

MAIZE GENETICS COOPERATION

NEWS LETTER

15

5-21

April 1, 1941

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Department of Plant Breeding  
Cornell University  
Ithaca, N. Y.

MAIZE GENETICS COÖPERATION  
DEPARTMENT OF PLANT BREEDING  
CORNELL UNIVERSITY  
ITHACA, NEW YORK

January 21, 1941

To Maize Geneticists:-

The call for material for the 1941 issue of the Maize News Letter has been delayed this year much longer than usual. This was the result of considerable uncertainty as to the source of support for the Maize Genetics Cooperation. While we can make no positive statements now, it seems likely that continued support of the Maize Cooperation at Cornell will be forthcoming from some quarter.

Items submitted for the 1941 News Letter should include new linkage data, descriptions of new characters, suggestions on breeding and cytological technique, and all similar material likely to be of general interest, and valuable to have on record.

We plan to print in the News Letter references to all important maize publications since our last issue. It will help to make this list more complete if you will send us the titles of papers in press, with the names of the journals which have accepted them.

The dead line on contributions is March 1, 1941. May we have your contribution soon?

Sincerely yours,

*A. C. Fraser*

A. C. Fraser  
Secretary

ACF:P

MAIZE GENETICS COÖPERATION  
DEPARTMENT OF PLANT BREEDING  
CORNELL UNIVERSITY  
ITHACA, NEW YORK

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April 1, 1941

To Maize Geneticists:-

At the request of Professor Emerson, I am taking over the job of Secretary of the Maize Genetics Cooperation. It is hoped that this arrangement will give continuity to the work of maintaining stocks and will enable us better to plan ahead.

Actually most of the detailed work with the stocks is at present in the hands of James E. Welch, one of our graduate students from Honolulu. Welch has a Ph.D. major problem on corn. He has made all of the pollinations of the "co-op" material this past summer and has proved very helpful in other ways.

You will be glad to learn that the Rockefeller Foundation has made a grant to Cornell University to cover the cooperative work with the maize stocks for three years, starting February 1, 1941. The Foundation has further indicated its willingness to consider a request for the renewal of the grant at the end of this period.

A. C. Fraser

Contents of the News Letter

I.	Secretary's note .....	Page 1
II.	Editorial Policy of Genetics .....	Page 3
III.	General News Items .....	Page 4
IV.	Miscellaneous Co-op Items .....	Page 49
V.	Maize Publications .....	Page 50
VI.	New Genes .....	Page 56
VII.	Maps .....	Pages 28 & 35.

## II. Editorial Policy of GENETICS

It will doubtless interest maize geneticists to know the editorial policy of GENETICS concerning the symbolizing of genes, linkage groups and chromosomes of maize. The present policy has been in use for sometime and seems to be satisfactory.

Arabic numerals are used to designate both linkage groups and chromosomes.

Literal superscripts are used to represent different members of an allelic series.

No subscripts are used to represent different genes which give similar phenotypes. The numeral shall be raised to the same level as the rest of the symbol, i.e.  $\underline{v}^3$  and not  $\underline{v}_3$ . The first member of such a series shall be designated only by the literal symbol without the accompanying numeral "one" e.g.  $\underline{bm}^1$  and  $\underline{al}^1$  shall be simply  $\underline{bm}$  and  $\underline{a}$ . This will prevent the confusion which would result from such symbols as  $\underline{a}^1$  and  $\underline{al}^1$  if the numeral "one" was used with  $\underline{a}$  but not as a subscript.

All gene symbols are italicized but the symbols T, Df and In representing translocations, deficiencies and inversions, respectively, are not italicized.

M. M. Rhoades

III. General News Items

California Institute of Technology,  
Pasadena, California

1. Cherry pericarp - An allele of R has been found in Pueblo Indian maize in which cherry pericarp color is associated with colored aleurone (i.e. R<sup>ch</sup>). It has been tested in back crosses to r-tester.
2. Long inversion on chromosome 2 - The inversion is well out toward the end of each arm, thus inverting four-fifths or more of the chromosome. Tests place the left break between gl2 and B, the right break far beyond v4 but in the v4-ch interval. In the homozygous inversion the map order is lg-gl2-v4-B-ch. Data on map distances are as follows:

	<u>Total</u>	<u>Crossovers</u>	<u>Percent</u>
lg-v4	851	321	37.7
gl2-v4	828	303	36.6
v4-B	2425	1006	41.5
B-ch	1205	300	24.9

3. Position of ba2 - A backcross culture homozygous for the long inversion but heterozygous for B, ba2 and v4 suggest that ba2 lies between B and v4. The data are

<u>B</u>	<u>v4</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1.2</u>
ba2		36 36	29 16	5 10	5 5

E. G. Anderson

Columbia University, New York City

1. Additional data on the location of Dt.  
In the News Letter of March 5, 1940, backcross linkage data for Dt and Wx and F<sub>2</sub> data for Dt and Sh were given. These data showed 41 percent recombination between Dt and Wx and 27 percent between Dt and Sh. The order apparently was Dt Sh Wx and the recombination value with Sh indicated that Dt should fall close to Yg2 near the end of the short arm of chromosome 9. The following data on the location of Dt were obtained this past year.

<u>Dt Sh</u>	x	dt sh	gave	<u>Dt Sh</u>	<u>Dt sh</u>	<u>dt Sh</u>	<u>dt sh</u>	<u>Total</u>
dt sh				617	266	305	588	1776

Dt Sh - 32 percent recombination

	<u>Dt</u>	<u>Yg</u>	<u>Wx</u>		<u>dt</u>	<u>yg</u>	<u>wx</u>	selfed
Dt	Yg	Wx	-	1450	dt	yg	Wx	- 385
Dt	yg	wx	-	38	dt	Yg	Wx	- 223
Dt	Yg	wx	-	360	dt	Yg	wx	- 63
Dt	yg	Wx	-	36	dt	yg	wx	- 238

Total 2793

Recombination values: Dt Yg 11 %  
 Dt Wx 42 %  
 Yg Wx 37 %

	<u>Dt</u>	<u>Yg</u>	<u>Sh</u>	<u>Wx</u>		<u>dt</u>	<u>yg</u>	<u>sh</u>	<u>wx</u>	selfed		
Dt	Yg	Sh	Wx	-	387	dt	Yg	Sh	Wx	-	52	Total : 779
Dt	yg	Sh	Wx	-	7	dt	yg	Sh	Wx	-	84	Recombination values:
Dt	Yg	Sh	wx	-	59	dt	Yg	sh	Wx	-	2	
Dt	yg	Sh	wx	-	2	dt	yg	sh	Wx	-	49	Dt Yg 10 %
Dt	Yg	sh	wx	-	35	dt	Yg	Sh	wx	-	1	Dt Sh 27 %
Dt	yg	sh	wx	-	10	dt	yg	Sh	wx	-	3	Dt Wx 44 %
Dt	Yg	sh	Wx	-	15	dt	Yg	sh	wx	-	9	Yg Sh 24 %
Dt	yg	sh	Wx	-	3	dt	yg	sh	wx	-	61	Yg Wx 38 %
												Sh Wx 20 %

These data indicate that the order is Dt Yg Sh Wx and they place Dt ten units beyond Yg. Creighton found only one percent recombination between Yg and the terminal knob on the short arm of 9 so there is some discrepancy here. It should be noted that in selfing a Dt dt plant three classes of seed are obtained, i.e. the Dt Dt Dt, the Dt Dt dt and the Dt dt dt classes. In this latter class possessing a single Dt allele the mutation rate is so low that a considerable number of Dt dt dt seeds were classified as dt because no dots (mutations) are evident. This fact introduces some error into the recombination values but nevertheless the order should be as indicated. The locus of Dt therefore lies beyond Yg and must be very near the end of the short arm of chromosome 9.

2. Mutation of a to different alleles.

Four alleles at the a locus have been described by Emerson and Anderson. These four are a, a<sup>P</sup>, A and A<sup>b</sup>. Only a has its mutation rate increased by Dt. Mutation of a to five different alleles has occurred in a Dt stocks. One of the five is a mutation to an allele similar to a in its effect on aleurone, plant and pericarp color but differs in that it is stable with Dt. This allele has been found several times. It is of some interest that these so-called stable alleles are not completely stable with Dt; an occasional dot is found in the aleurone (about .4 dot per seed in Dt Dt Dt seed) but these dots are commonly much smaller than normally is the case indicating that the mutations when they do occur take place at a relatively late stage.

A second allele is one identical in all respects with A. Out of twenty mutations tested, which give deep aleurone color and purple plant color with B Pl, eighteen of them were to A.

A third allele was found in the group of twenty mutations mentioned above. This allele produces deep aleurone and purple plant color but gives a recessive brown pericarp color with P. This is a new allele.

A fourth allele is one like A in its effect on aleurone and plant color but produces a red-brown pericarp color that is recessive to the red color produced by A but is dominant to the recessive brown of a. This is a new, previously undescribed allele.

The fifth allele found is one resembling a<sup>P</sup> in its effect on aleurone and plant color but giving a recessive brown pericarp color instead of the dominant brown produced by a<sup>P</sup>. This is also a new allele.

The data on hand indicate that mutations of a to different alleles do not occur with equal frequencies. Although four new alleles have already been found it may be expected that additional new ones will appear as these experiments are continued.

No effect of Dt on any locus other than a has been found. This is true for the unstable pericarp allele (P<sup>VV</sup>) as reported before and also for the unstable waxy allele.



3. Further studies on the behavior of the abnormal tenth chromosome. (See last News Letter)

Plants heterozygous for a normal chromosome 10 and an abnormal chromosome 10, differing from the normal in that it has a piece of chromatin attached to the distal end of the long arm as described by Longley (1937, 1938), give an unusual type of behavior for these two homologues. When used as the female parent the percentage of the basal megaspores receiving the abnormal chromosome 10 is approximately 67 percent instead of the expected 50 percent. The R locus was found to lie extremely close to the end of the short arm; there being one percent of recombination between R and the distal end of the short arm. This placing of R would mean that d<sup>7</sup> does not lie beyond R as Singh's data indicated. Crossover studies in the g R region showed no reduction in plants heterozygous for the abnormal chromosome so it is likely that the low recombination value between R and the end is the true distance and is not due to a reduction from the true value caused by the presence of the redundant piece of chromatin. Earlier, it was suggested that competition among megaspores might account for the excess number of eggs carrying the abnormal chromosome 10, i.e. in a considerable number of cases non-basal megaspores with the abnormal chromosome would develop into the embryo sac at the expense of basal megaspores with normal chromosomes 10. Examination of 200 young embryo sacs showed, however, that the embryo sac always arose from the basal megaspore so the above hypothesis can be definitely ruled out. The alternative explanation is that selective segregation during the two meiotic divisions results in the abnormal chromosome passing to the basal megaspore more frequently than expected on a random basis. This explanation is being tentatively accepted. There is no sterility on the ears so abortion of ovules with the normal chromosome 10 does not account for the discrepancy. Since the R locus is so close to the end of the long arm it may be used to mark the normal and abnormal chromosomes thus making it possible to collect a large amount of data. When pollen from a plant heterozygous for the two chromosome types is used it is found that pollen carrying the abnormal chromosome is at a disadvantage when competing with grains carrying the normal chromosome. Using the R alleles to mark the two chromosomes it was found in one experiment that 59.7 of the functioning pollen grains carried the normal chromosome. Since comparable results were obtained when different normal chromosomes 10 were used against the abnormal chromosome 10 it may be argued that the redundant piece of chromatin is not wholly inert but possesses some genetically active material.

If selective segregation is the correct explanation of the unusual results obtained on the female side it is of some interest to give the following results. In the summer of 1939, 75.7 percent of the individuals in a

population of 4,501 coming from female plants heterozygous for the two chromosome types carried the abnormal chromosome 10. A duplicate of the seed planted in 1939 was planted in 1940 but only 62.8 percent of the individuals in a population of 4,922 possessed the abnormal chromosome. Since the two lots of seed were identical it appears that environmental conditions influence the segregation of the heteromorphic bivalent. This behavior is similar to that found in certain insects where temperature differences determine whether the X or Y chromosome is extruded into the polar bodies.

