

MAIZE GENETICS COOPERATION

NEWS LETTER

19

February 15, 1945

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## I. REPORTS FROM COÖPERATORS

Bureau of Plant Industry Station and Cornell University,  
Beltsville, Md. and Ithaca, N. Y.

1. Tetraploid maize-Tripsacum hybrids. In 1942 the excised embryo technic was utilized to obtain two hybrids of tetraploid corn and tetraploid Tripsacum. Since these hybrids received two sets of chromosomes from each parent it was anticipated they would be fertile if the chromosomes comprising these sets synapsed to form bivalents. But these two hybrid plants proved to be completely sterile. They not only produced no functional pollen but when used as the seed parent in backcrosses to their parents no viable seed was obtained from them. A variable number of bivalents were formed and in addition there were always present from one to several multivalent complexes that could not be fully analyzed.

Compared with the elaborate technic of Mangelsdorf and Reeves a relatively simple procedure was employed to obtain these hybrids. The husks of the earshoots were opened sufficiently to permit a mixture of Tripsacum and corn pollen to be sifted in about the bases of the silks, the husks were then replaced about the earshoot and held in position by the glassine earshoot bag reinforced with rubber bands. Approximately three weeks after pollination the embryos of the partly developed kernels were excised and cultured in two ounce screw cap bottles on the sterile nutrient medium employed by Randolph and Cox for the culture of iris embryos (Proc. Amer. Soc. Hort. Sci. Vol. 43, 1943). As soon as a root system and seedling leaves were formed the seedlings were transferred to soil.

The two hybrids produced in 1942 resulted from the pollination of 14 earshoots of a synthetic tetraploid corn hybrid involving 5 different yellow dent lines (Stock A in accompanying table) with a mixture of tetraploid Tripsacum and tetraploid corn pollen carrying a full complement of genes for colored aleurone. Corn pollen was included with the Tripsacum pollen because Mangelsdorf and Reeves found that the presence of a certain number of normally developing corn grains on the ears aided the development of any rare hybrid kernels that might result from the functioning of Tripsacum pollen. Colored aleurone was involved to facilitate the separation of hybrid from the non-hybrid seeds.

In 1943 a further attempt was made to obtain additional hybrids for a more adequate study of their characteristics. Four vigorous tetraploid hybrids of commercial lines of yellow dent corn were selected as the seed parents. From a total of 38 pollinations 68 immature embryos or embryo-like structures were cultured. Most of these were inviable and the eight seedlings obtained from them proved to be non-hybrid corn seedlings.

The stocks used in 1944 to repeat the cross differed from those used in the preceding two years. These are listed as stocks B-F in the following table which summarizes the results obtained in 1942 and 1944. Stock B was a multiple recessive tetraploid combination of one or more recessive genes in each of the ten chromosomes ( $P^V$ -bm2, b-lg, A-cr, su, pr, y-pl, in, j, c-wx,  $R^E$ -g). Stocks C, D and E were, with respect to most of these recessives, duplex heterozygotes, the recessive stock having been crossed with an aB P1 lg type to produce C, and AB P1  $R^E$  type to produce D and with the inbred 187-2 to produce E. Stock F was an  $F_1$  hybrid of two commercial yellow dent lines, one of which was 187-2.

<u>Stock</u>	<u>Ears pol.</u>	<u>Embryos cultured</u>	<u>viable hybrid seedlgs.</u>	<u>Non-hybrid corn seedlgs.</u>
A	14	78	2	26
B	22	0	0	0
C	6	13	5	9
D	8	14	4	3
E	7	4	1	2
F	10	2	1	0

Perhaps the most interesting conclusion to be drawn from the results of these attempts in 3 different years to obtain hybrids between tetraploid corn and tetraploid *Tripsacum* is that hybrids may be obtained much more readily from certain stocks than from others. Gene differences affecting crossability may be involved, or, if the suggestion of Mangelsdorf and Reeves that corn carries segments of *Tripsacum* chromatin is to be taken seriously the possibility that such segments were present in the stocks which crossed most readily should be considered. However, there were no pronounced differences in knob frequency in the Stocks A-F; all had relatively few knobs.

The hybrids obtained in 1944 have not yet reached the sporocyte stage. One of the hybrids obtained in 1942 produced abundant tillers and has been maintained by vegetative propagation without difficulty; the other 1942 hybrid was less vigorous, produced few tillers and could not be kept alive by vegetative propagation. Extreme differences in the vigor of the 11 hybrids obtained from the 1944 crosses suggest that they may differ appreciably with respect to their chromosomal configurations.

2. Trisomic stocks. The number 1 trisome has been identified cytologically in stocks which gave trisomic ratios for bm<sub>2</sub>. All of the 10 trisomes have now been isolated and stocks of these are available in cultures known to be free of supernumerary B-type chromosomes.

Bureau of Plant Industry and Purdue University  
Beltsville, Md. and Lafayette, Ind.

Inheritance of susceptibility to Helminthosporium carbonum Race I. There are here submitted preliminary data on the linkage relations of the gene hm governing susceptibility to infection by H. carbonum Race I.

Earlier studies (Jour. Agri. Res. 63:331-334, 1941) and (Phytopathology 34: 214-222, 1944) have shown susceptibility to infection by H. carbonum Race I to be inherited as a monogenic recessive. Appropriate crosses were made by Dr. E. G. Anderson using a series of translocation stocks in which su endosperm was used as a translocation marker. The parents Pr and K61 are homozygous susceptible inbred lines of normal dent corn. The F<sub>1</sub> material was backcrossed with pollen from double recessives (sugary susceptible plants). Kernel separations were made of the backcross progenies, planted in the greenhouse and seedling inoculated at the 3-4 leaf stage. One week after inoculation disease readings were made. The data in table 1 definitely indicate that the gene hm is located on chromosome 1.

In table 2 a summary is given of a four-point test involving 9 backcross progenies. Further studies are underway in which backcross progenies  $\frac{p \text{ hm } br}{+ + +} \times \frac{p \text{ hm } br}{p \text{ hm } br}$  will be used. A series of translocations all involving chromosome 1, and supplied by Dr. E. G. Anderson, will also be under observation in 1945.

Table 1. Segregation of seedlings in which su endosperm was used as a marker for translocations

F <sub>1</sub>	Number kernels planted*		Sugary		Starchy		Chi Square Values	Range of "P"
	Sug.	St.	Res.	Sus.	Res.	Sus.		
suT1-4a x Pr	1344	1149	921	317	190	912	767.0	< .01
K61 x suT1-4a	924	894	664	176	150	703	642.0	< .01
suT2-4a x Pr	408	475	173	207	234	341	3.1	.2 - .3
K61 x suT2-4a	541	675	223	259	319	344	3.6	.1 - .2
suT2-4c x Pr	566	512	266	239	245	238	1.5	.3 - .5
K61 x suT2-4c	516	511	240	237	248	237	.3	.5 - .9
suTuT4-5b x Pr	458	476	199	206	230	230	.1	.5 - .9
K61 x suTuT4-5b	250	273	120	114	133	139	.3	.5 - .9
Pr x suT4-6a	478	495	190	205	240	221	1.3	.5 - .9
K61 x suT4-6a	443	484	187	181	255	218	3.0	.2 - .3
Pr x suT4-8	336	437	157	161	224	188	.2	.5 - .9
Pr x suT4-9a	548	545	227	219	244	249	.8	.5 - .9
K61 x suT4-9a	252	251	114	109	115	128	3.2	.2 - .3
K61 x suT4-10b	257	245	127	125	112	119	.2	.5 - .9

\* Also represents kernel ratio found on ears

Table 2. Four-point test for the gene hm, the F<sub>1</sub> genotype being  $\frac{hm + + +}{+ br f bm_2}$

Progeny No.	Parental Combinations		Reg.											Total	
	1	2	3	1 & 2	1 & 3	2 & 3	4	5	6	7	8	9	10		11
1	1	31	3	11	0	2	19	43	3	4	3	3	2	3	158
2	61	50	11	20	2	6	47	53	9	1	7	9	0	16	292
3	45	54	8	19	2	10	40	45	7	0	8	13	0	8	259
4	46	53	11	12	2	8	33	36	4	6	10	12	2	9	244
5	58	53	8	6	1	7	46	51	4	0	3	6	1	3	247
6	47	52	12	19	3	6	55	45	6	1	12	6	5	9	278
7	53	62	13	13	1	8	29	54	3	0	7	7	2	6	258
8	73	37	4	22	0	6	29	44	7	0	7	9	0	21	259
9	45	46	5	12	3	7	29	64	6	3	3	8	1	3	235
Total	459	438	75	134	14	60	327	435	49	15	60	73	13	78	2230
	897		209	74	762	64	133	91							
			9.4%	3.3%	34.2%	2.9%	6.0%	4.1%							

The indicated genetic map is:

hm 18.3 br. 10.3 f 44.3 bm<sub>2</sub>

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The following tables are compiled for the benefit of those using or wanting to use the sugary and waxy series of translocations for the study of economic or other characters in maize. The data included in tables 1 and 2 are the per cent of crossing over with su or wx in the heterozygous translocation plants, the position of the break in the other chromosome, and which alleles of Su su or Wx wx are present in each translocation. Tables 3 and 4 give a list of new semisteriles which small test plantings have shown to be linked to su or wx.

Table 1. Translocations closely linked with sugary.

	<u>Crossing over with su</u>	<u>Chro- mosome</u>	<u>Cyto- logical position</u>	<u>Linkage</u>	<u>Gene Combinations available</u>
1-4a	3.0	1		br-20-T-45-bm <sub>2</sub>	Su su
2-4(K-10)	(2.)	2		near B ( $\pm 8$ )	Su su
2-4(C-31)	close	2		near B ( $\pm 17$ )	Su
✓ 2-4a	3.5	2	2L.2	B-T-1.5-Y <sub>4</sub>	Su su ✓
2-4C	9.2	2		✓ 4--19.0-T-29.2-Ch	Su su
2-4(A-29)	6.1	2		✓ 4--22.3-T	Su su
✓ 4-5C	1.1	5		bm-3.5-T-15.5-pr	Su
✓ 4-5d	1.9	5		bm-2.5-T-5.5-pr	Su su ✓
4-5(X-6-77)	9.0	5		pr $\pm 16.4$	Su su
4-6a	4.5	6	6L.3	very close to Y	Su su
4-6C	2.	6		very close to Y	Su
4-7a	close	7	7L.3	near ra and gl	Su
4-8a	close	8	8L.1	T-34-msg-j	Su su
4-9(F-22)	4.2	9		c-wx-6.9-T	Su su
4-9a	{ 3. 20	9	9L.8	{ c-wx-11.5-T c-wx-31.0-T	Su su
4-9(A-26)	close	9		not tested	Su
4-10 b	4.0	10		near g	Su su
4-10(B-45)	close	10		T-8.8-g-R	Su
1,3,4,5,(B-2)	close	1,3,5		1 not tested, 3 near tg <sub>4</sub> , 5 near bm	Su su

Table 2. Translocations closely linked with waxy.

	Crossing over with <u>wx</u>	Chro- mo- some	Cyto- logical position	<u>Linkage</u>	<u>Gene combinations</u>
1-9C	12.1	1	1S 6	P-0.8-T	Wx wx
1-9a	11.2	1	1S.	P-21.2-T-35.6-br	Wx wx
2-9b	7.5	2	2S.1	ts <sub>1</sub> -5.3-T-7.8-√4	Wx wx
3-9a	3.6	3		near ts <sub>4</sub>	Wx wx
3-9C	7.6	3	3L.1	near ts <sub>4</sub>	Wx wx
3-9b	6.8	3		lg <sub>2</sub> -7.9-T-18.0-a <sub>1</sub>	Wx wx
4-9 (F-22)	6.9	4		su-4.2-T-Tu	Wx wx
4-9b	3.1	4	4L.6	su-Tu-13-21.9-T	Wx wx
5-9a	2.0	5	5L.6	bm <sub>1</sub> -pr-25-T	Wx wx
5-9 (X-14-111)	near wx	5		(near pr)	wx
6-9a	9.4	6	6S.	T-12.9-Y-P1	Wx wx
6-9b	3.8	6		near Y	Wx wx
6-9 (a-66)	12.2	6		near Y	Wx wx
6-9 (X-25-78)	3.4	6		near Y	Wx wx
8-9a	13.7	8	8L.2	T-30-msg-j	Wx wx
9-10b	5.7	10		T-8.8-g-R	Wx wx
9-10a	4.5	10	10L.9	g-R-3.2-T	Wx wx

Table 3. New semisteriles linked with sugary.

