spots on a dilute background	G R ^g k/g R ^r K	0/1,978	G (R) ^r K?	delayed cytology
Spots on a dilute background	g R ^g -14 K/G R ^g -14 k	7/25,561	G (R) ^g K	questionable non- crossover with a coin- cident g or K crossover.
Faint anthocyanin	G R ^g k/G R ^r K	0/4258	G (R) ^g k	non-crossover
Faint anthocyanin	G R ^g -14 k/g R ^r K	12/35,085	G (R) ^r K	non-crossover with a coincident co for g.
Weak anthocyanin	g R ^g co-1 k/G R ^v -1 k	4/6338	g (R) ^g k	unmarked
Weak anthocyanin	g R ^g nco-1 K/g R ^r k	2/25,241	g (R) ^g K	non-crossover
Dilute anthocyanin	G R ^g McB k/g R ^r K	8/27,757	g (R) ^r K	non-crossover
Dilute anthocyanin	g R ^g co-1 k/G R ^r k	1/5377	G (R) ^r k	unmarked
Dilute anthocyanin	g R ^g co-1 k/G R ^r k	13/28,739	g (R) ^g k	unmarked
Dilute anthocyanin	g R ^g co-1 k/G R ^v k	4/6338	g (R) ^g k	unmarked
Mottled anthocyanin	G R ^g -14 k/g R ^r k	----	G (R) ^g k	unmarked

* Parentheses indicate an intermediate (S) component.

** K₀ represents an altered knob-10 chromosome.

However, if it is postulated that R^r Cornell possesses a single (S) element, it is rather difficult to explain on this basis the occurrence of compound intermediate alleles from the same R^r allele, such as the spotted-dilute mutants. These mutants, which exhibit a combination of stippled-like spots on a fairly dilute background, could arise as the effect of single changes of (S) from a multiple S.S.S... complex. Alternatively, they could represent unstable R alleles. It is noteworthy that four, or possibly five, of the seven spotted-dilute mutants analyzed were also non-crossovers as were four of the mutants of intermediate seed-color.

Several additional intermediate alleles have been found in last summer's detassel plot and will be analyzed this summer.

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13. Behavior of altered knob-10 chromosomes.

As reported in the 1955 Maize News Letter a number of altered knob-10 rod chromosomes originated from a ring-10 heterozygote. A preliminary study has been made on three of these chromosomes to determine their effect on preferential segregation.

The following symbols are used to denote the different types of knobs: K , normal knob; k , knobless 10; K_S , approximately one-half of the original knob located at the end of 10-long; K_{iS} , about one-half of K -10 placed interstitially on 10-long; and K_O , chromosome lacking the knob but possessing the dissimilar chromomere pattern characteristic of normal knob-10 chromosome.

The data given in the following table came from plants heterozygous for the changed knobs.

Culture	Total Population	Number Colored Seeds	Number Colorless Seeds	% R
$R^r K/r^G k$ (control)	15,030	9,546	5,484	63
$R^r K_S/r^G k$	40,114	19,853	20,261	49
$R^r K_O/r^G k$	10,278	5,432	4,846	53
$R^r K_{iS}/r^G k$	16,632	7,993	8,639	48

These data show that normal segregation is restored in the presence of either K_S -10, K_{iS} -10, or K_O -10. This would suggest that the factor

responsible for preferential segregation is located in either the distal half of $\underline{K-10}$, or in the euchromatic segment distal to normal $\underline{K-10}$. Preliminary cytological studies indicate, however, that neo-centric activity which is characteristic of normal $\underline{K-10}$ is present in the $\underline{K_S}$ -chromosome. This is surprising since $\underline{K_S}$ shows no preferential segregation of \underline{R} . The objection may be raised that the $\underline{K_S}$ -chromosome possesses a deficiency which is reducing the normal female transmission of \underline{R} ; however, both pollen and ovule examinations have shown no evidence of abortion. The $\underline{K_O}$ -chromosome also exhibits no abortion in pollen or ovules. This has not been checked in stocks carrying $\underline{K_{1S}}$.

In addition, each of these knobs have been tested in compound with a normal knob-10. If both knobs are equally effective, a 1:1 ratio is expected. However, if the knobs have lost their ability to segregate preferentially, a normal knob ratio is expected. In this case, the normal knob showed a 68 \underline{K} :32 \underline{k} ratio.

Culture	Total Population	Number Colored Seeds	Number Colorless Seeds	% Normal K
R^r k/r^g K (control)	20,976	6,944	14,032	68
R^r $\underline{K_S}/r^g$ K	15,278	7,388	7,890	48
R^r $\underline{K_O}/r^g$ K	17,409	7,090	10,319	59
R^r $\underline{K_{1S}}/r^g$ K	20,327	9,063	11,264	56

These results are inconsistent with the data from table 1. The $\underline{K_S}$ chromosome, which exhibited no preferential segregation in the heterozygote, clearly shows full knob effect in compound with a normal knob-10. Also, the $\underline{K_O}$ -chromosome, which showed no preferential segregation in the heterozygote, exhibits some degree of preferential segregation in the homozygote. This chromosome has not been examined for neo-centromeres. The $\underline{K_{1S}}$ chromosome also shows some preferential segregation in the presence of normal $\underline{K-10}$, but abortion is not excluded.

At the present time an explanation of these results is not apparent, but it seems possible that the phenomenon of preferential segregation could be due to a combination of several factors.

This study includes other altered knob-10 chromosomes such as: one with approximately one-half of the knob on the end of 10-short; one with a normal $\underline{K-10}$ but without the dissimilar chromomere pattern; and one with normal $\underline{K-10}$ on 10-long and a modified $\underline{K-10}$ on 10-short.

14. Behavior of an attenuated knob-10 chromosome.

In the 1955 Maize News Letter it was reported that an attenuated knob-10 chromosome occurred spontaneously in an \underline{R} stock. The knob is rather slender and approximately twice as long as normal knob-10.

This knob (designated K_L) was tested for preferential segregation with a knobless and a normal \underline{K} knob-10 chromosome. The results are as follows:

Culture	Population	Colored Seeds	Colorless Seeds	% \underline{K}
$R^r K_L/r^E k$	12,873	8,324	4,549	64
$R^r K_L/r^E K$	15,284	6,156	9,128	59 (normal \underline{K})
$R^r k/r^E K$ (control)	20,976	6,944	14,032	68

These data show that the attenuated knob segregates preferentially in the heterozygote. In the homozygote, however, there is evidence of megaspore competition between the modified knob and the normal knob, as is shown by the distorted 1:1 ratio. Apparently, the normal knob chromosome has a selective advantage over the attenuated knob.

Two additional modified knob-10 chromosomes, which occurred spontaneously, have been found recently; one resembles K_L , and the other is smaller than normal \underline{K} -10. These have not been tested for preferential segregation.

15. Evidence of increased mutation frequency in presence of homozygous knob-10.

A homozygous knob-10 stock which was used as a male parent gave a high frequency of \underline{R}^E mutants in X-ray and ultra-violet treated plants, and in untreated plants (Genetics 1955). Since the frequency in treated plants was no greater than that in the control, the increased rate of mutation was not attributed to the effects of radiation. At that time there was no evidence available of high mutation rate in female gametes, since heterozygous knob-10 is commonly used in connection with the study of unequal crossing-over.

Subsequent experiments have confirmed this high mutation frequency in female gametes. The compound $\underline{g} \underline{R}^r \underline{K} / \underline{g} \underline{R}^r \underline{K}$, in 5711 tested gametes, yielded 17 colorless seeds. In plants heterozygous for \underline{K} -10, only 21

mutants occurred among 104,853 gametes tested. Thus the mutation rate for R in plants of K/K constitution was 29.8×10^{-4} , while in plants of K/k constitution the rate was 1.9×10^{-4} . These data do not come from sib comparisons.

The depression of R mutation rate in the presence of heterozygous knob-10 could be attributed to the presence of a modifier of mutation in homozygous knob-10 stocks. Alternatively, it could be due to an increase in the rate of unequal crossing-over. It is possible that pairing of homologous regions distal to R in K/K may favor unequal crossing-over, as it is known that heterozygous K-10 considerably reduces normal crossing-over between R and the end of normal chromosome 10. The homozygous knob stock, which was used, was not marked to determine unequal crossovers.

Several K-10 cultures including compounds marked for identification of unequal crossovers were grown in last summer's detassel plot in order to determine the extent to which mutants in homozygous K-10 plants are due to unequal crossing-over rather than to gene mutation. The modified knob-10 chromosomes were used in compound with a normal knob-10 to serve as a distinguishable marker distal to R. In addition, plants were grown which would give a direct comparison of seed-color mutations in K/K versus K/k sibs, and in K/k versus k/k sibs.

The following table presents the mutation rates which were found for each of these knob-10 compounds. The mutants will be examined cytologically this summer.

Culture	Population	Number Mutants	Mutation Rate (10^{-4})
<u>K/K</u>	5,711	17	29.8
<u>K/k</u>	104,853	21	1.9
<u>K_s/k</u>	34,478	13	3.4
<u>K_o/k</u>	130,030	25	1.9
<u>K_o/k</u> versus <u>k/k</u>	146,825	41	2.7
<u>K_s/k</u> versus <u>k/k</u>	77,200	24	3.1
<u>K/K_o</u> versus <u>K/k</u>	39,368	8	2.3
<u>K/K_s</u> versus <u>K/k</u>	9,543	3	3.1
<u>K/K_s</u> versus <u>K_s/k</u>	38,820	34	8.7
<u>K/K</u> versus <u>K/K_o</u>	43,095	31	7.1
<u>K/K_s</u> versus <u>K_s/K_o</u>	29,473	19	6.6

These data clearly show a low frequency of mutation in the presence of heterozygous knob-10 and in sib comparisons of types $\underline{K}/\underline{k}$ versus $\underline{k}/\underline{k}$ and $\underline{K}/\underline{K}_0$ versus $\underline{K}/\underline{k}$, which is essentially the same in knob composition as $\underline{K}/\underline{k}$ versus $\underline{K}/\underline{k}$. It is also evident from these results that the mutation rate is consistently high, with the exception of one cross, when one of the two genotypic classes includes homozygous \underline{K} -10. However, it is not as high as it is expected on the basis of the rate observed in $\underline{K}/\underline{K}$ plants (29.8×10^{-4}).

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16. Effect of Vg on development of the ligule.

Classifications for the ligule character were made among mature plants in several families segregating approximately equal numbers of normal and Vg (vestigial glume) individuals. All normal (non-vestigial) plants were found to have a normal ligule whereas all of the plants classifiable as Vg (vestigial) on the basis of reduced glumes associated with male and female florets were without ligules. These plants have a transverse ridge of compact tissue bordering the sheaths and blades of leaves but lack the membranous extension or flap which is characteristic of a normal ligule. Casual observation of these plants does not permit classification for the liguleless character since the leaf blades of Vg plants are oriented at a sharp angle with the culm as in normal plants, a habit which probably accounts for the earlier failure to recognize this character. Well over 100 field grown Vg and normal plants were classified this past summer for the ligule character; all Vg plants were liguleless while all of the non-vestigial plants had normal ligules. Since it appears that the liguleless character of Vg plants may be classified in the seedling stage, it should provide a valuable marker for chromosome 1 for which relatively few genes with seedling effects are known.

Since there is no basis on which to argue a homology between glumes and ligule, it is suggested that Vg may have a generally adverse effect on those meristems which, in terms of the cycle of development in the particular organ concerned, are initiated relatively late.

17. A possible clue to the nature of Dt action.

From individuals homozygous for \underline{A}^b (known to consist of separable elements each with greater than recessive \underline{a} effect) and crossed with pollen from \underline{aa} plants, individuals with recessive \underline{a} phenotype occur with great rarity. One such derivative from an $\underline{A}^b/\underline{A}^b$, Dt individual has been tested in preliminary fashion. Its phenotype is similar to that of recessive \underline{a} and it is likewise mutable. Moreover it is associated with recessive brown pericarp whereas \underline{A}^b has a dominant brown pericarp effect. While the occurrence of such an individual is reminiscent of changes of the type allele, \underline{A} , to \underline{a} in the presence of Dt it appears necessary in

the present case to account for the simultaneous change to the null condition of both the alpha and beta components of A^b , a requirement not easily satisfied on the hypothesis of gene mutation induced by Dt . Rather, it is contemplated that Dt may control an inhibiting element capable of influencing the adjacent alpha and beta components simultaneously. Critical evidence bearing on this hypothesis will await studies of reversions from the exceptional derivatives. McClintock based a similar argument on studies in which recessive a , in genetically $dt\ dt$ background, was held to yield somatic reversions as scored in the endosperms of individuals in which chromosome 9 aberrations had been induced. It is hoped that the findings reported here will afford a means of testing this hypothesis in studies dealing directly with an analysis of Dt -induced changes at the a locus.

18. The beta member of A^b complexes.

The association of crossing over with the isolation of the alpha (pale-acting) element of A^b (Ecuador extraction), establishes that this element is the left-most member of the A^b complex and, from the fact that A^b has an overall purple effect on pigmentation, provides a basis for the inference that the member on the right (beta) is an allele with purple effect. Since both A^b and its derivative alpha produce a dominant brown pericarp effect, an attempt was made to isolate the beta component in appropriately marked individuals on the assumption that this element, like the type A allele itself, has a red pericarp effect. In preliminary studies two individuals with red pericarp were isolated, both of which carried marker genes which indicated that there had been an associated crossover between the markers T 2-3d and sh_2 , a segment of about seven units and including the A locus. Moreover the markers carried by these derivatives are those expected if beta is located to the right of alpha in the A^b complex. More recently, eight additional derivatives with red-pericarp phenotype have been isolated in similar experiments and all appear to be crossovers but are subject to further critical tests to determine whether they carry the interchange marker and to test for contamination.

19. Evidence for the complexity of beta components of A^b complexes.

Several A^b complexes of Peruvian extraction (designated $A^b:P$) differ from the A^b of Ecuador extraction in regard to the order of the alpha and beta members. Thus, in the case of the latter, the order of members, stated with respect to the sh factor is alpha-beta- sh whereas the order in the $A^b:P$ complexes so far studied is beta-alpha- sh . This sequence in the latter case renders it technically much more feasible to isolate by crossing over the beta element of various $A^b:P$ complexes by taking advantage of the extremely close linkage between alpha and sh . Thus,

in $A^b:P$ (Lima) $Sh/a\ sh \times a\ sh/a\ sh$ crosses, about two-thirds of the colored-shrunken crossovers are determined to be beta-alpha- sh cases on the basis of a dominant brown pericarp (representing a crossover between alpha and sh); however, approximately one-third of the colored-shrunken crossovers have a red pericarp effect. Since it is known that the alpha components of these $A^b:P$ complexes produce a dominant brown pericarp effect, these latter must represent crossover isolations of the beta element following an exchange event between beta and alpha. It may be concluded that $A^b:P$ (Lima) carries a beta element with a red pericarp action. Similar studies carried out with $A^b:P$ (Cuzco) also yield colored-shrunken crossovers which in some cases are dominant brown in pericarp phenotype and in others are red. In addition, however, this complex yields colored-shrunken crossovers whose pericarp phenotype is red-brown and is distinct from the brown and the red phenotypes in the same families. It is assumed for the purposes of further analysis that $A^b:P$ (Cuzco) is at least a triple complex of the type: $\beta^{rb}-\beta^r$ -alpha, having two adjacent beta elements which differ in their determination of pericarp phenotype.

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1. $P_1 \times P_2$ vs. $F_1 + P_2$ as a criterion of overdominance in corn.

Overdominance may be due to heterozygosity per se, a divergent allele mechanism as postulated by East, an intermediate optimum, repulsion linkages and other hypothetical suppositions. If such gene actions are of importance at numerous loci certain breeding methods may be more effective than others. Hull (Jour. Amer. Soc. Agronomy 37: 134-145, 1945) outlined a selection method for specific combining ability based on the occurrence of overdominance. The common observation of corn breeders that many single crosses exceed the sum of the two inbred parents in yield is, according to Hull, indicative of many heterotic loci for yield. If the effects of alleles are strictly additive then the sum of the two homozygous lines which make up the F_1 can not be smaller than the single cross.

It is rather easy genetically to design cases in which the fallacy of the above argument becomes obvious. Say for example line A carries a homozygous recessive pale green allele and line B is homozygous for recessive sugary. Both alleles depress yield markedly. The F_1 will exceed the sum of the two parents not because of overdominance but simply because each line possesses the dominant allele to the other lines' recessive. If these two lines were also available without the pale green and sugary alleles one could produce the two identical single crosses except for the two mutant loci and compare them with the sum of their respective parents.

Such a situation was provided by two dwarf mutations in unrelated long time inbred lines. The inbreds denoted by ID_1 and IID_2 and the mutated lines denoted by Id_1 and IId_2 were intercrossed in the following manner: $ID_1 \times IID_2$, $Id_1 \times IID_2$, $ID_1 \times IId_2$ and $Id_1 \times IId_2$. These four entries were grown in randomized blocks with 16 replications. Data were collected on plant height, kernel row number, ear length and weight of shelled grain. Seed counts were made on seven replications only. Orthogonal partitions of the three treatment degrees of freedom were chosen according to pertinence of comparisons. The means and variances for the four parents were obtained in an experiment grown next to the above described test and reported on in Genetics 39: 908-922, 1954. Table 1 contains the means. The first six rows of the table are reproduced from the afore mentioned publication. The corresponding F-values are summarized in table 2, again the first two rows are a duplication from the paper in Genetics 39. Hull restricts his reasoning to yield only, but there seems to be no apparent reason to place limitations on his argument because heterosis is not confined solely to yield. In table 3 a number of comparisons for the different attributes are set out. The table is self explanatory. For example for yield the single cross $ID_1 \times IID_2$ when

Table 1. Means of five characters taken on two dwarf mutants, their motherlines and certain intercrosses among them.

Mutant or Cross		Plant height in centimeters	Number of seeds	Total kernel weight in grams	Kernel row number	Ear length in millimeters
Id ₂	(inbred)	92.30	426.90	81.40	15.20	174.90
IID ₂	(")	83.70	138.30	30.30	10.60	107.00
ID ₁	(")	188.58	701.65	168.23	15.43	214.06
IID ₂	(")	179.05	530.98	116.27	13.70	190.79
ID ₁ x IID ₂	(single cross)	254.91	903.59	292.53	16.59	259.48
ID ₁ x IID ₂	(")	240.19	840.52	261.62	18.25	254.34
Id ₁ x IID ₂	(")	224.24	848.12	275.46	16.64	267.83
Id ₁ x IID ₂	(")	211.29	822.96	258.60	17.13	255.32

Table 2. Variance ratios for 5 attributes taken on four F₁ hybrids.

Genotypic contrast	Plant height		Number of seeds		Total kernel weight		Kernel row number		Ear length	
	Differ- ence is	F-value	Differ- ence is	F-value	Differ- ence is	F-value	Differ- ence is	F-value	Differ- ence is	F-value
ID ₁ ID ₂ vs ID ₁ IId ₂ vs Id ₁ ID ₂ vs Id ₁ IId ₂		129.88**		1.77		12.60**		32.79**		7.28**
ID ₁ ID ₂ + ID ₁ IId ₂ vs Id ₁ ID ₂ + Id ₁ IId ₂	+	320.31**	+	1.94	+	29.93**	+	15.83**	-	4.19*
ID ₁ ID ₂ + Id ₁ IId ₂ vs ID ₁ IId ₂ + Id ₁ ID ₂	+	.27	+	.52	+	5.29*	-	18.76**	-	2.63
ID ₁ IId ₂ + Id ₁ ID ₂ vs ID ₁ ID ₂ + Id ₁ IId ₂	+	69.08**	+	2.83	-	2.59	-	63.76**	+	15.02**

* Exceeds 5 percent level of significance.

** Exceeds 1 percent level of significance.

Table 3. Comparison of crosses and lines.

