MAIZE GENETICS COOPERATION

NEWS LETTER

18

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The data presented here are not to be used in publications without the consent of the authors.

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I. IMPORTANT NOTICE

The Maize Genetic Coöperation News Letters carry a statement to the effect that the presentation of data in them is not regarded as constituting publication and that no such data are to be used in publications without the consent of the authors. A foreign geneticist and plant breeder, not working with maize, has published a review of News Letter 16, 1942. He was aware of the injunction and quoted it in the review. He included none of the data but did include the perhaps tentative conclusions drawn from the data by the authors. While, therefore, he obeyed the letter of the injunction, it can hardly be maintained that he accepted the spirit of the rule.

I conferred by letter with a number of the more active coöperators in this country. Replies ranged from one extreme to the other. Some thought that even such publication as had occurred might be disasterous and that, in the future, the News Letter should be sent only to those coöperators who contributed material. Others saw little danger, at this stage of our work, from such a review as had been published and suggested no change other than a rewording of the injunction. Most replies suggested a middle course between these extremes. I am, therefore, adopting the following procedure. This News Letter is being sent to those who are now coöperating or who have furnished material in the not too distant past. Further copies will be held here to be sent on request to other geneticists or breeders. I shall have to depend on my own judgment (good or bad) in determining whether particular requests shall be honored.

R. A. Emerson

II. FOREWORD (Swan Song)

I have been connected more or less intimately with Maize Genetic Coöperation from its beginning. Some years I have had to devote considerable time to it and other years almost none. On the whole I feel that I have probably done less than I should and certainly less than I am credited with having done. I am now an "emeritus" and rather enjoy it. I am anxious to complete (before my number comes up) certain maize genetic problems that have been underway for a long time and which will require yet further years of work. I am willing to admit no more than that I am not growing younger as the years go by. Any way I feel that, whether well or poorly, I have about done my stint and that some one else should soon assume responsibility for this coöperative effort. An appropriate time for a change is now when our most recent grant from the Rockefeller Foundation is to be closed out.

I shall, of course, retain an interest in this undertaking. If no other prior arrangement is made, I shall probably find myself planting certain genetic stocks again next spring and at pollination time shall wonder why I haven't yet learned to limit my planting to what I can take care of.

During the past year, many genetic stocks that were most in need of replenishment were grown and pollinated by Dr. M. J. Murray and Miss Rosalind Morris. Miss Morris has grown in the greenhouse many cultures showing seedling characters. When resort must be had to ears from normal plants of segregating cultures, it is important to determine which of the normals are heterozygous for the characters in question. Dr. Murray also spent much time in a study of the stocks on hand and of the available records and succeeded in bringing at least some measure of order into the rather chaotic situation that I had allowed to develop.

R. A. Emerson

III. REPORTS FROM COÖPERATORS

Bureau of Plant Industry Station, Beltsville, Maryland

A cross involving opaque-2 made in 1942 and selfed in 1943 segregated for an endosperm-color gene very closely linked with opaque. The gene has not been identified but since no gene affecting endosperm color previously has been reported in this region of Chromosome 7, the preliminary data are presented in the following table:

Flinty		Opaque-2		
Dark Yellow	Lemon Yellow	Dark Yellow	Lemon Yellow	Total
2337	21	42	752	3152

The data are not too satisfactory as considerable difficulty was experienced in classifying the opaque seeds for color. They indicate about 2 percent crossing over between the two loci. No symbol is suggested for the endosperm-color gene as too little information is available on it at the present time.

Merle T. Jenkins

Bureau of Plant Industry and Purdue University Department of Botany, Lafayette, Indiana

In 1941 one plant from a very uniform appearing ear-row of inbred Ky8 produced a self-pollinated ear segregating approximately 3:1 for salmon yellow and ivory colored kernels. When planted in a germinating bed the yellow seeds produced all green seedlings and the white seeds produced only albinos. In 1942 a row was grown from the yellow segregates and each plant self-pollinated. Of the 20 ears produced, 7 were homozygous yellow and 13 were segregating for yellow and white. Seedlings grown from these segregating ears gave the following totals:

	Seeds	Seedlings	
	planted:	green	white
Yellow seeds:	3910	3030	14
White seeds :	1104	11	785

Ten of the 11 exceptional green seedlings from white seeds were successfully transplanted and grown to maturity. Because of unfavorable conditions only five of the attempted self-pollinations were successful, but in every case both yellow and white kernels were produced. It appears probable that a single gene with a dual effect was involved in the original mutation, and that the aberrant seedling types were due to hetero-fertilization.

A. M. Brunson

Columbia University, Department of Botany, New York City

1. In a stock homozygous for the dominant Bt-1 allele a mutation occurred from Bt to bt^m. This new allele is unstable and mutates with a high frequency to Bt. Seeds of bt^m bt^m constitution are mosaics of normal and brittle tissue. Germinal mutations are numerous - 7.5% of the seeds on selfed bt^m bt^m plants are reverse mutations. The Bt alleles obtained by reverse mutation are stable. The bt^m allele occasionally mutates to a stable bt allele which is indistinguishable from the old bt allele. While genic modifiers influencing the mutability of the bt^m allele exist it is evident that this allele is intrinsically unstable, and this case is not similar to the a Dt situation.

2. Goldschmidt in the Proc. Nat. Acad. Sci. 1943 reports a situation in Drosophila melanogaster where the interaction of alleles at two different loci gives results somewhat similar to those reported for unstable genes. He suggests that the idea of unstable genes be abandoned, and that the so-called unstable genes of Drosophila and maize can be accounted for in terms of factor interaction, epistasis, and threshold conditions. He specifically cites the a-Dt case in maize. According to his interpretation the apparent mutations of a to A, believed to be induced by the Dt gene, are in reality cases where a new Dt allele (which will be represented Dt^A) produces the color ascribed to the A allele. He also states that no published data exist which negate his interpretation. Actually two decisive experiments have been published which establish the correctness of the mutation hypothesis. (1) The A alleles obtained by mutation from recessive a show the expected linkages with genes in chromosome 3. On Goldschmidt's scheme the color-producing allele would be in chromosome 9 since Dt is in that chromosome. (2) When a mutation of a to A occurs in a cell of a a Dt Dt constitution the constitution of that cell following mutation is A a Dt Dt. On Goldschmidt's scheme it should be a a Dt^A Dt.

M. M. Rhoades

3. The vascular bundles of corn leaves are surrounded by a single layer of bundle sheath cells possessing plastids differing in size and shape from the chloroplasts of the mesophyll cells. The plastids of the

mesophyll cells contain no starch; the sugars they produce are moved into the bundle sheath cells and there transformed to starch. Starch increasingly accumulates in the bundle sheath plastids in the day; during the night the starch is changed to soluble carbohydrates and translocation occurs. The plastids of the bundle sheath cells are usually devoid of starch by morning. These plastids contain a green pigment, presumably chlorophyll, but are of a lighter green color than are the chloroplasts of the mesophyll. Photosynthesis may occur in the bundle sheath plastids. However, the green color of the bundle sheath plastid is similar to that of the guard cells of the stomata. Sayre found that the guard cells of Rumex contained a light green pigment which was not chlorophyll. In view of the above facts it will be of interest to ascertain whether or not the green pigment in the bundle sheath plastids is chlorophyll.

Each of the bundle sheath plastids contains numerous, discrete regions, which may be likened to pyrenoids, in which the starch is deposited. It is surprising that the structure and functions of these unusual plastids have not been adequately described. Kiesselbach (1916 and cited in Weatherwax 1923) noted their abnormal size and shape but did not mention their function in starch synthesis. He believed these plastids had different shapes in fixed from those in living material. We have observed, however, the same variation in size and shape in both fixed and living cells.

M. M. Rhoades and Alcides Carvalho

Connecticut Agricultural Experiment Station
New Haven, Connecticut

1. Long-inbred lines of corn infrequently show heritable variations. A search among all the inbred material available over a period of several years has revealed deviating lines that differ from the original type in some distinct morphological or physiological character. Presumably these variations are single point mutations, although it is difficult to separate primary changes from delayed segregations. All variations so far found appear to be degenerative changes, reducing the ability of the plant to grow and to reproduce itself. They include delayed flowering, leaf blotching, narrow leaf, reduced plant size at maturity, crooked stalk and chlorophyll alterations.

All of these have occurred naturally. In X-rayed material less conspicuous variations have been found but these are not sufficiently well marked to segregate clearly.

