

MAIZE GENETICS COÖPERATION

NEWS LETTER

27

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March 17, 1953

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

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## I. ANNOUNCEMENTS

### 1. R. A. Emerson Memorial

The Department of Plant Breeding at Cornell University is pleased to announce that in all probability the R. A. Emerson Memorial will be completed within the present year. This Memorial will consist of a lighted glass exhibit case in which will be displayed a photograph of Dr. Emerson and changing exhibits of his work, together with current studies of the Department. The monetary goal originally set for the Memorial was \$500. At this date 44 contributions totaling \$302 have been received. Friends of Dr. Emerson who wish to contribute to the Memorial may send checks, payable to Cornell University, to Miss Frances Feehan, Department of Plant Breeding, Cornell University, Ithaca, New York.

### 2. Minutes of the 1952 Meeting of Maize Geneticists

The meeting of maize geneticists held at Cornell University (A.I.B.S. Meetings) on September 9, 1952, was attended by approximately 40 people. Discussion was centered around an agenda prepared by the Coordination Committee which had been appointed during the year by Dr. C. R. Burnham. A summary of the minutes of the previous meeting at Minneapolis in September, 1951, was read and discussed.

Dr. H. H. Smith, of Cornell University, gave a brief report on the present status of the Maize Genetics Cooperation. Maintenance of the Cornell stocks and their distribution are currently in the care of Miss Sherwood. Dr. Smith emphasized that after a long period of beneficent financing the Rockefeller Institute is withdrawing its support of the Cooperation this year (1953). Funds from this source are available only through June 30, 1953. While doubt was expressed concerning the source of funds to finance the maintenance and distribution of the Cornell stocks Dr. Smith reassured the group that there would be little difficulty in securing funds to finance the News Letter at Cornell.

Dr. M. M. Hoover gave a report on the status of the request submitted by the Illinois Station for funds from Research and Marketing 9B3, New Crops (North Central 7). The proposed project outlined the following objectives: (1) Maintenance and preservation of adapted genetic stocks; (2) Development of new combinations of testers; (3) Linkage determinations of unplaced genes; (4) Search for new genes. NC-7 funds could be applied legitimately to objective (1) above, involving maintenance and preservation of adapted genetic stocks. Mr. Hoover reported that the request for funds had been approved by the Technical Committee, NC7, at a meeting at Wooster, Ohio, August 25-26, 1952, and that the funds, \$2500 in amount, probably would be activated July 1, 1953.

Dr. M. M. Rhoades, in charge of the Illinois Program, reported that inventories of maize stocks would be solicited generally and that planting would be begun in 1953. It is intended to convert stocks to make them more adaptable. He announced that a copy of the project requesting funds from Research and Marketing would be sent to everyone on the roster of M.G.C.

Dr. E. G. Anderson raised the question of whether R. and M. funds could be employed for conversion of stocks. Dr. Hoover offered that these funds could legitimately support this activity. Dr. Rhoades indicated that additional funds to support the remaining objectives of the program would be sought at the University of Illinois.

Dr. Burdick raised the matter of the linkage assignments which had long ago been "farmed out" chromosome by chromosome to various maize geneticists. The general concensus seemed to be that this had proved a relatively unrewarding enterprise. In view of the absence of Dr. Burnham, who has in hand the data on the assignments, final action on this question was postponed until the next meeting.

Dr. Wright brought up for consideration the question of the status of the present Coordination Committee, and the floor was opened for nominations. A motion was made that the committee members be continued: Dr. Wright, Dr. Anderson, Dr. Eckhardt, Dr. Laughnan. Seconded by H. H. Smith and passed with no discussion.

Regarding the News Letter, Dr. E. G. Anderson commended Dr. Smith for the efficient manner in which he had handled the News Letter in the past, pointing out the great service which this publication renders to our group and to others and suggested that in view of lack of funds in the future to finance it a subscription fee of \$1 might be levied. Dr. Smith pointed out that funds are still available for 1953 publication but that editing may have to be done elsewhere than at Cornell. Dr. Rhoades indicated that a subscription fee would work an undue hardship on graduate students. Dr. Smith pointed out that he thought there would be no difficulty in financing the News Letter either at Illinois or at Cornell. It was agreed that there would be no current charge to Coop members for the News Letter. The News Letter topic was concluded with a strongly worded statement from Dr. Edgar Anderson who counseled upon the proper use and care of the publication.

The need for an up-to-date summary on maize linkages and for continuing work on this aspect of maize genetics was emphasized by Dr. E. G. Anderson.\* The matter of a current linkage summary was referred to the committee for further consideration.

John R. Laughnan

\*EDITOR'S NOTE: In regard to summaries on maize linkages it should be noted that the 1935 Summary of Emerson, Beadle, and Fraser is now available in limited numbers from the Department of Plant Breeding at Cornell. Moreover, the recent publication of J. Weijer in *Bibliographic Genetica* XIV (3-4) 1952 includes a compilation of maize genetic types as well as a complete bibliography.

## II. REPORTS FROM COOPERATORS

BROOKHAVEN NATIONAL LABORATORY  
UPTON, LONG ISLAND, N.Y.

Biology Department

1. Induction of Dominant Phenotype by Radiation.

This investigation was designed to study the effect of irradiation upon anthocyanin formation in the aleurone of a stock recessive for one of the factors whose dominant allele is ordinarily necessary for anthocyanin production. The recessive  $a_1$  allele was chosen for study. For the first series,  $a_1a_1A_2A_2CCRRPrprdt$  plants were grown in pails in a non-irradiation area and selfed or sibbed. At twenty-four or forty-eight hours after pollination, the plants were placed at various distances from a 145 curie  $CO^{60}$  source, and remained there until maturity (42-49 days). The ears were harvested and the kernels classified. A similar series was grown in a non-irradiation area and selfed or sibbed for controls. At a dose of 390 r/day of  $\gamma$ -irradiation approximately twenty-six percent of the endosperms show a mottled anthocyanin aleurone, at lower doses the percent of anthocyanin aleurones is correspondingly less. The majority of the mottled aleurones are pink, however an occasional aleurone will be purple or a mixture of pink and purple. The mottled areas are irregular in shape and vary in size. This phenotype appears to be similar to that previously described by Sager (Maize Genetics Cooperation News Letter 1948), Brawn (Maize Genetics Cooperation News Letter 1949), McClintock (unpublished) and others as "flush". In no instance did the mottled anthocyanin pattern appear definitely to be the dotted phenotype as first described by Rhoades, although it may be somewhat similar to the dotted phenotype recently described for an  $a_1$  allele by Nuffer (Maize Genetics Cooperation News Letter 1950).

A majority of the endosperms showing the mottled anthocyanin pigmentation appear to be associated with an undetermined germless condition (i.e. embryos fail to develop). This is also true for those carried thru the next generation. There are some kernels showing the "flush" endosperm in which the embryo appears normal.

Another class of kernels was found in which the aleurones were a mottled brown. These are also heritable and occurred chiefly at the higher doses.

For the second series, mature pollen from  $a_1a_1A_2A_2CCRRPrprdt$  plants was given 2000 r of x-ray and used to pollinate sister plants. Approximately two percent of the resulting aleurones were of the "flush" type.

In the controls one "flush" aleurone occurred in a total of 4905 kernels examined.

Further studies are in progress in an attempt to determine the nature and inheritance of this "flush" condition.

E. J. Dollinger

## 2. Linkage of bt<sub>3</sub> and pr.

In the 1952 Maize News Letter No. 26, p. 6., Matthews reported a new character shrunken<sub>3</sub> which was not allelic to sh<sub>1</sub> and sh<sub>2</sub>. This character which occurred in PI-183644 from Turkey, resembles brittle<sub>1</sub>, more than shrunken and has been renamed Brittle<sub>3</sub>. It is on chromosome 5 but possibly closer to pr than is bt<sub>1</sub>.

A cross of bt<sub>3</sub> x a<sub>1</sub> sh<sub>2</sub> gave 5 selfed ears with the following segregation among the colored seeds. (Since there is only about .25 percent crossing over between a<sub>1</sub> and sh<sub>2</sub> there would have been a very few sh<sub>2</sub> among the colored kernels). Pr + 481, Pr bt<sub>3</sub> 232, pr + 256, pr bt<sub>3</sub> 6, indicating about 15 percent linkage of Pr and bt<sub>3</sub>. Exact amount will be determined from backcross data in 1953.

Crosses will be made in 1953 between bt<sub>3</sub> and other bt stocks.

W. R. Singleton

## 3. Shrunken Stocks are Sweet.

In late summer last year it was noticed that kernels of nearly mature sh<sub>2</sub> stocks were noticeably sweet. Readings with a band refractometer ranged from 9 to 21 with one line averaging 19.4, while the low line averaged 12.8 on a reading of 10 plants. An inbred line of sh<sub>1</sub> was more uniform with averages between 15.3 and 16.0 for four progenies. It is suggested shrunken stocks be used for edible corn but the sugar content probably compares favorably with su stocks.

W. R. Singleton

CALIFORNIA INSTITUTE OF TECHNOLOGY  
PASADENA 4, CALIFORNIA  
and  
CITRUS EXPERIMENT STATION  
RIVERSIDE, CALIFORNIA

## 1. Chromosome placement of new genes from radiation.

Linkage tests of seedling mutants with endosperm marked translocations have determined the chromosome or linkage group for 14 of these mutants, and as our seedling tests are not yet completed, it is expected that several more will be placed. These 14 are as follows:

Character	Source	Chromosome
white seedling	4889	9
sienna	7758	8
yellow	7716	9 or 10
w(albino)	7716	3
w <sub>3</sub>	(old gene)	2
blue fluorescent no. 2		10
fungoid	8057	1
white (green base)	7263	6
zebra	5588	9
dwarf	p51	2
dwarf	7335	9
dwarf	8201	9
dwarf	8004	9
dwarf	8054	9

Some of the last four dwarfs are probably alleles but are of independent origin. They have not yet been intercrossed.

These are the results of seedling tests of crosses of genes with translocation cultures grown mostly for other purposes. Naturally the crosses were made with whatever suitably marked translocations happened to be available. The past year two blocks were laid out for this purpose, and crosses made in more orderly fashion. These have given us more adequate coverage for a larger number of genes, the results of which should be available next winter. The results to date are very encouraging and, we believe, amply justify using the endosperm-marked translocation technique for the placement of new genes in their respective linkage groups.

E. G. Anderson

## 2. A second blue-fluorescent seedling in maize.

One blue fluorescent character has been described (Teas and Anderson) which appears as a recessive in the seedling stage but acts as a dominant in the anthers. Linkage tests have placed the gene either in chromosome 5 or far out in the long arm of chromosome 9.

In 1950, three families from gamma ray and atomic bomb radiation each gave a single plant which segregated brilliant blue fluorescent seedlings. Paper chromatograms showed them to be different from the earlier type. Intercrosses also showed them to be different from blue fluorescent-1. The irradiated parents were widely different, but each had been pollinated by the same standard plant (3159-7) whose parentage involved only untreated CC5 and L317. Six other irradiated plants had been pollinated by the same standard, but only gave normal offspring. A repetition of all 9 families in 1952 yielded 7 additional plants which segregated blue fluorescent seedlings. The totals for the two plantings were:

Irradiated parent	normal	segregating fluorescent
3173-9	49	1
" -10	48	1
3175-2	44	3
" -4	52	0
" -5	45	1
3176-6	44	0
" -9	46	0
" -20	36	2
3177-14	42	2
Total	406	10

Thus only 2.5 per cent of the progeny of 3154-27 carried the mutant gene. The mutation was a spontaneous one and affected a sector including about one twentieth of the tassel.

Crosses were made with a series of waxy translocations. The test-crosses were made with a recovered waxy fluorescent. Seedling tests gave the following data:

Translocation	Total	Crossovers	Per cent
wx 1-9c	143	78	54.5
wx 2-9b	167	86	51.5
wx 3-9c	267	158	59.2
wx 4-9b	264	133	50.4
wx 5-9c	264	149	56.4
wx 6-9a	255	117	45.9
wx 6-9c	211	105	49.8
wx 8-9d	192	97	50.5
wx 9-10b	82	11	13.4

The linkage with wx 9-10b would indicate the gene location in chromosome 10, probably in the middle section.

E. G. Anderson

### 3. Linkage studies involving homozygous chromosome rearrangements.

During the course of linkage studies of chromosome rearrangements, a considerable amount of data has been accumulated on lg1-gl2 or C-wx linkage relations in various homozygous rearrangements. The chromosome rearrangements used are listed in Tables 1 and 2, together with their reported cytological positions. The cytological determinations listed are those which seem most nearly in accord with the present genetic information. The positions given for Inversion 2a are those reported by Dr. D. T. Morgan. The remainder of the determinations were made by Dr. A. E. Longley.



Table 1. Chromosome 2 rearrangements studied in homozygous condition.

Rearrangement		Cytological Position	
Inv 2	a	2S.7	2L.8
2-3	c	2S.5	3S.7
2-7	6372-2	2S.1	7L.2
2-8	6612-2	2S.4	8L.6
2-9	a	2S.5	9L.9

Table 2. Chromosome 9 translocations studied in homozygous condition.

Rearrangement		Cytological Position	
1-9	4398-4	1L.5	9S.2
1-9	4995-5	1L.2	9S.1
2-9	6656-4	2L.4	9S.3
3-9	c	3L.2	9S.2
4-9	5657-2	4L.3	9S.1
5-9	a	5L.8	9S.2
6-9	b	6L.1	9S.4
7-9	7074-6	7L.1	9S.8
8-9	6673-6	8L.3	9S.2

The genetic data have indicated that the point of translocation in chromosome 2 is proximal to the lg<sub>1</sub>-gl<sub>2</sub> region in each of the rearrangements listed in Table 1. Of the chromosome 9 translocations listed in Table 2, only 7-9<sub>7074-6</sub> is distal to C. The remainder are to the right of wx, though it is not certain that all are in the short arm of the chromosome. The map locations of most of the translocations discussed here were reported in the 1952 News Letter.

Plants homozygous for a chromosome rearrangement and heterozygous for the genes being studied were test-crossed reciprocally. The results are summarized in Table 3. Where recombination values from female and male transmission of the F<sub>1</sub> were not significantly different, only the totals were entered. In a few cases such data were tabulated separately, the values from female transmission being indicated by the letter F and those from male transmission by an M.

The Maize Linkage Summary indicates a map distance of 19 units for the lg<sub>1</sub>-gl<sub>2</sub> region and 26 per cent recombination between C and wx. The lg<sub>1</sub>-gl<sub>2</sub> recombination values in Table 3 are seen to be in rather close agreement with the standard map value, with the exception of the data involving 2-8<sub>6612-2</sub>. The recombination values there are somewhat higher in both female and male transmission. The C-wx combination values in homozygous rearrangements are in several cases considerably above the average reported in the Linkage Summary. In the case of 2-9<sub>6656-4</sub>, there is indication of a difference in the frequency of recombination in female and male transmission. Unfortunately, data from female transmission are available from only one plant. However, this same plant was used in two crosses as a pollen parent, with recombination values of 36.4 and 32.0 in the progeny (average value 33.8, based on 650 individuals).

Both 5-9a and 6-9b gave considerably lower recombination values, with the data from reciprocal crosses in close agreement. It may not be irrelevant

Table 3. Testcross data of  $lg_1-g_1_2$  and  $C-wx$  recombination values in homozygous chromosome rearrangements.

Rearrangement	Total Number	Total recombinants	%	Mean % Recombination*	Number**
<u><math>lg_1-g_1_2</math></u> Recombination					
Inv 2 a	4846	912	18.82	18.15 ± 2.34	4544
2-3 c	4953	990	19.99	20.42 ± 1.97	4953
2-7 6372-2	3111	561	18.03	18.22 ± 2.04	2945
2-8 6612-2	1932(F)	480	24.84		
	1072(M)	289	26.96		
	3004	769	25.60	25.41 ± 2.57	2826
2-9 a	5745	1231	21.43	21.61 ± 1.89	5651
<u>C-wx</u> Recombination					
1-9 4398-4	1732	583	33.66	33.70 ± 4.34	1732
1-9 4995-5	10805	3611	33.42	33.04 ± 1.79	10549
2-9 6656-4	157(F)	33	21.02		
	2654(M)	902	33.99	34.38 ± 1.55	2654
3-9 c	9526	2925	30.71	30.39 ± 2.00	9204
4-9 5657-2	9614	3255	33.86	34.02 ± 1.78	9402
5-9 a	8056	1993	24.74	24.48 ± 1.97	7887
6-9 b	2721	646	23.74	23.62 ± 2.52	2721
	1507(F)	487	32.32	32.21 ± 2.15	1507
7-9 7074-6	1442(M)	327	22.68	22.91 ± 6.70	1442
8-9 6673-6	3085	1082	35.07	35.13 ± 1.98	2961

\* Based on progenies larger than 100.

\*\* Total number of individuals in progenies larger than 100.

that both of these translocations display much non-homologous pairing and suppression of crossing over in the heterozygous condition.

Recombination values from female transmission were higher in 7-97074-6 than those from male transmission. In this homozygous translocation the C-wx region occupies its normal position with respect to the centromere of chromosome 9 but most of the long arm of chromosome 7 is attached distally. In the reconstituted 7<sup>9</sup> chromosome, therefore, the C-wx region is in the proximal portion of a long arm. It will be of interest to investigate the  $lg_1-g_1_2$  recombination value in homozygous 2-3a, in which the translocation point is distal to  $lg_1$ . In this case, as with 7-97074-6, a fairly long chromosome segment is attached distal to the region whose recombination values are being studied.

The data presented suggest that the recombination values of a region are dependent upon its position in the chromosome complement. It is not yet clear whether the important considerations are position with respect to a centromere or the tip of an arm, or whether factors such as the nature of adjacent chromatin or the lengths of chromosome arms are critical.

Earl B. Patterson

1. Viviparous<sub>1</sub> has been located as to chromosome with the aid of TB - 3a. An F<sub>1</sub> ear of a heterozygous vp<sub>1</sub> plant pollinated by TB-3a pollen was observed to be segregating viviparous seeds. This places vp<sub>1</sub> in the distal 9/10 of the long arm of chromosome 3 which is the portion of three translocated to the B centromere. Backcrosses of plants heterozygous for wx - T3-9a - vp<sub>1</sub> and wx - T3-9c - vp<sub>1</sub> to wx vp<sub>1</sub> produced 13.1% and 10.7% crossing over respectively between wx and vp<sub>1</sub>. Anderson (Genetics 23:307-313, 1938) reports 3.6% crossing over between T3-9a and wx and 7.6% crossing over between T3-9c and wx. The difference between the T-wx distances and the wx-vp<sub>1</sub> distances should approximate the crossover values expected between the translocations and vp<sub>1</sub>. This value is 9.5% for T3-9a and 3.1% for 3-9c.