Character	Difference represents	Result	Percent increase of cross over parent 1 + parent 2	Comparison represents	Result	Percent increase of cross over mean of parents
Plant height	$ID_1 \times IID_2 - (ID_1 + IID_2)$	-112.72	no	$ID_1 \times IID_2 - \frac{ID_1 + IID_2}{2}$	71.10	39
	$ID_1 \times IID_2 - (Id_1 + IID_2)$	78.91	45	$ID_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	166.91	190
	$Id_1 \times IID_2 - (Id_1 + IID_2)$	35.29	20	$Id_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	123.29	140
Number of seeds	$ID_1 \times IID_2 - (ID_1 + IID_2)$	-329.04	no	$ID_1 \times IID_2 - \frac{ID_1 + IID_2}{2}$	287.28	47
	$ID_1 \times IID_2 - (Id_1 + IID_2)$	338.59	60	$ID_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	620.99	220
	$Id_1 \times IID_2 - (Id_1 + IID_2)$	257.76	46	$Id_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	540.36	191
Total kernel weight	$ID_1 \times IID_2 - (ID_1 + IID_2)$	8.03	3	$ID_1 \times IID_2 - \frac{ID_1 + IID_2}{2}$	150.28	106
	$ID_1 \times IID_2 - (Id_1 + IID_2)$	180.83	162	$ID_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	236.68	424
	$Id_1 \times IID_2 - (Id_1 + IID_2)$	146.90	131	$Id_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	202.75	363

Table 3 (Continued)

Character	Difference represents	Result	Percent increase of cross over parent 1 + parent 2	Comparison represents	Result	Percent increase of cross over mean of parents
Kernel row number	$ID_1 \times IID_2 - (ID_1 + IID_2)$	-12.54	no	$ID_1 \times IID_2 - \frac{ID_1 + IID_2}{2}$	2.03	14
	$ID_1 \times IID_2 - (Id_1 + IID_2)$	- 9.21	no	$ID_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	3.69	29
	$Id_1 \times IID_2 - (Id_1 + IID_2)$	- 7.95	no	$Id_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	4.23	33
Ear length	$ID_1 \times IID_2 - (Id_1 + IID_2)$	-145.37	no	$ID_1 \times IID_2 - \frac{ID_1 + IID_2}{2}$	57.06	28
	$ID_1 \times IID_2 - (Id_1 + IID_2)$	-22.42	no	$ID_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	118.53	84
	$Id_1 \times IID_2 - (Id_1 + IID_2)$	-26.58	no	$Id_1 \times IID_2 - \frac{Id_1 + IID_2}{2}$	114.37	81

compared with the sum of the two parents gives an excess of three percent. This amount according to Hull must be due to overdominance. However, if the homozygous dwarf lines Id_1 x IId_2 are added up and contrasted to the hybrid Id_1 x IId_2 heterosis due to overdominance would jump to 131 percent. But since the difference between the normal inbreds and their dwarf counterparts is known to be due to mainly the strong effect of the recessive dwarf allele, the case for overdominance breaks down and resolves into a simple dominant-recessive relationship. It is not denied that some forms of overdominance, on whatever scale of observation it is measured, exist but simply to say that the excess in yield of a single cross over the sum of the two parents is attributable to overdominant loci is, as shown here, in many cases an unrealistic and unnecessary postulate.

Due to the fact that the four single crosses and the inbred parents were grown in two separate tests, although within a small and uniform piece of land, no error terms for testing differences were available. From the tables it appears clear that differences are so large and consistent as to eliminate a need for probability statements. However, data with identical and additional dwarf mutants will be forthcoming soon. These experiments will provide proper error terms.

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2. Studies on the inheritance of resistance to corn leaf rust, *Puccinia sorghi* Schw.

Genetic investigations on the inheritance of resistance to corn leaf rust, *Puccinia sorghi* Schw. were initiated at the Iowa State College in 1953. A rather heavy infection of rust that summer gave an opportunity to rate approximately 1700 inbred progenies and introductions of corn for field reaction to the fungus. Greenhouse seedling inoculations on 165 lines showing field resistance revealed that 25 strains possessed protoplasmic resistance to one or more biotypes of the pathogen. Subsequent tests of single cross combinations involving many of these lines have shown that 13 carry dominant genes for resistance and 12 have recessive genes. In addition to these, 13 strains show evidence for resistance but such resistance is incomplete or is modified by environmental conditions. (Studies at the University of Wisconsin have found resistance in 39 Mexican and South American types of which 23 have been shown to carry dominant genes for resistance and 2 appear to have recessive genes. These factors are being studied further in our program.)

Each gene conditioning resistance to rust is being transferred to inbred BL4 by the backcross method. This will serve three main purposes: (1) establish a set of sub-lines, or nearly "isogenic" lines, of B 14 which can be used in genetic studies of the pathogen; (2) the various genes conditioning resistance will be located in a stock which can be easily handled in the corn belt; (3) the sub-lines of BL4 will be used as a series of differential hosts for the identification of races within a pathogen. It will be desirable to add to the collection of resistant stocks any additional sources of protoplasmic resistance which other corn workers may have. Since interest will be only in the genes affecting host reaction to the fungus, such sources may be in various forms such as inbred lines, open pollinated varieties or hybrid combinations.

The relationships among the various genes for resistance are being determined by studies involving F_1 and F_2 progenies from single crosses among the resistant sources. Also, studies of F_1 , F_2 and backcross progenies involving resistant and susceptible strains are giving information on the number of factors reacting in a cross for a specific rust culture and whether or not these factors are dominant or recessive in behavior. At this time limited data are available, some of which are shown in the following table:

<u>Cross</u>	Number of Plants		Theoretical <u>Ratio</u>	χ^2 <u>Value</u>	P <u>Value</u>
	<u>Res.</u>	<u>Susc.</u>			
1 (K148 x BL4) F2	131	47	3:1	0.187	.50-.70
2 (K148 x BL4) B14	130	161	1:1	3.302	.05-.10
3 (GG208 x BL4) F2	64	31	3:1	2.951	.05-.10
4 (GG208 x BL4) B14	102	86	1:1	1.362	.20-.30
5 (Cuzco x BL4) F2	64	29	3:1	1.896	.10-.20
6 (Cuzco x BL4) B14	96	102	1:1	0.182	.50-.70
7 (Mex. 83 x B37) F2	79	20	3:1	1.215	.20-.30
8 (Mex. 83 x B37) B37	140	154	1:1	0.667	.30-.50
9 (B38 x W22) F2	74	22	3:1	0.222	.50-.70
10 (B38 x W22) W22	17	22	1:1	0.641	.30-.50
11 (P. I. 193906 x BL4) F2	11	53	1:3	2.083	.10-.20
12 (P. I. 193906 x B37) F2	15	59	1:3	0.883	.30-.50
13 (Pop 35 x W32) F2	8	90	1:15	0.612	.30-.50
14 (Pop 35 x BL4) F2	11	161	1:15	0.006	.90-.95
15 (Pop 36 x BL4) F2	9	85	1:15	1.773	.10-.20

These results indicate three types of gene interaction. In crosses 1 to 10 observed numbers show satisfactory fit to 3:1 for F₂ or 1:1 for backcrosses with resistance being dominant. Crosses 11 to 12 suggest that P.I.193906 carries one factor which is recessive in its behavior. In progenies 14-15 the data support a duplicate factor hypothesis in which both factors must be present in the homozygous recessive phase for resistance to be expressed. Additional F₂, backcross and F₃ progenies will be studied to verify these results.

Inbred B38 is resistant to 37 of 42 rust cultures with which it has been tested; K148 carries resistance to 36 of these same cultures. Cuzco has been resistant to 40 cultures to which it has been tested. GG208 has shown resistance to 37 of 38 cultures studied. Based on their reactions to the various cultures studied, these four sources appear to have different genotypes for resistance to corn rust. The other sources of resistance have been tested with varying numbers of rust cultures but none has shown resistance to as many cultures as the four listed above. Several of the sources studied appear to possess resistance to only one or a few of the rust cultures.

With the transfer of A. L. Hooker to the University of Wisconsin in December, 1954, this has become a cooperative project between the two institutions.

W. A. Russell
A. L. Hooker

3. Inheritance of corn borer resistance.

A study was made of the segregation of F₂ and first backcross generations of two crosses involving WF9 and M14 as susceptible parents and a resistant $\underline{gl}_7 \underline{v}_7$ chromosome 3 linkage tester stock. All plants were hand infested with corn borer egg masses. Notes were obtained on all plants for the glossy and virescent characters in the seedling stage and corn borer leaf feeding rating in late June.

The data for the WF9 x $\underline{gl}_7 \underline{v}_7$ cross are presented in Table 1. The range and distribution of borer ratings for the F₁ was very similar to that for the $\underline{gl}_7 \underline{v}_7$ parent. Both ranged from 1 to 5 with a mean of 2.5 for $\underline{gl}_7 \underline{v}_7$ and 3.1 for the F₁. WF9 was more susceptible with a range from 7 to 9 and a mean of 8.6. Homozygous susceptible plants appeared easy to distinguish from the homozygous or heterozygous resistant plants, but the latter two types were indistinguishable from each other. In the F₂ population 121 of 417 plants rated 7 to 9. If it is assumed that these classes included all plants homozygous for susceptibility and all other classes contain homozygous resistant and heterozygous types, 104 such plants rating 7 to 9 would be expected from the segregation of a single gene pair. In the backcross to WF9 160 of 309 plants rated in the

Table 1. Segregation for European corn borer resistance and for glossy and virescent seedlings in the cross WF9 x gl¹⁷ v¹⁷.

Entry	Phenotype	Total no. plants	European corn borer rating									Mean
			1	2	3	4	5	6	7	8	9	
WF9	normal	85							2	27	56	8.6
gl ¹⁷ v ¹⁷	glossy, virescent	101	20	34	26	19	2					2.5
F ₁	normal	111	5	28	40	31	7					3.1
F ₂	normal	325	27	61	40	50	22	18	11	22	74	4.9
	glossy, virescent	86	20	11	14	20	6	3	1	3	8	3.7
	glossy	3	1	1							1	4.0
	virescent	3	1	1							1	4.0
	Total	417	49	74	54	70	28	21	12	25	84	4.7
F ₁ x WF9	normal	309	18	30	31	42	23	5	6	38	116	6.1
F ₁ x gl ¹⁷ v ¹⁷	normal	164	18	43	40	43	16	3		1		3.1
	glossy, virescent	143	21	57	33	28	3	1				2.6
	glossy	3	1	1	1							2.0
	Total	310	40	101	74	71	19	4		1		2.8

7 to 9 class. This is very close to the 1:1 ratio expected from a single-locus segregation.

There appeared to be some association between the segregation of the borer resistance gene and that of the virescent and glossy genes. Some information on the genetic linkage value or cross-over percentage between these loci can be obtained from the glossy-virescent class of the F_2 . If all susceptible plants in this class are assumed to have resulted from the union of two cross-over gametes, the cross-over frequency can be estimated as the square root of the percent of the total glossy-virescent F_2 plants which rated 7 to 9. The cross-over estimate obtained in this case was 37 percent. Likewise, of 121 susceptible plants 14 plants or 11.6 percent were either glossy, virescent, or both. These also can be considered the result of the union of two cross-over gametes and can be used to estimate the percent crossing over. In this case the estimate obtained was 34 percent.

The data for the $ML4 \times \underline{gl}_7 \underline{v}_17$ cross are presented in Table 2. In the F_2 population 105 of 401 plants rated 7 to 9 for corn borer leaf feeding, and an additional 15 plants rated 6. Unless a rather high proportion of the plants rating 6 were assumed homozygous for susceptibility, the ratings did not deviate significantly from what would be expected from segregation at a single locus. In the backcross to $ML4$ 165 of 322 plants rated 7 to 9 approximating very closely the 50 percent expected from segregation of a single gene pair.

Linkage of the borer resistance gene with the $\underline{gl}_7 \underline{v}_17$ genes was indicated again in this cross. Of the 102 F_2 plants which were both glossy and virescent, 10 rated 7 to 9 for borer leaf feeding. Likewise, 11 of the 105 susceptible F_2 plants were either glossy or both glossy and virescent. Using the same assumptions and calculations as explained for the other cross, estimates obtained for the cross-over percentage were 31 and 32.

The data from both crosses could be interpreted similarly. Resistance appeared dominant in both cases and appeared to be conditioned by a single pair of genes. This gene pair was linked with the \underline{gl}_7 and \underline{v}_17 genes of chromosome 3 with cross-over values estimated at from 31 to 37 percent.

Table 2. Segregation for European corn borer resistance and for glossy and virescent seedlings in the cross M14 x gl₇ v₁₇.

Entry	Phenotype	Total no. plants	European corn borer rating									Mean
			1	2	3	4	5	6	7	8	9	
M14	normal	95						4	12	19	64	8.4
gl ₇ v ₁₇	glossy, virescent	102	19	33	29	21						2.5
F ₁	normal	105	2	14	28	39	12	8	1	1		3.7
F ₂	normal	293	19	51	35	57	25	12	24	25	45	4.9
	glossy, virescent	102	25	18	13	26	8	2	2	4	4	3.3
	glossy	6		1	1	2		1	1			4.3
	Total	401	44	70	49	85	33	15	27	29	49	4.5
F ₁ x M14	normal	322	7	27	19	60	32	12	26	57	82	6.1
F ₁ x gl ₇ v ₁₇	normal	168	19	30	38	64	14	1	2			3.2
	glossy virescent	130	18	48	35	27		1	1			2.6
	glossy	4	1		3							3.2
	virescent	3	2		1							2.0
	Total	305	40	78	73	95	14	2	3			2.9

4. Effectiveness of plant resistance in reducing corn borer damage.

Nineteen single crosses among three susceptible and four resistant inbred lines were evaluated for borer resistance and for yield. Yield data were obtained for each hybrid from one sprayed and two unsprayed treatments. Data are shown by types of crosses and by inbred lines in Table 1. Leaf feeding ratings for three S x S crosses, ten S x R crosses and six R x R crosses averaged 8.1, 4.9, and 2.5, respectively. Borer damage points per plant for the same crosses averaged 5.26, 2.46, and 1.32, respectively. The yield of the sprayed treatment exceeded those of the unsprayed treatments by an average of 12.0 bushels per acre for the S x S crosses, 5.6 bushels per acre for the S x R crosses, and 3.9 bushels per acre for the R x R crosses.

An item of interest is apparent in the data on the individual inbred lines. B14 crosses were susceptible to borer feeding as evidenced by both the leaf feeding rating and damage point counts, but the yield reduction attributable to borer damage was not as great as that in the hybrids of the other susceptible lines. On the other hand, N16 hybrids were intermediate to resistance to borer feeding; but the yield differences between the sprayed and unsprayed plots were second only to those of the 38-11 crosses. This would indicate that inbred lines may differ markedly in tolerance to first brood borer leaf feeding in addition to differing in actual leaf feeding resistance.

Table 1. Yields and European corn borer resistance ratings of 19 single cross hybrids.

Hybrids	Corn borer on unsprayed plots		Yields in Bu/A		
	Leaf feeding rating	Damage points per plant	sprayed	unsprayed	Difference
S x S	(3) 8.1	5.26	82.2	70.2	12.0
S x R	(10) 4.9	2.46	88.6	83.0	5.6
R x R	(6) 2.5	1.32	88.0	84.1	3.9
WF9 crosses	(6) 6.0	3.68	86.1	76.5	9.6
B14 crosses	(6) 6.1	3.36	87.5	82.8	4.7
38-11 crosses	(4) 6.2	3.47	84.4	73.8	10.6
R71 crosses	(5) 3.5	2.00	87.4	84.3	3.1
N16 crosses	(6) 4.8	2.61	90.9	81.0	9.9
(WF9x458-1) crosses	(5) 3.3	1.75	83.1	78.8	4.3
C. I. 31 crosses	(6) 2.7	1.02	90.9	89.6	1.3

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1. An a_1 mutable arising in pg^m stocks.

A newly arisen a_1 mutable that was segregating in a stock derived from a pale green mutable family was reported in the 1952 Maize News Letter. Tests were set up to determine the relationship of this new a_1 mutable to the Enhancer system controlling mutability at the pg locus; (i.e. $pg + En =$ mutable pg ; pg and no $En =$ stable pg .) One such test was designed to determine whether En is necessary for a_1 mutability. This was done by introducing pg^s (stable pale green, no Enhancer) into the a_1 mutable stocks that were not segregating mutable pg . This would test the presence of Enhancer in the a_1^m stocks. If a_1 mutability is controlled by En , all the pg seedlings arising from variegated kernels from the F_2 ears would be mutable. Following the selfing of these F_1 plants, (i.e. from the cross of a_1 mutable \times pg^s) a_1 mutable kernels were selected from F_2 ears and planted in seedling tests. Mutant pale green seedlings arising from these a_1 mutable seed were non-variegated or stable types indicating the absence of En to which pg seedlings respond. From this observation, it is evident that the factor that determines mutability at the a_1 mutable locus does not affect mutability at the pg locus. It is thus suggestive that this newly arisen a_1 mutable is not controlled by Enhancer.

Peter A. Peterson

2. Heterochromatin breakage with maleic hydrazide.

The hypothesis that maleic hydrazide causes selective breakage in heterochromatin was tested on strains of maize containing varying numbers of knobs. Germinated seeds of the strains Knobless Flint (0 knobs), IDT (4 knobs), HY (6 knobs) and Zapalote Chico (12 knobs) were treated with 10^{-3} molar and 10^{-4} molar maleic hydrazide for two hours and fixed 22 hours after the termination of treatment. Chromosome breakage was measured in terms of anaphases with bridges per anaphase. A strong positive correlation was found between knob number and bridges with an approximately five fold difference between the Knobless Flint and Zapalote Chico.

Anaphases with bridges/anaphase $\cdot 10^{-3}$ M. maleic hydrazide

Knobless Flint	IDT	HY	Zapalote Chico
8.3%	12.1%	20.5%	42.9%

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Sweet corn.

Seeds of the adapted inbreds, grown from soil blocks, have been bulked up. All produce good ears with sufficient seeds, except for NC-2 which, although a good combiner, is liable to produce an occasional four-rowed ear. Four inbreds have been hybridized with inbred C 13, already used in producing the John Innes Hybrids, to see whether suitable F_1 hybrids with higher row numbers are obtainable. These crosses will be tested in 1956.

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1. X-ray induced deficiencies and multiple embryo formation.

X-irradiation of the pollen results in an increase in the frequency of multiple seedlings in the F_1 (Jour. of Hered., 1951, pp. 90-93). A comparison of pollen abortion frequencies for plants originating from twin embryos and sibs from monoembryonic kernels suggested that chromosomal aberrations were concerned in the formation of multiple embryos. Ring chromosomes, dicentrics and losses of whole chromosomes were observed in aceto-carminic smears of young leaves of multiple seedlings. Recent preliminary data from marked crosses indicate that deficiencies induced in the sperm frequently result in cleavage of the embryo, leading to the formation of identical multiple embryos.

2. Monoploids following X-irradiation of the pollen.

Tester $lg_1 gl_1$ was crossed with pollen of inbred C13A irradiated at levels of 1000, 2000, and 4000 r. Monoploids were less frequent in the 3804 F_1 seedlings of the treated group than in the control population of comparable size.

3. Plasmodial microsporocytes, aneuploid metaphase I and asynapsis in X-ray induced twins.

Plasmodial masses of microsporocytes, presumably due to a premeiotic suppression of cytokinesis, were frequent in both members of a set of twins isolated from the F_1 following pollen treatment of 1000 r.

Hyperploid and hypoploid metaphase I figures also occurred. All of the pollen mother cells exhibited varying degrees of asynapsis. Metaphase counts of 19 plus a fragment and 19 were obtained for both members from aceto-carminic smears and crystal-violet sections of root-tips.

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1. N. J. 143y - A potent sweet corn fertility restorer.

The apparent scarcity of good fertility restorers in established sweet corn inbreds as well as in most sweet corn lines and varieties make the finding of such a strain of general interest. Seed of N. J. 143y-830-2, a remarkable combiner, was received in 1954 from Dr. Robert Snell of the New Jersey Agricultural Experiment Station. This inbred demonstrated its ability to restore fertility completely to sterile C13 of the T type, at this station in 1955. Dr. Snell says, "N. J. 143y was started in 1933 by Dr. Howard B. Sprague in a cross of Golden Giant sweet corn as seed parent with a 5th generation inbred of Northwestern Yellow Dent, selected for early maturity and smut and lodging resistance, as pollinator." It is possible then that the restorer factor found in this strain of sweet corn may have been transferred from field corn.

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1. Reversed germ.

On the ears of most varieties of corn the germinal face of each kernel is oriented toward the tip of the ear. Occasional kernels may be found, in which the orientation is toward the base of the ear spoken of in the literature as reversed germ (r.g.). Such kernels are found regularly in Country Gentleman sweet corn. The inheritance of the character was studied in dent corn lines which showed a relatively high percentage of reversed germ kernels and some crosses were also made with Country Gentleman. The character was found to be recessive and inherited as a maternal plant character.

Its morphology may be summarized as follows: In corn two spikelet primordia develop into one upper and one lower floret each. In most varieties the upper floret is functional and develops into a mature kernel while the lower one aborts. In Country Gentleman sweet corn the writer found that about 50% of the kernels were reversed when counted from the part of the ear where no rows could be detected. The interpretation is that here both florets develop, the upper one into a normal and the lower one into a r.g. kernel. From this fact it was concluded that the so called reversed germ kernel is not reversed at all, but has its position determined by the location of the second floret which is a mirror image of the first and thus is a mere consequence of the development of the second floret.