4. Singleton found a marked effect of the female parent on the functioning of sp1 pollen. Tests were made using four different r-testers to determine if a similar situation existed for sp2. The data obtained show no indication of an effect of these female parents on the functioning of sp2 pollen.
5. Jenkins gave the writer a selfed stock homozygous for mottled aleurone. He had found it extremely difficult to get a homozygous stock in which all seeds showed mottling since the mottled condition is extremely susceptible to the action of modifiers. This strain was turned over to the writer because it seemed possible that this case was similar to the a-Dt situation where one gene stimulates the mutability of another. The mottling proved to be caused by an r allele and was not due to another gene causing r to mutate. This allele is a new member of the R series. The mottled condition resembles most closely that produced by a single dose of R. It is not the same as the marbled and stippled alleles found in certain strains from Mexico and South America.

M. M. Rhoades

Connecticut Agricultural Experiment Station,  
New Haven, Connecticut

1. The "miniature seed" gene which markedly reduces the amount of tissue in the endosperm and embryo has no effect upon pollen tube growth and little or none upon plant growth. This is additional clear evidence that nuclear factors have a particular time for their action and are specific for certain tissues.
2. Wire stapling pliers are being used by many corn breeders to fasten paper bags on tassels and ear shoots in place of wire clips. The stapled bags are more secure and take less time to put on. The cost of the staples is about the same as for paper clips but more have to be used. (Stapler and staples made by Neva-Clog Products, Inc., Bridgeport, Conn.)

D. F. Jones

1. The mottling factor was given the symbol Mt in the Cornell Memoir 180. We have tested several stocks for mottling and have found all except one, C626 purple flint, to produce mottling in seeds of the constitution r r R. However C626 suppresses mottling when the pollen is applied to any r r stock. Hence, it seems to us that mottling is the recessive condition and no-mottling dominant. In 1940 evidence that the mottling factor mt and r are allelic, was obtained. The inbred C78 A C r pr mt (mottling) had been crossed by C626 A C R Pr Mt (no mottling). The F<sub>1</sub> hybrid was selfed and also pollen was applied to a r mt stock. One ear backcrossed gave 120 colored (none mottled) and 133 colorless. Three selfed ears gave 825 colored (no mottled kernels) to 268 colorless. Although these data are fragmentary they indicate that R and Mt are allelic or very closely linked, much closer than the 12% of crossing over originally calculated by Kempton. Further evidence will be obtained in 1941. I should be glad to receive additional stocks of A C R that are known not to produce mottling.

2. Status of Connecticut Sweet Corn Hybrids. Possibly the maize geneticists will be interested in an item regarding the practical phase of genetics. Sweet corn hybrids developed by the Connecticut Experiment Station are increasing in use each year. In 1940 approximately 500,000 pounds of seed were produced. This amount is sufficient to plant 50,000 acres or 10% of the total sweet corn acreage in the country. More than 95% of this production had C13 as one parent. This is an early inbred almost immune to bacterial wilt. The use of this inbred in the early hybrids has practically solved the bacterial wilt problem for early corn. This inbred was first distributed in 1936, 73 pounds being sold. Four years later it was used in the production of approximately 475,000 pounds of seed. The three principal hybrids comprising this inbred are Spancross (C4.13), Marcross (C6.13) and Carmelcross (P39. C13). Considerably more seed will be produced in 1941 as well as seed of three new hybrids, C23.P39, C27.P39, and C15 x C13. A letter of March 3 from one of the leading producers of hybrid sweet corn seed states that now Marcross (C6.13) is second to Golden Cross Bantam in poundage, and that all open pollinated varieties are falling off rapidly. Hybrid corn is one of the best examples of the contribution of Genetics to practical agriculture.

W. R. Singleton

1. Endosperm divisions have been examined further for determining types of aberrant mitoses in lines showing high rates of mosaic formation on the mature kernel. Evidence for a relation between aberrant chromosome

divisions and observed genetic changes was obtained from control pollinations. The female parent was the same in both crosses. The resulting seed of one cross gives a high frequency of variegation, whereas from the other pollen parent there are very few or no mosaics observed. Cytological study of the endosperm divisions from both pollinations (10-12 days after pollination) showed a mean difference in percent of aberrant divisions of 3.24 (3431 divisions observed.  $P = .01-.05$ ). This is a highly significant difference although many of the aberrant divisions are probably associated with changes that would not be observed genetically.

F. J. Clark

Cornell University, Ithaca, N. Y.

I am indebted to Dr. M. J. Murray for indispensable help in making the records to be reported here.

1. The order of br f - as noted in the News Letter of 1940, page 17, Bryan (News Letter 1938, page 5) had questioned the published order of the genes br and f. My report of last year was not wholly satisfactory because I was obliged to limit it to plants recorded as f. The records reported here were made last summer and are taken mostly from 5-point tests involving br f an and, in addition, gs or bm2 and another chromosome-1 gene or translocation. They are assembled here for more ready reference as 3-point tests (items 1 and 2 below)

Regions

<u>Item</u>	<u>Genes</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
1	br f an	512-376 888	26-25 51 4.4%	78-125 203 17.5%	12-3 15 1.3%	1157
2	br f an	1109-853 1962	26-44 70 3.2%	92-73 165 7.5%	7-2 9 0.4%	2206

<u>Item</u>	<u>Genes</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>	<u>Reference</u>
3	br f an	347	22 4.8%	77 17.0%	7 1.6%	453	N.L. '40, p.17
4	br f an	760	40 4.2%	156 16.3%	4 0.4%	960	L.S. '35, p.35
<u>Total</u>							
1-4	br f an	3957	183 3.8%	601 12.6%	35 0.7%	4776	
5	br f ad	975	47 4.0%	141 12.1%	3 0.3%	1166	L.S. '35, p.35
6	as br f	263	93 24.7%	21 5.6%	0	377	L.S. '35, p.35
7	br f Kn	446	21 3.3%	148 23.1%	25 3.9%	640	N.L. '38, p. 5

Item 2 (above) includes cultures involving translocations which apparently reduced crossing over. Both lots indicate the order to be br f an. Results reported in last year's News Letter (item 3) and various records published in the Linkage Summary (items 4-6) are included for comparison. The locus of ad is very near that of an and, therefore, to the right of br as is Kn also, while as is certainly to the left of br. Bryan's records are repeated in item 7.

It is obvious from these records that, in my material, f is to the right of br. Bryan's records do not agree with mine, but they are not wholly conclusive, because, on the assumption of either order of br f, the double crossovers are so nearly equal to the single crossovers in the short region.

2. Loci of chromosome-1 translocations. Further tests of the linkage relations of several chromosome-1 translocations have been made. The genes included in these tests are br f an and either gs or bm2.

These records indicate that T1-6a, T1-10a, T1-7b and T1-7c are to the left of br in the order given here with T1-6a relatively far from br and T1-7c relatively near it. T1-5a appears to be very near to and to the right of f, between it and an. T1-3d and T1-4 are between an and gs and relatively near an. Crossing over percentages between these several translocations and br, as reported here, are,

for the most part, in close accord with those reported by Anderson (N. L. 1938, p. 6). Agreement is good also between the placements reported here and Anderson's cytological observations, except for T1-7c.

Five-point Translocation Tests

Region	T1-6a : +	T1-10a : +	T1-10a : +	T1-7b : +	T1-7b : +
	+ : br	+ : br	+ : br	+ : br	+ : br
	+ : f	+ : f	+ : f	+ : f	+ : f
	+ : an	+ : an	+ : an	+ : an	+ : an
	+ : bm2	+ : gs	+ : bm2	+ : gs	+ : bm2
0	137	118	73	93	110
1	30	5	8	4	3
2	5	2	1	4	
3	34	14	18	3	7
4	101	55	52	17	59
1-2	1				
1-3	1	2	5	2	
1-4	17	5			
2-3	2	1	2		
2-4	6	1	10	1	
3-4	17	1	1	1	
1-2-3	1	2	1		
1-2-4				1	
1-3-4		1			
2-3-4					
1-2-3-4	—	—	—	—	—
Total	352	207	171	126	179

Percent recom- bina- tion	T-br	14.2	T-br	7.2	T-br	8.8	T-br	5.6	T-br	1.7
		T-f	17.3	T-f	8.2	T-f	9.4	T-f	8.7	T-f
	T-an	31.2	T-an	13.5	T-an	26.3	T-an	10.3	T-an	5.6
	T-bm2	48.4	T-gs	38.2	T-bm2	47.4	T-gs	23.0	T-bm2	38.5
	br-f	4.2	br-f	2.9	br-f	0.3	br-f	4.8	br-f	0
	br-an	17.9	br-an	10.1	br-an	18.7	br-an	9.5	br-an	3.9
	br-bm2	45.1	br-gs	37.7	br-bm2	44.5	br-gs	20.6	br-bm2	36.9
	f-an	14.5	f-an	10.1	f-an	17.0	f-an	4.8	f-an	3.9
	f-bm2	46.2	f-gs	38.7	f-bm2	46.2	f-gs	19.1	f-bm2	36.9
	an-bm2	39.9	an-gs	30.4	an-bm2	40.8	an-gs	15.9	an-bm2	33.0

	Tl-7c	:	+		+	:	br		+	:	br		+	:	br		+	:	br	
		+	:	br		+	:	f		+	:	f		+	:	f		+	:	f
Region		+	:	f	Tl-5a	:	+		+	:	an		+	:	an		+	:	an	
		+	:	an		+	:	an	Tl-3d	:	+		Tl-3d	:	+		Tl-4	:	+	
		+	:	gs		+	:	bm2		+	:	gs		+	:	bm2		+	:	bm2

0	160		142		119		59		185
1	1		5		5		2		4
2	9		6		4		4		4
3	4				1				4
4	20		72		9		36		125
1-2	3								
1-3			1						
1-4	6		5		1		1		3
2-3			1						1
2-4	2		3		1		1		3
3-4	1		2		1		2		8
1-2-3	1								
1-2-4									
1-3-4									1
2-3-4							1		
1-2-3-4									
Total	207		237		141		106		338

	T-br	2.9	br-f	8.8	br-f	4.2	br-f	2.8	br-f	2.4
	T-f	6.3	br-T	9.4	br-an	7.8	br-an	8.5	br-an	3.6
Percent	T-an	12.6	br-an	26.3	br-T	9.2	br-T	9.4	br-T	7.7
recom-	T-gs	16.9	br-bm2	47.4	br-gs	13.4	br-bm2	40.6	br-bm2	40.5
bina-	br-f	6.3	f-T	0.3	f-an	3.5	f-an	5.7	f-an	2.4
tion	br-an	10.6	f-an	18.7	f-T	4.9	f-T	6.6	f-T	5.9
	br-gs	17.9	f-bm2	44.5	f-gs	17.6	f-bm2	39.6	f-bm2	40.4
	f-an	5.8	T-an	17.0	an-T	1.4	an-T	2.8	an-T	4.1
	f-gs	14.5	T-bm2	46.2	an-gs	8.5	an-bm2	35.8	an-bm2	40.2
	an-gs	15.0	an-bm2	40.8	T-gs	8.5	T-bm2	38.7	T-bm2	41.4

3. Tassel-seed 3 and tassel-seed 6 - The results of tests reported in the 1940 News Letter by Lindstrom (p. 25) and by me (p. 16) suggest that Ts3 is between an and gs, while Ts6 is near bm2 and probably to the right. The records reported by Lindstrom, tho conclusive in showing that Ts6 is near bm2, are inconclusive with respect to whether Ts6 is to the right or the left of bm2. Where one region is as long as that between br and bm2 and the other as short as bm2 to Ts6, double crossovers are apt to be as frequent as are singles in the short region. My last year's records, involving an and either gs or bm2 are unsatisfactory because of the wide differences between complementary classes of crossovers. The records

presented here are equally unsatisfactory for the same reason. They are given first in a table as 4- and 5-point tests with complementary crossover classes combined.