Homozygous vp<sub>1</sub> seeds do not develop aleurone color in the presence of the genes A<sub>1</sub>, A<sub>2</sub>, C and R. There are two possible explanations for the absence of color in these seeds; 1) it could be the result of some direct action of vp<sub>1</sub> upon the formation of the aleurone pigment or 2) the gene could act by first inducing premature germination which in turn prevents the formation of color in this layer. The cross with TB-3a suggests that the first hypothesis is correct. The seeds in this cross all carried the genes A<sub>1</sub>, A<sub>2</sub>, C and R. However, the viviparous seeds instead of having colorless aleurones were colored while some of the dormant seeds were colorless. Thus, it is probable that the lack of color in the aleurone is not caused by the premature germination but rather is the result of some more direct action of vp<sub>1</sub>. If this is true, then the viviparous seeds with colored aleurone in the above cross result from the union of polar nuclei with a hyperploid sperm carrying vp<sub>1</sub> in duplicate while the deficient sperm (deficient for the vp<sub>1</sub> locus) unites with the egg nucleus. The dormant colorless seeds result from the reciprocal fusions. (In both of these classes of seeds the ovules functioning in fertilization carry vp<sub>1</sub>.) The cross with TB-3a also suggests that vp<sub>1</sub> is similar to vp<sub>5</sub>, vp<sub>7</sub> and vp<sub>8</sub> in that vivipary is determined by the genotype of the embryo and is independent of the genotype of the endosperm.

The following linkage information on several of the other viviparous mutants has been obtained.

vp<sub>2</sub>  
vp<sub>2</sub> - (4.0)\* - bm<sub>1</sub> - 19.0 - pr  
vp<sub>2</sub> - 1.1 - T4-5i

\*This is a maximal value. Non-viviparous ears in this crossover class will need to be tested further.

VP5    WX - 3.98 - T1-9c - 25.9 - VP5

VP9    WX - 5.4 - T5-9<sub>a76</sub> - 20.8 - VP9

VP9 - 8.5 - gl<sub>1</sub>

Donald S. Robertson

Brittle endosperm-2 and brittle endosperm-1.

Counts of F<sub>2</sub> kernels from brittle-2 times sugary 1 showed 545 normal kernels to 542 mutant kernels (sum of sugary and brittle) suggesting that bt<sub>2</sub> is near sugary in the proximal portion of the short arm of chromosome 4. Chemical analyses of mature brittle-2 and normal endosperms are shown in the accompanying table.

Carbohydrate analyses for ontogenetic series of brittle-1 and brittle-2 compared are shown in the second table. The homozygous mutant was from selfed plants, the control in each case was from a normal line of fairly similar background pollinated by the respective mutant. The brittle-1 and brittle-2 are in general quite similar with respect to their effects on reducing sugar sucrose and water-soluble polysaccharides. Reducing sugars were higher in both mutant types than in their respective normal counterparts from 33 days on. Sucrose was very much higher in both from 21 days on. Water-soluble polysaccharides, however, were very little different in the mutants than in the normals. Preliminary starch determinations in these samples indicate that brittle-1 and brittle-2 store much less starch at all sampling dates than do the normal. Previous work has shown that sugary-1 also accumulates much less starch than normal. But sugary has large amounts of water-soluble polysaccharide whereas brittle-1 and brittle-2 accumulate much greater quantities of sucrose at mid- and late development than have been found for sugary.

Howard Teas  
James Cameron (Citrus Exp. Sta.)  
Anna Teas

Table 1. Chemical constituents of brittle-2 and normal endosperms from three F<sub>2</sub> segregating ears.

	Percentage by weight	
	bt <sub>2</sub>	Bt <sub>2</sub>
Fat	7.3	1.5
Protein	17.0	15.2
Reducing sugars	7.7	.7
Sucrose	4.1	.05
Water-soluble polysaccharide	.4	.7
Starch	33.4	54.0

Table 2. Carbohydrate content of developing endosperms of Bt<sub>1</sub> versus bt<sub>1</sub> and Bt<sub>2</sub> versus bt<sub>2</sub>.

Days after pollination	Carbohydrate content mg. per endosperm					
	Reducing sugars		Sucrose		Water-sol	polysac
	Bt <sub>1</sub>	bt <sub>1</sub>	Bt <sub>1</sub>	bt <sub>1</sub>	Bt <sub>1</sub>	bt <sub>1</sub>
14	2.8	2.6	3.4	3.9	.2	.3
21	3.6	3.2	4.8	8.9	.7	.7
25	3.6	4.4	4.4	18.1	.7	1.7
33	.9	4.0	.3	26.0	.8	1.9
39	.3	3.3	.2	21.2	1.3	1.6
46	.3	2.1	.6	4.4	7.3*	2.2
	Bt <sub>2</sub>	bt <sub>2</sub>	Bt <sub>2</sub>	bt <sub>2</sub>	Bt <sub>2</sub>	bt <sub>2</sub>
14	4.3	3.5	1.8	2.1	.2	.2
21	3.2	5.3	2.0	18.2	.4	.5
25	4.6	4.4	4.7	24.0	.9	.7
33	3.7	4.6	6.4	26.4	1.8	.9
39	1.0	4.5	.1	25.2	1.4	1.2
46	.6	5.0	.1	14.7	2.5	1.2

\*Probably an abnormally high value.

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION  
NEW HAVEN 4, CONNECTICUT

1. Cytoplasmic pollen sterility.

Additional evidence has shown clearly that the different sources of cytoplasmic pollen abortion behave differently in crosses with the same inbreds. Many lines that cannot be sterilized satisfactorily by one source can be sterilized completely by another and maintained in a sterile condition for successive generations in backcrossed lines and in first generation crosses. On the other hand, inbreds that cannot restore fertility to a cytoplasmic sterile line of one source may be able to restore fertility to the same inbred line when sterilized by a different source. This shows that the various sources of cytoplasmic sterility differ in their interaction with the same genomes. Five different sources are being studied.

All sterile lines that have been converted to a uniform type and maintained by backcrossing in successive generations (some for eight generations) have shown a few plants returning to partial fertility. These plants that are apparently not outcrosses occur with low frequency, usually not more than 1 in 800 to 1000. No completely fertile plant has been found so far but they produce sufficient pollen to be maintained by self-fertilization. The offspring are variable in the number of anthers exposed

and in the amount of normal pollen produced. Some individuals return to complete sterility but, so far, none have been restored to complete fertility. These partially fertile plants cannot be attributed to outcrossing and must be due either to variation in the cytoplasmic state or mutation to pollen restoring genes. These possibilities are being tested by crossing by normally fertile lines free from restoring genes and on to completely sterile lines of the same genic constitution.

## 2. Testing for heterosis from inter-allelic interaction.

In a backcrossing experiment extending over ten generations, dominant gene markers were introduced into a relatively homozygous, long inbred line by outcrossing and backcrossing. The backcrossed lines each segregating for one of the dominant gene markers were gradually reduced in the amount of heterosis until there was no measurable difference in average height between the backcrossed line and the original recurrent parental line. One of the gene markers, Yy, endosperm permits a critical comparison between individuals grown from seeds produced on the same ears. The plants heterozygous for the gene marker were 0.8 inches taller than the plants homozygous for this marker. The two other markers used showed similar differences. The significance of these differences is being determined. This difference in the Y and y individuals is an increase in height of 1.3 percent over the homozygous sib plants. The original heterosis was a 33 percent increase in the first generation hybrid.

The evidence shows clearly that a large number of genes are involved in heterosis as measured by height of plant. Many of these are on the same chromosomes and are closely linked with these gene markers which were selected at random for their position on the chromosomes.

D. F. Jones

CORNELL UNIVERSITY  
ITHACA, NEW YORK

## 1. Cytoplasmic pollen sterility.

The experiment of 1951 as previously reported (Maize News Letter 1952) was continued on a limited scale. A preliminary study has been made, completing the examination of pollen samples for viability. The general result obtained continues to support a potency difference of the plasmagene. The microscopic readings also indicate a positive correlation between the size of the pollen grain and its viability. The diameter of the viable pollen grains ranged from 70-82 microns whereas the range of non-viable ones was between 40 and 45 microns.

The high potency of Ky 21 as a fertility-restorer over Minn. A 71 and Wis. W9 is re-confirmed. In single crosses of Ky 21 with Iowa I205<sup>t</sup> the percentage of viable pollen grains was 94.8% whereas those of crosses between I205<sup>t</sup> and A71 and W9 were 0% and 0% respectively.

In 1951 ears were taken from plants in 4 otherwise highly sterile lines that showed a relatively high percent of pollen shedding. Seed from these ears was planted in 1952. The percent of pollen viability of these plants on the average shows a significant regression toward sterility and also a polymodal distribution pattern. This is an agreement with the postulation advanced by Gabelman that pollen abortion was due to a particulate cytoplasmic factor and that the presence of one or more of these cytoplasmic particles in the microspores resulted in their failure to form functional pollen.

A limited experiment designed to test the transmission of sterilizing plasmagenes through the pollen grains of the restored single crosses also has been continued. The restored plants (C106<sup>ts</sup> x Ky21) were used to pollinate a normal fertile inbred (C106). The S<sub>1</sub> of the three-way cross showed no significant difference from the S<sub>0</sub> as far as pollen viability is concerned. The experiments will be continued in 1953 and the preliminary studies made in 1952 will be reported later in greater detail.

H. L. Everett and T. T. Chang

## 2. Cold tolerance in maize inbreds.

During the summer of 1952 some exploratory work was undertaken to determine the ability of certain inbred lines to germinate under controlled low temperature (10°C ± 1°). The experiments were carried out in deep freeze units with each kernel in a separate aseptic culture tube on an agar medium of mineral salts. Germination counts were taken daily for more than thirty days. Results may be summarized as follows:

Inbred	% Germination @ 10°C.
Wisc. W23	96.7
Minn. A152	75.0
Ill. A	10.0
Mo. G	7.5

It is interesting to note that while the inbred Mo. G showed the lowest germination at 10°C., once the cultures were exposed to room temperatures almost perfect germination was recorded. This occurred after the inbred had been held at 10°C. for as long as two months.

R. Rabson

## 3. Heterosis in albino seedlings of corn.

The objective of this work was to determine to what degree hybrid albino seedlings show heterotic vigor, and the ratio of this vigor in comparison with green seedlings from kernels of a single ear.

Materials used in this study were segregating lines which have been selfed for three or more generations and crosses between these selections. Light endosperm and albinism occur together as a pleiotrophic gene effect in these lines. Hence, segregating ears are chosen from the selfs and crosses to compare normal and albino seedlings. The first seedling trials

were grown in flats with five randomized blocks. These seedlings were grown in the dark to eliminate the effects of photosynthesis. Measurements of seedling heights, fresh and dry weights were made after 25 days and are reported in the following table:

Table 1.	Seed weight gm.	Plant height cm.	Fresh weight gm.	Dry weight gm.
Albino:Parents average	0.2033	28.0	0.769	0.0681
hybrid	0.2633	33.1	1.085	0.0892
hybrid increase	0.0600	5.1**	0.316**	0.0211*
% increase	23.0%	15.4%	29.1%	23.6%
Green:Parents average	0.2111	37.0	1.025	0.0784
hybrid	0.2655	43.9	1.472	0.1033
hybrid increase	0.0544	6.9**	0.447**	0.0249**
% increase	20.4%	15.6%	30.3%	24.1%

\*\*Difference is highly significant.

\*Difference is significant.

Further tests are in progress to determine similar values under greenhouse conditions. Comparisons of normals and albinos in regard to etiolated growth and phototropism are also being made.

S. Galal Sayed

#### 4. Effects of antibiotics on growth of corn seedlings.

Preliminary experiments have been conducted to determine the effect of soil treatment with various antibiotics on the growth of corn seedlings.

Treatment consisted of daily watering with a solution of the specific antibiotic. Height measurements were taken every three days for a period of 15 days, and green and dry weights determined at the end of this period.

Treatments with 7 ppm of procaine penicillin G and streptomycin sulfate have resulted in no significant differences in plant height, green weight, or dry weight of the field corn single cross B8 X Oh51A. Solutions of these antibiotics were applied to both sterilized and unsterilized soil. Terramycin, applied in concentration of 5 ppm, has resulted in a slight decrease in plant height and green weight.

Further studies are being planned to investigate the effects of concentration and amount of antibiotic applied, condition of soil, treatment of seed with disinfectants, and seed stock used for treatment.



### 5. Frequency of monoploid corn plants.

The frequencies of naturally occurring monoploid plants have been determined for the following seed stocks.

<u>Seed Stock</u>	<u>Pollen Parent</u>	<u>Number of monoploids Per 1,000 Seed Tested</u>
(B8 X Oh51A)(NY3 X D50)	Randolph 50167	.64
	aBPlCRgPrlg	
B8 X Oh51A	"	1.5
NY3 X D50	"	.3
B8	"	1.8
Oh51A	"	.5
NY3	"	.7
D50	"	.8
Cornell-11	"	.1
Randolph 50167	B8	.6
Randolph 50167	Oh51A	.3
Randolph 50167	Chase H225	.7

Only 13% of all monoploid plants set seed when self-pollinated. However, when pollinated with normal pollen of diploid plants, approximately 80% of the monoploid plants set viable seed.

R. R. Seaney

DEKALB HYBRID SEED COMPANY  
DeKalb, Illinois

### 1. Haploidy.

Following Chase's procedure our attempts to establish haploid lines have not been successful. We have, however, succeeded in isolating 26 haploid plants after processing 291,583 seedlings. To date none of them has been fertile enough to self-pollinate or the time of silking has failed to coincide with anthesis.

One of the best marker stocks is the Emerson brown aB Pl type which gives good aleurone color in the female parent and a strong root color in the zygote. The ideal marker is, of course, one which will induce the largest number of haploids, a uniformly dark aleurone, and a high concentration of anthocyanin. The female parents which produce the least amount of anthocyanin upon exposure to light and the best pigment coloration when crossed with a marker stock are most desirable.

Oddly enough, the approximate ratio of 1:10,000 obtained for induced haploidy, corresponds closely with the frequency of natural occurrence of polyembry (double-diploid, double diploid-haploid, or triple diploid embryos). In one study of seedling from germination samples of commercial seed fields, it was found that 210,100 seeds yielded 22 polyembryonic specimens, mostly

all double-diploid in nature. The previously mentioned 291,583 seedlings surveyed for haploidy yielded only 8 double-diploid embryos. It is of course not known how many haploids occurred in the germination samples observed from the commercial seed fields.

However, the above frequencies suggest that haploidy could occur and also account for the occasional off-type ears which are found on the sorting belts of both foundation and commercial production and are "inbred" in appearance yet fail to closely resemble either parent.

## 2. Sugar stalk corn.

Studies have been continued with sugar content of cornstalks where selections are being made for higher sugar content. A series of 3-way crosses and one four-way cross yielded the following data:

<u>No. of different Stalk Samples</u>	<u>Single cross</u>	<u>x No. of different inbred lines</u>	<u>% Sugar*</u>
62	C103xT1	10	13.34
83	T1xC103	11	12.87
68	C103x83	8	13.11
39	83xC103	7	13.48
48	T1x83	6	11.77
53	83xT1	6	11.98
54	(38-11xC103)x83	8	13.95

\*For comparative readings in the field a Bausch and Lomb Hand Refractometer was used. Samples were taken at the "hard-dough" stage.

## 3. Male sterility.

Paired progeny selection continues for converting key inbred lines to a sterile cytoplasm. Non-pollen restorers are being selected in male parents for female (seed parent) single crosses while pollen restorers are being selected for both parents of the male single cross. Samples from foundation seed stocks are being tested this winter (1952-53) at various locations in Florida, Texas, Mexico, and the greenhouse (DeKalb) for fertility.

Last summer pilot production fields involving male sterile single crosses averaged less than 0.5% for pollen fertility. The sterile seed fields showed a considerable increase in yield over the normal seed fields.

Loring M. Jones

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## 1. Maize breeding.

Three synthetic varieties are being produced, two of them in the current way, with inbreds that we made from the varieties Yellow Synthetic (University of Minnesota) and Hays Golden; the other one, by the strain

building method, out of the variety Midland. The variety (Midland) has been improved and is used in the south of our country. This is the first dent variety that has been distributed and grown in the country regularly.

We have produced a commercial dent-flint top-cross and distributed it for the first time this year. This top-cross has yielded significantly more than the standard varieties Midland and Colorado Klein in all the trials grown in the last three years.

As part of our work in corn breeding we have developed some seventeen inbred lines. They are now being used in single crosses to predict doubles. Those inbreds listed below are available if any corn breeder is interested to try them.

No. of Inbred	Years of Inbreeding	Origin
C15-1	7	Colorado "La Estanzuela"
C15-2	6	" " "
C16-1	7	Colorado Klein
C16-2	"	" "
C31-1	"	Hays Golden
C31-2	"	" "
C31-3	6	" "
C2-1	7	Yellow Synthetic (Univ. of Minn.)
C2-2	"	" " " " "
C2-3	"	" " " " "
C2-4	"	" " " " "
C2-5	"	" " " " "
C2-6	"	" " " " "
C2-7	"	" " " " "
C2-8	"	" " " " "
C6-1	"	Improved Leaming
C6-2	"	" "

R. Constancio Lazaro

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1a. Fossil maize pollen from Mexico.

Through the kind cooperation of Professor Paul B. Sears of Yale University and Mrs. Kathryn Clisby, research associate, Oberlin College, the authors have had an unusual opportunity to study fossil grass pollen secured from deep cores taken in Mexico City.

In the course of analyzing pollen content of the core samples Mrs. Clisby observed large grass pollen grains of such size as to preclude the reasonable possibility that they were derived from species of native wild grasses yet extant in the Valley of Mexico. Careful study of the material,

in particular the very large grains from the 70 meter level, however, suggested to the authors three possibilities for the origin of the fossil pollen: *Tripsacum*, maize, or the presumed hybrid of *Tripsacum* and maize, teosinte. If the grains proved to be those of maize, as seemed most reasonable on the basis of size (111.0 - 133.0 $\mu$  by acetylation method) they would extend the fossil record of Indian corn far beyond presently known evidence. (Mangelsdorf, P. C. and C. E. Smith. *New Archaeological Evidence on Evolution in Maize*. Bot. Mus. Leaflets Vol. 13: No. 8. 1949.)

In order to obtain a critical basis for identification of the fossil pollen an extensive study was made of the size ranges of the pollen of *Tripsacum*, teosinte and maize. To sustain a uniformity in the data all preparations were made by the acetylation method and permanent slides prepared with glycerine jelly mounting medium. A total of nine species of *Tripsacum*, 2 collections of teosinte and three varieties of maize were used for purposes of measuring. It early became evident that very considerable size range exists within each of the three genera. In the case of *Tripsacum* average values for the long axes of the grain varied between 41.9 $\mu$  (*T. latifolium*) and 58.2 $\mu$  (*T. pilosum*); in teosinte, 79.2 $\mu$  and 86.5 $\mu$ ; in maize 117.3 $\mu$  and 120.6 $\mu$ . Unpublished data furnished by Dr. P. C. Mangelsdorf, shows that pollen of certain varieties of maize are far smaller than the three varieties of maize measured in this study, and, indeed, fall well within the range of teosinte and even that of the largest *Tripsacum* grains. It is apparent, therefore, that size alone cannot be utilized for critical identification of presumed fossil corn pollen unless sufficient individual grains can be measured and plotted on size-frequency curves to show statistical probability of one of three possibilities. Owing to the small number of individual grains from the cores, however, this procedure was not possible.