One of the r.g. lines used showed a considerable variation in r.g. kernels (0 - 63.7%). This was explained as being due to variable expressivity of the gene or genes involved. All ears but two had some r.g. kernels. Thus penetrance seemed to be complete, the two exceptional ears probably being contaminations. A study of 30 ears from the r.g. parent, the F_2 and the backcross to the r.g. parent revealed that the r.g. kernels are not distributed at random on the ear. Based on the average of the 30 ears 3.9% of the r.g. kernels were found in the upper third of the ear, 7.4% in the middle and 14.1% in the lower third of the ear. Another study of a possible relationship between kernel number on the ear and r.g. kernels revealed that in general the average percent abnormalities decreased as the kernel number increased. This apparent relationship found in the r.g. line was present to a much less degree in the segregating population.

The inheritance study which included both parents, F_1 , F_2 and both backcrosses revealed the following facts:

The character is due to one major and one minor gene, either factor alone or both together causing the reversed germ character. The minor factor gives an intrinsic low percentage of reversed germ kernels. The backcross ratio was 1:3 and the F_2 ratio was 9:7. Some exceptions were found to these ratios. Some backcrosses, in which a different normal had been used, segregated in a 1:7 ratio. The results indicate that normals may carry factors affecting the inheritance of this character, with some indication of a dominance effect.

Reciprocal crosses between the r.g. line and Country Gentleman sweet corn lead to the conclusion that ear type, i.e. presence or absence of rows as well as reversed germ kernels are maternally transmitted.

A second r.g. line received from Dr. F. S. Warren, Central Experimental Farm, Ottawa, Canada had a much higher percentage of reversed germ kernels (93.5% in the original ear). It also behaved as a recessive character. Crosses between the two lines indicated they carry different genetic factors.

2. Striate-2 (sr_2).

This character has been reported under the name waseca stripe in the Corn News Letter 27 (page 66) and 29 (page 54). Further linkage data on it were obtained in 1955. These confirm its location on chromosome 10. The genetic constitution of the striate stock with respect to the aleurone color series was found to be $A_1A_1A_2A_2A_3A_3$ cc rr ii (not a_3a_3 as was previously stated).

The following data were obtained from backcrosses, F_2 's and combined backcross and F_2 data, and originated from ears segregating for one color factor (R) only. Heterogeneity tests were applied to the different groups of data and indicated that the data were homogeneous. The following table shows the source of the data, number of plants classified and the percent crossing over. All crosses were in the coupling phase.

<u>golden₁ vs r.</u>		
Source	N	% c. o.
3 point backcross test	436	20.0
F_2 data	231	18.5
(3:1)(1:1) data	1360	16.0

<u>striate₂ vs r.</u>		
3 point backcross test	436	25.0
F_2 data	231	31.5
all backcrosses	1796	25.1

<u>striate₂ vs golden₁</u>		
3 point backcross test	436	44.9
F_2 data	231	45.0
(3:1)(1:1)	1360	40.0

The detailed data on the three point test are as follows:

grs	129	g++	38	gr+	49	g+s	3	total	436.
+++	118	+rs	42	++s	53	+r+	4		

Therefore the order of the genes is golden₁ - R - striate₂, as already reported. (Corn News Letter 29).

The striate stock had also been crossed on to nana-2. From three F₂ progenies it was concluded that nana-2 was independent of R and of striate-2. One ear segregated for Pr vs pr: 82 PrNa: 14 Prna: 13 prNa: 27 prna. The data suggest linkage between nana-2 and pr.

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Breeding for sugars in the corn stalk after maturation of the grain.

Breeding work suggested to us by Dr. D. F. Jones in 1950 was continued during 1955. Partial reports have been published in the Maize News Letters of 1952, 1953, and 1955.

In 1951 Dr. Jones sent us seven inbred lines and five hybrids, and in 1954 eleven more hybrids. From 1951 to 1955 American and indigenous inbreds were selected for high refractometrical readings of stalk juice after the grain was mature (i.e., with less than 30% moisture). The same material was selected for greenness of leaves and stiffness of stalks. Pure inbreds were not affected by this selection. Heterozygous lines were, on the contrary, deeply affected. American and indigenous inbred lines were combined in 3-way crosses and single crosses to test general and specific combining ability for these characters. The three combinations: "American" X "American," "American" X "indigenous," and "indigenous" X "indigenous" were tested. The number of hybrids tested in 1955 was 304.

The 1955 results show the possibility of obtaining hybrids with very high refractometrical stalk juice readings which remain green when the grain has matured (having 25% moisture content). These hybrids should also show a very high yield and the grain should contain a large amount of protein.

1. Recovered inbreds.

In the last year, 1955, second cycle inbreds, recovered by back-crossing from single crosses of "American" X "American," were tested for the character being selected. The comparison of crosses of C103 and corresponding crosses of (TL. C103II)_S₃ is interesting. See Table I.

2. Some cases of dominance for high refractometrical readings.

As Dr. D. F. Jones reported, the refractometrical readings of F₁'s are lower than the refractometrical readings of the corresponding parents. (Report of 7th North. Corn Improv. Conference). In our trials, 10 out of 111 different crosses were exceptions to this general rule; single crosses between them show refractometrical readings equal or superior to

Table I. A comparison of the combining ability of C 103 and (TL-C 103^{II})-S₃.

Trial	Hybrids	Grain yield (15.5% moisture) Kgs./Ha.	% grain moisture at harvest	Stalk juice refractometrical reading at grain harvest
V	(M.B.G. 404 x W22) x C103	8,603	29.9	10.23
V	(M.B.G. 404 x W22)x(TL-C103 ^{II})-S ₃	9,430	28.4	11.06
	Difference	+ 827	-1.5	+0.83
V	V30 Commercial	8,766	28.1	8.57
V	V31 Commercial	7,337	22.8	3.36
V	V32 Commercial	6,728	28.5	9.25
T	W22 x C103	12,030	26.0	10.45
T	W22 x (TL-C103 ^{II}) S ₃	12,780	26.6	8.38
	Difference	+ 750	0.6	-2.07
T	BL4 x C103	11,225	27.4	7.67
T	BL4 x (TL-C103 ^{II}) S ₃	13,144	26.9	8.67
	Difference	+1,959	-0.5	+1.00
T	P8 x C103	12,581	26.7	7.10
T	P8 x (TL-C103 ^{II}) S ₃	13,502	27.2	8.57
	Difference	+ 921	+0.5	+1.47
T	MOG x C103	12,053	28.0	7.03
T	MOG x (TL-C103 ^{II}) S ₃	13,980	25.8	8.16
	Difference	+1,927	-2.2	+1.13
S	(P8 x W22) x C103	8,562	31.2	8.90
S	(P8 x W22) x (TL-C103 ^{II}) S ₃	11,057	30.0	8.40
	Difference	2,495	-1.2	-0.50
T	T43= A, Standard Commercial	10,118	25.3	--
T	T44= B, Standard Commercial	10,859	25.0	--
T	T42= C, Standard Commercial	10,649	24.4	--
S	S28= A, Standard Commercial	10,079	28.1	--
S	S27= C, Standard Commercial	10,450	31.9	--
	Average difference with standard hybrids.	+2,849	+0.7	+1.87
	Average difference between homologous hybrids.	+1,767	-0.4	+0.31

the highest parent. This complementary action was evident also in the 3-way crosses. See Table II.

3. Correlation between high corn protein percentage, refractometrical reading of stalk juice, and greenness of the vegetative part of the plant after grain maturation.

In the Maize Newsletter 29, we reported a parallelism in inbred lines between refractometrical readings (after grain maturation) and kernel protein percentage. In the 1955 trials, seven hybrids were analyzed for grain protein: one standard hybrid (Ohio M 15) and six other experimental ones superior in their refractometrical readings and greenness of leaves after grain maturation. The protein percentage in these six "sweet stalk hybrids" was higher than the protein percentage in the standard hybrid--13.63%-15.58% as compared to 11.98% for the latter. Among these seven hybrids there is no correlation between protein percentage and reduction in yield. Each sample analysis was representative of the four replications for each hybrid. Fertilizers applied by the hectare were: N = 140 Kgs.; P₂O₅ = 108 Kgs.; K₂O = 60 Kgs. See Table III.

4. Evaluation of hybrids with high refractometrical stalk juice readings compared with evaluation of standard hybrids.

Table III is a summary of the productivity and evaluation of the standard hybrids in comparison with experimental hybrids with a high content of sugars in the stalk at the time of grain maturation. To obtain the average productivity of standard hybrids those with the highest grain yield were considered from each trial: Ohio M 15; Indiana 251 A; Bear 31; Dekalb 505; and Clyde B 31. (Ohio M 15 was the best standard hybrid in 3 different trials.) To obtain the average productivity of hybrids with high percentage of sugar in the stalk, the hybrids with the highest yields --of grain, of green leaves, and of fermentable sugars--were considered for each trial. The trials were run as randomized blocks of four replications.

5. Persistence of sugars in the stalk.

After harvesting the mature ears on October 17th, the plants of three experimental hybrids with high refractometrical readings and the plants of four standard hybrids remained in the field for later observations. On November 22, after six consecutive nights of frost (from minus 2° C to minus 5° C), the refractometrical readings were determined. The results are recorded in Table IV. The stalks of standard hybrids were, on the whole, lodged and rotten. The stalks of the hybrids with high refractometrical readings were, on the contrary, still stiff and erect.

6. Applications and implications.

The best utilization of the plants of such hybrids after the grain is harvested is being considered. Leaf silage is much appreciated by

Table II. (Refractometrical readings were made when grain was harvested.)

Trial	Experimental Hybrids	P ₁	P ₂	M P ₁ P ₂	F ₁	% moisture at harvest	Grain yield Ks./Ha.	Grain % protein
X	MBG 68 x MBG 3	13.57	12.15	12.86	13.33	24.6	9,035	15.25
U	MBG 68 x MBG 3	13.57	12.15	12.86	15.08	24.0	8,343	15.56
X	MBG 68 x MBG 404	13.57	11.40	12.48	15.68	27.0	8,574	13.63
M	MBG 3 x MBG 404	12.15	11.40	11.77	12.78	---	---	---
U	(MBG 3 x MBG 404) x MBG 68	12.15-11.40	13.57	12.67	14.34	25.4	9,257	---
V	(MBG 404 x W22) x MBG 68	11.40-12.80	13.57	12.83	13.57	28.9	9,431	14.38
V	(MBG 404 x C103) x MBG 68	11.40-8.90	13.57	11.86	13.91	27.4	9,104	14.81
M	MBG 404 x MBG 235	11.40	6.62	9.26	10.02	---	---	---
FAO Va.	(MBG 3 x MBG 404) x MBG 624	12.15-11.40	13.30	12.53	14.01	---	---	---
M	(MBG 3 x MBG 404) x MBG 624	12.15-11.40	13.30	12.53	9.42	---	---	---
U	MBG 68 x MBG 624	13.57	13.30	13.43	14.08	26.2	9,360	13.88
X	MBG 68 x MBG 624	13.57	13.30	13.43	10.95	29.2	9,000	---
Ob	MBG 104 x MBG 68	6.7	13.57	10.13	14.06	---	---	---
X	MBG 3 x MBG 96	12.15	11.78	11.96	12.51	26.1	5,350	---
Fert	MBG 3 x MBG 96	12.15	11.78	11.96	14.51	---	5,350	---
	Commercials							
X		---	---	---	---	22.2	8,902	---
X		---	---	---	---	22.4	7,803	---
X	Ohio M 15	---	---	---	---	26.8	9,152	11.88
X	Indigenous variety	---	---	---	---	25.6	5,916	---
U	Ohio M 15	---	---	---	---	26.5	9,252	11.88
U		---	---	---	---	24.5	8,115	---
U		---	---	---	---	25.0	8,011	---
V	Ohio M 15	---	---	---	---	23.1	8,666	11.88
V		---	---	---	---	22.8	7,337	---
V		---	---	---	---	28.5	6,728	---

Table III.

	Hybrids with the best performance			
	Experimentals of highest yield of: grain, green leaves and fermentable sugars	Standard Americans of highest grain yields		
Number of hybrids averaged	27	7		
American scale cycle in days	117	119.00		
Kgs. yield of grain/Ha. (15.5% moisture content)	10,753	9,370.00		
Litres of 100% alcohol/Ha. calculated from fermentable sugar content of juice stalk (+)	772	305.00		
Litres of 100% alcohol per 100 kgs. stalks	3.21	2.13		
Kgs. of green leaves/Ha.	12,496.00	practically 0		
Refractometrical reading when grain was harvested	10.8	8.6		
Grain moisture content at harvesting	27.8	28.1		
<u>Feeding value, estimated in Spanish pesetas/Ha.</u>				
For grain	32,259.00	28,110.00		
For green leaves	4,998.40	Not valuable		
For solid of the stalk juice	<u>5,497.80</u>	Not valuable		
TOTAL pesetas value	42,754.00	28,110.00		
Increase in value in pesetas over the standard hybrids	14,645.00	0.00		
Increase over the standard hybrids expressed in %	52.0%	0.00		
Feeding value of the plants compared with the feeding value of the grain of the experimental hybrids	32.5%	0.00		
--- THE RANGE WAS ---				
	Kgs. Yields/Ha. of:			Refract. reading
	Grain (at 15.5% m)	Solid of stalk juice	Green leaves	
Experimental hybrids	13,975 to 7,469	3,395 to 792	20,000 to 7,469	14.3 to 7.55
Standard hybrids	10,895 to 6,550	945 to 523	DRY	9.9 to 7

Table IV.

	Refractometrical readings on different dates			% of stalk juice on the dates		% grain moisture at Oct. 17 (harvesting day)
	Oct. 17th Harvesting Day	Oct. 27th	Nov. 22nd (first frost on Nov. 16)	Oct. 17th (harvesting day)	Nov. 22nd (first frost on Nov. 16)	
Experimental hybrids	13.7	14.6	12.3	76.1	69.7	25.0
Standard hybrids	8.0	--	Lodged and rotten	58.9	Rotten	22.7

oxen. The solids of the stalk juice (more than 70% consists of fermentable sugars) can be utilized as raw material for industrial purposes.

A genetic investigation of the kinds of sugars in the stalk juice of different inbreds is being considered as well as a study of the genetical and physiological interaction of these sugars with protein formation in the kernel. Correlations between high refractometrical readings, high percentages of grain protein and high yields of grain are interpreted as:

- a) The genetical and physiological interactions of different functions that determine heterosis.
- b) Selection for plant survival permits an extension of the period for protein formation, as well as carbohydrate accumulation in the stalk.

An extensive paper on these studies is being prepared for publication.

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1. Ear with inserted tip ear.

In 1954, an unusual ear with an added ear on the tip was found in the 4th generation selfed progeny of the single cross Tx4R3 X T528. This pistillate segment had the characteristic appearance of a staminate segment sometimes found inserted in ears except in this case the added ear has a normal cob and is enclosed by a separate husk in addition to the main husk that covers both ears. Selfed progeny from the lower ear reproduced like progeny in 1955. Seeds taken from the bottom ear and the tip ear are viable, but it has not been determined whether seed from the tip ear will reproduce this characteristic.

2. White endosperm seeds from crosses of yellow inbreds.

Single crosses between the yellow inbred line Mo. 567, which was inbred for at least 10 generations, with other yellow inbreds give F₂ ears segregating for yellow and white kernels. The yellow kernels vary in density of yellow. Some yellow inbred lines, such as Oh29, when

crossed with Mo. 567 give F₂ ears segregating approximately 3 to 1 for yellow and white kernels, whereas Mo. 567 crossed with other yellow inbreds do not appear to give the same ratios. When these white endosperm kernels first appeared in crosses involving Mo. 567, they were thought to be due to contamination. To be sure that some plants of Mo. 567 might not give such progeny a number of plants were selfed and at the same time outcrossed to Ohio 29. In all instances the F₂ seed from these outcrosses segregated for white endosperm kernels.

3. Longevity of yellow inbred lines.

Seventy-one inbred lines which were last grown in 1949 were stored at room temperature both as shelled and unshelled seed with the shelled and unshelled seed of each line stored in the same kraft paper bag. In January of 1955, the seed was planted in sand with 5 replications of 20 seeds each for both the shelled and unshelled seed. The seed was not previously treated with a fungicide. Germination percentages for the 71 lines tested indicated a very slight advantage for shelled seed (12.5%) compared with ear storage (11.2%). Two inbreds, C17 and W74, gave a higher germination for ear storage seed, whereas in most of the remaining group that germinated, the trend favored the seed stored as shelled grain. The number of inbreds grouped in the various germination classes are as follows:

<u>Germination</u> <u>Range</u> %	<u>Inbreds</u> No.
0	12
1-5	16
6-10	14
11-15	8
16-20	7
21-25	1
26-30	5
31-35	2
36-40	3
41-45	3
above 46	0
	Total 71

The three inbred lines germinating above 40% were Mo. 567, R62, and W62. Anyone desiring detailed information on germination percentages for the remaining group may have it upon request.

4. Tasselless Maize.

In the 1955 Maize Genetics Cooperation News Letter, B. H. Beard reported the progeny from tasselless cultures obtained from a cross made at the University of Missouri. Similar plants made at Missouri in 1955 continued to produce tasselless plants but in addition gave several plants with double tassels developing from branching above the ear bearing node. Since the total number of plants observed was small, definite ratios of normal to abnormal plants could not be established. Sufficient seed is now available to make more detailed observations in 1956.

5. A high Amylose starch.

Numerous defective endosperm types that might give higher than normal amylose starch (25-30%) have been selected and sent to the Northern Regional Utilization Branch, Peoria, Illinois for amylose determinations by Dr. M. M. MacMasters and associates. To date only one such defective has been found that offers much promise (Amylose content 37-40%). This defective was among a group obtained from L. A. Tatum at the Kansas Agricultural Experiment Station. Its parentage was Cassell O. P. It seems to be a form of "dull" with a sort of a "soft velvety sheen" appearance. Two extractions of this strain have been given the temporary designation of ha_m122 and ha_m123 . So far this strain has not been identified as possessing an allele of any known defective endosperm gene. When crossed and backcrossed to Argentine waxy the waxy selected seeds give an amylose content ranging from 7.0 to 10.0 percent compared with 3.0 to 5.0 percent for Argentine waxy. Reciprocal crosses were attempted in 1955 between ha_m and Kramer's high amylose strain (Maize Genetics Newsletter #29). Only F_1 seed for the cross made on ha_m was obtained, and its amylose content was 27.0 percent indicating that the factor responsible for the increased amylose content is not allelic to the factor causing high amylose in Kramer's strain.

Abnormal Types Derived from the South African Corn Breeding Program.

6. Christmas tree tassel.

A South African yellow flint inbred line, E800-1, was found to possess a dark green tassel with stiff branches. These branches were progressively shorter from the base to the apex to form a perfectly conical shaped tassel. Furthermore, the anthers were a dark purple, and with the dark green background, the tassel at the time of pollen shedding gave the appearance of a lighted Christmas tree.

7. Modified teopod type.

A third generation self from what was supposed to be a cross of "lazy" by "dwarf" produced plants whose ears were similar to teopod. It varied from teopod in that a single ear was borne on the stalk without branching plus a single ear located at the base of the tassel region. Furthermore, the tassel region was composed of a number of very short leaves placed over one another to give an appearance of scales and a single tassel branch protruded from the end of this region. The plants produced sufficient pollen under South African conditions but varied from plant to plant under Missouri conditions.

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8. Test of doubleness at C^i -C-c locus.

Assuming C^i to be compound, its order and constitution may be CI, IC, cI, or Ic. In a test for separability of two components, crosses have been set up to obtain C-carrying C^i from the last two structures, in case this is necessary:

+ C^i +/yg C sh x yg c sh;
select yg C^i + and + C^i sh;
backcross to yg c sh.

The final backcross provides tests of all four possibilities for the structure of C^i , through the detection of exceptional colored kernels arising by crossing-over. Selection of crossovers for the markers should serve to increase the likelihood of recovering CI from cI, or IC from Ic, among the individuals given in the final backcross.