Four of the natural variations have been crossed back with the normal lines from which they come. All have given the surprising result of a hybrid-vigor effect. The F_1 plants are either taller, greener, broader in leaf and stalk, earlier in flowering or more productive of grain. The differences are small but measurable. If it is proved that these differences involve only a single gene this would be clear evidence that heterosis is something more than an accumulation of non-allelic dominant favorable growth factors.

It may also be questioned fairly whether these are actually the degenerate types that they seem. From evidence previously reported these reduced lines may give superior results in outcrosses. Since these mutations presumably originate in the heterozygous condition, the plants containing them should be more vigorous than the homozygous individuals in the same line and are likely to be selected for propagation. This was actually the case in the blotched leaf line that came originally from a plant selected as superior in height of stalk and ear development to the other plants in the same self-fertilized progeny. This is additional evidence to show why inbred lines are difficult to maintain in a constant and uniform condition.

It may also explain why some of the poorest lines are so useful in production of commercial hybrids. For example, Iowa L317, C.I. 540 and 4-8 are notably unsatisfactory as inbreds but are used in hybrids that are widely grown. Combining ability results from a complementary action that is not clearly indicated in the homozygous condition and apparently involves an equilibrium of genic material that is not as yet fully understood.

2. The reciprocal crosses reported last year, made between inbreds with extreme differences in kernel size (Rice pop and Reid dent) again showed significant differences in early growth. These differences almost entirely disappeared by flowering time. The combined average days to tasseling and silking were 81 for the pop inbred and 66 for the dent. The two reciprocal crosses were 66 and 65. The crossed plants from the larger seeds flowered one day earlier. Differences in tillering also went with the larger initial growth, where the seed was produced by the non-tillering parent. The average number of tillers this year is dent 0, dent x pop 2.7, pop x dent 2.1 and pop 2.9.

3. Plants grown in the greenhouse and transplanted to the field are sometimes shorter at maturity than plants grown from the same seed sown directly in the field. Very small, immature seeds from ears that are harvested at an early milk stage usually produce plants that grow to normal height and productiveness. This suggests that tall plants that are difficult to pollinate might temporarily be reduced in height advantageously. Possibly better means could be devised to do this, such as bending the plants to the ground in the early stages of growth and allowing them to grow upright. The basal part could be held down by covering with soil, fastening with a wire staple or tying to adjacent plants.

D. F. Jones

4. Considerable heterosis is manifest when Purdue 39 is crossed with Connecticut 30, a reduced type of P39. The P39.C30 hybrid in 1942 produced 25-30% more grain than P39. The hybrid also grew faster than either parent. The C30 type plant is recessive to P39 and the P39.C30 hybrid gives good monogenic ratios in both F_2 populations and in backcrosses to C30. C30 arose in 1933 in a selfed ear of the P39-16 stock of the Crookham Company, Caldwell, Idaho. Since there was no evidence of outcrossing it is assumed that C30 is a mutation. The interesting question is whether the heterosis found last year in the P39.C30 cross was produced by the same factor causing the C30 plant to be reduced or due to other factors that may have mutated since the C30 was separated from Purdue 39. Crosses made last year may give information on this point. C30 was crossed by several different sub lines of Purdue 39 maintained in different places and quite distinct in themselves. It will be interesting to see if as much hybrid vigor is obtained when P39-16 is crossed by C30 as when other more remotely related lines are crossed. The data on hand are insufficient to justify any conclusion regarding the nature of the hybrid vigor encountered in this intra-inbred hybrid. It could be explained by the

interaction of alleles, divergent in function as suggested by East. Further study is necessary to determine whether the factors responsible for heterosis are allelic or not. Whatever the explanation this phenomenon like hybrid vigor between different inbreds, may have its practical application before we understand fully the cause of the hybrid vigor. If the yield of Purdue 39 can be increased 25% or even 10% by first crossing with C30 it would seem logical for the seedsmen to use the C30.P39 hybrid in production fields wherever P39 is ordinarily used as the seed parent. Since it has been found that C30 hybrids are equal if not superior to P39 hybrids, seedsmen might well utilize the hybrid vigor of the P39.C30 hybrid in their seed fields to increase their seed yield without sacrificing in any way the quality of the finished hybrid.

5. Effect of C30 on the production of new mutants.

In the cross of P39 x C30 several cases of defective and germless seeds have been encountered. The number of segregating progenies has been small and consequently no rate has as yet been determined. It is our belief that a rate exceeding the normal mutation rate will be found when more data are accumulated. Besides germless and defective seeds, a virescent seedling was found to be segregating in a selfed progeny of the cross P39 x C30. No such virescents have been observed in either P39 or C30. The virescent when selfed produced 100% virescent seedlings. The inheritance of the new virescent will be determined. Also P39, C30 and the F_1 hybrid will be examined cytologically.

6. A light yellow factor or yellow reducer has been found in a stock of white sweet corn, Early Pearl. In changing Early Pearl from white to yellow this character was observed. Such yellow reducers are common in certain of the late white varieties of field corn grown in the south but are not frequently encountered in sweet corn. The ones we have always observed it in are Early Pearl, Sugarsweet or Cupid, and Hayes White. These varieties are similar and probably have a common origin. The new light yellow is dominant over the intermediate or darker yellow and in the F_2 gives a good ratio in most sweet corn crosses of 3 light yellow: 1 darker yellow. When backcrossed to the regular yellow a good 1:1 ratio of light: dark is obtained. If backcrossed to light yellow the kernels are all light. The light yellow condition is homozygous in one of our commercial inbreds C35, derived from the Yellow Pearl. At the eating stage of ears heterozygous for light yellow no segregation for the light yellow factor can be detected, the color being a good medium yellow. Apparently the color is reduced during the drying process.

7. "First" Maize Breeder had Crossing Plot at New Haven in 1836.

In the 1845 issue (Vol. 2, p28) of the Cultivator magazine occurs an interesting letter from Noyes Darling, a New Haven lawyer and judge, telling how he developed a variety of sweet corn. The full letter will be published shortly, probably in the Journal of Heredity. We enclose an excerpt giving his procedure the first year, 1836.

"1st year. I had a very early yellow corn, but quite diminutive in its growth - the stalks not over 3 feet in height, and the ears not over 4 inches in length. Late in the season I planted this in a patch of sweet or shriveled corn, then considerably grown. As soon as the tops or blossoms of the yellow corn protruded, they were cut off, in order that the early corn might be impregnated only by the sweet corn. The result this year was yellow corn of the usual size and appearance."

This then appears to be the first crossing plot in which one variety was detasseled to be pollinated by another although James Logan had cut tassels off of corn 100 years earlier in his experiments to determine whether pollen was necessary for fertilization. However Darling's experiment seems to be the first time a maize breeder had detasseled a variety of corn in order to make a controlled pollination. From the sweet-flint cross, by selection he produced

an early white sweet corn that matured on July 18 in New Haven, a very early corn. He described his experiment in a concise, accurate fashion that would serve as a model for scientific reporting today.

W. Ralph Singleton

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Ithaca, New York

Aberrant pericarp-color ratios. In last year's News Letter (17:8-10,1943), I reported a disturbance of pericarp-color ratios unlike that caused by the recessive zygotic lethal, zl. Selfed red ears gave progenies with approximately equal numbers of red and of white eared plants instead of the expected 3-1 ratio. Such red eared plants, when used as pollen parents in crosses with white gave progenies with about four times as many whites as reds. Only part of the red ears of such cultures gave aberrant progenies. The possibility of this disturbance being transmitted thru the egg had not been determined.

More data of the same kind and a few new data are now available. The new and older data are summarized in the accompanying table.

Normal and aberrant pericarp and cob-color ratios

Line No.	Progeny of line No.	Parental genotypes ♀ ♂	Progenies: No. of cultures	Phenotypes and No. of individuals: R-R	W-R	W-W	Approx. ratios	Remarks
1	-	W-R x R-R	2	26				
2	1	$\frac{W-R}{R-R}$ (x)	11	651	182		3:1	Normal
3	1	" (x)	3	175	153		1:1	Aberrant
4	1	W-W x $\frac{W-R}{R-R}$	9	402	391		1:1	Normal
5	1	"	7	290	1125		1:4	Aberrant
6	5	$\frac{W-W}{R-R}$ x W-W	6	197	-	199	1:1	Normal
7	5	$\frac{W-W}{W-R}$ x W-W	8		225	203	1:1	Normal
8	6	$\frac{R-R}{W-W}$ (x)	8	125	-	114	1:1	Aberrant
9	7	$\frac{W-R}{W-W}$ (x)	6	-	140	40	3:1	Normal
10	7	" (x)	1	-	14	11	1:1	Aberrant

The pollen parents of the two F_1 cultures shown in line 1 were from the same stocks of chromosome 1 markers, P br f an gs, both homozygous for red pericarp and red cob, R-R. The pistillate parents were from unrelated stocks with colorless pericarp and red cob, W-R. Of 14 F_2 cultures, 11 (line 2) showed normal 3:1 segregation and 3 (line 3) gave aberrant ratios approaching 1:1. Other F_1 R-R plants were backcrossed as pollen parents to stocks with colorless pericarp and white cobs, W-W. Of 16 such backcross cultures, 9 (line 4) gave

normal 1:1 ratios and 7 (line 5) gave aberrant ratios approaching 1:4. Six red eared plants (line 6) and eight red-cob whites (line 7) of the aberrant backcross cultures were again backcrossed this time as pistillate parents; and all gave normal 1:1 ratios. Eight red eared plants (line 8) from these normal second backcross cultures when selfed gave only aberrant cultures. Finally, six red-cob whites from the second backcross cultures (line 9) gave normal ratios on selfing and one (line 10) gave an apparently abnormal ratio.

