MAIZE GENETICS COOPERATION

NEWS LETTER

21

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

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

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To Maize Geneticists :-

This is a call for material for the 1947 Maize Co-op News Letter. The dead line on contributions is February 15.

Since there have been many changes in personnel following the war your cooperation is requested in correcting any errors in mailing addresses and suggesting names of interested investigators who may not be on our present list.

Comments: The Maize Genetics Cooperation has received a generous grant from the Rockefeller Foundation to continue operation. Mr. James. E. Wright, Jr. has been enrolled for part time student help. Requests for seed of our genetic stocks has shown an upward trend.

Sincerely yours,

H. H. Smith

H. H. Smith

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Ed. note: A change in size of page from previous issues was necessitated by a shortage of mimeograph paper.

I. REPORTS FROM COÖPERATORS

California Institute of Technology
Pasadena, California

Alignment of translocations on chromosome 2.

Translocation	Cytological position	Linkage	Number of plants
2-3a		near lg_1	Burnham
2-6b	S.75	gl_2-3.9-T-0.9-B	2008, 3152
2-3c	S.65	B-0.5-T-4.9-sk	3317, 183
1-2b	S.6	B-5.3-T-1.4-sk	1176, 1176
2-9a	S.65	sk±0.5	784
2-3d	S	sk-8.5-T-12.5-v_4	447, 939
2-9b	S.1	ts_1-5.0-T-7.8-v_4	662, 1542
2-5a	L.1	T-7.3-v_4	Rhoades
2-4d	L	ts_1-9.6-T-8.8-v_4	125, 1059
2-5b	L	T-5.0-v_4	185
2-10a	L.2	ts_1-13.5-T-6.5-v_4	384, 1145
2-7b	L.25	ts_1-15.3-T-5.4-v_4	470, 1091
2-6d	L.3-	ts_1-26.6-T-4.2-v_4	403, 754
2-6c	L.3	ts_1-12.3-T-1.7-v_4	594, 1869
1-2(17)		ts_1-10.7-T-1.1-v_4	375, 481
2-4a	L.3	ts_1-12.9-T-1.0-v_4	395, 1522
1-2c	L.3	ts_1-8.5-T-0.3-v_4	649, 1164
2-6a	L.3	v_4±1.1	354
2-7c	L.3+	ts_1-v_4-1.0-T	592
2-3b		ts_1-v_4-4.0-T	1412
2-4b	L.6	ts_1-v_4-5.6-T	1207
2-4c	L.8	v_4-19.0-T-34.2-ch	1098, 1317
2-4(a-29)		v_4-22.3-T	622
Inv.	L.7+	v_4-34.5-T-30.4-ch	447, 447

E. G. Anderson

Ira W. Clokey

California Institute of Technology, Pasadena, California

Linkage and cytological data on translocations, to add to the list reported in the 1946 News Letter, pages 34 and 35

Translocation	Chromo-some	Locus of break	Linkage	Chromo-some	Locus of break	Linkage
2-3d	2	S.	sk-8.5-T-12.5-v_4	3	L.	na-13.0-T-7.1-a
2-4a	2	L.3	ts_1-12.9-T-10-v_4	4	L.2	su-3.3-T-14.0-Tu
2-4b	2	L.6	ts_1-v_4-5.6-T	4	L.4	Tu-gl_3-15.0-T
2-4c	2	L.8	v_4-19.0-T-34.2-ch	4	S.1	su-9.1-T-30.8-Tu
2-4d	2	L	ts_1-9.6-T-8.8-v_4	4		near Tu
2-4(a-29)	2	L	ts_1-v_4-22.3-T	4		su-5.6-T-18.8-Tu
2-5a	2	L.1	B-T-7.3-v_4	5	S.1	T-1.5-bm_1-pr
2-5b	2	L	B-T-5.0-v_4	5		bm_1±1.
2-6a	2	L.3	v_4±1.1	6	S.1	T-9.6-Pl-sm
2-6b	2	S.75	gl_2-3.9-T-0.9-B	6	L.65	Pl-sm-3.3-T
2-6c	2	L.3	ts_1-12.3-T-1.7-v_4	6	L.3	near Y
2-6d	2	L.3	ts_1-26.6-T-1.1-v_4	6	L.3	near Y
2-7b	2	L.25	ts_1-15.3-T-5.4-v_4	7	L.2	T-1.3-ra-gl_1
2-7c	2	L.3	ts_1-v_4-1.0-T	7	L.1+	T-5.7-ra-gl_1
2-9a	2	S.65	sk±0.5	9	L.65	C-wx-30.7-T
2-9b	2	S.1	ts_1-5.0-T-7.8-v_4	9	L.2	C-wx-7.5-T
2-10a	2	L.2	ts_1-13.5-T-6.5-v_4	10	L.7	T-1.9-g-R

E. G. Anderson

Columbia University
New York, New York

1. A new mutable gene.

Mutable alleles have been found at the P, Bt, and Wx loci. These mutable alleles may be described as recessives with a high mutation rate to the dominant allele. In addition there is the genically induced mutability of recessive a by the Dt gene. The effect of Bh on recessive c probably belongs in this category. A new type of mutable allele has recently been found. A dominant A allele mutates with high frequency in both somatic and germinal tissue to an intermediate allele producing light aleurone color and red-brownish plant color. The effect on pericarp color has not yet been determined. An example of the mutation rate of this mutable A allele (designated A^m) is as follows: The cross of a x A^m gave 74 kernels with self-colored aleurone, 61 kernels mosaic for deep and light colored aleurone, and 24 with light colored aleurone. At least two different intermediate alleles, differing in intensity of color in aleurone and plant, have been found.

2. Directed segregation.

A derived strain from a complex translocation involving chromosomes 5 and 3 has the following constitution: Nine normal bivalents, including chromosome 5, and a chain of three consisting of a normal chromosome 3, a short arm, and a long arm of chromosome 3. When this chain of three is present in plants with a certain genetic background, the orientation of the chain on the metaphase I spindle is approximately random, i.e., orientation of the chain leading to alternate segregation of the three members and giving euploid combinations occurs in 50 per cent of the P.M.C., while a linear orientation leading to aneuploid gametes occurs in 50 per cent of the P.M.C. In other strains, differing in genetic modifiers from the above, the orientation of the chain is such that in about 95 per cent of the cells the normal chromosome 3 passes to one pole while the other two members of the chain pass together to the other pole. Here we apparently have a case of genic control of orientation, and hence segregation. This finding is of interest in connection with the breeding behavior of Oenothera translocations.

3. Maize strains with 11 bivalents.

From the translocation mentioned above it has been possible to obtain plants with 11 pairs of chromosomes. They carry no duplication of genetically active chromatin. This increase in chromosome number was a consequence of the breaking of the centromere of chromosome 3 into two portions with both the short and long arms receiving part of the parental centromere.

M. M. Rhoades

New allele of Ga_1 on chromosome 4.

In the course of studies on a new chlorophyll striping character, a super-allele of Ga_1 on chromosome 4. was found. This allele, Ga^s, is dominant over Ga. Small ga pollen does not function on Ga^s silk even in the absence of competition with Ga or Ga^s pollen. Out of 14 such crosses only one seed developed on one ear. The other 13 ears were completely devoid of seeds. This is interesting in view of the fact that ga pollen does function on Ga silk when there is no competition with Ga pollen. Selfing of plants heterozygous for Ga and Ga^s using sugary as a marker, Ga su/Ga^s Su, showed that Ga^s pollen functions in the production of approximately 66 per cent of the kernels when competing on Ga^s silk. This super-allele appears to be independent of the striping.

Drew Schwartz

Studies with mutable waxy.

An allele at the waxy locus (wx^m), which mutates with a high frequency to Wx in both endosperm and germinal tissue, is under investigation. This allele is intermediate between Wx and wx^s; $Wxwx^m$ plants segregate approximately 3 Wx:1 wx^m; and wx^mwx^s plants approximately 3 wx^m:1 wx^s. (Ratios deviate from 3:1 in some cases due to germinal mutations.)

Typically, a wx^mwx^s plant when selfed gives three classes of kernels: About 1/4 waxy, less than 3/4 mosaic (waxy with various sized spots of normal starch), and a variable number (often 5-20 per cent) of kernels with normal starch endosperm.

The most readily observable mutation both somatically and germinally is from wx^m to Wx. Mutation rate comparisons made between different stocks by counting the numbers of Wx kernels produced in crosses wx^mwx^m backcrossed or selfed, indicate differences of the following order of magnitude:

	wx^m	Wx	wx^s	% Wx
S-43-12 selfed	140	4	1	2.7%
S-47-2 x wx^s	199	41		17.0
9903-10 selfed	63	24		27.5
9903-4 selfed	53	34		39.0

The mutable allele probably also mutates to wx^s. Four ears from a cross wx^swx^s x wx^mwx^m threw 5.3 per cent wx^s seed. A mosaic kernel when grown and selfed gave the phenotypic ratio 29 Wx:212 wx^m; 19 wx^s - the 29 Wx and 19 wx^s kernels arising by mutation. These seeds are being grown now to establish their genotype.

In a few stocks, kernels have been found consisting entirely of normal starch except for many small scattered waxy spots. Since in

these cases the rest of the ear bore all normal starch kernels (Wx by mutation), these spotted kernels may represent reverse somatic mutations of a somewhat unstable Wx' allele back to wx.

A study of the distribution of Wx and wx pollen grains in alcohol preserved tassels from $wx^m wx^m$ plants (Wx grains stain blue and waxy stain red with weak IKI) indicates that mutations may occur so early in tassel development as to affect an entire branch, or even a few neighboring branches. On the other hand, some branches carry anthers segregating in varying ratios, indicating later mutations. Mapping of ears from crosses $wx^m wx^m$ x $wx^s wx^s$ has not revealed any sectored pattern as yet.

Ruth Sager

Connecticut Agricultural Experiment Station
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Varieties of corn grown in the Northeast and in the Middle West at the same latitude are noticeably taller in the East. Several environmental conditions are involved in this growth difference, principally light intensity and temperature. Plants of many species, including maize, grown under tobacco shade cloth are significantly taller and broader in leaf than plants from the same lots of seed grown in full sunlight. Under the cloth shade the temperature is the same as outside but the humidity is higher and the light intensity is lower. The same effect is noticed in the field where short-stalked varieties of corn are grown in single rows between taller varieties. Where there is a wide alley between ranges the plants at the ends of the rows are shorter than those in the center of the rows, the plants graduating in height. Here humidity and temperature are the same but light intensity varies.

Some corn seedlings started in the greenhouse and set outdoors were shorter at maturity than plants from the same seed started outdoors. This indicated that temperature in the early stages of growth had an effect. To test this, seeds of a uniform, vigorous, first generation hybrid (Wf9 x P8) were germinated in an incubator at about 30° C. until the shoots and roots were from one fourth to one half inch long. Three different lots of sprouted seedlings, were held at 40, 50 and 60° C. for one hour. They were then planted in pots and left in the greenhouse until it was certain the plants would grow. They were then set in the field alongside plants from the same lot of seed sown in the open ground at the same time the treated seedlings were started in the incubator. Some of the treated seedlings died but enough were started in each lot and later thinned to give an even stand of plants in the field.

All three lots of heat-treated seedlings were shorter in height, less vigorous in growth throughout the season and later in flowering than the treated plants. All lots grew to full maturity and were measured after growth had ceased. The results are: Control 101: 40° C. 87; 50° C. 89; 60° C. 93 inches in height. The differences between the three

temperature treatments are small. All three averaged 90 compared to 101 inches in height for the control.

The result that was not anticipated was the pollen sterility in all treated lots. Normal tassels were produced with well-developed florets but the anthers were small and shriveled and for the most part remained enclosed in the glumes. In view of the fact that high temperatures sterilize the male germ cells in animals, from amphibians to mammals, these results are highly significant. This influence on growth is an anti-vernalization effect and may have wide usefulness in the production of hybrid seed especially if shown by other plants as well as maize.

D. F. Jones

A second "Teopod" mutation.

Another mutation to Teopod or a similar character, has occurred. This mutant was discovered by Dr. Bailey Pepper of the New Jersey Experiment Station in a field of sweet corn growing in New Jersey. We obtained seed from Dr. C. M. Haensler of the New Jersey Station. It was grown under the name of "Corn Grass" because it was much more like a grass than normal corn. The blades of the leaves are narrow and there are many tillers giving a grassy appearance. In the field the plants do not exceed three feet in height and look much less like normal corn than the Teopod of Lindstrom. However until the two stocks have been tested by crossing it is not possible to state whether they are allelic. These tests will be made in 1947.

The "second Teopod" was first grown in Connecticut in 1945. Seed from the mutant produced two kinds of plants, normal and Teopod, in approximately equal numbers. The normal plants were recessive. Open-pollinated seed from the Teopod plants gave in 1946 a 1:1 ratio for normal and Teopod. In the field in 1945 and 1946 no tassels of any kind were produced. The stock has been maintained by backcrossing to normal corn.

In the 1946-1947 greenhouse, crop grown under a shorter day, tassels with apparently good pollen have been produced.

The "Teopod" reported here makes many brace roots beneath the leaf sheaths. Some of these grow to be several inches in length. It occurred to us we might propagate these asexually and an attempt was made. The cut stalks rooted and lived for several weeks. Had the attempt been made earlier in the summer, it is possible they might have been successful.

One is forced to speculate whether mutations to such bizarre types as Teopod may have any bearing on the origin of corn. If a single gene can change the habit of a corn plant so completely, might not a reverse mutation have originally occurred to give us normal corn ? Possibly the ancestor of maize may have been something more like one of the Teopods.