Because of the paucity of structural features and the undistinctive sculpture pattern on the pollen exines of the three genera, it became necessary to utilize some other means of distinguishing the three pollen types. Consideration of the problem led to one other possibility, viz., a comparison of the ratio in size which exists between the pore of the pollen grain and that of its longest axis. In order to demonstrate this ratio, 50 additional grains were measured from each preparation, with respect to these dimensions. The measurements were averaged and the ratios computed from the averaged values for each slide. The results showed unusual consistency, the ratio of pore to axis being an unexpectedly conservative value, and, from the data at hand, significantly different in the three forms in question. The numerical values computed are:

<u>Species</u>	<u>Pore:Axis Ratio</u>
1. <i>Tripsacum lanceolatum</i>	1:3.99
<i>T. dactyloides</i>	1:4.15
<i>T. laxum</i>	1:3.89
<i>T. australe</i> #1	1:4.04
<i>T. australe</i> #2	1:4.03
<i>T. pilosum</i>	1:3.97
<i>T. latifolium</i>	1:3.90
<i>T. maizar</i>	1:4.10
<i>T. sp.</i>	1:4.12
2. Teosinte annual (Guatemala)	1:5.70
Teosinte " (Guatemala)	1:5.38
3. Maize; Thayer Flint	1:6.53
" ; Knobless	1:6.52
" ; Thompson Flint	1:6.23
4. Mexican core pollen at 70.3 - 70.5 meters (average of 2)	1:6.6

Although these data are limited to approximately 600 pollen grains the differences are so consistent, both with respect to individual grains as well as with averages of many, that the pore-long axis ratio appears to be a perfectly valid method of distinguishing maize pollen from that of its near relatives. It may be noted also, in connection with this analysis, that teosinte, a putative hybrid between maize and *Tripsacum* shows an intermediate value both in over-all size, and, more significantly, in the pore ratio. The intermediate value is well in keeping with the postulated hybrid origin of teosinte.

Because of the evidence obtained in this study it is the opinion of the authors that the fossil grass pollen from Mexico City can be none other than that of maize. Future discovery may perhaps modify this conclusion, but from the facts now at hand it is the only conclusion possible.

Although palynological and geologic conclusions have not yet been drawn as to the actual antiquity of the deeper portions of the Mexican cores, it is apparent that they extend well back into the late Pleistocene. (Sears, P. B. Palynology in southern North America 1: Archaeological Horizons in the Basins of Mexico. Bull. Geol. Soc. Am. 63: 241-254. 1952) If this is the case the fossil corn pollen with which we are concerned probably antedates the advent of man in North America, and, as such, indicates the existence of wild maize in the Valley of Mexico during some early stage of the Wisconsin glaciation, if not during the last interglacial (Sangamon).

Elsa S. Barghoorn  
and  
Margaret K. Wolfe

### 1b. The occurrence of pre-colonial maize on Cape Cod, Massachusetts

In the course of palynological investigations of a fresh water bog, Small Swamp, on Cape Cod a number of pollen grains identifiable as maize, Zea Mays, have been encountered at significantly deep levels in the deposit. They were first found at a depth of 92 inches and more recently at a depth of 150 inches. The grains after acetylation, range in size from  $84\mu$  to  $97\mu$  along their long axes, and hence are well within the size range of maize pollen. It has been postulated by Barghoorn and Wolfe, above, that a further criterion for the distinction of maize pollen from that of other large grass pollen is the ratio between pore diameter and the long axis of the grain. This ratio in the case of maize fluctuates between 1:6.0 and 1:7.3 with a very consistent mean value of 1:6.5. The Cape Cod fossil grass pollen meets both the criterion of large size and that of the pore:axis ratio typical of maize, the fossil grains showing a pore ratio in two cases of 1:6.7 and in two others 1:7.0.

The antiquity of the maize pollen from Small Swamp cannot be determined until the pollen spectrum of the deposit has been completely analyzed. However, if a maximum value of the rate of accretion of the peat is accepted as 12 inches per century it can be concluded that the fossil corn pollen is on the order of 1200 years old. If this estimate be correct, it indicates the presence of agriculture in New England at a surprisingly early date.

Patrick Butler  
and  
Elso Barghoorn

### 2. Geographical and genetic variation in pollen size.

When a study of the fossil maize pollen from Mexico, reported above, was begun it soon became apparent that very few comparable data on size and other characteristics of maize pollen are available. A study was therefore undertaken of pollen from the maize varieties of this hemisphere. The pollen was obtained from ripe anthers of herbarium specimens of tassels all grown in the vicinity of Cambridge. The pollen was mounted in lactic acid which causes it to swell to approximately its original size. Twenty-five grains from each tassel were measured for maximum diameter under the microscope with an eyepiece micrometer. Altogether 17,350 grains from 694 plants from the maize of fifteen different countries were measured. The results in terms of modal frequencies are set forth in Table I.

Subsequent studies have revealed that there are sources of error in these data. For example, free pollen which has been shed from dehiscing anthers is usually larger than pollen teased from a ripe anther. Also there is some variation in pollen size from season to season in the same stocks. However, the data in Table I represent rather large samples and are so consistent in certain characteristics that they are believed to be significant.

Table 1. Geographical Variation in Pollen Size

Country of Origin	No. Plants	No. Pollen Grains	Diameter in microns		
			Modes		
			1	2	3
U. S. (Inbred strains)	50	1250	90		
Mexico	47	1175	90		
Guatemala	115	2875	92	100	
Salvador	5	125	92	96	100
Honduras	43	1075	92	96	100
Costa Rica	35	875	90	96	100
Nicaragua	13	325	90	100	
Panama	7	175	100		
Colombia	65	1625	90		
Venezuela	16	400	90		
Ecuador	52	1300	90		
Peru	63	1575	90	100	
Bolivia	130	3250	90	96	100
Paraguay	39	975	92	96	100
Brazil	14	350	92	102	
Totals	694	17,350			

The most interesting feature of the frequency distributions with respect to pollen size is that the curves are often bimodal or trimodal and there seem to be significant geographical regularities in size frequencies. In Central America for example, Honduras, Salvador and Costa Rica, adjoining countries, have frequency curves with modes at 90-92, 96, and 100 microns. Guatemala and Nicaragua, which lie to the north and south respectively of these three countries, have curves with modes at 90-92 and 100 microns. Mexico, which is still farther north, and Panama, which is farther south, each have curves with only one mode, which in Mexico is at 90 and in Panama at 100 microns. In Central America the center of diversity with respect to pollen size occurs in Honduras and diversity decreases in both directions from the center.

A similar situation exists in South America. There the center of diversity in pollen size is in Bolivia and Paraguay, whose curves for pollen size have modes at 90-92, 96 and 100 microns. The curves for Brazil and Peru are bimodal with peaks at 90-92 and 100-102 microns. Ecuador, Colombia and Venezuela, adjoining countries, all have unimodal curves with modes at 90 microns.

Pollen size is in some cases a plant character affecting all pollen grains in the tassel. But in some instances size is directly determined by the genes within the pollen grain and there is segregation for size within a single anther. A hybrid of P39 with a Bolivian variety, for example, produced pollen grains of two sizes in approximately equal numbers, the smaller with a mode at 90, the larger with a mode at 102 microns. There are apparently at least two distinct genotypes in maize with respect to genes for pollen size acting in the haploid state. There may be several

more. It will be important to determine how many different genes and chromosomes are involved in pollen size and whether selective fertilization which might act as an isolating factor occurs when there is segregation for pollen size.

An attempt has been made to correlate pollen size with other characteristics of the corn plant. When all of the data available are considered it is difficult to show any strong correlation. There are, however, correlations within certain smaller samples of the population. In Mexican races of maize, for example, pollen size tends to be correlated with ear length (style length?). In pop corn varieties there is a significant correlation between pollen size and kernel size. This is shown in Table 2, where pop corn varieties, arbitrarily placed in three groups with respect to kernel size, are compared in pollen size.

Table 2. Relation between size of kernels and diameter of pollen grains in microns in pop corn varieties.

Size Kernels	No. Strains	Pollen Grains	
		No.	Mean
Small	9	1800	91.6
Medium	15	3000	96.1
Large	7	1400	100.3

Since domesticated grasses usually not only have larger pollen grains than their wild counterparts but are also larger in other organs, including the caryopsis, it is possible that variation in pollen size in maize is the product of genes affecting the size of plant parts in general. Genes of this kind may have played a very important role in the evolution of the species under domestication.

P. C. Mangelsdorf

### 3. Geographical variation in gene frequencies.

While growing the races of maize of the countries of this hemisphere as part of a general taxonomic study, it seemed desirable to obtain data on gene frequencies of several genes which are easily tested and for which there is no strong presumption of selective value. Genes for which such tests have been made are Pr on chromosome 5, I on chromosome 9 and Ga on chromosome 4. All of these genes may belong to allelic series and no attempt has been made to distinguish between the different alleles. The test for both Pr and I, for example, involved a pollination of the stock A C R pr i by representative varieties from Latin America and by U. S. inbred strains, and no attempt was made to distinguish between the degrees of development of purple aleurone color or the inhibition of aleurone color. The data obtained from these studies are as follows:



Table 3. Percentage frequency of three genes in U. S. inbreds and in maize varieties of Latin America.

Country	Percentage Frequency		
	Pr	I	Ga
U. S. (inbreds)	98	0	0
Mexico	67	50	56
Guatemala	82	29	43
Honduras	63	77	69
Salvador	50	--	--
Costa Rica	55	50	57
Nicaragua	67	55	54
Panama	30	60	--
Colombia	86	11	26
Ecuador	93	13	25
Peru	96	25	7
Bolivia	95	22	10
Venezuela	69	19	50
Brazil	75	25	20
Paraguay	75	19	--
Cuba	33	17	--

Although the samples are far from adequate as a basis for final conclusions, several facts are quite clear.

Adjoining countries usually have similar frequencies for the same gene. Thus, the frequency of Pr is high in all of the Andean countries, Peru, Ecuador, Bolivia, Colombia and Venezuela. It is lower in the South American lowland countries, Brazil and Paraguay, and still lower in the countries of Central America with the exception of Guatemala which resembles the Andean countries.

The situation with respect to the I gene is similar to that for the Pr gene except that it is in reverse. The Andean countries have a relatively low frequency of I, the South American lowland countries a slightly higher frequency. The countries of Central America all have a relatively high frequency of the I gene except Guatemala, which resembles the South American countries more closely than it resembles the adjoining countries.

The frequencies of the Ga genes resemble the frequency of the I gene. The Andean countries are lowest, the South American lowland countries are somewhat higher, and the Central American countries (again with the exception of Guatemala) highest.

The consistent resemblance of Guatemala to the Andean countries in frequencies of these three genes is probably highly significant. Earlier studies of the maize of Guatemala and Southern Mexico have revealed strong affinities of some of the Guatemalan maize to the maize of Bolivia, Peru, Ecuador and Colombia.

Another conclusion which may be drawn from these data is that the maize of the United States is unique so far as these particular gene frequencies are concerned, Pr having a higher frequency and I and Ga lower frequencies than in any other country of this hemisphere. So far as gene frequencies are concerned the U. S. maize resembles that of Guatemala more closely than it does that of Mexico. However, when gene frequencies are broken down by states and departments it is apparent that the maize of the United States is related to the maize of eastern Mexico, which in turn is derived from the maize of southern Mexico and northwestern Guatemala. The maize of the U.S., at least so far as it is represented by inbred strains of commercial varieties, is, however, still unique when compared to the maize of most of this hemisphere.

P. C. Mangelsdorf

#### 4. Tests for weak alleles at the Tu-tu locus.

In earlier tests it was found that when maize varieties of Latin America are crossed on an inbred strain of half-tunicate tu<sup>h</sup> tu<sup>h</sup> there is marked variation in the development of the glumes on ears of the F<sub>1</sub> plants. Variation ranges from ears in which only the basal kernels are partly covered with glumes, to ears in which all kernels are completely covered. Some of this variation is undoubtedly due to modifying factors and some, perhaps, to environmental influences. There is, for example, some variation in glume development in the same stock from season to season. Much of this variation, however, may be due to differences in alleles at the Tu-tu locus in the Latin American varieties, some of which, although ordinarily regarded as non-tunicate, have glumes appreciably longer than those of most of the commercial varieties of the United States. The Mexican variety Chapalote, for example, has glumes about as long as the kernels.

A rather sensitive test for allelism at this locus has now been developed. Varieties with longer than average glumes, thought to be weak forms of tunicate, are crossed with an inbred strain of sugary, P39 for example, with short glumes. The F<sub>1</sub> hybrid is crossed by a non-sugary inbred strain of half-tunicate tu<sup>h</sup> tu<sup>h</sup>. If the stock being tested carries an allele somewhat higher (or lower) in the series than that brought into the cross by the sugary parent, there is segregation in the backcross generation, the differences between the two original genes being exaggerated by the presence of the tu<sup>h</sup> gene. Thus a cross of non-tunicate, tu tu, by weak-tunicate, tu<sup>w</sup> tu<sup>w</sup>, when backcrossed to half-tunicate, tu<sup>h</sup> tu<sup>h</sup>, yields two genotypes, tu<sup>w</sup> tu<sup>h</sup>, tu tu<sup>h</sup>, in equal numbers. If the parents differ with respect to sugary endosperm then the backcross also yields two genotypes, Su Su and Su su, in approximately equal numbers. The test for allelism, therefore, usually involves first, the occurrence in the backcross generation of two more or less distinguishable classes with respect to the development of glumes, and secondly, the linkage of these classes with the two genotypes involving sugary. This second test is necessary to exclude the possibility that variation in glume length is the product of major modifying genes on other chromosomes.

The data so far obtained from tests of this kind are summarized in Table 4. In all of the crosses included in this table two classes with respect to glumes have been distinguished and these classes have shown some degree of association with the two genotypes involving sugary. The average percentage of crossing-over is 37.1. This is within the range of data previously reported for crossing over between Su and Tu, but is somewhat higher than the average. This can be attributed to the fact that the classification with respect to glume length is seldom perfect.

Table 4. Tests for allelism and linkage at the Tu-tu locus.

Cross	<u>Longer Glumes</u>		<u>Shorter Glumes</u>		Total	No. Cross-overs
	<u>Su su</u>	<u>su su</u>	<u>Su su</u>	<u>su su</u>		
Guatemala 197 x P39	18	19	19	33	84	33
Ecuador 1195 x P39	19	10	13	20	62	23
Chapalote x P39	28	15	22	26	91	37
<u>Pr</u> Tester x P39	31	15	13	29	88	28
<u>Pr</u> Tester x Conn. 75	19	10	17	22	68	27
Conn. 75 x Ecuador 1197	30	59	60	26	175	56
Honduras 1639 x P39	24	49	38	24	135	48
Venezuela 1536 x P39	32	50	53	43	178	75
				Totals	881	327
				Average Percent Crossing Over		37.1

Additional tests in which both parents were either Su Su or su su so that linkage relations could not be determined indicate that Conn. 75 and P39 have different alleles and that Chapalote and Pr Tester are also different. In both cases two distinguishable classes for glume length occurred.

The combined data indicate that

1. P39 carries a higher allele than Venezuela 1536 and Honduras 1639.
2. Guatemala 197, Ecuador 1195, Chapalote, Pr Tester, and Conn. 75 all carry higher alleles than P39.
3. Pr Tester has a higher allele than Conn. 75.
4. Chapalote has a higher allele than Pr Tester.

Since all of these stocks have shorter glumes than those conditioned by the allele tu<sup>f</sup>, although they have not been tested in crosses with it, it now appears that there are at least seven alleles at this locus, Tu, tu<sup>h</sup>, tu<sup>f</sup>, tu plus three types of weak tunicate which lie between tu<sup>f</sup> and tu and to which symbols have not yet been assigned.

In addition to the crosses listed in Table IV and those mentioned elsewhere we have had one cross, Peru 1715 x P39, in which there was no segregation for glume length. There has also been one cross, Brazil 1691 x P39, in which segregation for glume length occurred but was not associated with segregation for sugary. This cross, however, happened to be segregating for several other characters including cob color, and the longer glumes proved to be linked with the P factor on chromosome 1. The glumes in the Brazilian parent of this cross are not at all like the glumes of weak tunicate, being quite stiff and horny, and resembling the glumes on ears of derivatives from maize-teosinte crosses.

The alleles at the Tu tu locus furnish a substantial sum of variation and, as is shown later, affect other characters of the plant and are undoubtedly a factor in the evolution of maize under domestication. Judged by their appearance and by the glumes produced on F<sub>1</sub> ears when they are crossed with half-tunicate, the majority of inbred strains of field corn in the U.S. are non-tunicate, but some of the sweet corn inbreds including P39 are weak tunicate.

#### 5. Effects of alleles at the Tu-tu locus.

The most conspicuous effect of the Tu gene is to accentuate - on some genetic backgrounds to exaggerate - the development of both the staminate and pistillate glumes. Not so readily apparent is the fact that this gene frequently causes the rachis to be more slender. This suggests that there is competition between the glumes and the rachis for the energy available for the development of the ear. Since the rachis represents the "system of supply" to the kernels, it is possible that reducing the glumes and increasing the rachis may also lead to an increase in total grain production.

Since we now have available a series of alleles at the Tu-tu locus it is possible to study the effect of different alleles upon the glume/rachis ratio. In order to make such a study we are developing, by repeated backcrossing to the inbred A158, isogenic stocks for comparing the different alleles on a uniform genetic background. Several additional years will be required to complete the study but the preliminary results already available from stocks not yet completely isogenic have proved to be interesting and significant.

The glumes were separated from the rachis and both were weighed. The lemmas and paleas which are enclosed in the glumes were weighed with the glumes. The results are shown in Table 5.

Table 5. Effects of alleles at Tu-tu locus on the relative development of glumes and rachis of the ears.

Genotype	No. Ears	Weight in Gms.			Ratio Gl./Rach.
		Total	Glumes	Rachis	
<u>Tu tu</u>	2	17.62	14.34	3.28	4.38
<u>tuh tuf</u>	3	23.99	17.21	6.78	2.54
<u>tuh tu</u>	6	21.76	13.24	8.52	1.56
<u>tuf tu</u>	3	22.48	11.86	10.62	1.12
<u>tu tu</u>	5	20.93	9.94	10.49	.95

The data show that the total weight of the cob (glumes, lemmas, paleas and rachis) does not vary greatly with different genotypes, but the glume/rachis ratio varies decidedly and consistently from 4.38 in the genotype Tu tu to 0.95 in the genotype tu tu.

The effect of the alleles upon potential grain production is not so easily measured, at least in these ears all of which were hand-pollinated and not completely filled. Potential grain production was estimated by multiplying the average number of rows x average number of kernels per row x average

weight of kernels from a well-filled portion of the ear. The results, although not consistent in all respects, since these ears are not from completely isogenic stocks, are still significant (Table 6). Accompanying an increase in the size of the rachis are slight increases in kernel-row number, number of kernels per row, total number of kernels and perhaps in average weight of kernels. All of these factors combine to produce a substantial and fairly consistent increase in total potential grain production. In these preliminary tests genotype tu tu is slightly lower in potential grain production than the genotype tu<sup>f</sup> tu, but the difference is probably not significant and can be attributed to a single atypical ear with unusually small kernels included in the study.