Four- and five-point tests with Ts3 and Ts6

Regions	+ : br + : f + : an Ts3 : + + : gs	+ : br + : f + : an Ts3 : + + : bm2	+ : br + : f + : an Ts3 : +	+ : br + : f + : an + : gs Ts6 : +	+ : br + : f + : an Ts6 : + + : bm2	+ : an + : gs Ts6 : + + : bm2
0	88	68	104	82	26	152
1	4	7	11	6	2	56
2	21	15	22	32	12	35
3	21	14	19	35	22	11
4	33	30		31	1	
1-2			4	1	1	16
1-3			1	5		1
1-4		2		2		
2-3			5	3	3	
2-4	3	9		16		
3-4	16	5		19		
1-2-3			4			
1-2-4				1		
1-3-4				1		
2-3-4	2	1		1		
1-2-3-4	—	—	—	—	—	—
Total	188	151	170	235	67	271

Percent Recombination

br-f	2.1	br-f	5.9	br-f	11.9	br-f	6.8	br-f	4.5	an-gs	26.9
br-an	16.0	br-an	22.5	br-an	22.9	br-an	28.1	br-an	25.4	an-Ts6	33.6
br-Ts3	34.6	br-Ts3	34.4	br-Ts3	33.0	br-gs	46.8	br-Ts6	53.7	an-bm2	38.0
br-gs	42.0	br-bm2	44.4	f-an	20.6	br-Ts6	45.5	br-bm2	55.2	gs-Ts6	19.2
f-an	13.9	f-an	16.6	f-Ts3	27.1	f-an	23.0	f-an	23.9	gs-bm2	22.9
f-Ts3	32.5	f-Ts3	28.5	an-Ts3	17.1	f-gs	46.8	f-Ts6	52.2	Ts6-bm2	4.4
f-gs	41.0	f-bm2	41.1			f-Ts6	45.5	f-bm2	53.7		
an-Ts3	20.8	an-Ts3	13.3			an-gs	27.2	an-Ts6	37.3		
an-gs	30.3	an-bm2	36.5			an-Ts6	39.6	an-bm2	33.8		
Ts3-gs	28.7	Ts3-bm2	31.2			gs-Ts6	30.2	bm2-Ts6	1.5		



The data, as presented in the accompanying table indicate that Ts3 is between an and gs, and Ts6 near bm2 and to its left. The unsatisfactory nature of the data is well shown when arranged as 2-point tests involving an and either Ts3 or Ts6, as follows:

$\frac{+ \text{Ts3}}{\text{an} +}$	+Ts3	++	anTs3	an+	Total
	64	39	0	85	188
	56	16	4	75	151
	<u>63</u>	<u>25</u>	<u>4</u>	<u>78</u>	<u>170</u>
Total	183	80	8	238	509

Total Ts3 = 191, non-Ts3 = 318  
 " an = 246, non-an = 263

$\frac{+ \text{Ts6}}{\text{an} +}$	+Ts6	++	anTs6	an+	Total
	77	80	13	65	235
	24	16	9	18	67
	<u>112</u>	<u>63</u>	<u>28</u>	<u>68</u>	<u>271</u>
Total	213	159	50	151	573

Total Ts6 = 263, non-Ts6 = 310  
 " an = 201, non-an = 372

In the cultures involving Ts6, an was strikingly and Ts6 somewhat deficient. In the Ts3 cultures, an was slightly and Ts3 decidedly deficient. The striking feature of these records, however, is the discrepancy between complementary crossover classes, ++ to an Ts6 being over 3 to 1 and ++ to an Ts3 10 to 1.

It seems likely that some, perhaps many, plants recorded as +Ts6 may have been an Ts6. The tassels were not removed and in many cases, ears failed to develop, and it is difficult to determine an from the tassels alone of Ts6 plants. With Ts3 and an, experience of some years has led me to question whether there may be an inhibiting effect such that, when heterozygous Ts3 and homozygous an are together, both characters generally fail to develop. But no adequate test of such a notion has been attempted.

4. The locus of vestigial - A 5-point test of Vg with br f an bm2 has given the following results from the F<sub>1</sub> genotype

$\frac{+ \text{Vg} + + +}{\text{br} + \text{f an bm2}}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>1-3</u>	<u>1-4</u>	<u>2-4</u>	<u>3-4</u>	<u>Total</u>
164	5	1	42	103	4	2	1	15	337

Per cents of recombination are as follows:

br-Vg 3.3, br-f 3.9, br-an 19.6, br-bm2 44.8, Vg-f 0.6,  
Vg-an 18.4, Vg-bm2 44.8, f-an 18.1, f-bm2 45.1, an-bm2 35.9.

Sprague (Jour. Heredity 30: 143-145, 1939) has shown that Vg is between br and f, a locus supported by the data presented here. I cannot, however, agree with his suggested order of f Vg br bm2. His three-point test, involving a very short region with a very long one, is unsatisfactory as pointed out by him, but the data as reported suggest the order br Vg bm2. His four-point test, again involving a very long region with very short ones, as a whole indicates the order suggested by him, but, when bm2 is disregarded, the resulting three-point data are:

$\frac{+ \text{ Vg } +}{\text{br } + \text{ f}}$	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
	53	2	6	0	61

These data, obviously, afford no evidence of the order of the genes except that Vg is between br and f.

5. Tests of knotted, perhaps involving an inversion - Bryan (N.L. 1938, p. 5) reported Kn in this relation: br 7.2 f 27.0 Kn 24.1 Bm2. My last year's report (N.L. 1940, p. 17) was: an 22.5 Kn 25.2 Bm2 and an 22.6 Kn 9.6 gs. These 1940 reports were condensed from five-point tests including also br and f. In the five-point records given here those reported last year are combined with those obtained last summer.

Tests involving Kn

	+ : br		+ : br		+ : br
	+ : f		+ : f		+ : f
Regions	+ : an		+ : an		+ : an
	Kn : +		Kn : +		Kn : +
	+ : gs		+ : bm2		
0	82		140		107
1	4		4		
2	3				
3	23		46		44
4	6		39		
1-2	7		2		
1-3	1		1		
1-4			2		
2-3	1				
3-4	1		19		
1-2-3	4		1		
1-2-4	<u>1</u>		<u>2</u>		
Total	133		256		151

	br-f	12.8	br-f	4.7	br-f	0
	br-an	6.8	br-an	2.7	br-an	0
Per cent	br-Kn	26.3	br-Kn	28.1	br-Kn	29.1
Recom-	br-gs	30.8	br-bm2	35.9	f-an	0
bination	f-an	12.0	f-an	2.0	f-Kn	29.1
	f-Kn	27.1	f-Kn	27.3	an-Kn	29.1
	f-gs	30.1	f-bm2	35.1		
	an-Kn	22.5	an-Kn	26.2		
	an-gs	27.1	an-bm2	35.5		
	Kn-gs	6.0	Kn-bm2	24.2		

It is obvious from these records that Kn is between an and gs and relatively near the latter. The recombination percentages for regions to the right of an are about those usually observed, but those in regions between br and an are far from normal. These differences in the two regions to either side of an are seen more readily perhaps when the data are assembled as three-point tests:-

<u>+ Kn +</u>	<u>0</u>	<u>1</u>	<u>2</u>	<u>1-2</u>	<u>Total</u>
an + gs	96	29	7	1	133
		21.8%	5.3%	0.8%	
<u>+ Kn +</u>	146	47	43	20	256
an + bm2		18.4%	16.8%	7.8%	
<u>+ + +</u>	507	12	4	17	540
br f an		2.2%	0.7%	3.1%	

The data of the br-f-an array might indicate that the order of genes is not that given here. But the only order suggested by these data, on the basis of the usual criteria of three-point tests, is br-an-f. Since the chromosome-1 tester stocks employed in these tests are the same ones used in other tests (sections 1 and 2 of this report), no such assumption is tenable. It seems more likely that we are here dealing with a heterozygous inversion involving much of the region from br to an. This assumption is supported by the marked reduction in observed percentage of recombination, particularly in the f-an region, and by the appearance of more double crossovers than of singles in either region.

6. Tests of miscellaneous genes with chromosome-1 markers - Twelve genes, whose linkage had not been previously determined, have been tested with several chromosome-1 markers. Tests of some of these were reported last year (N. L. 1940, p. 18) with only one clear indication of linkage, namely, bm2 with v19. The data given in the accompanying table were obtained from F<sub>2</sub> cultures of last summer. Percentages of recombination have been calculated with the help of Immer's tables. Many of the relatively large deviations from 50 per cent are not statistically significant. Percentages that show significant deviations from 50, or deviations on the border line of significance, are accompanied by their respective probable errors. The tests of this year are inadequate for much of the short arm of chromosome 1, since, except for sr, the markers used are all in the long arm.

The frequency arrays for bm2 and v19 from last year's report and from records of last summer are:

	$\frac{+ \quad \underline{bm2}}{\underline{v19} \quad +}$	++	<u>bm2</u> +	+ <u>v19</u>	<u>bm2</u> <u>v19</u>	Total
N. L. 1940, p.19		42	25	21	0	88
New cultures		<u>60</u>	<u>42</u>	<u>37</u>	<u>6</u>	<u>145</u>
Total		102	67	58	6	233

Recombination percentage =  $16 \pm 4.3$

It seems clear that v19 is in chromosome 1. Attempted tests with gs have failed. It is not known, therefore, whether v19 is to the left or the right of bm2.

Tests of non-linked genes

Chromosome-1 markers

New genes	<u>sr</u>	<u>msl7</u>	<u>br</u>	<u>f</u>	<u>an</u>	<u>gs</u>	<u>bm2</u>
at	58	-	49	54	52	43	42
bm3	50	-	57	48	57	41	-
g2	51	-	40	46	46	36±4.5	34±3.7
ms5	60+	-	38±4.2	47	37	41	53
ms6	55	-	41	41	34±5.9	35	42
ms9	36	-	32±7.1	-	-	-	-
msl10	-	-	47	37±4.9	44	-	52
msl13	53	-	46	49	49	60+	-
msl14	-	-	41±4.2	41±4.2	40±4.3	49	-
na2	48	55	-	-	38	40	-
yg3	46	-	47	47	38	-	38
vl9	42	-	44	55	38	-	23±5.3
*vl9	-	<u>F</u> 52	58	-	51	-	<19

\* From N. L. 1940, p. 18

R. A. Emerson

1. Some additional data on chromosome VII. Field counts.

(a)  $\frac{+ + +}{v5 \text{ ra gl}} \times v5 \text{ ra gl}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>1 &amp; 2</u>	<u>Total</u>
686	52 6.7%	41 5.2%	3 .4%	782

(b)  $\frac{+ + +}{ra \text{ gl ij}} \times ra \text{ gl ij}$

<u>0</u>	<u>1</u>	<u>2</u>	<u>1 &amp; 2</u>	<u>Total</u>
169	10 4.6%	35 16.1%	4 1.8%	218

(a)  $v5 \ 7 \ \frac{ra \ 6}{ra \ 6} \ \frac{gl}{gl} \ 18 \ ij$

(c) Antherless (at), unlinked, is very clear cut and gives sharp classifications in the field. An  $F_2$  involving at, v5, and ra showed at to be independent of the other two genes.

(d) In making notes on v5, it is best not to wait until toward the close of the growing season. A number of plants often develop stripes only on the lowest leaves. These should be marked, since if seasonal or soil conditions are adverse, the lower leaves may die and such plants will be classed as green.

A. C. Fraser

(a) Any virescent-1 stock coming from the Co-op or from me must be used cautiously; there seems to be another virescent mixed in. Can anyone send me a stock known to be v1?

(b) In a backcross of about 400 seedlings the alien virescent mentioned above showed no linkage with wx. Of the 182 virescents in this backcross, 108 of them showed normal green stripes. This is suspiciously close to a 9:7 ratio.

(c) A number of chlorophyll types (g, w, l and v) are being inbred by repeated backcrossing to the same inbred. The purpose is to get genetically uniform types for physiological study. Seed of the various types (twice backcrossed) are available to any one desiring it.

(d) In connection with the above mentioned inbreeding program, I should like very much to obtain seeds of two or three different pale greens (esp. lethal ones) and of any other green seedlings that die. Will several of you who have such stocks send in a few seeds, please?

(e) Can anyone send me some g3 seed? That in the Co-op seems not to carry g at all.

(f) A summary table of all my slit blade cultures is given below to show some of the abnormal ratios obtained. The division of the  $F_2$  cultures into groups is arbitrary and hard to justify except on the grounds of convenience. Note that both B.C. &  $F_2$  totals show too many Sb plants.

	<u>Sb</u>	<u>sb</u>	<u>Ratio</u>
Sum of B.C.	495	384	1.29:1
Sum of F <sub>2</sub> (less than 4:1)	3083	1001	3.08:1
Sum of F <sub>2</sub> 4:1-7:1	2138	458	4.67:1
Sum of F <sub>2</sub> (greater than 7:1)	<u>633</u>	<u>69</u>	<u>9.2:1</u>
Sum of all F <sub>2</sub>	5854	1528	3.83:1

(g) Small F<sub>2</sub>'s last summer showed no linkage of bm3 or wa to sh, wx, or gl4; nor of sb to lg2, Ts5, j, sh, wx, gl4 or gl. Several attempts have failed to show any linkage of my gl4 to yg, sh, or wx. (This is not the gl4 of Burnham.)