	<u>Backcrosses with su</u>		<u>Gene Combinations</u>
	<u>Total</u>	<u>Crossovers</u>	
a-57	36	0	Su
I-10	38	3	su
K-17	107	3	Su su
X-1-1	39	3	Su su
X-2-64	36	2	Su su
X-17-108	near su		su
X-19-5	near su		su
X-47-41	39	0	su
X-57-31	30	1	su

Table 4. New semisteriles linked with waxy.

	Backcrosses with wx		Gene Combinations
	Total	Crossovers	
a-76	34	2	Wx
F-24	96	7	Wx wx
bp	near wx		wx
X-7-39	40	3	Wx wx
X-10-6	37	0	wx
X-11-73	37	5	Wx wx
X-22-92	39	1	Wx wx
X-23-158	39	5	Wx wx
X-26-8	35	2	Wx wx

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Translocations and centromere positions. Translocations are especially useful in determining the location of genes in relation to the centromere and other visibly differentiated regions of the chromosome, due to the fact that their position in the chromosome can be determined cytologically and their linkage relations with known genes also can be determined. The following is a summary of available data on the relative positions of translocations and genes in the neighborhood of the centromeres in chromosomes 1 to 9 inclusive, with a few records for chromosome 10. These data were compiled chiefly from Dr. Anderson's records while in residence at the California Institute of Technology for several months in 1942 and 1944.

Chromosome 1. - Information on translocations in the short arm of chromosome 1 was summarized by Anderson in 1941. The gene P is about two-thirds of the distance out on the short arm. A minimum map distance from P to the centromere may be determined from % 1-9a which is known to be located in the short arm. On the basis of 730 plants the per cent of crossing-over between P and T 1-9a was found to be  $21.2 \pm 2.5$ . Thus the location of the centromere in the linkage map is 21.2 units or more to the right of P.

A number of translocations in the long arm of chromosome 1 give less than 5 per cent of the crossing-over with brachytic. These are distributed from about L2 to about L6. The gene br is probably located in the neighborhood of L3 or L4. Only 2 of the translocations in the long arm are definitely placed to the left of br. T 1-6a was reported by Burnham and Cooper and Cooper and Burnham to be in the

long arm of chromosome 1 a short distance from the spindle insertion. From their diagrams and figures a position of about L2 is indicated, which is also in accord with other data. The map position, based on 75 plants, is given as 13.4 units to the left of br. T 1-6b has been described by Burnham. The locus in chromosome 1 is given as L2.5. Very good linkage data involving 952 plants place the translocation to the left of br with 3.8 per cent of crossing over. (Data by Burnham cited by Emerson, Fraser and Beadle, 1935). These data merely show that br is between one-quarter and one-half the distance out on the long arm. The map position of the centromere must be some where between the locus of T 1-9a, 21.2 units to the right of P and the locus of T 1-6a, 13 units to the left of br. This is a very long region. If crossing over were equally distributed over this portion of the chromosome we might expect the centromere to be about midway between P and br.

Chromosome 2. - The map location of the centromere can be rather closely delimited by a number of translocations in the interval between ts and v<sub>4</sub>. Several of these will be considered. T 2-9b is located cytologically at 2S1 and 9L2. Linkage tests give the order definitely as B-ts-T-v<sub>4</sub>. Crossing over between the nearest genes was

$$\begin{aligned} \underline{ts-T} &= 33/622 = 5.0 \text{ per cent} \\ \underline{t-v_4} &= 121/1528 = 7.9 \text{ per cent} \end{aligned}$$

Since the break in chromosome 9 is known to be in the long arm (Anderson, 1938), the wx gene is carried in the 9<sup>2</sup> chromosome. Tests of linkage relations in the homozygous translocation can be used to verify the location of the break in chromosome 2. These tests gave the following results, showing that the break is between ts and v<sub>4</sub>.

$$\begin{aligned} B - \underline{ts} &= 27\% \\ \underline{ts} - \underline{v_4} &= 55\%, \text{ or independence.} \\ \underline{wx} - \underline{B} &= 21.3\% \\ \underline{wx} - \underline{v_4}, \text{ repulsion series} &= 51.5\% \\ \underline{wx} - \underline{v_4} \text{ coupling series} &\text{ in } 50.1\% \end{aligned}$$

The wx gene is carried in the 9<sup>2</sup> chromosome.

The linkage of wx with B and its independence of v<sub>4</sub> establishes the break in the short arm of chromosome 2 between B and centromere. The linkage of B and ts shows the break in to the right of ts and the independence of ts and v<sub>4</sub> locates the break between those genes. Thus the centromere is at least 5 units to the right of v<sub>4</sub>.

T 2-5a was studied by Rhoades and described cytologically as in the long arm of chromosome 2 near the centromere. Linkage tests give the order as B-T-v<sub>4</sub> with 7.3 per cent of crossing over between T and v<sub>4</sub>.

T 2-10a is located at L2, with the break in chromosome 10 well out on the long arm, 2 to 3 cross-over units to the left of g. The order on chromosome 2 is ts-T-v<sub>4</sub> and the data on crossing over are as follows:

$$\begin{aligned} \underline{ts-T} &= 11.4 \text{ per cent} \\ \underline{T-v_4} &= 6.6 \text{ per cent} \end{aligned}$$

Linkage data in the homozygous translocations are as follows:

$$\begin{aligned} \underline{B-ts} &= 16.+ \text{ per cent} \\ \underline{B-g} &= 20 \text{ per cent} \end{aligned}$$

Since g is distal to the break in chromosome 10 the B-ts section of chromosome 2 must include the centromere, i.e., the translocation must be in the long arm of chromosome 2.

These data may be summarized as follows:

T 2-9b	<u>ts-5.0-T-7.9+-v<sub>4</sub></u>	short arm
T 2-5a	<u>ts -T-7.3 -v<sub>4</sub></u>	long arm
T 2-10a	<u>ts-11.4-T-6.6-v<sub>4</sub></u>	long arm

The centromere must be 5 or more cross-over units to the right of ts and 7.3 or more units to the left of v<sub>4</sub>. Since there is usually some suppression of crossing over in the heterozygous translocations, the total map distance of the ts-v<sub>4</sub> interval is uncertain. The normal value is probably about 20 units. The centromere is probably a little closer to ts than to v<sub>4</sub>.

Chromosome 3. - The summary of translocations involving chromosome 3 published by Anderson and Brink places the centromere in the general neighborhood of ts<sub>4</sub>. Since then additional data on T 2-3b has indicated that ts<sub>4</sub> is in the long arm of chromosome 3. This translocation shows about 4 per cent of crossing over with v<sub>4</sub>. The order is probably B-sk-v<sub>4</sub>-T. Linkage tests in homozygous T 2-3b stocks give the following cross-over values.

$$\begin{aligned} \underline{B-sk} &= 39/399 = 9.+ \% \\ \underline{B-v_4} &= 128/289 = 44.3 \% \\ \underline{B-ts_4} &= 495/1171 = 42.3 \% \\ \underline{ts_4-1g_2} &= 27/135 = 20.0 \% \\ \underline{v_4-ts_4} &= 10/59 = 17.+ \% \end{aligned}$$

These data all agree in placing the translocation beyond v<sub>4</sub>, consequently in the long arm of chromosome 2. The linkage of ts<sub>4</sub> with B and v<sub>4</sub> in the homozygous translocation places the break between the centromere and ts<sub>4</sub>, and shows that it is the long arm that is involved. From this it may be concluded that the centromere is to the left of ts<sub>4</sub>, i.e., between d and ts<sub>4</sub>.

Chromosome 4. - A number of translocations in the proximal regions of both arms of chromosome 4 adjacent to the centromere all show close linkage with su, usually accompanied by much suppression of crossing over. These data indicate that the centromere is in the general region of the su locus. Data on T 2-4c place su in the short arm. This translocation is very near the centromere in the short arm of chromosome 4, and is far out on the long arm of chromosome 2 between v<sub>4</sub> and ch. Linkage data from homozygous T 2-4c show ts<sub>5</sub> and su to be linked and su to be independent of Tu. Thus the break is to the right of su. Further data on this homozygous translocation areas follows:

$$\begin{aligned}\frac{\text{su-v}_4}{\text{su-ch}} &= \frac{401/1057}{247/525} = 37.94 \text{ per cent} \\ \frac{\text{su-ch}}{\text{Tu-ch}} &= \frac{247/525}{193/429} = 47.0 \text{ per cent} \\ \frac{\text{Tu-ch}}{\text{su-ch}} &= \frac{193/429}{247/525} = 44.9 \text{ per cent}\end{aligned}$$

From heterozygous stocks of this translocation chromosome 2 linkage relationships and adjacent to the break were:

$$\frac{\text{v}_4-19.94-T-29.3-\text{ch}}{\text{su-9.1-T-30.8-Tu}}$$

for chromosome 4:

$$\frac{\text{v}_4-19.94-T-29.3-\text{ch}}{\text{su-9.1-T-30.8-Tu}}$$

The linkage of su with v<sub>4</sub> in the homozygous translocation demonstrates that the translocation must be between su and the centromere of chromosome 4. This places the centromere at least 9 units to the right of su on the linkage map.

Chromosome 5. - The position of the centromere in relation to the known genes of chromosome 5 was determined very accurately by Rhoades in 1936, with the aid of a fragment of chromosome 5, which apparently consisted of the centromere and the entire short arm of the chromosome. In the metaphase of the first meiotic division in the microsporocytes the fragment formed a trivalent with the two normal number 5 chromosomes in approximately half of the cells; in the remainder of the cells it was present as an univalent that was rarely included in either daughter nucleus. From the known cytological behavior of the fragment the expected back cross ratio from fragment plants of the constitution AAa with a in one of the normal chromosomes was calculated to be 5A:3a or 37.5 per cent of recessives. This ratio differs sufficiently from the ordinary 1:1 back cross ratio of disomic inheritance so that with the aid of the fragment chromosome genes located in the short arm could be distinguished from those located in the long arm of chromosome 5.

Another test employed by Rhoades to identify the genes in the short arm was the occurrence of fragment-carrying plants homozygous for the recessive gene in the back cross progenies of fragment plants carrying a recessive allele in one of the normal number 5 chromosomes. If the locus under consideration was in the short arm none of the

fragment-carrying plants would be homozygous for the recessive allele, barring rare exceptions resulting from chromatic crossing over.

Utilizing these tests it was found that the A<sub>2</sub> and bm loci were in the short arm and bt, pr, vs, v<sub>2</sub> and v<sub>12</sub> were in the long arm of chromosome 5. The available cytological and genetical data from translocations involving chromosome 5 confirm the findings of Rhoades relative to the position of the centromere between the bm and bt loci.

Chromosome 6. - There are available six translocations recorded cytologically at about 6L2 or 6L2.5. These are T 1-6c, 2-6c, 4-6a, 4-6b, 4-6c and 6-9b. All are closely linked with Y and are definitely to the left of P<sub>1</sub>. All show a reduction of crossing over between Y and P<sub>1</sub> to 5% or less, in the heterozygous condition. Proven cross-overs with Y have not as yet been obtained for study. With so much suppression of crossing over, little can be inferred as to the location of the Y locus with reference to the centromere. Translocations in the satellite or nucleolar region are located well to the left of Y. Data on 3 translocations between the centromere and the nucleolar region are too meagre to give any satisfactory evidence as to the position of the centromere.