Table 6. Effects of alleles at the Tu-tu locus on potential grain production.

Genotype	No. Rows	Potential Kernels		Kernel Weight	
		Per Row	Total	Average	Total
<u>Tu tu</u>	13.0	22.5	293	.242	70.9
<u>tu<sup>h</sup> tu<sup>f</sup></u>	15.3	27.0	413	.187	77.2
<u>tu<sup>h</sup> tu</u>	14.0	32.8	459	.224	102.8
<u>tu<sup>f</sup> tu</u>	14.0	34.7	486	.233	113.2
<u>tu tu</u>	14.0	33.2	465	.227	105.5

The data in Tables 5 and 6 indicate that the evolution of the ear of maize may be, in large part, the product of changes in glume-rachis relationships with these, in turn, affecting grain production. It is not yet certain that wild corn was of the genotype Tu Tu (for the gene Tu may prove to be a pseudo-allele which arose under domestication) but it must certainly have been some form of a pod corn. The earliest cultivated corn found in archaeological sites has glumes and rachises similar to those characteristic of tu<sup>f</sup> and tu<sup>h</sup>. Mutations at the Tu-tu locus have created considerable variation in the glume/rachis ratio involving a secondary but highly important effect upon grain production. Both human selection and natural selection operating in a man-made environment would tend to favor the lower alleles and to work toward the extinction of the higher ones. Evolution of the ear of maize seems, therefore, to be, in substantial part, the product of evolution at one gene locus - the Tu-tu locus on chromosome 4.

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and  
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#### 6. Effects of the Tu gene on the tassel.

The Tu gene, in addition to causing the development of glumes enclosing the kernels of the ear, has numerous effects upon the tassel. In the homozygous condition it frequently causes the production of massive tassels bearing a mixture of staminate and pistillate spikelets. In some stocks the tassels are monstrous and exhibit varying degrees of male and female sterility. Plants bearing monstrous tassels are usually earless. These facts have led some students of maize to question the possibility that the tunicate character might be a primitive one, once characteristic of wild maize. It is possible

by repeated backcrossing to appropriate stocks, especially certain popcorn varieties, to provide the Tu gene with a modifier complex in which the tassel is not monstrous but is a normal grass inflorescence quite similar in its botanical characteristics to the inflorescences of corn's relative Tripsacum. Nevertheless, it is possible that a study of more or less monstrous tassels in which the several effects of the Tu gene are greatly exaggerated might yield valid clues to the mechanisms involved in its effects.

Detailed studies of numerous tassels of Tu Tu plants reveal that the sterility which occurs is sometimes more apparent than real. The pistillate spikelets are usually fertile if their silks, which appear about two weeks earlier than those of tu tu sibs, are promptly pollinated. The proportion of staminate spikelets is often greatly reduced and on some tassels there are none. On others, the anthers of the staminate spikelets fail to develop completely, especially those occurring in spikelets with massive glumes. In still other tassels the staminate spikelets bear well-developed anthers which are not exerted. These contain normal pollen, which is functional if the anthers are crushed between the fingers and applied to fresh silks. In some spikelets the anthers dehisce and shed their pollen without becoming exerted. The development of functional anthers is promoted by the removal at an early stage of the massive central spike which apparently draws heavily upon the total energy. During the past summer we successfully made a number of pollinations with pollen collected from apparently sterile Tu Tu plants.

Detailed morphological studies have also been made to determine how other parts of the tassel are affected by the Tu gene. Tassels from sib plants of three genotypes, Tu Tu, Tu tu, and tu tu, were directly compared. The results are shown in Table 7. One effect not shown by these data is the elongation of the rachilla which bears the caryopsis. In occasional spikelets this becomes so long that the kernel is borne on a long stem projecting beyond the glumes.

It is obvious from the data in Table 7 that the Tu gene causes a shortening and thickening of the internodes immediately below the tassel as well as the internodes of the branches of the tassel itself. The number of spikelets is greatly increased. The glumes, as well as the lemmas and paleas, are elongated, and there is a marked change in the ratio of total spikelet weight to rachis weight. All of these changes can be attributed to a single basic change, probably of a hormonal nature, which diverts the energy of the plants into its terminal inflorescence instead of its upper, ear-bearing, lateral branches. This diversion is easily prevented by removing the tassels at an early stage, whereupon the lateral ear-bearing branches usually develop.

Some of the effects of the Tu gene can be duplicated in nontunicate plants by growing short-day tropical maize under short-day treatment until the embryonic tassels begin to differentiate. When short-day treatment is terminated at this point and the plants return to a strongly vegetative phase, the tassels which finally emerge are frequently massive, sometimes pollen-sterile, and usually have elongated staminate glumes similar to those of plants of the genotype Tu Tu.

In modern corn varieties, often characterized by a single thick stalk, the diversion of the plant's energy to a single terminal inflorescence may well result in a state of physiological unbalance and a disorderly differentiation and development of its several parts. In wild corn, perhaps a freely-tillering plant with numerous slender stalks, the concentration of energy in the terminal inflorescences may have produced quite normal tassels. The tunicate character is not per se a monstrosity, although on modifier backgrounds provided by some modern varieties it may become one.

Table 7. Effects of the Tu gene on characters of the tassel.

Characters	Genotypes		
	<u>TuTu</u>	<u>Tutu</u>	<u>tutu</u>
Aver. length of 3 terminal internodes, cms.	8.47	15.17	21.49
Aver. diameter of 3 terminal internodes, cms.	0.65	0.55	0.40
Weight of tassel, gms.	48.4	20.5	3.2
Weight of glumes, gms.	33.6	15.2	2.1
Weight of rachises, gms.	9.3	4.9	1.0
Glume/rachis ratio	3.61	3.10	2.10
No. of branches per tassel.	35	25	18
No. of spikelets per tassel.	2445	1826	1228
Distance between spikelets, cms.	0.16	0.22	0.28
Lower glume length, cms.	1.89	1.48	0.96
" " width, cms.	0.57	0.54	0.39
Lower lemma length, cms.	1.84	1.02	0.80
" " width, cms.	0.56	0.36	0.18
Lower palea length, cms.	1.27	0.95	0.83
" " width, cms.	0.17	0.22	0.24
Upper glume length, cms.	1.91	1.40	0.92
" " width, cms.	0.63	0.58	0.37
Upper lemma length, cms.	1.34	0.69	0.65
" " width, cms.	0.48	0.22	0.11
Upper palea length, cms.	0.86	0.62	0.77
" " width, cms.	0.42	0.20	0.16

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#### 7. Mutagenic effects of teosinte chromatin in maize.

For some years we have been developing a series of stocks in which chromosomes of several varieties of teosinte are incorporated by repeated backcrossing, singly or in combination, into three different inbred strains of maize. On several occasions mutations have been noted in these teosinte derivatives and we have suspected that teosinte chromatin is in some way mutagenic when transferred to maize. Recently we have summarized data which tend to lend weight to this suspicion.

Fifteen different mutations have now been noted in the teosinte derivatives. Among these are ten defective seeds, two virescents, two albinos and one sugary endosperm. In all cases where the teosinte chromosomes have been identified chromosome 4 is one of the chromosomes or the only chromosome involved. Chromosome 4 from three different varieties of teosinte has been associated with mutations. Only three of the defective seed mutants have so far been tested for linkage. All are located on chromosome 4 closely linked to the Su locus. These three defectives are slightly different phenotypically, but whether they represent different mutations at different, closely-linked loci or recurring mutations at the same locus has not been determined.

All mutations so far noted have occurred when the teosinte chromosome was either known to be or suspected to be heterozygous. The mutations have occurred in relatively small populations, not more than six to twelve plants of each stock being grown each season. The relatively high frequency of mutations and the fact that they apparently occur only in heterozygotes suggests strongly that they are the product of crossing over, perhaps unequal crossing over, between maize and teosinte chromosomes. Sax (1931) suggested some years ago, on the basis of other evidence, that crossing over may be a primary cause of mutation. This possibility is being tested but the problem is complicated by a lack of good workable genes on both sides of the Su locus.

If these mutations are indeed the product of unequal crossing over then it is probable that minute duplications, less easily detected than ordinary mutants, are also occurring. Many of these may actually be beneficial in a domesticated species in creating new more complex "genes" which serve as a new source of variation and which may be an important factor in the evolution of this species.

Since maize hybridizes freely with teosinte and since in such countries as Mexico there is a constant reciprocal introgression of one species into the other, it may well be that a substantial part of the variability of modern maize is the product not only of Mendelian recombination of genes from the two species, but also of the mutagenic effects of teosinte chromatin in maize. At least this possibility merits a thorough study. Any suggestions from other students of maize for designing critical experiments in connection with such a study will be welcomed.

P. C. Mangelsdorf

#### 8. Tripsacoid maize in South America.

Evidence is accumulating that maize with Tripsacoid characteristics occurs not only in Mexico and Central America but also rather widely in South America. The following items, none in itself conclusive, add up to a rather suggestive total. Some of these items may be mentioned elsewhere by others, but it seems worth while to summarize them here since the writer, on a recent trip to the countries of South America, has had an unusual opportunity to synthesize more-or-less isolated items of evidence.



A. We have received from Ing. Urbano F. Rosbaco in Argentina a strain of "Maize Amargo" which in its ear characters is the most Tripsacoid maize yet discovered. The glumes are thickened and indurated as in segregates of maize-teosinte and maize-Tripsacum hybrids. Plants of this maize, like the "Maiz Indio" of Colombia, tiller freely, have hispid leaf sheaths and thick drooping leaves. "Maiz Amargo" is somewhat resistant to the attacks of grasshoppers and other insects and this fact coupled with the resemblance of its ears to segregates of maize-teosinte and maize-Tripsacum hybrids led Ing. Rosbaco to suspect Tripsacum contamination. The chromosome-knob number of this maize, however, is low, suggesting that if it is the product of a maize-Tripsacum hybrid it may have had a knobless species of Tripsacum as one of its ancestors.

B. A variety of maize in Brazil received from Dr. Brieger has long stiff lower glumes. This character is being transferred by repeated backcrossing to the U. S. inbred A158. It appears to behave in inheritance as a unit character although it may involve a group of genes rather than a single gene. The unit character, whatever it may be, involves the first chromosome and is linked with the  $P$  factor on that chromosome with 34.6 percent of crossing over. This is believed to be the first instance of locating on a chromosome a Tripsacoid character occurring in an established variety of maize.

C. Dr. F. Brieger in Brazil has in his collections at Pirizicaba a very maize-like Tripsacum obtained from the island of Marajo near the mouth of the Amazon. This Tripsacum is completely sterile. Preliminary studies show it to have 20 chromosomes. Dr. Brieger suggests that this Tripsacum may be a derivative of a maize-Tripsacum hybrid. (See also the description of "Maiz Indio" in the report of the Rockefeller Foundation Agricultural Program in Colombia).

P. C. Mangelsdorf

#### 9. New collections of prehistoric maize.

Preliminary studies have been made on two collections of archaeological maize.

The first of these, excavated by Mr. Reynold J. Ruppe of the Peabody Museum of Harvard University, comes from Cebollita Cave in New Mexico. It is regarded on the basis of pottery and other cultural traits as comparatively recent. The earliest maize, comprising carbonized ears with kernels intact, is a small-seeded flint corn, probably a pop corn, showing affinities with the primitive pop-corn races of Mexico, Chapalote and Nal-Tel, recently described by Wellhausen *et al.* It is definitely non-Tripsacoid. The later corn is strongly Tripsacoid and includes some specimens which are almost exact counterparts of segregates of maize-teosinte hybrids.

The second collection representing the LaVorra culture comes from a cave in Taumulipas, Mexico, excavated by Dr. Richard MacNeish of the National Museum of Canada. The earliest of this maize is dated by Carbon 14 determinations of other associated remains at  $4445 \pm 280$  years. This maize is closely related to the Nal-Tel race of Yucatan and Campeche in Mexico. Some of it is, however, more primitive than modern Nal-Tel, having longer glumes and

more slender rachises. The smallest cob in this collection is almost an exact counterpart, in both size and botanical characteristics, to the smallest cob of the corn from Bat Cave described earlier by Mangelsdorf and Smith.

There is some evidence of evolution in the LaPerra maize. The larger cobs with larger rachises and shorter glumes were all found in the upper strata. No strongly Tripsacoid cobs were found in any strata.

Since the LaPerra culture represents a transition from food gathering to food growing, the earliest maize found in this site may be not far removed from wild maize. Indeed, in the light of the fossil maize pollen found in the Valley of Mexico and mentioned earlier, it is even possible, though perhaps not highly probable, that the most primitive LaPerra maize is wild maize. Students of maize, including the present writer, have supposed that maize as we know it could not have existed in the wild because it lacks a means of dispersal. But if the ears of wild maize were small and numerous, and not completely enclosed in husks, the means of dispersal may have been adequate.

Neither of these collections of prehistoric maize lends any support to Randolph's suggestion that Tripsacoid characters are relict characters stemming from corn's ancestor. No strongly Tripsacoid cobs occur in the LaPerra maize at any stage, while in the material from Cebollita Cave the earliest maize is definitely non-Tripsacoid and the more recent maize is highly Tripsacoid. A similar situation occurred in the Bat Cave maize reported several years ago.

Incidentally, a study of prehistoric maize combined with studies of pod corn and derivatives of maize-teosinte hybrids has produced several criteria for distinguishing weak forms of pod corn from Tripsacoid maize. In the former the upper and lower glumes are similar in length and texture and the lemmas and paleas of both the fertile and sterile florets are well developed. As the cobs deteriorate the lemmas and paleas disappear first leaving both glumes. In the final stages of deterioration the entire spikelets are lost leaving only the rachis. In Tripsacoid maize (as in both *Tripsacum* and teosinte to an even greater degree) the lower glumes are thicker and more indurated than the upper and the lemmas and paleas of the sterile floret are not strongly developed. As the cobs of Tripsacoid maize deteriorate the upper glumes disappear with the lemmas and paleas leaving the rachis with the lower glumes still projecting. Cobs of Tripsacoid maize are not at all suitable for one of the homely uses to which corn cobs are traditionally put.

P. C. Mangelsdorf

#### 10. Additional data on chromosome-knob numbers.

Earlier studies by Longley, by Mangelsdorf and Cameron and by Reeves have indicated that diversity with respect to chromosome knobs is highest in the general region of Guatemala and decreases in proportion to distance from this center.

Additional determinations of knob numbers have been made in maize varieties from Latin-American countries. Two new techniques employed in connection with these studies have proved useful. The first involves crossing the Latin-American varieties with an inbred strain of Wilbur's Flint whose chromosomes are knobless and possess good spreading characteristics. Cytological studies are made in material collected from the  $F_1$  plants in which the knobs are always heterozygous and the spreading qualities usually good. Also it is much easier in these  $F_1$  hybrids, than it is in the Latin-American varieties themselves, to estimate correctly the stage at which meiosis occurs. The delay of one generation in obtaining material for cytological study is more than compensated for by the several advantages gained.

The second technique involves the storage of cytological material at low temperature in a deep freeze. The storage is in 70 percent alcohol at  $0^\circ\text{F}$ . or less. The material keeps indefinitely with little or no deterioration. Excellent preparations have been made from material three years in storage.

Table 8. Chromosome-knob numbers in Latin-American maize.

Country	No. Varieties	Knob Number	Knob-number Frequencies														
			0	1	2	3	4	5	6	7	8	9	10	11	12		
Mexico	57	4.72	3	4	5	5	8	8	7	4	10	2	1				
Guatemala	7	2.29	2	2	1	1						1					
San Salvador	4	5.75				1	1		1				1				
Honduras	21	6.38			1		3	3	6	1	4	2					1
Nicaragua	14	5.28	1				5	4	1			2	1				
Costa Rica	8	3.50			1	2	5										
Panama	1	5.00							1								
Colombia	43	5.74	1		3	2	3	5	13	7	3	2	2	2			
Ecuador	28	0.78	13	9	5	1											
Peru	75	1.73	30	12	12	4	8	4	5								
Bolivia	27	0.81	14	7	3	3											
Venezuela	14	5.63				4	4	5		1	2	1				2	
Brazil	7	3.71		1	1	1	1	2	1								
Uruguay	1	0.00	1														
Paraguay	4	2.75	1			1	2										
Argentina	1	5.00							1								

Total 317

Knob numbers have now been determined in one plant each of 317 varieties from 16 different countries. The results which are shown in Table 8 are, with some exceptions, in general agreement with earlier determinations. The maize of Colombia shows a greater diversity than had previously been recognized. The varieties of Ecuador, Peru and Bolivia are not as preponderantly knobless as previous data had indicated. Many of the varieties from Peru included in these studies and not previously studied came from the Peruvian coast.

It is planned in the near future to summarize all available data on chromosome-knob numbers in maize.

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#### 11. Restoration of fertility to cytoplasmic male-sterile corn.

The cytoplasmic male-sterile inbreds C106-sterile and Tx203Ms used in these studies derive the male-sterile character from the Texas variety Golden June, a derivative of Mexican June.

In contrast to the condition reported by Bauman (1952) in which each inbred of the 250 tested restored fertility completely to the KyS cytoplasmic male-sterile line, few inbreds so far tested restore fertility to the Texas cytoplasmic male-sterile lines. Forty-two inbreds have been tested for genes restoring fertility to Tx203Ms and C106-sterile. The  $F_1$  progenies of Tx203Ms and C106-sterile x Inbreds were classified as: sterile - plants which rarely exerted anthers and dehisced no viable pollen; partially sterile - plants containing a few spikelets with exerted anthers dehiscing viable pollen in variable amounts; fertile - plants all of whose spikelets contained normally exerted anthers dehiscing abundant viable pollen.

Of the inbreds tested four (9.5%) restored fertility completely in the  $F_1$  and four (9.5%) produced  $F_1$  progenies segregating fertile plants. It should be possible to isolate lines homozygous for fertility-restoring genes from inbreds whose  $F_1$  progenies segregate fertile plants, and these could be used in single crosses as effectively as lines already homozygous for fertility-restoring genes. As more inbreds are tested, additional lines will undoubtedly be found which carry fertility-restoring genes, however, the indications now are that the majority of U.S. inbreds lack such genes. It is desirable, therefore, to find other sources of fertility-restoring genes. One such source is to be found among Latin American maize varieties.

A total of 124 varieties of Mexican, Central and South American maize varieties have been tested for fertility-restoring genes. Of the 124  $F_1$  populations resulting from crossing C106-sterile by various Latin American varieties, 96 were tested in both 1951 and 1952. In only one of these was there a significant variation in classification, probably due to sampling errors. A larger percentage of lines containing fertility-restoring genes was found among the Latin American varieties than among U.S. inbred lines. 13.7% of the varieties tested restored fertility completely in the  $F_1$ , while 45.9% produced  $F_1$ 's segregating fertile plants. Besides serving as an additional source of fertility-restoring genes, some of these varieties may also prove to be valuable sources of germplasm for improving corn in the U.S. (Wellhausen *et al*, 1952).