W. R. Singleton

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The relation of plant colors to total dry weight in maize.

A number of years ago Brink (Jour. Amer. Soc. Agron. 26: 697-703, 1934) reported the relative yielding capacity of four different anthocyanin plant-color types, namely, purple A B Pl, sun red A B pl, dilute purple A b Pl, and dilute sun red A b pl. The stocks were so bred that all four classes occurred with approximately equal numbers in each of the 11 families involved in the test and so that the residual genotypes of the four color classes were approximately the same. Somewhat more than 3500 plants were observed and yields were reported as average dry weight of ears per plant in pounds as follows: Purple .433, sun red .569, dilute purple .561, dilute sun red .511. Thus dilute sun red, the prevailing color type of the country, yielded significantly more than purple and both sun red and dilute purple significantly more than dilute sun red.

The writer has made similar tests, using total dry weight of plant as the criterion of yield. The genes b and pl were derived from two dilute sun red (A b pl) inbred dent lines and their dominant alleles from several genetic stocks, including purple A B Pl, brown a B Pl, and reddish brown a^p B Pl. Each of these genetic stocks was crossed with each dilute sun red inbred and purple plants of the resulting progenies were backcrossed from one to three times with the same or the alternate inbred. Some of the cultures, therefore, were little if any more vigorous than the inbred lines and some showed marked heterosis. The four color types of any one culture, however, were comparable and occurred in approximately equal numbers. In table 1 are shown the average dry weights per plant in grams for the several color types of each of 14 cultures.

Table 1

Culture number	Number of plants	Mean dry weight per plant			
		A B Pl	A B pl	A b Pl	A b pl
1	90	142	111	98	110
2	76	129	132	129	110
3	91	165	163	150	145
4	92	133	145	145	127
5	93	206	217	229	184
6	73	78	82	118	78
7	96	204	229	222	230
8	89	161	162	146	150
9	89	118	103	122	104
10	89	187	207	227	222
11	74	117	122	115	117
12	76	68	88	77	74
13	96	202	181	186	199
14	94	186	172	185	203
Total	1218				
Average of mean dry weights		150	151	153	147

In addition to backcrossing heterozygous purple plants of table 1, certain sun red and dilute purple plants were backcrossed with one or other of the same dilute sun red inbreds. Results are shown in table 2.

Table 2

Culture number	Number of plants	Mean dry weight per plant			
		A B pl	A b pl	A b Pl	A b pl
15	76	143	110		
16	89	129	124		
17	86	128	134		
18	80	123	110		
19	82	132	128		
20	79	108	103		
21	91	222	238		
22	95	195	192		
23	94	201	194		
24	95	195	217		
25	88	120	106		
26	83	72	75		
27	92	259	251		
28	92	206	201		
Total	1222				
Average of mean dry weights		160	156		
29	84			143	146
30	91			149	152
31	89			166	153
32	72			136	113
33	75			157	113
34	80			140	120
35	74			126	118
36	61			71	85
37	92			253	254
38	94			199	199
39	72			196	171
40	31			202	184
41	26			215	209
Total	941				
Average of mean dry weights				166	155

From the results presented in table 1, it is obvious that purple plants were not appreciably less in dry weight than sun red and dilute purple plants. The dilute sun red plants were lowest in dry weight but not markedly less than the other three color types. The results given in table 2 were similar to those of table 1. In one lot of cultures, dilute sun red plants were slightly less in weight than sun red ones. In the second lot of cultures, dilute sun red again was less in weight than dilute purple; and the difference here is greater than in the other tests.

On the whole and in so far as the results here reported are concerned, it can be said that in segregating cultures, dilute sun red plants were slightly less in total dry weight than were plants of the other color types. Whether or not the fact has any significance, it should be remembered that, in all these tests, comparisons have been made between homozygous dilute sun red and heterozygous purple, sun red, and dilute purple.

Among genes other than B and Pl that are related to plant colors of maize, the A a pair is of fundamental importance. In most instances, only in the presence of dominant A do anthocyanin pigments develop. Where A results in purple or red, its recessive alleles usually give brown or have no appreciable effect on color. Accordingly several tests have been made of the possible influence of A and of some of its alleles on dry weight of plant. Certain colorless (green) types were crossed with the two dilute sun red inbreds used in the tests noted above. The F_1 plants were backcrossed to the colorless parent. Three sets of cultures were grown from the following crosses: (a B pl x A b pl) x a B pl, (a b Pl x A b pl) x a b Pl, and (a b pl x A b pl) x a b pl. In each set of cultures, two color types were represented. The results are given in table 3.

The records of table 3 reveal small but not consistent differences in total dry weight of plant between colored and colorless individuals of the several cultures. In averages of mean dry weights, sun red plants were about five per cent lighter than the corresponding colorless ones, while dilute purple and dilute sun red plants were heavier than their colorless sibs by six and three per cent, respectively. With the genotypic backgrounds here involved, there was relatively little effect of A and of its recessive allele a on total dry weight of plant.

There remains to be considered a possible difference between the influence of A and of some of its recessive alleles when the background genotype contains both dominant B and dominant Pl. In one lot of tests purple A B Pl was crossed with brown a B Pl and backcrossed once with the same brown. The results are recorded in the first section of table 4. Another allele of A, namely, aP, gives a reddish brown plant when in combination with B and Pl. Reddish brown was crossed with one of the two dilute sun red inbreds and the purple plants resulting were backcrossed once or twice with the same reddish brown. Recessive a2 with B and Pl gives brown plant color. This brown was crossed with reddish brown and the resulting purple F_1 plants were backcrossed with reddish brown. The genotypes concerned here are as follows: (A a2 B Pl x aP A2 B Pl) x aP A2 B Pl. All these progenies, segregating purple and reddish brown, are recorded in the second section of table 4.

Table 3

Culture number	Number of plants	Mean dry weight per plant					
		A B pl	a B pl	A b Pl	a b Pl	A b pl	a b pl
42	83	150	157				
43	73	158	138				
44	88	162	163				
45	70	176	180				
46	81	159	169				
47	88	182	215				
48	78	210	221				
49	52	189	227				
50	65	184	196				
51	57	188	193				
Total	735						
Average of mean dry weights		176	186				
52	47			144	130		
53	37			171	170		
54	42			143	105		
55	69			186	175		
56	73			171	163		
57	76			165	167		
58	79			169	163		
59	70			193	158		
60	70			166	183		
61	70			174	169		
Total	633						
Average of mean dry weights				168	158		
62	71					185	195
63	63					180	170
64	37					181	155
65	60					146	158
66	57					171	174
67	48					172	162
68	51					146	137
69	57					132	139
70	46					181	159
71	59					167	164
Total	549						
Average of mean dry weights						166	161

Table 4

Culture number	Number of plants	Mean dry weight per plant					
		A B Pl	a B Pl	A B Pl	a^p B Pl	A2 B Pl	a2 B Pl
72	48	150	134				
73	80	95	75				
74	83	109	96				
75	80	97	88				
Total	291						
Average of mean dry weights		113	98				
76	61			126	96		
77	61			119	81		
78	71			111	84		
79	61			115	85		
80	49			156	138		
81	40			128	115		
82	81			112	89		
83	63			142	114		
84	56			126	122		
85	66			140	101		
86	76			157	106		
Total	685						
Average of mean dry weights				130	103		
87	59					167	141
88	68					170	128
89	41					173	147
90	45					162	119
91	75					154	127
92	67					163	117
93	83					171	124
94	92					136	135
95	73					140	103
96	77					117	95
97	73					207	182
98	67					140	91
99	78					172	131
Total	898						
Average of mean dry weights						159	126

Brown plants of the genotype A a2 B P1 were crossed with one of the dilute sun red inbreds, with purple, and with reddish brown. In all instances the resulting F_1 purple plants were backcrossed with A a2 B P1. Here then the brown plant color is conditioned not by an allele of A but by an allele of A2. The cultures involving A2 and a2 are listed in the third section of table 4.

Cultures segregating for purple and brown plant color, as shown in table 4, whether the brown color is conditioned by a, or its allele a^P, or by a gene of a different chromosome a2, all exhibit consistent results. The averages of the mean dry weights are greater in each of the three lots of cultures by from 15 to 26 per cent for the purple than for the brown plants. Moreover in each of the 28 cultures of table 4 without a single exception, the purple plants are heavier than the brown ones.

Since for one of the genes conditioning brown plant color, namely, a, no consistent effect on weight was found when A and a were combined with B p1, b P1, and b p1 (table 3), it seems reasonable to assume that the lighter weight of brown plants conditioned by a, a^P, or a2 in contrast with purple plants conditioned by the dominant alleles of these genes, results from some deleterious effect of the brown pigments in the physiology of the plant, rather than from a direct effect of the recessive genes or of growth factors closely linked with them.

R. A. Emerson

Florida Agricultural Experiment Station
Gainesville, Florida

Mendelian interpretation of offspring-parent regressions.

Dr. K. Mather on his recent visit to this country discussed some extensions of methods proposed by Fisher, Immer and Tedin, (Genetic 1932), for estimation of dominance bias in quantitative inheritance.

My own attack in the last News Letter is also an extension of the same. My approach seems to have some advantages from employing highly inbred or homozygous parents. Uncertainty on linkage effects is largely eliminated. Dominance does not reduce correlation between phenotypes of homozygous parents and the gametes they produce. I have found no particular advantage in requiring equal frequency of a and A alleles by confining study to populations which stem from a single selfed heterozygote in each case. Samples of homozygous lines, selected or otherwise, seem to be satisfactory. If all of this be true the method must have a wide utility and may be presented again from more of a Mendelian and less of a mathematical viewpoint.

If the heterozygote aAbBcCdD is crossed to the multiple recessive tester aabbccdd, testcross progeny may be classified on kinds and frequencies of four distinct qualitative characters to obtain a reflected view of dominant alleles in gametes of the heterozygote. This is the

method of classical genetics. It has been seldom noted here that regression of number of plus characters in testcross progeny on number of dominant alleles in parent gamete is 1.0. Every plus allele in a gamete provides a plus character in the zygote, regardless of linkage.

The top dominant AABBCCDD is clearly worthless as a tester. Offspring-parent regression is zero. Intermediate testers are efficient in inverse proportion to the number or proportion of loci of AA type. Thus if testers in general are of aa type at one half of the loci which are heterozygous in the F_1 to be analyzed, a dominant allele in F_1 gametes will provide a dominant character in testcross progeny in one half of the cases. In the other half the dominant character is always provided by the tester and a dominant allele in the F_1 gamete can add nothing more. Regression is one half. Reduction of regression by dominant genes in the tester is purely a dominance effect. This dominance effect is reduced one half by selfing the testcrosses.

It hardly seems necessary to labor with the transfer of these concepts to the general field of multigenic inheritance where effects of the several genes combine in a single quantitative measure, and where dominance is taken into account quantitatively. In the former case, concern is primarily with frequencies. Basic effects of genes and dominance effects are both tacitly defined as unity throughout. In the latter case the two effects must be defined separately and quantitatively. We cannot assume that either is unity since we are concerned with degree of expression, not with just whether the character is or is not expressed.

In my attack the array of F_1 gametes is replaced with an array of gametes from an array of homozygous parents. The purpose is no longer to obtain a reflected picture of the gametic array. That array is already revealed in the array of homozygous parents. The purpose now is to estimate regressions of testcross progeny on gamete or homozygous parent with different testers. If both the bottom recessive and top dominant were available as testers, decline in regression from one case to the other would reveal directly the average degree of dominance. But neither of those two testers is likely to be available in multigenic cases. We are restricted to a study of regression relations with such testers as we may be able to develop.

For quantitative definitions of basic gene effects and dominance effects we may well employ the general scheme of Fisher, et al (1932) which is essentially that of Fisher in his 1918 paper on correlation between relatives, and of Mather on his recent visit. If the basic, phenotypic effect of substituting A for a is "d", phenotypes of aa, aA, AA are 0, d, 2d. The heterozygote is strictly intermediate. But if there is in addition an interaction of a with A to provide also a dominance effect "kd", the phenotypes are 0, d+kd, 2d. These quantities are deviations from a working origin at aa. Deviation of the heterozygote from strict intermediacy is kd, (h in the notation of Fisher, et al).

For a multiple set of genes a_1A_1, a_2A_2 - - - a_nA_n, we may as well let d and kd be average values for the several loci. Then if gene action is additive each genotype is evaluated (estimated) by summing the

several d's and kd's. The simplest case is n = 2. The checkerboard frame is

P_2		a_1a_2	A_1a_2	a_1A_2	A_1A_2
		0	2d		4d
4d	A_1A_2	2d 2kd	3d kd	3d kd	4d 0
	a_1A_2	d kd	2d 2kd	2d 0	3d kd
2d	A_1a_2	d kd	2d 0	2d 2kd	3d kd
0	a_1a_2	0 0	0 kd	d kd	2d 2kd

P_1

Table 1 -

Phenotypes of the 3 parent classes are written on the margins along with the gametes of each class. Phenotypes alone are written in interior cells for offspring. It may be desirable in teaching to write genotypes also in the cells and to evaluate some of them by counting a d for each A allele and a kd for each aA locus or each interaction of unlike alleles. It may also be desirable to write genotypes of parents and evaluate them, noting absence of dominance effects.

Table 1 is a simple regression surface. Our avowed purpose is to study the effect of k on the shape of the surface that we may interpret shapes of data surfaces in terms of k, average degree of dominance.