John Shafer

Cornell University and the

United States Department of Agriculture

1. Trisomic stocks. An effort was made during the summer of 1940 to assemble a set of all the known trisomic stocks, to produce stocks of those which were missing, and to make appropriate crosses to build up reserve stocks of all of the trisomes for the future use of cooperators. It was found that seed was available of all of the trisomes except one and four. Individual trisomic plants lacking B chromosomes were selected by actual chromosome counts in each of the eight available stocks. Genetic tester stocks were also examined cytologically in an effort to get together two complete sets of testers lacking B chromosomes, each set to have different endosperm or seedling genes with one good gene in each chromosome. These two sets of testers to be used for crossing alternately with the different trisomic stocks in order to maintain vigorous, genetically identifiable trisomic stocks for general use. Unfortunately, several of the present trisomic stocks are very much lacking in vigor and uniformity and are segregating for various lethals, with the result that although we started the season with five or more trisomic seedlings in each of the eight stocks, at

the end of the season we had not more than one or two poor trisomic ears from two or three of the stocks. But from the other trisomic stocks we have anywhere from 3 to 10 good trisomic ears.

It is especially important in working with trisomic plants to have vigorous, uniform stocks. A number of the trisomic types are inherently weak. In fact the trisomic plants in most of the trisomic stocks apparently come chiefly from the smaller seeds and are apt to be weaker than their disomic sibs in the seedling stage; at least it was our experience that from 75 to 90 percent of the smallest seeds from trisomic ears of the 8 different trisomics we worked with produced trisomic individuals. It would be highly desirable also to maintain a high degree of uniformity of plant type in the trisomic stocks in order to be able to pick as many as possible of the trisomic individuals on the basis of their phenotypic appearance. As an experiment in this direction, we crossed a number of different trisomic plants with pollen of several different inbreds which were known to contain no B chromosomes to see what the trisomics would look like in the various F<sub>1</sub> populations. In our cultures last summer we could, with reasonable accuracy, distinguish the trisomic plants from their disomic sibs in our stocks of numbers 5, 8, and 9, with indications that at least several others could be detected phenotypically in more uniform material.

Another procedure for obtaining very uniform trisomic stocks is to isolate the various trisomes from the selfed progeny of triploids obtained by intercrossing diploids and tetraploids derived from a common inbred parent. In attempting to do this we have learned from experience that it is advisable to start with a very vigorous inbred; otherwise the triploid progenies from which the trisomes must be isolated are rather weak and not too satisfactory to work with.

It is expected that the two missing trisomes, numbers one and four, will be available for distribution next year. Selfed ears showing trisomic ratios for su and similar material segregating for bm2 were obtained last summer from individual plants in triploid progenies known from chromosome counts to have from one to three extra A chromosomes.

Technical assistance for much of the routine cytological work in connection with these trisomic stocks was furnished by the Maize Cooperation.

2. Genetics of the B chromosomes and their derivatives.  
The B chromosomes are by no means genetically impotent as was formerly believed and is still being reiterated in current literature on maize cytogenetics. It is true that in small



numbers they appear to produce no discernible effects; they are transmitted more readily than any known A chromosome fragments through both pollen and egg and their presence in genetic stocks seems not to have interfered with genetic analysis of mendelizing characters. But this does not necessarily mean that they are genetically inert or devoid of hereditary potentialities. In summarizing my data on the behavior of the B chromosomes that have been accumulated over a period of years in attempts to solve the enigma of their origin and fundamental nature, there are some rather interesting conclusions that can be drawn with reasonable assurance that they may mean something.

Although individual plants with relatively few B chromosomes are indistinguishable from their no B sibs, higher numbers of B chromosomes produce marked effects: More than 13-15 cause some reduction in fertility; more than 23-25 cause a marked reduction in both fertility and vigor; more than 30 occur rarely and the plants are very weak, produce mostly aborted pollen and set little or no seed.

In reciprocal crosses of plants with 1 B x 0 B, the B chromosome is transmitted about equally well by the pollen and egg to about one-third of the progeny. Exceptional plants with 2 or more Bs appear in these crosses more frequently when the B is carried by the pollen parent.

Reciprocal crosses involving 2, 3, and 4 Bs with no B plants are markedly dissimilar: when the Bs are carried by the seed parent, the numbers in the progeny tend to be intermediate between the parental numbers, but when they are carried by the pollen, the 0 B, 2 B and 4 B classes are predominant. This was true of both meiotic and somatic counts, the total number of individuals involved in these crosses being 398.

The B chromosome plants do not breed true for any given number of B chromosomes, regardless of whether the number is odd or even. When selfed, or when plants with the same number of Bs are sib crossed, less than one-third of the progeny have the parental number of B chromosomes. Various numbers are represented in the populations, the mean number being approximately the same or slightly less than the parental number for plants with from 1 to 17 B chromosomes. The total number of plants studied in these selfed and sib-crossed progenies was 988.

Numbers higher than either parent appeared frequently in crosses between plants with different numbers of Bs ranging from 1 to 20, but in the progenies of plants with more than 20 Bs they appeared less frequently. The mean

number of Bs in the progenies of plants with from 1 to 10 Bs when intercrossed was essentially the same as the mean parental number; with higher parental numbers whose means ranged from 11 to 20.5 the mean number in the progeny was less than the parental mean by from 10 to 30 percent. These data were from 65 cultures which included a total of 983 plants.

Irregular assortment in meiosis, somatic nondisjunction and double division in somatic mitosis possibly due to irregular timing of centromere division, are some of the characteristics of B chromosome behavior responsible for the extreme variation in number observed in the progenies of B chromosome plants. Although the number of Bs in an individual plant is not necessarily the product of the contributing gametic numbers since changes in number may occur in outogamy due to mitotic irregularities there is little evidence of selective elimination of gametes except among very high B chromosome plants. There is no evidence from these experiments on the breeding behavior of the Bs to support the contention of Darlington, presented in a recent discussion of "the activity of the inert chromosomes" (sic) in maize, that there exists a population pressure maintaining an equilibrium distribution of the B chromosomes at relatively low levels in different stocks. In fact the results suggest that higher numbers than are present in most natural populations would readily be tolerated. It seems quite possible that the B chromosomes are on the increase in at least some varieties of maize.

No disturbed ratios were obtained from  $F_2$  and backcross data involving B chromosome stocks crossed with 43 known genes distributed throughout the 10 linkage groups. The linkage relations of these genes are indicated on the accompanying map in which the tested genes are underscored. This map also includes tentative assignments of centromere positions based on information kindly furnished by Anderson, Rhoades and Burnham, the more definitely placed centromeres being represented by an oval drawn with a solid line and those less definitely placed being similarly represented by a dotted line. Disturbed ratios have been obtained with the gene sb, together with some evidence that the reduction in the number of recessives in the segregating progenies was proportional to the frequency of the B chromosomes. (See also Shafer's discussion of sb ratios in this News Letter) This would be expected if the B chromosomes carried the normal Sb allele. Unfortunately the linkage relations of sb are unknown.

These gene tests involving the B chromosomes have an important bearing on the fundamental question of the origin of the B chromosomes. If the centromere positions indicated on the linkage maps are even approximately correct, it is

apparent that the tested genes giving undisturbed ratios in the presence of B chromosomes are distributed among 17 of the 20 normal A chromosome arms. Only 3 arms, the short arm of 8 and 10 and the long arm of 9, do not include at least one tested gene. If a test of one or a few genes were sufficient to exclude a particular chromosome arm from further consideration as the source of the B chromosome, the problem of the origin of the Bs would be much simplified, but in my opinion such tests would not be sufficient. It is altogether possible, in my opinion, that only part of a particular arm is represented in the B chromosome. For example, it might consist of an A chromosome centromere plus some adjacent euchromatin, but not necessarily all of the euchromatin of any particular arm, and in addition heterochromatin from the same or some other chromosome. This suggestion as to the possible mode of origin of the typical B chromosome may seem unnecessarily involved. However, there is a rapidly accumulating body of evidence that the chromosome is not as stable a unit as it was once thought to be. In fact it is surprising that chromosomes maintain any individuality whatever as separate and distinct morphological entities for extended periods of time in the light of the numerous types of reorganization to which they are subject. Furthermore, the typical B chromosome has a distinctive prophase morphology unlike that of any one region of similar length among the A chromosomes ordinarily present in existing types of maize. This is not an off-hand statement based on casual observation, but is the conclusion arrived at after making a very critical survey of the meiotic prophase morphology in well over fifty varieties of maize representing all of the known types of flour, flint, dent, pop and sweet corn, a survey that was conducted primarily to throw light on the origin of the B chromosomes. This does not mean that there may not be in existence today types of maize containing an A chromosome or segment thereof that is identical with the B chromosome. Or it may be that such a chromosome existed in primitive strains of maize that are no longer in existence. The fact that the B chromosome ordinarily does not synapse with any of the A chromosomes suggests that it is not of recent origin, but synaptic behavior alone should not be considered as proof of this assumption.

There is the further possibility that hybridization with relatives of maize may have been involved in the origin of the Bs, but in my opinion the possibilities of a more direct mode of origin are by no means exhausted.

In a further search for clues to the origin of the Bs, it would seem highly desirable to examine additional types of maize especially from regions where primitive stocks may still be in existence. Also more extensive tests of known genes should be made in the search for alleles of B

chromosome genes; possibly Sb is one such allele, but additional cytological and genetical tests are needed to establish this. If the suggestion made above concerning the origin of the Bs is valid, and if there is a tendency in maize as in *Drosophila* for heterochromatic regions to be populated with fewer genes than are the euchromatic regions, the best chance of finding alleles of known genes in the B chromosome would be to test especially genes lying near the centromeres in the linkage maps. These genes may actually be an appreciable distance cytologically from the centromeres. But if the proximal euchromatic region of the B is in approximately the same relative position with reference to the centromere that it was in the A chromosome from which it originated, some of these nearby genes should be represented by alleles in the euchromatin of the B, which constitutes approximately one-third of the total length of the chromosome. A certain number of these nearby genes have already been tested as indicated on the linkage map. An especially good test involved chromosome 5 in which Rhoades' data from his telocentric fragment has given us the best evidence we have of the location of a particular centromere relative to neighboring genes. His evidence tells us that the closely linked genes, bm and bt, are definitely on opposite sides of the centromere. These two genes, as well as a2 in the short arm and bm, pr and v2 in the long arm of this chromosome gave normal backcross and  $F_2$  ratios in the presence of B chromosomes. Thus these tests would seem to exclude the possibility that the regions in which they are located are involved in the makeup of the B chromosome.

A notable characteristic of the B chromosomes is that they are like the A chromosomes in being susceptible to breakage, with the resultant loss of acentric segments of chromatin or rearrangement of parts. But there is this distinction that the supernumerary B chromosomes can undergo a greater variety of such morphological changes than can the A chromosomes without deleterious effects, and their monocentric derivatives can be readily maintained in culture for further study. Over a period of years a considerable number of such B chromosome derivatives have arisen in my stocks, the first of these being the C chromosome that was described back in 1928. Since most of these elements have been detected in root tip figures being examined for chromosome count, they have been grouped for convenience in four reasonably distinct size classes or types, based on their appearance in the somatic metaphase. These include (a), the C type that is somewhat shorter than the B chromosome but definitely elongated in contrast to (b), the D type that is essentially spherical with a diameter roughly equivalent to the diameter of an ordinary chromosome, (c), the E type that is of approximately the same size as the undivided satellite of chromosome 6, and (d), the F type that is distinctly smaller than the E type and in fact is

only slightly above the lower limit of visibility of the photomicroscope.

On the basis of this classification there can be no additional new types of still smaller B chromosome derivatives, at least not until the electron microscope is utilized in the study of chromosomes. (Incidentally, this series of chromosome types from B to F, if interpreted in the reverse order, makes a very convincing demonstration of the de novo origin of chromosomes.) In the meiotic prophase morphological distinctions within these size groups can be detected and may be classified accordingly.