1955 data on the final backcross:

Colorless shrunken class				
<u>Est.</u>	<u>Examined</u>	<u>Plants</u>	<u>Per plant</u>	<u>cases</u>
	69,250	182	380	1 Sh?
Yellow-green colorless non-shrunken				
	218,900	581	377	3 Sh (Separate plants)

In 288,150 gametes, one colored case found on an ear of the sh class, may be a Sh contamination; three colored cases found on ears of the yg Sh

class, one extra small, one extra large, and one near eartip. All cases thus appear very tenuous, and may be contaminations. These are to be tested for validity in 1956. Accepting these four cases for the present, insofar as they can possibly reflect crossing-over events, maximum map distances can be calculated for C to I, depending upon the assumed structure of Cⁱ:

1. I C: All four cases could be crossover-derived, and both classes of plants can be considered as tests. In the 288,150 gametes, half were tested for crossing-over: $4/144,075 = 0.0028$ map units maximum.
2. C I: Only the one case in the sh group could be derived by crossing-over: $1/144,075 = 0.00069$ map units maximum.
3. I c: Only the sh group tests this, since crossover-derived I C individuals would be restricted to this selected class. The one case here could possibly prove valid. Taking into account the Cⁱ - Sh map distance (4 units), the number of plants tested, and the number of kernels per plant, a maximum distance of 0.11 map units can be derived.
4. C I: Only the yg group tests this, in a fashion similar to assumption 3. No cases fit the assumption of crossover derivation. Assuming one case, and considering yg - Cⁱ map distance (20 units), a maximum of 0.14 map units can be derived.

Tests of cases, of case-carrying plants, and of additional final backcrosses are planned for 1956.

9. Mutation of Cⁱ.

In hand-pollinated Cⁱ/Cⁱ x c, 9,402 gametes gave no mutations. In Cⁱ/Cⁱ x C, 11,970 gave three variegated colored kernels. The constitution of such mutant derivatives will have a bearing upon the structure of Cⁱ (see above). Three previously found colored kernels, obtained from Cⁱ/Cⁱ x C in an undetermined total in 1953, were also variegated. Of the latter three, one failed to germinate, one appeared to carry normal, unchanged Cⁱ, and one was deficient for Yg. The last case has since been tested, and appears to carry a terminal deficiency, with the break distal to Cⁱ. Presumably the variegation in the original kernel was due to a breakage-fusion-bridge cycle, with loss of Cⁱ in sectors. The three new cases will be tested in 1956, and a large-scale mutation test is intended, to determine the constitution of mutants obtained from Cⁱ.

10. Combinations of aleurone-color factors.

Most of the paired combinations of a₁, a₂, bz₁, c, Cⁱ, r, pr, and in, both doubly homozygous and segregating for one or the other factor,

are available for the use of any cooperators who wish them. In addition, multiple combination stocks are available of the following selfs:

$A_1 a_1 bz bz c c$	and triple recessive
$A_1 a_1 a_2 a_2 bz bz$	and triple
$A_1 a_1 a_2 a_2 r r$	and triple
$A_1 a_1 a_2 a_2 bz bz c c$	and quadruple
$A_1 a_1 a_2 a_2 bz bz r r$	and quadruple
$A_1 a_1 a_2 a_2 bz bz c c r r$	and quintuple
$A_2 a_2 bz bz c c$	and triple
$A_2 a_2 bz bz r r$	and triple
$a_1 a_1 A_2 a_2 bz bz c c$	and quadruple
$a_2 a_2 bz bz C c$	and triple

11. A line with 2-3% haploids.

A genetic inbred obtained from C. R. Burnham in 1950 for use as a purple-aleurone stock has been found to have a very high frequency of haploids in self progenies. The line was an accession from Northrup King Seed Company, "late Mexican meal corn, red collar," and is a white endosperm, purple-seeded floury type. It has been designated as "stock 6" for identification. Self progenies from two different sources were planted in 1955: One source Stock 6 maintained by selfing, and the other haploid x sib (1952) selfed two generations. The haploids are easily recognized in the field, since stock 6 is very uniform: haploid individuals are zebra-striped, small, narrow-leaved, erect, linear-sectored with white, and generally "male-sterile." The following counts were made in 1955:

<u>Source</u>	<u>Haploids</u>	<u>Total</u>	<u>% haploids</u>
Stock 6 selfs	15	760	1.97
(hap. x sib) selfs	<u>35</u>	<u>1,222</u>	<u>2.86</u>
Totals	50	1,982	2.52

Poisson distributions show that the two sources do not differ significantly from their sum, and that the difference between the two is barely significant at the 5% level. Further counts in 1956 should determine whether a difference exists.

In outcrosses of stock 6 (R^E) by a R^r haploid tester, selfs from haploid x sib were used as eggparent, and seedlings were classified by

tip color in the bench:

<u>Total</u>	<u>Green:</u>	<u>Diploids</u>	<u>Died</u>	<u>Haploids</u>	<u>% haploids</u>
1,085	13	4	3	6	0.55

The difference between 0.55% and 2.52% (or 2.86%) is highly significant. Tests are underway to determine the source of this difference in frequency.

Ample seed of the stock is available.

12. Test for non-homologous crossing-over in translocation heterozygotes.

In meiocytes heterozygous for a translocation, the commonly observed non-homologous pairing might result in occasional non-homologous crossing-over. The products of such events would be short interstitial deficiencies and insertions, including the segment between crossover and break. If the break is near a known dominant gene, deficiencies could be detected as "mutations" to the recessive, and could be verified by their transmission frequency and cytology. It is to be expected that the frequency of such events would be very low, for intuitive reasons as well as for the lack of previous detection of events of this sort. A small test of several translocations was run in 1955, crossing heterozygous translocation, homozygous dominant for nearby gene, to the recessive.

<u>Transl.</u>	<u>Test genes</u>	<u>Number</u>	<u>Cases</u>
3-9f	sh	2,378	0
2-9c	wx	4,937	0
6-9 8536-12	y, sh	6,718	0
8-9 8525-1	sh, wx	2,822	0
6-9 8439-6	y, sh	120	0
5-9 8457-5	sh	2,297	1 sh
4-7a	su	1,320	0
4-5g	su, pr	3,739	0

The one sh exception will be tested for transmission of C. T5-98457-5 involves 5L.76, 9S.84.

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13. Chromosome 9 mapping.

Stocks on hand:	da ₁ ?	ms ₂₀
ar	Dt ₁	PG ₁₁ PG ₁₂
au ₁ au ₂ ?	g ₄	sa ₁ ?
bk ₂	gl ₁₀ (Sprague)	sh ₁
bz ₁	gl ₁₅ (gl _H)	v ₁
c	l ₆	wc
c ¹	l ₇	wx
d ₃	ms ₂	yg ₂

Stocks of any others would be appreciated. Does anyone have any of the following?

cr ₂	re ₃
Da ₂	sc ₂
de ₁₅	su ₃
gm _e	v ₁₅
o ₃	w ₁₁
pk	yf
Pr ₂	

14. A possible homozygous viable deficiency in the long arm of chromosome 1.

The bz₂ locus which has been described and located cytologically on the long arm of chromosome #1 (Newsletter 28, 29) has shown linkage with an₁. The data listed below indicate that bz₂ is located between an₁ and gs:

Cross: an Bz gs/An bz Gs x an bz gs
(bz seeds only)

<u>Parentals</u>	<u>Region 1</u>	<u>Region 2</u>	<u>Doubles</u>	<u>Total</u>
21	3	2	0	26

The distance between \underline{bz}_2 and \underline{an}_1 has become important because of the discovery that one of the radiation-induced anther-ear mutants (\underline{an}_{6923}) found by Anderson has an associated bronze aleurone effect. A cross of \underline{an}_{6923} with a \underline{bz}_2 tester gave all bronze seeds indicating that the two \underline{bz} characters are allelic. The allelism of \underline{an}_1 with \underline{an}_{6923} has not yet been determined but might reasonably be expected. If so then \underline{an}_{6923} probably represents a rather sizable deficiency which is homozygous viable and which includes at least two previously established loci.

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15. Instability of the α and β components of the A_1 locus.

A rather large population of $\underline{A}^b \underline{Sh}_2 \underline{et/a-x2} \underline{Et}$ plants, which were pollinated by $\underline{a} \underline{sh} \underline{et}$ in order to determine the types of mutants that would be produced without the conventional type of crossing-over, yielded a single dilute \underline{Sh} seed with frequent full colored dots. Using Laughnan's $\alpha \beta$ designation of the components of the \underline{A}^b locus this case appeared to be a change of β to an unstable recessive form while α remained unchanged. When the dilute mutant was placed in a marked heterozygote with a null allele for the \underline{a} locus ($\alpha \beta^m \underline{Sh/a^s sh}$), and backcrossed to the recessive ($\underline{a^s sh}$), four colorless \underline{Sh} dotted seeds were obtained. Each appeared to have lost α but retained the unstable β . Subsequent tests showed that they had lost the dominant brown pericarp effect that is characteristic of α . There were no genetic markers to the left of α so there was no way of determining whether the loss was by mutation or by crossing over. These cases probably are examples of an unstable β by itself.

Another type of change was observed in two cases from $\alpha \beta^m$. This type was colorless \underline{Sh} but had both dilute and full colored sectors suggesting that both α and β had become unstable. The tests for pericarp color revealed that they retained the dominant brown expression of α . There is some indication that mutability of these components may be influenced by a second factor, but in any case it is neither \underline{Dt} nor \underline{Ac} .

16. The effect of \underline{Dt} on the mutability of an A_1 allele.

The positive effect of \underline{Dt}_1 on the mutability of one A_1 allele was reported in the 1955 Newsletter. However the allele used ($\underline{A:D2}$) was one which had originated as a mutant from \underline{a}_1 through the action of \underline{Dt}_1 and therefore might have retained a susceptibility to \underline{Dt} action. Four natural occurring \underline{A}_1 alleles which have had no history of \underline{Dt} association have been tested for mutability of female gametes in presence of \underline{Dt} . Two failed to give any recessive mutants in large populations while the other two gave an occasional case. It was thought that perhaps increasing dosage of \underline{Dt} would increase the frequency of these cases. To test this a

male stock carrying one of the two more promising alleles, A:Provo, and also carrying two Dt genes, so as to increase the basic rate, was crossed on two female stocks which differed only in their Dt constitution. The first was a^s sh₂ dt, and the other a^s sh₂ Dt₁ Dt₂. Seeds from the dt ear stock have two doses of Dt contributed by the male parent, while those from the Dt ear stock have six doses of Dt (four from the female and two from the male). The seeds produced were examined for 1/8 + a Sh₂ aleurone sectors which represent A — a mutation occurring after fertilization takes place. As can be seen in table 1, the Dt female parent yielded significantly more mutant sectors than did the dt parent. Thus by increasing Dt dosage it is demonstrated that Dt can cause a naturally occurring A₁ allele to mutate at an increased frequency.

Table 1. Mutation of A:Provo expressed in aleurone sectors.

Parents	Population	1/8 seed or more		
		<u>a sh</u>	<u>a Sh</u>	<u>A sh</u>
<u>a^s sh, Dt</u> x <u>A Sh, Dt</u>	3521	8	9	0
<u>a^s sh, dt</u> x <u>A Sh, Dt</u>	4362	14	1	0

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1. Enzyme studies in corn.

In the 1955 Newsletter a communication from this laboratory dealt with the influence of seed irradiation upon the activities of certain enzymes in preparations of green seedlings grown from the irradiated seeds. Appreciable increases in the specific activities of peroxidase, phosphatase, polyphenolase, and catalase, together with reduced seedling height, were found to result from seed treatment with X-rays or thermal neutrons. During the past year these observations have been confirmed using a different lot of L289 x L205 seed for the treatments. In addition, experiments with seedlings grown from maleic hydrazide-treated seeds have disclosed that this chemical treatment produces effects on the above four enzyme activities and on seedling stature which appear similar to the effects brought about by seed irradiation. Seedlings which were reduced in stature by virtue of decreased growing period and lowered temperature during growth were also used in enzyme assays. In these cases, however, reduced seedling stature tended to be associated with either slight decreases or only very small increases in the specific activities of peroxidase, phosphatase, polyphenolase, and catalase. Metabolic

differences between seedlings which are stunted because of age or temperature effects and seedlings which are small because of the effects of seed treatment with X-rays, thermal neutrons, or maleic hydrazide are thus clearly indicated.

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1. Number of genes involved in pollen fertility restoration.

Fifteen inbred lines of corn which had been previously reported as restorers to Texas Cytoplasmic male sterility were found to restore fertility in North Carolina. These lines are K6, R6, R7, K55, NC77, Mp307, K63, Ky21, Kyl22, Tl15, Tx127C, TxGJ39, T208, NC212, and a Mississippi inbred, Yel-Jel 81-1-1-1-1.

Additional studies, in general, support the hypothesis that each of these inbreds possesses at least one dominant gene for pollen fertility restoration. The following steps were used in arriving at this conclusion:

1. Seventy eight of the 105 single crosses possible among the 15 inbreds were made.
2. All of these single crosses were crossed with a Texas source of male sterile cytoplasm.
3. Approximately 30 plants of each progeny were grown and classified for pollen shedding.

Of the 78 crosses studied 72 were entirely fertile. Sterile plants did occur in the remaining 6 crosses with a frequency of approximately 1 sterile plant to 30 fertile plants. These sterile plants might be explained by a difference in loci involved in fertility restoration in the two inbreds, the genes being located close enough together so that crossing over between the two loci, which would result in a gamete with genotype for sterility being formed, would occur in about 12% of the meiocytes. Seed mixture or pollen contamination might also explain a few sterile plants.

Ratios in backcross data involving plants of the constitution cytoplasmic male sterile x (cytoplasmic male sterile x restorer inbred), did not deviate significantly from a 1:1 ratio which also indicates that each of the following inbreds possesses a single dominant gene for pollen fertility restoration: K63, Mp307, Ky21, Kyl22, NC77, and K55. These ratios are based on populations of approximately 60 plants each.

The inbreds Oh29 and K64 which have been reported as restorers in other states were found to have little value as restorers in North Carolina. These inbreds when crossed with Texas male sterile cytoplasm restored only partial fertility.

2. Linkage relationships of restorer genes.

The data from a linkage study using backcross data show a loose linkage of the restorer gene or genes in Mp307, NC77, and K55 with the gene a_1 on chromosome 3. The crossover percentages and P values for linkage as calculated by the X^2 test are shown in the table below.

Inbred	Phenotypic Class	No. Plants	Crossover %	P Value for Linkage
K55	Fertile, A	169	44.6 ± 2.02	<.01
	Sterile, A	139		
	Fertile, a	132		
	Sterile, a	168		
	Total	608		
Mp307	Fertile, A	226	45.6 ± 1.73	.02 - .01
	Sterile, A	184		
	Fertile, a	193		
	Sterile, a	224		
	Total	827		
NC77	Fertile, A	193	40.3 ± 1.88	<.01
	Sterile, A	141		
	Fertile, a	136		
	Sterile, a	214		
	Total	684		

3. Influence of length of day on pollen fertility restoration.

Since male sterile material shows a tendency toward fertility under the short day lengths in Florida during the winter an experiment was set up during May in the greenhouse to determine the effect of long day length on materials with restorer genes. Supplementary lighting was provided from 11 p.m. to 2 a.m. from the first week after the seed was planted until maturity. No appreciable response to the increased photoperiod was observed with the exception of progenies of (male sterile x K63) and (male sterile x Tx581) in which sterile plants did occur. However, in a number of progenies the size of tassels was greatly reduced and the very small tassels produced little or no pollen. The fifteen good restorers mentioned in the paragraph above with the exception of K63 showed no sterility under the long day conditions.

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1. Inbreeding depression in inter-variety populations of open-pollinated varieties of corn and interaction of non-allelic genes.

Experimental evidence on the importance of interactions among non-allelic genes is being sought in statistical genetic investigations with corn. Vetukhiv (Evolution 8:241-251, 1954) measured survival to adulthood as an index of viability of the larvae in geographical strains of three species of *Drosophila* and in the F_1 and F_2 populations from crosses among strains within the species. In crosses between strains within two of the species F_1 's were superior to both parent strains and the F_2 's were inferior, at least to the average for the parent strains. The results were interpreted as indicative of epistasis as an important aspect of genotypic variation at the inter-strain level, if not within strains. An experiment, similar to that conducted by Vetukhiv, was carried out with corn in 1955 using the Jarvis, Indian Chief and Weekley open-pollinated varieties and the F_1 and F_2 of the three possible crosses among them. If heterosis in these crosses, reported earlier (see American Naturalist, in press), is entirely due to allelic gene interaction (dominance) the F_2 should be intermediate in mean yield between the F_1 and the average for the two parent varieties in contrast to the type of results obtained by Vetukhiv and explainable on the basis of epistasis.

The parent varieties, F_1 and F_2 (inter-se mated F_1) of each population were grown in replicated plots at three locations and the results for yield are reported below.

Entry	Jarvis x Indian Chief (lbs/plant)	Jarvis x Weekley (lbs/plant)	Jarvis x Indian Chief (lbs/plant)
F_1	.40	.44	.50
F_2	.39	.40	.47
Parents	.36	.37	.42

These results do not support the hypothesis that epistatic effects are important in genetic variation of segregating populations of the cross of two open-pollinated varieties of corn.

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1. Suppressive action of I.

A single dose of I is sufficient to completely inhibit the production of aleurone color against two doses of C. The suppressive action of I becomes incomplete against four doses of C. Endosperms of the constitution I/CC/CC show considerable pigmentation. Such endosperms were obtained by using plants carrying a duplication of the short arm of chromosome #9 as the female parent in crosses to I.

2. Stable ring chromosome.

A stable chromosome #9 ring has recently been isolated. Cytologically, this ring cannot be distinguished from the unstable ring from which it was derived. The ring carries the dominant C marker. In backcrosses of plants of the constitution cc + ring to cc testers no color variegation is observed; only self-colored and colorless kernels are found. No dicentric rings are observed in mitotic anaphases.

3. Mutable c.

A mutable c allele has been found which frequently mutates to C in both somatic and germinal tissue. It has been possible to select for early and late occurrences of the mutations. Crosses to Ac testers have failed to reveal any Ac activity. The cytological picture is normal. There is no sign of chromosome breakage. The mutations from c to C are not accompanied by variegation of any of the proximal markers as might be expected if the mutation involved chromosome breakage and was followed by sister union. Clusters of germinal mutations on the ears have not been found.

Drew Schwartz

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1. Kys male sterile inheritance.

When cytoplasm of five standard inbred lines were substituted for that of inbred Kys, comparable classes of normal, sterile and partially filled pollen plants were produced. The cross (Kys mm*ssxNormal Inbred MMSS) x Kys mm ss gave 147, 90 and 62 plants of the classes normal pollen,

partially filled pollen, and male sterile respectively. The cross (normal inbred x Kys) x Kys gave 99, 63 and 31 plants of the same respective classes.

Certain inbred lines were found to differ from others in regard to M and S constitution. Among these were Kansas K64 and P.A.G. 287. All F_1 plants of the cross Kys (mm ss) x K64 were normal for pollen type. Test crosses made with Kys sterile plants (Mm ss) x K64 yielded 43 normal : 46 partial pollen plants. This ratio is evidence that the genotype of K64 is mm SS. Testcrosses of Kys male sterile x (Normal Inbred x Kys), or Mm ss x (MMSS x mmss) gave 3 partial to 1 normal pollen plant. Actual numbers obtained were 92 partial : 34 normal. This indicates that mm Ss plants are phenotypically normal pollen producers.

Testcrosses similar to those made with K64 indicated that P.A.G. 287 is also homozygous recessive mm, but that some plants of this line may segregate for Ss. Testcrosses of one P.A.G. 287 strain (mm SS) gave evidence that heterozygous Ss segregates normally and is transmitted normally by pollen of plants that are recessive mm. The testcross was made of the genotypes, Mmss x (mm ss x mm SS) and yielded 36 normal : 17 partial pollen plants : 15 male sterile compared to the expected 34:17:17.

F_1 reactions indicating other than the MM SS constitution were observed for ML4, Oh7, and P.A.G. 169. This type of male sterility is not practical as a means of eliminating detasseling in hybrid production fields because no more than an average of 50% of a given population can be sterile.

Charles W. Ogle

* Dominant MS²¹ gene.

2. A simple method for inoculating breeding material with Helminthosporium turcicum.

Epidemics of Northern Corn Leaf Blight, caused by the fungus Helminthosporium turcicum, have been induced by using quantities of inoculum made from pure cultures of the fungus. (1) This method involved laboratory preparation of the cultures and considerable time in making repeated applications to the breeding material.

Methods were described in 1952 for using diseased corn leaves as a source of infection. (2)

A simple way of initiating and spreading Northern Corn Leaf Blight was tried in our breeding nursery at Tuscola, Illinois in 1952.

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- (1) Elliott, C. & Jenkins, M. T. Helminthosporium turcicum Leaf Blight of Corn. PHYTOPATHOLOGY 36: 660-666, 1946.
 (2) Robert, A. L. & Findley, W. R. Jr. Diseased Corn Leaves as a Source of Infection and Natural Epidemics of Helminthosporium turcicum. PLANT DISEASE REPORTER 36: 9-10.

Leaves from corn plants which were heavily infected with Helminthosporium turcicum were collected from our 1951-52 winter nursery located in southern Florida in the spring of 1952. The leaves were dried by storing in a room with uncontrolled temperature. They were later ground up by running them through a hammer mill with a 1" screen.