In practice the homozygotes a_1a_1 A_2A_2 and A_1A_1 a_2a_2 are ordinarily indistinguishable. This means that the two center columns and two center rows of table 1 may as well be pooled to conform with the situation of data on a quantitative character. Pooling provides,

P_2				
	4d	2d 2kd	3d kd	4d 0
	2d	d kd	2d kd	3d kd
	0	0 0	d kd	2d 2kd
		0	2d	4d

P_1

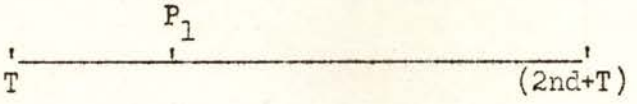
Table 2 -

Note that the entry in the central cell, e.g., of table 2 is the mean of the four central cells of table 1. It is the predicted (average) result of crosses of homozygotes of the types indicated on the margins. Deviations of the four crosses from the mean are deviations from regression due entirely to dominance, to variations in degree of heterozygosity, specific combining ability. These variations are not predictable from data on the parents. The teacher should write frequency distributions of individual crosses in each cell of table 2 along with the means given here.

Note further that, while tables 1 and 2 represent two-factor checkerboards of classical genetics with gametes of F_1 recorded on the margins and F_2 phenotypes in interior cells, the view here is arrays of homozygous lines on the margins with F_1 phenotypes of crosses of such lines in cells of the tables. Subsequently, interior values will be referred to as F_1s in agreement with modern corn breeding practice. The two situations are strictly analogous only when a and A are equally frequent in the sample of homozygous parents.

If table 2 is expanded to include many loci, parent values are 0, 2d, 4d, - - - - 2nd. A statement of the mean F_1 of any cell in terms of parent values would be the general regression function of F_1 on P_1 and and P_2. The solution of this problem was given in the previous News Letter. The mean of any cell in a table of the type of table 2, may be calculated by solving a smaller checkerboard. Detailed arrays of gametes of the two parent types are written on the margins. But this is merely taking the product of two gametic arrays, a fundamental principle of Mendelism. Hence, if u and w are the proportions of loci AA in P_1 and P_2 respectively, gametic arrays are represented in general by $(1-u)a + uA$ and $(1-w)a + wA$. In all of the crosses of P_1 type parents x P_2 type parents together, expectations are $(1-u)(1-w)aa$, $[u(1-w) + w(1-u)]$ aA, uwAA. The sum of these three proportions, each multiplied by n and by the respective phenotypes 0, d+kd, 2d, is the expected increment of mean F_1 over the multiple recessive T. Making the substitutions $u = (P_1-T)/2nd$ and $w = (P_2-T)/2nd$ provides the desired function.

The concept $u = (P_1-T)/2nd$ might be presented effectively to a class by laying off an arbitrary scale to represent the range of phenotype from



bottom recessive to top dominant. The scheme is to count 2d for each locus AA as the increment above T, hence, 2nd where all n loci are AA. The position of any homozygote P_1 on this scale reveals directly the proportion of loci AA in P_1, $u = (P_1-T)/2nd$.

The purpose of T is to adjust for the possibility that the phenotype of the bottom recessive is not zero on the data scale.

It is instructive to verify from table 2 results reported last year. The left column may represent a series of hybrids having a common parent P_1, the tester, which is aa at each locus. Lines being tested are represented on the parallel margin as different values of the variable P_2. It is clear that if the tester is completely recessive, every substitution of AA for aa in P_2 will provide a substitution of aA for aa in F_1. Regression of F_1 on P_2 is (aA-aa)/(AA-aa) or (one basic gene effect plus one dominance effect)/(two basic effects) or (1+k)/2. Note that the increment from one cell to the next, left column of table 2, is d+kd and that the corresponding increment in the P_2 column is 2d. The ratio is (1+k)/2. When P_1 is aa throughout $P_1-T = 0$. Substitute in last year's formula for bp to obtain $bp = (1+k)/2$, if $P_1-T = 0$.

Similarly from the right column of table 2, $bp = (1-k)/2$, when P_1 is AA throughout, $(P_1-T) = 2nd$. Expansion of table 2 to include many loci will not provide different results.

If, as in most actual cases, some proportion u of the loci of P_1 is AA and 1-u is aa, the weighted mean increment of F_1 is $[n(1-u)(d+kd) + nu(d-kd)]/n$. Or the weighted mean of slopes is $(1-u)(1+k)/2 + u(1-k)/2 = (1+k)/2 - uk$. Substituting $u = (P_1-T)/2nd$, $bp = (1+k)/2 - (k/2nd)(P_1-T)$.

If bp is (1+k)/2 in the left column of table 2 and (1-k)/2 in the right column the increment of bp across the table is $[(1-k) - (1+k)]/2 = -k$. The concurrent increment of u is 1, and of P_1 it is 2nd. Regression of bp on u is -k and on P_1 it is -k/2nd, as the formula $bp = (1+k)/2 - (k/2nd)(P_1-T)$ expressly states.

Thus, the values reported last year may be verified and their interpretations clarified by direct inspection of table 2.

If it is not immediately obvious that the regression estimates are unaffected by linkage and by relative frequencies of a and A alleles, except as noted, the student may need to work out some specific examples with numerical values assigned to d, kd, q, and per cent crossover and calculate regressions by machine formulas as well as by direct substitution in present formulas.

It is also clear that bp for the midcolumn or midrow of table 2 is one half, and that mean bp for all three columns or all three rows is one half. This latter case of mean bp for the whole table is the one usually calculated for regression of offspring on one parent. If a and A alleles are equally frequent, frequencies of the three columns are expected in the ratio 1:2:1 and dominance effects on regression are effectively cancelled. Note that bp is always one half if k = 0. But if a alleles are in the minority, the frequency of the right column will be greater than that of the left column and expectation is that dominance will depress mean partial regression below one half. This seems to be an adequate explanation of low regressions of yields of corn hybrids on yields of inbred parents. No alternative explanations of higher order interactions of genes or of inefficient plot technic appear to be necessary.

The function, $F_1 = b_{1a}P_1 + b_{1b}P_2 + b_2P_1P_2 + C$
may be fitted to data on samples of homozygous parents and the several F_1 crosses, or F_2 by selfing F_1. For F_1 data, estimates of b_1 are estimates of $(1+k+kT/nd)/2$, on the assumption of additive gene action. Estimates of b_2 are estimates of $-k/2nd$. Regression of bp on P_1 or on P_2 is the same estimate of $-k/2nd$.

As indicated last year, the general regression function may be solved to obtain estimates of bottom recessive, top dominant, and average degree of dominance. From the regression of bp on P_1, the estimate of P_1 for bp = 0 may be obtained. This is the critical value of P_1. Such a tester combines equally well with poor, medium and good lines on the average. Better testers may be expected to combine better with low lines than with high lines, bp is negative.

The several estimates reported last year are in all respects surprisingly consistent with the hypothesis of overdominance in vigor of corn. Tests of significance of b_2 reported last year are apparently in error. The appropriate test is for significance of departure from linear regression (Snedecor 14.3). By this test no single estimate of b_2 is significantly different from zero which may mean merely that numbers are too small. The crucial point for overdominance is whether k is significantly greater than 1. An additional set of data from C. M. Woodworth, Oren Bolin and Earl R. Leng of the Illinois Experiment Station gives essentially the same picture. The critical value of P_1 is 4.4 bu./A. Yields of inbred parents range from 2 to 40. Mean yield of F_1s is 103.

We have then one more set of data consistent with the others in supporting the conclusion that the more vigorous inbred lines in hand are worthless or worse as testers for general combining ability, since bp is zero or negative with such lines as testers.

That the few sets of data are not crucial for overdominance is not surprising. They would not be crucial even if the test for k greater than 1 showed high significance in each case. So few cases of monogenic inheritance and linkage would not prove the chromosome theory of heredity. When many more sets of data on different types of characters in both cross- and self-fertilized species have been analyzed we may have a clearer picture of where and to what extent dominance bias occurs. But even then

the results can hardly be conclusive and we will probably still need to be content with theories which agree best with the whole body of evidence.

There is a suggestion in corn yield data that the relative order of rank within either a group of inbred lines or within a group of hybrids may be quite different in two different environments. Further, the shape of the fitted regression surface may also vary greatly in response to environmental effects. If alleles A' and A perform different functions in the sense of East, A'A' may be usually inferior but sometimes superior to AA. The heterozygote A'A if better buffered to environmental shifts may be on the average superior to either homozygote. In these events, A will probably be the more frequent and also the dominant favorable in the usual environment. But the possibility exists that in some environments A' will be the dominant favorable, with dominance still in the direction of greater vigor. The dominant favorable A' will be in low frequency. The ratio k of an average dominance effect to an average basic effect may be changed and with it the equilibrium gene frequency ratio. All of these shifts will be likely to appear in the regression analyses for a given sample of stable lines and F_1s in different environments.

Fred H. Hull

Addendum.

Since the above report was typed I have received from Dr. Paul H. Harvey yield records on 12 lines and the 66 F_1s and have now completed the first part of the analysis. Yields of lines (selfed four times) ranged from 12 to 24 bu./A. Mean F_1 is 46. The critical value of P is 25, one bushel above the top line. These data seem to agree with the other sets and the conclusions drawn from them in all respects.

These last results have given me sufficient confidence to propose a further attack for which a considerable body of data is now available, - data on F_1s but not on the parent lines. Mean F_1 for any column of table 2 may be considered a measure of the general combining ability G of the constant parent for that column. It is easily demonstrated that G is a linear function of P. Hence, we may as well estimate the G value of a tester which provides zero partial regression of F_1 on G. Where the several F_1s of a group of lines have been tested in as many as four replications, one half of the replications may be employed to estimate G values for the lines. The remaining replications may estimate F_1s. Correlation of experimental errors in the two estimates are thus eliminated. The analysis, as before, is to run the simple regression of each F_1 column on the parallel column of G; then to run the simple regression of the first order regressions on G values of the respective constant parents; and finally to estimate G for bp = 0. If this critical value of G is within the range of the data the only direct interpretation I have found is over-dominance.

This kind of analysis has been run with the data on Late Yellow Single Crosses from the cooperative tests of the U.S. Department of

Agriculture with Ohio, Indiana, Illinois, Kansas, Nebraska and Oklahoma in 1943. Mean G for each line was based on the data of five states for analysis with F_1 data of the sixth state in each case. The critical value of G is below the G measure of the top line in three cases and slightly above in two cases. In the sixth case the trend of regression is upward and the data are apparently not consistent with any dominance bias toward high yield. Interstate correlations of G values of the ten lines are mostly positive but not very large. This kind of analysis is apparently of some worth where such data are available but it would seem that the attack outlined in the preceding paragraph would be more efficient and also applicable to more data.

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1. Midcob color described by Demerec some years ago is probably due to one of the alleles of the R series. At least the gene responsible for it shows close linkage with G on chromosome 10. Color in the cob is associated with colored internodes in the stalk.

2. In various strains of the Guarany corn of Paraguay mid-cob color is frequently associated with a faint purple color on the pistillate glumes or bracts. The gene responsible for this color is an allele of Pl and shows linkage with Y on chromosome 6. In the presence of B the purple glume color becomes very intense and is also extended to the leaves and stalks. This new allele, or another in the series, seems also in certain stocks to be responsible for the basal glume in the tassel.

3. Most of our time and space this season was devoted to determining on which chromosomes are located the multiple-factor segments which distinguish maize and teosinte. Relatively isogenic stocks, homozygous for one or more multiple-factor segments, were produced by crossing four varieties of teosinte with an inbred strain, backcrossing three times to the same inbred, and selfing. These were then crossed to a nine-gene linkage tester and backcrossed to a second nine-gene tester. The ears in these populations were then classified with respect to presence or absence of the multiple-factor segments from teosinte. Such classifications are far from completely accurate, because the effect of the segments vary with the influence of several genes in the tester stock, especially j and g. Linkages can be detected, however, even when the classification is purely arbitrary, although exact crossing-over percentages cannot be determined from these particular studies. The results of these tests are shown in the accompanying table. Analysis of the data was greatly simplified by the use of McBee punched cards which can be sorted with a simple, inexpensive tumbler.

Table I. Summary of linkage relations of the multiple-factor segments derived from four varieties of teosinte

Variety of teosinte	Number of segments	Linkage with chromosome number									Total number chromosomes tested
		1	2	3	4	6	7	8	9	10	
Florida	1	-	-	+	-	-	-	-	-	-	1134
"	1	-	-	+	-	-	-	-	-	-	1530
"	1	-	-	-	+	-	-	-	-	-	1575
"	1	-	-	-	+	-	-	-	-	-	1512
"	2	-	-	+	-	-	-	-	+	-	1512
"	2	-	-	+	+	-	-	-	-	-	828
"	2	-	-	I	+	-	-	-	-	-	1386
"	2	+	-	-	+	-	-	-	-	-	675
Summary	12	+	-	+	+	-	-	-	+	-	10152
Durango	1+	-	-	I	+	-	-	-	-	-	567
"	1+	I	-	-	+	-	-	-	I	-	756
"	2	+	I	+	-	-	-	-	-	-	1305
"	3	-	-	-	+	-	-	-	+	-	1494
Summary	7	+	-	+	+	-	-	-	+	-	4122
New	1	-	-	-	-	-	I	-	I	-	1539
"	1+	I	-	-	+	-	-	-	-	-	855
"	2	I	-	-	+	-	I	-	-	-	1575
"	2	-	-	-	+	-	-	-	I	-	1440
Summary	6	I	-	-	+	-	I	-	I	-	5409
Nobogame	1	-	-	-	+	-	-	-	-	-	1359
"	1	-	-	-	+	-	-	-	-	-	765
"	2	-	-	-	+	-	-	-	I	-	1521
"	2	-	-	+	+	-	-	-	-	-	1602
Summary	6	-	-	+	+	-	-	-	I	-	5247
Grand Summary	31	+	-	+	+	-	I	-	+	-	24930

+ = Linkage
I = Indication of linkage
- = Independent inheritance

The important fact gained from this study is that the multiple-factor segments which distinguish maize and teosinte are located on chromosomes 1, 3, 4, and 9 in Florida and Durango teosintes. In Nobogame teosinte which had previously been shown to carry only three major segments, chromosomes 3, 4, and 9 are involved. In "New" teosinte chromosomes 3, 4, 9, and possibly 7 are involved. The remaining chromosomes appear to carry none of the major multiple-factor segments which distinguish maize and teosinte. They are probably not lacking in genes which effect the various characters which distinguish the two species but these are either modifiers or segments too small to be detected by the methods followed in this experiment which depend wholly upon dominant or partially dominant effects.