In summary, it should be noted that red eared plants of aberrant cultures when selfed or used as pollen parents in backcrosses to white, transmit the disturbance to some but not to all cultures of the next generation. When used as pistillate parents in such backcrosses, no disturbance is shown in the following generation, but both red eared plants and red-cob whites of that normal generation give aberrant results when grown one further generation.

From all this, it is clear that the disturbing factor is carried by a part (presumably one-half) of the female gametes and by a part (materially less than half) of the functioning male gametes. In its adverse effect on the functioning of male gametes, it is similar to the Ga reported by Rhoades (News Letter 17:7, 1943). I am, therefore, assigning to it tentatively the symbol Ga4.

Since there is evidence (tho slight) of crossing over between Ga4 and the pericarp-color locus and of differential functioning of male gametes, these two variables can be evaluated by use of F_2 or backcross ratios only when adequate data are available for a third nearby gene. The percent of crossing over can be determined directly, however, from the ratios of aberrant to normal cultures from (1) F_3 from reds of aberrant F_2 cultures and (2) from progenies of reds and/or red-cob whites of backcross cultures where Ga ga reds are used as the pistillate parents of the backcrosses. In these cases, the ratios of aberrant to normal cultures should be quite independent of the percent of functioning Ga pollen.

Limits can be set for the two variables by use of F_2 and backcross ratios of red to white. Thus, the observed 53 percent red eared plants of F_2 might be accounted for by various combinations of the two variables with extremes from zero crossing over with 6% functioning Ga pollen to 6% crossing over with zero functioning Ga pollen. But the observed 27 percent red eared plants in backcross cultures indicate very different limits for the two variables, namely, from zero crossing over with 27% functioning Ga pollen to 20% crossing over with 12% functioning Ga pollen. Since the crossover percentage must be the same for the two types of cultures, one of three conclusions must follow, namely, (1) my hypothesis is wrong (2) my calculations are wholly inaccurate, or (3) pollen functioning is affected adversely much more when the pistils to which it is applied are heterozygous for Ga than when they carry only ga. If the latter is true, the gamete factor, Ga4, may be regarded as dominant as is Ga1.

R. A. Emerson

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Chromosome 1.

Cross $\frac{Ts_3 \quad +}{+ \quad Kn}$ x inbred (ts_3 kn)

Ts_3 +	Ts_3 Kn	+ +	+ Kn	Total
78	2	5	68	153

% recombination = 4.6

Chromosome 2. Tetraploids

In the course of his intensive work on tetraploids, L. F. Randolph created a stock containing the genes lg, gl, b, v4 and a corresponding stock containing the dominants. Both stocks were homozygous A_1, A_2, A_3 and also Rg which is necessary for definite classification of the genes B-b in the seedling stage. The stocks were multiplied and then selected for distinct expression of the four marker genes. Following this, J. E. Welch studied the linkage relations of plants duplex for each of the four genes when backcrossed to the multiple recessive. Beginning at this advanced point, I can contribute some additional information.

The cross of a plant duplex for all four markers $\frac{+ \; + \; + \; +}{+ \; + \; + \; +}$ $\frac{lg \; gl \; b \; v}{lg \; gl \; b \; v}$ by a multiple recessive one $\frac{lg \; gl \; b \; v}{lg \; gl \; b \; v}$ should give as a parental class ratio four plants simplex for all genes $\frac{+ \; + \; + \; +}{lg \; gl \; b \; v}$ $\frac{}{lg \; gl \; b \; v}$ to one plant duplex for all genes $\frac{+ \; + \; + \; +}{lg \; gl \; b \; v}$ $\frac{}{lg \; gl \; b \; v}$ to one multiple recessive plant $\frac{lg \; gl \; b \; v}{lg \; gl \; b \; v}$ $\frac{}{lg \; gl \; b \; v}$. Numerous other arrangements are possible in plants derived from crossover gametes; but for any one gene, the individual plant should have the recessive allele represented either two, three or four times. The last type is obvious phenotypically since it is homozygous for a recessive marker. Further, a cross of this nature should and did segregate in the ratio of 3.6 - 5 dominants : 1 recessive for each of the four genes.

If several individuals with dominant phenotype are selected from such a backcross progeny, and again backcrossed to the multiple recessive, one should find that certain of their progenies give simplex ratios for all four gene members.

Twenty individuals were tested; their distribution is as follows:

2 duplex ratios for all four genes
1 duplex ratios for lg, gl and b; simplex ratio for v
1 duplex ratios for gl, b, and v; simplex ratio for lg
1 duplex ratios for lg and v; simplex ratio for gl and b
4 duplex ratio for v; simplex ratios for lg, gl and b
2 duplex ratio for lg; simplex ratios for gl, b and v
9 simplex ratios for all four genes

The study of progenies, derived from backcrossing plants simplex for each gene to the multiple recessive stock, should give the most direct measure of recombination frequency in a tetraploid for comparison with those in similar diploid stocks.

While 4,315 mature plants were studied, obviously only part of these may be used in the calculation of recombination frequencies from simplex ratios for any given region. The data are tabulated as a three-point test for lg, gl and b and as a two-point test for b and v_4. This enables one to utilize larger numbers than would be possible in a 4-point tabulation. No records were used unless the ratio of dominant to recessive allele was a good fit for a 1:1 ratio. In this manner, any possible effects of either differential viability or poor expression are kept at a minimum. Note that the total is smaller for the 2-point test as a number of cultures were not usable since the v_4 class was deficient.

0	(+ + +	1033		0	(+ +	484
	(lg gl b	1036			(b v_4	427
1	(+ gl b	196		1	(+ v_4	352
	(lg + +	192			(b +	359
						1622
2	(+ + b	181				
	(lg gl +	219				
1 &2	(+ gl +	55				
	(lg + +	54				
		2966				

786 b : 836 + D/P.E. = 1.9
779 v_4: 843 + D/P.E. = 2.4

1500 lg : 1466 + D/P.E. = 0.9
1506 gl : 1460 + D/P.E. = 1.3
1467 b : 1499 + D/P.E. = 1.0

The diploid recombination values used in the following table are taken from Fraser, Jour. Hered. 30: 375-378, 1939.

	4n	2n	Difference
lg - gl	16.8±0.46	19.5±0.40	2.7±0.61
gl - b	17.2±0.47	21.6±0.41	4.4±0.62
b - v_4	43.8±0.83	33.2±0.47	10.6±0.95

The observed differences between 2n and 4n are significant, but a discussion of the possible causes is too lengthy for this preliminary report.

Chromosome 7.

Certain stocks of the late Professor A. C. Fraser, and several of the co-op stocks as well, contain a factor for defective seeds. This recessive factor reduces seed size to 1/16 - 1/4 that of normal and is somewhat variable in expression. Defective seeds entirely fail to germinate in weak lines but may produce 1/4 - 1/8 sized plants in vigorous stocks. As a new defective seed mutant, this one would hardly command any attention. However, this semi-lethal was isolated by selfing cultures containing the genes in v5 ra gl and these same cultures had previously shown unequal parental and crossover classes in 3 point tests. One may presume that this semi-lethal is linked rather closely with these markers and is the cause of these aberrant ratios. It is unlikely that this recessive by itself can account for the marked differences obtained in linkage results in different lines, unless it has an effect on crossing over when present in the heterozygous condition. This has not been studied. One might easily ascribe ears segregating for this gene to the effects of poor pollination, but ears segregating approximately 3:1 have been recovered from normal seeds taken from a segregating ear.

M. J. Murray

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Quantitative characters and dominance

Use of third degree statistics with this problem has been illustrated by Fisher, Immer, and Tedin (Genetics 17:107, 1932).