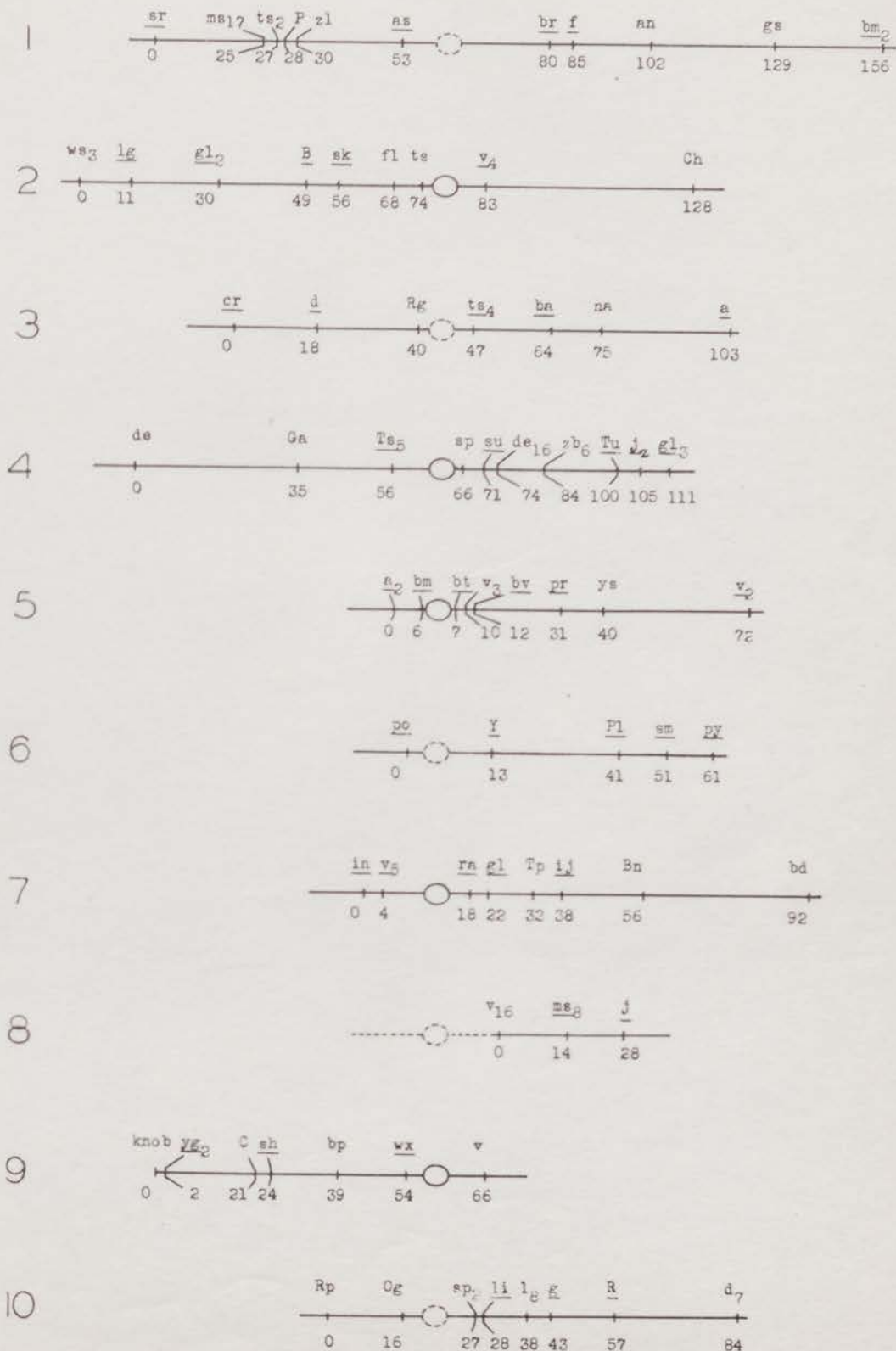
The B chromosome derivatives are proving very useful in studies of the relative genetic potency of different parts of the B chromosome. Data are available at the present time which suggest that the sterility-inducing effects of the B chromosome are to be attributed to factors localized chiefly in the proximal euchromatic region of the chromosome.

There is some evidence that other mutant derivatives of the typical B chromosome, such as extensions of the long arm or additions to the rudimentary short arm, occur from time to time, but these are less easily detected in somatic figures because of their greater similarity to the shorter A chromosomes.

The occurrence of distinctly dibranched B type chromosomes in maize has been described from somatic figures by Darlington and others in recent years. But in these cases the position of the centromere has very probably been misinterpreted. The typical B chromosome when viewed in somatic metaphases often exhibits what appears to be a subterminal constriction, especially after fixation with fluids that shrink the chromosomes. This is not a true centric constriction but is actually the weakly chromatic region between the proximal knob adjoining the centromere and the distal heterochromatic portion of the chromosome. This interpretation is quite obvious if one is familiar with the pachytene structure of the B chromosome and follows the transformation accompanying the shortening of the B chromosome during the late prophase and early metaphase of the first microspore division where the distinction between euchromatin and heterochromatin in these stages is clearly apparent in good preparations. Many pachytene figures of the typical B chromosome do, however, show the presence of a rudimentary short arm consisting of a very few small chromosomes. This arm is often folded back against the proximal knob on the opposite side of the centromere, thus making the centromere appear truly terminal.

L. F. Randolph

MAIZE LINKAGE MAPS  
WITH TENTATIVE ASSIGNMENTS OF CENTROMERE POSITIONS



Illinois Agricultural Experiment Station,  
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1. In further studies on genes h (starchy endosperm) and fl2 (floury endosperm), h was found to be hypostatic to sul and wx; and fl2 hypostatic to sul. Gene h is linked with fl2 with 4% crossing-over, and with dl, with 25% crossing-over. This puts both genes in chromosome 3, but the exact loci are not yet determined. If it is assumed that h is approximately at 60, then fl2 would be near ts4 or Rg.

W. J. Mumm

1. A sugary type of endosperm which was discovered at this Station several years ago appears to be identical with su2 as indicated by crosses. In inbred Os 426, one of our hybrid corn producers, Robert Bear, Decatur, Illinois, found an ear segregating for yellow vs. white endosperm, and normal vs. viviparous kernels. All the normal kernels were yellow and all the white viviparous. The gene for vivipary involved is likely vp5 which Doctor Lebedeff reported in the 1940 News Letter. Another of our hybrid corn producers, Royal Oakes, Bluffs, Illinois, discovered a dwarf in a double cross. This dwarf as grown in 1940 was 56 cm. high; tassel, large, spreading, and productive of pollen; and leaves large and dark green giving a vigorous appearance to the plant. Crosses indicate the gene involved is not dl, and the new dwarf does not answer the description of other dwarfs listed in Cornell Memoir 180.

C. M. Woodworth

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1. A valuable mutation. The ministry of agriculture in Venezuela has received numerous requests from the farmers for a variety of sweet corn which would do well under tropical conditions. There has been no way of filling these requests, however, because Venezuela has no sweet corn of its own, and all the imported varieties have failed to give desirable results.

There are at least two ways of getting good sweet corn for this country. One is to import unadapted varieties of sugar corn and cross them with the adapted varieties of starchy corn and continue selfing and back-crossing until the sugary character becomes established in an adapted variety. Another method is to make a large number of selfs in the best varieties of starchy corn and watch for the appearance of sugary as a result of a mutation. This is the procedure that was chosen, mainly because inbred lines were needed anyway for the production of hybrids. In September, 1939, 135 varieties of open-pollinated corn from various countries were planted to select the best ones and to make selfs.

During the first two generations of inbreeding, there were no mutations to sugary in approximately 3,000 selfs. In the third generation, however, in which there were approximately 1,500 selfs, two ears segregated for sugary. One of these was in the best inbred line that had been developed from an open-pollinated variety from Cuba and is probably sugary-1 (su). It segregated 216 Su to 72 su. The other sugary appeared in another inbred line from the same source and may be su<sup>am</sup>. This ear had 478 kernels of which 10 were very sugary, 106 had a dull endosperm, and in the remaining 362 kernels there was a continuous gradation from slightly dull to clear endosperm. Test for allelism with known stocks of su and su<sup>am</sup> will be made.

Some of the seeds from these two ears have been planted and there should be no question about the development of suitable sweet corn varieties in the near future.

2. Late plants. Two second generation inbred lines segregated for late-maturing plants in 1940, but there were numerous differences between the late segregates of one culture and those of the second culture. Inbred line number 40-156 consisted of 10 plants of which 8 grew normally and produced ears, one grew about 7 months without shedding pollen, and one which was apparently a late type was broken by a workman. Inbred line number 40-290 consisted of 5 plants of which 3 were like the normal plants of 40-156 and two were late like those of the other culture but differed from them in that they were dwarfs instead of giants.



Culture	Type of Plant	Days to Pollen	Total number of nodes	Nodes with brace roots above ground	Height cm.	Length of first 5 inter-nodes cm.	Average circumference of first 5 internodes cm.
40-156	:Late	:207++	: 26	: 15	: 255	: 11.0	: 10.8
40-156	:Normal	:104	: 14	: 1	: 184	: 12.6	: 7.3
40-290	:Normal	: 98	: 13	: 1	: 175	: 12.0	: 7.1
40-290	:Late	:207++	: 21	: 11	: 33	: 1.2	: 6.0

The late types died about January 15, 1941 from lack of water. The giant plant from culture 40-156 subdivided near its top, producing 10 branches each of which contained a small tassel that was nearly exposed at the time the plant died. This giant type may be the same mutant character that was originally reported by Brunson and has since appeared in the cultures of Bryan and Emerson.

The dwarf type of late plant in culture 40-290 still had its tassel deeply enclosed in the leaves when it died from lack of water. Perhaps this mutant form of plant is the same as the one described by Antonio E. Marino in "Una variacion 'tardia' en maiz" (A late variation in maize), *Revista Argentina Agron.* 6 (3): 237-240, 1939.

3. In three different inbred lines of corn, ears have been found in which there is no definite orientation of the kernels in spite of the straightness of the rows. The germ of the kernel may face the tip, or the butt, or either side. Other ears in the same cultures were normal.
4. Twin kernels. One ear in a second generation inbred had 287 kernels of which 68 were normal; 210 had streaks on the backs of the kernels, indicating a tendency toward the production of another germ; and 9 had two fully developed germs, one on each side of the kernel. Apparently the tendency toward twinness segregates about 3 to 1.
5. Hard starch vs. soft starch. Among 140 self-pollinated ears in second generation inbred lines developed from an open-pollinated variety of flint corn, one ear was found in which 130 kernels were of the flint type and 41 were capped with soft starch. The segregation was discontinuous. There were no "dents" in any of the kernels.

D. G. Langham

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Linkage Tests

Chromosome 10.

<u>Genes</u>	<u>Phase</u>	<u>XY</u>	<u>Xy</u>	<u>xY</u>	<u>xy</u>	<u>Total</u>	<u>% Recomb.</u>
<u>Og na2</u>	CB.	39	20	37	50	146	39
<u>Og na2</u>	CS	129	40	39	21	229	42

Note on na2 = Material from Cornell under No. Co 37-172 and designated na2.

<u>gl d7</u>	CS	53	9	17	4	83	45
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Mutation - YY → Yy. Verification of this one-kernel mutant from over 7200 kernels reported in 1940 News Letter. This white was tested against the y gene in Evergreen sweet corn, in a white dent inbred and in Hickory King. All progeny were white, indicating that this mutant involved the standard Y gene.

E. W. Lindstrom

North Carolina Agricultural Experiment

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"Intersectional" hybrids (Corn Belt lines crossed with local strains) of the following types have been tested: single crosses, top crosses, multiple top crosses, three-way crosses, and double crosses. The average of all "intersectional" hybrids was 20.8 percent in 1939 and 18.2 percent in 1940, higher than the average grain yield of the local varieties. These hybrids were made up entirely at random except for morphological observations of the parent lines. Besides grain yield the "intersectional" hybrids approach or equal the local varieties in pest resistance and grain quality. When compared with Corn Belt double crosses, the "intersectional" hybrids are much superior in general adaption to North Carolina conditions.

In six locations across the state 5 x 5 lattice square designs on 1/140 acre plots were utilized in 1940. The lattice square design showed an average gain in precision of at least the equivalent of an extra replication in a complete randomized block design. Complete randomized blocks of more than 30 entries have proved very unsatisfactory in our studies. Since 5 x 5 lattice squares have been of doubtful value in the Corn Belt, it seems worth while to mention our results on the heterogeneous soils of the Southeast.

Paul H. Harvey

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1. A new gene for pollen abortion, pa, is located in chromosome 1. Plants heterozygous for pa are semisterile in the pollen and have normal ears. It is transmitted rarely if at all through the pollen, but gives normal ratios through the eggs. The locus of pa is between P and br, the recombination values being: P-30-pa 34 br. It differs from sp and sp2 in that pollen carrying it is for the most part devoid of starch.

Cytological examination shows no visible deficiency in chromosome 1.

C. R. Burnham

The following chromosome map shows the loci of those interchanges for which there is cytological information. It is based on data presented in previous Coop Letters, whatever has been published and in addition unpublished data of Dr. C. R. Burnham. The scheme Anderson has used is followed, the breakage points being measured from the spindle fiber insertion region in tenths of the length of the particular arm in which the break occurred. Interchanges for which only genetic information is available are not listed.