It should be noted that chromosome 6 was not represented in the nine-gene linkage tester. Previous studies on crosses of Florida teosinte with a stock including $\underline{bm_1}$ on this chromosome gave no indication that it is involved in the four major segments.

The exact location of these segments and their length is yet to be determined. The segment on chromosome 1 shows very weak linkage with $\underline{bm_2}$ and since previous experiments with Florida teosinte had shown one of the segments to be strongly linked with P at the opposite end it is probable that this segment involves part of the short arm of chromosome 1. There is some crossing over within the segment.

The segment on chromosome 3 shows 25-30 per cent of crossing over with A. This segment is usually transmitted intact. Crossing over, if it occurs at all, is not readily detectable.

The segment on chromosome 4 includes the Su locus. There is considerable crossing over (about 30 per cent) within the segment.

Nothing is known about the position of the segment on chromosome 9, or the amount of crossing over which occurs within it.

The effects of the different segments are alike but not identical. All reduce the size of the seeds, and the diameter of the ear. All of them increase the prominence of the glumes and the number of ears produced on a single plant. At least two of these segments contribute very noticeably toward the reduction of number of rows of grain. In another experiment single segments were first rendered heterozygous by crossing with the original inbred strain, and the hybrid was then crossed with a second inbred to produce a vigorous and uniform F_1 in which approximately half of the plants were heterozygous for the segment. Ears from plants heterozygous for the segments average two rows of grain less than those which lacked the segments.

The segments have no discernible effect upon the pairing of spikelets or response to length of day. It is probable that they carry genes affecting these characteristics but that threshold limitations prevent single spikes from appearing at these levels.

The corresponding segments derived from different varieties of teosinte are similar in the nature and magnitude of their effects. In each case the segment on chromosome 4 is the most "potent." In each case this segment exhibits crossing over within the segment. Furthermore,

a stock derived from Florida teosinte and homozygous for the segment on chromosome 4 is almost identical with a corresponding stock derived from Nobogame teosinte. Differences in teosinte varieties are attributable to: (1) Differences in the number of major segments; (2) the genetic nature of the maize varieties into which they have become incorporated; and (3) the probable presence of additional smaller segments or modifying factors.

We have some evidence that a single segment in heterozygous condition can increase yields appreciably, the extent to which this happens depending in part at least upon the kind of germ plasm with which it is combined. Hybrids involving some inbred strains are noticeably improved when small amounts of teosinte germ plasm are included.

It has so far been impossible to detect these segments cytologically. Stocks heterozygous for the segment on chromosome 4 occasionally exhibit a region of weak pairing on chromosome 4, but since similar regions are found on other chromosomes little significance can be attached to this. Apparently the segments are at least partly homologous to the corresponding regions of maize chromosomes so that there is no regular and distinct failure of pairing.

The new data seem to establish beyond any reasonable doubt the hybrid nature of teosinte. At least the varieties so far studied are nothing more than maize which has been contaminated by another species. The contamination is not a random one but involves multiple-factor segments of four, or in the case of Nobogame teosinte, three chromosomes. These foreign genes must have come either from Tripsacum, or from a "pure" variety of teosinte now extinct or yet to be discovered.

P. C. Mangelsdorf

(Ed. note: In correspondence Dr. Mangelsdorf has written, "I have an abundance of seeds of several nine-gene multiple testers and shall be glad to share it with anyone who wants some.")

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"Scattergrain" white double crosses.

In the fall of 1945 a number of farmers' fields of hybrid corn were reported in Kentucky, Tennessee and Indiana which failed to set seed properly. In several fields examined near Henderson, Kentucky, the seed set ranged from as low as about 20 per cent to 85 per cent or better. The difficulty received considerable local publicity and the hybrids concerned were locally designated as "scattergrain" hybrids. The trouble was restricted to white hybrids but the reports indicated that hybrids from several different seed corn companies were involved. Evidence

pointed to male sterility on a field-wide scale as the cause of the poor seed set. The amount of sterility occurring in the same hybrid varied from field to field and seemed to be worse in bottom-land fields that were planted late.

On the basis of information obtained on the pedigrees of some of the offending hybrids, seed of a series of reciprocal single crosses was collected or produced in the greenhouse during the winter of 1945-'46. Observational plantings of these singles and several of the "scattergrain" double crosses were made at Lexington, Berea and Henderson, Kentucky, and at Beltsville, Maryland, in 1946. The data obtained do not permit a critical analysis of the cause of the sterility as, for some unexplained reason, the sterility occurred with a much lower frequency in the single crosses than in the double crosses. Sufficient data were obtained on the sterility, however, to suggest the following as important contributory factors:

1. The sterility seems to occur only in crosses which have a cytoplasmic contribution from 33-16, an old inbred line developed in Indiana.
2. Sterility in the hybrids also is influenced by contributions from the male parent. The substitution of only one line in the male parentage of one of the "scattergrain" double crosses, completely eliminated the sterility in the resulting double cross.
3. The expression of the sterility is very subject to environmental influence.

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Inflorescence structure and row number.

Two abnormalities have previously been described which affect row number in maize, each in its own particular way. (1) Multiplication, recently described by Cutler, produces two spikelets where normally there would be one. In its lowest expression it is responsible for the occasional kernel squeezed in between the regular rows of northern eight- and ten-rowed flints. In its most extreme development it produces the crowded and apparently rowless ears commonly seen in parts of Central and South America. (2) Condensation (Anderson, Ann. Mo. Bot. Gard.) is a telescoping of successive internodes and is most easily analyzed in the tassel. In its extreme form it produces an eliptical or flattened, more or less fasciated ear. In its less extreme expressions it is responsible for most row numbers of 16 or above.

While these phenomena are not unknown in other grasses, as has been demonstrated by Cutler, they are both of them of a more or less teratological nature and it seemed probable that a study of the inflorescence structure in varieties of maize which have neither condensation nor multiplication might be illuminating. A special effort has been made to study such strains and, as anticipated, the structure of their inflorescences (tassels and ears) is much simpler than in other kinds of corn. Particularly as it concerns the central spike of the tassel, it does not seem to have been previously described. It is not spiral but whorled. There are two extreme types, those with whorls of two and those with whorls of three.

Old-fashioned eight-rowed flint corns are an example of one extreme. Their central spikes are in whorls of two pairs of spikelets, each whorl bearing its spikelets at right angles to the whorls immediately above or immediately below. The uppermost tassel branches are also clearly in whorls of two. The other extreme type is found in certain persistently 12- and 14-rowed strains of corn from South America and the Southwest. They have a structure similar to the eight-rowed flints but the central spike has whorls of three pairs of spikelets and the upper portion of the tassel has whorls of three branches. In the Great Plains there are varieties with from 10 to 14 rows. When they are without condensation they show various mixtures of two-whorled and three-whorled.

The apparent spiraling of the central spike is due to the regular alternation of two patterns of spikelet position from node to node. In the eight-rowed flints, for instance, if the spikelets are on the north and south sides at one node they are on the east and west at the next, then the north and south again, and so on. In the 12-rowed corns there is a similar alternation from positions A, C, E, to positions B, D, F, and then back again to A, C, E, producing a six-ranked spike. Since each spikelet pair on the ear produces two kernels of corn the ear-equivalent of a four-ranked spike will be an eight-rowed ear; for a six-ranked spike it will be a 12-rowed ear. The structure of the tassel in these eight- and 12-rowed races is almost transparently simple. The addition of a little condensation or multiplication, however, produces an organ so difficult to analyze that until these less complicated types had been studied the basic whorling was pretty completely concealed.

These observations allow us to put forward a series of hypotheses as to the various processes affecting row number in North American corn. They have already been tested genetically in part; further experiments are under way. The hypotheses are as follows:

There are at least four quite different characters which affect row number in maize. Each operates a different lever so to speak. (1) Maize is fundamentally either in whorls of two branches or whorls of three, or in various mixtures between these two extremes. There are indications that the genetic differences between the two-whorled and the three-whorled are multiple factorial.

In North America this basically simple difference is complicated by the almost universal presence of (2) Condensation. Preliminary genetic results suggest that this may be a single recessive gene, with a number

of modifying factors which usually hold down the expression of this fundamentally teratological condition. In Central and South America (3) Multiplication is also an important factor in differences in row number. Nothing is yet known about its inheritance but various states of the phenomenon are known from very slight to very extreme. Except in an occasional inbred it is of little consequence north of Mexico. In addition to the above processes, row number can also be affected by the development or lack of development of the second floret as in Country Gentleman sweet corn and in various strains from South America.

These hypotheses can all be tested by orthodox genetic methods as soon as there are available multiple marker stocks which exhibit extreme values for the above phenomena, viz., condensation vs. non-condensation, three-whorl vs. two-whorl, multiplication vs. no multiplication.

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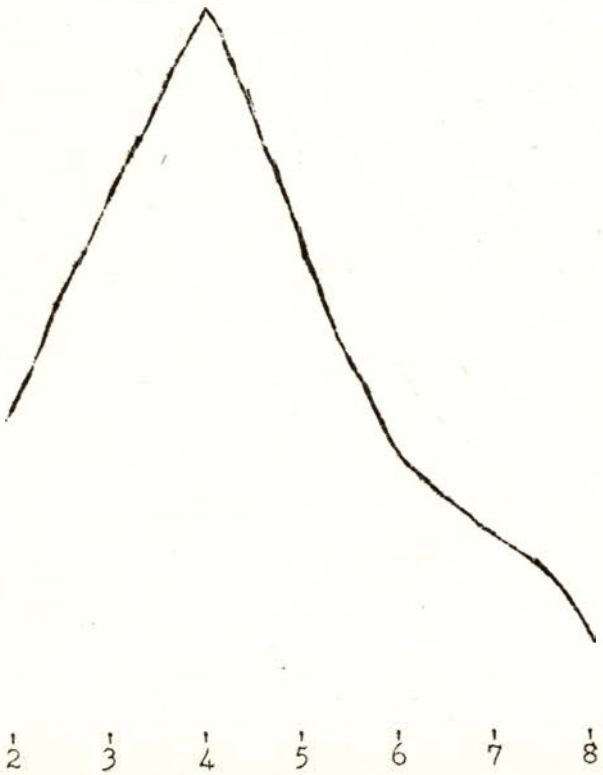
Among 80 dent corn inbreds of commercial importance, chromosome knob numbers range from 2 to 8 with a frequency distribution as follows:



The modal knob number is 4 with 3 and 5 as the two next most frequent classes. Knob number is strongly associated with at least two

morphological characters - number of rows of kernels and development of husk leaf blades (flag leaves). As knob numbers decrease, row numbers decrease and flag leaves become more pronounced. It is assumed that low knob numbers, low row numbers and long flag leaves were introduced into Corn Belt dent corn from Northern flint varieties. It is interesting and perhaps significant that these characters are so strongly linked that even after a century of breeding they still remain together in dent corn inbreds.

Although exceptions have been observed, there is also an overall correlation between high knob number and shape of ear. For example, those inbreds which approach Mexican Pyramidal in ear shape usually fall into the higher chromosome knob groups.

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New alleles of A.

The alleles A^b and aP, originating from Ecuador and Peru, respectively, are associated with brown, P-determined, pericarp color (Emerson and Anderson, Genetics 17:503-509. 1932). Both alleles are dominant to A (North American origin), which is associated with red pericarp color. Several mutants having intermediate plant color effects and arising spontaneously from A^b have a brown pericarp effect which likewise is dominant to the red of A (Stadler, News Letter 17:20-21. 1943). The divergent action of the A alleles of North and South American origin is revealed further in a series of dosage and dominance studies conducted by the author (Microfilm Abstracts 7: No. 1) and is being investigated further using exotic material collected from isolated regions of Peru and kindly supplied by the Pioneer Hi-Bred Corn Company, Johnston, Iowa. Some results of the preliminary work are reported here.