Chromosome 7. - Translocation 2-7b is located about one-fourth of the way out on the long arm of chromosome 7 and at about the same relative position on the long arm of chromosome 2. Linkage tests place it near ra, with slightly less than one per cent of crossing over. Linkage tests in the homozygous translocation show linkage of ra and gl, which places the translocation to the left of ra. This is also confirmed by the linkage of B and ra ( $B-ra=167/462=36.1\%$ ). Since B is in the short arm of chromosome 2 and is thus in the 2<sup>1</sup> chromosome ra must be in the translocated portion of chromosome 7. Several translocations in the short arm of chromosome 7 have been tested for linkage with ra as follows:

T 1-7d	S <sub>4</sub>	5/231	=	2.2%
T 2-7c	S <sub>1+</sub>	24/376	=	6.4%
T 5-7d	S <sub>1</sub>	14/153	=	9.2%

Chromosome 8. - The only gene known to be located in chromosome 8 are in the distal region of the long arm. From the data of Anderson (1939) the location of the centromere must be 30 units or more to the left of msg.

Chromosome 9. - Translocation 5-9a is located in the short arm of chromosome 9 near the centromere and is about 2 cross-over units to the right of wx. This places the centromere at least two units to the right of wx. T 3-9a in the long arm of the chromosome gave 3.6% of crossing over with wx, indicating that the centromere is probably not far beyond the minimum of 2 units. The gene y has not

been located definitely but is believed to be in the long arm not far from the centromere (Beadle 1932, Burnham 1934b). Its map position is 12 units from wx.

Chromosome 10. - The only chromosome 10 genes which have been tested with translocations are g and R. Both are located far out on the long arm, apparently beyond L.6. Translocations to the left of L.3 have given from 9 to 23 per cent of crossing over with g. Probably there are different amounts of suppression involved. The centromere must lie at least 15 units to the left of g.

8-10a	S.6	17.0	104/613
8-10c	S.4	22.8	122/535
9-10b	L.1-	8.8	12/135
6-10a	L.1	9.6	33/342
3-10a	L.1+	15.7	74/471
1-10a	L.3	15.3	21/137

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1. Linkage relations of the bronze locus.  $F_2$  data suggested that bronze (b<sub>z</sub>) belonged in chromosome 9 and was located to the left of C. Backcross data obtained this past year show that the order is C-sh-b<sub>z</sub> with b<sub>z</sub> approximately 2 cross-over units from sh.

Summary of  $\frac{C \ Sh \ bz}{c \ sh \ Bz} \times \frac{c \ sh \ bz}{c \ sh \ Bz}$

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)
C	c	C	c	C	c	C	c
Sh							
<u>bz</u>							
1396	1354	76	65	15	31	0	0

C-Sh 4.8% recombination  
 Sh-Bz 1.6% "  
 C-Bz 6.4% "

Summary of  $\frac{Sh}{sh} \times \frac{Bz}{bz}$

$\frac{Sh}{Bz}$	$\frac{Sh}{bz}$	$\frac{sh}{Bz}$	$\frac{sh}{bz}$	Total	6040
2952	54	62	2972		

Sh-Bz 1.92% recombination

2. Cross sterility. A new mutant was found in 1942 showing a chlorophyll striping. No seeds were obtained from a large number of crosses in which this mutant plant was used as the female parent although these plants were self-compatible. Normal siblings were self- and cross-compatible. In many ways this situation is comparable to that previously reported by Demerec for crosses involving rice pop as the female parent.

3. Blotched aleurone. In the 1935 linkage summary the blotched aleurone gene (Bh) was shown to give 26% recombination with Y; no other linkages involving Bh were reported. This past summer I obtained data showing that Bh was close to Pl. I mentioned this to Dr. Emerson and he dug up from his old records data which show the same close linkage. I was interested in the Bh locus because of the Bh-c interaction. As Emerson found out years ago seeds of A R c Bh are not colorless but have irregular patches or blotches of color in the aleurone. In order to test the hypothesis that Bh was a gene stimulating the mutability of recessive c in the same way that Dt affects a I made a number of crosses involving a chromosome 9 lacking the C locus. The deficient chromosome 9, obtained from McClintock, had lost that portion of the short arm from the terminal knob to and including the C locus. Sh was not included in the deficiency. Plants carrying this deficient chromosome with the Sh allele and a normal chromosome 9 with recessive c and sh were pollinated by c sh Bh pollen. The Sh seeds had the C locus represented by a single recessive c allele while the sh seeds had three recessive c alleles. The two classes of seeds were examined for the grade of blotching. The data clearly show that seeds with one c allele have less aleurone color than do seeds with three c alleles. The Sh and sh phenotypes have no effect on the degree of blotching. This dosage effect of c would seem to indicate that the Bh-c situation is comparable to the Dt-a.

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1. Six deviating lines, originating as mutations in long inbred strains, have been compared in the heterozygous condition with their normal and deviating homozygous parental lines. In all cases there was an increase in size of plant (height, width of leaf, width of stalk) and in yield of grain and a hastening of the time of flowering when compared to the mean of the parents. When compared to the larger or earlier parent in each case there are definite increases in yield in four cases ranging from 17 to 104 per cent. Increases in height in four cases varied from 3 to 9 per cent over the taller parent. Time of flowering was intermediate in two cases and earlier than the earlier parent in two cases.

When outcrossed to unrelated normal lines and compared to the same crosses made with the normal parent the differences are small and show significant increases for the deviating line in only one case. Due to the very dry season and poor location this trial is not as conclusive as it may be possible to obtain.

In every case except one the deviating line is less productive than the line from which it originated and thus appears to be a degenerative change. A narrow leaf variation produces taller plants which flower earlier than the normal line. The stalk is more slender and has much less leaf area. This deviating line in previous years has been noticeably less productive but in the replicated yield test this last year it proved to be considerably more productive. Possibly this is due to the earlier maturity in a very dry year. If it proves to be more productive from now on it will be the first variation in inbred corn to be better in ability to reproduce its kind.

2. Attempts to shorten corn plants for convenience in pollination were not entirely successful. Two single crosses (Hy x L317 and Hy x 540) planted at two different times, May 27 and June 8, were bent to the ground and tied with binder twine to the adjoining plant on July 14. At this time the first planting was 3-4 feet and the second planting about 2 feet high. The plants were about one foot apart in the row. All of the plants had such a strong pull toward the erect position that all were injured to a certain extent by the string cutting into the stalks. Some plants were completely severed below the growing point and thus committed suicide rather than be tied down! Short plants were tied above the growing point. These bowed upwards between the base and place of attachment and tried to grow out of the leaf sheaths and were badly stunted. The treated plants in both plantings were shortened about 15 inches in ear height. The first planting was shortened 22 inches in average height of stalk to tip of tassel and the second planting 11 inches. The treated plants were also delayed a day or two in time of tasseling and silking. Both

pollen and seed production were seriously reduced by this treatment. Possibly the plants can be tied more loosely using a larger and softer cord. Care must be taken to tie the plants well below the growing point.

Plants that were bent over and covered with soil straightened out and were not reduced in height or delayed in flowering. Plants with half of each leaf cut off before flowering were not shortened in height but were so delayed in flowering that many of them never produced either tassels or ears!

Plants grown from seeds in which the embryo was cut out and attached to endosperms of the same or different genetic constitution were kept in the greenhouse for several weeks and later set in the field. Compared with untreated plants of the same type these plants were noticeably shortened. Since other plants grown for an equal length of time in the greenhouse were not shortened it may be that the embryo excision had something to do with this change.

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1. White-capped red pericarp. In News Letters 16 and 17 (1942 and 1943), I presented data indicating that white-cap red pericarp of such varieties of maize as Bloody Butcher is not a member of the multiple allelic series at locus P as has been supposed and suggested that this color is conditioned by multiple genes as in quantitative inheritance, one or more of which are closely linked with P. In Bloody Butcher white-cap red pericarp is associated with red cob (C-R), while in Northwestern Dent an apparently identical pericarp color is associated with white cob (C-W). Northwestern Dent alone was involved in the earlier work which had led to the idea that white-cap red was allelic to P, and Bloody Butcher alone was involved in the results reported in recent News Letters. It became important, therefore, to repeat the study with Northwestern Dent in order to determine whether the apparently identical pericarp color of the two varieties is inherited in the same way. Results to date indicate that intensity of color of white-cap red of Northwestern Dent also is conditioned by multiple genes, one or more of which are linked with P. But certain complications have arisen which give the whole problem added interest---- not to say added perplexity.

For comparison with more recent data, there are here presented records from News Letter 16 (1942), including  $F_2$  and backcrosses of Bloody Butcher, C-R, with colorless inbreds, W-W. Pericarp-color grade "0" is colorless and "6" is about the intensity of Bloody Butcher.

Table 1.

	Cob Color	Pericarp-color grades							Total	Mean grade
		0	1	2	3	4	5	6		
C-R/W-W	{ R	32	4	45	58	72	113	17	341	3.6
	{ W	49	4	24	25	13	3	—	118	1.6
C-R / W-W W-W / W-W	{ R	48	6	38	41	40	37	2	212	2.7
	{ W	119	2	7	41	28	5	—	202	1.4

Cob color here shows approximately normal mono-genic segregation, but the ratios of colored to colorless are not those typical of mono-hybrids. The mean grade of pericarp color of red-cob segregates is materially higher than that of white-cob ones. The four possible combinations of cob color and pericarp color appear with frequencies indicating linkage.

The same type of cross was repeated with  $F_4$ C-R and W-W segregates from the original Bloody Butcher cross. The results are:

Table 2.

	Cob	0 - 1 - 2 - 3 - 4 - 5 - 6							Total	Mean
		0	1	2	3	4	5	6		
C-R/W-W	{ R	—	5	5	17	34	39	3	103	4.0
	{ W	5	5	7	11	2	—	—	30	2.0
C-R / W-W W-W / W-W	{ R	—	1	4	30	29	9	—	73	3.6
	{ W	31	5	14	15	—	—	—	65	1.2

Here again segregation of cob color is normal and the mean pericarp-color grade is higher for red-cob than for white-cob segregates. But one color-class, W-R, did not occur and the ratios of colored to colorless pericarp are far from those typical of mono-hybrids.

White-cap red pericarp of Northwestern Dent, associated with white cob, C-W, also has now been studied. Crosses of this variety with a red-cob colorless-pericarp inbred, W-R, selfed and crossed with W-W are recorded below.

Table 3.

	Cob	0	1	2	3	4	5	6	Total	Mean
C-W/W-R	{ R	31	21	19	33	24	12	2	142	2.3
	{ W	--	2	3	9	11	13	7	45	4.0
$\frac{C-W}{W-R}/W-W$	{ R	83	--	1	--	--	--	--	84	.02
	{ W	1	16	19	18	5	--	--	59	2.2

Northwestern Dent was also crossed with an  $F_4$ W-R segregate from the original cross of Bloody Butcher with W-W, and  $F_1$  was out-crossed with an  $F_4$ W-W segregate of the same original cross. The data obtained are given below.

Table 4.

	Cob	0	1	2	3	4	5	6	7	Total	Mean
C-W/W-R	{ R	41	24	16	27	23	26	3	2	167	2.5
	{ W	--	--	4	24	18	22	9	1	78	4.1
$\frac{C-W}{W-R}/W-W$	{ R	60	9	--	--	--	--	--	--	69	.13
	{ W	2	10	24	54	11	1	--	--	102	2.6

The two crosses behaved essentially alike. There was some departure from 3:1 and 1:1 ratios for cob color. The striking features of these records are (1) the absence of the W-W color class in  $F_2$  and the near absence of it in the out-cross to W-W, (2) the relatively few ears and low grade of the C-R class in the out-cross, and (3) the higher mean grade of white cob than of red-cob ears in both  $F_2$  and the out-cross. Thus, in the Northwestern Dent crosses pericarp color, particularly of the higher color grades, tends to be associated with white cob rather than with red cob the reverse of that in the Bloody Butcher crosses. In short, the tendency is to maintain the parental associations of cob and pericarp colors.

Crosses of C-W with W-R, not involving Northwestern Dent but rather C-W and W-R segregates from the original crosses of Bloody Butcher, C-R, with W-W inbreds, have given results wholly unlike those in which Northwestern Dent was used as the C-W parent. The available data are given below.