As is customary, the map presents the cytological lengths of the chromosome which are in proportion, using chromosome 10 as 100 units. The length of each arm is given at the spindle fiber attachment region, the total chromosome length being the total of the two arm lengths. The long arm/short arm ratio is given at the bottom of the map.

The following example illustrates the use of the map: translocation 1-2a is listed as 2a on chromosome 1 opposite .7 on the long arm; on chromosome 2 it is listed as 1a opposite the locus .6 on the long arm. When more than one break has occurred at the same point, they are grouped together. For example, there are 5 translocations at locus .3 on the long arm of chromosome 2. Breaks which have occurred in the satellite of chromosome 6 are grouped in that region but their position in the satellite arm is not definitely known. 6-9a occurred in the nucleolus-organizer region. 2-6a and 5-9a involved the short arm of chromosome 6, but their relation to the spindle fiber insertion region is not known, hence they are given 0+ ratings.

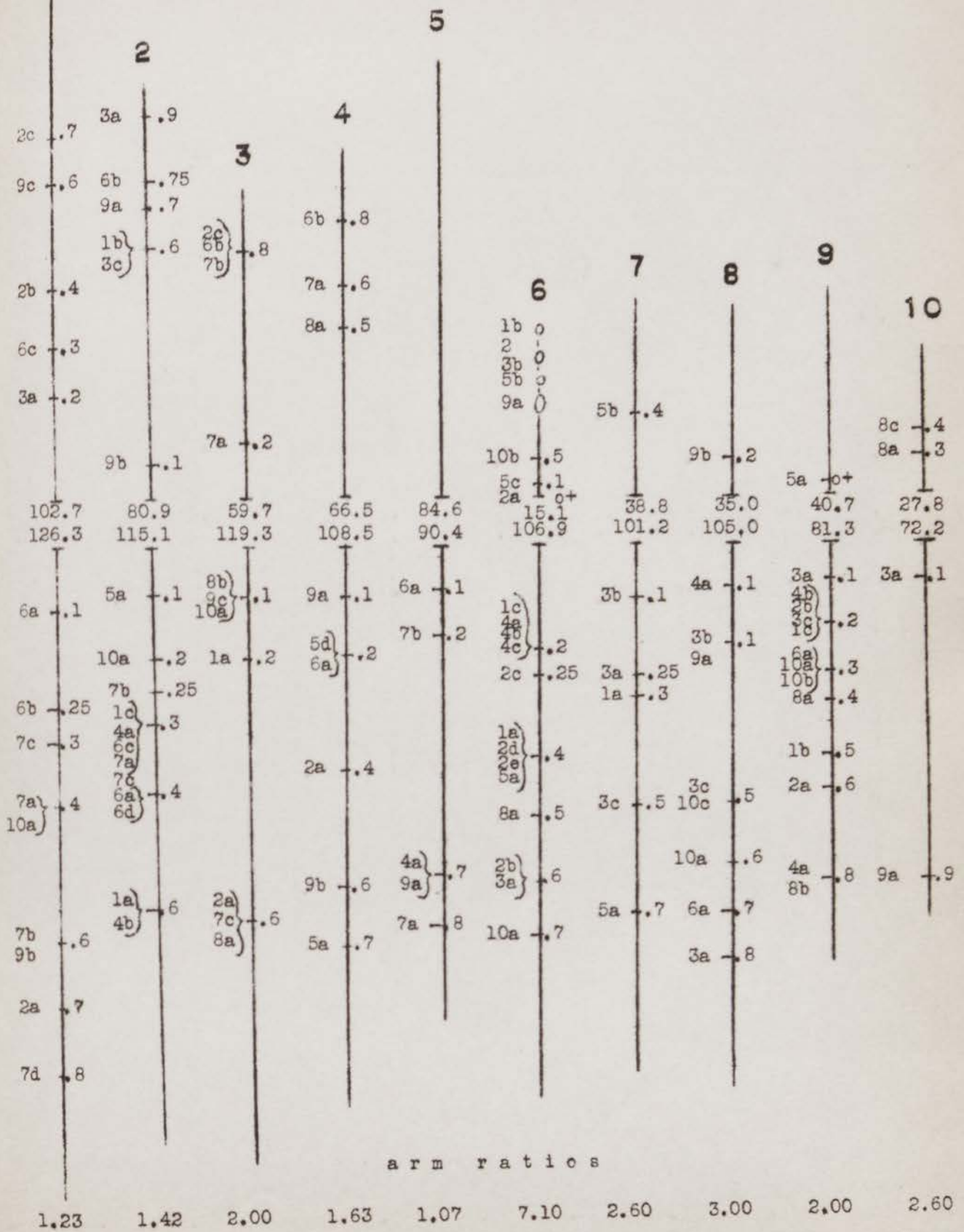
On completing this map Dr. C. R. Burnham has given advice and suggestions and a final check on the figures.

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Edward Garber

with locations of cytologically placed translocations



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Comparison of the Genetic Effects of Xrays and Ultraviolet Treatment. In 1939 and 1940 an attempt was made to determine the relative frequency of mutation and other types of genetic alteration induced by comparable doses of Xrays and ultraviolet. Since there is no physical basis for equating doses of the two radiations, it is necessary to make the comparison on the basis of some biological equivalent, for example, to determine the effect upon mutation of two doses equal in inducing deficiencies or translocations. But since previous studies had shown that the deficiencies and translocations induced by ultraviolet are of types different from those produced by Xrays (or include various types in widely different proportions), the doses equivalent on the basis of one chromosomal effect would be widely different from those equivalent on another.

The doses used therefore were chosen arbitrarily at levels suited to the significant determination of mutation frequency, and their equivalence may be judged only by the frequencies of the various alterations detected. The Xray doses used are relatively low, so as to permit the survival of as many plants as possible and the production of well-filled ears, which is essential for the determination of mutation rates. The ultraviolet doses used are close to the tolerance limit for the wave lengths represented.

Since both types of radiation produce defective plants of various kinds, it is essential to reduce losses to a minimum and to consider the individuals lost as well as the survivors in the interpretation of the results. The populations used represent the entire seed population from the treated ears, and special precautions were taken to secure maximum germination and survival. Plants which died early or which failed for other reasons to yield a pollen specimen were classified as "+" (apparently normal plants, accidentally lost) and "-" (apparently defective plants). The treatments compared, populations used, frequency of endosperm deficiency (A, Pr, Su), and losses to pollen shedding are shown below:

	No. Seeds	Endo-: sperm: deficien-: %	Embryo-: tion	Un-germi-: nated	Lost Died Early + -	No Pollen + -	: Hap-:loid	: Excluded	: Contam-:inated	: Popu-:lation
λ3022	210	43.1	19	12	10 8	0 0	2	0	159	
λ2967	160	28.8	7	10	1 3	0 2	1	0	136	
250 r	420	3.0	11	11	3 7	1 1	0	2	384	
500 r	217	7.4	8	7	3 4	2 4	1	0	188	
Control	1016	0.3	8	9	20 1	0 1	2	0	975	

Frequency of Pollen Segregation in F<sub>1</sub>. In populations so large as those required for the determination of mutation rates (particularly with low doses and control progenies), it is not feasible to determine the frequency of deficiencies and translocations by the direct cytological examination of every plant. Some indications regarding the frequency of chromosomal derangements may be obtained from the frequency and type of pollen segregation in F<sub>1</sub>. Pollen segregation was recorded as to percentage and type of defective pollen, the types ranging from "a" (significant reduction in size but normal development of contents) to "e" (practically empty). In the table which follows, types a and b are listed as "subnormal", types c, d, and e as "aborted," and segregations of both classes in the same individual as "mixed,"

The following facts determined from investigations in previous seasons are of help in the interpretation of the pollen records:

(1) "Directed segregation" in maize translocations is absent or extremely rare. The plants with segregating defective pollen therefore include all of those in which translocation has occurred as well as those with deficiencies.

(2) Gametophytic lethals at points of translocation are absent or very rare. If, as a result of "position-effect" or other causes, there were a tendency for mutational effects at the breakage points, it might be expressed by failure in development or functioning of the pollen carrying the translocation chromosomes. This does not occur. It is therefore possible to discriminate between segregating defective pollen due to translocation and that due to deficiency by transmission tests.

(3) F<sub>1</sub> plants with segregating defective pollen include many with cytologically detectable deficiencies not associated with translocation. Among pollen segregating plants from Xray treatment, these deficiencies include some which are obviously intercalary. Most of the cytologically detectable deficiencies are found in plants with "aborted" pollen, but in short intercalary deficiencies defective pollen is frequently of the "subnormal" class. The deficiencies from UV observed cytologically include none which is clearly intercalary. In all of the UV deficiencies so far observed cytologically the segregating pollen is of the "aborted" type.

(4) Among the plants with segregating defective pollen, the proportion due to translocation is much lower with ultraviolet than with Xrays. With high doses of ultraviolet, translocations unquestionably are induced, but the great majority of these are "deficiency-translocations"; that is, plants in which one or both of the chromosomes involved in the translocation has lost a segment. These deficiency-translocations are usually very defective plants, and their frequency depends in large part upon the precautions taken to insure survival of the poorest plants of the progeny. Translocations of this type may not be detected by transmission tests; they may be identified only by direct cytological examination of the F<sub>1</sub>.

The frequency of segregating defective pollen in these cultures is listed in the next table. The numbers and percentages given in parentheses represent the frequencies when each "high-sterile" is taken to represent two segregating factors for sterility.

	No. Exam.	Semi-sterile Sub.Ab. Mix.		High-sterile Sub. Ab.Mix.				Low Sterile	Total	%
X3022	159	10	15	1	0	2	3	1	32(37)	20.1(23.3)
X2967	136	13	8	0	1	2	1	2	27(31)	19.9(22.8)
250 r	384	13	23	2	0	8	2	1	49(59)	12.8(15.4)
500 r	188	9	21	6	0	12	6	5	59(77)	31.4(41.0)
Control	975	3	4	0	0	0	0	2	9(9)	0.9(0.9)

Low Deficiency Rate in Embryo vs. Endosperm with UV. In both UV progenies the frequency of plants with segregating defective pollen was about 20 per cent. There is reason to believe that many of these are due to causes other than deficiency (notably to mutations producing subnormal pollen). But even if all were due to deficiency, their frequency is



far lower than would be anticipated from the endosperm deficiency rates. The seeds planted showed endosperm deficiencies amounting to about 36 per cent for the marker genes A, Pr, and Su; these could represent only a small fraction of the deficiencies present in the entire ten chromosomes of the treated gamete. With equal deficiency frequency in the embryo, almost all of the F<sub>1</sub> plants should have segregating defective pollen due to deficiency, and many should have several deficiencies.

At one marked locus, a direct comparison may be made. The seeds planted in the two UV progenies included 71 endosperm deficiencies for A; the F<sub>1</sub> plants included no A-deficiencies.

Although induced deficiencies are relatively rare in the F<sub>1</sub> embryos, it is certain that they are not wholly absent. The treated pollen carried the dominant markers A B P1 R<sup>F</sup>; the UV families included five genetically marked deficiencies and several unmarked deficiencies which were identified cytologically in defective plants. Only one deficiency (a monosomic for chromosome #6) was found in the much larger control population.

Frequency of Translocation. In certain cultures, translocation frequency was determined by direct cytological examination of the F<sub>1</sub> plants in every plant with segregating defective pollen. The cultures examined included the entire population given the ultraviolet treatment "X2967" and the entire population from one ear given the Xray dose "250 r" and one ear given "500 r." The results are shown below:

Population		Segregating Pollen			Diakinesis Association	
		Semi-Sterile	High-Sterile	Low-Sterile	Inter-change	Deficiency-Association
X2967	136	21	4	2	0	3
250 r	97	14	0	0	4	2
500 r	83	20	7	3	11	6

It is noteworthy that deficiency-associations are found with Xray as well as UV treatment, but in the former they occur with a larger number of interchange-associations, while with the latter they do not.

Frequency of Translocation in Control. The spontaneous frequency of translocation is of interest in determining whether the occurrence of chromosome interchanges following

ultraviolet treatment is an effect of the treatment. Among the translocations observed in UV-treated progenies to date, although as previously mentioned the majority are deficiency-translocations, there are two or possibly three which appear to be regular segmental interchanges. Although such translocations have previously been found in untreated maize populations, there is no basis for an estimate of their spontaneous frequency. The large control in this experiment included only nine plants with segregating defective pollen; the progeny tests from these showed that two of them transmitted through pollen the factor for aborted pollen segregation. Diakinesis examination in these progenies showed in both cases the presence of chromosome interchange producing a ring-of-four at diakinesis. The spontaneous frequency of chromosome interchange thus appears to be appreciable, and the number of interchanges observed following ultraviolet treatment is not significantly higher than that in untreated material.