The less powerful but more ready attack with means does not require so extensive nor intricate data. Essentially the method is to test for departure from the additive scheme except for dominance by comparing F_2 mean with the mid-point of F_1 and parents, and backcross mean with mid-point of F_1 and parent. Some extension of the method is proposed and illustrated below.

Denote: n - number gene pairs heterozygous in cross; n_1 - plus pairs in parent farther from F_1; n_2 - pairs in near parent; $n_1 + n_2 = n$; α - aA effect minus aa effect; k - dominance factor, (AA-aA)/(aA-aa); R - minimum phenotype summing effects of pairs aa or AA in both parents and aa effects of n pairs; FP - parent farther from F_1; NP - near parent; - etc.

For the additive scheme with pure parents;

$$FP = n_1\alpha + n_1 k\alpha + R \qquad (1)$$

$$NP = n_2\alpha + n_2 k\alpha + R \qquad (2)$$

$$F_1 = n\alpha + R \qquad (3)$$

$$F_2 = 3/4\ n\alpha + 1/4\ nk\alpha + R \qquad (4)$$

$$FB = 1/2\ n\alpha + 1/2\ (1 + k)\ n_1\alpha + R \qquad (5)$$

$$NB = 1/2\ n\alpha + 1/2\ (1 + k)\ n_2\alpha + R \qquad (6)$$

Eliminating R from (1) to (6) and combining n_1 and n_2 provides seven not entirely independent estimates of (1-k) $n\alpha$ and an eighth comparison $(2F_2-B) = 0$. Take: P - sum of parents; F - sum of F_1 and F_2; and B - sum of backcrosses. For Lindstrom's data on relative yields of three inbred lines of maize and their hybrids (Proc. 7th. Int. Gen. Cong.):

	(1-k) $n\alpha$	d
$4(F_1 - F_2)$ =	136.8% F_1	15.1
4/3(F-P)	124.5	2.8
2(B-P)	142.0	20.3
$(2F_1-P)$	127.6	5.9
$2(2F_2-P)$	118.4	-3.3
4(F-B)	89.6	-32.1
$2(2F_1-B)$	113.2	-8.5
Mean	121.7	$(2F_2-B)$ = 11.8; should be 0.

Lindstrom's data probably are a fair representation of the usual result - see Neal, J. Am. Soc. Agron. 27: 666.

The seven estimates of (1-k) $n\alpha$ are expected to be homogeneous and $(2F_2 = B)$ on the additive scheme, with no restrictions as to linkage, or as to degree, direction or other variation of dominance, or variation of Alpha.

In the event of no significant departure from the additive scheme the mean estimate of (1-k) $n\alpha$ may be of value to the breeder without further resolution into its factors. The quantity (1 + k) $n\alpha$ or $(n\alpha + nk\alpha)$ estimates total range of genetic variation for the specific cross with free assortment. Distance from the lower extremity to F_1 is $n\alpha$; from F_1 to upper extremity is $nk\alpha$. The two are equal with no dominance. With dominance their difference is (1 - k) $n\alpha$. Total depression by inbreeding is 1/2 (1 - k) $n\alpha$; depression from F_1 to F_2 is 1/4 (1 - k) $n\alpha$.

Taking the present case as additive, $k = (-121.7/n\alpha) + 1$. Then, $n\alpha$ must be as great as 121.7% F_1 if the conclusion of negative k is to be avoided. The factor k varies from unity for no dominance, through zero for complete dominance to negative values for over-dominance, "super-dominance," or "diverse alleles". With the conclusion of "complete" dominance (k = 0) $n\alpha$ must be taken 121.7 and the minimum phenotype minus 21.7 Taking the minimum at zero, $n\alpha$ is 100% and k is minus 21.7 The correct explanation of heterosis for yield in maize may lie somewhere between those somewhat arbitrary limits, involving both negative R and negative k. Note that on the additive scheme F_1 will not exceed the sum of parents without negative R or negative k, yet most maize inbred yields are less than one-half of F_1 yield. If k be negative, selection for increased

inbred yield will tend towards lower F_1 yield.

The obtained value of 121.7 places expected yield of a homozygote from these crosses at 39.2% F_1, which is higher than usually obtained. The example may not be strictly additive. For further illustration of method, four of the seven estimates of $(1 - k)\, n\alpha$ involve (-P) with average deviation plus 6.4, indicating that slightly higher inbred yields may be expected with the present hypothesis.

Cross of heterozygous maize varieties - Tuxpan x Golden Cross Bantam

	F_2		Backcross to G.C.B.			S.D.	
	0	C*	0	C**	$(1-k)n\alpha$	F_2	sk
Number leaves	13.7	13.9	12.0	11.6	+1.7	1.47	-3
Height, feet	7.5	7.3	5.4	5.9	+2.7	1.00	-2
Days to silking	73.9	70.9	66.6	65.2	-6.9	4.47	+3
Tassel length, ins.	17.4	16.6	14.6	14.7	+3.2	2.28	-1
Silking shoots	4.7	4.8	6.5	5.5	+2.8	2.30	+4
Ear diameter, cm.	4.4	4.6	4.2	4.3	+0.1	0.37	0
Cob diameter, cm.	2.5	2.5	2.3	2.3	-0.1	0.26	0
Husk length, cm.	24.0	24.6	21.1	22.8	-3.2	2.96	0
Ear length, cm.	19.1	19.6	18.1	18.6	+5.3	2.84	-1?
Husk extension, cm.	5.0	5.2	3.0	4.3	-8.0	3.33	+3
Number tillers	.9	.97	1.1	1.3	+0.9	0.91	+5
No. kernel rows	13.4	13.3	11.6	12.0	+0.4	2.27	+1

* Mid-point between F_1 and mean of parents.

** Mid-point between F_1 and Golden Cross Bantam.

sk Inspection grade of skewness: grade 5 as 1/2 of a normal distribution.

Although these records are from heterozygous parents they show generally good agreement with the additive hypothesis. Interpretation for any character will involve first the comparison of F_2 and backcross means. Where agreement seems good, $(1 - k)\, n\alpha$ is next compared with skewness as to magnitude and direction. Finally, $(1 - k)\, n\alpha$ as a measure of dominance bias is considered with some measure of variation. Number of silking shoots and number of tillers have apparent skewness opposed in direction to the dominance bias. For tillers the explanation seems to lie in a piling up of nearly half of the frequency in the zero class; the character is not expressed to the left of or below zero. No explanation for silking shoots is apparent.

It is indicated that continued inbreeding would increase total husk length 1.6cm., while ear length would be shortened 2.6 cm. Husk extension would then increase about 4.0 cm. with inbreeding and decrease with crossbreeding of inbreds.

Powers (J. Agr. Res. 63: 161) presents records on plant height in centimeters for four tomato crosses. Mean estimates of $(1 - k)\, n\alpha$ are:

	Danmark	Johannisfeur
Red Currant	25.3	10.8
Johannisfeur	13.8, 7.1*	
Bonny Best		1.1

* Records for two years

The seven individual estimates on which each of the above is based do not show marked heterogeneity within any set in the writer's judgment. Variance of $(1 - k)\, n\alpha$ is apparently much greater between than within these crosses. Deviation from 0 of $(2F_2 - B)$ is slight in each case. The cross Johannisfeur x Bonny Best was discussed separately by Powers. He found departure of F_1 from mid-point of the parents not significant. F_1 and F_2 seem almost identical. Yet the seven estimates of $(1 - k)\, n\alpha$ are, 0.24, 1.31, 1.28, 1.04, 1.84, 1.36, 0.80; all positive, suggesting the expected mean may be some small positive value due to some degree of dominance bias, geometric interaction, or non-linear scale of environmental effects. Since $(2F_2 - B) = 0.28$, dominance may be the favored conclusion.

For the cross Danmark x Red Currant the far parent is 16.6 cm. from F_1. Since $(1 - k)\, n\alpha = 25.3$ cm. the minimum phenotype, R, is 25.3 cm. farther from F_1 than is the maximum. It would appear that the far parent Red Currant has plus gene values not found in the other parent sufficient to explain the excess of F_1 over the taller parent. The writer sees no suggestion of negative k or negative R in the three crosses which have F_1s taller than the taller parent.

Powers has noted that dominance bias may be affected by environment, which view is supported by the two records for separate years on one cross. Extensive analysis by higher order statistics, not being easily repeated, might be of doubtful value, if confined to one season or location.