1. Dominance effects of Peruvian alleles associated with full purple-aleurone color (A-P). Small progenies from individual, open-pollinated, Peruvian ears were planted at Columbia, Missouri, in 1945 and crosses were made on aa and on A-. The progenies of the A crosses with those Peruvian plants which were shown to be homozygous for alleles determining full-purple aleurone color were planted at Ames, Iowa, in 1946. Since the A- plants in the 1945 crosses were either AA or Aa, two kinds of progenies were expected; designating the A-P alleles carried by any individual Peruvian plant as $A\text{-}P_1$ and $A\text{-}P_2$ these progenies were expected to contain plants of the following genetic constitutions:

Cross (1945)	Types in progeny (1946)
$A/A \times A\text{-}P_1/A\text{-}P_2$	$A/A\text{-}P_1$; $A/A\text{-}P_2$
$A/a \times A\text{-}P_1/A\text{-}P_2$	$A/A\text{-}P_1$; $A/A\text{-}P_2$; $a/A\text{-}P_1$; $a/A\text{-}P_2$

Both types of progeny afford a test of the dominance effects of the

Peruvian alleles, the first in compounds with the A allele and the second in heterozygotes with both the A and a alleles. Crosses were made on individual plants within progenies using aa Dt Dt plants as a pollen source. Progeny type was thus distinguished by the presence or absence of dots and this was also the basis for distinguishing A/A-P from a/A-P plants within progenies of the second type. Seven such progenies representing the test of A-P alleles of separate origins in Peru were classified for pericarp color; the available data are summarized in the following tables.

		A/A - P	
Family	Cross	red	brown
117	A/A x A-P/A-P	4	7
119	Same	9	14
120	Same	20	0

		A/A - P		a/A - P	
Family	Cross	red	brown	red	brown
118	A/a x A-P/A-P	3	4	2	3
122	Same	4	5	2	1
123	Same	0	3	0	3
124	Same	5	0	2	0

In spite of the small numbers involved in these progenies it is obvious that the A-P alleles of isolated origin are not similar in their effects on pericarp color. Moreover, in the cases of four of the seven progenies (all excepting families 120, 123 and 124) the two A-P alleles associated in individual Peruvian plants show contrasted behavior. The data suggest that A-P alleles, so far as these progenies represent them, are of two types: One determining red pericarp color and indistinguishable from A; the other determining brown pericarp color and having an effect completely dominant to that of A. There is no evidence for the existence of an A-P allele having a brown pericarp effect which is recessive to A, unless it be found that the progenies of the red pericarp types in families 117, 119 and 120 segregate ears showing brown pericarp color.

2. Dominance effects and response to Dt among Peruvian mutants of the aP and a type. Some of the Peruvian plants which were crossed to A tester in 1945 were not homozygous A-P; six of the test cross ears gave 50:50 ratios for purple; colorless aleurone and two gave 50:50 ratios for purple; pale aleurone. In each of these eight cases some of the seeds having colorless or pale aleurone showed dots. Since the tester parent was a^{dt} a^{dt} RR CC DtDt in constitution, the presence of these dots establishes with certainty that the colorless and pale seeds are due to mutant alleles at the A locus; if a dominant dilution factor or a recessive factor other than a were responsible for the dilution effects the

seeds would be expected to be without dots. This apparently is the first report of the occurrence of recessive a in South American material; since five of the six Peruvian plants which were found to be heterozygous for a were of separate origin this mutant probably is widely distributed in Peruvian material. It is likely that these types failed to be recognized earlier because of the frequent occurrence in Peruvian material of the recessive forms of the genes R and C, which complement A in pigment production and because they may not have been studied in backgrounds providing the Dt gene which is specific for a.

The action of the pale mutants (designated a^{P}-P) was studied further in progenies providing the combinations a^{P}- P/a and a^{P}-P/A. In the cases of both pale mutants, the combinations with recessive a were invariably associated with brown pericarp color, as were those with A. To test the response of the a^{P}-P alleles to the Dt gene, crosses were made between a^{P}-P/a and the tester a^{dl} a^{dl} Dt Dt (the a^{dl} gene does not mutate under influence of Dt). Without exception, the pale seeds (a^{P}-P/a^{dl}, Dt) on ears from these crosses were without dots, whereas colorless seeds (a/a^{dl}, Dt) on the same ear were dotted. Hence, both a^{P}-P alleles are similar to a^{P} in their pericarp color effects and response to Dt, though they may differ from each other and from a^{P} in the matter of their determination of plant and aleurone pigmentation.

Similar studies are in progress with the six Peruvian a mutants (designated a-P). The limited data which are available at the time point to a divergence in type of action within the a-P group as well as between members of that group and recessive a. All six members are associated with brown pericarp color as determined in heterozygotes with a. Dominance effects in compounds with A have been determined for only two of the six mutants but in both cases there is complete dominance over the red effect of A. This is the first knowledge of an a allele which is associated with colorless aleurone and brown plant color, in which respects it is recessive to A, and yet shows complete dominance to A in its effect on pericarp color. Of the four a-P mutants tested for response to the Dt gene, one proved to be dottable, the other three being without response. The two mutants mentioned as showing dominance to A in pericarp color effect do not respond to Dt. Except for the products of X-ray and ultraviolet treatment there are no past reports of a mutants which fail to respond to Dt; Rhoades (News Letter 15: 6. 1941) describes an a mutant which is indistinguishable from a with the exception that it shows much reduced response to Dt, but this allele, unlike the a-P alleles, is recessive to A in pericarp color effect. The lack of response to Dt reported here for three naturally occurring a-P mutants suggests that the failure to dot in the presence of Dt is not a valid criterion of deficiency at the A locus.

The evidence reviewed here adds to an already complex picture of gene action at this locus. Most significant, from this standpoint, is the evidence on the extreme antimorphism of at least two of the a-P alleles. The antimorphic effects of certain of the A alleles have been reviewed previously (Microfilm Abstracts 7: No. 1). The evidence is not in support of certain hypotheses, notably those of Wright and Stern, which have been advanced to explain antimorphic effects. It is suggested that the antimorphic behavior of the alleles of A may be explained on the basis of an hypothesis which holds a single gene capable of entering into

two different reactions. It is the purpose of further investigation of the Peruvian alleles reported on above to provide additional tests of this hypothesis.

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For a few years observations have indicated that teosinte has more tolerance to heat and drought and possibly more resistance to certain diseases and insect damage than corn. Efforts to improve inbred lines of corn by modifying them with teosinte characters have progressed far enough to give a suggestion of the results to be expected. Various Texas lines were crossed with Florida teosinte, backcrossed to corn from once to three times, and selfed each generation afterwards. In the development of the modified lines, no effort was made to select by observation among the segregates available for use. Plants were selfed at random, and only those plants or ears that were seriously affected with such abnormalities as disease, insect damage, and sterility were later discarded.

Tests of the desirability of the modified lines as compared to the original (unmodified) corn lines were of two kinds: (1) Tests of the lines themselves to compare their tolerance to artificially applied heat; (2) Yield tests of the various lines crossed to a common tester, conducted under field conditions.

1. Heat-tolerance tests. The procedures followed in making tests for tolerance to heat were based on those used for several years at the Kansas Agricultural Experiment Station, although in some respects there are considerable differences between the Kansas methods and mine. Inbred plants of Tx4R-3 and of eight modifications of it were grown and given artificial heat treatments in an oven in six replications, each replication being grown and treated at a different time. Glazed pots with top inside measurement of four inches were used. The pots were selected for uniformity. The soil used for the first five replications was a thorough mixture of sandy loam and compost. That used for the sixth was relatively homogeneous Houston Black Clay.

In each replication, five pots of each line were planted, and an effort was made to have a final stand of two plants to the pot. This procedure usually resulted in 10 plants of each line for each replication.

The plants were given the artificial heat treatment when 13 to 15 days old. The oven used was electric, automatically controlled, with forced ventilation. It was designed for other purposes, and the fluctuation in the temperatures obtained led to some difficulties. However, after a few replications had been treated for practice, the method was found to be usable.

Prior to each application of heat, the soil in the pots was

well-saturated with water. The pots were randomized in the oven and kept under heat treatment for eight hours at 55° C. After the treatment was complete, the plants were kept in the greenhouse for 5 to 30 days without water while the readings of the results were taken. It was found most practicable to take the first reading about 24 hours after treatment, because the extent of the damage to the plants was more readily determined after this lapse of time. The best method found of recording the results was to tabulate the number of days that each plant lived after treatment. In most of the replications no plants were living 10 days after treatment, and those which did live this long or longer were considered not to have been killed by the treatment.

For the purpose of analyzing and studying the results, it was found desirable to assemble all the data for each entry into a single score. In order to accomplish this objective, the combined number of days that all the plants of an entry lived after treatment was adopted as the score. Thus, in the fifth replication of modified line No. 1, the 10 plants lived the following numbers of days: 3, 6, 3, 20, 3, 17, 3, 3, 5, 15. But, since a plant is not considered to have been killed by the heat treatment when it lived 10 days or longer, all numbers above 10 were reduced to 10, and therefore the numbers actually added in order to get the score of this entry were 3, 6, 3, 10, 3, 10, 3, 3, 5, and 10. The score of this entry, therefore, is 56. The highest possible score is 100, and the lowest is zero. The score of each entry is shown in table I, the various lines being listed in descending order of their observed tolerance to heat:

Table I.

	Replications						
Lines	1	2	3	4	5	6	Average
3	45	38	20	85	100	62	58.3
9	32	26	30	100	96	60	57.3
5	47	22	12	90	96	30	49.5
6	28	22	16	71	100	59	49.3
4	26	22	16	60	94	61	46.5
Tx4R-3	36	18	10	50	87	42	40.5
1	22	32	26	77	56	26	39.8
2	18	14	20	30	93	33	34.7
7	36	14	16	34	69	30	33.2

For significance, .05 = 14.6

Since the difference necessary for significance on the .05 level is 14.6, the indication is that two of the lines modified with

teosinte characters are more tolerant to heat than the original line Tx4R-3. Whether tolerance to heat and to drought are related phenomena, as reported by some investigators, has not been determined in this study. However, the yield tests, to be discussed in the following paragraphs, were conducted with that possibility in mind.

2. Yield tests. One yield test was conducted each year from 1943 to 1946 on hybrids involving the group of Tx4R-3 lines tested for heat tolerance, and several tests were conducted on certain other groups. In all the yield tests, the uniform tester was a single cross, commonly one with which the original inbred is combined when put into agricultural use. One or more checks were always included. Except where the contrary is indicated, one check was the original inbred crossed with the uniform tester, and various hybrids whose usual performance was known were often used as supplements.

The most satisfactory results of yield tests were obtained with groups of lines other than Tx4R-3 and its modifications. Although results of the heat tests indicate that additional tolerance has been introduced into Tx4R-3 by crossing it with teosinte, no field test has shown convincingly that the yielding ability of any of the modified Tx4R-3 lines should be adjudged superior to that of the original. Tests conducted during 1945 and 1946 showed only that some of the modified lines were in the same class with the original Tx4R-3 and that others were inferior. As would be expected, one or more modified lines gave actual yields greater than the original Tx4R-3 in each test conducted, but in none of these instances was the difference significant. It should be pointed out, however, that tolerance to drought did not have a fair chance to manifest itself in terms of yield in any test conducted on the Tx4R-3 group. In 1943 and 1944 the yield tests were a failure, principally because of poor stands and accidental damage. In 1945 and 1946 there was no appreciable drought during the critical part of the season.

More interesting results of yield tests were obtained with a group of modified Tx127C lines. A small portion of the results of the two tests conducted in 1945 and 1946 is shown in table II.

The 1945 test of the Tx127C lines contained 36 entries and the 1946 test contained 25 entries. Since the two tests did not contain the same entries, but had only certain ones in common, it is impracticable here to combine all the results briefly in one table. However, the following table does include the highest-yielding entry and one check in each test. The lowest-yielding entry tabulated here from the 1945 test stood 14th among the 36 in the test, and the lowest shown from the 1946 test stood 16th among the 25 in the test. A blank indicates the omission of the entry from the test.

Table II.

Pedigree*	Average yield bu. per acre 1945	1946
42116-21-2	44.8	59.5
42116-25-3	42.6	
Tx. Hybrid No. 18 (Ck.)	40.8	
42116-15-2	39.4	65.7
42116-27-1	38.2	49.3
42116-28-5	37.0	55.4
42116-28-4		45.6
Tx127C (Ck.)		44.0
Difference for significance, .05	7.26	9.75
Difference for significance, .01	9.63	12.06

*The tester in each instance was Tx173D x Tx203

It may be observed from these results that some of the Tx127C modified lines, such as 42116-21-2 and 42116-15-2, show considerable promise. It is interesting that some of them gave improved yields during a season when there was no serious drought or other hazard to which teosinte is known to be especially tolerant. Of course there are possible explanations. It seems fairly probable that the introduction of teosinte germ plasm into Tx127C resulted in modified lines with more remote relationship to the tester. Remoteness of relationship between the two parents of a cross is often believed to be an important factor affecting hybrid vigor. Another possible explanation is simply that additional "yield genes" have been acquired from teosinte.

A few teosinte-modified lines of Tx132A and Tx102A have been developed and tested, but the results to the present do not indicate appreciable improvement in them.

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A pair of genes influencing the intensity of yellow endosperm color was reported in the Maize News Letter for January 31, 1944. Segregations of 3 dark yellow to 1 lemon yellow were obtained in selfed progenies. The gene in question was closely linked with opaque-2 in chromosome 7. No symbol was suggested. The situation with regard to the genes for endosperm color is not entirely clear. Five genes have been numbered and one or two additional genes apparently are known. It is suggested that the pair of genes discussed here be designated as $\underline{Y_8}$ $\underline{y_8}$.