The results suggest that UV treatments produce a significant increase in the frequency of deficiency-translocations, without appreciable effect upon the frequency of segmental interchanges.

Mutation. The mutations determined were those involving endosperm characters, defective seeds, germless, and seedling abnormalities. Each of these types may be determined by examination of the selfed ears of the  $F_2$  plants or of the 100-seedling progenies grown from each of these ears. All of the mutations which are not clear-cut and unmistakable in the  $F_2$  culture are checked for recovery in  $F_3$  from heterozygous  $F_2$  plants. The analysis of the check-progenies of 1940 is not yet completed, and the data therefore are given separately for number of mutations and number of doubtful mutations, the latter being those subject to the  $F_3$  check. The percentages in the table are provisional percentages representing the clear-cut mutations plus half the doubtful mutations. Confirmation tests so far completed indicate that the final percentages will be somewhat higher than those here given.

	Endosperm			Germless			Seedling			Total %
	n	M	M? %	n	M	M? %	n	M	M? %	
X3022	62	5	5 12.1	110	2	11 6.8	107	11	2 11.2	30.1
X2967	93	4	8 8.6	82	0	6 3.7	81	4	1 5.6	17.9
250 r	250	1	2 0.8	298	0	1 0.2	299	1	2 0.7	1.7
500 r	143	5	7 5.2	133	1	2 1.5	126	1	1 1.2	7.9
Control	613	0	7 0.6	766	0	1 0.1	764	1	2 0.3	1.0

The mutations included, together with many useless types, a scattering of promising viable mutants affecting endosperm and seedling characters. The number of mutants is considerably larger than that shown in the table, since several other treatments were handled similarly. In all of these the  $F_2$  ears which yield the mutations are segregating for Y and P<sub>1</sub>, permitting a three-point test for chromosome 6 mutants, and are segregating also for single markers on chromosome 2, 3, 4, 5, 9, and 10. Doctor C. R. Burnham is undertaking the location of some of the more promising mutants.

Comparative Mutation Rate from Xray and UV. As the table indicates, mutations were considerably more frequent from UV than from Xrays, in spite of the fact that the Xray doses used produced considerably more translocations and probably more deficiencies.

Actually the mutation rate from UV is considerably higher than is indicated by these data. Among a sample of pollen grains treated with UV, because of the high absorption in passing through the pollen grain contents, only a small proportion receive a heavy dose at the site of the gametic nucleus, and many receive no effective dose at all. The mutation rate among the effectively-treated pollen grains therefore is much higher. Many of these include two or more independent mutations.

It is probable also that many of the segregating pollen defects (particularly of the subnormal class) are due to mutation expressed in the gametophyte generation rather than to deficiency. Since intercalary deficiencies are so rare and mutations are so common with UV treatment, it seems probable that the high frequency of subnormal pollen segregation following UV treatment is largely or wholly the result of gametophytic mutations, and is another expression of the high frequency of mutation induced by this agent.

#### Technic for Identification of Gametophytic Mutations.

In the mutation technic used in the experiment just described, gametophytic mutations are not detected if they have no visible effect upon pollen development; and if they produce defective pollen, they are not distinguishable from short deficiencies. Another difficulty is that many of the sporophytic mutations are questionable because of possible over-lapping of the normal phenotype.

Both of these difficulties may be avoidable, for limited chromosome regions, by the use of inversions to inhibit crossing-over. A trial of this method with one inversion was made in 1940, in an experiment comparing UV and Xray treatments in a manner otherwise similar to that of the experiment just described. The method may be used more effectively with a combination of inversions in various chromosomes.

The treated parent was I wx; the untreated parent carried rearrangement-9 (McClintock 1939) with i Wx. This rearrangement eliminates crossovers in a large part of chromosome 9. The F<sub>2</sub> seeds therefore are of three types -- one fourth I wx, homozygous for the treated normal chromosome; one fourth i Wx, homozygous for the untreated chromosome; and one half I Wx, heterozygous for the treated and untreated chromosomes. Induced chromosome 9 alterations are linked with I wx. They are manifested in three ways:

(1) By pollen defects linked with wx. In iodine-stained pollen specimens extremely slight effects on pollen size or development may be recognized, far below the limit of detection in unlinked segregation.

(2) By modified ratios for I and Wx. Gametophyte mutations or deficiencies without visible effect on pollen development, if they prevent functioning of pollen, modify the 3:1 ratios to 2:2 and 4:0 respectively. If they permit reduced functioning, they permit the segregation of a reduced proportion of wx seeds. (A reduced proportion of wx seeds may result also from a Ga-mutation inhibiting functioning if separated from the rearrangement by crossing-over.)

(3) By seed and seedling mutations linked with I Wx. Here also the linkage permits the detection of some mutants which would be doubtful or undetectable without linkage.

The mutants are crossed with C Wx (normal chromosome) for genetic location in three-point tests. Gametophyte mutations not transmitted through pollen may be recovered from the heterozygous I Wx seeds, and when pollinated by C Wx (normal) yield heterozygotes in which the location of the Ga-factor may be determined by crossing on C wx or c wx. Deficiencies and other chromosomal alterations not lethal to the female gametophyte may be recovered similarly, for cytological examination in plants free from the rearrangement.

The spontaneous frequency of the various types of alteration is shown in the same F<sub>2</sub> ears by segregations of the same kinds linked with i Wx instead of I wx.

The results of this experiment, as regards chromosomes other than #9, were similar to those of the previous experiment, except for differences incidental to the use of different wave lengths and dosages, which will not be discussed here.

The number of chromosome 9 alterations of each type identified is shown below:

	Treated Chromosome-9			Untreated Chromosome-9
	UV λ2967	UV λ2537	Xray 600 r	
Population	457	263	288	1008
(1) Defective Pollen				
Aborted	2	0	3	0
Subnormal	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{2}{5}$	$\frac{0}{0}$
Total	2	0	5	0
(2) Low Transmission 12 (Pollen Normal)		4	2	0
(3) Mutation				
Endosperm	3	2	0	0
Germless	1	0	0	0
Seedling	$\frac{2}{6}$	$\frac{2}{5}$	$\frac{1}{1}$	$\frac{1}{1}$
Total	6	5	1	1

These constitute a representative sample of the genetic alterations induced by Xrays and UV, all located within a region well suited for critical comparison genetically and cytologically.

Qualitative Comparison of Induced Mutations. The very high frequency of UV mutations, with the much lowered frequency of chromosomal derangements, suggests that these may include types of mutation not included among the Xray mutants, and may be relatively free from the various sorts of pseudo-mutation which occur under Xray treatment as by-products of induced chromosomal derangement.

The problem is to find criteria which may be applied to distinguish types of "mutation." Possible criteria available in maize include the following:

(1) Gametophyte viability. Many induced mutations are of lowered viability in the gametophyte, particularly as shown by reduced transmission through male germ cells. Differences in viability among mutants are usually regarded as characteristic of the different mutant alleles, the higher viability of standard alleles being considered the result of natural selection.

This view is contradicted by results with the known spontaneous mutations in maize. A large number of mutants representing various endosperm genes is available, and in

these gametophyte viability and male transmission are regularly normal. This suggests that the low viability of induced mutants may be due to the loss of something more than the dominant allele which is assumed to have mutated.

Transmission of the mutant through pollen, in competition with the normal non-mutant pollen grains, provides a very rigorous test of gametophyte viability, which may be applied to mutations at any locus.

(2) Use of genes which mutate normally to an intermediate allele. Spontaneous mutations of  $R^F$ , identified by colorless seeds, are regularly mutations to small  $r^F$ , as previously reported. Recent studies have shown that  $R^F$  mutates also, and with comparable high frequency, to  $R^G$ . It does not mutate spontaneously, or at most does so very rarely, to  $r^G$ . This may mean that the effect of  $R^F$  on anthocyanin coloration of the aleurone and of the plant is due to two separate but very closely linked genes, but whether this is true or not, the fact provides a convenient method for distinguishing between spontaneous mutations at this locus and the type of pseudo-mutation which could result from haplo-viable deficiencies.

A similar situation may apply at certain other loci. Recent trials show that the gene  $A^b$  also mutates spontaneously, with a fairly high frequency, to an intermediate allele. The results of an experiment in which the suspected mutations were identified by loss of aleurone color and all were subsequently checked by progeny tests show the following frequencies:

Stock	Mutation to $a^P$	Mutation to $a$
$A^b A^b$	0/55,765	25/36,661
A A	0/19,587	0/9,431

The  $a^P$  mutants, when combined with the appropriate complementary genes, have the red-brown plant color and brown pericarp characteristic of the standard  $a^P$ , although some of the mutants show a somewhat deeper color in aleurone and plant than the standard. Nine of these mutants have been tested for dominance of the brown pericarp effect. In all of these the effect is dominant as in the standard  $a^P$ .

(3) Reverse mutability. The analysis of the action of  $Dt$  by Rhoades makes possible the effective application of this criterion in the case of apparent mutations to  $a$ .

It is not applicable to the  $a^p$  mutations from  $A^b$ , since  $Dt$  is without effect on  $a^p$ . Whether it is applicable to all mutant  $a$ 's, or to the colorless mutations from all  $A$ 's, also remains to be seen, since the present stocks of  $a$ , on which  $Dt$  is effective, trace to not more than two original sources. Reversability of a mutant  $a$  under the influence of  $Dt$  is good evidence against deficiency, but failure of a mutant to be reverted by  $Dt$  is not convincing evidence against intragenic mutation.

(4) Detailed analysis of phenotypic effect. In the case of the genes affecting anthocyanin pigmentation, mutant phenotypes may be compared quite precisely by the use of methods developed by Karrer, Robinson, Scott-Moncrieff, and others for the identification of the various anthocyanin pigments. A study of the anthocyanin pigments in maize now being made by J. E. McClary indicates that there is a very rich variety of these pigments in maize, including several which do not commonly occur among the flower pigments genetically studied by the English workers.

One of these is the anthocyanin pigment which occurs together with a flavonol in the  $a^p$  stock. In the presence of  $B$  and  $P_1$ ,  $A^b$ , like  $A$ , produces chrysanthemine, but  $a^p$  produces an anthocyanin of distinctly different properties. The dark  $a^p$  obtained by mutation from  $A^b$  apparently produces the same pigment in larger quantity.

#### Comparison of X-ray and UV Induced Mutations of A.

Mutations and deficiencies involving the  $A$  locus may be identified by seedling examination of  $F_1$  plants from the cross  $a \times A \ B \ P_1 \ R^+$ . A very large number of plants of this constitution have been examined following treatment of the male parent with X-rays, and the green seedlings saved for identification of the mutation or deficiency. The majority of such plants turn out to be distinctly defective in growth and to have segregating aborted pollen. A small proportion approximate normal growth, but these also have defective pollen. Among them a few are found with segregating pollen of the subnormal type. Two plants were found in which the  $A$  effect had been lost, the plant was of normal vigor, and the pollen was completely normal in appearance. Both plants had the phenotypic appearance of typical  $a \ B \ P_1$ . They are designated  $a^{X4}$  and  $a^{X6}$ . In addition one plant of  $a \ B \ P_1$  phenotype and normal vigor, but with segregating subnormal pollen, was included in the further tests. It is designated  $a^{X1}$ .

In similar progenies of plants from UV treated pollen, the frequency of loss of the A effect is very much lower, as noted in connection with the experiment first described. Such plants may be found, however, by growing large enough progenies of F<sub>1</sub> seedlings, and we have so far identified about fifty of them. Among these, four individuals showed loss of the A effect but fully normal pollen. All of the others had aborted pollen, and in all cases this was empty or nearly empty. Three of the four mutants showed the phenotype of a B Pl. They are designated a<sup>U3</sup>, a<sup>U15</sup>, and a<sup>U18</sup>. The fourth mutant, though green as a seedling, showed faint anthocyanin coloration in later growth and deepened to a light purple at maturity. It is designated A<sup>lt</sup>.