There is of course, no new principle involved in the analysis by comparison of means suggested here. More efficient statistics for judging significance in some of the comparisons may be developed perhaps. If values of k, n, and alpha could be resolved by extensive analysis the quantity $(1 - k)\, n\alpha$ would still be of prime interest as a measure of dominance depression of efficiency of selection. Progress in breeding towards an objective involving several quantitative characters may sometimes be hastened by an efficient balancing of backcross and selection pressures. Those characters which have strong dominance depression away from the objective will be more difficult to recover from crosses by selection. Insofar as possible such characters should be collected in the recurrent parent, and thus largely recovered by backcrossing.

In the event of negative k (aA increment exceeds AA increment), regression of phenotype on number of plus genes (A) will rise to a point beyond which the mean effect of an (A - a) substitution is negative because of increasing homozygosity. From this point the F_2 distribution of

phenotype will be doubled back on itself with respect to gene number values. Analysis by comparison of means will not be distorted. Presumably, analysis by higher order statistics may also not be distorted but that must be investigated.

Analysis by comparison of means would seem to be a ready method where more extensive analyses cannot be employed or a reasonable preliminary to more powerful methods.

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Linkage relations of gl_4

$$\frac{su\ Gl_4\ Tu}{Su\ gl_4\ tu} \times su\ gl_4\ tu$$

Su Gl_4 Tu	Su Gl_4 tu	Su gl_4 Tu	Su gl_4 tu	su Gl_4 Tu
20	3	9	33	18

su Gl_4 tu	su gl_4 Tu	su gl_4 tu
7	1	6

Su — 30.8 — Gl_4 — 20.6 — Tu

43.3

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1. Midcob color. This character is difficult to study in this climate. Samples of the same inbred material were grown in 1941 and in 1942. In several cases a line that had red midcobs in 1941 was classified as having colorless ones in 1942. The ears in both cases were brought in at maturity and dried in the drier for final classification. 1942 was an unusually wet year, especially during August and September. Even under conditions where the ears matured and dried well in the field as in 1943, many ears classified in the field as having colorless midcobs were found to be colored after drying. Proper conditions for complete maturity and drying appear to be essential.

In 1943, apparent linkage was found between an interchange T5-6 and midcob color (30% recombination in 172 plants), indicating at least one midcob color factor may be in chromosome #5 or #6. A new factor for shrunken endosperm (sh2), one of Stadler's x-ray mutants is linked with pr. Backcross data: 150 Pr Sh + 45 Pr sh + 51 pr Sh + 164 pr sh indicate 23.4% recombination. Its location in the chromosome has not been determined.

2. Dominant White Cap (W^c) appears to be in chromosome 1 based on the linkage observed with interchange 1-9c and the lack of linkage with 9-10a. Also there was no linkage with wx (using pollen classification for wx). Data with 1-9c (1942 and 1943): W^c = 80 semisteriles + 28 normals; yellow cap = 47 semisteriles + 74 normals or about 33% recombination. Dr. Hayes' earlier tests with bm2 were negative, while with gs there was a loose but significant linkage (P = .05 - .02). Such a linkage value would indicate W^c might be near br.

3. Zebra striped zb6. (Hayes, H. K. and Chang, M. S. Genetics 24: 60. 1939) was crossed with zb1, zb2, and zb3 and found to be genetically different from these three.

zb1 is not in chromosome 6, as shown by a trisomic test (C. Lazaro)

4. Fasciated ear appears from my F_2 results to be a dominant character, not a recessive as listed in the Cornell Linkage Summary. (This stock is Coop. #39-25-6).

5. Crosses between interchanges involving the same two chromosomes.

T2-4a x 2-4c	=	semisterile F_1
T2-4a x 2-4b	=	"
T2-4b x 2-4c	=	"
T2-6c x 2-6d	=	20% sterility on ears, pollen also low
T2-9a x 2-9b	=	semisterile
T5-7a x 5-7c	=	29% sterility on ears (pollen also low)

The low sterility was thought to be the result of survival of a certain class of spores which ordinarily aborts. In crosses involving two interchanges in which the two breaks are close together and in the same relative position with respect to the spindle fiber (the same interchange having its break in each chromosome closer to the spindle fiber than does the other one) certain spore classes should be deficient for only one short region. According to the cytological data available, in T2-6c the breaks are in the long arms at .3 and .25 respectively from the S.F. in chromosomes 2 and 6; while in 2-6d they are also in the long arms but at .4 and .4. Deficiency tests for genetic loci in the two F_1 hybrids showing low sterility were all negative:

for T2-6c x 2-6d : ms, si, pb were tested for chromosome 6
lg gl, v4, ba2, ts were tested for chromosome 2.

T5-7a x 5-7c : bv gl6 for chromosome 5
sl, bd, gl, ra ij for chromosome 7

It seems probable that none of the genes tested is in the region suspected of being deficient.

C. R. Burnham

6. Red glume collar. Certain inbred lines and genetic stocks show a band of red color near the base of the glumes of the tassel. Most stocks are green at this point. The color may show only when the tassel is fully out of the boot, but it may show earlier. A few segregating progenies indicate

that in these cases the red differs from green by a single dominant factor. A backcross test involving this character and also Y and Pl indicates that red glume collar is closely linked with Pl (6.6% recombination), but the data did not indicate the probable order.

Another red glume collar character is found in B pl stocks, but in cultures segregating B-b, the collar color has always been associated with B.

C. Lazaro and C. R. Burnham

Young tassels of both types b pl red collar and B pl red collar were wrapped up in black paper to exclude the light. In the first type (linked with Pl), the collar color developed in all cases in the absence of light. When the second type (associated with B) was bagged, the sun red color on the glumes did not develop, but the collar was colored, although not as intensely as that in the type linked with Pl. It appears, therefore, that the collar color is not a sun red color even in the type which is associated with B.

C. Lazaro

7. Trisomic tests with unlinked genes. Trisomic tests for chromosome 6 and the following genes were negative: zb, gl6, gl9 (trisomic plants had an excess of gl progeny as compared with the 2n), and v9. A seedling dwarf (one of Stadler's designated temporarily as ds-3) may be in chromosome 6 by this trisomic test.

Linkage data with other factors were obtained along with the tests for linkage in chromosome 6. The possible linkages are as follows:

Genes	N	Segregating for new characters	χ^2 for indep. test	Recom. ± S.E.
pr - ws	104	3:1	P = .02	35.5±6.1
W^c - si?*	164	15:1	P = .02	
Y - gl-11	283	3:1	P = <.01	38.5±3.3
Y - w (in gl6 culture)	202	3:1	P = <.01	27.0±3.8
Fl - gls-3	276	3:1	P = <.01	12.0±3.6
gls-3 - tw?**	276	excess for 15:1	P = <.01	1.0±1.7
Fl -tw?	276	"	P = <.01	
1 aleur. factor - tw3	579	"	P = <.01	38.0±6.2
Fl - tw3	218	"	P = .02-.01	
gl - tw3	561	"	P = <.01	28.0±5.6

* This silky is one that appeared in an F_2 of a single cross here.
**This tw was linked in coupling with the gls-3, one of Stadler's mutants.

Negative results by the χ^2 for independence test were obtained for the following linkage tests: zb with lg; ws with Y Pl B rg; gls-1 with B lg nl?; nl? with B lg; ds-3 with su, pr Y colorless aleurone (9:7). gl6 with Y; gl9 with Y bt? and zg3 with Y and colorless aleurone (3:1)

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1. Gene Variability. The study of R alleles which Fogel and I reported in the 1943 News Letter has been continued, with the addition of a series of r^r types and with further study of specific modifiers of R action and of environmental conditions affecting it. All or nearly all of the 22 R^r's originally included appear to be distinguishable in their effect upon plant color, but since some of these differences are slight they require confirmation in experiments in which modifier action may be excluded more critically than is possible by repeated parallel backcrossing.

For this purpose we have used colorless aleurone mutants of several of the original R^r alleles, since as previously reported spontaneous mutations of $R^r \rightarrow r^r$ have no appreciable effect upon the plant-color action. For example six R^r alleles (Boone, 997, Cornell, Quapaw, Ponca, and Black Beauty) form a group characterized by rather strong pigmentation, though distinguishable in parallel backcrosses by slight though consistent differences. Colorless aleurone mutants of Cornell and Quapaw were crossed with other members of the group, and backcrossed by rg. This yields progenies in which the Cornell or Quapaw phenotype may be compared with the phenotypes of similar alleles in sib plants, the aleurone color difference providing a completely linked marker. Such comparisons, so far as they have gone, confirm the reality of the small differences observed between members of this group. A similar method may be used for the study of "non-linear" variation in the action of the different alleles (News Letter 1943, page 20), and here the mutant r^r's may be supplemented by naturally occurring r^r's. We are using the latter chiefly for this purpose.