Inoculations in the field were made on a susceptible single cross hybrid and on numerous susceptible x resistant crosses by dropping a quantity of the ground up infected leaves into the whorl of each plant when they were approximately 24" tall.

Infection was not well established until after tasseling. By harvest time infection was so severe that no differences in resistance were apparent on the susceptible x resistant crosses.

In 1953 a very susceptible single cross hybrid was used as a "spreader" row. Each row of breeding material was bordered by a "spreader" row which resulted in a planting pattern where every third row in the nursery was the susceptible single cross. Only the "spreader" rows were inoculated using the method described above. Infection became well established in the inoculated rows at tasseling time. Natural infection resulted in the breeding material after tasseling and was of such a magnitude as to allow effective selection to be practiced at harvest time.

This method of inoculation has been used on a large scale for the past three years in our disease breeding nursery. It involves a minimum of facilities and labor and has produced artificial epidemics without failure during the period mentioned.

Lyle E. Oncken

3. Environmental effects on fertility of restored sterile hybrids.

Thirty-six different restored 4-way hybrids were made up in the following manner: One pollen parent inbred, heterozygous for the I153 "F" gene was crossed with the other pollen parent inbred, which was heterozygous for the K55W "F" gene. The resultant pollen single (carrying "T" cytoplasm) was used as male on appropriate "T" sterile seed parents. Each of the resulting 36 restored 4-way were compared with a blended 1:1 sterile and normal version at 11 locations in 1955. The results were as follows:

<u>LOCATIONS</u>	<u>50-50 BLEND % FERTILE</u>	<u>RESTORED HYBRID % FERTILE</u>
1. Lincoln, Nebraska	55.7	59.2
2. New Cuyama, California	51.6	55.3
3. Franklin, Kentucky	44.9	50.2

<u>LOCATIONS</u>	<u>50-50 BLEND % FERTILE</u>	<u>RESTORED HYBRID % FERTILE</u>
4. Ithaca, Michigan	59.1	64.8
5. Tuscola, Illinois	52.0	61.5
6. Huntsville, Alabama	62.7	68.8
7. Carrollton, Missouri	64.6	79.0
8. Monroe, Iowa	86.6	88.4
9. Aurora, Illinois	55.6	63.9
10. Aurora, Illinois*	55.1	68.2
11. Aurora, Illinois**	56.8	54.4

* With 1400 lbs. sugar added per acre

** With 1400 lbs. Nitrogen added per acre

The fertility of the restored material was in close agreement ($r=.901$) with fertility of the checks at the different locations.

Similar results were obtained in 1954 when eleven 4 ways, made up alternately with 3 different "F" gene sources, each of these being produced both (1) with, and (2) without "T" cytoplasm in the pollen parent, were compared for tassel fertility with corresponding normal version at 9 locations.

In neither 1954 nor 1955 during this study, was it possible to differentiate between fertility of normal 4-way varieties, and those restored with the "F" gene of Il53, K6, K55, Tx127C, etc. in any variety, at any location, or under any condition, within limits of the sensitivity of techniques employed.

Donald L. Shaver*

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1. Yields of cytoplasmically pollen sterile hybrids, compared to their normal counterparts.

Normal and sterile forms of four double crosses and two single crosses (the sterile hybrids were made with T cytoplasm) were grown in 3 locations (Iowa, Illinois, and Ohio) at rates of 7, 10, 13, 16, 19 and 22 thousand plants per acre in 1955. The average yield of the normal

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hybrids was 101.97 bushels per acre. That of the sterile hybrids was 102.01 bushels per acre. The difference was not significant. However, analysis of variance indicated that the following interactions were highly significant: (1) cytoplasm x hybrids; (2) cytoplasm x locations; and (3) cytoplasm x rates of planting. Normal and sterile forms of one hybrid in which S cytoplasm was used for the sterile form also were entered in this test. Analysis of variance showed a highly significant difference between cytoplasm in favor of the sterile, and a highly significant interaction between cytoplasm and locations.

Donald N. Duvick

2. Knob numbers of elite vs. non-selected inbreds.

Chromosome knob numbers of 52 inbreds developed without selection (News Letter, 1954) were compared with knob numbers of 95 elite lines. The mean number of knobs of the non-selected lines was 3.1 as compared with 4.2 for the elite lines. The modal class for each of the two groups was 3. A somewhat higher mean number of knobs of selected lines can probably be explained as resulting from selecting against flint-like inbreds in the corn belt.

3. Cytology of homozygous diploids.

Progenies of eight inbred lines derived from monploids through chromosome doubling have been checked for pachytene pairing at meiosis. Although the lines were two and three generations removed from their monploid parents each appeared to be phenotypically homozygous. Two of the eight progenies exhibited cytological evidence for heterozygosity in the form of one or more short, non-paired chromosomal segments. Internal segments only were considered and no attention given to the rather frequent occurrence of unpaired ends. In most cases chromomere patterns of the unpaired chromosomes were visibly different. No evidence of non-pairing was observed in progenies of the remaining six lines. In these few auto-diploids the number of progeny exhibiting heterozygous segments seems to be about the same as that occurring in many inbred lines developed by continuous self pollination and suggests that complete homozygosity, if ever present, persists through relatively few generations.

4. Comparative grain yields of random and selected inbreds.

Among a group of inbreds produced in the absence of artificial selection, 20 were selected in the S_6 generation which on the basis of their phenotype appeared to merit testing for combining ability (a type of visual selection similar to that commonly practiced in corn breeding). At the same time an equal number of lines from the same population were selected at random. Top cross yields (using a composite as a tester) of

the two groups were compared in tests grown in six locations of two replications each. Mean grain yields of the two groups were as follows:

Selected lines 86.66 Bu/A
 Unselected lines . . . 86.64 Bu/A

The top yielding line in the test was a selected one which produced 5.8 Bu/A more than the best unselected line, although the difference was not significant statistically. Among the twelve top yielding lines, seven were unselected and five selected; the twelve lowest yielding lines consisted also of seven unselected and five selected.

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1. An unstable compound locus, a_1^{Pm} .

Rhoades reported the origin of a mutable locus at A_1 in the 1950 News Letter. Aged seed carrying $a_1^{P1}/a_1^{P1} Dt/Dt$ was crossed by an a/a strain. Three separate mutations arose involving one or more kernels. Two of these mutants resembled the a_1 allele and were relatively stable. The third was a highly mutable form of the a^P allele, a^{Pm} .

Stocks carrying a^{Pm} ($A_2C R B_2$) exhibit a pale aleurone which is mosaic with deep and colorless sectors. The plant color produced by this allele ($B P_1 B_2$) is reddish-brown with stripes of deep purple and brown tissue. The pericarp is dominant brown in a^{Pm} (P) stocks with occasional red sectors. Germinal and somatic mutations from pale to deeper and to lighter levels of anthocyanin intensity occur at high frequencies. Changes in mutability often occur jointly with changes in level. The mutation rate may vary for different forms or states of the a^{Pm} allele; however, some representative mutation rates follow:

- a_1^{Pm}
 (Pale mosaic)
- to germinal, stable, deep alleles - 1 in approximately 20,000 gametes
 - to germinal, stable, light pale alleles - 1 in approximately 10,000 gametes
 - to germinal, stable, colorless alleles - 1 in approximately 4,000 gametes
 - to germinal, stable, colorless plus dot alleles - 1 in approximately 100 gametes
 - to germinal, stable, medium pale alleles - 1 in approximately 30 gametes.

These germinal mutation rates in contrast to what is observed somatically indicate infrequent mutations to the deep level. Somatic deep sectors are abundant but generally they are very small. If these represent mutations, it is likely that their late occurrence is responsible for the low number of germinal changes.

The stable mutants from a^{Pm} may be grouped into four general classes: I - deep aleurone, red pericarp; II - pale aleurone, dominant brown pericarp; III - colorless aleurone, recessive brown pericarp; and IV - colorless aleurone, dominant brown pericarp. Of 66 analyzed mutants, 8 are of class I, 23 - class II, 31 - class III, and 4 - class IV. Since the parent allele was mutable and exhibited pale aleurone and dominant brown pericarp, Class I alleles were derived by an event affecting the mutability, aleurone, and pericarp portions of the A_1 locus. Class II alleles, however, arose from events affecting only the mutability component of a_1^{Pm} . Alleles of Class III again involve changes at the mutability, aleurone, and pericarp components. Changes at the mutability and aleurone components but not the pericarp component are involved when Class IV mutants arise.

One interpretation of this mutation pattern is that separable genic units at A_1 control the mutability, aleurone, and pericarp characteristics. Evidence for the presence of a mutability factor at A_1 is ample. There is a genetic factor for variegation in characters controlled by A_1 which is not segregated from A_1 ; nor has this factor been separated from A_1 by crossing-over. The existence of a spreading effect phenomenon involving A_1 and a closely associated gene on chromosome 3 indicates the presence of a mutability factor in this region, as does the alteration of the a_1-sh_2 crossover rate by a_1^{Pm} derived alleles.

Laughnan has shown that two components, $-$ and $_{-}$, controlling aleurone color exist in the allele A^b . It is possible that similar components are present in a^{Pm} . An $_{-}$ -like component is suggested by the similarity in phenotypes produced by a^{Pm} and the A^d () alleles described by Laughnan. Moreover, a large number of the pale self mutants derived from a^{Pm} are phenotypically identical to the A^d alleles arising from A^b : Peru. A deep $_{-}$ -like component is thought to be present because of the large number of deep sectors which occur on plants carrying a^{Pm} . The germinal mutations to the deep level indicate that these events actually are mutations at A . The large number of somatic alterations renders improbable the possibility that these are intragenic changes converting the pale component into a deep component. The possibility that $_{-}$ is present in the a_1^{Pm} allele but is inhibited in its expression by $-$ or the mutability factor or both is more likely. That a_1^{Pm} contains P^b is suggested by the Class III and IV mutants, both of which exhibit colorless aleurone. Class III mutants produce recessive brown pericarp while dominant brown pericarp is characteristic of Class IV mutants. Thus, it is possible for mutational events to occur which affect both aleurone and pericarp properties and others which affect aleurone but not pericarp properties. The separate existence of a pericarp component in a_1^{Pm} seems likely.

The linear arrangement of the four components at the A_1 locus may be computed by observing the mutational patterns of a_1^{Pm} . The evidence available indicates the sequence is $\beta - M - \alpha - P^b - - sh_2$.

2. A case of "spreading effect" involving the A_1 locus.

Among the mutants arising from a_1^{Pm} , one ($a_1^{P_{L14}}$) exhibited simultaneous alterations at the A_1 locus as well as at an adjacent locus. The allele arose as a single, light pale, self-colored, exceptional kernel in the cross $a_1^{Pm} Sh_2 / a_1^{Pm} Sh_2 \times a_1 sh_2 / a_1 sh_2$. When the kernel was grown and the plant self-pollinated, the resulting ear demonstrated that the new pale type was inherited in the typical Mendelian fashion, and that the new type could not have been the result of a foreign pollen grain. The kernels from this ear fell into an approximate $3(a_1^{P_{L14}} Sh_2)$ to $1(a_1 sh_2)$ ratio. A fraction of the pale kernels were germless while only two germless kernels were found in the $a_1 sh_2$ class. In addition when the germed kernels were grown, some of the seedlings were both devoid of chlorophyll and markedly deformed. This aberrant seedling type was with one exception, confined to the $a_1^{P_{L14}} Sh_2$ class. Furthermore, approximately 40 mature plants have been grown from the $a_1^{P_{L14}} Sh_2$ kernel class from self-pollinated heterozygotes and in every case these plants have proved to be heterozygous. Table 1 gives the results of a classification of kernel and seedling types in the progenies of two self-pollinated plants heterozygous for $a_1^{P_{L14}} Sh_2$ and $a_1 sh_2$.

Table 1. Kernel and seedling frequencies among the progenies of selfed heterozygotes.

Kernel Phenotype	Kernel Classification			Seedling Classification		
	Number Classified	Germless Kernels	Germed Kernels	Number Classified	Deformed-Albino Seedlings	Normal Seedlings
$a_1^{P_{L14}} Sh_2$	308	65	243	216	27	189
$a_1 sh_2$	117	2	115	72	1	71

It is clear that a gene or closely linked genes control these abnormal kernel and seedling types, for when they are considered together the aberrant types make up one-fourth of the progeny. Furthermore, the single exceptional seedling found in the $a_1 sh_2$ class and possibly the two germless $a_1 sh_2$ kernels indicate that crossing-over may occur between A_1 and the gene controlling these deformed seedlings.

Several explanations are possible for the results described above. Two simultaneous independent point mutations involving these two genes is highly improbable. A deficiency of the chromosomal region including the two linked genes is possible. However, the detection of crossing-over

between the two genes rules out this hypothesis. The results may be explained by a spreading effect, such as that found by McClintock, which is caused by the inhibition of closely linked genes. The available evidence supports the last hypothesis.

The new gene controlling albinism has proved to be not allelic with W of Stadler and Roman, for plants of the constitution $a_1^{PL14} Sh_2/a - x_1$ are normal.

3. The effect of a mutability factor on crossing over in an adjacent region.

McClintock has reported an effect of a mutability factor (Ds) on crossing over in 9S. In spreading effect cases in which both Sh₁ and Bz were inhibited by the mutability factor, crossing over within this region was not detected. In addition the segments on either side of the inhibited region exhibited a recombination rate which was normal in some cases and increased in others.

The following experiment deals with a mutability factor M, which is present at the A₁ locus and which might exert an effect on crossing over in the A₁-Sh₂ region. The control stocks contain a variety of alleles at A₁ and are derived from different genetic backgrounds. They are similar, however, in that none contain known mutability factors. The experimental stocks were all derived from a highly inbred strain containing the allele a₁Pm. Thus, if genetic variability is a cause of varying recombination rates, these differences should be the more evident in the control. A mutability factor, M, is present at the A₁ locus in the parental stock and it persists in various states of inhibition and mutability at the locus in the derived stocks. This is demonstrated when the derived alleles revert, as they occasionally do, to the original a₁Pm condition.

Since crossing over within the A₁-Sh₂ region is low, a large total number of gametes has been scored, yet the number of recombinant gametes remains small. Thus, instances producing gametes which might be mistaken for crossover gametes should be taken into account. This mistake could be made if the A₁ allele in the A₁Sh₂ gamete mutated to the colorless level giving an a₁Sh₂ gamete. This mutation rate among the control stocks which contain stable alleles is negligible, and could not be an important factor in altering the control recombination rate. However, the experimental alleles were derived from a mutable locus, and although the alleles are true breeding, they are not always stable. Consequently, this mutation rate should be considered when the recombination rate is computed and a corrected rate should be given. Cases in which mutations of this type are occurring may be indicated by an unbalance in the two recombinant classes in favor of the a₁Sh₂ class, which resembles the mutant gametes. In the data given the numbers are so small that this unbalance could easily be accounted for merely on a chance basis. However, it is not believed to be a coincidence that all three alleles which show measurable mutation rates have an excess of the a₁Sh₂ recombinant class over the A₁sh₂ class. Table 1 shows recombination, mutation, and corrected recombination rates for these control and experimental stocks.

Table 1. Crossing over within the a_1 - sh_2 region in stocks carrying various A_1 alleles.

Allele	Origin	Recombination Rate			
		Total Gametes Scored	Recombinant Gametes		Percentage of Recombination
			A sh_2	a Sh_2	
A	A-standard	4,495	4	5	.200
A	A-standard (repulsion)	13,079	17 ^(A Sh_2)	8 ^(a sh_2)	.191
A ^b	A ^b : Ecuador	4,937	3	4	.142
A ^{d-st}	A ^b : Ecuador by crossing-over	8,770	4	12	.182
A ^{d-6}	A ^b : Ecuador by crossing-over	6,625	5	6	.166
Control value for stable alleles		37,906	68		.179
A ^R	From a ^{p_m} mutation to true breeding alleles	4,030	2	4	.149
A ¹	" " " "	3,772	0	2	.053*
A ²	" " " "	4,770	6	5	.273*
A ⁴	" " " "	3,761	8	7	.398*
a ^{P1}	" " " "	8,547	3	3	.058*
a ^{P2}	" " " "	9,001	18	16	.378*
a ^{P3}	" " " "	13,900	9	22	.223
a ^{P4}	" " " "	12,720	10	14	.189
a ^{PL14}	" " " "	3,110	0	5	.161

*Significantly different from the control value at the .001 level.

Table 1. (Continued)

Allele	Mutation Rate			Corrected Recombination Rate (Percentage)
	Total Gametes Scored	Mutant Gametes (to the recessive a_1 allele)	Percentage of Mutation	
A	----	----	----	----
A	----	----	----	----
A ^b	----	----	----	----
A ^{d-st}	----	----	----	----
A ^{d-6}	----	----	----	----
A ^R	14,469	7	.048	.101
A ¹	20,226	5	.025	.028*
A ²	4,007	0	.000	.273*
A ⁴	----	----	----	----
a ^{P1}	15,771	0	.000	.058*
a ^{P2}	2,096	0	.000	.378*
a ^{P3}	6,261	0	.000	.223
a ^{P4}	10,441	7	.067	.122
a ^{PL14}	----	----	----	----

* Significantly different from the control value at the .001 level.

The data illustrate that over half of the stocks carrying derived alleles show recombination rates which are different from the control values at the .001 level of significance. Both decreases and increases in the rate of recombination are indicated and these are not correlated with the deep or pale level of the particular A_1 allele.

4. The effect of the mutability factor at a^{Pm} on gene loss in endosperm tissue.

In the 1955 News Letter Fradkin reported that Modulator was effective in producing gene loss in endosperm tissue. M_p located on chromosome 1 or elsewhere in the genome can increase gene loss in chromosomes 9 (C and Wx) and 5 (Pr). This effect was presumed to be due to increased chromosome breakage in the presence of M_p . Muffer presented similar data in which gene losses were controlled by the mutability factor Dt . Endosperm with a single dose of Dt exhibited a loss frequency for A_1 and Sh_2 which differed significantly from the control. Here chromosome 3 losses were apparently controlled from chromosome 9.

Some preliminary counts have been made on experiments testing the effect of the mutability factor at a^{Pm} on gene loss, and the results are somewhat different from those in the above experiments. Losses of a linked gene (Sh_2) are considerably more frequent in the presence of the mutability factor (M) than in the controls (Table 1.). When a gene (Bz) on another chromosome (9) is considered, endosperm with and without the mutability factor differed only slightly in percentage of bz sectors. The greater rate of loss occurred in the control (Table 2).

Table 1. Somatic losses of Sh_2 in endosperm tissue.

Cross	Unsectored kernels	Sh_2 -sectored kernels	Total	Percent sectored
$a sh_2/a sh_2 \times A Sh_2/A Sh_2$	986	304	1290	23.6
$a sh_2/a sh_2 \times a^{Pm}Sh_2/a^{Pm}Sh_2$	255	610	865	70.5

Table 2. Somatic losses of Bz in endosperm tissue.

Cross	Unsectored kernels	Bz -sectored kernels	Total	Percent sectored
$bz/bz A/A \times Bz/Bz a/a$	2798	163	2961	5.5
$bz/bz A/A \times Bz/Bz a^{Pm}/a^{Pm}$	1999	40	2039	2.0

Since M affects the loss of Sh₂ but not of Bz it appears that this mutability factor is behaving differently from Mp and Dt. The mutability factor located on chromosome 3 seems to control chromosome 3 gene losses but not chromosome 9 losses. The spreading-effect properties of M described above may be responsible for the somatic losses of Sh₂ activity, and M may lack the non-specific chromosome breakage properties of Mp.

5. More evidence of shrunken-floury's effect on protein synthesis.

A supposed effect of the gene sh^{fl} on protein synthesis was reported in the 1955 News Letter. The evidence was morphological in nature and involved abnormalities in the endosperm, aleurone, and in microsporogenesis. Proof of this supposition lay in a chemical comparison of the proteins in sh^{fl} and Sh^{fl} (normal) tissue.

Since determinations of total nitrogen in mutant and normal kernels failed to reveal a significant difference, an attempt was made to fractionate the proteins, making use of their varying solubilities. In this way a somewhat more refined comparison of the proteins of the two kernel classes is possible.

Mutant and normal kernels were classified from self- or sib- pollinated ears produced on plants heterozygous for sh^{fl}. Only ears with an extreme expression of shrunken-floury were used. Those with segregating modifiers which bring the expression of sh^{fl} toward normal were avoided in these tests. The kernels were finely ground and samples of two to four grams were weighed out. These were placed in 125 ml. Erlenmeyer flasks for extraction. The samples were successively extracted with water, 1.0 N potassium chloride, 80% ethyl alcohol, and 0.2% sodium hydroxide. Hence, the protein fractions will be referred to as water, salt, alcohol, and base soluble, and insoluble proteins. Twenty-five ml. of solution were used for each gram of the sample, and the extraction was continued for 24 hours. Kjeldahl nitrogen determinations were made for each fraction and these values were converted to protein by multiplying by the 6.25 factor. Since the separate ears varied in the percentage of kernel weight which was protein, a better comparison was obtained by computing the percentage of the total protein which resided in the particular protein fraction. Table 1 gives the results of five ears whose mutant and normal kernel classes were fractionated as above. The values cited are average values for two replications.