Table 5.

Cob		0	1	2	3	4	5	Total	Mean
C-W/W-R	{ R	15	15	17	27	20	6	100	2.4
	{ W	12	4	5	12	1	--	34	1.6
C-W/W-R W-R/W-W	{ R	20	16	20	16	--	--	64	1.6
	{ W	24	12	14	--	--	--	50	0.8

Here again cob color segregated normally. The striking features of these data are (1) the relatively high frequency of the W-W class--all but absent in the Northwestern Dent crosses--(2) the high frequency of the C-R class in the out-cross, and (3) the higher color grade of red-cob ears. In short the behavior of these crosses of C-W/W-R, in both F<sub>2</sub> and the out-cross generations, was much less like the behavior of crosses of the same color types when C-W came from Northwestern Dent than like the cross of C-R/W-W when C-R came from Bloody Butcher.

Eight F<sub>3</sub> cultures have been grown from the three color classes, C-R, C-W, and W-R, obtained in F<sub>2</sub> from the cross of Northwestern Dent, C-W, with an inbred W-R. The results are given below.

Table 6.

Cob Color	F <sub>2</sub> Pericarp grade	Cob Color	F <sub>3</sub> progenies								Total	Mean grade
			Pericarp-color grades									
			0	1	2	3	4	5	6	7		
R	0	R	20	--	--	--	--	--	--	--	20	0
R	2	R	--	1	7	6	3	--	--	--	17	2.6
R	3	{ R	4	2	1	2	8	2	--	--	19	2.7
		{ W	--	--	--	--	11	4	1	1	17	4.5
R	4	{ R	3	3	1	1	10	1	1	--	20	3.0
		{ W	--	--	--	1	--	6	1	--	8	4.9
R	5	{ R	--	--	3	3	1	3	1	--	11	3.6
		{ W	--	--	--	--	1	1	3	--	5	5.4
W	3	W	--	--	3	17	15	2	--	--	37	3.8
W	6	W	--	--	--	--	4	3	23	5	35	5.8
W	6	W	--	--	--	--	3	10	13	3	29	5.6

As in  $F_2$ , the pericarp-color grade is higher when associated with white than with red-cob; and as in  $F_2$ , the W-W class did not occur. In one case the  $F_2$  recombination class C-R apparently bred true in  $F_3$  for the presence of both cob and pericarp color. It is evident that diverse intensities of pericarp color can be isolated by inbreeding and selection when Northwestern Dent is involved in crosses with colorless pericarp just as is true of Bloody Butcher crosses as reported in News Letter 17 (1943).

From this report and earlier ones, it can be said that the intensity of white-cap red pericarp of such maize varieties as Bloody Butcher and Northwestern Dent and of their crosses with colorless-pericarp strains, is influenced by genes whose action is like that of genes conditioning other quantitative characters. It can also be said that some of these genes are linked with the gene for red or white cob.

To assume that some of the effective genes of Bloody Butcher are represented by ineffective alleles in Northwestern Dent and that the reverse is true of other such genes, and further to suppose that some of them are more closely linked with the cob-color alleles, is of little help without the added assumption of interaction of some intensity genes with red cob and of others with white cob. On such assumptions it might be expected that an  $F_4$  C-W individual from a cross involving Bloody Butcher would have at least some of the genes of Bloody Butcher with the same linkages and interaction with red cob as in Bloody Butcher. Such C-W plants might then be expected to behave differently in crosses with W-R from that of the C-W plants of Northwestern Dent. It is not worth while at the present stage of the study to go into further detail about this complex and somewhat hazy hypothesis. The principal thing to be said in its favor is that it seems amenable to experimental genetic test.

2. Linkage of 4-row ears. Some years ago, I obtained results suggesting that a gene for the 4-row type of ear is in chromosome 6 well to the right of Pl. Four-row cultures were, therefore, crossed with 8-row translocation 6-10a. Y y and Pl pl were also involved. Backcross progenies were grown last summer. There was marked deficiency of 4-row plants as has been observed frequently before in dealing with this character. From a total of 295 plants of the backcross, the following per cents of recombination were found.

Y-Pl	29.5	Y--4-row	41.7
Pl-T	34.2	Pl--4-row	44.7
Y-T	49.5	T--4-row	51.2

From these results it is clear that, if a gene for the 4-row condition is in chromosome 6, its locus is to be sought to the left of Y rather than to the right of Pl.

3. Among the seed stocks belonging to the late Dr. A. C. Fraser were several noted as "segregating for w and l." Seed from a few of these cultures was planted in the greenhouse for student use and they were found, without exception, to be segregating for a dwarf as well as for w or l. The dwarf was later identified as pigmy and the white seedling as wl. Lebedeff, News Letter of March 6, 1938, reported 4.8% recombination between w and py, assuming one w py, none of which were actually found. Among 413 seedlings we likewise found no w py plants, further indicating the close linkage between these loci.

	<u>++</u>	<u>+ py</u>	<u>w +</u>	<u>w py</u>	<u>Total</u>
$\frac{+ \text{ py}}{w +}$	212	98	103	0	413
	<u>w - py</u> 10.1 % (assuming 1 <u>w py</u> )				

The origin of the luteus in this material is unknown. There is no record of outcrossing and, so far as we can determine, it first appeared in S<sub>4</sub> of the cross +/w x py/py. Whatever luteus this may be, it is also linked with pigmy, as indicated by the following data:

	<u>++</u>	<u>+ py</u>	<u>l +</u>	<u>l py</u>	<u>Total</u>
$\frac{+ \text{ py}}{l +}$	635	253	292	2	1182
	<u>lx - py</u> 9.2 %				

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Heterosis, grain yield. For homozygous parents and linear interaction of non-allelic genes, in the notation of Fisher et al Genetics 17:107, 1932, d is (AA-aa)/2, h is the deviation of aA from the midpoint between aa and AA.

$$\begin{aligned} P_1 &= 2n_1d + R \\ P_2 &= 2n_2d + R \\ \hline P &= 2nd + 2R \end{aligned}$$

$$\begin{aligned} F_1 &= n(d + h) + R \\ F_2 &= n(d + \frac{1}{2}h) + R \\ \hline F &= 2nd + 3/2nh + 2R \end{aligned}$$

$$\begin{aligned} B_1 &= \frac{1}{2}n(d + h) + n_1d + R \\ B_2 &= \frac{1}{2}n(d + h) + n_2d + R \\ \hline B &= 2nd + nh + 2R \end{aligned}$$

$\phi$  is the phenotype, n is number loci heterozygous in  $F_1$ , R is the least homozygote available by segregation.

Analysis of data

	Maize yield		Danmark x Height	Tomato, Powers <sup>3</sup>	
	Neal <sup>1</sup>	Lindstrom <sup>2</sup>		Red Current Fruit wt.	Johannis.x Red C Fruit wt.
Estimates of 2nh	(All records per cent of $F_1$ )				
4( $F_1-F_2$ )	148.1	136.8	76.0	+ 7.2	+ 36.0
2( $2F_1-P$ )	124.4	127.6	58.5	- 751.7	- 625.1
2( $2F_1-B$ )		113.2	62.8	- 241.6	- 228.8
2( $2F_2-P$ )	130.3	118.4	41.0	-1510.6	-1486.3
4/3( $F-P$ )	126.4	124.5	52.6	-1004.7	- 845.0
4( $F-B$ )		89.6	49.6	- 490.4	- 493.6
2( $B-P$ )		142.0	54.2	-1261.8	-1021.5
Mean 2nh	132.3	121.7	56.4	- 750.5	- 666.3
( $F_2-\frac{1}{2}B$ )		- 5.9	- 3.3	- 67.5	- 67.3
P	75.6	72.4	141.5	950.7	836.6

<sup>1</sup>J.A.S.A. 27:666, 1935.    <sup>2</sup>Proc. 7 Int. G.C.    <sup>3</sup>J.A. Res. 63:149, 1941.

The close agreement of Neal's and Lindstrom's data in the above analysis seems to indicate strongly that grain yield is a function of heterozygosis. For any locus,  $(aA-aa) - (AA-aA) = (h+d) - \sqrt{2d-(h+d)} = 2h$ . The interval from the least homozygote to the heterozygote minus the interval from the heterozygote to the top homozygote is 2h for one locus or 2nh for n loci, if h and d values are essentially the same for all loci.

For all values of h or h/d (any degree of dominance) the 7 estimates of 2nh (table) are a homogenous set, except for non-genetic fluctuations. Heterogeneity indicates interaction of non-alleles.

The three quantities,  $(P = 2nd+2R) > (F_1 = nh+nd+R) > 2nh$  must lie in that or the reverse order with each interval in any case equal to  $\frac{1}{2}\sqrt{n(h-d)-R}$ . If h=d (dominance complete) the intervals are estimates of R. On that assumption the mean estimate of R for the two maize records is minus 26.5% $F_1$ . If R cannot be negative the minimum estimate of R equal zero provides the minimum estimate of h equal 1.7d.

The top homozygote is (P-R). For these records it cannot be estimated larger than 74% $F_1$  if negative R is to be avoided.

The data on tomato weight and estimates of 2nh from them may seem to suggest a complication of interactions, although the two sets of 2nh are quite similar. It is proposed to separate allelic from any regular non-allelic interaction graphically. The points  $P_1$ ,  $B_1$ ,  $F_1$ ,  $F_2$ ,  $B_2$  and  $P_2$  are plotted with the scale on the  $\phi$  axis being that of the actual data and on the x axis that of allelic but no non-allelic interaction. Lay off a wide interval from  $P_1$  to  $P_2$  on the x axis. Trial positions of  $F_1$  may then be taken with  $F_2$  midway between  $F_1$  and the mean of parents and each backcross midway from  $F_1$  to the recurrent parent. The best trial position of  $F_1$  should be  $2(F_1 - F_2)$  from the mean of parents in the direction indicated by the data, since  $F_1$  and  $F_2$  have the same gene number and their comparison will be least affected by non-allelic interaction. If the 6 plotted points do not seem to lie on a smooth curve  $F_1$  is to be shifted right or left with  $F_2$  and backcross shifts being  $\frac{1}{2}$  of the  $F_1$  shift until the best fit to a smooth curve is obtained. The curve presumably represents regular non-allelic interaction or regular interaction with environment. Allelic interaction is evident in the 7 estimates of 2nh which should be a uniform set.

In this way, close fits to smooth curves were obtained with Power's data on the crosses Danmark x Red Current and Johannisfeur x Red Current with  $F_1$ s just slightly to the right of the parental midpoint towards heavier fruit. The curves lie between  $\phi = kx^3$  and  $\phi = b^x$  over most of the range. Both agree closely with the hypothesis of very slight dominance of heavier fruit and strong, regular interaction of non-alleles. The interaction may of course be little more than the cubic relation of weight or volume to linear dimension.

A slightly poorer fit was obtained for Johannisfeur x Bonny Best but the same dominance bias and interaction is evident. The two records on Danmark x Johannisfeur did not provide consistent solutions, perhaps because the parents are too close together. That difficulty would always appear with yield records on inbred maize.

Complementary interaction is not regular in the above sense. It might become evident in the  $(F_2 - \frac{1}{2}B)$  comparison and in aberrations from regular interaction in the above graphical analysis. With 2-factor interaction,  $F_2$  is  $9/16$  and  $\frac{1}{2}B$  is  $8/16$  of the interval from  $\frac{1}{2}P$  to  $F_1$ ; both are  $8/16$  without interaction. There is no evidence of complementary interaction as a factor of heterosis of maize yield or of tomato plant height. There seems to be no evidence for complementary interaction for tomato weight except in the cross Johannisfeur x Bonny Best. If the curve for that cross is plotted by neglecting the  $F_2$  to obtain the best fit with  $F_1$  and backcrosses the  $F_2$  deviation from the curve is large and positive which may indicate complementary interaction for heavier fruit. Plotting  $3\sqrt{\phi}$  or  $\log \phi$  might bring the complementary interaction out more clearly.