The chief characteristics of these induced mutants, with reference to the criteria which have been mentioned, are as follows:

(1) Phenotype. Except in the case of A<sup>lt</sup> no consistent difference has been found in the phenotype of the mutants and that of a. In all six the aleurone is wholly colorless with C R A2, and the plant is typically brown with B Pl. The pericarp is red with A P but has not yet been seen with a P. With a<sup>U3</sup> B Pl a considerable amount of purple pigmentation was observed, chiefly in the upper half of the lower leaf sheaths, but similar coloration has been found in a B Pl plants extracted from the same culture. In segregating progenies from a<sup>mutant</sup>/a x a B Pl and a<sup>mutant</sup>/a x a<sup>P</sup> B Pl, it was not found possible to distinguish the mutant a from the standard a in any of these six cases.

The phenotype of A<sup>lt</sup> is clearly distinguishable from A, a, and a<sup>P</sup> in plant color, but it is not always distinguishable from a<sup>P</sup> in aleurone color. The plant color at maturity (with B Pl) is more similar to A than to a<sup>P</sup>, and the plant does not appear brown at any stage. The cob is reddish purple. The extracted pigment includes a considerable quantity of anthoxanthin as well as anthocyanin. The purified anthocyanin is distinct from both chysanthemin (A) and the anthocyanin of a<sup>P</sup>.

(2) Gametophyte viability. a<sup>X1</sup> is transmitted through female germ cells but in reduced proportion, seldom in more than 30 per cent of the expected number. Seeds heterozygous for the variant are reduced in size. There is no transmission of the type through pollen of the heterozygous plant.

a<sup>X4</sup> and a<sup>X6</sup> show full viability in the female gametophyte, and the seeds are full size. Although the pollen in both these types is fully normal in appearance, transmission of



the mutant is reduced in pollinations from heterozygous plants, ordinarily to 25 to 40 per cent of the expected numbers.

Self-fertilization of  $A/a^{X6}$  plants yields no colorless seeds, even though the same pollen used on a  $C R$  testers both before and after selfing shows transmission of the mutant  $a^{X6}$ . This type therefore appears to be zygotically lethal when homozygous. The same result is obtained with  $a^{X4}$ , though the trials in this case are less extensive.

$a^{U3}$ ,  $a^{U15}$ , and  $a^{U18}$  show full male and female viability and transmission.  $A^{it}$  is also fully viable in male and female gametophytes and regular in transmission.

(3) Relation to  $Dt$ . The reaction to  $Dt$  is determined chiefly by examination of the aleurone of seeds produced by the cross  $a^{mutant}/a^p Dt Dt \times a^{dotless} Dt Dt$  in comparison with sister ears of  $a a^p Dt Dt$  similarly pollinated. Supplementary determinations have been made in other ways.

None of the mutants show regular dotting comparable to that of  $a$ . Occasional seeds may show a single dot, but this may be ascribed to the  $a^{dotless}$  tester as well as to the  $a^{mutant}$ . Evidence on dotting in the homozygous  $a^{mutant} Dt$  combination is still scanty and has shown no dots so far.

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Although I am concerned primarily with corn breeding, I have started genetical studies of corn grown in Puerto Rico. There are many mutants found in local corn, such as white and yellow seedlings, various other chlorophyll deficiencies, male and female sterility, narrow leaf, tassel seeds, vivipary, brown midrib, red pericarp, variegated pericarp, and others. Whether these mutants have been introduced from the North, and subsequently incorporated into local corn, or are local in origin it is difficult to tell with certainty. However, it is well known that corn from the mainland is not adaptable to local conditions, and the few attempts to

introduce it to Puerto Rico have failed. The corn imported from other regions, such as Santo Domingo, Cuba and Argentine is used exclusively for feed.

Many crosses were made between some of these mutants and unrelated stocks, and  $F_2$ 's and backcrosses are expected to be raised this spring. For the present I want to mention two interesting cases: brown midrib and tassels, and forked or split stem.

Brown midrib and tassels. The  $F_1$  data suggest that we have a new dominant mutant, tentatively designated Bm-b, for the development of brown pigment in midrib and tassels. The color appears rather late, before tasseling, and varies in intensity especially in tassels, sometimes approaching color of tassels of a B Pl plants.

This mutant was found in one of the inbred lines. Bm-b plants were selfed and crossed to three unrelated stocks. The selfed plants had also red pericarp and cob. The five  $F_1$  crosses segregated in the following ratio:

<u>Bm-b</u> <u>P<sup>VV</sup></u>	<u>Bm-b</u> <u>p</u>	<u>bm-b</u> <u>P<sup>VV</sup></u>	<u>bm-b</u> <u>p</u>
193	2	0	183

The result suggests that Bm-b is closely linked with P. The presence of the red pericarp in Bm-b plants, as well as the development of anthocyanin in seedlings of all  $F_1$  plants indicate that the development of brown color in tassels and midrib is not due to a. Also there is evidence that we are dealing with red and not cherry pericarp, as there is no Pl involved in these crosses.

Forked or split stem. A number of plants were observed in several cultures in which the stem is split or forked. The forking may occur in any node. If forking takes place at the node below the ear, then two ears and tassels are formed.

From two selfed forked ears 44 plants were raised, all of which were normal, non forked. The  $F_1$  between forked and normal plants yielded:

	<u>Normal</u>	<u>Forked</u>
	153	2
	22	2
	26	0
	<u>15</u>	<u>1</u>
Total	216	5

IV. Miscellaneous Co-op Items

1. Co-op stocks. An effort is being made to grow each stock in our collection at least once every three years. To maintain vigor, especially in the naturally weaker stocks, we shall follow a practice started a few years ago. The co-op stocks are crossed with standard inbreds I (U.S. No. 204) and II (West Branch). The desired characters are then recovered from each of these hybrids, and crosses are then made between these desired sorts from the two sources.
2. Assignments of chromosomes for mapping. In News Letter 13, April 15, 1939, page 39, there is given a list of persons who are mainly responsible for linkage studies on the different chromosomes, and for the building up of linkage stocks. At the Christmas meetings in 1940, this list was examined by the co-operators present, and a few changes were made. The revised assignments follow:

Chromosome 1	-	Emerson
Chromosome 2	-	Rhoades and Clokey
Chromosome 3	-	Brink and Woodworth
Chromosome 4	-	Singleton and Brunson
Chromosome 5	-	Burnham and Cartledge
Chromosome 6	-	Burnham, Lebedeff and Stadler
Chromosome 7	-	Jenkins and Fraser
Chromosome 8	-	Sprague and Perry
Chromosome 9	-	Shafer and Eyster
Chromosome 10	-	Lindstrom

3. Personals.

- (a) Carlos A Krug of Sao Paulo, Brazil, is spending a year in this country, with the special purpose of studying the genetics and cytology of citrus, at Riverside, California. Krug brought to the U.S.A., 60 types of maize collected by his assistant in Bolivia, Peru, Ecuador, and Columbia. These have been added to the Co-op stocks. Small amounts of seed can be spared to cooperators who are especially interested.
- (b) D. G. Langham of Venezuela is in this country for a few months, for the purpose of collecting corn and of working on a special problem in connection with his research.
- (c) Two of our number, M. M. Rhoades and B. McClintock, will be at Cold Spring Harbor this summer, along with Muller, Wright, Nebel and other geneticists.
- (d) R. A. Emerson left Ithaca early in February for a six-weeks vacation in Florida.

V. Maize Publications

Since the preparation of the list of publications in News Letter 14, March 5, 1940, the following articles have appeared in print:-

- Anderson, E. G. and Brink, R. A. - Translocations in maize involving chromosome 3. *Genetics* 25: 299-309, 1940.
- Andres, J. M. - Analisis genetico del color de endosperma en algunos maices comerciales Argentinos. *Inst. Genet. Univ. Buenos Aires* vol. 1: 25 p., 1939.
- Avery, G. S., Jr., Creighton, H. B. and Shalucha, B. - Extraction methods in relation to hormone content of maize endosperms. *Amer. Journ. Bot.* 27: 289-300. 1940.
- Beard, D. F. - Relative values of unrelated single crosses and an open-pollinated variety as testers of inbred lines of corn. Abstr. Ph.D. thesis, Ohio State Univ. 33: 9-18, 1940. (Includes discussion of susceptibility to *Diplodia Zeae*).
- Bercaw, L. O., Hannay, A. M. and Larson, N. G. - Corn in the development of the civilization of the Americas. A selected and annotated bibliography. U.S.D.A. *Agr. Econ. Bibl.* 37: 195 p., 1940.
- Bonnett, O. T. - Development of the staminate and pistillate inflorescences of sweet corn. *Journ. Agr. Res.* 60: 25-37, 1940.
- Borgeson, C. and Hayes, H. K. - The Minnesota method of seed increase and seed registration for hybrid corn. *Journ. Amer. Soc. Agron.* 33: 70-74, 1941.
- Buss, H. - Die Problemstellung in der deutschen Maiszüchtung. *Deut. Land. Presse.* 67: 87, 1940.
- Capinpin, J. M. and Rollan, A. O. - Hybrid vigor in the first generation crosses between strains of Cebu corn. *Philipp. Agr.* 28: 491-503, 1939.
- Carnegie Institute Washington - Maize cultivation in northwestern Guatemala. (Compiled from data collected in the field by Raymond Stadelman). *Carnegie Inst. Wash. Pub.* 523: 83-263. 8 pl. map, 1940. Processed.

- Clark, F. J., and Copeland, F. C. - Chromosome aberrations in the endosperm of maize. *Amer. Journ. Bot.* 27: 247-251, 1940.
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- Eckhardt, R. C., and Bryan, A. A. - Effect of the method of combining the four inbred lines of a double cross of maize upon the yield and variability of the resulting hybrid. *Journ. Amer. Soc. Agron.* 32: 347-353, 1940.
- Eckhardt, R. C. and Bryan, A. A. - Effect of the method of combining two early and two late inbred lines of corn upon the yield and variability of the resulting double crosses. *Journ. Amer. Soc. Agron.* 32: 645-656, 1940.
- Edwards, E. T. - The American hybrid maize programme. *Journ. Austral. Inst. Agr. Sci.* 6: 146-153, 1940.
- Fujita, T. - <sup>II</sup>Über die Organstellungen bei Maiskolben, Japan. *Journ. Bot.* 10: 113-140, 1940.
- Gaessler, W. G., Hixon, R. M. and Haber, E. S. - The quantity of pericarp in several hybrids and inbred strains of sweet corn. *Iowa State Coll. Journ. Sci.* 14: 379-383, 1940.
- Gini, E. - Estudios sobre esterilidad en maices regionales de la Argentina. *Anales Inst. Fitotecn. Santa Catalina (La Plata, Arg.)*. 1: 135-158, 1940. (Eng. Sum.)
- Graner, E. do A. - Variacoes do valor de "linkage". *Revista Agr. (Piracicaba)* 15: 168-175, 1940. (Eng. Sum.)
- Haber, E. S. - Sweet corn hybrids. *Iowa Agr. Exp. Stat. Bull. N.S. P15*: 437-468, 1940.
- Heyne, E. G. and Brunson, A. M. - Genetic studies of heat and drought tolerance in maize. *Journ. Amer. Soc. Agron.* 32: 803-814, 1940.
- Hirschhorn, E. and Hirschhorn, J. - Accion del pH sobre los caracteres culturales del carbon del maiz. *Ustilago Zeae (Beck) Ung. Physis (Buenos Aires)* 18: 223-251, 1939.

- Hoerner, I. R., and Snelling, R. O. - Effect of pollination upon chemical composition of silks of certain inbred lines of maize. Journ. Amer. Soc. Agron. 32: 213-215, 1940.
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- Randolph, L. F. and Hand, D. B. - Relation between carotenoid content and number of genes per cell in diploid and tetraploid corn. Journ. Agr. Res. 60: 51-64, 1940.
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Papers in Press

Longley, A. E. - Knob positions on teosinte chromosomes.  
Journ. Agr. Res.

\_\_\_\_\_ - Chromosome morphology in maize and its  
relatives. (A review). Submitted to Botanical  
Review, but not yet accepted.

Saboe, L. C. and Hayes, H. K. - Genetic studies of smut  
reactions in maize by means of chromosomal trans-  
locations - Submitted to Journ. Amer. Soc. Agron.

VI. New Genes

1. Five alleles of a for aleurone color. No symbols given as yet. See contribution by M. M. Rhoades, Columbia University, item 2.
2. A new member of the r series for aleurone color. See report by M. M. Rhoades, item 5.
3. New gene for pollen abortion pa contribution of C. R. Burnham, item 1.
4. An R<sup>ch</sup> allele of R contribution of E. G. Anderson, item 1.
5. Mutations produced by irradiation. See contribution by L. J. Stadler and co-workers.
6. Bm- b- brown midrib and tassel. Contribution of Lebedeff from Univ. of Puerto Rico.