The alleles of B (News Letter 1943, page 22) appear to be fully as variable as those of R, and since the range in plant-color phenotype is even wider, they may be better suited to the identification of small differences. Among 14 B^w's compared, 6 were selected as standards to represent distinct levels spaced roughly between b and B, and in each of these a stock of B-gl rg was established. These alleles listed in ascending order of effectiveness, are designated as follows:

1. B^w (Boone) 3. B^w (Clarage) 5. B^w (Lookout)
2. B^w (Young) 4. B^w (La Paz) 6. B^w (Seattle)

Additional B^w's, both from existing stocks and from mutations of various B's, have been crossed each with the standard B^w-gl strains which appear to be just below and above them in effectiveness, and backcrosses of these hybrids will determine their position in the series. For further mutation work, Anderson's In2 (v4 B Gl lg) stock is being extracted in homozygous combination with r^g since B^w mutations induced in this stock may be crossed with the naturally-occurring alleles to produce backcross progenies with virturally complete linkage of marker genes.

Miss Elizabeth Somers is making a detailed histological study of the development and distribution of anthocyanin under the action of R and of B.

2. Gene Action. Among tissues capable of anthocyanin production there are marked differences in response; cells of certain types produce

anthocyanin readily with any R-allele above the R^g level, while cells of other types may produce anthocyanin only in the presence of the strongest R^r alleles. For example, among epidermal cells of the leaf, there are distinctive differences in the reaction of the long, narrow cells over the veins, the long and short surface cells, the stomatal cells, the hairs and the specialized cells at the base of the hairs, and the paired silicaceous and suberized cells. Anthocyanin is formed much more readily in the epidermis than in the underlying mesophyll cells, but in the chlorophyll-lacking sectors of japonica plants it is produced abundantly in mesophyll cells also. The same is true of certain white and virescent types, and in normal green plants the mesophyll cells of the auricle (which lack chlorophyll) are well colored by even relatively weak alleles. With strong B alleles, green mesophyll cells containing anthocyanin are more frequently found.

The alleles of R and B thus provide a series of reagents, so to speak, for the study of tissue differentiation. Thirty years ago Keeble, Atkins, and others showed certain interesting relations between anthocyanin patterns and the occurrence of oxidase systems detectable by the use of histochemical test-substances. Mr. Fogel has undertaken a study of this kind with maize, which is however still in a preliminary stage.

The study of competitive action of certain A alleles (News Letter 1943, page 21) is being continued in collaboration with John R. Laughnan. The dominant action of aP upon plant color is manifested with all of the visibly weakened A alleles tested (A^w, a^{lt}, A^{br}, A^{rb}). The alleles A^{br} and A^{rb} (both obtained by Rhoades, out of a by Dt) are purple plant types distinguished from A by their reduced effect upon pericarp color. When these are compared with A in sib plants (in backcross progenies marked by et), they show slight but distinct reduction in anthocyanin pigmentation of the plant as well.

The dominant effect of aP upon plant color is shown also, to a slight extent, by certain A's which appear to have full plant color and pericarp color effect. The different A's used were extracted, after parallel backcrossing to a C R, from various stocks, chiefly the Indian strains used as foundation material for the R and B studies. With some A's the difference between A/aP and A/a sibs is clear enough to permit reasonably accurate prediction of the genotype at the flowering stage, and this identification may be made somewhat more accurately by testing the extracted pigment. The difference is due to the presence of varying quantities of yellow pigment in addition to the purple. With other A's and with A^b, no difference is found. The aP reaction thus serves as a sensitizer for the recognition of differences between the A alleles, and indicates the occurrence of considerable additional allelic variability at this locus. Conversely, the extent of the effect varies among different pale alleles obtained by mutation from A^b (News Letter, 1943, page 21), when these are tested against a common A. All of the pale alleles showing the dominant plant color effect have

dominant brown pericarp action; the two pale aleurone alleles with recessive brown pericarp ($\underline{A}^{w}$ and $\underline{A}^{lt}$) give negative results in parallel tests.

Mr. Laughnan is making a chemical and spectrographic study of the pigments involved in the action of the A alleles, and is developing methods for the quantitative study of the mixed pigment phenotypes.

3. Spontaneous Mutation. The frequency of spontaneous mutation to colorless aleurone types varies widely in different R alleles. The most mutable of the alleles studied is $\underline{R}^{r}$ (Cornell), which yields r mutations at the rate of about 2 per 1000 gametes. At the other extreme are a few alleles which give no mutations in populations of 25,000 to 100,000 gametes.

As previously reported, differences in mutability are inherent in the gene itself, since they are maintained when a highly mutable and a rarely mutable allele are combined in a heterozygote, so that the mutations must occur in precisely comparable cells. This comparison is made possible by the fact that the mutations affecting aleurone color do not affect plant color, and in a heterozygote $\underline{R}^{1}\ \underline{R}^{2}$, in which plant color is distinct in the two alleles combined, the identity of the gene mutating is readily determined. For example, when R (Cornell) is combined with an $\underline{R}^{g}$ of low mutability, the mutants produced by the F_1 plants are almost exclusively r (Cornell).

In addition, however, there is a pronounced effect of modifiers upon the frequency of R → r mutation. Homozygous R (Cornell) stocks extracted from crosses of the type mentioned show lowered mutation rates, in some cases much lowered. Different homozygous strains extracted from the same F_1 plant show distinctly different rates.

Mutations to colorless plant types ($\underline{R}^{r} \rightarrow \underline{R}^{g}$) occur at appreciable rates in certain alleles, and the variation between $\underline{R}^{r}$ alleles in frequency of mutation to $\underline{R}^{g}$ appears to be uncorrelated with that of mutation to $\underline{r}^{r}$. R (Cornell) is very low in frequency of mutation to $\underline{R}^{g}$, while certain other R alleles yield plant color mutations at moderately high rates, none however approaching the frequency of aleurone color mutations in R (Cornell). The frequency of mutation to $\underline{r}^{r}$ and to $\underline{R}^{g}$ in the same plant (male germ cells) was tested extensively in 2 plants of R (Columbia), with the following results:

Plant	Mutations to $\underline{r}^{r}$	Mutations to $\underline{R}^{g}$
1	6/12,525	3/11,804
2	5/ 8,459	3/ 8,020
Total	11/20,984	6/19,824

Mutations of $\underline{R}^{r}$ to intermediate levels appear to be very rare. On the contrary B mutates frequently to intermediate levels, and no mutations of B to b have been found. The $\underline{B}^{w}$ alleles occurring by mutation differ widely in level of action. In this respect B resembles $\underline{A}^{b}$, which as previously reported mutates frequently to different levels of $\underline{a}^{p}$ type and rarely if ever mutates spontaneously to a.

4. Comparison of X-ray and Ultra-violet Mutation. Following the experiment on X-ray and ultra-violet mutation of A previously reported (News Letter 1941, page 45-47, 1942, page 24-27), Roman and I set up a somewhat similar experiment with A^b. This was designed to take advantage of the fact that the spontaneous mutations of A^b are to an intermediate allele and are therefore clearly distinguishable from the effects of deficiency. The previous experiment had shown that the apparent mutations induced by X-rays were in fact minute deficiencies, and that the apparent mutations induced by ultra-violet were distinctly different and behaved as if they represented transformation of the gene to a recessive allele. It did not, however, exclude the possibility that the ultra-violet mutations were still more minute deficiencies, or cases of destruction of the single gene. With A^b this distinction could be made, if ultra-violet mutations actually are mutations of the type represented by spontaneous mutation of the same gene.

Extensive pollinations with untreated, UV-treated, and X-rayed pollen of a single A^b plant were made upon ears of a Dt, and numerous deficiencies and mutations were identified in the progeny. But the experiment failed in its main objective, because the natural frequency of mutation of A^b to a^p is so high that no significant increase in a^p mutations was produced by the treatments used.

The results, however, give additional support to the indication that the UV mutations are true gene mutations in two ways.

(1) No apparent mutation of A^b to a was found in the very extensive ultra-violet series.

(2) Among the endosperm mosaics induced by ultra-violet treatment, there were several cases in which a mosaic of clearly pale aleurone tissue showed typical dots of Dt type. Although an endosperm sector does not permit progeny testing, these can only have resulted from mutation of A^b to a^p, induced by the ultra-violet treatment. An endosperm mosaic of pale appearance could result from any one of numerous causes, but it could not provide a background for visible dots of A tissue unless it resulted from a change in A-action, and this background could not be pale if the A loss were due to deficiency.

The effect of ultra-violet treatments upon A^b mutation is sufficiently frequent for detection in the endosperm and not in the embryo because of the much higher frequency of induced alterations in endosperm than in embryo, which has previously been reported as characteristic of ultra-violet treatment.