Data from  $F_2$  and  $F_3$  populations indicate that a single gene is responsible for restoration of fertility in two U.S. inbreds tested, while two genes are indicated in a third inbred. Chi-square tests for goodness of fit to an assumed ratio of 3 fertile:1 sterile were applied to six  $F_3$  progenies from the cross Tx203Ms x K55. Chi-square values for all of these progenies were low

and equivalent P. values ranged from P.10 to P.90. The Chi-square value obtained for an assumed ratio of 3 fertile:1 sterile from one F<sub>2</sub> progeny of the cross Tx203Ms x 127C lay between P.30 and .50. The Chi-square value obtained for an assumed ratio of 9 fertile:7 sterile in one F<sub>2</sub> progeny of the cross Tx203Ms x K64 lay between P.80 and .90. In the two F<sub>2</sub> progenies, partially sterile and sterile plants were grouped and treated as steriles. This was done on the assumption that the partially sterile plants do not carry fertility-restoring genes but, due to the action of segregating modifying genes and/or environment, produce some viable pollen. In addition two F<sub>3</sub> populations from the cross Tx203Ms x K55 contained only fertile plants, 20 and 23 in the respective populations. One F<sub>3</sub> population of the cross Tx203Ms x 127C contained 56 plants all of which were fertile. These three F<sub>3</sub> populations containing only fertile plants must have resulted from the unconscious selection of F<sub>2</sub> plants homozygous for the fertility-restoring factor. That two factors are involved in fertility-restoration in K64 is indicated by the marked deviation from a 3:1 ratio and by the high P value obtained for the assumed 9:7 ratio.

An investigation of the number of factors involved in fertility-restoration by Latin American lines has been begun. Fertile plants among the F<sub>1</sub> populations of one Mexican and two Bolivian varieties (C106-sterile x Latin American Variety) were backcrossed to C106-sterile. The Chi-square values obtained for the assumed ratio of 1 fertile: 1 sterile in the three backcross progenies were low. These ratios indicate that a single gene is responsible for fertility-restoration.

Knob counts from 58 of the Latin American varieties tested for fertility-restoring genes were obtained from Table 17 of Races of Maize in Mexico (Wellhausen et al, 1952) and from Mangelsdorf and Paxson (this issue of the News Letter). Forty-five varieties from ten countries had average knob numbers ranging from 4.5 to 9.5. Among these, four (16%) of the 25 varieties producing completely fertile or segregating-fertile F<sub>1</sub> progenies had fewer than 5.5 knobs, while nine (45%) of the 20 varieties producing completely sterile or segregating-partially sterile F<sub>1</sub> progenies had fewer than 5.5 knobs. These figures indicate a correlation between high knob number and fertility restoration but do not show whether knobs restore fertility or are associated with genes which do so. Thirteen varieties from Ecuador, Peru, and Bolivia had low average knob numbers, 1.5, 2.5 and 0.57 respectively. No correlation has been found between knob number and fertility restoration in the varieties from these countries.

Meiosis in male-sterile plants of the stocks studied appear to be normal. This is in agreement with the condition reported by Rhoades (1933) in another male sterile. Degeneration of the microspore in sterile plants occurs after the formation of the quartet of pollen grains. Degeneration varies within individual anthers from completely empty pollen grain walls to pollen grains containing varying quantities of protoplasm.

Gabelman (1949) has postulated certain particles one or more of which when present in a pollen grain produce sterility. Rhoades (1950) has suggested that differences in mitochondria might be responsible for cytoplasmic

male-sterile plants arising from male-fertile progenies containing the gene *iojap* in the homozygous condition. Pollen mother cells as well as somatic tissues from leaf and glume epidermis, root tip, scutellar and endosperm tissue from C106-sterile and C106-fertile have been examined in an effort to determine whether any visible differences exist between the cytoplasm or cytoplasmic organells of fertile and sterile plants. Janus Green B, Pinacyanol, and Neo-tetrazolium chloride have been used to stain living tissue, while Zirkle's modification of Erliki's fixative and Heidenhain's hematoxylin have been used in sectional material. Neo-tetrazolium chloride seems to be the most promising of the stains used thus far. It permits utilization of the squash technique on both living and fixed material. Since nuclear structure is not brought out with Neo-tetrazolium chloride, young tassels have been divided, half being stained with Neo-tetrazolium chloride, half fixed in alcohol:acetic acid. Aceto-carmin staining of pollen mother cells indicates the meiotic stage of the nuclei in corresponding areas of the other half of the tassel. No differences in the appearance or number of mitochondria have been observed in either the somatic or germinal tissue so far examined. Since pollen degeneration occurs after the completion of meiosis, continued observations of the later stages of pollen formation may uncover some differences between mitochondria in C106-sterile and C106-fertile.

John R. Edwardson

## 12. Pilosity and hispidulousness of the leaf sheath.

The leaf sheath of corn exhibits hairs of two distinct types, long slender hairs causing pilosity and short hairs resulting in hispidulousness. Both types have been found present on all maize examined although with considerable variation. The gross and microscopic morphology of the pilose and hispidulous hairs have been studied in a large number of varieties and races of maize in order to determine the range of variation.

The pilose hairs are long single cell outgrowths of the epidermis about 4.5 mm. long, at the base of which is a ring or collar of enlarged epidermal cells formed by an elongation, in a direction perpendicular to the epidermal surface, of cells immediately surrounding the hair. The diameter of the collar varies only slightly from plant to plant being about 0.25 mm. with an average height of 0.12 mm. Beneath the collar is an area of cell proliferation produced by the second layer of epidermal cells; embedded in this mass of cells is the swollen end of the hair.

No pattern of arrangement of the pilose hairs has been observed, except that they occur only in the grooves formed by the ridges overlying the vascular bundles of the sheath. There is a complete range in the distribution on the sheath from a few sparsely scattered hairs along the edges at the top of the sheath to a dense covering of the entire sheath.

The hispidulous hairs are microscopic single cell prickles involving only the outer layer of epidermal cells in their formation. They vary in length from about 0.05 mm. to about 0.25 mm., and may be straight or curved. In all the varieties of corn studied these prickles project from the epidermal

surface at an angle less than 90 degrees in a basipetal direction. Their distribution is fairly uniform over the entire length of the grooves where the hairs are located. They tend to lie in rows since their presence does not disturb the pattern of the epidermal cells as does the pilose hairs.

A distribution study by countries was made of the variation for these hair types for 508 varieties of Latin American maize. The plants for this study were grown and examined in the field at Weston, Massachusetts. In order to insure uniformity of sampling, the plants were not classified until anthesis, and the second sheath above the uppermost ear was chosen for examination.

Pilosity was divided into five arbitrary classes based on the amount of leaf sheath covered. Class 1 had hairs only on the edges of the sheath; class 2 had hairs covering about one quarter of the sheath; class 3 had hairs present for about one half the length of the sheath; class 4 had hairs three quarters of the way down the sheath; class 5 had hairs on the entire sheath.

The results of this classification were grouped according to country of origin. The data showed that the highest percentage for each country fell in class 2, and that adjoining countries tended to resemble each other. The center of diversity with respect to pilosity is in Guatemala.

The data suggest that the degree of pilosity represented by class 2 may be the normal or "wild" condition and may have been the condition existing in primitive maize. Present variation could be explained on the basis of the introduction into some varieties of a second factor.

Two possible sources for the introduction of a second pilosity factor are Cacahuacintle, a pre-Columbian race of Mexican maize, and Tripsacum pilosum. At present the evidence on this point is not at all conclusive.

A similar distribution study was made for hispidulousness but with less clear-cut results. Hispidulousness was divided into four classes on the basis of the roughness of the leaf sheath as determined by feel with the fingers. Those sheaths which gave no sensation of roughness were called class 1; and those which gave a very strong sensation were classified as class 4.

An analysis of this distribution indicated that adjoining countries tended to be similar. The highest percentage in the Central American countries fell in class 2 and in the South American countries in class 3.

Genetic studies of pilosity and hispidulousness have been in progress for the past three years. Several Latin American varieties were crossed with a multiple-tester strain having marker genes on nine chromosomes (chromosome 5 excepted) and the  $F_2$  and backcross progenies classified. The varieties used were pilose (class 5) from Mexico and Guatemala, hispidulous (class 4) from Nicaragua, and near-glabrous varieties (class 1 for both pilosity and hispidulousness) from Peru and Colombia. The  $F_2$ 's and backcrosses with the multiple-tester were classified for the two leaf sheath characteristics and for the nine marker genes. The results of these studies showed strong evidence

of linkage between pilosity and the gene I on chromosome 3 and wx on chromosome 9. There was some indication of linkage between hispidulousness and lg on chromosome 2 and wx on chromosome 9.

John B. Paxson

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1. Monoploid maize meiosis. Monoploid meiosis was studied in some fifty plants obtained from Dr. S. S. Chase. Details of irregularities were noted in relation to chiasma-formation, bivalents, homologous vs. non-homologous pairing, pachytene configurations, secondary association, and irregular spores. Zygotene and pachytene strands were observed to be double. Földbaks and pairing between two non-homologous chromosomes were noted and discussed. Bridges, fragments, bivalents and chiasmata were also noted and discussed.

2. Cytogenetic comparison of maize homozygous diploids and inbreds.

The homozygous diploids studied were crossed onto I205 X L289 and the 555 F<sub>1</sub> plants of 58 progenies carefully examined phenotypically for pollen sterility in field and laboratory, and cytologically for structural heterozygosity. A small percentage of F<sub>1</sub> showed pollen sterility but no structural aberrations were observed. The F<sub>1</sub>'s were found to be vigorous, uniform, and in all respects normal.

The homozygous diploids derived from monoploids were then compared with inbreds by studying the hybrid progeny of each crossed onto the commercial single cross I205 X L289 and the F<sub>1</sub> of each subjected to detailed cytogenetic study. No particular difference between homozygous diploids and inbreds was noted in percentage of pollen sterility, phenotypes, appearance of mutants, or structural heterozygosity. An inversion, possibly associated with a deletion, was observed cytologically in the F<sub>1</sub> from one inbred, the hybrid of which had 50 per cent pollen sterility.

Dr. Lee Ford

3. Gene frequencies in a strain of Reid Yellow Dent

A long term experiment was started in 1948 with the objective of obtaining information on the validity of certain assumptions in population genetics. Population size, randomness of mating, equilibrium, mutation rate, gene frequency, etc. are some of the commonly used terms in the mathematical-statistical treatment of genetic problems. Actual experimental data, though, are rather limited, with the possible exception of *Drosophila*. The first phase of this study has been completed and will be briefly reported below.

A strain of open pollinated Reid Yellow Dent served as source. 801 selfed ears were obtained in 1948, representing a random sample of the variety. Approximately 50 seeds per ear were germinated in the greenhouse and classified for recessive seedling mutants; 70 kernels were checked for 'germless seed.' The results are set out in Table 1. In previously reported experiments in corn of this sort the frequency of the character but not of the alleles were



recorded. Since a number of different loci might be responsible for the expression of a character, it was thought desirable to actually determine the frequency of each recessive allele by intercrossing all progenies which segregated for the same character. This test for allelism among viable types was made by plant to plant intercrosses. For the lethal types, however, it was necessary to grow the material in paired rows. The results are set out in Table 2.

It should be noted that the number of progenies tested for allelism is usually smaller than the number originally classified. This loss is due to improper sampling, non-heritable cause of the expression, poor stand, etc.

During the course of the study one new seedling character was found. It is tentatively designated as 'mottled albino green.' The seedling leaves are characterized by small normal green spots on an albino background. Only the first 3-5 leaves are affected. Greening occurs rapidly.

The mutation rates for the lethals in Table 2 are estimated by the use of the relationship  $q^2 = u$ , where  $q$  is the frequency of the recessive lethal and the  $u$  the mutation rate from the dominant to the recessive condition. Under a certain mutation rate and gene frequency one can calculate the number of generations required to reach the equilibrium level. A number of assumptions, however, are involved in such a calculation.

In a continuation of this experiment an attempt will be made to find out how rapidly the equilibrium values are approached. Ears of the original sample which did not segregate in the  $S_1$  were thought to be free of defectives. A composite of these ears was grown under isolation and a sample saved from each crop harvested. If these samples are analyzed in the same manner as the material reported above, then it should be possible to obtain some estimates on the speed with which equilibrium is approached by the different alleles.

J. F. Schuler  
and  
G. F. Sprague

Table 1. Frequency of Occurrence of Segregation for Various Characters in a Sample of Selfed Ears from the Variety Reid Yellow Dent.

Character	No. of ears segregating	Frequency expressed as	
		% of total	% of segregates
Germless	87	10.86	36.56
Yellow-green	44	5.49	18.49
Virescent	25	3.12	10.50
White	28	3.49	11.77
Luteus	15	1.87	6.30
Pale green	10	1.24	4.20
Glossy	7	.87	2.94
Dwarf	8	1.00	3.36
Stripe	6	.75	2.52
Miscellaneous	<u>8</u>	<u>1.00</u>	<u>3.36</u>
	238	29.69	100.00

Table 2. Estimated Gene Frequencies and Mutation Rates for the Various Mutant Alleles.

Character	Allele	Frequency of occurrence	Observed gene frequency	Estimated mutation rate
Yellow-green (viable)  (lethal)	yg a	2	.00126	
	b	1	.00062	
	c	1	.00062	
	d	1	.00062	
	e	20	.01248	155.7 x 10 <sup>-6</sup>
	f	10	.00624	38.9 x 10 <sup>-6</sup>
	g	3	.00187	3.5 x 10 <sup>-6</sup>
	h	2	.00125	1.5 x 10 <sup>-6</sup>
	i	2	.00125	1.5 x 10 <sup>-6</sup>
	j	1	.00062	.38x 10 <sup>-6</sup>
	k	1	.00062	.38x 10 <sup>-6</sup>
	l	1	.00062	.38x 10 <sup>-6</sup>
	m	1	.00062	.38x 10 <sup>-6</sup>
Luteus	l a	7	.00437	19.1 x 10 <sup>-6</sup>
	b	2	.00126	1.5 x 10 <sup>-6</sup>
	c	1	.00062	.38x 10 <sup>-6</sup>
	d	1	.00062	.38x 10 <sup>-6</sup>
	e	1	.00062	.38x 10 <sup>-6</sup>
Stripe	str a	3	.00187	
	b	1	.00062	
White	w a	21	.01310	171.6 x 10 <sup>-6</sup>
	b	1	.00062	.38x 10 <sup>-6</sup>
Glossy	gl 3	4	.00249	
	a	1	.00062	
	b	1	.00062	
	c	1	.00062	
Dwarf	d a	6	.00375	
	b	1	.00062	
Miscellaneous		1	.00062	
		1	.00062	
		1	.00062	

JOHN INNES HORTICULTURAL INSTITUTION  
Hertford, England

1. Breeding projects.

Inbreeding has been continued: Northern Cross and Dependogold are providing desirable inbred lines, while sugary derivatives of Cinquantino gave second generation inbreds with good, early germinations. Golden Standard Maize, Cinquantino flint and other maize types are also being inbred. A preliminary growing of Russian maize, obtained through the Board of Trade, showed they grew well here but set seed far too late. They are doubtless mechanical mixtures of yellow and white seeded forms.

As low germination hinders sweet corn production in England, the effects of date of harvesting seed were studied using inbred C 13 and J.I. Hybrid No. 1. Hybrid seed could be harvested over a wide period: from 24 September to end of October, without detriment to germination. C 13 germination was high only for seed picked on 24 September, germination rapidly falling off with later harvestings. Earlier seeds probably gave reduced germinations because they were immature, while falling off in later ones was possibly due to fungal attacks.

In collaboration with Mr. Newell, it was found that sweet corn raised in soil blocks in glasshouses and frames, and then transplanted are earlier, more vigorous and better yielding than direct sowings. Maize normally dislikes transplanting. More important is that they escape detrimental effects of low temperatures on germination and frit-fly attacks. Soil blocks are economically advantageous for sweet corn as a horticultural crop in England.

Gordon Haskell

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1. Breeding for sugar in the stalk.

From 30,000 selfed plants on which sugar determinations had been made refractometrically, 800 ear progeny from plants with high sugar content were planted in 1952. Again selfed plants (approximately 8000 plants) were checked refractometrically for sugar content. There was a correlation between the average single ear determinations of 1951 and the average determinations of ear progenies in 1952.

2. Trials of hybrids for grain and sugar.

Two tests were grown. The first field trial with 36 hybrids was raised at Pontevedra (Atlantic coast); the second trial with 9 hybrids was grown in Barcelona (Mediterranean coast). The highest yields of grain and dry matter in the juice are reported below:

Pontevedra:

	(M)*	(P)*	(L)*
Experimental hybrid 5 =	11,450	653	30
Experimental hybrid 10 =	10,630	834	35

Barcelona:

	(M)	(P)	(L)
Experimental hybrid 3	7,140	1,047	22
Experimental hybrid 10	6,950	1,366	24

\*(M) = Kgs. of corn/Ha. at 15.5% moisture.

(P) = Kgs. of dry matter in the juice/Ha.

(L) = % of moisture at time of harvest.

Conditions that favor grain production also have a positive influence on dry matter content (sugar) in the juice, especially conditions which contribute to stalk constituents after grain maturation. The characteristics permitting a high grain production are not antagonistic to a favorable sugar metabolism in the stalk juices.

### 3. Specific combining ability in relation to classes of sugars in stalk juices.

Six parent inbreds of hybrids entered in the trial at Pontevedra were classified as to the predominant class of sugar produced in the stalk juices. Use was made of the following symbols:

a = reducing sugar  
b = non-reducing sugar

Their hybrids were classified as:

- 1 = Homozygous a x a and b x b
- 2 = Heterozygous a x b
- 3 = Mixtures (a x b) x b and (a x b) x a

Differences in the average grain yields between the groups are reported below:

	Yield of grain Kg./Ha.	Groups Compared	"t"
1. Homozygous	9,441	1-2	4.2**
2. Heterozygous	10,461	1-3	3.2*
3. Mixtures	10,215	2-3	1.2

\* = Significant at  $P < 0.05$

\*\* = Significant at  $P < 0.01$

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and  
Jose L. Blanco

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1. A serological investigation of 2 inbreds.

It seems logical that there should be some degree of protein specificity differentiating inbred lines of corn. If such is the case, then different lines could be distinguished from each other serologically provided that our techniques are refined enough to detect the limited differences which are present.

Rabbits were the animals immunized. The inbred lines of corn, Hy and WF9, were used to induce antibody formation. 100 seeds of each inbred were soaked for 18 hrs. in distilled water at 0°C. and the embryos excised. These were ground into fine particles and extracted in Bloor's mixture for 14 hours. This solution was filtered and the precipitate extracted in a buffered salt solution for 30 hrs.

The rabbits used were bled and the sera checked against an aliquot of the protein solution of the two inbreds to check for acquired immunity for these particular proteins. All tests were negative.