The reader should be warned that application of the above graphical analysis to data involving little or no non-allelic interaction and strong interaction of alleles as in tomato plant height may produce a straight line with the 6 values spaced the same on both axes or a smooth curve through P<sub>1</sub>, B<sub>1</sub>, F/2, B<sub>2</sub> and P<sub>2</sub>. In the latter event the six values will agree with the hypothesis of no allelic interaction on the x axis. The factor of curvature here is h. I do not now have the function.

For linear interaction of non-alleles, theoretical regressions in F<sub>2</sub> and backcross of  $\phi$  on x (gene number) are:

$$F_2; \phi = \frac{-hx^2 + (2n-1)dx + 2nhx + R}{2n-1}, \quad d\phi/dx = d + \frac{(2n-2x)h}{2n-1}$$

$$B_n; \phi = \frac{nd + (n-2n_b)hx}{n} + \frac{2n_b h}{n} + R, \quad d\phi/dx = d + \frac{(n-2n_b)h}{n}$$

n is the number of loci heterozygous in F<sub>1</sub>; n<sub>b</sub> is the number of n loci fixed AA in the recurrent parent.

These equations seem to be mainly useful for the solution of theoretical problems. For example, the backcross distribution is not skewed by any degree of dominance even though the recurrent parent is fixed AA at all n loci, (n<sub>b</sub> = n). The slope is then (d-h) or zero if h = d. If h > d the slope is negative —  $\phi$  decreases as the number of plus genes increases. If n<sub>b</sub> is zero the slope is (d+h) — positive unless h is negative and greater than d.

F<sub>2</sub> regression is a second degree parabola with slope a function of -2hx. The F<sub>2</sub> distribution is skewed by dominance. The familiar case (h = d) involves the left branch of the parabola from (0,R) rising with decreasing slope to the vertex at (x = 2n - 1/2), then dropping slightly to (x = 2n). This function may be employed with the normal frequency table to construct a theoretical distribution for any number of loci and any degree of dominance to show that maximum skewness is reached when h = d; and that skewness then decreases with increasing h. The demonstration is facilitated by working with one pair of genes. Thus if A'A' equals AA, and A'A is some greater value, d is zero and h is relatively large. The F<sub>2</sub>, (1/4 A'A' + 1/2 A'A) becomes (1/2 A'A', AA + 1/2 A'A). This distribution or the product of any number of such distributions is symmetrical. If d is now allowed to take increasing positive values, skewness increases up to h = d. East's alleles of divergent function would not intensify skewness of F<sub>2</sub>.

The conclusion of h > d for maize yield is supported by failure of mass and ear row selection, by failure of synthetic combinations of selected inbreds, by superiority of hybrids of inbreds

of diverse origin, and by the success of modern maize breeding itself. If  $h$  is not greater than  $d$ , mass or ear row selection will probably continue to surpass present maize breeding technic, because of more frequent recurrence of selection. But if  $h > d$ , present technic is the only method so far tried which should effect appreciable improvement. No degree of allelic interaction will confuse selection among  $F_1$  hybrids of homozygous lines. However, selection favoring the heterozygote loses efficiency rapidly. It is questionable if the expectation of continuing success with present technic can be supported in Mendelian theory.

Selection may be measured by the deviation of the mean of a selected group from the original mean in terms of the standard deviation of the original. Thus "student" noted selection effects of 12 and 7 sigma for high and low oil in the Illinois experiments. If the selected group may be represented by a tail of the normal area cut off above  $x = t$ , and the mean of the tail is  $s$ ;  $s = (\text{ordinate at } t) / (\text{area beyond } t)$ , or  $(P_t)$ . Then  $1/P_t$  is the number of individuals from which selection of the top one may be expected to effect a selection differential of the given value of  $s$ . The highest value of  $s$  calculable from a 15-place table of areas and ordinates of the normal curve, (W.P.A. City of New York) is 8, for which  $1/P_t$  is 222,222,000,000,000. This is roughly 2000 times the number of maize plants grown in the world in one season. That the low oil result ( $s = 7$ ) might have been obtained by selection among 400,000,000 homozygous lines is plausible. The high oil result ( $s = 12$ ) is 4 billion million times as difficult. Selection of the top 10 from 26 provides an  $s$  of one in the absence of gene interaction and environmental effects. Eight recurrences of such selection will effect an  $s$  value of 8 if variability is maintained as it was in the selection for oil. A total of 208 plants is required. From this viewpoint the oil selection results do not seem improbable as the work was done; they do seem very improbable in the face of much inbreeding.

The  $s$  value of the top one of 11, 185 singlecrosses from at least 150 inbred lines is about 4. This might be a yield increase of about 40% over original stock. The genetic variance of singlecrosses is the same as for single plants of original crossbred stock. Sigma in this case is then 10% of the original mean yield. This seems a fair estimate of the present Florida situation. The problem now is how much effort will be required for further gains. If each cycle of inbreeding must begin at the same level as the first, as indicated by the yield of synthetic combinations of selected lines and nearly all other available evidence, it will be necessary to identify the best single cross among 1,300,000 from 1600 homozygous lines to effect a further improvement of 10%. Gaining 10% again beyond that will be truly difficult, even though the genetic variation may remain unimpaired in the process as suggested by oil selection results.

A breeding technic has been proposed to deal with the case  $h>d$ , Hull, Recurrent Selection for Specific Combining Ability in Corn. J.A.S.A. in press. The method is recurrent selection in a crossbred lot for combining ability with a specific homozygous line. Selection is among testcrosses of single plants of the crossbred lot to the homozygous tester line. For any locus heterozygous in the crossbred lot and  $aa$  in the tester the testcrosses are:  $aa$ ,  $(aa+aA)/2$ , and  $aA$ , or if the tester is  $AA$  they are:  $aA$ ,  $(aA+AA)/2$ , and  $AA$ . The three testcrosses are separated by equal intervals,  $(d+h)/2$  in the first case and  $(d-h)/2$  in the second. The essential point is that the three values are equally spaced as would be the three genotypes in a crossbred population without dominance. This type of selection avoids the confusion of dominance or allelic interaction even though  $h>d$ . The price is some loss of variance. It also allows maximum frequency of recurrence of selection. Maximum frequency of recurrence with respect to resistance to insects and diseases as well as to yield and any other desirable characters would seem to be obtained by simultaneous selection.

Tomato weight and height have been included for contrast with maize yield. Estimates of  $2nh$  involving  $(-B)$  are smaller than those involving  $(-P)$  for both maize yield and tomato weight.  $B$  values might suffer less distortion from non-allelic interaction than  $P$  values since the former are nearer the center. The slightly excessive value of  $B$  in Lindstrom's data may indicate nothing more than a little heterozygosity remaining in the parent lines. Strong allelic interaction is indicated for maize yield. Tomato weight records indicate very slight allelic interaction but strong non-allelic interaction. Both the maize yield and tomato weight situations seem improbable. If the tomato weight interaction is the cubic relation of volume to linear dimension, why does not this function appear in the relations of  $aa$ ,  $aA$  and  $AA$  at one locus? Why would it not appear in the maize yield between non-allels? Why does  $h>d$  appear only in grain yield of maize; not in components, e.g. ear length and diameter, plant height, stalk diameter etc.? Tomato height in  $F_1$  exceeds the greater parent but not the sum of parents ( $P$ ). There is no evidence here of  $h>d$  and slight evidence of non-allelic interaction.

The enormous selection intensities available by properly controlled recurrent selection provide a tool for investigation of physiological limits, limits of recombination, and perhaps detection of aggregates of natural or induced mutations in a group of numerous small genes.

Appendix - January 10, 1945: Hayes et al, J.A.S.A. 36:998, 1944; data on synthetic, mean of parent lines and mean  $F_1$ . From  $F_1$  minus synthetic the estimate of  $2nh$  is 160%  $F_1$ . The  $(2F_1 - P)$  estimate of  $2nh$  is 127%  $F_1$ . If  $h = d$ , and  $R = 0$ , then  $F_1 = 2nh$ . Decline from  $F_1$  to  $F_2$  or synthetic is  $2nh/2N$ , where  $N$  is number of lines. On the foregoing assumptions, expected decline of Hayes' synthetic is  $100/16$  or 6.25 %  $F_1$ . If  $R$  is 20 %  $F_1$ , expected decline of synthetic is 5 %  $F_1$ .

The actual decline of 10%  $F_1$ , may be evidence of  $h > d$ , non-allelic interaction, or  $R < 0$ . Taking  $R = 0$ , no interaction, then  $h = 4d$  for the  $F_1$  - synthetic comparison, and  $h = 1.74d$  for  $(2F_1 - P)$ .

Kiesselbach, J.A.S.A. 22:614, 1930;  $F_2$  and  $F_3$  of 21 single-crosses,  $h = 1.98d$ .

Richey et al, J.A.S.A. 26:196, 1934;  $F_2$  10 double crosses,  $h = 1.55d$ .

Neal, loc. cit.,  $F_2$  10 double crosses,  $h = 1.72d$ .

If  $R$  is some positive value all of the above estimates of  $h$  must be revised upward.

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1. Pod corn. The sterility of homozygous pod corn is largely due to an excessive vegetative proliferation which may take various forms. Ts<sub>5</sub> is an important modifier to Tu; it brings Tu under "control" and prevents some of the unrestrained proliferation which characterizes Tu under some conditions.

Tu can also be brought under control by various unidentified genes in the modifier complex. It can be assumed that Tu is frequently a monstrous character because it is the product of the "wild" gene superimposed upon modern varieties which lack the modifiers which in wild maize must have kept the character under control. If this assumption is sound then modifiers of Tu should be particularly abundant in primitive varieties of maize. The nearest approach to "primitive" maize which we have so far discovered is the maize of the Guarany Indians of Paraguay. When this is crossed with Tu and the hybrid repeatedly backcrossed to Guarany, the glumes of the Tu tu plants are decidedly reduced. Other stocks are now being tested for their modifier complexes with regard to Tu.

We now have a homozygous true-breeding pod corn. Tu Tu plants with both staminate and pistillate fertility were found some years ago but such plants are very difficult to self because of the long interval between silking and anthesis. Selfing, however, has finally been accomplished.

The hybrid of pod corn and Guarany mentioned above has unexpectedly furnished a most striking demonstration of the real nature of the ear of maize. Under certain conditions Guarany maize has a tendency to produce a partially indeterminate ear, which once protruding beyond the husks elongates considerably. Tu accentuates this

tendency. During the past year we have obtained ears which are normal at the base but enormously elongated at the tip. This "stretching" shows that the ear of maize is fundamentally a simple spike with pairs of spikelets in whorls at the nodes of the rachis.

2. Maize-teosinte crosses. Studies of the genetics of maize-teosinte crosses have been greatly facilitated by the development of a stock with a marker gene on each of nine chromosomes, ten if the other parent is pr. (bm<sup>2</sup> lg a su Pr Y/y gl j wx g) This stock has been inbred and is uniform. Needless to say it is weak, so weak that most of the plants are barren and many do not shed pollen. But difficult as it is to maintain the stock is extremely valuable. It imparts considerable vigor to its crosses and it permits the investigator to control nine of the ten chromosomes in a single cross.

This stock was crossed with two varieties of teosinte, Durango and Nobogame. F<sub>2</sub> results are shown in the accompanying table. In the Nobogame cross the nine marked chromosomes segregate independently of each other as would be expected if no translocations, "sticky" chromosomes or other complicating factors are involved. In the Durango cross there are two significant deviations, one in the direction of linkage between Su and J and another indicating "repulsion" between Wx and Gl. There are additional deviations approaching statistical significance in the Durango cross.

In addition to the nine marker genes the plants in both crosses were scored for five characteristics, in which maize and teosinte differ. One of these, a red spot at the base of the staminate glumes, Bs, is also found in some maize varieties, particularly South American and is not regarded as an important character from the standpoint of differentiating maize and teosinte. The remaining four are characters involved in interspecific differences. They are (with the teosinte characters listed first):

1. Tr Two-ranked vs. many-ranked ear or central spike.
2. Pd Single vs. paired spikelets.
3. Sd Strong vs. weak response to length of day.
4. G. S. (Glume Score) Prominent horny glumes vs. inconspicuous membranous glumes.