This heightened frequency of endosperm alterations may be used to simplify various studies involving ultra-violet effects, and to make possible certain studies which otherwise could not be carried out. For example, it would be very desirable to determine the effect of varying ultra-violet wave lengths on the frequency of mutation. The action spectrum for A-losses in endosperm has been determined, but these include both deficiencies and mutations, and presumably consist very largely of deficiencies. It would not be possible to make significant comparisons of wave length effectiveness in inducing mutation if the mutations could be identified only by the growing and testing of progeny plants.

The use of $\underline{A}^{b}$, with recognition of mutants by the $\underline{a}^{p}$ phenotype, as described above, is effective for identifying positive cases of mutation in the endosperm, but it is not suited to quantitative work because of frequent failure of $\underline{a}^{p}$ sectors to color positively. Laughnan and I have therefore made use of a different method, which permits identification of the alterations in the endosperm but with confirmatory tests on the plant grown from the accompanying embryo.

Pollen of homozygous A A with the recessive markers gl3 and j was used on ears of a-X1/$\underline{a}^{p}$. The x-ray mutants a-X1, a-X2, etc., are inviable when homozygous and in all possible combinations inter se, and sectors homozygous or hemizygous for them are also inviable (News Letter, 1942, page 25). If all X-ray induced A-losses involve the loss of the associated viability factor, X-rayed pollen will never yield a colorless seed or sector; if any apparently colorless or sectorially colorless seed is found, it may be tested by growing the plant to determine whether the female gamete was a-X1 or $\underline{a}^{p}$. A colorless seed yielding a plant not heterozygous for $\underline{a}^{p}$ is selfed or tested for the recessive markers to exclude the possibility of pollen contamination.

The A-losses shown by $\underline{a}^{p}$ tissue include the deficiencies plus the mutations among the seeds from $\underline{a}^{p}$ gametes; those shown by a tissue include the mutations alone among the seeds from a-X1 gametes. Control pollination by a C R on a number of ears of the female stock show that ♀ gametes of $\underline{a}^{p}$ and a-X1 functioned in approximately equal numbers.

In the limited populations now completed, X-ray treatment has failed to yield colorless seeds or sectors. Ultra-violet treatment has given 3 proven cases of colorless sectors. The total number of A-losses in endosperm in the ultra-violet population on which the tests have been completed was 92. This indicates a ratio of deficiency to mutation of about 86:3 under ultra-violet treatment for the A stock used in the experiment. This is not greatly different from the proportion found among progeny plants representing A losses in the embryo.

The induced alterations classified as mutations are subject to the same reservations regarding their genetic nature as are the ultra-violet mutations identified in progeny plants following treatment of A. The method permits the determination of relative frequency of mutation (in this sense), with a fraction of the effort required in determining mutation from progeny plants. By this method it is feasible to compare the effect of different wave lengths upon deficiency and mutation simultaneously, and to compare different A alleles in relative frequency of mutation. With slight modifications the method may be used also for the identification of gene mutations of $\underline{A}^{b}$ critically distinguishable from the effects of gene-deficiency.

The results of the above experiment have a further interest in connection with the problem of the endosperm-embryo difference in frequency of ultra-violet alterations. The cause of this difference is unknown, and the most plausible guess has been that it is somehow connected with the difference in breakage-fusion phenomena in endosperm and embryo, which might appropriately be termed the McClintock effect. It might be expected that deficiencies, initiated by equal effects of the treatment upon the two sperm nuclei, might differ greatly in frequency of realization under

the very different conditions of endosperm and embryo. But this experiment indicates that the heightened frequency of alterations in the endosperm applies to mutations as well as deficiencies.

While the various experiments with induced mutation of A and A^b indicate that ultra-violet treatment produces true gene mutation and that X-ray treatment does not, they are disappointing in their failure to yield induced gene mutations which may be established in stocks subject to critical analysis. This is due to the failure of the A^b experiment described on an earlier page of this report. The advantage of regular spontaneous mutation to an intermediate allele, which makes A^b suitable for this experiment, applies also to R^r, since its spontaneous mutations are regularly to R^g rather than to r^g. In the case of R^r distinct alleles are available, including types with varying frequency of spontaneous mutation. Mrs. Elena Perak has undertaken an extensive study of the effects of X-ray and ultra-violet treatment upon mutation of various R^r alleles.

5. Effect of X-rays upon Dominant Mutation of a. No dominant mutations have been found in X-ray progenies of maize in experiments in which hundreds of recessive mutations have been observed. The evidence against the occurrence of dominant mutation induced by X-ray is however inconclusive, for the following reasons:

(1) The number of genes capable of showing dominant mutation may be much smaller than the number capable of showing recessive mutation, since many genes may be already fixed by natural selection at a level maximal for gene action. The possibility of inducing dominant mutation can, therefore, be tested critically only with known recessives.

(2) Among known recessives many may be themselves deficiencies and, therefore, incapable of dominant mutation. Critical evidence of failure to mutate to a dominant allele therefore may be obtained only from recessive genes which have previously been known to mutate to a dominant allele.

(3) The only recessive alleles which meet this requirement are the variegation genes, which may be regarded as unstable recessive mutating frequently to a dominant allele. In these the spontaneous frequency of dominant mutation is so high that an effect of X-rays in inducing additional dominant mutation probably would not be appreciable.

It is possible to avoid these difficulties in the case of one gene. The recessive a1 has several known dominant alleles. The effect of Dt proves that it is capable of dominant mutation. In the absence of Dt it is not mutable, and would therefore permit recognition of even a slight effect of X-rays in inducing mutation. Since the effect of mutation is recognizable in minute sectors the treatment may be applied in a fairly advanced stage of endosperm development, so that many hundreds of cells are tested for mutation by the examination of a single endosperm. It is therefore possible to test for the occurrence of this mutation in practically unlimited populations.

The seed to be irradiated was produced by the cross a a X A a, both parents being homozygous for dt dt and for the complementary factors required for aleurone color. The endosperms of half of the seeds produced are A a a. These serve to indicate the size of sectors resulting from genetic

alterations induced by irradiation at the stage chosen, since induced deficiencies of A result in sectors of colorless aleurone. In the colorless seeds, induced dominant mutation of any one of the 3 a genes would result in a corresponding sector of colored aleurone. The colored seeds thus provide a basis for calculation of the number of opportunities for detectable mutation in the colorless seeds, and a basis for comparison of the relative frequency of induced dominant mutation and deficiency. Treatment was applied 73-81 hours after pollination.

The mutability of the a gene in both parental stocks was tested by crossing with a^{dl} Dt, a^{dl} being an a allele with negligibly low dominant mutation rate in the presence of Dt. From the results of these crosses the number of dominant mutations which would be expected in the a a a seeds under the influence of various doses of Dt may be calculated.

The results show failure of X-rays to induce dominant mutation in a population estimated at 5,700,000 cells, each containing three a's capable of mutation. The cell population of equal size in sib seeds yielded approximately 100,000 losses of A (deficiencies or recessive mutations) from cells containing only one A gene each. The number of mutations to A which would have occurred in the same populations under the influence of Dt, calculated from the test crosses mentioned, was over 16,000 for a single dose of Dt, or about 16 times this number for homozygous Dt Dt Dt seeds.

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During the past few years, a number of terminal deficiencies of the short arm of chromosome 9 have been isolated. Each deficiency arose as the consequence of a meiotic breakage of the short arm of chromosome 9 following crossing over in plants heterozygous for a chromosome 9 with a duplication of the short arm or for a structural rearrangement of the segments of chromosome 9. In each case, the extent of the deficiency was determined at pachytene in the F_1 plants which had received a normal chromosome 9 from one parent and a recently broken (deficient) chromosome from the other parent. Tests showed that deficiencies which ranged from minute to one-third of the distal segment of the short arm were all female transmissible. Those which extended into the first distinct chromomere were transmissible through the pollen. None of the longer terminal deficiencies were male transmissible. Because of the male and female transmission of the very short terminal deficiencies, plants which were heterozygous for these deficiencies were self-pollinated to determine if viable endosperms and embryos could be obtained which were homozygous for these deficiencies. In these F_1 plants, the normal chromosome carried c and the deficient chromosome carried C. The C mutant is located in the short arm within the 5th or 6th chromomere from the distal end. In these F_1 plants, 30 individuals were classified as having received a broken chromosome 9 which was deficient for only the knob. Self-pollinations of these heterozygous deficient plants gave typical ratios of 3 C to 1 c. The endosperms and embryos in both classes of kernels were normal. Plants arising from both the C and c kernels were likewise normal in appearance. Cytological

examination of some of these F_2 plants showed the presence of the two deficient chromosomes 9. It may be concluded that a homozygous deficiency of the knob does not obviously alter the appearance and functioning of any tissues.