Significant differences between the nitrogen content of sh^{fl} and Sh^{fl} kernels exist in the water, salt, and alcohol soluble fractions. The differences within the base soluble and insoluble fractions are not significant. The shrunken-floury class contains about 1.74 times as much water soluble "protein" as the normal class. Differences of the same type occur in the salt soluble fraction, but the factor is 1.60. These differences are compensated for in the alcohol soluble fraction where the shrunken-floury class has a little more than one-half the protein of the normal class.

Table 1. Comparison of the protein fractions of sh^{fl} and Sh^{fl} Kernels.

Protein Fraction	Ear Number	sh ^{fl} *	Sh ^{fl} *	sh ^{fl} /Sh ^{fl} Ratio
Water Soluble Fraction	1	15.48%	9.70%	1.60
	2	18.65	12.47	1.50
	3	19.95	12.60	1.57 m = 1.74**
	4	21.86	10.41	2.10
	5	22.78	11.77	1.93
Salt Soluble Fraction	1	10.58%	6.75%	1.57
	2	12.35	9.86	1.25
	3	10.36	8.44	1.23 m = 1.60**
	4	12.53	5.84	2.15
	5	12.57	6.92	1.82
Alcohol Soluble Fraction	1	22.66%	28.61%	0.79
	2	15.48	29.82	0.52
	3	17.06	31.38	0.54 m = 0.56**
	4	23.20	43.69	0.53
	5	14.57	33.32	0.44
Base Soluble Fraction	1	26.88%	31.89%	0.84
	2	27.12	27.63	0.98
	3	22.66	25.94	0.87 m = 0.97
	4	27.63	23.12	1.20
	5	25.05	26.57	0.94
Insoluble Fraction	1	24.35%	23.19%	1.05
	2	25.47	21.78	1.17
	3	29.56	21.69	1.36 m = 1.13
	4	14.75	16.86	0.88
	5	24.90	20.93	1.19

* Percentage of the total nitrogen appearing in the given fraction.

** Significantly different from 1.0.

One interpretation which might be placed on these results is that the gene sh^{fl} is blocking the conversion of the simpler proteins (water and salt soluble) to the more complex (alcohol soluble) proteins. It is likely that the water and salt soluble fractions contain proteins of lower molecular weight than the protamines of the alcohol fraction, and it is possible that some of these simpler components are unconverted substrates of the alcohol soluble proteins. Proof of this will require a more involved chemical treatment, but it seems certain that sh^{fl} is involved in protein metabolism. It exerts its effect at sometime after the incorporation of nitrogen and it hinders the production of certain of the more complex proteins.

Shrunken-floury has been tested for allelism with a number of endosperm mutants and was found to be allelic with a gene in the Co-op stock labelled " sh ," Singleton. This symbol is apparently tentative and, I suggest the locus be called shrunken-floury due to the obvious floury nature of the kernel.

D. L. Richardson

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1. Races of maize in Central America.

In cooperation with the National Research Council, we have made a collection of the maize of the countries of Central America. The collection comprises 1,148 entries, representing all the countries from Guatemala to Panama.

Preliminary studies of the collections looking toward classification and a description of the races has begun. Although there is a wide diversity of maize in Central America, especially in Guatemala, it turns out that the majority of types in Central America have already been recognized elsewhere, either in Mexico or in Colombia.

We now recognize fifteen races, of which six are predominantly highland, and nine lowland. The list follows.

Highland Races

1. Serrano, which is a counterpart of the Colombian Sabanero and the Mexican Cacahuacintle. It has six sub-races.
 - a. Cristalino Amarillo
 - b. Cristalino Blanco
 - c. Harinoso Blanco

- d. Harinosa Negro
 - e. Grueso (fasciated, a Guatemalan development)
 - f. Salpor (fasciated, a Guatemalan development)
2. Sanmarceño, a race common in San Marcos in Guatemala and intermediate in its characteristics between Serrano and Oloton.
 3. Oloton, previously described for Mexico and a close counterpart of the Colombian Montaña.
 4. Comiteco, a race previously reported in Mexico.
 5. Punta, a race still not well defined, with small, sharply tapering ears. This may be an ancient indigenous race. Only a few collections of it have been made.
 6. Harinoso Occidental, not found in pure form but the influence of such a race is evident in many collections. It is probably the parent of the race Salvadoreño, and probably came originally from South America.

Lowland Races

7. Nal-tel, one of the ancient indigenous races of Mexico.
- 7a. White Nal-tel, similar to Nal-tel, except that it has white endosperm. This, rather than yellow Nal-tel, is probably one of the ancestors of Dzit-Bacal.
8. Punta (lowland), similar to the Punta from the highlands. More collections are needed to define this race.
9. Tepecintle, previously reported from Mexico, although it probably originated in Guatemala. This race is believed to be one of the ancestors of most of the modern dent corns in Mexico and the U.S.
10. Dzit-Bacal, previously described from Yucatan and Campeche in Mexico.
11. Salvadoreño. This race, especially common in Salvador, has a white flour corn as one ancestor. The other ancestor may be Nal-tel or a form of Punta.
12. Clavillo, a slightly modified counterpart of the Colombian Clavo, a slender-eared corn with flexible cob.
13. Panama 8-rowed. An eight-rowed flint, of which there are only a few collections.

Table 1. Races of maize of Central America compared in knob numbers.

HIGHLAND RACES			LOWLAND RACES		
Races	Altitude (Feet)	Average Knob Number	Races	Altitude (Feet)	Average Knob Number
1. Serrano			6. Nal-tel		
a. Cristalino Amarillo	9,026	3.24	a. Yellow	2,887	9.82
b. Cristalino Blanco	9,275	3.49	b. White	2,916	5.73
c. Harinoso Blanco	8,087	4.69	7. Tepecintle	500	5.27
d. Harinoso Negro	8,557	3.39		3,150	7.81
e. Grueso	7,087	5.60		2,600	9.04
f. Salpor	7,980	2.82	8. Dzit-Bacal	2,900	6.66
2. Sanmarceño	7,841	4.31	9. Salvadoreño		
3. Oloton	6,189	3.96	From Salvador	-	6.36
4. Comiteco	5,819	5.34	From Honduras	-	5.03
5. Punta	6,426	6.78	From Nicaragua	-	7.41
			10. Clavillo (Costa Rica)	-	8.21
			11. Panama 8-rowed	-	4.82
			12. Lowland Elotes	3,200	8.06
			13. Tuxpeño	-	4.77

Table 2. Races of maize of Central America compared in external characters of the ears.

Races	Length cm.	Diameter cm.	Row No.	Shank Diameter mm.	KERNEL CHARACTERS			Denting*
					Width mm.	Thickness mm.	Length mm.	
Serrano								
a. Cristalino Amarillo	13.3	3.8	10.3	10.9	9.4	5.3	10.1	1.3
b. Cristalino Blanco	11.2	3.9	11.0	15.2	9.5	4.9	11.1	1.8
c. Harinoso Blanco	15.7	4.6	11.0	14.1	10.9	6.2	11.9	1.3
d. Harinoso Negro	12.3	4.0	10.7	12.8	9.6	5.1	11.4	1.4
e. Grueso	10.3	3.4	-	7.7	8.0	6.0	8.0	1.0
f. Salpor	19.7	5.7	13.0	23.5	11.8	5.9	13.1	1.2
Sanmarceño	16.4	4.2	8.8	16.5	12.0	5.6	11.8	2.0
Oloton	22.3	4.7	11.9	16.3	9.9	5.7	10.8	1.7
Comiteco	21.7	5.0	13.4	18.0	10.0	5.0	11.4	1.6
Punta	12.4	3.5	12.0	12.0	8.5	4.6	9.5	1.3
Nal-tel								
Yellow	12.0	3.3	11.3	10.7	8.2	4.0	9.4	1.5
White	12.7	3.6	10.0	12.4	8.7	4.0	9.9	1.9
Tepecintle	18.0	4.9	15.5	14.7	8.9	4.5	11.0	1.8
Dzit-Bacal	17.4	3.6	10.0	9.7	10.0	4.3	11.0	2.0
Salvadoreño	10.3	3.6	11.0	5.8	8.0	5.4	8.1	2.0
Lowland Elotes	14.2	4.1	12.0	12.8	9.1	4.3	10.1	1.4
Tuxpeño	17.8	4.9	14.0	17.4	9.3	4.2	12.6	2.0

* Visual estimate recorded on an arbitrary scale 0 = None; 1 = Intermediate; 2 = Maximum.

Table 3. Races of maize of Central America compared in characters of the plants.

	Days to Flowering	Height Cms.	L E A V E S				No. of Nodes to Ear
			Total No.	Length cm.	Width cm.	No. Veins	
Serrano							
a. Cristalino Amarillo	82	242	14	95	11	26	7
b. Cristalino Blanco	86	240	14	91	12	27	6
c. Harinoso Blanco	114	291	16	98	8	23	7
d. Harinoso Negro	87	255	14	95	11	24	6
e. Grueso	116	275	16	101	11	25	8
f. Salpor	90	288	16	104	9	25	8
Sanmarceño	111	316	17	111	10	23	9
Oloton	123	325	18	120	9	27	9
Comiteco	120	294	18	115	9	26	-
Punta	114	318	16	108	9	26	8
Nal-tel							
Yellow	85	140	14	80	9	24	6
White	84	145	14	85	8	26	6
Tepecintle	115	150	16	85	10	28	8
Dzit-Bacal	110	165	14	85	10	22	7
Salvadoreño	90	132	14	77	8	24	6
Clavillo (Costa Rica)	102	165	18	100	9	27	9
Panama 8 rowed	125	112	15	72	6	26	8
Lowland Elotes	89	152	15	75	9	25	6
Punta Lowland	92	150	17	90	8	25	8
Tuxpeño	125	205	18	110	12	32	-

14. Lowland Elotes, white dent corns with colored aleurone, used primarily for roasting ears.
15. Tuxpeño, previously described from Veracruz in Mexico. It is probably a fairly recent introduction.

The close resemblance of a number of Guatemalan races to Colombian races supports the hypothesis (Wellhausen *et al.*, 1952) that the evolution of maize in Mexico (and parts of Central America) is the product of hybridization between ancient indigenous races and South American races introduced into this region in pre-Columbian time.

Data on knob numbers, ear and plant characters are given in Tables 1-3.

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1. Inbreeding with "Santa Rosa" and "Ampero," two commercial varieties, is being carried on in order to obtain white endosperm strains to be used in single and double crosses. Some white endosperm strains introduced from Mexico were mixed and gave a population very promising for our conditions.
2. Some sweet corn strains too late for Connecticut which were given to me by Dr. W. R. Singleton thirteen years ago were mixed and are growing as a good population in Brazil. Selection is being carried on to isolate three main endosperm types: white, yellow and orange varieties of sweet corn.
3. Synthetic populations with yellow endosperm derived from two very productive commercial varieties of Brazil, "Armour"--a yellow dent endosperm type and "Santa Rosa"--a yellow and white dent endosperm type, are under investigation. These improved populations will be compared with their parents and hybrids between them will also be made in order to check the combining ability of the varieties with the hope of producing a good commercial hybrid.
4. Stocks for linkage tests involving the main genes in all 10 chromosomes that I made up while in the States in 1942 have been preserved and sometimes crossed with Brazilian material in order to improve their vigor.

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1. Origin of cultivated corn races in the southern part of South America.

Flint-Races: The most common type is the Orange Flint which is subdivided into a large number of local races, and belongs to the general group of the Carribean Flints and must have migrated along the Atlantic Coast, before Columbus, to the southern corn limit in Argentina. There is an indigenous group of White Flint in north-western Argentina, which goes under the name of Calchaqui Flint, since it occurs in the area which was once occupied by this now extinct Indian tribe. There are three more types, two of which are most probably old synthetics: the Amarillo of Uruguay and Argentina, which probably is derived from a cross between Soft Guarany Yellow Corn and Cateto types, and the Cristal of Southern Brazil and Paraguay, probably derived from crosses between Soft Gusrany Yellow and Calchaqui. Finally there is the Canario de Ocho, of Uruguay and northeastern Argentina with slender eight rowed ears and large kernels, which is a rather isolated type since no eight rowed types occur anywhere in the South American lowlands.

Of these flint types, the Orange Yellow Flint is the most cultivated; it constitutes the Argentinian export type. However it seems as a general rule that the maximum ceiling of combining ability of these flints is rather low, and thus they do not constitute a type which recommends itself for modern breeding work, as shall be shown later in this report.

Dent Races: There are two indigenous dent races in southern South America: The Capio of the high Andean valleys in northwestern Argentina and the Caingang Soft Dent (white) in southern Brazil. The latter has probably contributed to the formation of some old synthetics but the main bulk of Dent Types has been imported from abroad from the United States, since there is no record whatsoever about importation from Mexico. It is rather difficult to obtain exact information but there seem to have been several importations of U.S. Dents through government agencies in at least the last fifty years, and there have been probably some importations before this time, and also through refugees from the U. S. Civil War. In many cases, the type of ears and kernels still permits us to state which U. S. variety had been imported, but it is of special importance that in some areas, notably in Sao Paulo State, a natural synthetic of U. S. Dent and Cateto is forming. Paulista Dent thus has an origin somewhat similar to that of U. S. Corn Belt Dent, which is also considered to be a synthetic between dent and flint types. It is very highly productive with a much higher ceiling of combining ability than Cateto, and has harder kernels of much deeper orange color than U. S. dent. It will be shown later that Paulista Dent represents a very promising type for new breeding programs.

2. The structure of indigenous and other synthetics.

Our studies of indigenous races lead us to conclude that they represent what is generally called today a balanced synthetic, i.e., a population which under a given type of mass selection maintains its hybrid vigor and does on the whole not suffer from natural inbreeding. Furthermore, since inbreeding causes immediately a very significant loss of vigor, it must be concluded that we are dealing with a system of heterotic factors where any degree of homozygosity already acts very strongly. As has been shown (Brieger in "Handbuch of Pflanzenzüchtung, Parey-Berlin 1955), panmixis produces in such a system the inevitable appearance of some homozygotes of various degrees, and if they should reach maturity, the total yield of the mature plants, heterozygotes and homozygotes combined, will be below the maximum yield possible, if there were only heterozygotes. This loss of yield probably does not appear in the indigenous synthetics, since here plant vigor is already so affected by any degree of inbreeding that these homozygotes will usually not reach maturity. Thus in synthetics the loss actually consists of those plants which are eliminated either by natural competition or by roguing, and the yield of those plants which reach maturity will not differ much from the maximum yield. This conclusion induced me to postulate (Genetics 1950) that the best method for obtaining commercial synthetics is to combine inbreds with a high combining capacity but with a low inbreeding minimum. It must, however, be admitted that such synthetics will have considerable disadvantages. Their yield must remain well below maximum if no strong roguing is carried out, which would in turn require a rather dense sowing to guarantee full stand even after intensive roguing. Thus there will be a serious loss, either by having to plant an excessive number of seeds or by having below maximum yields. If, on the other hand, lines are used with a rather high inbreeding minimum, the homozygotes formed by panmixis will cause a certain loss in yield of the synthetic when compared with hybrids. However recent data on synthetics have shown that this loss is not necessarily serious. Thus I have to correct my suggestion, and this correction is being made in our breeding program, that lines with a maximum combining ability and a good performance as inbreds should be used.

F. G. Brieger

3. Cross-sterility factors in pop corn races.

Using descendants of Pira, the Colombian pop corn type, we notice a high degree of cross-sterility in advanced generations, and thus a test was carried out including some 100 different origins of South American pop corn, in order to test for the frequency of occurrence of cross sterility. A number of plants of each sample were pollinated by a common variety, and the frequency of fully sterile, half fertile and fully fertile ears determined. These samples gave a complete series from complete

cross sterility to complete cross fertility; the latter were samples which on the whole showed a higher degree of infiltration from flint corn. The frequency of half-fertile ears was correlated to the degree of sterility in samples with 100 to 60% sterility and also in those samples with from 100 to 60% of full fertility. In the middle group the percentage of half fertile ears increased, and the maximum was reached in samples with about equal parts of fully sterile, half fertile and fully fertile ears. New samples will now be selected out of this lot, in order to verify the genetic basis of the different types obtained.

It can be however already accepted as a fact, that the cross sterility factor is of very common occurrence in nearly all pop corn races. This raises several interesting questions on the history of corn and on the question of population genetics. It is hardly possible to assume that this isolating gene has been introduced by man into this oldest racial type of corn, and we must determine where it may have come from in the beginning and if it came from the wild grasses which entered into the composition of the most primitive cultivated corn. Next it would be very interesting to know what caused the loss of this cross-sterility system when the higher developed races of corn appeared, such as flint, floury and dent races. Since there is no reason to suppose that the cross-sterility factor in these populations differs from other genes, it will mutate recurrently to the cross fertility genes. If the difference between these two types of factors has to do with rate of pollen tube growth, then the new genes for a slower growth rate can hardly have had any possibility of accumulating in the population and thus of increasing their frequency. Thus if the cross-sterility factors were eventually lost, some special situation of selection against them must have appeared. No definite conclusions can be drawn as yet, and the complete analysis of these indigenous races will be necessary.

F. G. Brieger
J. T. A. Gurgel

4. Performance of yellow dent corn varieties from the southern States of Brazil.

In a special randomized block design including 300 samples of yellow dent corn from Sao Paulo State, with 3 replications in 5 blocks per replication of 60 plots each for the same number of samples and 4 plots for randomized checks and further with systematic check every 16 plots, we obtained a frequency distribution of the yields as shown in table 1. As the main check we used H-4664 (I.A.) which is the best semi-dent double hybrid now in distribution.

The error between samples, with regards to the general mean, was of course highly significant. Upon comparing sample yields with the check double hybrid H-4624 (I.A.) it became evident that one sample was numerically superior to the check, about 63 samples or 21% were equal to it at

Table 1. Frequency distribution of yields of yellow dent corn samples from Sao Paulo State, Brazil.

Kg/ha Intervals	1.76 to 2.00	2.01 to 2.25	2.26 to 2.50	2.51 to 2.75	2.76 to 3.00	3.01 to 3.25	3.26 to 3.50	3.51 to 3.75	3.76 to 4.00	4.01 to 4.25	4.26 to 4.50	4.51 to 4.75	4.76 to 5.00	Total
Number of samples	1	2	4	15	28	48	65	60	44	26	6	--	1	300
%	0.33	0.67	1.33	5.00	9.33	16.00	21.67	20.00	15.67	8.67	2.00	--	0.33	100%

2.45(1%) ← general mean → 4.27(1%)
 2.67(1%) ← 3.47 → 4.49(1%)

3.86(1%) ← 4.66
 3.61(1%) ← H-4624(check)

Table 2. Frequency distribution of yields of yellow corn samples from Sao Paulo State, according to sample denominations.

Denom- ination of samples	Kg/ha														Total
	1.76 to 2.00	2.01 to 2.25	2.26 to 2.50	2.51 to 2.75	2.76 to 3.00	3.01 to 3.25	3.26 to 3.50	3.51 to 3.75	3.76 to 4.00	4.01 to 4.25	4.26 to 4.50	4.51 to 4.75	4.76 to 5.00		
Itaici	-	-	-	-	-	-	2	-	-	1	-	-	1	4	
Armour	-	-	-	-	5	5	13	19	10	7	1	-	-	60	
Argentino	-	-	-	2	4	3	6	6	9	6	-	-	-	36	
Caiano	-	-	1	5	3	14	7	6	7	-	1	-	-	44	
Amarelão	-	1	-	3	8	6	15	13	6	6	3	-	-	61	
Sta. Catarina	-	-	-	1	1	1	3	1	-	-	-	-	-	7	
Cunha	1	1	1	-	3	1	3	1	-	1	-	-	-	12	
Others	-	-	2	4	4	18	16	14	12	5	1	-	-	76	

$2.45(1\%)$ ← general mean → $4.27(1\%)$
 $2.67(1\%)$ ← 3.47 → $4.49(1\%)$

$3.86(1\%)$ ← 4.66 →
 $3.61(1\%)$ ← $H=4624(\text{check})$ →

Table 3. Frequency distribution of yields of yellow dent corn samples from Santa Catarina and R. G. Sul States, of Brazil.