During the past season data were obtained on a three-point backcross test involving the cross $\frac{+\ +\ +}{\underline{o_2}\ \underline{y_8}\ \underline{v_5}}$. These data are reported below:

Parental combinations		Recombinations					
		Region 1		Region 2		Region 1 & 2	
404	374	6	11	21	23	0	0
778		17		44		0	
		2.0%		5.2%		0.0	

The gene order indicated is $\underline{o_2}$ - 2.0% - $\underline{y_8}$ - 5.2% - $\underline{v_5}$.

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Natural teosinte-corn hybrids in Guatemala.

Teosinte occurs as a weed in corn fields over extended areas in the Jutiapa - Progresso - Lake Retana area in south central Guatemala and in the San Antonio Huixta area in the northwestern part of the country. Botanists who have visited these areas, including Weatherwax, Kempton and Popenoe, noted the absence of hybrids in the fields where corn and teosinte were growing together and flowering at the same time. This was surprising in view of the fact that the two species were known to hybridize readily under controlled conditions and their hybrids are fully fertile.

The Jutiapa - Progresso - Lake Retana area was visited in

November, 1946, with Dr. I. E. Melhus, Director of the Iowa-Guatemala Tropical Research Center. A thorough search for natural hybrids was made in corn fields containing teosinte as a weed extending for 40 kilometers along the highways in this area. No hybrids were discovered. Extensive collections of corn and teosinte seed were made from these fields and it is planned to grow this seed to determine whether natural crossing occurred during the current season in fields observed to have corn and teosinte of the same stage of maturity growing in juxtaposition.

Subsequently, the San Antonio Huixta region was visited together with Dr. George Semenuik. As a result of an extended search in this area approximately 30 hybrid plants were discovered. With very few exceptions all of these plants apparently were first generation hybrids having typical four-rowed ears. One hybrid plant with eight-rowed ears and one with predominantly two-rowed ears similar to the teosinte parent were found. Open-pollinated seed from these plants was harvested for a study of the progeny.

An unsuccessful attempt to hybridize Guatemalan Tripsacum and corn.

Having been successful in obtaining hybrids between diploid and tetraploid forms of corn and Tripsacum dactyloides native in the United States, the possibility of obtaining similar hybrids involving corn and Tripsacum species which are native in Central America was investigated. Tripsacum dactyloides is not known to occur in Latin America. Of the various species which do occur there, all that have been studied have proved to be tetraploids with approximately 72 chromosomes.

Since very special conditions are required to obtain hybrids of diploid Tripsacum dactyloides and diploid corn, the possibility seemed very remote that the tetraploid Tripsacum of Central America would hybridize with the diploid corns of that region. However, in developing an hypothesis of the origin of modern varieties of cultivated corn based on the assumption that teosinte resulted from the hybridization of Tripsacum and corn and that the chromosome knobs and various other important characters of corn came from Tripsacum by way of teosinte, Mangelsdorf and Reeves assumed that natural hybridization of Tripsacum and corn did occur in Central America. Hypotheses are of little value unless they can be tested. Fortunately, a direct test of this hypothesis, formulated nearly 10 years ago, involved no special difficulties. Tripsacum and corn were found to be in flower at the same time in readily accessible areas in the neighborhood of Guatemala City and Antigua at altitudes of approximately 5,000 feet. More than 200 ear shoots of native corn plants from three different fields were carefully pollinated with Tripsacum pollen from plants collected in their natural habitat in the same region. In making pollinations by applying a mixture of Tripsacum and corn pollen directly to the bases of the corn silks and in culturing the embryos of resulting aborted seeds, the same technique was used that previously had been successful at Ithaca in obtaining a considerable number of Tripsacum-corn hybrids. From three to four weeks after pollination each ear was carefully scrutinized for possible hybrid seed, the embryos of seeds suspected of being hybrid were cultured in a sterile nutrient agar and flown directly to Ithaca where their chromosome number was determined from root-tip counts. There were no hybrid seedlings. All had 20 chromosomes.

This test failed to confirm the assumption of Mangelsdorf and Reeves that in the recent past Tripsacum and corn hybrids occurred in western Guatemala, subsequently designated by Mangelsdorf and Cameron as the secondary center of origin of cultivated maize. However, it would be desirable to make additional tests employing other species of Tripsacum which are found elsewhere in Central America. Also, a careful search should be made for diploid Tripsacums throughout Central America.

L. F. Randolph

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Linkage data on several unlinked characters were gathered and analyzed by graduate students.

1. The silky which appeared in the F_2 of a cross between two inbred lines segregated in an F_2 to give a ratio of 15 normal : 1 si and approximately 3:1 in a backcross.

Red collar (base of tassel glumes) vs. green segregated 9:7 in F_2 in one of these cultures. Based on small numbers, si was independent of red collar, sr, and ms (this ms was supposed to be ms_1 but did not show linkage with sr, also the ears were normal). Red collar was also independent of this same ms and sr. This silky shows no linkage with ms_1.

Backcross tests indicated no linkage between Pl and red collar, a result differing from that reported previously (News Letter 18:16-17. 1944 - Pl vs. red collar = 6.6 per cent recombination). This difference is explainable if red collar is due to complementary factors.

Antonio Marino

I. Z. Hasanain

2. Woodworth's vp gives no evidence of linkage with ms_1. To determine the order of Y, pb, and ms; all very closely linked, Y + ms/y pb+ plants were crossed with y pb ms/+. One y + ms and one y pb ms were obtained, suggesting that this is the order of the three genes.

H. A. McLennan

F. H. White

3. One stock from X-ray treatment has 10 chromosome pairs and about 20 per cent of pollen abortion. The sterility shows linkage with factors in chromosome 2: 43.5% with gl_2, 34.6% with B, and 15.5% with v_4.

Preliminary cytological examination reveals bridges with fragments, indicating an inversion is the probable cause of the sterility, and that the centromere is outside the inversion. The ears show normal fertility.

W. A. Russell

4. A survey of the knob numbers (and where possible the positions) in 20 inbred lines used in the breeding program here is being made to determine possible relationships with plant characters and with combining ability. The knob number varies from two to at least eight.

M. V. Vachhani

The dominant white cap ($\underline{W}^c$) endosperm factor is linked with brittle stalk ($\underline{bk}_2$) in chromosome 9, the backcross numbers being 135 $\underline{W}^c$ +, 67 $\underline{W}^c$ $\underline{bk}$, 65 $\underline{w}^c$ +, 143 $\underline{w}^c$ $\underline{bk}$, or 32.2 per cent recombination. With T 8-9a there was 30 per cent recombination ($\underline{W}^c$ - T 8-9a = 18:33:68:25). Since tests reported previously indicated no linkage with waxy (News Letter 18: 16. 1944) the order appears to be $\underline{wx}$ - $\underline{bk}_2$ — $\underline{W}^c$; or $\underline{wx}$ - T 8-9a — $\underline{W}^c$.

A brown midrib character which appeared in a $\underline{sh}$ $\underline{wx}$ $\underline{gl}_{10}$ culture seems to be genetically different from the other three brown midribs, and therefore is $\underline{bm}_4$.

Viviparous ($\underline{vp}_5$) is the same as Woodworth's $\underline{vp}$ as shown by intercrosses. Tests are in progress to determine the linkage group to which $\underline{vp}_5$ belongs. This will also locate one of the factors for yellow endosperm (unless $\underline{vp}_5$ itself causes the color effect).

Progress in building large rings (See News Letter 20:16. 1946).

The different rings of six chromosomes produced as the first step in the program were backcrossed to normals; the progeny were grown and examined for pollen sterility. In each case, plants approximately 75 per cent sterile were identified. These should be carrying the crossover which combines the two parental translocations in one gamete. Similarly, backcrosses of the F_1 ⊙ 10 from 1-5-6-7 ⊙ 8 x ⊙ 4 were grown. It is hoped that the selected ears represent the desired crossovers, but the sterility classes were more difficult to distinguish by the "pocket microscope" method used in the field.

Chromosome disjunction (See News Letter 19:31. 1945).

In plants heterozygous for T 5-6c, the low percentage of crossing over with the chromosome 5 inversion in the translocated chromosome as compared with the amount observed with the inversion in the normal chromosome can now be explained without resorting to "position effect". When Dr. A. H. Sturtevant saw the data, he suggested that the cytological data on crossing over (percentage frequency of the crossover type or "half disjunction" quartet) did not measure crossing over within the inversion in both cases. When we drew the chromosomal diagrams (checked later) they

showed that this was true. When the inversion is in the translocated chromosome, crossovers within the inversion do not give rise to the cytologically recognizable "half-disjunction" quartets; whereas when the inversion is in the normal chromosome these crossovers are recognizable in that manner. In the one case these quartets result only from crossing over between the translocation break (center of the cross) and the new position of the centromere, consequently comparable to that in the stock heterozygous T 5-6c but homozygous for the inversion.

C. R. Burnham

Linkage data calculation (See News Letter 20:18. 1946).

Fisher (Amer. Nat. 80:568-578. 1946) has presented a simple method of scoring linkage data by using maximum likelihood formulas. To make it readily understood, we have illustrated its application to F_2 and F_3 data commonly encountered in plant material (now ready to be submitted for publication). The formulas, for the scores (remainders) of maximum likelihood formulae when p = one half is substituted (50 per cent recombination), are:

Source of data	Formulas for scores (c) at p = one half *	Information (i) per F_2 plant or F_3 line at p = one half
Backcross	$2\,(a - b - c + d)$	4
F_2	$4\left(\frac{a}{9} - \frac{b + c}{3} + d\right)$	16/9
F_3 from Ab F_2 plants	$4/3\,(k - 2\,j)$	32/9
F_3 from aB F_2 plants	$4/3\,(m - 2\,l)$	32/9
F_3 from AB F_2 plants	$4/9\,(8e - f - g - h - i)$	128/81
F_3 from doubly heterozygous F_2 plants	$4\,(h - i)$	16

* Suitable for repulsion, change signs for coupling.

By substituting the observed values for a, b, c, d, e, etc., the score (c) for each source of data is obtained.

The total amount of information furnished by the data is ni, where n is the number of plants or of F_3 lines and i is the information per plant or line. Fisher shows that $\sum c^2/I$ is distributed as χ^2. Each such c^2/I value for each source of data, having one degree of freedom, tests the significance of the deviation from 50 per cent recombination. Then $\chi^2 = (Sc)^2/SI$ tests the deviation from 50 per cent for the pooled data with one degree of freedom. The difference $\chi^2 = S\left[\frac{c^2}{I}\right] - \frac{(Sc)^2}{SI}$ tests

heterogeneity, the degrees of freedom being (N-1) where N is the number of sources of data pooled. For this test a value of p sufficiently close to the best estimate of p should be used. The ratio $\overline{Sc}/SI$ provides an estimate of the correction to be applied to $p = 0.5$ to obtain the p value which best fits all the sources of data.

H. H. Kramer

C. R. Burnham

Study and use of trisomics.

1. The frequency of transmission of trisomics without root-tip chromosome counts can be determined by crossing each trisomic with a homozygous translocation involving that chromosome. The trisomic F_1 plants will show low pollen sterility (25-30 per cent) as compared with the 50 per cent shown by their diploid sibs. With experience the difference can be recognized easily even in the field with the "pocket microscope". I have used it satisfactorily for chromosome 6, using T 5-6a.

2. It would also be desirable to make the trisomic analysis usable by those not able to get chromosome numbers counted. At present only plants trisomic for chromosomes 5 and 7 are phenotypically distinguishable in most crosses, but not in all.

Two tertiary trisomic stocks for each crhomosome might be established so that between them the entire chromosome in question would be represented in trisomic condition. If the piece of the attached non-homologue which is also trisomic came from chromosome 5 or 7, it might serve to identify the desired tertiary trisomic plants. Since these tertiaries would also differ from primary trisomics by having approximately 15 per cent of pollen abortion while the primaries would be normal, pollen examination could be used as a supplementary check if desired or if the phenotypes were not distinct.

In place of the 10 primary trisomics, 20 tertiary types would be used for a complete test of the 10 chromosome or linkage groups.

For example, the series might be established from 2n + 1 (No. 1 chromosome trisomic) x T 1-5; 2n++ 1 (No. 2 chromosome trisomic) x T 2-5, etc., selecting the translocation in each case in which the break in 5 was near the middle of the chromosome, assuming a plant trisomic for nearly half of 5 would be most likely to be phenotypically distinct. Two tertiaries would be established for each cross. A series with chromosome 7 also might be usable.

C. R. Burnham

Chromosome disjunction.

In discussing with many others the problem of getting lower sterility from large rings, the possibilities of genic control were suggested. On this basis, a planned search for factors affecting chromosome

behavior at meiosis, such as changed chiasma frequency or position, may be needed. Those studying inbred lines for knob number might be on the lookout for such effects at diakinesis and metaphase. Such stocks would be of interest for other problems also.

Since such factors are likely to be recessives, it will be necessary to study selfed lines from X-ray treatment rather than the immediate plants obtained from the use of X-rayed pollen. I wish to acknowledge the assistance of H. A. McKennan, F. H. White, and K. Hanson.

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Effects of the major plant color genes upon kernel weight in maize.

Brink (1934) has demonstrated that maize plants belonging to the anthocyanin series of color types differ significantly in their average production of grain. Comparison of the four anthocyanin types led to the conclusion that purple was much inferior to dilute sun red, while dilute purple and sun red exceeded dilute sun red in average yield per plant. Subsequent unpublished results indicate that there is probably no significant yield difference between sun red and dilute sun red. Two trials in successive seasons in which dilute sun red (A b pl) and triple recessive green (a b pl) were compared, suggest that dilute sun red has a significantly greater yield.