Langham's symbols for the first three characteristics are used although the characters involved did not prove to be simple monofactorial in their inheritance in these crosses. All of these characters showed linkage with each other and all but the second showed linkage with one or more of the nine marker genes.

3. Chromosome segments from Florida teosinte. The segments of chromatin or blocks of genes which distinguish Florida teosinte and maize have been transferred by repeated backcrossing to a uniform inbred strain of maize. Two of these have now been crossed with the nine-gene multiple tester stock previously mentioned and backcrossed

to the multiple recessive. Here we are studying only the dominant effects of the chromatin segments from teosinte.

One of these segments proved to be linked with A on the third chromosome the other with Su on the fourth. In both cases the segments are somewhere near the center of the chromosome, the segment on the fourth includes the Su locus, the segment on the third shows approximately 25% crossing over with A, which is known to be near the end of the chromosome. Both segments have the same kinds of effects. Both reduce the number of rows of grain, the size of the seed and affect the development of the pistillate glume structure.

The segment on the third chromosome is usually inherited intact but that on the fourth is frequently broken as a result of crossing over. Parts of the segment have the same general effects as the entire segment, but in a smaller degree.

It is quite possible that the problem of inheritance of row number in maize is complicated by small segments of this kind originally derived from *Tripsacum* through admixture with teosinte. The crosses of Nobogame and Durango teosinte previously mentioned showed that genes involved in the difference between the two-ranked and the many-ranked condition occur on at least seven of the nine chromosomes tested. These are probably the same kind of genes which account for differences in number of rows of grain in some varieties of maize.

Summary of Linkages in Teosinte Crosses

Nobogame x Multiple Tester - F2

	Em <sub>2</sub>	Lg	A	Su	Y	Gl	J	Wx	G	Tr	Sd	Pd	G.S.	Bs
Durango x multiple tester - F2	Em <sub>2</sub>	-	-	-	-	-	-	-	-	+	-	-	-	-
	Lg	-	-	-	-	-	-	-	-	+	-	-	-	+
	A	-	-	-	-	-	-	-	-	I	-	-	I	-
	Su	-	-	-	-	-	-	-	-	-	-	-	+	-
	Y	-	-	-	-	-	-	-	-	+	-	-	+	-
	Gl	-	-	-	-	-	-	-	-	I	-	-	+	-
	J	-	-	-	+	-	-	-	-	+	-	-	+	-
	Wx	-	-	I	-	-	+	-	-	+	-	-	-	I
	G	-	I*	-	-	-	-	-	-	-	-	I	-	I
	Tr	-	+	+	+	-	-	+	+	-	-	+	+	+
Sd	-	-	-	-	-	-	I	-	+	+	+	+	+	-
Pd	-	-	-	-	-	-	-	-	-	+	+	+	+	-
G.S.	-	-	+	+	-	-	+	+	+	+	+	+	+	-
Bs	-	+	-	-	-	-	-	-	+	+	+	-	-	-

- + = Linkage
- I = Indication of Linkage
- = Independent Inheritance
- \* = Deviation in Direction of Repulsion

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1. Glossies. Glossy S-2 (one of Stadler's mutants) is the same as gl<sub>6</sub>, leaving gl S-1 and gl S-3 which are not completely tested.

2. White Cap. Additional backcross data show linkage between W<sup>c</sup> and T<sub>1</sub>-9b (31.3% recomb. in 208 plants); W<sup>c</sup> and T<sub>1</sub>-9c (26.0% in 127 plants) and new data show no linkage with T<sub>1</sub>-10a (149 plants). The breaks in chromosome 1 are: .6 long arm, .6 short arm, and .4(-) long arm respectively. The breaks in chromosome 9 in the first two interchanges are at .5 long arm and .2 long arm respectively. These data indicate chromosome 1 is not the one carrying white cap. A previous test with 9-10a (break at .3 long arm of 9) had shown no positive evidence of linkage from which it was concluded that W<sup>c</sup> is in chromosome 1 (1944 news letter). Closer examination of these data shows 35.4%±S.E. 5.1% recombination in one culture, independence in a second, while the combined results do not deviate significantly from 50%. In a backcross linkage test on 190 plants there was no linkage between W<sup>c</sup> and P. In the same culture f was segregating 3:1 with no indication of linkage. W<sup>c</sup>, therefore, is probably not in chromosome one, but in chromosome 9. If so it is probably in the long arm since a test with waxy showed no linkage (1944 news letter).

3. Midcob color. Some evidence of linkage between red midcob color and yellow endosperm was obtained, although the results were complicated by the presence of both W<sup>c</sup> and pale yellow endosperm. Certain cultures segregate clearly 3 red: 1 colorless midcob; others show an excess of the colorless midcob class.

4. Miscellaneous. The character brown midrib-3, bm<sub>3</sub>, is closely linked with sugary-1. F<sub>2</sub> repulsion data were: 111 Su Bm, 63 Su bm, 57 su Bm.

Vivipary-5 (vp<sub>5</sub>), reported by Lebedeff (coop. letter of March 5, 1940, page 14) as closely linked with yellow (probably Y) is not linked with the Y<sub>1</sub> in chromosome 6; since vp<sub>5</sub> and ms<sub>1</sub> segregate independently. On ears segregating 9 yellow : 7 white or pale yellow, vp<sub>5</sub> showed about 1% of recombination with yellow.

Another vivipary from C.M. Woodworth which has not been tested against vp<sub>5</sub> shows close linkage with yellow on ears segregating 3 yellow : 1 white.

Before the ears had dried in the field, viviparous seedlings from both sources were transferred to soil in the greenhouse. In all cases they proved to be albinos. Although many of these had shown some pale green color underneath the husks, this color soon disappeared.

Piebald-5 (pb5) was reported by Lebedeff in the same news letter to be linked with Y and Pl. This is confirmed by a test which shows close linkage with ms1, and also by the independent segregation of pb5 and vp5.

I have been unable to identify the zg3 character obtained originally as Co 306-1 (x) - A B pl Y zg3.

5. Partial sterility studies. One case with about 75% pollen abortion and a ring of 8 chromosomes (originated by x-ray treatment of a homozygous 5-7 interchange stock) was identified by Mr. Lazaro as involving chromosomes 1,5,6 and 7. In new data from crosses of normal x 75% sterile plants, the offspring included 75% sterile:semisterile:normal::273:71:181. Six different semisterile plants derived from the ring-of-8 were shown by him to have a single ring of 4 chromosomes one of which was number one, while in no case was number 6 involved.

A stock homozygous for the interchanges involved in the ring-of-8 (1-5-6-7) has been established.

6. Chromosome disjunction. In an abstract (Records Genetics Society-1944, p, 14) it was reported that chromosome disjunction in a plant heterozygous for interchange T5-6c was markedly changed when the position of the chromosome 5 centromere was shifted nearer the center of the cross by the presence of a homozygous inversion in chromosome 5. It was also reported that the amount of cytologically observed crossing-over when the inversion was heterozygous was different depending on whether the inversion was present in the interchanged chromosome 5 or in the non-interchanged 5. Cytologically the pairing configurations in the two cases should be similar. It was thought possible that some additional change might have accompanied the crossing-over by which the inversion was introduced into the interchanged chromosome 5. Accordingly a prophase study of the following homozygous stocks has been made: inversion in chromosome 5 T5-6c, and T5-6c plus inversion. Fortunately one of the breaks in the inversion and in T5-6c was in a heavy chromomere region, while the second was in a region with small chromosomes. Positions of breakage and rearrangement could be clearly recognized. The stock combining both also appeared to have the exact morphology expected. The differences in crossing over mentioned above appear to result from some other cause.

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Maize in Mexico. Maize in Mexico may ultimately be of practical importance to the U. S. corn belt because it constitutes such a reservoir of genic variability. We may also find that we must study Mexican varieties in order to understand our own, since our ultimately came from the south. This will be rather difficult since the whole pattern of variation in Mexican maize is so different and so much more complex than that in the U.S. The over-all morphological diversity in the maize of a single Mexican town may be as great as in all of the U.S., yet in another Mexican region 300 miles away the varieties may be entirely different but quite as varied. These regional differences are due in part to the great differences in altitude, temperature, rainfall, and growing season which characterize Mexican agriculture.

During my six months in Mexico I attempted to make a reasonably complete survey of the regions around Guadalajara (Jalisco, western Mexico) and Mexico City, with scattering collections through the intervening area. A random sample of 25 ears was taken from each field or corn crib and 15 measurements were made on each ear. A few collections have been examined cytologically for knob number and tested genetically for c, r, and pr. The following generalizations are already established.

1. Maize of western Mexico. In spite of much variation in color, row number, and Kernel size, the maize of western Mexico is prevailingly long and slender-eared, tapering somewhat to the base and long and irregularly to the apex. Its husks are so tight that there are usually conspicuous striations running lengthwise of the ear. The row number is commonly 8 to 12, the kernels are frequently broad, seldom pointed, and the denting is slight or none. The plants are strong-rooted and stiff stalked. Chromosome knob numbers are high (10 or more) and the knobs are large. The recessive genes r, c, and pr are common.

2. Maize of the Mexico City Region. The maize of this region is prevailingly short-eared and sharply and regularly tapering to the apex. Row numbers are usually above 12, the kernels are more or less pointed and are frequently strongly dented. Chromosome knobs are 0 or a very few. The plants are shallow rooted, the tasselbranches few in number and the leaves broad.

In the intervening area between Mexico City and Jalisco an intermediate and variable type is commonly grown. This is particularly true of the Mexican corn belt (the "Bajío"), centered about the state of Guanajuato.

A few outstanding varieties have wide distribution and deserve special attention.

1. Maíz dulce, the sweet corn of western Mexico is in general unlike the corn of that region and shows striking similarities to similar sweet varieties in highland South America. Dr. Kelly and I have published a detailed report on it. (Ann. Mo. Bot. Gard. 1943).

2. Cachuzintle, a large kernelled white, flour corn grown in the region around Mexico City and southward. Its plant type is strikingly unlike the other maize of that region. It is "popped" by cooking in rapidly boiling water.

3. "Elote" corns with colored aleurone. Throughout all these regions varieties with colored aleurone (both Pr and pr) are almost universally grown. They are said to be sweeter than the other varieties and are favored for green corn on the cob (elote) and parched cornmeal (pinole). Some of them have fine wrinkles and look as though they might carry su and an inhibitor.

4. Popcorns. There are at least 3 popcorns in Mexico if we include cachuzintle under that name. The other two are morphologically very different from each other in everything but popping ability. They are: Maíz reventador, the Jalisco variety for which I have recently (Ann. Mo. Bot. Gard. 1944) published a detailed report and the rice pops of Toluca and other towns near Mexico City. The latter are similar to the semi-pointed dent corns of the same region in plant and tassel characters and are grown inter-mixed with them.

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1. Gamete Selection in Corn Breeding. The method of corn improvement commonly known as "selection in self-fertilized lines" has been remarkably effective in the development of types of corn far superior to any previously existing variety in yield and in other agronomic characters of practical value.

The general experience of corn breeders and the results of the experimental studies of breeding methods which they have made indicate that, if this job were to be done over, it would be possible to make comparable advances at a much smaller cost in time and labor. The chief results of the method experiments, as related to yield improvement, may be summarized as follows:

- (1) Visual selection for yield is practically ineffective. The extent to which a plant of given genotype will contribute to yield in hybrids can only be determined by yield testing of its hybrid progeny. The factor limiting the scope of breeding operations is the number of items which may be adequately tested for yield.

- (2) The combining value of a given genotype varies considerably in combinations with different genotypes. General combining value may be tested effectively in practice by crosses on mixed populations.
- (3) The inheritance of yield genotype is in general in agreement with expectation based on the hypothesis of complementary dominant favorable factors.
- (4) There is little or no advance in yield genotype in the course of inbreeding and selection as ordinarily practiced in the production of inbred lines. This fact, convincingly demonstrated by Jenkins, is the basis for current attempts to improve the efficiency of the breeding technic, for it shows that the method owes its success not to selection in self-fertilized lines, but to the unrecognized differences in genotype of the foundation plants.