Injections of the protein extracts were given intravenously in four doses. Dose sizes were 50 mg, 100 mg, and 200 mg of extracted protein in solution. The rabbits were injected with these doses at three day intervals. Eleven days after the last injection the sera were checked for antibody content. The titer was ca 1:5000. The rabbits were bled 13 days after the last injection; the sera obtained were filtered through a Seitz filter and stored at -2°C.

It was thought that the proteins common to both WF9 and Hy would induce the formation of antibodies which could be removed by the heteroantigen leaving in the sera antibodies of a more specific nature. These antibodies would react with the homoantigen but not with the heteroantigen. If the protein components of the embryos of both inbred corn lines were similar then no reaction would be obtained using the homoantigen after the treatment of the antisera with the heteroantigen.

One cc. aliquots of antisera from the immunized rabbits were placed in tapered centrifuge tubes and .5 cc aliquots of heteroantigen were added. The tubes were shaken for 10 minutes and then centrifuged for 30 minutes at 1200 rpm. After this treatment all tubes had a considerable amount of precipitate. The controls, which consisted of antiserum alone, protein extract alone, protein extract plus water, and antiserum plus water were treated in the same fashion. No precipitate formed in the controls.

Subsequent treatments consisting of the addition of the heteroantigen to the antisera after centrifugation to remove precipitate of previous treatments failed in most instances to remove all of the antibodies capable of reacting with the heteroantigen, and leave antibodies specific for the homoantigen.

Some of the tests did give the results expected if there was a serological difference between the two inbreds, but the results were not consistent enough to prove the existence of such a serological difference.

The sera were also tested by means of the precipitin technique. Tubes in which the reactions were read were made from glass tubing having an inside diameter of 4 mm, and cut to a length of 5 cm. Approximately .2 cc. of serum was run into the bottom of a tube and the same amount of diluted protein extract introduced above the serum. The results of the precipitin reactions are given in table I. In this table, the serum against which the extracts of the inbred lines of corn listed were run is designated as the antiserum. In recording the reactions, a heavy flocculent precipitate of considerable depth at the interface of the antiserum and the extract was read as a four-plus reaction, a reaction showing less depth was read as a three-plus reaction, a light but definite reaction was called a two-plus, and a very light reaction was read as a 1-plus reaction.

Table 1. Precipitin Reactions

Hy antiserum	Extract	Dilution of Extract					
		*1:5	1:10	1:20	1:40	1:80	1:160
1	Hy	++++	+++	++	+	+	+
1	WF9	++++	+++	++	+	+	-
WF9 antiserum							
2	WF9	++++	+++	+	+	+	+
2	Hy	++++	+++	++	+	+	-
3	WF9	++++	++	+	+	-	-
3	Hy	++++	+++	+	+	-	-

\*Dilutions given in the table are to be multiplied by 100.

The data in table 1 indicate that if specific differences exist between these two inbred lines the precipitin technique is too crude to detect them.

Gerald Clary

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Colombia, South America

### 1. Agricultural Program.

The varietal improvement of maize and wheat were the two first projects undertaken by the cooperative agricultural research program of the Colombian Ministry of Agriculture and The Rockefeller Foundation. This program began in May, 1950.

A basic phase of the corn improvement program has been the systematic collection of the native varieties. 1193 samples were collected in Colombia

prior to January 1, 1953. Approximately 40% of the corn growing areas of the country are still to be collected. Two trained field collectors will continue until the job is completed.

The collections are being evaluated from the standpoint of desirable agronomic characteristics for use in a breeding program. They are also being grouped into races on the basis of their natural relationships. At least 15 races have been identified so far. Several more will undoubtedly be identified as more detailed studies are made.

Some of the races are of interest for their desirable agronomic characteristics, and others from the standpoint of their primitiveness. One race is extremely interesting in view of the climatic conditions and cultural practices to which it is adapted. This is a small eared popcorn to which has been given the name "Chococito" because it is found distributed along the Pacific Coastal Plain in the Department (State) of Choco. (Also, it is often called "Maiz Indio" by the natives). The annual average rainfall in this region is among the highest in the world, varying from 300 to over 400 inches per year. The very high temperature and relative humidity are characteristic of a low elevation tropical rain forest region. Perhaps more interesting than "Chococito's" adaptation to adverse climatic conditions is the fact that this race thrives with probably the minimum cultural care from man of any corn on record. The seeds are planted broadcast in usually a small plot of land alongside a river which has previously been cleared from rain forest. They are not covered by soil but only by the leaves and plant residue from the shrubby growth that is felled after the seeds are scattered broadcast on the surface of the ground. Usually the corn is not cultivated or weeded even once from planting to harvest.

The National Research Council in cooperation with the Rockefeller Foundation initiated a program in 1951 to collect and preserve the indigenous corns of the Americas. Colombia was designated as the center responsible for collecting and preserving the corns of the Andean region of South America. This region includes most of Venezuela and Bolivia and all of Colombia, Ecuador, Peru, and Chile. The number of collections from each country to date is as follows: Venezuela 256, Colombia 1139, Ecuador 218, Peru 275. Collecting in Chile and Bolivia has not yet been started. It is planned to continue the collecting work, which is being carried on collaboratively by the agricultural research technicians in the respective countries and the center in Colombia, until the entire Andean region is thoroughly sampled. Seed of each collection will be kept viable at the corn germplasm bank in Medellin, Colombia and will be made available on request to all research workers in corn genetics and corn improvement.

## 2. *Tripsacum* Collected in Colombia, Ecuador, and Venezuela.

On the corn collecting trips in the Andean region of South America, the field collectors have been on the look-out for *Tripsacum* growing wild. It has been found growing in six locations in Colombia, five in Venezuela, and one in Ecuador. These locations are:



Colombia.-

	Elevation in meters.
1. El Morro, Cajambre, and Buenaventura. Valle	40
2. Joaquinquito, Naya, and Buenaventura, Valle	8
3. Marcelo, Calima, and Buenaventura. Valle	25
4. Rio Dulce, and Villeta. Cundinamarca	980
5. El Dinde, La Plata, and Rio Paez. Huila	950 - 1100
6. Afueras Gramalote. Santander del Norte	1020

Ecuador.-

1. Kilometer 106, Railroad Guayaquil-Quito, Huigra, and Naranjapata.	550
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Venezuela.-

1. Kilometer 19, Highway San Cristobal-San Antonio. Tachira	880
2. Highway La Quinta-Seboruco, Rio La Grita. Tachira	800
3. Las Cruces, Ejido-Parroquia. Merida	1180
4. Confluente Momboy-Motatan, near Valera. Trujillo	500
5. Kilometer 18, Quiriquire-Maturin. Monagas	70

Herbarium specimens of all the *Tripsacums* found are kept at the Facultad de Agronomia, Medellin, Colombia and duplicate specimens are sent to the USA for identification. The studies of identification have not yet been completed. Living specimens from Colombia and Ecuador are growing at the Experiment Station "Tulio Ospina", Medellin. Those from Venezuela were transplanted on the Experiment Station Farm of the Instituto Nacional de Agricultura, Maracay, Venezuela. It is planned to transfer living specimens of these to Medellin in the near future so that all of the *Tripsacums* found in the Andean region will be brought together at one place and propagated for the convenience of anyone who is interested in studying them.

3. Resistance to *Helminthosporium* sp. and *Puccinia sorghi*.-

*Helminthosporium* leaf spot and rust, *Puccinia sorghi*, are probably the two most damaging diseases of corn in Colombia. The most common species of *Helminthosporium* involved is *turcicum*, but preliminary studies indicate that one and perhaps two other species are present.

Experiments were conducted to determine the genetic basis of resistance to those two diseases. The resistance or susceptibility to each of these diseases was found to depend primarily on a single pair of factors which are independently inherited. Dominance was not discernible in either pair of genes. There are numerous modifiers in each case (the exact number was not determined) that affect in a minor way the intensity of the attack. These modifiers did not, however, obliterate the ratios conditioned by a monofactorial segregation for each disease. Data were obtained in Medellin, Colombia in 1951 on ten F<sub>2</sub> families with 1910 plants, six backcross families

to the resistant parent with a total of 1340 plants, and 10 backcross families to the susceptible parent with 1813 plants.

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The Analysis of Diallel Crosses

1. Introduction.

Hull (1946) has developed methods of analyzing data from diallel crosses of homozygous lines using regression techniques and has applied them in particular to the estimation of dominance in maize yields.

Recently we have developed a different approach to the same problem based on Mather's (1949) components of variation, D and H. We have been experimenting with diallel crosses of Nicotiana rustica and have analyzed various quantitative characters of these plants. We have been able to prove conclusively that in some cases genic interaction may cause spurious over-dominance, and, in the absence of such interaction to obtain reasonably accurate estimates of the dominance ratio, asymmetry of gene distributions, etc. We have also analyzed some maize yields from various sources and although these analyses do not provide quite the best illustrations of our method, we thought it would be of interest to report them here for comparison with Hull's method.

2. Definitions and basic formulae.

A diallel table is an arrangement in a square of  $n^2$  observations from a set of diallel crosses among  $n$  parents, the rows and columns of the square corresponding to the offspring of each parent. The  $n$  homozygous parents themselves form the diagonal of the table. It is easy to test whether there are significant differences between the reciprocal crosses, and, whether these exist or not, reciprocals may be averaged so that rows and columns contain the same figures and will be termed arrays.

Following Mather (Mather, K. Biometrical Genetics. Methuen. London. 1949) we suppose that the quantitative character is polygenically controlled and there are in fact  $g$  genes represented by more than one allele in the parents. If each gene has just two alleles then for the  $i$ th locus we define

$2d_i$  = difference between the homozygotes

$h_i$  = difference between the heterozygote and the mid-homozygote

$u_i:v_i$  = ratio of numbers of positive and negative homozygotes in the parents

( $d_i > 0$ ;  $h_i$  may take sign;  $u_i + v_i = 1$ ;  $i = 1, 2, \dots, g$ )

The dominant homozygote is that which deviates from the mid homozygote in the same direction as the heterozygote.

When the  $g$  genes have independent actions and are distributed independently in the parents the following statistics may be obtained from the diallel table.

$$F_1 \text{ mean} - \text{parental mean, } F_1 - P = \sum 2u_i v_i h_i$$

$$\text{Variance of parents, } V_p = \sum 4u_i v_i d_i^2$$

$$\text{Variance of the families of the } r\text{th array (including the common parent), } V_r = \sum 1u_i v_i (d_i - h_i)^2 + \sum 2u_i v_i (d_i + h_i)^2$$

$$\text{and its mean value, } V = \sum u_i v_i (d_i^2 - 2(u_i - v_i)d_i h_i + h_i^2)$$

$$\text{Covariance between the families of the } r\text{th array and their non-recurrent parents, } W_r = \sum 1 2u_i v_i d_i (d_i - h_i) + \sum 2 2u_i v_i d_i (d_i + h_i)$$

$$\text{and its mean value, } W = \sum 2u_i v_i d_i (d_i - (u_i - v_i)h_i)$$

which is also the covariance between parents and their offspring means.

Variance of the array means,  $V_M = \sum u_i v_i (d_i - (u_i - v_i)h_i)^2$  ( $\sum$  is over  $i = 1$  .....  $g$ ,  $\sum_1$  over genes with positive homozygotes in the  $r$ th parent,  $\sum_2$  the negative ditto). There is also an environmental component of these statistics which will be given later.

### 3. Testing the hypotheses.

The hypotheses from which the formulae of the previous section were deduced are

- (i) Homozygous parents.
- (ii) No multiple allelism.
- (iii) Genes independently distributed in the parents.
- (iv) No genic interaction on the scale in use.

When these hold good the difference  $W_r - V_r$  has the value  $W_r - V_r = \sum u_i v_i (d_i^2 - h_i^2) = W - V$  independently of  $r$ . Heterogeneity of this difference indicates that one or more of the hypotheses fail and two methods are available for testing this.

In the first, the variance of  $W_r - V_r$  is compared with a theoretical variance obtained from the diallel table to give an approximate  $X^2$  test of significance. As the form of the theoretical variance is complicated, only the numerical results of its use will be quoted.

The second method uses the graph of  $W_r$  against  $V_r$  which should be a straight line of unit slope. The statistical inequality  $W_r^2 \leq V_r V_p$  means that

all the points  $(V_r, W_r)$  of the graph line on that part of the line  $W_r - V_r = W - V$  inside the parabola  $W_r^2 = V_r V_p$ . Though  $(V_r, W_r)$  are not a set of independent observations, but are correlated second degree statistics, an approximate test of the validity of the above hypotheses is to fit a regression line to the points  $(V_r, W_r)$  in the usual way. Failure of the hypotheses is indicated either by a nonsignificant regression in a sufficiently extensive experiment or, when the regression is significant, by a significant deviation of the slope from unity. Non-significance of regression may also arise if all  $h_1 = 0$ , but this may be tested separately.

All the formulae of this and the previous section apply to the means of  $F_2$ s from selfed  $F_1$ s if  $\frac{1}{2}h_1$  is substituted for  $h_1$  so that  $F_2$  data may be tested and analyzed in the same way. Further, the graph of  $F_2$  array variances (or covariances) against  $F_1$  variances (or covariances) should be a straight line of slope  $\frac{1}{2}$ . A linear test which is also available is that  $P + F_1 - 2F_2$  should be zero. The empirical value can be compared with the standard deviation derived from the environmental variation of parental,  $F_1$  and  $F_2$  means to give a test of significance.

When failure of the hypotheses has been demonstrated it is not easy to decide from  $F_1$ s alone just which ones have failed. However, the possible use of an unsuitable scale can be detected by plotting  $W_r - V_r$  against the array means to see if there is a definite trend from which a new scale may be deduced by the usual variance stabilization method. When it is not possible to remove the variation in  $W_r - V_r$  by rescaling, the  $(V_r, W_r)$  graph can be examined. It may show some points deviating markedly from the line of unit slope through  $(V, W)$  though even these must of course be inside the limiting parabola. The four hypotheses are discussed in turn and we suppose for convenience that in the graph the OW axis is vertical and the OV axis horizontal.

When there is no dominance ( $h_1 = 0$ ) the line is a tangent to the limiting parabola, but if there is dominance the line is a chord cutting off an area of the parabola which increases as the amount of dominance increases.

- (i) Heterozygosity in a parent moves the corresponding point above the line and reduces the apparent amount of dominance.
- (ii) As long as there is no segregation, multiple allelism can be regarded as polygenic biallelism exhibiting genic interaction or distributional association.
- (iii) Correlated association of alleles in the parents causes points to deviate either side of the line.
- (iv) Genic interaction moves the corresponding points either above or below the line depending on whether it moves the double heterozygote nearer to or further away from the mid-homozygote.

When there is little dominance, neither (i) nor (iii) causes any trouble while in (iv) the limiting parabola forces any deviation to be below the line which accords with the fact that interaction must move the double heterozygote away from the mid homozygote in this case.

Usually in practice only one or two points deviate strongly and then the results from the progeny of the corresponding parents can be removed from the diallel table and the theory of section 2 applied to the smaller sub-table.

Maize-yields (Kinman and Sprague, 1945). This is a set of  $F_1$  and  $F_2$  means from a diallel cross of 10 lines labelled Hy, R46, B2, WF9, 38-11, K159, Oh07, Oh04, WV7 and A14 in the original paper and now renumbered 1 to 10 respectively.

The graph of  $W_r - V_r$  against array means revealed no trend so that rescaling is not suggested.

$F_1$ . The first test of heterogeneity of  $W_r - V_r$  gave  $\chi^2_9 = 32.756$  which is highly significant ( $P < .001$ ). The greatest improvement was obtained by removing the progeny of line (1) ( $P = .05 - .02$ ) and then either line (3) ( $P = .20 - .10$ ) or line (7) ( $P = .30 - .20$ ).

The regressions in the second method were all highly significant ( $P < .001$ ). For the whole table  $b = 0.676 \pm 0.108$  which on removing the progeny of line (1) improved to be  $b = 0.754 \pm 0.098$ . Removing (1) and (3) gave  $b = 0.788 \pm 0.075$  while (1) and (7) gave  $b = 0.808 \pm 0.086$  which is not significantly different from  $b = 1.000$ .

$F_2$ . The first method gave  $\chi^2_9 = 7.263$  which is not significant ( $P = .70 - .50$ )

The slope of the regression line was  $b = .707 \pm .114$  which barely differs significantly from 1.000 ( $P = .05 - .02$ ). Removing (3) which lies farthest from the regression line only improved the slope slightly.

As expected the reduced heterozygosity in  $F_2$  makes it more difficult to detect anomalies.

Linear test.  $P + F_1 - 2F_2 = 5.66$  which, using what we estimate to be the errors of the means is highly significantly different from zero. This is reduced to 3.41 by removing line (3) and the further removal of line (2) reduces it to 1.74.

These tests show conclusively that interaction of some sort was present, probably in many of the crosses, but that it had altered considerably over the two years in which the  $F_1$  and  $F_2$  were grown. However line (3), i.e. (B2), was picked out by all the tests.

In our Nicotiana experiments we have found little evidence of interaction in flowering time, but in height a few lines exhibit marked interaction and do so consistently in  $F_1$  repeated over two years and also in an  $F_2$  and a backcross.

#### 4. Dominance

Once the data has been shown to satisfy the hypotheses of section 2 or the awkward lines have been removed, the formulae of that section may be applied. If  $E$  is the environmental variation (assumed to be independent of the genotype) of an  $F_1$  mean, the formulae may be written

$$V_P = D + E$$

$$V = \frac{1}{4}D + \frac{1}{2}H_1 - \frac{1}{4}F + \frac{n+1}{2n}E$$

$$W = \frac{1}{2}D - \frac{1}{4}F + \frac{1}{4}E$$

$$V_M = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + \frac{1}{2}\frac{1}{n}E$$

where

$$D = \sum 4u_i v_i d_i^2$$

$$H_1 = \sum 4u_i v_i h_i^2$$

$$H_2 = \sum 16u_i^2 v_i^2 h_i^2$$

$$F = \sum 8u_i v_i (u_i - v_i) d_i h_i \quad \text{and } E \text{ is estimated from reciprocal}$$

differences or block differences if the experiment is replicated. The peculiar coefficients of E and its occurrence in W are caused by the use of means of reciprocals and by each array having an observation in common with the parental array.

$H_1/D$  measures dominance since  $H_1$  and D are weighted means of  $h_i^2$  and  $d_i^2$  respectively, the weighting being in favour of genes with both alleles represented equally in the parents. This ratio may be measured graphically. In the (Vr,Wr) graph let the line of unit slope through the mean point (V,W) cut the OW axis in A and let the parallel tangent to the limiting parabola cut this axis in B. Then (except for the correction for E),  $AB/OB = H_1/D$ .

$H_2/4H_1$  provides an estimate of the mean value of  $u_i v_i$  (with maximum value  $\frac{1}{4}$  when  $u_i = v_i = \frac{1}{2}$ ) and so shows whether or not positive and negative alleles are present in equal proportions. Genes having the greatest values of  $h_i$  have the greatest weight in the estimator which thus provides no evidence about the distribution of allelic pairs exhibiting no dominance.

F is an indicator of the relative frequencies of dominant and recessive alleles and is positive if there is an excess of dominants.