In 1938 and 1939 the writer conducted three additional experiments at Madison, Wisconsin, in an effort to clarify the status of those color types which had given inconsistent results and in order to include the brown class (a B Pl) which had not occurred in earlier trials. A number of ears resulting from the backcross A_1a_1 Bb Plpl x a_1a_1 bb plpl were obtained. Two experiments, the first including 12 backcross families in three randomized replications and the second, with 18 families in two replications, were grown in 1938. A third experiment (12 families, 3 replications) was grown in 1939. The heterozygous A B Pl plants used in backcrossing were not closely related to the a b pl stock and the segregating progenies exhibited considerable hybrid vigor. Five-eighths of the residual heredity in each family was derived from commercial strains of yellow dent corn adapted to Southern Wisconsin conditions.

The plants were classified as to color type and distinctively tagged. No attempt was made to distinguish the a B pl and a b Pl plants from a b pl in the green class. The frequencies of each type within each row were determined; the mature ears from each color group in a row were harvested together. The samples were dried to a uniform moisture content, shelled, and the shelled corn weighed to the nearest ounce.

The mean shelled grain weights per plant for each plant color class in experiments I and III appear in table I.

Table I.

Mean grain weights per plant by color classes

Phenotype	Experiment I (1938)		Experiment III (1939)	
	No. plants	Mean in lbs.	No. plants	Mean in lbs.
A B Pl (purple)**	674	.307(6)	600	.282(6)
A b Pl (dilute purple)	681	.361(3)	641	.323(2)
A B pl (sun red)	694	.355(4)	686	.318(4)
A b pl (dilute sun red)	686	.372(1)	682	.331(1)
a B Pl (brown)**	698	.344(5)	602	.305(5)
a B pl, a b Pl, a b pl (green)	2002	.368(2)	2000	.319(3)
Total	5437		5211	

** Highly significant differences between this and other classes.

The analysis of variance for each of these experiments reveals that the low yield of purple is highly significant in both cases and that brown with a significantly greater yield than purple is significantly below the yields of the remaining four classes. The relative standings of the six color types with respect to mean grain weight are indicated by the numbers in parenthesis in table I. Dilute sun red has the largest mean in each experiment, the value being significantly (P = .01) greater than the pooled mean of the green, dilute purple and sun red classes in each case. In a combined analysis of experiments I and III the difference between dilute sun red and sun red is highly significant.

The results from experiment II are consistent with the other two experiments with respect to the purple and brown classes. The differences are again highly significant. The mean of sun red is second highest in the experiment instead of fourth as in I and III. This high value for sun red in experiment II is subject to question, however, for when the analysis is based upon kernels per ear instead of kernels per plant, sun red is fourth highest while the relative standings of the other are but slightly changed. In this experiment, also, sun red contributes disproportionately to the variance. The error term is larger than in the other experiments making it impossible to pool the results of experiment II with the others. A summary of experiment II and the total frequencies of each color type are presented in table II.

Table II.

Mean grain weights per plant by color classes

Phenotype	Experiment II (1938) No. plants	Mean in lbs.	Total plants I + II + III
A B Pl (purple)**	806	.320(6)	2080
A b Pl (dilute purple)	803	.370(3)	2125
A B pl (sun red)	884	.376(2)	2264
A b pl (dilute sun red)	920	.379(1)	2290
a B Pl (brown)**	848	.345(5)	2148
a B pl, a b Pl, a b pl (green)	2555	.367(4)	6558
Total	6816		17,465

** Highly significant differences between this and other classes.

A chi-square test for the correspondence of the observed frequencies of plants in each color class to the expected 1:1.1:1:1:3 backcross ratio reveals that the frequencies shown in table II have a probability of .01. The largest deviations occur in the purple class which is smaller than expected and the dilute sun red class which is larger than expected. Since these are the classes which have the lowest and highest mean grain weights, respectively, it appears that the same genotypes which influence kernel weights also influence viability. Relatively large negative deviations also occur in dilute purple and brown, while the sun red frequency exceeds the expected. It seems probable that the dominant gene, Pl, has an adverse effect upon viability.

Plants with the purple phenotype carry the three dominant genes A B Pl and are much less productive than those plants in which one or more of these dominant factors is not present. The brown plants which have the genes B and Pl are at a similar but less marked disadvantage. The dominant genes were always present in heterozygous condition. Since the presence of a single gene A is the only known condition which differentiates the purple from the brown type within a given family, it appears likely that this gene acting in conjunction with B and Pl results in a decreased storage of starch in the kernels. In contrast it is found that dilute purple, dilute sun red, sun red, and green, all have higher mean grain weights than brown. In the three anthocyanin color classes A is present, but b, pl, or b pl are homozygous. The heterogeneous green class includes combinations of a with b, pl or both in homozygous condition. Therefore, it may be concluded that the B Pl gene interaction is effective in reducing the mean weight of grain per plant, presumably by affecting starch storage

during development. The gene, A for anthocyanin pigment, in combination with B Pl increases the effect.

The relatively higher yield of dilute sun red in all three experiments is noteworthy because this is the genotype which is virtually universal among North American varieties of dent corn. While the evidence is hardly adequate to demonstrate that this genotype is always superior in grain yielding potentiality, the fact that A b pl yields are probably significantly greater than those of A B pl is suggestive. In sun red as in purple and brown the development of deeply pigmented tissues must immobilize considerable quantities of carbohydrate which might otherwise be stored in the seeds.

The possibility that the results reported are actually caused by other genes, rather closely linked to the three segregating color genes cannot be entirely rejected on the experimental evidence now available. The foregoing conclusions are based upon a rather homogeneous sample of residual heredity tested in a single locality. Until further evidence is available on the point, however, it would be inadvisable to introduce B and Pl as markers in dilute sun red commercial breeding stocks.

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1. Breeding program.

Brazil may not yet be ready for large-scale introduction of hybrid corn and premature widespread use might lead to a loss of valuable genetical and breeding material in the numerous local populations. In view of these considerations, I have tried since 1937 the following program of establishing homogeneous self-propagating populations.

(a) Selection of the initial material which may either consist of plants of local populations or hybrids combining desired characters.

(b) Selfing during three to four generations and elimination of all pedigree lines which contain undesirable characters.

(c) Sib and between-line crosses during about three generations; selecting the most vigorous combinations, eliminating any hybrid showing undesirable characters; and maintaining all families separately (pedigree).

(d) Thus, the final stage is reached after about seven to eight generations and all the selected families are united into one population which is maintained by open pollination and simple mass selection for stock seeds.

Final results have been obtained by this method in establishing new sweet corn varieties: Piracicaba white P678, P18, orange P9, etc. Satisfactory, though only preliminary results have been obtained also with hard orange flint (cateto) and with yellow dent. After having essentially solved the question of producing sweet corn for our climate, we are now concentrating on the hard orange flints.

The theoretical basis of the process "controlled pollination-pedigree-breeding" is easily explained. It consists in producing a population essentially homozygous for all desired characters, such as grain color and texture, ear size and form, plant height and relative position of ear (slightly above the middle of the plant); and heterozygous for the main factors giving vigor. That such a combination of homozygosis and heterozygosis is possible, was proved in indigenous corn which is on the one side very homogeneous for many seed and plant characters, but at the same time extremely susceptible to close inbreeding.

In Piracicaba sweet corn which is a new synthetic variety we have started the routine work of selfing in order to produce ultimately hybrid seeds.

2. Chemical composition of grain.

The following results were obtained in an analyses of a few of our varieties. The analyses were carried out by the chemists of the "Refinacões de Milho Brazil, S.A." in São Paulo.

			Hard Flint		Dent	
			Cateto P-104	Cateto P-114	Dente P-111	Dente P-113
Water	(Umidade)	%	12.81	12.93	13.45	13.61
Protein	(Proteina)	%	10.33	8.58	3.84	8.84
Oil	(Oleo)	%	4.20	4.21	3.92	4.52
Sugar	(Acúcar)	%	0.60	0.68	0.83	0.79
Dextrin	(Dextrina)	%	1.58	1.45	2.00	1.80
Starch	(Amido)	%	66.98	68.60	67.71	66.89
Fiber	(Fibra)	%	2.15	2.25	1.95	2.15
Ash	(Cinza)	%	1.35	1.30	1.30	1.40
Total		%	100.00	100.00	100.00	100.00

Sweet Corn Piracicaba

	White	Orange	Horticulture
Umidade	11.48	11.63	11.95
Proteina	11.21	12.61	11.56
Oleo	7.61	6.74	7.99
Acúcar	3.86	3.53	3.21
Dextrina	22.36	22.78	23.63
Amido	38.38	38.01	36.15
Fibra	3.10	2.80	3.25
Cinza	2.00	1.90	2.25
Total	100.00	100.00	100.00

Note: The three samples of sweet corn contain about five to six per cent of soluble starch, included in the total starch content.

The analyses were carried according to "Food Inspection and Analysis" by Albert E. Leach, S.B. Fourth, 4th edition, p. 304.

There is evidently a very pronounced variation in oil and protein content. Piracicaba sweet corn contains twice as much oil (seven per cent) as the flints and dents. The protein content is also rather high: 12 per cent of total weight or 13.5 per cent of dry weight in sweet corn and 10 per cent in total weight or 11.6 per cent of dry weight in one of the hard flints.

We hope to be able to carry out the analyses on a larger scale this year.

3. Resistance against the grain weevil and moth.

A series of observations have shown beyond a doubt that one type of yellow dent (Monte Olimpo P111) is relatively less attacked by these insects. The studies are being continued.

4. Linkage tests.

The collection of linkage tests is now in the hands of Mr. Nelson Kobal, in continuation of the work by Dr. Graner who has left our Department. Some new lines have been incorporated and others are being constructed. We hope to furnish next year a complete list of our stocks. We expect also to be able from now on to furnish limited numbers of segregating ears for class work.

5. Tunicate.

The work on South American Tunicate is practically concluded. There seems to be no essential difference, either genetically or in phenotypic variability, between pod corn from São Paulo, Minas Gerais or Bolivia. There cannot be any doubt, as far as the seed formation in the tassel is concerned, that there is no difference between homozygous and heterozygous pod corn. Thus, there should not exist any difficulty in maintaining homozygous pod corn through the seeds in the tassel, without the necessity of using in addition a tassel seed factor.

6. Collection of indigeneous corn.

The studies on authentic indigeneous corn are being continued and I hope to publish soon the first results, together with Dr. Cutler. There seems now to be little doubt that one may classify to some extent native corn in accordance with the grouping of the Indian tribes. The main bulk of our collection has been furnished by tribes of the Tupi-Guarany group. There is comparatively little difference between the types cultivated by the Emeremhon (north of the smouth of the Amazon), the Cayabi and other tribes (North Mato-Grosso, almost in the middle of Brazil), the Paragayans and the Chiriguanos (Northern Argentina). The predominant types are: Soft large-grained yellow (aleurone color); semi-hard white;

orange, variegated or red pericarp with some tendency towards dent. There are two rather primitive types; the large ears with flexible rachis and half-submerged grains from northern Mato-Grosso (Caiabi and Bororo Indians) and the small grained pointed pop corns of the Tupi-Indians, which contain many "Tripsacoid" characters.

Both the corn cultivated by the Chavantes of Central Brazil and numerous types cultivated by the Cainguang of Parana in the South are completely different, without the predominance of yellow and orange types.

No explanation has as yet been found with regards to the hard orange flints called in the Argentine and Urugaya "Colorado" and "Quarantino", and in São Paulo "Cateto". It may be extracted from crosses of soft yellow and pointed pop.

The genetical analysis of the material is being continued. In the color of red or purple (Pr/pr) aleurone as contrasted to colorless, at least three factors are involved, one the dominant inhibitor Ci. There is at least one dominant inhibitor of yellow endosperm in pointed pop. Floury has more often a polyfactorial basis, rather than the simple fl gene. Waxy seems rather common. Nothing as yet can be stated with certainty about the large number of plant, cob and glume colors. Rose or wood-colored husks are due to new alleles of the P-series.

The Mendelian ratios in Paraguay corn are all perfectly normal. In Bororo corn a gametophyte factor in the IX chromosome causes a deficiency or excess of recessives.

7. Cytology and studies on sterility.

The material from the margins of the Amazon River is characterized by a considerable sterility and we hope to decide this year whether it is simply phenotypic or is a cytological complication.

In several lines of indigenous corn the pollen is heteromorphic or dimorphic.

In Cateto the frequency of different types of defective seed is remarkable. Nothing is known as yet about the frequency of B-chromosomes in this material, though we hope to get fuller information next year.

8. Origin of corn.

Since full accounts have been published no details need be given. Accepting the eastern foothills of the Andes from Peru-Acre down to the Chaco as the center of origin, there are evidently two main centers of domestication: The Quechua group in the Andes and the Tupi-Guaranis in the plains. This year new material from outside these regions will be studied; material from Southern Brazil and, in the north, material from Colombia.

9. Relations between corn and teosinte.

Both comparative morphological and genetic studies convinced me that teosinte is an independent genus, different from both Zea and Tripsacum. A full account is under publication.

The genetical analysis of Zea-Euchlaena hybrids continues. The phenotype of the F_1 and the segregation in the F_2 depend to a large extent upon the varieties used in the cross. Corn characters are less dominant in the order: Piracicaba Sweet, Paulista Pod, Paulista Pointed Pop; and teosinte characters are less dominant in the order: Mexican teosinte and Guatemala teosinte.