Origin	Kg/Ha														Total
	1.51 to 1.75	1.76 to 2.00	2.01 to 2.25	2.26 to 2.50	2.51 to 2.75	2.76 to 3.00	3.01 to 3.25	3.26 to 3.50	3.51 to 3.75	3.75 to 4.00	4.01 to 4.25	4.26 to 4.50	4.51 to 4.75		
No. of samples	-	1	-	3	2	6	13	8	17	12	3	3	-	68	
S.C. %	-	1.47	-	4.41	2.94	8.83	19.12	11.76	25.00	17.65	4.41	4.41	-	100.00	
No. of samples	1	-	-	1	2	5	5	4	2	2	3	2	1	28	
R.G.S. %	3.57	-	-	3.57	7.14	17.87	17.87	14.28	7.14	7.14	10.71	7.14	3.57	100.00	

2.26(1%) ← general mean → 4.58(1%)
 2.51(1%) ← 3.42 → 4.33(1%)
 3.66(1%) ← 4.57
 3.41(1%) ← H-4624(check)

the 1% limit of significance, and the rest of 237 samples were inferior to it. Thus it is evident that the Paulista Dent types under cultivation by farmers and not yet explored by breeders, offer excellent material for new breeding projects, and it must be expected that some of the 63 samples equal to the best double hybrid in this experiment may give still higher yields after improvement through breeding.

Since little is known about the detailed history of Paulista Dent and of the real meaning of names used among farmers, sample means were grouped in accordance to names (Table 2). These data seem to indicate that there is really some systematic difference between samples with identical names. Those received under the name of Itaici and Armour tend to yield more and those under the names of Cunha and Sta. Catarina (i.e. grown under this name in Sao Paulo) tend to yield less than average.

In another yield trial including samples of yellow dent corn from the Southern States of Brazil--Santa Catarina (68 samples) and Rio Grande do Sul (28 samples) with two replications and with H-2464 (I.A.) as check distributed in systematic arrangement, we obtained the frequency distribution of yields shown in table 3. Thus it is evident that these more southern dents do not differ much in yield from the Paulista Dent. It must however be considered that dents from Rio Grande do Sul frequently show in Sao Paulo a lack of adaptation and undesirable plant characters.

Classifications for plant vigor, lodging, ear height, and ear appearance were also made. In the material from Sao Paulo we found in general much lodging. Among the southern samples, those from Santa Catarina have a better performance in agronomic characters than those from Rio Grande do Sul. These samples from Santa Catarina came mainly from one region near the sea coast, populated by a special type of farmers, in small holdings and of North European origin.

E. Paterniani

5. Performance of yellow-orange flint hybrids.

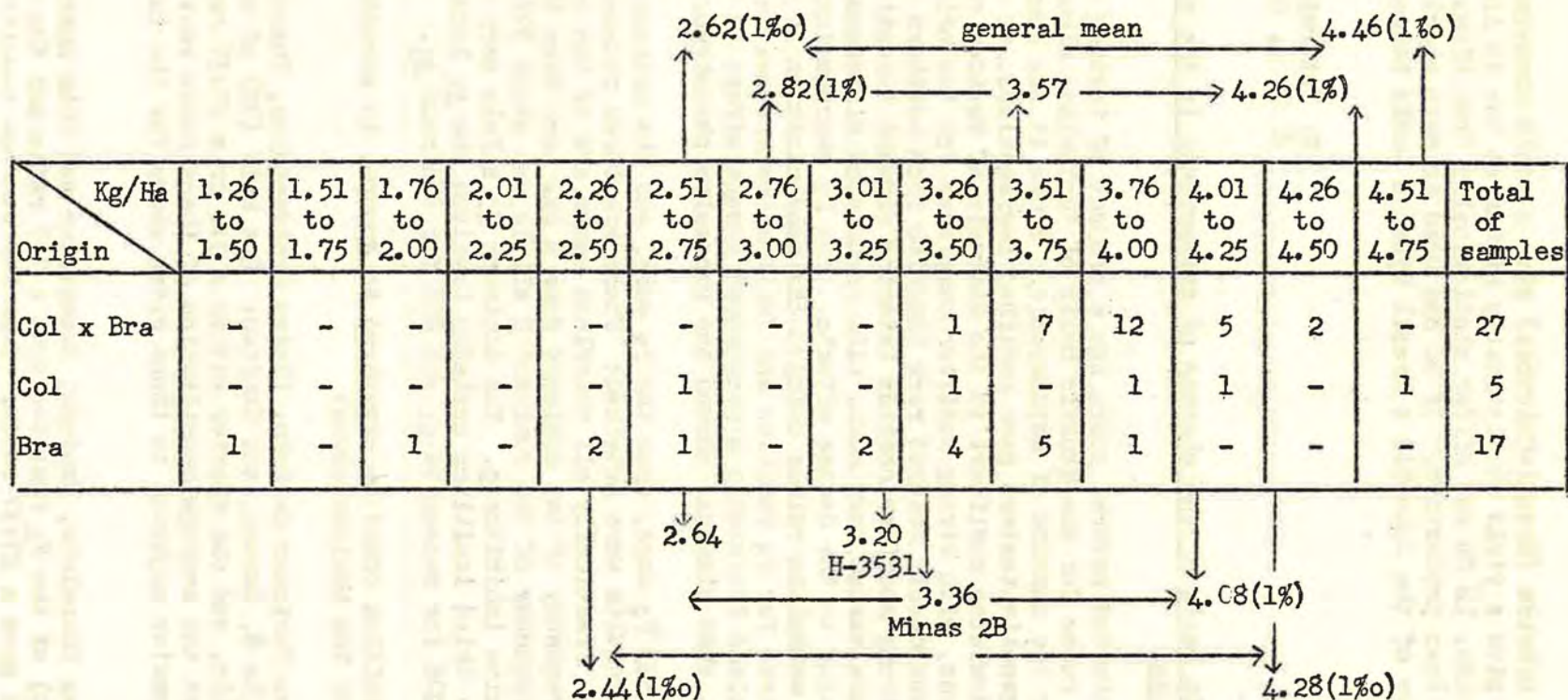
A yield trial carried out in 1951-52, but not yet published, compared hybrids between Brazilian inbreds with those between Brazilian and Colombian strains, received from the Agricultural Colombian Program (Dr. L. M. Roberts). One of our problems in breeding yellow flint is the low ceiling of combining ability, which seems typical of the Brazilian "Cateto." Table 4 shows mean yields, with the 49 samples arranged into two groups (results of a simple 7 x 7 lattice, with 4 replications). As checks we used the two best double hybrids then in distribution, and still in use today.

It is evident that a considerable increase of yield, well beyond that of hybrids of Brazilian lines (Cateto), is always obtained after introducing Colombian germplasm. If we take the hybrid Minas 2B, all

Table 4. Frequency distribution of yields of yellow flint hybrids and varieties according to the origin of their inbred.

(Col x Bra = double hybrids with lines from Colombia and Brazil)

(Col; Bra = Hybrids or varieties, of either Colombia or Brazilian origin only)



but one of 27 hybrids (Brazil-Colombia) give a yield numerically superior while 7 in 27 give a yield statistically higher at the 1% limit. Of the Brazilian hybrids, 12 do not differ statistically from Minas 2B and 5 are statistically less productive. If we had used as main check H-3531 (I.A.), the superiority of the Colombia x Brazil hybrids would become still more pronounced.

E. Paterniani
J. T. A. Gurgel

6. The genetic basis of the absence of anthocyanin in the aleurone of indigenous races.

Brieger started several years ago a project of testing a large number of indigenous races for the genetic basis of "colorless aleurone," and especially for the absence of anthocyanin. Since it was found that direct crosses with genetic testers gave modified segregations, we used Brieger's method of randomizing modifiers in the analysis of Mexican races. The indigenous races, with strong modifier complexes for "colorless," were crossed with one deeply colored race (Negrito from northern Colombia, which has a strong modifier complex favoring pigment formation). The color in F_1 ears varied very much, with pronounced differences in reciprocal crosses owing to the dosage effects. The F_2 segregations gave approximately normal mendelian ratios owing to the randomization of the modifiers. The same was true for F_3 families and for the backcrosses to tester lines, but there remained frequently a pronounced dosage effect in the sense that heterozygotes, when simplex, showed the recessive phenotype.

From the 523 F_2 ears, from the F_3 ears, and the crosses with testers the following results were obtained: There are three recessive inhibitors involved. Practically all colorless races are of the constitution rr, and the frequency of the dominant gene R was less than 10%; at the C locus the frequency of the dominant C allele was about 50% as was that for the recessive inhibitor c. The dominant C^I allele very rarely occurred. The third inhibitor probably involved the A₁ locus with a frequency of 20% for recessive a₁ and 80% for dominant A₁.

The F_2 families could be organized in groups, in accordance to the constitution of the Mexican races:

Group 1: races Harinoso de Ocho, Elotes Occidentales, Tuxpeño, and samples Coahuila 8, Carmen, and Capiten: One half (92) of the F_2 families gave a 9:7 ratio, and one quarter either a 3:1 or a 27:37 ratio. It can be assumed that the average constitution of these races was: rr Cc Aa, with the frequencies adjusted to those given above for the individual alleles.

Group 2: races Chapalote, Vandeño, Reventador and Cuba Amarillo: About two thirds (72) of the F_2 families gave a 9:7 ratio and the remaining one third (42) gave a 27:37 ratio. Thus the average constitution of the

racess was rr cc Aa.

Group 3, race Celaya: The relatively few F_2 families gave the following ratios: 7 (3:1) - 7 (9:7) - 15 (27:37) - 1 (1:3 or 3:13). Thus we must accept as the average constitution, as in group 1, the formula rr Cc Aa, with an occasional substitution of c by the dominant inhibitor.

Group 4, races Rabloncillo, Tehua, Tepecintle, Zapalote Grande, sub-race Perla and sample Guanajuato 61: There were 80 families with a 9:7 ratio, 102 with a 27:37 ratio and 20 with either a 1:3 or 3:13 ratio. The average constitution must thus have been the same as in group 2, with an occasional substitution of the recessive c inhibitor by its dominant inhibitor allele.

It could also be shown that all abnormalities observed can be attributed to dosage effects, which cause simplex heterozygotes to give the recessive (colorless) phenotype. For this purpose we first determined what should be in each case the results expected from a dosage effect, and then verified that these results were in fact observed: (a) The families segregating for the ratios 3:1 or 1:3 in all groups and 9:7 in groups 2 and 4 should give, and gave an asymmetrical distribution in the direction expected, i. e., in favor of high frequencies of colorless kernels in all but the 1:3 ratio, where the higher frequencies were in the colored kernel class. (b) The families with a 9:7 ratio in group 1 showed, besides the asymmetry in the direction of colorless kernels, also an excess of colored kernels in some ears, which were the result of dosage effect in ears which should have segregated in a 3:1 ratio but had their ratio considerably altered by dosage. (c) The ears of the 27:37 group showed a bimodal distribution, owing to the shift of ears of the 9:7 group and of the 27:37 ratio towards higher frequencies of colorless kernels.

No other exceptions were observed, and it may be stated that the frequency of contamination, and also of heterofertilization was very low.

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1. The origin of diminutive B-type chromosomes in maize.

The chance discovery of an exceptional plant in a progeny heterozygous for the B-9a translocation gave clues that seemed to explain the origin of diminutive B-type chromosomes. The following excerpt from an abstract of the article appearing the American Journal of Botany

(January 1956) outlines the changes that are necessary to produce from a normal B, a diminutive B chromosome.

"The heterochromatic areas of a B chromosome when they are not paired with the homologous areas of a second chromosome frequently are folded back on themselves at mid-prophase to simulate a paired condition. Similar pairing is found between the distal and proximal sections of the long arm of the B chromosome in B-A translocations. The dyscentric pairing of the two sections of a B is such that exchanges occur to give a diminutive B-type chromosome or a dicentric chromosome and an acentric fragment."

One plant appeared in a progeny from the above exceptional plant that had only a short section of the long arm of the B chromosome inserted at the mid-point of 9. It is thought that this second exceptional plant arose because there had been an exchange or crossover in the loop formed by the inserted B cutting off an acentric fragment and leaving a much shorter insertion from the B chromosome.

This second plant further substantiates the view that the heterochromatin of a B when dyscentrically paired will have crossing over, and that this crossing over may occur at different areas of the long arm of B.

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1. Variation in color intensity and frequency of sectoring in separate self-red mutations from a given variegated pericarp allele.

Red pericarp families derived from mutant red (self-colored) kernels on variegated ears of a given origin were divided into two groups: those containing Modulator (Mp) somewhere in the genome and those lacking Mp altogether. The presence of Mp was determined by testcrossing to appropriate Dissociation (Ds) stocks, and scoring for the phenotypes expected from chromosome breaks. The frequency of changes to or toward colorless (sectoring) was then measured.

It was found that families which were derived from independent red mutations on the same variegated ear, and which did not contain Mp anywhere in the genome, sometimes differ significantly in the frequency of pericarp sectoring. However, larger and more frequent differences were found between comparable families which contained Mp than between those which do not contain this factor. The data thus show that the families lacking transposed Mp, in general, are more stable for pericarp than those which contain it.

To obtain additional information on the effect of M_p on stability of P^{rr} expression, inbred 90RR (red pericarp and cob) was crossed with near-isogenic stocks of inbreds 22R and 4Co63, each inbred being represented in the crosses by both variegated and colorless pericarp stocks. The two groups of families derived from the crosses with 22R did not differ in the frequency of pericarp sectoring. However, one of the crosses made with 4Co63 differed from the others. This family, resulting from the mating 90RR x 4Co63 medium variegated, showed a relatively high frequency of pericarp sectoring.

Families that were scored for the frequency of pericarp sectors were scored also for color intensity against a set of standard ears. It was found that both the families which contained M_p and those lacking it occasionally differed in color intensity. No consistent relationship between variations in color intensity and the frequency of pericarp sectoring was found.

G. H. Clark

2. Effect of heterozygosity for variegated pericarp on mutation to red and to light variegated.

The rate of somatic mutation of the variegated pericarp allele (P^{vv}) to red (P^{rr}) usually is much lower in homozygous P^{vv}/P^{vv} than in heterozygous P^{vv}/P^{wr} plants. Emerson reported this relation in 1929, and it has been confirmed since in a number of our stocks. It is now well established that mutations of variegated to light variegated, related in origin to the reds, also occur. An experiment was made to measure the frequencies of these two mutant phenotypes among the offspring of otherwise near-isogenic homozygous and heterozygous variegated pericarp plants.

A P^{vv} allele of common origin was incorporated into the yellow dent inbreds W22 and W23 (P^{wr} , colorless pericarp, red cob). Fifth backcross generation P^{vv}/P^{wr} (variegated pericarp, red cob) plants in both the W22 and W23 series were selfed to provide homozygous variegated (variegated cob) and heterozygous variegated (red cob) plants. Both classes of plants were then pollinated with P^{ww} (colorless pericarp and cob). The progeny from the $P^{vv}/P^{vv} \times P^{ww}$ and $P^{vv}/P^{wr} \times P^{ww}$ matings were classified for pericarp phenotype into medium variegated, light variegated, red, and colorless pericarp with red cob. The following table shows the distribution of the progeny from the testcrosses:

Pericarp class	W22				W23			
	Homozygous		Heterozygous		Homozygous		Heterozygous	
	No. of Plants	Per-cent	No. of Plants	Per-cent	No. of Plants	Per-cent	No. of Plants	Per-cent
Medium var.	4325	94.7	2137	45.8	6114	90.5	3293	40.9
Light var.	108	2.4	48	1.0	337	5.0	329	4.1
Red	132	2.9	52	1.1	302	4.5	411	5.1
P^{wr}	0	0	2433	52.1	0	0	4018	49.9
Total	4565		4670		6753		8051	

It will be seen that in the W23 series the frequencies of reds in the progenies of heterozygous and homozygous parent ears are approximately the same. Since there are two P^{VV} alleles in the homozygote which could mutate to red and only one in the heterozygote, the mutation rate is roughly twice as high per P^{VV} allele in heterozygotes as in homozygotes. It is apparent from the data that a similar relationship exists also in the light variegated class: per P^{VV} allele in the parent, somewhat less than twice as many light variegateds appear among the offspring of heterozygotes as among the offspring of homozygotes.

The P^{VV} allele shows a markedly lower rate of change to both red and light variegated in the W22 than in the W23 background. Furthermore, the frequency of red and light variegated is slightly more than twice as high in the progeny of homozygotes as in the progeny of heterozygotes. This stock, therefore, is an exception to the rule of greater instability of P^{VV} in heterozygotes.

These data, and the results of other studies still in progress, point to three phenomena as being involved in the coincident occurrence of red and light variegated mutants: (1) "release" of Modulator (M_p) from the P locus, (2) "capture" of M_p at one or another chromosomal site (see *Genetics* 37: 519-544 and 39: 724-740) and (3) increase in number of Modulator units, in certain cases, in the mutation process.

R. I. Brawn
R. A. Brink

3. Gene order in the vicinity of the P locus, chromosome 1.

Emerson (1939, *Genetics* 24) established the order $ms_{17} - 1.7 - ts_2 - 1.3 - P \rightarrow br$. Hayes (1938, M.G.C. News Letter) placed zb_4 in chromosome 1 by showing 31% crossing over with brachytic, 28% with fine stripe, and 7% with the P locus. Since P is distant from br and f , Hayes' data suggested that zb_4 was between P and br , and thus proximal to P .

Anderson (1941, *Genetics* 26) located translocation 1-2b (1S.44) on the opposite side of P from ts_2 , about 3.8 units proximal to P .

The following results from this laboratory show that zb_4 actually is distal to P . (See Table 1.)

The 1955 results of Brink clearly indicate that zb_4 is on the opposite side of P from $Tl-2b$.

The Knott and Valentine pooled results establish the order $zb_4 - ts_2 - P$, with distances essentially $zb_4 - 4 - ts_2 - 3+ - P$. The distance of 7 units between zb_4 and P is in agreement with the findings of Hayes.

F ₁ genotype	Parental combinations		Recombinations				Total	Source of data
			Region 1	Region 2	Regions 1 & 2			
$\frac{+ \text{ p}^{\text{WR}} \text{ T1-2b}}{\text{zb}_4 \text{ p}^{\text{WW}} +}$	353	*	4 *	10 *	0	0	367	R. A. Brink
			1.09%	2.72%				
$\frac{+ + \text{ p}^{\text{VV}}}{\text{zb}_4 \text{ ts}_2 \text{ p}^{\text{WR}}}$	4305	3561	172 175	136 104	6**	***	8459	D. R. Knott, 1952 Wis. Ph.D. thesis
			347	240				
$\frac{+ + \text{ p}^{\text{VV}}}{\text{zb}_4 \text{ ts}_2 \text{ p}^{\text{WR}}}$	200	*	17 *	3 *	0	*	220	F. Valentine
	4505		189	139	6	=	4839*	
			3.91%*	2.87%*	0.12%*			

* zb_4 not classified and/or included.

** Classification for both ts_2 and zb_4 was verified by progeny tests.

*** This class is omitted because of difficulty in classifying some plants for ts_2 even after progeny tests.

Perhaps T1-2b reduced crossing over between zb₄ and P in Brink's data. The Wisconsin data show rather more crossing over between ts₂ and P than reported by Emerson.

This region of chromosome 1, therefore, may be mapped as follows:

zb₄ - 4 - ts₂ - 3+ - P - 3 - T1-2b

D. R. Knott
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R. A. Brink

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1. Linkage of Co.

In the News Letter No. 24 (1950), I described plants with chocolate colored pollen due to a gene Co which is located in the 10th chromosome and is linked with the gene li. In further research a linkage of 21.7% between Co and sp₂ has been found.

2. Frequency of natural mutations to white seedlings in some inbred lines.

In some inbred lines hand-pollinated for 10 to 25 years some white seedlings have appeared. In the table below the frequency of these mutants is expressed per 10,000 plants in the inbred lines from different indigenous varieties of maize (I-VIII) and after different 10 to 25 generations of selfing.

Inbred lines	Generation with mutants	No. of white seedlings per 10,000 plants
S _I -26	11	5
S _I -54	14	3
S _I -73	12	7
S _{II} -58	21	6
S _{II} -6	10	10
S _{II} -15	18	9
S _{III} -35	17	4

(Table continued)

Inbred lines	Generation with mutants	No. of white seedlings per 10,000 plants
S _{IV} -47	12	15
S _{IV} -64	10	12
S _V -34	15	5
S _{VI} -43	16	8
S _{VII} -58	10	3
S _{VIII} -81	25	9

3. Hybrids between Z. M. rostrata and other types.

31 different inbred lines originating from 9 different indigenous varieties of maize have been crossed with inbred lines of flint, dent, sugary, and pop maize of different shape and size kernels and of different size and percentage of cob. The F₁ generation has been investigated in details including the combining ability of the different inbreds. The results are being prepared for publication.