The equations for  $F_2$  may be derived from these as mentioned in section 3 and so provide independent estimates of dominance, etc. E in this case will contain a component due to genetic variation within  $F_2$  families.

Maize yields These are from three different sources (see table). No estimate of E was given and it has been ignored in obtaining the results in the table. Interaction is present in all sets of data, but only that of Kinman and Sprague has been investigated fully. (Kinman and Sprague. Jour. Amer. Soc. Agron. 1945)

All the data show overdominance, an even distribution of positive and negative alleles, and equal frequencies of dominant and recessive alleles. Since the two lines removed from the  $F_1$  of Kinman and Sprague correspond to points in the (Wr,Vr) graph on either side of the regression line, the

dominance ratio has not been affected. (In our height data from Nicotiana rustica the removal of the progeny of 3 interacting lines out of the 8 used brought about the striking reduction of  $H_1/D$  from 2.2 to nearly zero.) The agreement between  $F_1$  and  $F_2$  is good enough considering that interaction is definitely present.  $k$  is the value of  $h/d$  obtained by Hull's method. It is about half our value of  $\sqrt{H_1/D}$  except for  $F_2$  when a zero result was obtained.

Order of dominance. The points in the  $(W_r, V_r)$  graph are in order of dominance along the straight line from the (possibly fictitious) complete dominant with minimum  $V_r = \sum u_i v_i (d_i - h_i)^2 = V_D$  to the complete recessive with maximum  $V_r = \sum u_i v_i (d_i + h_i)^2 = V_R$ . It can be shown that unless  $h_i/d_i$  is constant these lie somewhat inside the limiting parabola. However, assuming that  $(V_D, W_D)$  and  $(V_R, W_R)$  are at the intersection of the  $(V_r, W_r)$  line and the limiting parabola, we can find their values if necessary. Then an estimate of the ratio of the numbers of dominants to recessives in each parent under certain restrictions about equality of gene effects is  $\frac{V_R - V_r}{V_r - V_D}$  and over all

parents is  $\frac{V_R - V}{V - V_D} = \frac{\sqrt{(DH_1)} + F}{\sqrt{(DH_1)} - F}$  This is close enough to unity in all the maize data.

If there is a strong correlation ( $p$  in the table) between the dominance order (given by  $V_r + W_r$ ) and the parental order of magnitude, it is possible to predict the values of the complete dominant and recessive parents from the values of  $V_D$  and  $V_R$ . When this correlation is negative these are the values of the maximum and minimum parents possible, and vice versa for a positive correlation. (In  $K$  and  $S$  data,  $F_1$ , these limits are 51.9 and 2.3) If there is little correlation between dominance order and parental magnitude (as in our Nicotiana data) no such prediction can be made.

##### 5. Accuracy of the estimates.

It can be mentioned briefly that we have two ways of estimating the accuracy of these variance components.

Firstly, a certain analysis of variance of the diallel table enables exact significance levels to be obtained for  $V_M$ ,  $H_2$ ,  $(H_1 - H_2)$ ,  $((n + 2) H_2 - H_1)$  and  $(P - F_1)^2$ . These determine whether there is significant dominance and heterosis and, when significant, whether the estimate of  $uv$  differs significantly from either of its bounds,  $\frac{1}{4}$  and  $\frac{1}{n + 2}$ .

Secondly, the  $n$  estimates,  $W_r - V_r$ , of  $\frac{1}{4}(D - H_1)$  enable an error to be derived from  $D$ ,  $H_1$ ,  $H_2$  and  $F$ . This is the source of the standard errors given in the table.

The results and analysis of our measurements of flowering time, leaf length and height in Nicotiana rustica will be published later, together with a more detailed exposition of the theory and methods.

Source of data	F <sub>1</sub>	Kinman and Sprague F <sub>1</sub> (omitting Hy & Oh07)	F <sub>2</sub>	Nilsson Leissner (1927)*	Stringfield (unpublished, quoted by Hull**)
D	180.22 ± 46.73	229.44 ± 37.00	180.22 ± 13.78	1775.10	260.19
H <sub>1</sub>	1521.80 ± 95.77	1855.22 ± 82.74	1349.54 ± 112.97	27478.43	2605.13
H <sub>2</sub>	1464.77 ± 83.60	1811.26 ± 74.00	1201.42 ± 98.60	25837.99	2530.74
F	45.77 ± 110.59	-8.77 ± 90.63	88.32 ± 65.22	1102.72	159.77
√(H <sub>1</sub> /D)	2.91	2.84	2.84	3.93	3.16
k	1.64	-	0.00	2.05	1.88
uv	0.241	0.244	0.224	0.235	0.243
<i>P</i>	-0.902	-0.784	-0.770	-	-

\*Hull, F. Maize Genetics News Letter 20. 1946.

\*\*Nilsson Leissner. Journ. Amer. Soc. Agron. 1927.

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1. A-B interchanges as a method of screening for new mutants in specific segments.

The use of A-B interchanges in assigning the linkage group of a previously isolated recessive factor makes it possible to obtain information in the  $F_1$  generation. Where large numbers of unplaced mutant factors are available and the problem is that of assigning these to their respective linkage groups the conventional use of A-B translocations should prove a great advantage over the older method. Considered from the point of view of maize genetics as a whole the placement of such large numbers of factors more or less at random on the chromosome maps is a highly desirable enterprise since it stands to benefit all maize geneticists in the long run. However experimental studies often place a premium on several marker genes in a particular linkage group, in a single arm or even in a restricted region of a particular arm of a chromosome. Considering the current status of chromosome maps in maize that aspect of a problem which poses these requirements often must either be dropped or postponed until our present "shot-gun" method yields the desired markers. The numerous stocks of reciprocal translocations which are now available may be the solution to this problem in some cases but have the disadvantage that the phenotype of this kind of marker is manifest only in the mature plant; moreover the associated effects on crossing over and gametophyte viability are disadvantages in numerous studies. Some method is required which will enhance the frequency with which plants carrying new mutant genes may be recognized and which will at the same time screen for mutants which have a favorable location in terms of the requirements of specific studies.

The A-B interchanges should prove to be ideal testers for this purpose. According to the method proposed here a pollen parent carrying a selected reciprocal A-B interchange is crossed, not with plants carrying a previously selected mutant character whose linkage placement is sought, but with normal plants. Since, following non-disjunction in the second microspore division of the pollen parent, the great majority of immediate offspring (embryos or endosperms) are deficient for the acentric portion of the A-chromosome which is translocated to the B chromosomes, any mutations which occur in the corresponding segment in the normal plant, which are incorporated in functional megaspores and which finally come to reside in hypoploid complements should be immediately expressed and identified. Thus each  $F_1$  hypoploid plant or endosperm tests a single gamete of the normal plant for mutation of previously unidentified genes lying in the specified segment. In contrast, by the present method of obtaining new mutants, an entire  $F_2$  progeny is required to test single gametes. The method proposed here has the same advantage as that enjoyed in studies dealing with the isolation of visible mutations carried in the X-chromosome of Drosophila males, the latter being from the standpoint of most of the sex-chromosome material, haplo-X.

In addition to the expected greater efficiency in the recognition of newly arising mutants this method is expected to have the following advantages: (1) Depending on the particular A-B interchange employed a variety of

A-chromosome segments may be screened for mutation; (2) In the case of hypoploid mutant embryos the deficient complement is not expected to transmit through the gametophyte and since the mutant gene is carried on a normal chromosome the progeny of the selfed, mutant hypoploid should be composed entirely of plants which are homozygous for the mutant factor and have an entirely normal complement of chromosomes; (3) The incorporation of desired gene combinations or structural modifications into the background of the new mutant stocks need not await the discovery of a desired new mutant factor. Stocks with the desired combinations may be utilized directly as the egg parent in the cross with the interchanged tester parent.

The degree of application of the proposed method would be a function of the variety of A-B interchanges available. While stocks involving such interchanges for almost half of the 20 chromosome arms in maize are now available studies involving the remaining arms would not be aided by this method. Moreover, the technique does not lend itself to the isolation of mutants lying in close proximity to their respective centromeres. A further disadvantage which applies to the isolation of seedling mutants by this method lies in the fact that the hypoploid plant is often less vigorous than the normal plant.

We are at present studying the feasibility of this method and are utilizing several A-B interchanges and analyzing mutations in both the embryo and endosperm. A recent search for mutants among the seedling progenies of crosses of normal plants with a plant carrying the T B-3a interchange gave encouraging results. At the present time it is not possible to state the frequency of mutant embryos among these progenies since the analysis is not complete and moreover there is always the tendency to select as possible cases the plants with slight as well as striking deviations from normal. However, there were included among selected cases a number of striking virescent, albino, glossy, pale-green and luteus plants. In a number of families there occurred several individuals with the same striking singular phenotype. These are expected in the event that mutations in the egg parents occur early enough to be included in a number of megasporocytes.

In a cooperative program among maize genetecists aimed at finding and mapping new mutant genes previous methods would require that the various cooperators exchange stocks carrying the newly-isolated recessive factors which would then be crossed with numbers of tester stocks to facilitate the placement of the mutant factors. If the method discussed here proves feasible it would not require this exchange and incidentally save considerable bookkeeping. Each cooperator would be responsible for the current mapping of a single arm or chromosome and would cross to screen for and deal with only those mutants occurring on that arm or chromosome.

## 2. A test of Goldschmidt's hypothesis of the "sensitive" segment.

The occurrence of a number of cases of closely linked genes with similar effects has suggested to Goldschmidt that the adjacent member alleles in such series may represent not factors with separate identity in the classical sense, but impairments at various points within a segment the whole of which is concerned with the development of normal phenotype for the character involved. This is an engaging hypothesis and to the extent that

evidence confirms it as an explanation for such closely linked systems it would supplant the hypothesis which argues the origin of such loci through duplication. It has the further merit that it may be tested readily for it requires that mutations of independent origin at a "locus" be distributed essentially at random within the hypothetical, sensitive segment and hence leads to the expectation that most combinations of heterozygotes of such mutant types give rise to reversions to wild type associated with crossing over within the specified segment. Most heterozygotes involving mutant alleles now available at particular loci in maize would not represent valid tests of this hypothesis, for in this material new alleles have been sought ordinarily among the progenies from crosses of normal plants with those carrying a mutant allele. Barring a position effect, this method favors the isolation of alleles which, on the above hypothesis, lie at the same point within the hypothetical segment. The hypothesis is being tested in maize under conditions which, it is hoped, will eliminate this bias. Plants which are homozygous for the A factor are crossed with T B-3a plants carrying A on the interchanged segment. Hypoploid endosperms among the progeny (see discussion under previous heading) will appear colorless if there has been a mutation of A to its recessive form in the egg parent. If there exists a relatively extended segment on the chromosome within which slight impairments at any one of a number of points may produce the effect of recessive a the isolation of mutants from such hypoploid progenies should insure that a random sample of mutants representing aberrations at various points within the hypothetical segment is obtained. Heterozygotes of these mutant forms may then be made in various combinations and analyzed for the occurrence of reversions associated with crossing over in the region concerned. The C and R loci are being analyzed in the same manner using appropriate A-B translocation stocks. We would be happy to receive, from cooperators, stocks carrying mutants of the above types which may have been obtained incidentally in crosses involving pollen parents carrying A-B interchanges.

John R. Laughnan  
and  
E. H. Coe, Jr.

### 3. Sublethal concentrations of formaldehyde and phenol

In a preliminary trial of the mutagenic effects of formaldehyde and phenol, solutions of various concentrations were injected into the tassel area, at the sporocyte stage, with a hypodermic needle. The sublethal concentrations for these two substances are:

Phenol: 0.5% to 1.0% by weight.

Formaldehyde: 1:160 to 1:320 dilution of commercial formalin.

Concentrations greater than these resulted in death of the tassel.

E. H. Coe, Jr.

#### 4. The effect of $sh_2$ on carbohydrate reserves in maize endosperm

Quantitative determinations of reducing sugars, sucrose, water-soluble polysaccharides and starch in mature endosperms indicate that the shrunken phenotype of  $sh_2$  is associated with a striking difference from normal in carbohydrate reserves. To facilitate a valid comparison of the effect of the  $sh_2$  factor with that of  $su_1$  studies were carried out on the selfed progenies of plants heterozygous for both factors ( $Su\ su\ Sh\ sh$ ). Four phenotypic classes are represented among the progeny: normal ( $Su\ Sh$ ), sugary ( $su\ Sh$ ), shrunken ( $Su\ sh$ ) and sugary-shrunken ( $su\ sh$ ). While normal kernels store carbohydrate predominantly in the form of starch there is a progressive decrease in this component among the other classes in the order named. Conversely, sugars are lowest in normal kernels (1.8%) and highest in the sugary-shrunken class (32.0%), the latter type having only one-tenth the normal amount of starch. The differences in sugar content are due primarily to sucrose which alone accounts for 28% of the dry weight of sugary-shrunken endosperms. Water-soluble polysaccharides which represent 30% of the weight of sugary ( $su\ Sh$ ) kernels (a long established observation) are nearly absent in the other types. The following general interpretation of the action of these genes is suggested. In the development of normal ( $Su\ Sh$ ) endosperms there is an uninterrupted conversion of sucrose and reducing sugars to starch. The  $su$  gene determines a partial block in synthesis at some point following the condensation of sugar residues but prior to the formation of starch. The unusually high sucrose and low starch levels of  $Su\ sh$  endosperms suggest that the  $sh_2$  factor blocks synthesis at an earlier stage than does  $su$  and may be concerned with the enzymatic degradation of sucrose. The  $sh_2$  factor may be of some value in the sweet corn industry either as a substitute for, or in combination with, the  $su$  gene.

John R. Laughnan

#### 5. Two new pairs of duplicate factors

An  $F_2$  progeny obtained through the kindness of the DeKalb Hybrid Corn Co. was found to segregate close to 1/16 glossy seedlings. Progenies of selfed, normal sibs of these glossy plants segregated  $\frac{1}{4}$  glossy, 1/16 glossy or were non-segregating in frequencies approximating those expected if the glossy character is inherited on a duplicate factor basis. Linkage tests in  $F_2$ , repulsion phase, place one member of this duplicate pair on the fourth chromosome close to  $su_1$ , the other in linkage group 2 near  $v_4$ . The recessive forms of a second pair of duplicate factors are associated with a new albescent character. One member of this pair is placed approximately 25 recombination units to the left of  $gl_6$  on chromosome 3. The linkage relation of the other member is not established.

John R. Laughnan

#### 6. The mutable pale green locus

The mutable pale green phenotype was found in material provided by Dr. E. G. Anderson which had been exposed to irradiation from the Bikini atom bomb.

Two distinct seedling phenotypes are associated with the pg complex; a stable-type (pg<sup>s</sup>) characterized by its uniform "pale green" color with occasional sectors of green stripes and a variegated-type (pg<sup>m</sup>) containing numerous dark green stripes on a pale green background. There is experimental proof that these green stripes represent mutations of pg to the normal allele. Pg.

These two phenotypes appear, together with the normal green plants, in three characteristic ratios in the F<sub>2</sub> progenies: (1) 3:1 for green to stable pg - the s class; (2) 12:3:1 for green to mutable pg to stable pg - the m & s class; and (3) 3:1 for green to mutable with a low and variable fraction of stables - the m class.

There are various lines of evidence to show that the m & s class is due to the presence of an independently segregating factor, En, increasing mutability at the pg locus. Such a factor acting on pg is suggestive of the Dt influence on a<sub>1</sub> and of the Ac effect on Ds-controlled loci. When mutable plants homozygous for independent En (pg En) are outcrossed to various agronomic lines, the following results are obtained:

<u>Pollen parent</u>	<u>Classes of F<sub>2</sub> progenies</u>			
	<u>G</u>	<u>s</u>	<u>m &amp; s</u>	<u>m</u>
1950 43-54	4	0	22	2
1950 43-57	15	0	29	2
Total	19	0	51	4

When pg plants from the unexpected m type progenies are further tested in the F<sub>3</sub>, they behave like members of the m class.

The mutability of the m class is autonomously controlled -- i.e. En is located adjacent to the pg locus (pgEn). When pollen parents containing homozygous pgEn are outcrossed to lines, the following results are obtained:

<u>Pollen parent</u>	<u>Classes of F<sub>2</sub> progenies</u>			
	<u>G</u>	<u>s</u>	<u>m &amp; s</u>	<u>m</u>
1950 66-108	11	3	10	54
1950 40-37	1	1	5	17
1951 388.1	0	0	2	7
1951 647-3	24	1	11	12
1951 283-1	21	2	3	20

In addition to the m-type F<sub>2</sub> progenies, two unexpected classes- the m & s and s - also appear. Their frequency is interpreted as indicative of a high rate of change from pgEn (m class) to pg En (m & s) and pg (s class). Transposition of En from its position adjacent to the pg locus results in its appearance at another position in the chromosome complement. Plants from the

newly-arisen m & s type behave as if En were independently segregating and those in the s class lack En.

Tests show that En is not present in 20 agronomic lines examined.

Rate and direction of mutation. -  $pg^S$  mutates to  $pg^m$  in a low frequency (1/420). The occurrence of  $pg^m$  seedlings in  $pg^S$  stocks is correlated with the sectors of mutability observed in  $pg^S$  seedling leaves. This is indicative of the appearance of En in somatic tissue. The isolation of one m-type progeny from the outcross of  $pg^S$  indicates that this new En lies adjacent to the locus.

$pg^m$  mutates to  $pg^S$  at the rate of approximately 2.5% - 4% in the gametes of  $pg^m$  P<sub>1</sub> pollen parents. In the F<sub>1</sub> plants, the rate is approximately 17%. A number of explanations, such as different rates of mutation in homozygotes versus heterozygotes and the presence of non-specific modifiers in the P<sub>1</sub> plants reducing mutation rate, may account for this difference.

The autonomous and independent En differ in their phenotypic expression and in their relative stability in that the latter is characterized by a pattern of later occurring mutations and has not been found to mutate.

In addition to the location of En adjacent to the locus and on an independently segregating chromosome, En was found in one instance to be linked with pg at a distance of approximately 36 cross-over units. This third location of En is further evidence that it undergoes transposition.

A hypothetical representation of the pg complex is diagrammed below:

$pg^S$  =  $Pg(I)$  -stable type seedlings  
 $pg^m$  =  $Pg(I)En$  -mutable seedlings: the autonomous location of En.  
 =  $Pg(I) En$  - mutable seedlings: the independent location of En.  
 Green =  $Pg$  - Normal wild allele of all lines.

According to this scheme, the mutable locus represents the association of an inhibitor (I) with the normal dominant allele Pg resulting in a pale green phenotype. The loss of (I) under the influence of En is manifested in the mutation of pg to Pg. This scheme fits McClintock's concept which considers that mutation of unstable genes represents the removal of an inhibitory locus adjacent to the dominant allele.

Two new mutables ( $a_1^m$  and  $w_x^m$ ) arose in  $pg^m$  families containing the dominant alleles A<sub>1</sub> and W<sub>x</sub>.