Seven of the original F_1 plants were classified as having a chromosome 9 which was deficient for the knob and the adjacent segment of thin chromatin which joins the knob with the first distinct chromomere. Self-pollinations of these plants likewise gave typical ratios of 3 C to 1 c. The endosperms and embryos were normal in appearance. In all 7 cases, the seedlings arising from these kernels segregated in the ratio of 3 green to 1 pale-yellow. The pale-yellow seedlings are normal in morphology but die following exhaustion of food supplies in the kernels. Linkage of the pale-yellow phenotype with C, carried by the deficient chromosome, was obvious in each case. Through genetic and cytological means, it was possible to determine in each case that the recessive pale-yellow phenotype is produced as a consequence of the homozygous deficiency. Intercrosses between plants heterozygous for these 7 pale-yellow mutants showed that all 7 were either identical or allelic. The recessive mutant yg2 is known to be located close to the end of the short arm of chromosome 9. Combinations of a chromosome 9 carrying yg2 with any of the 7 deficient chromosomes 9 produced only normal green seedlings and plants. It may be concluded that the deficiencies which produce the pale-yellow phenotype are not long enough to include the Yg2 locus.

In six F_1 plants, the broken chromosome 9 was classified as being deficient for a terminal segment which extended into and included a part of the first distinct chromomere. These deficiencies were slightly longer than those which produced the pale-yellow phenotype. Following self-pollinations of these plants, normal F_2 ratios of 3 C to 1 c appeared in four of the six cases and a slight reduction of the C class in two of these cases. When these kernels were germinated, white seedlings segregated in ratios expected from a recessive mutant. In all cases, linkage of the white seedling mutants with C was obvious. It was possible to determine for each case that the white seedling phenotype resulted when these seedlings were homozygous for the deficient chromosomes 9. Intercrosses of heterozygous deficient plants of all 6 cultures were made to determine the allelic relations of the white seedling mutants. White seedlings segregated in the F_1 following all 15 combinations, indicating that the white seedling mutants were allelic if not identical. Intercrosses between plants heterozygous for the 7 pale-yellow producing deficiencies and the 6 white producing deficiencies gave rise to the typical pale-yellow phenotype in one-fourth of the progeny of all 42 crosses. It was determined that the pale-yellow phenotype arose following combinations of the two deficient chromosomes in a zygote. Thus, the deficiency mutants pale-yellow and white are allelic. Pale-yellow is dominant over white. This would be expected because the residual homozygous deficiency following combinations of the two deficient chromosomes is only that which would produce the pale-yellow phenotype.

Plants heterozygous for the 6 white seedling producing deficiencies were crossed by plants homozygous for yg2. In the progeny of all 6 crosses, a ratio of 1 green plant to 1 yellow-green plant appeared. Appropriate tests showed that the yellow-green plants were those which had received the

deficient chromosome 9 from the heterozygous parent. Therefore, it may be concluded that the white mutants are allelic to yg2, with yg2 dominant over white. This would be expected if the terminal deficiencies causing the white seedling mutants included the locus of Yg2. From the point-of-view of genetic analysis, the pale-yellow and white seedling mutants are comparable in all ways to other known recessive mutants in maize. The allelic expressions of pale-yellow and white and yg2 and white, and the non-allelic expression of pale-yellow and yg2 would be difficult to interpret following a purely genetic analysis. These results are readily interpretable when the cytological conditions are known. The phenotypic expression following combinations of any two of the three mutants may be considered a reflection of the residual effects of over-lapping deficiencies.

The mutants pale-yellow and white are repeatedly produced following the meiotic breakage of chromosome 9. Among 2577 such recently broken chromosomes 9 which were tested, 55 gave rise to the pale-yellow phenotype and 33 to the white phenotype. In contrast to most mutation inducing agents, the chromosomal breakage mechanism is a "mutation" inducing process which "induces" the same mutant time and again.

Barbara McClintock

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Unfortunately, I have been unable to make any worth while contribution to the News Letter. For the past few years my genetic research has been largely restricted to an attempt to keep some of my stocks from extinction in hope of better times to come.

I have, however, made fairly satisfactory progress with the sweet corn breeding. In a randomized block test that I ran last summer one of my hybrids out-yielded Golden Cross Bantam by about 85% (dry weight of shelled grain) and yielded about 90% as much as Trucker's Favorite. This Hybrid is perhaps 10-14 days earlier than T. F. and might average a little, perhaps a day, later than G.C.B. In quality, it is about the same as G.C.B. In what amount to "blind-fold" tests since the culture numbers meant nothing to the tasters, this hybrid got 15 votes and G.C.B. got 13 in direct comparison, a pretty good 1:1. Ears are slightly bigger but not quite so smooth as those of G.C.B.

In a smaller yield test planted about six weeks later, (hotter, drier weather and shorter days) this hybrid showed up much better in comparison with G.C.B.

Ioana and G.C.B. are the two sweet corns recommended for this area. Ioana was a little better than G.C.B. in the early tests but not nearly so good in the later test.

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1. Flint and Dent Corn. The improved yellow corn, Maiz Amarillo VENEZUELA -1, which is being distributed to the farmers of this country for commercial production, is neither dent nor flint corn but rather an intermediate between the two, with variations toward both extremes. This intermediate type, often referred to as tropical flint, is preferred to dent corn because it is more resistant to damage by the ever-present grain weevil.

Considerable difficulty has been encountered in maintaining this variety as a tropical flint. The farmers who make no selection in their corn complain that after two or three generations VENEZUELA-1 degenerates, that is, the amount of soft starch increases. Even in the Experiment Station where there has been selection for tropical flint ears during the past eight generations, the soft starch type reappears in considerable quantity at each harvest. The ears of the true flint type are scarce.

In this connection it is worthy to note that the dent corn from the United States and from Argentina become extremely soft under these conditions and little hard starch is developed.

2. Tall Corn. In the lowlands of this country where the soil is relatively fertile nearly all the local varieties of corn are extremely tall and the ears are often six to ten feet from the ground. The improved type, VENEZUELA-1, was especially popular when introduced to the public because it was shorter than the local varieties and had a low set ear. It has been discouraging to find that each year this corn is becoming taller and the ears are farther from the ground. Mass selection for low growing plants with their corresponding low set ears has been practiced for eight generations with little permanent success.

3. White Corn. Corn, prepared in a multitude of ways, is the principal food of the people of this country. Due to custom, the people of the central part prefer white corn while those of the eastern and western parts prefer yellow corn. When the corn improvement program was initiated in 1939, emphasis was placed on the selection of high yielding varieties of yellow corn with the hope that the people in the central region would take advantage of the improved seeds and perhaps learn to like yellow corn over a period of time, and thereby improve their diet. During the past two years this faint hope has been realized in certain areas in which the improved yellow corn, VENEZUELA-1, has given as much as 100% increase in yield over the local white varieties.

But in spite of this indication that a change in custom might be possible, we have finally yielded to public pressure to develop improved varieties of white corn (as a matter of fact, both white and yellow corn have been included in the corn improvement program since 1939, but the hybrids and the improved varieties of white corn have not been publicized). The few kernels of white corn which always appear in some of the ears of the variety Maiz Amarillo VENEZUELA-1 have been used as the basis of a new variety, Maiz Blanco VENEZUELA-3. From many thousands of ears of VENEZUELA-1, several hundred ears segregating white kernels were shelled together and planted in a small field. Before pollination the weakest plants

were eliminated. At the time of harvest, two kinds of ears were found: those with all of the kernels yellow and those with some kernels white and some yellow. The yellow ears were discarded. Of the ears with both white and yellow kernels, the best were shelled together and the seeds were placed on tables where a group of women picked out the white kernels by hand. (The white kernels were not all pure white; some were a faint yellow). They were planted in several experiment stations and with several farmers for propagation.

The harvest from these propagation plots was not completely white but is commercially acceptable. Further selection is being carried on to improve this new variety, VENEZUELA-3, but this slightly mixed type is being distributed to the farmers for commercial production. In the yield tests conducted in five different states this year, the varieties, VENEZUELA-3 and VENEZUELA-1, were nearly identical in plant type and in yield.

D. G. Langham

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V. SEED STOCKS PROPAGATED IN 1943

Dr. Murray and Miss Morris grew over 200 cultures and hand-pollinated approximately 1600 ears. These cultures consisted mostly of stocks that had been listed in earlier News Letters, that were in need of replenishing, or that were several years old and liable to loss of viability.

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