Jenkins' results suggest the possibility that an appreciable fraction of the individual plants in open-pollinated varieties may be as high in yield genotype as the best present inbred lines. Obviously, the identification of these plants near the beginning rather than near the end of the breeding operations would make for greater efficiency, for it would concentrate the analysis upon populations with the highest content of desirable genotypes. In the few outstanding selected strains it would be feasible to use test-controlled selection in the first selfed generation, where genetic variability is at its maximum. Such selection might reasonably be expected to accomplish further improvement in yield.

This is an effective and practicable method for the further sampling of the open-pollinated varieties. It is not widely used in corn breeding at present, chiefly for these reasons:

- (1) The frequency of high yield genotypes among the plants of open-pollinated varieties is low enough to make their identification much less economical than that of comparable genotypes in populations of various types which may be produced by the use of the highly improved lines now at hand.
- (2) The exceptional genotypes identified are virtually unselected as regards characters other than yield. Some of these characters are very important in practice, often more important than a considerable increment in yield.

The critical factor determining the practical feasibility of varietal sampling is the frequency in the varieties of genotypes

approximating the yield level of the present elite strains. The limiting data available (all for trials in single seasons) indicate rather high variability in yield genotype among plants of open-pollinated varieties, averaging about 9% of the mean yield after removal of the variance due to experimental error. The distribution of yield level in these populations is normal. The data unfortunately do not show where the present elite lines would fall upon these distribution curves. The general experience of corn breeding in the past 20 years is probably a better basis for estimating the frequency of plants in the foundation varieties which approximate the elite yield level. On this basis a fair estimate of this frequency is 1 or 2 per cent.

Despite its relatively low return, the further sampling of the open-pollinated varieties is essential. The greater part of the hybrid corn now grown is the product of various combinations of about a dozen inbred lines. Each of these represents a single gamete genotype, fixed as a homozygous diploid for controlled combination. These, with the additional lines of promise for further breeding, constitute a minute sample of the gamete populations of the foundation varieties. To confine further breeding to the recombinations of this small group of genotypes is to reduce its ultimate possibilities to an extent which cannot be accurately estimated from available evidence but which must be pretty drastic. Moreover, any new line produced from the recombination of the old lines is limited in its practical use, for no line gives good combinations with lines to which it is related.

Now these varietal populations, in which 1 or 2 per cent of the members reach the elite level, are populations of open-pollinated plants. Each plant represents a random combination of two gametes of the varietal gamete population. The yield potential of the plant is the result of dominant factors contributed by the two parental gametes. The frequency of genotypes of unusually high (or low) yield-potential must be much higher in the gamete population than in the population of open-pollinated plants. In a variety in which plants of yield potential equal to the elite lines occur at a rate of about 1 per cent, gametes of correspondingly high average yield potential constitute almost 10% of the gametic population. This group includes the tail of the frequency curve, and the best 1-2% may be genotypes well in advance of the elite level. Gametes constituting 1% of the population represent a level of yield potential occurring among the open-pollinated plants with a frequency of only about 1 in 10,000. Such genotypes may represent a level of efficiency in grain production which has not been closely approached by selections made from the open-pollinated plants.

The term "yield potential" (YP) as here used refers to the capacity of the genotype for contributing to yield in specific hybrid combinations. Detailed definition and illustration of the concept of yield potential must be omitted here for brevity, but it may be briefly described as follows: The yield potential of a homozygous individual, with reference to any homozygous biotype used as a

tester, is (for given conditions) the excess in yield of the  $F_1$  or test-cross over the tester biotype. The YP of the gamete genotype of this individual is one-half of this value. When the tester is a hybrid or mixed population, the YP of the tested individual is the excess of the  $F_1$  over a hypothetical yield which would be produced by biotypes representing the gamete population of the tester. This quantity is indeterminate, but since it affects all test cross yields equally its determination is unnecessary. In practice, YP with reference to a hybrid or mixed tester may be determined as accurately as to a homozygous tester, since the number of plants of each test-cross required for an adequate yield test is large enough to render negligible any variation due to individual plant variability.

In the absence of direct evidence, it is necessary to make certain assumptions regarding the inheritance of YP. The validity of these assumptions for the present purpose does not require that they be precisely correct in specific instances but rather that they represent correctly the general or average interaction of the factors involved. All assumptions regarding inheritance of YP in this discussion are derivable from two postulates which are in harmony with the evidence now available but which still require direct experimental verification. These postulates are as follows:

- (1) The YP of an individual is the sum of the YP's of its parental gametes.
- (2) The mean of the YP's of the gametes produced by an individual is equal to the mean of the YP's of its parental gametes.

In the initial stage of an isolated corn breeding program, the gamete cannot be made the unit of selection, since there is no homogeneous gamete population with which the varying gametic series may be combined for comparative testing. It is therefore necessary to select among the plants produced by the random combination of gametes of all levels. After an initial series of inbreds distinctly superior to the varietal means has been established, it is possible to use these inbreds in further sampling of the varieties, and in this procedure the gamete may be the unit of selection.

Gamete selection in practice would ordinarily involve two steps:

- (1) The selection, on the basis of outcross yield tests, of individual plants of a variety/inbred population, and
- (2) A similar test-controlled selection in the first generation self-progeny of the outstanding individuals identified in the first step. This would ordinarily be followed by continued selfing, with visual selection, to fix a line homozygous for the desired agronomic characters as well as yield genotype.

For some purposes continued selfing would be unnecessary; notably for the extraction of plants of value in complex crossing. Complex crossing for the extraction of improved lines has been little used in corn breeding, chiefly because of the limited number of good lines available. But homozygosis is not essential in the strains used in complex crossing, and the heterozygous strains identified in the plant selection and gamete selection tests may be used without sacrifice of the established inbreds.

The technic may be illustrated by an experiment now in progress. The variety used is Midland, which has given exceptionally good yields among open-pollinated varieties in central and southern Missouri and in other localities in the southern Corn Belt. The inbred used is WF9, which is outstanding in performance among lines now available in the Corn Belt, though it is a little too early to make full use of the growing season in Missouri. It is one of the parents of U. S. 13(WF9/38-11 x L317/Hy) the hybrid now most widely grown in Missouri.

Each Midland/WF9 plant is selfed and is outcrossed on a tester stock, in this case L 317/Hy. Each outcross tests the yield potential of one Midland gamete added to that contributed by the uniform gametes of WF9. Similar outcross tests on L317/Hy are made for comparison from the line WF9, and from  $F_1$ 's of WF9 with various inbreds of outstanding performance in this region.

Any Midland/WF9 plant which excels the performance of WF9 in outcross yield tests under varying and representative conditions represents a Midland gamete superior in yield potential to WF9, in a combination in which WF9 is very effective. The selfed progeny of such a plant provides a population in which further improvement by test-controlled selection should be possible. This selfed progeny is comparable to the  $F_2$  of a cross of WF9 with an unrelated elite line. As compared to such  $F_2$ 's it has, in addition to its possible advantage in yield genotype, the merit of avoiding interbreeding of the tested lines. A derivative of WF9 x L317 cannot be used effectively with either WF9 or L317; a derivative of WF9 x Midland can be used with any other line except WF9.

In comparison with selfs of plants selected from the pure variety, the variety/inbred selfs have certain distinct advantages and disadvantages. For brevity the former will be referred to as the plant-selection series and the latter as the gamete-selection series.

The chief advantage of the gamete-selection series is the expected superiority in yield potential of the best individuals in the population, or in the limited sample of the population which may be effectively tested for yield-genotype. It has in addition the following noteworthy advantages:

(1) A probably greater range of segregation for yield potential in the selfed progeny of the selected individual. This segregation is

the basis for any further improvement in yield which may be made by a second application of test-controlled selection in the selfed progeny of the selected plant. The extent of this segregation is dependent upon the difference in the specific yield-controlling genes contributed by the parental gametes. The yield potential of the selected plant would benefit as much, on the average, from five such genes, each contributed by both parents, as from ten, each contributed by only one of the parents. But the possibility of further improvement in yield potential would come only from the latter.

It would be expected that a self of an outstanding Midland plant, representing a combination of one superior Midland gamete with another, would be heterozygous for fewer yield factors than a self of a Midland/WF9 plant of equal yield potential, representing a combination of a superior Midland gamete with a superior gamete type of unrelated origin. The evidence available is very limited, but indicates that this difference is an important one.

(2) A better opportunity for extracting a line satisfactory in characters other than yield. In a series of Midland selfs, the only selection for such characters previous to yield testing would be that made among the individual foundation plants. It may be expected that the plants of highest yield potential might in many cases be unsatisfactory in other respects. The series of Midland/WF9 selfs is also virtually unselected, but since each plant is heterozygous for the favorable agronomic characters of WF9 it should be possible, in the extraction of homozygous lines from the selfed progeny, to avoid undesirable characters which are not common to the Midland selection and to WF9. This advantage will vary with the line used, but in major characters such as strength of stalk, for example, any elite line selected for use in this type of experiment would provide some insurance against the weaknesses likely to be met within unselected genotype of the open-pollinated varieties.

The chief disadvantages of the gamete-selection series are the following:

(1) In gamete selection it is impossible to fix the genotype selected from the variety; it can be used only to extract a combination of this genotype with some other genotype chosen in advance, (such as the WF9 genotype in the present example). The line ultimately derived from this combination is restricted to use in crosses not involving WF9. In plant selection a new line is derived which may be combined with other lines without restriction, and which may be crossed for further improvement with lines chosen after the properties of the selected Midland line are known.

(2) In yield testing to compare the value of the Midland gametes, the gametic genotypes compared represent only half of the genotype of the plants which are tested; in plant selection the genotypes compared are the total genotypes of the plants tested. A more accurate yield test is therefore required to detect significant

differences in the gamete-selection series. The accuracy of yield tests is limited, and this imposes a minimum limit to the difference in yield potential which may be used in breeding. Furthermore, increased accuracy is expensive, and reduction of the standard error to one-half requires yield tests about 4 times as extensive. If differences only half as large are to be detected, only about one fourth as many items could be tested with equivalent outlay.

The gamete-selection series would involve smaller differences than the plant-selection series, but the differences to be expected are considerably more than half as large. The net variability of the outcross test yields, after removal of the superimposed variability due to experimental error, is the measure of the yield potential of the plants tested. The yield potentials of a series of open-pollinated Midland plants are the sum of the yield potentials of the male and female gametes combined. These may be represented as follows:

YP of Male Gametes	$A \pm \sigma_A$
YP of Female Gametes	$B \pm \sigma_B$
<hr style="width: 50%; margin: 0 auto;"/>	
YP of O. P. Plants	$(A + B) \pm \sqrt{\sigma_A^2 + \sigma_B^2}$

In wholly unselected series, A and B are equal and the yield potential of the open-pollinated plants is  $2A \pm \sqrt{2} \cdot \sigma_A$

The yield potentials of the  $F_1$  plants of WF9 x Midland would be as follows:

YP of Male Gametes	$A \pm \sigma_A$
YP of Female Gametes	$C \pm 0$
<hr style="width: 50%; margin: 0 auto;"/>	
YP of $F_1$ Plants	$(A + C) \pm \sigma_A$

The number of tests of adequate precision that could be made with a given outlay would be about half as great for the gamete-selection series as for the plant-selection series. In view of the increased frequency of exceptional genotypes in the gamete selection series, the smaller sample would have a much higher probability of including exceptional Midland genotypes than the larger.

During the past season direct evidence on some of these points was secured in a yield test, conducted in collaboration with D. C. Anderson, at Malta Bend, Mo. The items tested included outcross tests (on L317/Hy) of the following:

- (1) 41 Midland plants
- (2) 37 Midland/WF9 plants
- (3) the line WF9, (entered for increased precision as 4 items)
- (4) 6 other elite lines (38-11, R136, 940, C.I.7, Kys, and K4)
- (5) 10  $F_1$ 's of elite lines, included to check the additive inheritance of YP.