4. The heritable proliferation of tassels.

This character was described in News Letter No. 27 (1953) and has since been studied cytologically. The sporocytes of these plants are smaller than in the normal plants and the membrane is very brittle. In the pachytene stage the chromosomes surround the nucleolus very closely and appear quite different from those of the normal plants. The haploid number is usually 10 chromosomes, but in some plants a large chromosome which often breaks in two parts at the centromere region has been observed. The results are prepared for publication.

A. Tavcar

IV REPORT ON MAIZE COOPERATIVE

Work of the past year has been directed chiefly toward increasing seed supplies and confirming genetic constitutions of improved stocks. A partial conversion of all genetic stocks is being made to the inbred lines M14, W23, and Oh51A in order to improve their vigor and range of adaptation. A large number of segregating F₂ families were grown the past summer, and seed increases from mutant segregants obtained. The stage in conversion to inbred background which has been reached varies considerably with different stocks. Conversion of dominant traits is in general straightforward and rapid, while conversion of multiple recessive gene testers, especially those involving aleurone color traits, requires extensive confirmation of genotype at each step.

In many of the stocks, traits have appeared that were not indicated in the original pedigrees. The most frequent of these are liguleless, glossy, virescent, or dwarf. An attempt is being made to note in the pedigrees all unidentified traits that are observed. Since, in many cases, stocks free of such extraneous traits are not yet available, it will be helpful in supplying stocks if correspondents in their requests indicate those instances when the presence of certain classes of traits would interfere with their immediate uses.

Many of the older gene traits are still not represented in this collection. The majority of these may be presumed to be lost. However, it is urged that all recipients of the News Letter check their own stocks for the presence of any useful traits that should be added to the Cooperative collection. It is important that this be done now to prevent unnecessary further loss of valuable traits.

During the past year about a hundred traits have been added to the collection. The majority of these are unidentified, and their listing must await seed increase and the completion of allelism testing where necessary.

To eliminate space-consuming repetition of stock lists, a complete listing of available genetic stocks is not included in this issue. The stocks which follow represent traits or combinations supplementary to those listed in last year's News Letter. Additional copies of the previous catalog of stocks are available upon request. Requests for genetic stocks or for last year's report should be sent to the Botany Department, University of Illinois, Urbana, Illinois. Newly-available stocks are as follows:

Chromosome 1

ad₁ bm₂; seg P^{rr}, Kn
an₁ bm₂; seg sr, P^{rr}, br₁, gs₁

seg an₁, Kn, bm₂
 br₁ f₁ bm₂; seg P^{rr}, an₁, gs₁
 br₁ f₁ bm₂; seg P^w, an₁, gs₁
 seg Kn, Ts₆
 P^{rr} gs₁ bm₂; seg br₁, f₁, an₁
 prw
 P^w; seg ad₁ an₁ (coupling)
 P^w; seg zb₄ ts₂ (coupling)
 P^w hm br₁ f₁
 seg sr zb₄ P^w (coupling)
 vp₈
 zb₄ P^w
 zb₄ P^w bm₂
 zb₄ P^w br₁

Chromosome 2

lg₁ gl₂ b fl₁ v₄; seg ws₃
 lg₁ gl₂ b v₄; seg fl₁, sk
 lg₁ gl₂ b v₄; seg gs₂, Ch
 lg₁ gl₂ b v₄; seg sk
 ws₃ lg₁ gl₂ b

Chromosome 3

a₁ Ga₇
 A₁ g₃⁷
 a₁ sh₂ et; Dt₁
 ba₁
 seg ts₄, lg₂, na₁

Chromosome 4

su₁ gl₃; seg Tu
 su₁ j₂ gl₃
 Ts₅ su₁

Chromosome 5

A₂ bm₁ pr₁ ys₁; seg v₂
 gl₁₇ bt₁

Chromosome 6

po y
 y at si
 Y Pl sm; seg py

Chromosome 7

gl₁ sl Bn
 ij¹
 in; pr

Chromosome 8

v₁₆ j₁; seg ms₈

Chromosome 10

na₂ R

Varieties

Ladyfinger Popcorn

Multiple gene stocks

A₁ A₂ C R^g Pr B pl lg₁ fl₁ y
 bm₂ lg₁ a₁ su₁ pr Y gl₁ j₁ wx g₁

E. B. Patterson

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3. A summary of an extensive screening project for "T" and "S" sterile cytoplasm restorers.

A large number of sources of germ plasm were sampled for restoring genes for the "T" and "S" sources of sterility. These gene sources are being practically evaluated as will be discussed later.

Upon summarizing results, an attempt was made to correlate frequency of restoring gametes with the geographic origin of the source material. Geographic areas were arbitrarily set-up as follows:

Area

- 1 New England and No. Eastern Canada
- 2 Extreme No. Western Corn Belt, centering in South Dakota.
- 3 Eastern Corn Belt, centering in Pennsylvania.
- 4 Middle Corn Belt, centering in Illinois and Iowa.
- 5 South-western United States and No. Mexico
- 6 South-eastern United States, centering in Georgia.
- 7 Carribean Islands and So. Florida.
- 8 So. Mexico and Central America.
- 9 Northern half of So. America.
- 10 Southern half of So. America.
- 11 Mediterranean Countries.
- 12 So. Africa and Ethiopia.
- 13 Northern Europe.
- 14 South East Asia and India.
- 15 No. East Asia and Japan.
- 16 Australia.

All possible correlations were run on data from areas 2, 3, 4, 5, 6, 7, and 8, in order to determine the degree to which origin affected the relationship between occurrence of restorers in this material. Results were as follows:

	r =	d/f
Between T completes and T partials	.235	15
" " " " S completes	-.106	6
" " " " S partials	.243	6
" " partials " S completes	-.266	6
" " " " S partials	.141	6
" S completes " S partials	.544	6

Table 1.--"T" Texas Type Sterility.

Area	No. of varieties or sources sampled	No. of plants sampled	No. of Gametes sampled	% Completely restoring gametes	% Partially restoring gametes	% Non-restoring gametes
1	8	21	211	3.8	0.9	95.3
2	26	143	205	2.6	5.6	91.8
3	8	66	921	8.8	4.0	87.2
4	165	736	10,498	6.3	3.2	90.5
5	71	370	5,333	13.4	2.7	83.9
6	116	356	5,112	10.5	3.0	86.5
7	21	156	2,266	25.8	9.1	65.1
8	10	37	533	34.3	5.4	60.3
9	10	26	387	8.8	2.3	88.9
10	64	64	896	23.5	13.5	63.0
11	745	766	10,677	9.6	10.4	80.0
12	53	53	747	12.3	4.8	82.9
13	66	77	1,082	1.4	6.1	92.5
14	23	41	563	38.5	3.7	57.8
15	10	10	134	6.7	7.5	85.8
16	25	25	339	13.9	5.6	80.5

Total 1,421 2,947 41,754
Average all readings not weighted by areas. 10.7 5.8 83.5

--"S" Connecticut - U.S.D.A. Type Sterility.

1	7	10	137	0.7	65.0	34.3
2	22	79	1,083	4.0	70.1	25.9
3	6	52	740	1.9	64.2	33.9
4	138	491	6,940	2.5	42.6	54.9
5	69	314	4,508	3.8	70.4	25.8
6	125	335	4,808	14.8	75.9	9.3
7	21	130	1,835	3.7	66.9	29.4
8	7	29	397	3.5	69.0	27.5
9	1	5	78	0	29.5	70.5
11	1	13	182	0.6	45.6	53.8
13	1	11	154	0	59.7	40.3
14	3	19	268	0	46.3	53.7
15	1	1	11	0	45.5	54.5

Total 402 1,489 21,141
Average all readings not weighted by areas 5.6 61.2 33.2

Next, all possible correlations were run on data from the 32 best sampled varieties (individual data not shown here), in order to determine the degree to which varieties affected the relationship between occurrence of restorers in this material. Results were as follows:

Between T completes and T partials	r = .130	d/f 31
" " " " S completes	r = .014	31
" " " " S partials	r = .079	31
" " partials " S completes	r = -.028	31
" " " " S partials	r = -.154	31
" S completes " S partials	r = .025	31

The reader is left to his own interpretation as to the meaning of these correlation values, only one of which approached significance.

It would seem that the most important information presented here is the estimate that material derived from regions 5, 6, 7, 10, 12, 14, and 16, provides the most abundant sources of T restorers, while region 6 seemed to be the only area abundant in good "S" restorers. Also, assuming that we have made an unbiased sampling of Zea Mays, then the general frequency of complete and partial restoring gametes for "T" and "S" cytoplasm for the species may be shown in the following table.

	No. sources sampled	Percent complete restoring gametes	Percent partial restoring gametes	Percent Nonrestoring
T cytoplasm	1421	10.7	5.8	83.5
S cytoplasm	402	5.6	61.2	33.2

The expectation that restorer characters should most likely enjoy their greatest frequency in areas where the corresponding cytoplasm originated, makes this summary a matter of interesting speculation.

4. Investigation of new sources of restorer genes.

Texas cytoplasm restorers. More than 200 new "T" restorer sources have been found. Work is now in progress to determine if any of these new sources are different from or non allelic to the presently used "T" locus to be found in K6, Ky21, K55, Tx127c, I153, A344, etc.

"S" cytoplasm restorers. More than 100 sources of restoration for this cytoplasm have been screened out. Explanation of mode of inheritance of restoration of this cytoplasm from this work is far from conclusive, and further investigation of these sources is being directed entirely to a better explanation of gene action involved. The difficulty lies in establishing what might constitute a valid genic background. This work

involves use of WF9 MS (S) x M14 as tester parent, and hence future information will by necessity include the assumption that this single cross does in fact represent a valid threshold from which to measure factors affecting restoration of "S" cytoplasm, since the recycling technique in use progressively removes restoring factors from the original source genic backgrounds (usually O, P.) and inserts these factors into the WF9 x M14 background in the usual backcross rate of 50% per generation.

33-16 cytoplasm restorers. Mode of inheritance of restorer mechanisms found in six inbred lines is being investigated, assuming the Inb. WF9 constitutes a valid "threshold."

5. Investigation of new sources of sterility.

More than 30 new sources of male sterility, including one derived from Vg stocks, have been collected and confirmed as being cytoplasmic. These new sources have been organized into a project to differentiate these from known sources of sterility and from each other by means of restoration patterns.

Information so far shows that at least 2 of these new sources are extremely similar to, and probably the same, as the 33-16 type. One was derived from a sweet variety, and the other from a blue seeded flint variety.

6. Estimate of frequency of occurrence of "sterile" cytoplasm in Zea Mays.

One hundred different, randomly selected, non central corn belt varieties were collected and organized into a project to insert the nuclear complement of a specific strain of WF9 into each of the cytoplasm carried by the 100 varieties.

As a side light of this project, now in the BC3 stage, there has so far been conclusive evidence that fully six of the original sources carried "sterile" cytoplasm, assuming that WF9 represents a valid genic background for classifying cytoplasm as "sterile" or "fertile." (There is also some evidence that 3 additional sources may carry weaker male sterilizing characters)

If it is assumed that these 100 random (non corn belt) varieties represent an unbiased sample of Zea Mays, then it must be concluded that at least 6% of the divisional entities of the species carry cytoplasm that must be classified as "sterile" in the presence of the WF9 nuclear complement.

7. Restoring tendencies in inbred ML4.

Information from second winter generation 1954-55, summer 1955, and first winter generation 1955-56, based on observation of 1597 plants of 92 testcross progenies support an assumption that the seemingly complex inheritance of restoration in this inbred could trace to a single factor or closely linked complex which is expressed in 70 percent of homozygous individuals as either partial or complete fertility, and in 35 percent of heterozygous individuals as either partial or complete fertility.

A project for removing this factor(s) by outcrossing to non-restoring, non-recurrent parents, and backcrossing six times to ML4, while holding heterozygosity by means of testcrosses, is now nearly complete. The above observations are based on testcross observations during backcross generations 2, 3, and 4.

	Number plants observed	Number progenies observed	Number progenies Heterozygous (50% assumed)	% Sterility in Heterozygous progenies	% Partial Fert. in Heterozygous progenies	% Fert. in Hetero- zygous progenies	% Sterility in Homozygous progenies	% Partial Fert. in Homozygous progenies	% Fertility in Homozygous progenies
Spring 1955 (Florida)	282	23	11	53	5	42	18	11	71
Summer 1955	739	34	17	70	27	3	31	55	14
Fall, 1955 (Florida)	576	35	18	64	33	3	35	57	8
Ave. of 3 Gen. weighted by seasons	1579	92	46	62	22	16	28	41	31
Ave. for 3 Gen. of whole pop. observed	1579	92	46	<u>65</u>	25	10	<u>30</u>	47	23

It should be noted that even though this work was begun with an unselected version of ML4, the above estimates would be biased in the later generation data, if "Within line" variability existed in our strain of ML4, because of an unavoidable and progressive tendency to select for the less restoring substrains, if they existed.

8. Restoring tendencies in Minn. A344 and Kansas 55W.

Information up through the BC5 recovery generation indicates that restoring tendencies of A344 and K55W can be easily and simply eliminated by removing a single, dominant gene. Procedure has been to outcross these lines to sources of the recessive "F" gene, and backcross until reaching the BC6 generation, while holding heterozygosity at the "F" locus by means of testcrosses.

Infrequent and haphazard occurrence of extremely weak partials, in addition to the expected fertiles, in these test cross progenies, has not been investigated, but is assumed to result from changing complementary relationships at other loci during the recovery segregations.

No ordinary or obvious morphological or genetic characters have so far been found to be closely linked to the restorer locus.

9. Description of two proposed breeding methods for introduction of restorers into "problem" inbred lines.

Using the "Eckhardt" method of recovery, and alternating one or two winter generations with a summer crop, a few lines show normal 1:1 segregation in the winter backcross population. The succeeding summer generation may show no normal fertiles at all, and only a few partials, this latter generation typically being one of the middle or later backcross generations.

It is widely suggested that such exceptional phenomena must relate to the possibility of having by-passed needed complementary genes during a generation (presumably in Florida) grown under a non-critical environment. It is also widely suggested that individuals for backcrossing should be selected from large populations only under a critical environment (presumably summer). Because, however, of the great expanse of time involved in recovering lines by such a one generation per year procedure, plus the fact that even any one summer environment may well fail to be "critical," two other procedures are being attempted.

The first merely involves straight backcrossing until the first non-fertile (partial) generation is reached. Sibbing between partials, across as much family relationship as possible, should then reconstitute the "threshold" complementary gene level with a very reasonable frequency, assuming dominant and independent (excluding complementary) action of the threshold genes. Backcrossing might then be resumed on the resulting normal fertiles of the next generation, followed again by a sib generation as necessary.

The second method merely involves backcross recovery in the absence of sterile cytoplasm, where "F" heterozygotes are identified by means of

a sterile tester. Such a procedure would make it possible to easily introduce the "F" locus into a problem line, but it would be almost categorically impossible to also bring in any or few of the threshold genes. Since, however, only a small portion of lines lack such a threshold (presumably composed of only a small random portion of an essentially dominant series of alleles), it would seem likely that the odds against any resultant four-way hybrid lacking such a minimum threshold would be very heavy indeed.

It is hoped that the reader does not interpret any claim to originality for the actual techniques described above, except perhaps as they may be applied.

10. A single plot testing technique for the agronomic evaluation of substrains of recovered restoring versions of inbred lines.

Three hundred and one substrains of recovered restoring versions of several standard lines were tested in 1955, using a single plot technique.

Testcross seed was made up using a "T" sterile version of the appropriate seed line as the female parent. Male parents were individual BC6 recovery plants of an inbred line, heterozygous at the "F" locus.

Testing was done by planting the resulting seed, segregating about 1 sterile: 1 fertile, in single, bordered plots 30 plants long. At flowering time, the fertile segregates were tagged. At harvest time, yield and other data were gathered separately from both the sterile and fertile segregates. Performance will be calculated by expressing yield of fertile segregates in terms of percent of yield of sterile segregates, reduced or weighted to a single plant average.

It would seem likely that, testcrossing during the BC6 generation, resultant sterile and fertile segregates would differ genetically only by the chromosome segment carrying the "F" locus. Thus, if it can be shown that steriles and fertiles differ, this difference must relate to agronomic characters linked to the restorer. Hence differences within a line, within an "F" gene source would probably relate to the amount or length of the non-recurrent "F" segment, and differences within a line between "F" gene sources would probably represent an estimation of the general differences between agronomic factors closely linked to the "F" locus between gene sources.

Thus the method may be an efficient and timely means of selecting best recovered individuals within a recovery family, and will most certainly provide an accurate comparison between sources, of agronomic factors linked to the restorer. This latter consideration may well prove to be the most logical criterion to use in making final choice of "F" gene sources to use.

The efficiency of an adaption of this technique is being preliminarily evaluated as a possible device useful for usual testing needs.

(Actually, some strains were testcrossed before BC6, in order to make use of the summer of 1955 for testing).

11. Use of the Homestead, Florida location in three generations per year breeding programs.

Six complete, successive generations involving a comprehensive and extensive array of corn breeding projects were grown during the two calendar years beginning September 1953, and ending September 1955, alternating two winter generations at Homestead with one summer generation in the Corn Belt.

Material involved in these nurseries ranged in maturity from Northern corn belt lines to "deep" south material. Usual planting dates for the fall generation were September 5-11, and for the spring generation were December 5-21, and for the summer generation were May 1-11.

Porous, higher, rockland soils were utilized for the fall "rainy season" crop, and lower marl (glade) soils for the spring "dry season" crop. By far the most critical aspects of this program have been

1. Need for adequate plant food supplies to replace leaching losses from open rockland soil.
2. Adequate and timely irrigation facilities for fall nursery on rockland soils with extremely low water holding capacity.
3. Adequate insect control during "off season" fall crop, when general insect population level is extremely high.
4. Satisfactory seed germination in the second winter generation, which is planted at mid-winter when low soil temperatures sometimes prevail in the cool, moist glade soils.

It is assumed that corn does best in the deeper, older, finer types of rockland soils, and has done very well in such soils known to be heavily infested with the common tomato and garden bean nematode. It is reportedly sensitive to the extreme pH of newly scarified soils.

Average breeding success during these four winter generation ran higher than during the two interspersed summer generations.

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Information from projects carried on while at Pfister's Associated Growers, Inc.

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3. Big rings.

Work is continuing using the method of intercrossing interchanges with a common chromosome, then selecting the recombinations which combine the parent interchanges. A 1-7-5, 3-2-4, 8-9-10 and probably 3-2-4-9 have been obtained. Certain combinations needed have not appeared but other interchanges have been substituted. Also other combinations are being built for use in the later stages, using the procedures suggested by Inman (Corn News Letter #29, p. 55.)

Crosses between the various stocks were grown last summer. The largest ring should have had 14 chromosomes. The tassels looked and felt like those of a male sterile. Only occasionally did an anther extrude. Limited pollinations made by teasing out the pollen gave no seed set. When they were pollinated with normal pollen there was some seed set. It is hoped that some crosses will shed pollen even with a big ring present. Some variation has been noted for a ring of 10, depending on the cross or the season.

4. Big rings in barley.

There may be some interest in the information that in barley a homozygous stock has been obtained which gives a ring of 6 in crosses.

Tests using closely linked genetic markers are being used in corn and in barley to aid in selecting the desired crossovers.

Also the ring of 6 barley has been irradiated.

5. Crossing over in ♂ and ♀.

Tests for differences in crossing over in male and female were continued. For the su-la region, two exotic strains, maize Chapaloti and long ear Papago were tested. Both gave higher values in the ♂ but the Papago strain gave a considerably greater difference; For maize chapaloti: 11.7% in the ♂, 8.0% in the ♀, for Papago: 14.1% and 6.3%.

Using other standard stocks, there was no consistent difference in the su-tu-gl regions of 4, or in d-Rg-lg in 3. Limited tests on jm in 8, P-zb₄ in 1 and su zb₆ Tu in 4 showed no significant differences.

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6. Deficiency - duplication studies.

Genetic evidence for an intercalary deficiency was found in the progeny of the cross (Tl-9a x Tl-9c) x *argentina* (ar ar). From a total of 1625 plants grown, 207 plants were observed showing the ar phenotype. Also in the cross (Tl-9a x Tl-9c) x Tl-9c x ar ar, 127 ar plants were observed in a total of 577 plants grown and from the cross (Tl-9a x Tl-9c) x Tl-9a x ar ar, 14 ar plants were observed from 77 plants grown. In sporocytes taken from plants of the cross Tl-9a x Tl-9c, 10 bivalents were observed at diakinesis. Folded loops were observed on chromosome 1 and open loops were observed on chromosome 9 at pachytene.

E. Turcotte