In the F_2 and subsequent generations many new combinations have appeared and I am trying to stabilize them; especially intermediate types and what may be called new teosinte "varieties". Among the attempted combinations one may be especially interesting: The combination of corn ear characters and the resistance of teosinte against inbreeding.

The photo-thermo-periodicity of Euchlaena is rather interesting. Using earliness in flowering as a measure, we may establish generally the following order from the earliest to the latest: Mexican teosinte, F_1, Corn F_1, and Guatemala teosinte. However, in the very rainy summer of 1945 and 1946 the order was maintained with one exception. Mexican teosinte and all teosinte-like segregates in F_2 or later generations became as late as Guatemala teosinte or later still, some not flowering at all; while the F_1 hybrids retained their relative position as indicated in the sequence above. The corn-like segregates and the intermediate forms behaved more or less like the F_1 hybrids.

The analysis of individual gene segregations is under way with the intention of determining the intensity of gametophyte and of zygote elimination both of which are considerable.

10. Publications.

Since all of our papers have been published in Journals with a limited distribution, I am including a list as follows:

Published papers.

1938 - F. G. Brieger - Problemas de melhoramento do milho. Revista Agr. 13:3-18.

F. G. Brieger - Hibridos de milho com referência especial â precocidade. Revista Agr. 13:3-13.

F. G. Brieger e E. A. Graner - Variacões quantitativas do milho "Santa Rosa". Revista Agr. 13:3-24.

F. G. Brieger e E. A. Graner - Analise da precocidade no milho. Revista Agr. 13:3-17.

1943 - F. G. Brieger - Origem do milho. Revista Agr. 18:409-418.

E. A. Graner - Endosperma amarelo do milho. Revista Agr. 18:443-445.

1944 - F. G. Brieger - Estudos experimentais sòbre a origem do milho. Anais Escola Sup. Agr. "Luiz de Queiroz". 1:226-278.

E. A. Graner e G. O. Addison - Meiose em Tripsacum australe Cutler e Anderson (T.dactyloides subsp-hispidum Hitchcock). Anais Escola Sup. Agr. "Luiz de Queiroz", 1:213-224.

1945 - F. G. Brieger - Estudos geneticos sôbre o milho tunicata. Anais Escola Sup. Agr. "Luiz de Queiroz". 2:211-238.

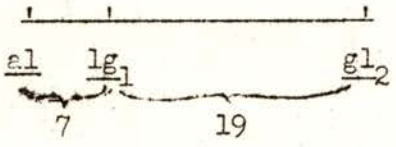
F. G. Brieger - Competicão entre Megaspôrios em Milho. Anais Escola Sup. Agr. "Luiz de Queiroz". 2:239-267.

F. G. Brieger - Estudos sôbre a inflorescência de milho com referência especial aos problemas filogenéticos. Bragantia. 5: 659-716.

H. C. Cutler - Espiguetas de dois grãos no milho. Anais da Escola Sup. Agr. "Luiz de Queiroz". 2:423-430.

F. G. Brieger

1. The al gene (y_3) is seven units from lg_1 in chromosome 2. Its locus in relation to lg_1 and gl_2 is:



2. The y_x gene of Dr. A. M. Brunson, white seeds and albino seedlings (News Letters 18:2-3. 1944 and 20:23-25. 1946) is now called Y_7 and is a new complementary to Y_1 and Y_3. Crosses with y_1 and y_3 gave the following results:

(a) $Y_1y_1Y_3Y_3Y_7y_7$Bnbn) ⊗

Pedigree (1946)	Classes	Seeds	Seedlings obtained: Green	Albion (y_7)	Total of seedlings
11-19 ⊗	Yellow-orange	240	231	5	236
	Lemon-yellow (Bn)	101	5	70	75
	White	100	59	25	84
Total		441	295	100	395

(b) ($Y_1Y_1Y_3Y_3Y_5Y_5Y_7Y_7$Bnbn) ⊗

Pedigree (1946)	Classes	Seeds	Seedlings obtained: Green	Albescent (y_3)	Albino (y_7)	Total of seedlings
153-10 ⊗	Yellow-orange	210	192	2	4	198
	Yellow (Y_5)	59	0	51	1	52
	Lemon-yellow(Bn)	75	1	0	69	70
	White	8	0	0	5	5
Total		352	193	53	79	325

Neither cross shows independent segregation for lemon-yellow seeds and albino seedlings. In some strains only the triplex and duplex seeds for lemon-yellow can be separated from the white ones and if this should be the case, the lemon-yellow seeds would give about 50 per cent of green and 50 per cent of albino seedlings (3 green : 4 albino). The $\underline{Y}_7$ gene shows linkage with the lemon-yellow class. In cross (b) the yellow seeds ($\underline{Y}_5$) also show linkage with $\underline{Y}_7$.

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1. Catalogue of A-B interchanges.

Ten interchanges between A-type and B-type chromosomes have been obtained from pollen treated with X-rays. In the list that follows, the A-chromosome involved in each interchange is indicated by the numeral in the symbol designating the interchange. The A-chromosome in one of the interchanges (TB-A?) is unknown and in another (TB-8?) the identification of chromosome 8 is based on a few rather poor pachytene figures and may be incorrect. The letters S and L refer to the short and long arm, respectively, of the A-chromosome. The distance from the centromere to the point of breakage in the A-chromosome is given as the decimal fraction of the length of the arm in which it occurred.

Interchange	Breakage Point in A-chromosome
TB-1a*	L .2-.3
TB-1b	S .1
TB-4a	S .2
TB-6a	within nucleolar-organizing body
TB-7a	L .9+
TB-7b	L .3
TB-8?	L .3-.4
TB-9a	L .5
TB-9b	S .4±
TB-A?	unknown

*The interchange was originally thought to involve chromosome 2 and was listed as T2-B in Maize News Letter 16: 1942.

The points of breakage in the B-type are as follows: In TB-1a, TB-4a, TB-7a, TB-7b, and TB-8?, they are at or near the junction of the euchromatic and the distal heterochromatic regions. In the others, excluding TB-A? for lack of evidence, the breaks are well within the heterochromatic segment.

2. Behavior of A-B interchanges.

The genetic behavior of TB-1a, TB-1b, TB-4a, TB-7b, and TB-9b

has been investigated in some detail. The results were essentially the same for all five interchanges and can be summarized as follows: The interchange chromosome B^A, which carries the centromere and proximal portion of the B-type and a distal segment of A-chromatin, undergoes non-disjunction in the division of the generative nucleus. The result is that the gametes of a single pollen grain are not alike. One is deficient for the B^A chromosome; the other carries it as a duplication. Both gametes are functional.

When plants that are normal are pollinated with pollen of this kind, two types of seeds are obtained: (1) One has a hyperploid (for B^A) embryo and a deficient endosperm; (2) the other has a deficient embryo and presumably a hyperploid endosperm. If the normal plant used in this cross carries a recessive endosperm gene, the dominant of which is present on the B^A chromosome, the deficient endosperm can be identified by the appearance of the recessive character. Thus, sugary kernels are obtained from the cross, Normal (su su) x TB-4a (Su Su). The hyperploid and deficient embryos have been identified by both cytological and genetical methods.

The interchange chromosome (A^B) carrying the A-centromere shows regular behavior in the division of the generative nucleus. Both interchange chromosomes are transmitted in normal fashion through the eggs.

The rate of non-disjunction, as estimated from the results of crosses involving TB-4a and TB-9b, is very high, approaching 100 per cent. In other words, the B^A chromosome undergoes non-disjunction in the division of nearly every generative nucleus. It seems to be quite regular in behavior in the meiotic divisions and in other mitoses.

3. Genetic location of breakage points.

The location of the point of breakage in the A-chromosome of an A-B interchange may be determined genetically if appropriate recessive testers are used. This has already been illustrated in the case of TB-4a, using the sugary gene. If the corresponding dominant allele is distal to the point of breakage (i.e., in the B^A chromosome), the deficient F_1 progeny will show the recessive character. If it is proximal to this point, the dominant character will appear. The following table gives the results which have been obtained for interchanges tested in this way.

Interchange	Point of Breakage
TB-1a	Proximal to f
TB-4a	Proximal to su
TB-7b	Between v5 and ra
TB-9b	Between sh and wx

4. Evidence of selective fertilization.

A pollen grain in which mitotic non-disjunction has occurred has one gamete lacking a B^A chromosome and another gamete carrying it in two doses. In the double-fertilization process, either gamete may fertilize the egg; the other fuses with the polar nuclei. If fertilization can

occur in either direction at random, we would expect the two types of seeds described in Section 2 to be formed in equal numbers. The frequency of either type would not be expected to exceed 50 per cent of the total progeny, a value corresponding to a rate of non-disjunction of 100 per cent.

In some of the crosses between normal female parents and male parents homozygous for either TB-4a or TB-9b, the percentage of seeds with a deficient endosperm was far in excess of 50 per cent. In the crosses involving TB-9b, a c-tester stock, homozygous for sh and wx as well, was used as the seed parent. The interchange chromosomes comprising TB-9b carried the corresponding dominant alleles. Wx was present in the 9^B chromosome, C and Sh in the B^9 chromosome. The F_1 seeds with an endosperm deficient for B^9 were colorless, shrunken, and starchy.

It was thought, at first, that the excessive number of seeds with a deficient endosperm indicated an outright loss of the B^A chromosome in some of the second microspore mitoses. Suppose that the B^A chromosome lags in this division and is lost to both gametes. Each occurrence of this kind would produce not only a deficient endosperm but also a deficient embryo in the same seed. This result could be distinguished readily from the result of non-disjunction by an examination of the plants obtained from these seeds.

A cytological examination has not yet been accomplished. A genetic test was possible in the crosses involving TB-9b, through the use of scutellum color as an indicator of the presence of C (and therefore B^9) in the embryo. The scutellum is colored when C is present in addition to certain other factors, and is colorless in its absence. Some of the c-tester plants used in these crosses were homozygous for the complementary factors. The F_1 seeds with colorless endosperm were examined for scutellum color and the following results were obtained.

Cross	Colorless endosperm: Colored scutellum	Colorless endosperm: Colorless scutellum	Colored endosperm	% Colorless endosperm
119-11 x 96-8(TB-9b)	227	5	121	66
119-4 x 96-8	95	1	52	66
119-3 x 96-23	129	0	99	57

It is evident from these data that the hypothesis of "outright loss" is untenable as an explanation of the excessive frequency of colorless kernels. The colored scutellum in seeds with a colorless endosperm shows that B^9 is present in the embryo but absent in the endosperm. This would be expected from mitotic non-disjunction. The six exceptional colorless seeds may represent errors in classification since scutellum color varied in intensity and was faint in some embryos. It is also possible that they are due to heterofertilization. The F_1 seeds will be grown this summer for a further check of their constitution with respect to B^9.

The results so far point to the conclusion that, in some crosses at least, the reciprocal types of double-fertilization do not occur with equal frequency. There is a marked tendency for the hyperploid gamete to fertilize the egg and the deficient gamete of the same pollen grain to fuse with the polar nuclei.

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Effect of the de_{17} allele on seed development.

The de_{17} allele in corn reduces kernel weight to 25 per cent of normal, or less. It shows regular Mendelian transmission. A fair proportion of seeds on the best ears are viable. Once past the seedling stage de_{17} indviduals develop into vigorours and fertile plants which, however, are about one foot shorter than their normal sibs. The stock has been propagated in homozygous condition for several generations.

Defective and normal kernels are obtainable at will by pollinating de_{17} plants with de_{17} and De_{17} pollen, respectively. De_{17} kernels develop as well on de_{17} plants as on normals. Defective and normal caryopses increase in weight at the same rate up to nine days after pollination. At 12 days the defective kernels have fallen slightly behind the normals in dry weight. The difference is much larger at 16 days, and continues to increase rapidly up to 24 days beyond which time the defectives make little growth.

Histological studies reveal a relationship between the initial divergence in weight of the two classes of kernels and the differentiation of an absorbing region in the endosperm. Between six and 12 days the cells on the basal surface of the endosperm facing the placental region in normal kernels become elongated, the nuclei move to the inner end of the cells, and the cytoplasm assumes a dense, fibrillar appearance. The basal cells of the endosperm in defective seeds do not become similarly transformed into absorbing elements. Rather, they enlarge about equally in all dimensions and become highly vacuolate. A few days later the cells in this region in defectives begin to break down. Eventually many cells in the basal area and in the adjoining central region of the endosperm collapse and thus become entirely non-functional in the transfer of nutrients to the seed.

The parenchymatous cells of the placenta are quickly and extensively depleted of their total contents by the regularly differentiating normal endosperm. The corresponding cells in kernels possessing defective endosperms are more slowly and less completely depleted. The difference appears to be a direct function of the absorptive capacities of the normal and defective endosperms.

A definite conclusion cannot be reached from the available data whether the de_{17} allele exerts a direct parallel action on endosperm and embryo, or acts directly on the endosperm only. The severely restricted development of the defective endosperm in itself is sufficient to account for the failure of many of the associated embryos to reach a viable condition and for the others to yield weak seedlings. The somewhat shorter stature of adult de_{17} plants, as compared with their normal sibs, may be due either to the handicap incurred at the seedling stage because of poor seed development or to this factor plus a continuing but only mildly deleterious effect of the de_{17} allele on later growth.

R. A. Brink

D. C. Cooper

II. MAIZE PUBLICATIONS -- 1946

(Including certain 1945 publications not previously listed and some early 1947 publications.)

Altstatt, George E. A new corn disease in the Rio Grande Valley. Plant Dis. Reporter 29(20):533-534. 1945.

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