Groups (1) and (2) each included 27 plants representing a wholly unselected sample, with additional plants from visual selection which proved unrelated to yield. These two groups thus represent respectively the zygote and the gamete population of the Midland stock used. The test was planted as a 10 x 10 triple lattice, with 12 replications.

Calculation of the data is not yet completed but the results in general are evident from direct calculation as a randomized block experiment. On this basis the least significant difference is 4.5 bu. per acre. The test-cross yields of the Midland plants varied from 60.3 to 77.8. Those of the 7 elite lines ranged from 61.8 to 77.0, that of WF9 being 64.1 bu. per acre. The test-cross yields of the  $F_1$ 's and parent inbred lines were in general in good agreement with expectation on the additive basis, though the differences between the lines crossed are not large enough to make this a very significant test of YP inheritance. The test-cross yields of the Midland/WF9 plants indicated yield levels for homozygotes of the Midland gamete genotypes ranging from 46.8 to 83.8 bu. per acre.

Seed was produced in 1944 for a further trial of plant and gamete selection in the varieties, Kansas Sunflower, Clarage, and Midland, with certain modifications of method. It may be desirable in practice to apply gamete selection not to the unselected gamete population but to a selected population secured from the exceptional plants identified by a preliminary test-controlled plant selection. To test the feasibility of this modification, the unselected plants in the varieties mentioned are selfed and test-crossed as before and are also crossed on the inbred line selected for use in gamete selection. The gamete selection series from unselected plants may be made up from these crosses, and that from selected plants or mixtures may be made up from them after the plant selection tests have been made. Each variety thus yields three distribution curves, representing the unselected plant population, the unselected gamete population and the selected gamete population. Among the inbred lines included for comparison are K4, a line of excellent performance which was extracted from Kansas Sunflower, K201C, an excellent line extracted from Midland; and 3 Ohio lines which represent the best extractions previously made from Clarage. The position of these lines on the plant and gamete distribution curves of their parent varieties should provide a more definite basis for estimating the possibilities of plant and gamete selection as compared with the methods used in producing our present inbreds.

L. J. Stadler

2. Redox relationships in the development of anthocyanin. Keeble and Armstrong, Wheldale-Onslow, Atkins, and others have presented evidence suggesting the presence of oxidase enzymes and an oxidation system associated with the development of anthocyanin. In repeating the studies made by these early workers it is possible, in the light of revised redox methods, to correct several of the interpretations of the

use of oxidase indicators, and it now appears that the oxidase enzyme of the earlier workers is in fact a lipid absorptive and oxidative system. It became increasingly apparent during the course of the present study that there is a localized absorption of the oxidized form of the common redox indicators in unsaturated fats present in anthocyanin bearing cells. The oxidation of p-phenelenediamine,  $\alpha$ -naphthol, leuco methylene blue and related indicators prior to their introduction into sections of r<sup>ch</sup> and r<sup>g</sup> tissue will give, in uniform and comparably cut sections, a greater localization of colored indicator in r<sup>ch</sup> tissue. An iodimetric method applied to this absorptive system, in appropriately prepared tissue, has made possible a qualitative study of differences between colored (r<sup>ch</sup>) and colorless (r<sup>g</sup>) tissue and has given an exact iodine number for different tissues where weak anthocyanin development, dependent upon R alleles, is to be compared with more strongly colored r<sup>ch</sup> tissue.

Iodine absorption is always greater in anthocyanin bearing cells; hence practicable microscopic qualitative observations may be compared with macroscopic anthocyanin distribution, and differences in intensity of pigmentation, by using the iodine number as a qualitative guide. The higher iodine absorption of anthocyanin bearing tissue may be seen to be localized in free plasmal lipids, in lipid material localized in "mitochondrial" or lipoclastic bodies in the cell, and in lipids impregnating cellulose walls. The lipids are highly unsaturated condensation aggregates and not true glycerides. They are not readily soluble in ordinary fat solvents but are soluble in petroleum ether after preliminary hydrolysis of the tissue and extraction with an alkaline/alcoholic mixture. The unsaturated lipids in colorless (r<sup>g</sup>) tissue have a higher peroxide number as determined by oxidation of ferrous ammonium sulphate. The extracted lipids from r<sup>ch</sup> tissue have 40% greater absorptive capacity (Wij's Iodine Method) than comparable extracts from r<sup>g</sup> tissue. Presented in the table below are the iodine numbers of leaf tissue of r<sup>ch</sup> and r<sup>g</sup> sib comparisons, as determined by halogen solutions of increasing concentration. The samples were hydrolyzed to prevent iodine addition to starch and to facilitate iodine addition to unsaturated bonds; they were dried under nitrogen to constant weight and a standard iodine method with thiosulphate titration was used and endpoints were determined galvanometrically in some cases. The samples used ranged in weight from 0.020 mg. to 0.155 mg. so that the method may be applied to small samples of tissue that are held in ethyl alcohol (not above 50%), in order to remove chlorophyll, anthocyanin, etc., with frequent changes of alcohol to facilitate elution. At all stages in the process storage under nitrogen prevents oxidative degradation and a drop in iodine values.

Halogen solutions of increasing concentration

	I	II	III	IV
r <sup>ch</sup>	3.55	9.24	12.55	50.54
r <sup>g</sup>	2.21	6.91	10.34	44.22

Using the methods outlined above a study was made of the development of pigment in excised leaves in culture. It was found that additions of dilute emulsions of unsaturated fats (corn oil, soybean oil, linseed oil) and various terpenes. (thujone, etc.) greatly increased the production of pigment, but only when sugar was also present. Glucose solutions ( $16 \times 10^{-3}$  molar) were less effective than glucose ( $8 \times 10^{-3}$  molar) plus unsaturated fat emulsions (.4%). Holding the cultures under anaerobic conditions (under nitrogen) for the first two days of a culture study inhibits production of anthocyanin but increases overall pigmentation after aerobic conditions are restored. In the table below are the iodine numbers from a typical sugar culture experiment. A marked decline in iodine number in r $\bar{g}$  and a final rise in rch with pigmentation is clearly demonstrated.

All tissue from same leaf

	r $\bar{c}h$	r $\bar{g}$
Fresh Tissue	45.95 (colorless)	51.90 (colorless)
Sugar/Anaerobic	41.70 "	44.22 "
Sugar/Same as above, but exposed to air one day.	50.54 (Anthocyanin)	40.02 "

In vitro preparations of anthocyanin extracts and unsaturated fat emulsions reveal that anthocyanin is a hydrogen acceptor and acts to dehydrogenate and oxidize the fat, and the anthocyanin becomes partially reduced and in some cases irreversibly reduced. This dehydrogenation of fat emulsions by anthocyanin is stronger when water extracts of r $\bar{c}h$  tissues are added to the emulsions. Microscopic sections of anthocyanin-bearing tissue held under anaerobic conditions and at a pH of 7.0 to 7.4 show a reduction (loss of color) of anthocyanin in lipid granules in the plasma under intense illumination and a restoration of color on diminishing the light. This is direct evidence of a reversible redox relationship between lipids and anthocyanin pigments.

It is generally true that anthocyanin bearing cells are epidermal, hypodermal or bundle sheath cells which have an excess of lipid material, and it is a general rule that cells low in lipids are lacking in anthocyanin. This fact may be determined by iodine staining in combination with extraction methods outlined above. It is illustrated in corn by the siliceous epidermal cell which, unlike its couplet partner, the fat-bearing suberized cell, lacks anthocyanin unless cultured in sugar/fat media under nitrogen followed by oxygen. Fatty and other organic acids, as revealed through the use of polychrome stains and direct acid value determinations are present in anthocyanin bearing cells before pigment is produced and there are apparently less free acids after pigment production.

Preliminary trials on B determined pigmentation indicate there is in lipid/pigment development a redox relationship similar to that obtaining in R $\bar{r}$  alleles. Trials on the other higher plants

(*Andropogon*, *Coleus*, *Petunia*, *Acer*, etc.) reveal a similar redox problem in floral and autumnal anthocyanin development.

In summation, it now appears that the oxidase system, believed by early workers to be causal in anthocyanin development, is in reality a reflection of the oxidized and dehydrogenated state of lipids which absorb and possibly oxidize redox indicators. The absorption of iodine by these dehydrogenated lipids reveals qualitative but not absolute quantitative differences between pigmented and non-pigmented tissues. Anthocyanin acts *in vitro* to bring about the dehydrogenation of fats, and wherever anthocyanin appears in the plant associated with a lipid system the fats are more dehydrogenated than in comparable non-pigmented tissue.

D. S. Van Fleet

3. Comparison of ultraviolet and X-ray deficiencies. Earlier examinations of ultraviolet induced deficiencies in maize indicated that they were terminal, whereas X-ray deficiencies appeared to be usually, perhaps always, internal. Since non-homologous pairing of pachytene chromosomes frequently occurs, this point could be settled only by a study of a chromosome arm with a terminal cytological marker. In order to select plants with breaks in this arm, a gene affecting a seedling character was essential. Enoades reported bronze (bz) in the short arm of chromosome 9 (corn letter 1943). It was found that in the presence of certain  $R^2$  alleles, distinct color developed at the tip of seedling leaves with Bz but failed to develop with bz. Deficiencies of the bronze locus were induced by irradiation of mature pollen from a knob-bed-9 stock, wx-Bz-knob. Pollinations were made on a homozygous or heterozygous bz stock, Wx-bz. The colorless-tip  $F_1$  plants which subsequently developed bronze pigment instead of anthocyanin furnished the cytological material. The usual acetocarmine smear technique was employed.

In the ultraviolet group, 3513 seedlings were examined of which 9 possibly tipless died in early seedling stage and 9 were bronze plants. In the X-ray group, 1670 seedlings were examined, of which 7 possibly tipless died in the early seedling stage and 11 were bronze plants. The cytological study of the bronze plants is summarized in the table.

Kinds of Chromosomal Change

No. bz plants	Haploid	1 break		2 break rearrangement			Not ana- lyzed
		Term. def.	Int. def.	Ring Chro- mosome	Def. trans.		
Ultra- violet							
9	2	4	0	0	2	1	
X-ray							
11	0	0	1	3	5	2	

In the ultraviolet material single breaks in the short arm of chromosome 9 gave terminal deficiencies (with the loss of the knob) in 4 plants. The shortest deficiency, about one-third of the arm, removed the bronze locus and gave less than 1% crossing over between the break and the wx locus. In two cases breaks in different chromosomes were followed by rearrangement in such a way that parts of both chromosomes were lost and only one translocation chromosome survived. These have been called deficiency translocations. In pachytene the translocation chromosome pairs homologously with parts of the two normal chromosomes, and the two single strands usually pair non-homologously to give a three-armed translocation figure. At diakinesis and metaphase I, this association appears as a chain of three chromosomes or, less frequently, as a pair and a univalent. Anaphase I shows 9-10 separations or occasionally 9-9 with a lagging univalent. Pachytene preparations were not clear enough to determine exact points of breakage in the chromosomes.

All X-ray deficiencies resulted from rearrangements involving two breaks within the same cell. In one case both breaks were in the short arm of chromosome 9, giving an internal deficiency. In 3 cases breaks occurred in both arms of 9, a ring fragment which included the centromere being formed. Five deficiency translocations were found. In the case giving the best cytological preparations (involving chromosomes 9 and 5) both breaks appeared to be at or very near the spindle fiber regions. There were no cases of terminal deficiency.

Many plants with deficiency translocations (in this and other material) show a higher percentage of normal pollen than can be accounted for by random distribution of the three associated chromosomes at the first meiotic division.

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### III. SEED STOCKS PROPAGATED IN 1944

Slightly more than 200 cultures were grown last summer. About half of these were the  $F_1$  hybrids between weak stocks and non-related inbreds made by Dr. Murray in 1943. A few plants were selfed in each of these cultures. This program was carried along by growing still other weak stocks and crossing them with inbreds. It is hoped that in the course of a few years most of the useful genes can be put into vigorous combinations of this kind. In cooperation with Dr. Randolph, a beginning was made of the transfer of a good marker gene or two to each of the trisomic stocks now available. Combinations involving trisomic V, VI, IX, and X were obtained this year.

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