Peter A. Peterson

### 7. Mutation of $a_1$ to $a^s$ -stable

As is well known, the Dt gene induces the mutation of the  $a_1$  allele to A, which results in the appearance of dots on otherwise colorless kernels. Occasionally, colorless kernels appear which do not respond to Dt; these have been designated a-stable ( $a^s$ ). Studies were undertaken to analyze the mutation of  $a_1$  to  $a^s$ . The isolated but regular occurrence of dotless kernels on normally dotable ears suggests that the mutation of the  $a_1$  allele to  $a^s$  arises following a meiotic event. A series of crosses were made to test the hypothesis that a factor necessary for dotting was lost by crossing-over. Crosses with appropriate markers indicate that the mutations of  $a^s$  are not related to crossing-over. Further insight into the problem was obtained by testing the role of the Dt gene in the mutation of  $a_1$  to  $a^s$ . In the cross, where mutations of  $a_1$  to  $a^s$  are being tested for their occurrence in the absence of the Dt gene, no mutations have been found in a population of 6525 gametes tested for dotless kernels. Since the rate of mutation of  $a_1$  to  $a^s$  in the presence of Dt is .25% in these tests, approximately 12 cases would be expected if Dt were not responsible for the origin of  $a^s$ . This indicates that few, if any, mutations of  $a_1$  to  $a^s$  occur in the absence of Dt. The above results suggest that Dt conditions the change not only to higher alleles as has previously been shown (Rhoades), but also to the colorless stable allele,  $a^s$ .

Peter A. Peterson

### 8. Cytogenetic studies with a paracentric inversion.

Inversion 3a is a paracentric inversion in the long arm of chromosome 3. The proximal break occurred 0.4 of the length of the long arm from the centromere and the distal break was very near the free end. The Lg<sub>2</sub>, A<sub>1</sub>, and Et loci all lie within the limits of the inversion. Recombination between these loci was greatly reduced in inversion heterozygotes; the only effective recombination coming from double exchanges, the frequency of which indicated the absence of chromatid interference.

Table 1. Backcross data from the cross of N lg a x In Lg A/N lg a.

Individuals were scored as heterozygous for the inversion or homozygous normal on the basis of pollen abortion. Since Lg and A are both included within the inverted segment, region (1) consists of the interval between A and the distal breakage point, region (2) is the A-Lg interval, and region (3) lies between the Lg locus and the proximal breakage point of the inversion.

(0)	(1-3)	(2-3)	(1-2)	(1-2)	(2-3)	(1-3)	(0)	Total
Lg	Lg	lg	lg	Lg	Lg	lg	lg	
A	A	A	A	a	a	a	a	
<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>	
1403	7	5	3	3	3	7	1208	2639

Recombination values: Region 1 0.8%  
 Region 2 0.5%  
 Region 3 0.8%

% double crossover strands 1.1 (28/2639)

On the basis of cytological observations (see table 3) the expected frequency

of double crossover strands when the In/N plants are used as the male parent is 1.5. The difference is not significant.

Table 2. Backcross data from the cross of In Lg A/N lg a x N lg a.

The regular offspring received a chromosome 3 with a full complement of genes in either the normal or inverted order from the maternal parent. The hypo-hyperploid individuals arise from megaspores with a chromosome 3 deficient for the tip of the long arm but redundant for varying portions of the proximal region of the long arm. Crossover regions are identical with those in table 1.

Regular offspring							Hypo-hyperploid offspring								
(0)	(1-3)	(2-3)	(1-2)	(1-2)	(2-3)	(1-3)	(0)	Lg	Lg	lg	lg	Lg	Lg	lg	lg
956	9	2	5	4	1	10	731	A	A	A	A	a	a	a	a
								<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>	<u>In</u>	<u>N</u>
								3	1	9	7	1	0	7	1

% double crossover strands is 1.8. Expected with no chromatid interference 1.87.

The hypo-hyperploid individuals in table 2 possess a deficient-duplicate chromosome 3 which arises from breakage of dicentric bridges. Approximately one-half of the deficient-duplicate chromosomes possessed an inverted, and the others a normal sequence. There was no transmission of deficient-duplicate chromosomes through the pollen. Transmission through the ovules was variable, depending upon the length of the duplicated piece. An average transmission value of 25% was found.

Cytological observations of bridge frequency are given in table 3.

Table 3. First and second meiotic anaphase configurations in In/N microsporocytes.

		Anaphase I			Anaphase II (Single cell counts)	
<u>no bridge</u>	<u>1 bridge</u>	<u>1 bridge</u>	<u>no bridge</u>	<u>2 bridges</u>	<u>no bridge</u>	<u>1 bridge</u>
<u>no frag.</u>	<u>1 frag.</u>	<u>no frag.</u>	<u>1 frag.</u>	<u>2 frags.</u>		
925	577	37	87	19	458	17
56.2%	35.1%	2.2%	5.3%	1.2%	93.2%PMC	6.8%PMC

Studies with individuals carrying two inverted chromosomes, one of which was deficient-duplicate, placed the Lg<sub>2</sub> locus 12 recombination units from the proximal break of the inversion. Similar studies with plants carrying two normal chromosomes, one of them a deficient-duplicate, indicated that the Et gene was 3 recombination units from the distal break.

The frequency of recovered deficient-duplicate chromosomes and the amount of ovule abortion were both higher than that expected if the basal megaspores receive broken chromosomes derived only from cells with double bridges at anaphase I or single bridges at anaphase II. It was concluded that some of the broken chromosomes delivered to the basal megaspore came from breakage of single bridges at anaphase I.

M. M. Rhoades and  
Ellen Dempsey



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1. Location of factors for corn borer reaction

A borer resistant inbred line, Minn. A411 whose resistance came from the Oh7 inbred, was used in crosses with chromosomal interchange stocks from E. G. Anderson. As far as possible, the interchanges selected had breaks near the middle of each arm. The general plan was to cross susceptible interchanges with the resistant inbred line and to backcross the semisterile  $F_1$  plants to the inbred line showing the recessive borer reaction. Since resistance proved to be dominant, the  $F_1$ 's were backcrossed to a susceptible inbred A344, a selection from the Iowa 153 inbred. Several interchange lines proved to be resistant and were not usable in this analysis of A411.

The plants were hand infested with borer egg masses. The individual plants were classified by pollen examination in the field and later each was classified (5 grades) for the degree of leaf feeding and of stalk damage. The P values for the  $X^2$  tests for independence, based on an average of 167 plants (range from 119 to 192 plants) per test, are summarized in the following table:

	P values for $X^2$ test for independence based on total hand infested plants:		Factor located in
	<u>leaf feeding</u>	<u>stalk damage</u>	
1-9b	.20-.10	<.01**	
2-3c	.30-.20	.30-.20	
2-6c	.30-.20	.10-.05	
2-7c	.95-.50	.50-.30	
2-9b*	.30-.20	.95-.50	
3-5a	.05-.01*†	.10	
3-6 Conn	.05-.01*†	.50-.30	
3-7c	.05-.01*†	<.01**	3L
3-9c*	.05-.01*†	<.01**	3L
3-9x23-158*	<.01**	.05-.01*†	3L
4-9 D25*	<.01**	<.01**	4L
5-9a	.05-.01*†	.05-.01*†	5L
6-9x25-78*	.50-.30	.95-.50	
6-10a	.30-.20	.95-.50	
8-9x22-92*	.50-.30	.95	
9-10b*	.20-.10	.05-.01*†	

\*Translocations with WF9 (susceptible) background  
\*†, .05-.01 = significant    \*\*, <.01 = highly significant

The data indicate that the resistance of the A411 inbred is due to at least one gene in the long arm of chromosome 3 and one in the long arm of 4, and probably another in the long arm of 5. (The cooperation of Dr. E. H. Rinke and F. Loeffel in the corn breeding project and Dr. F. J. Holdaway and his assistants in Entomology is acknowledged.)

M. A. Ibrahim and  
C. R. Burgham

2. Analysis of a multiple break translocation stock produced by X-raying T5-7b

The stock homozygous for these translocations, when crossed with T5-7b, produced a (·)6 indicating they differ by two interchanges. When that same stock was crossed with standard normal, a (·)8 was produced involving chromosomes 1-5-6-7. The derived types of (·)4 and (·)6 from the latter cross (Coop Newsletter #20, p. 15, 1946) have been analyzed at pachytene and the available genetic data summarized. Cytological studies showed that the breakage positions in the most numerous type of derived (·)4, T1-5, were probably at 1S or L .6 and 5L.4. No linkage data were available for chromosome 1, but for chromosome 5 linkage data indicated the break was in the long arm. For the other type of derived (·)4, T6-7, the breakage points were at 6L.3 and 7S.3. At diakinesis in plants from the cross of plants homozygous for a derived (·)6 (T5-6-7) with plants homozygous for the parental interchange T5-7b there was only a (·)4 chromosomes attached to the nucleolus indicating these two lines differ by only one interchange. Conclusions as to the probable original breakage positions should be possible from this information. It should be possible then to plan further crosses to utilize the T1-5-6-7 stock in the production of larger rings.

Aly Mohamed  
and  
C. R. Burnham

3. Inheritance of pericarp tenderness in sweet corn

Segregating material using interchange markers will be grown next summer to attempt to locate factors for tender pericarp in sweet corn.

Aly Mohamed

4. Crossing over differences in ♂ and ♀

Studies are underway to make these tests for regions which may be near the centromeres. For many, stocks have to be synthesized, but a few more results have been obtained:

Tester parent	F <sub>1</sub> het.	F <sub>1</sub> heterozygote used at † <sup>o</sup>		F <sub>1</sub> heterozygote used as ♂	
		number	% recomb.	number	% recomb.
+lg <sub>2</sub>	$\frac{Rg +}{+ lg_2}$	618	26.7	262	35.1
$\frac{+d}{++}$	$\frac{Rg +}{+ d_1}$	897*	9.6*	347*	16.4*
y pb	$\frac{+ +}{y pb}$	304	1.64	394	5.8

\*recombination calculated by product method for (3:1) (1:1) ratios

Crossing over values are higher in the  $\sigma^1$ . Similar differences were reported in the 1950 Coop Newsletter #24, p. 56; for sh-wx, the difference was most pronounced in plants heterozygous for T5-9a, less so in those homozygous for the translocation or without the translocation. In that report, the upper row of data for each group is from the heterozygote used as the  $\sigma^1$ , the lower row is from the heterozygote used as the  $\sigma^2$ --this was not indicated in that summary.

Mr. E. Clark is studying crossing over in chromosome 9 in reciprocal crosses in a series of translocations involving the short arm of chromosome 9.

#### 5. Set of translocation markers.

From the translocations listed by Drs. Longley and Anderson, a set has been selected which it is hoped will, with a few additions, test adequately all the arms of the 10 chromosomes. These have been crossed to an early, a medium, and a late inbred and will be backcrossed for several generations to furnish the set in uniform backgrounds.

#### 6. Chromosome segregation in translocations in relation to crossing over

A. The spore quartet data on the frequency of quartets having one or two of the spores with a diffuse nucleolus are, for two stocks heterozygous for In5a:

	<u>one-diffuse quartets (%)</u>	<u>two-diffuse quartets (%)</u>
<u>T5-6c +</u> + In 5a	45	16.7
<u>T5-6c In 5a</u> + +	12.3	35.8

The lower frequency of "one-diffuse" quartets in the second stock is due to the fact that the crossovers cannot be detected in the entire interstitial segment, part of which is in the inversion. The higher frequency of "two diffuse" quartets in the second stock is due to adjacent-1 segregation following single crossing over or 3-strand doubles occurring within the inversion. This is the first evidence for adjacent-1 segregation following crossing over in an interstitial segment in corn translocations.

B. Crosses between translocations are being selected so that crossover frequency in the differential segment may be measured by the spore quartet technique, and compared with the frequency of recovered genetic crossovers in the same region.

Preliminary breeding tests indicate that crossovers occurring in the differential segment are recovered, indicating again that adjacent 1 segregation occurs following such crossing over.

(5-6c x 2-5b) x normal = 22.4% of crossovers (normals and combined T2-5-6)

(1-10(4885-1) x 6-10b) x normal = 4.1% of crossovers (normals and combined T1-10-6)

For the latter, the percentage of crossover type quartets was 4.8% for the (·)6 F<sub>1</sub> plants and 4.8% for plants heterozygous for T6-10b alone. These cytologically observed values must be divided by 2 to be comparable with the 4.1% observed in the backcross progeny.

More data from these and several other crosses of the same type will be obtained next summer.

#### 7. Progress in production of large ring in corn

Certain of the translocation intercrosses from which basis permanent rings of 6 were expected failed to produce the necessary crossovers to proceed with the original plan. Intercrosses for a new plan of producing a complete ring utilizing translocations with more favorably placed breakage points, i.e. which involve longer differential segments, were made the past summer.

C. R. Burnham,  
assisted by Ed Clark

#### 8. Inheritance of Waseca stripe

This character is recessive and very similar to japonica (j<sub>1</sub>) in chromosome 8, but it shows to some extent in the seedling stage. It was first found in 1947 in the corn breeding work at the Waseca station by Dr. E. L. Pinnell, where it arose from an F<sub>2</sub> of A347 x K230. It probably was an out-cross of an F<sub>1</sub> to some source of white endosperm, because it also has white endosperm. Intercrosses showed it was not japonica or ij. Among the crosses of this stripe as ♀ with different 'B' chromosome translocation testers, supplied by Dr. H. Roman, the one with translocation TB-10 threw Waseca stripe plants in F<sub>1</sub>, indicating this factor is in chromosome 10.

F<sub>2</sub> populations from a cross involving golden-1 and this stripe appear to confirm this linkage, although the numbers are small and striped plants were greatly deficient due to poor growing conditions. Further information on this topic will be sought next summer.

Gertrud Joachim  
and  
C. R. Burnham

#### 9. Inheritance of Reaction to the Chlamydozoospores of Corn Smut, Ustilago zea (Beckman) Unger Derived from a Single Cross.

Two compatible lines of corn smut (10A4 x 17D4) obtained from the Department of Plant Pathology, University of Minnesota, were inoculated into

plants in the field. The chlamydospores from the galls obtained from this cross were stored and used for inoculation on the material tested for smut reaction. The spores were measured out, mixed in a given quantity of water and sprayed on the plants. A resistant inbred line derived from Minnesota 13, the same one used by Saboe in earlier studies, and a susceptible inbred, Baker 164, together with material from the backcrosses, were sprayed with this suspension just as the tassel emerged from the boot.

Sixteen chromosomal interchange stocks, which were susceptible to smut, were crossed with the resistant Minnesota 13 line and only semisterile  $F_1$  plants were backcrossed both to the resistant and susceptible parents. These tested sixteen of the twenty arms of the ten chromosomes. The backcross progeny were inoculated. From the backcross to the resistant, there were 3.62 per cent of smutted plants and from the backcross to the susceptible parent, there were 29.13 per cent smutted plants. These results show that the resistance of this inbred is dominant for this one lot of chlamydospores. The inoculated Minnesota 13 showed no smutted plants while the susceptible Baker 164 showed 63.6 per cent. The uninoculated Baker 164 showed only 3.11 per cent of smutted plants.

Significant deviations from independence of smut reaction and semisterility, a P value less than .001 were observed with interchange 2-7c, 3-5a, 3-6a, 3-7b, 4-5c, 4-6 (57-31) and 5-9a and .05-.02 for 2-9a and .02-.01 for 1-4a for the progeny from backcrossing the semisterile  $F_1$ 's to the susceptible parent.

The associations indicate that the difference in reaction of these two inbreds to this corn smut inoculum is governed by at least 5 or possibly 6 factor pairs. The inferred location of these factor pairs (or linked groups of factors) is as follows: In the short arms of chromosomes 4 and 9, in the long arms of chromosomes 3, 5 and 7 and another possibly in the short arm of chromosome 3.

The assistance of C. R. Burnham in planning the genetic tests is acknowledged.

J. J. Reilly

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#### 1. Additional Dt loci.

As a result of testing 97 races of corn of diverse origin for modifiers of mutation at the  $A_1$  locus, two possible additional Dt loci have been discovered. (The gene  $Dt_1$  discovered by Rhoades is located on the short arm of chromosome 9 and causes the gene  $a_1$  on chromosome 3 to mutate to its dominant allele  $A_1$ .) The first of these two was found in the Brazilian variety "Cateto". Preliminary linkage evidence has shown it to be linked to the gene Y with about 22.5% recombination. Other crosses have clearly demonstrated that it is not an allele of  $Dt_1$ , and is not linked to

either sh<sub>1</sub> or wx. It has therefore been tentatively located on chromosome 6.

Except for location on different chromosomes Dt<sub>1</sub> and Dt<sub>2</sub> have not been found to be distinguishable. From a selfed ear of an a<sup>m</sup> a<sup>m</sup>, Dt<sub>1</sub> dt<sub>1</sub>, Dt<sub>2</sub> dt<sub>2</sub> plant it was found that 1, 2, and 3 doses of Dt<sub>2</sub> give a near exponential increase in dot number as the Dt dosage is increased. This is similar to the behavior of Dt<sub>1</sub> under the same conditions.

In combination Dt<sub>1</sub> and Dt<sub>2</sub> supplement each other in dosage expression. Thus while two doses of Dt<sub>1</sub> give about the same dotting frequency as two doses of Dt<sub>2</sub>, the combination of two doses of each (giving a total of four doses) produces ten times as many dots.

It will be interesting to see what the seeds from a selfed ear of an a a, Dt<sub>1</sub> dt<sub>1</sub>, Dt<sub>2</sub> dt<sub>2</sub> plant will show. They will range in combined Dt dosage from 0 to 6 doses in the endosperm.

The second Dt gene was found in a Peruvian race. It has not yet been located and could be an allele of either Dt<sub>1</sub> or Dt<sub>2</sub>.

The three known occurrences of Dt genes reported to date are from widely separated unrelated races of corn. The first (Dt<sub>1</sub>, reported by Rhoades) was found in Black Mexican sweet corn, which is a North American variety of possible Central American origin. The second (Dt<sub>2</sub>) is from a Brazilian yellow flint type, and the third is from a purple aleurone Peruvian race.

## 2. A new pale aleurone gene.

A selfed ear in a culture that was homozygous for all the genes required for full purple aleurone color was found to be segregating for a pale aleurone effect. The ratio was 3 full colored: 1 pale. Approximately three fourths of the pale seeds had many small full purple aleurone sectors suggesting frequent reversion to the normal type. One explanation for this behavior would be that the effect was due to a recessive pale aleurone factor which was unstable in the presence of a dominant modifier. Purple seeds from this ear gave plants with normal anthocyanin pigmentation whose ears included some which were homozygous colored and others which were segregating for colored and pale seeds. The sectored pale seeds gave green plants with red anthocyanin sectors. They produced ears with all pale seeds but which segregated for stable and unstable seeds. The pale stable seeds gave all green plants which produced ears with only pale stable seeds. Tests on a<sub>1</sub>, a<sub>2</sub>, c, f, and b<sub>2</sub> testers have shown that the effect is not allelic to any of these. Therefore it must be a new gene affecting anthocyanin pigmentation of both aleurone and plant tissues. It has been tentatively designated pa (pale aleurone).

M. G. Nuffer

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1. Effects of X-ray and thermal neutron radiations of dormant seeds of maize on the immediate generation.

Dormant seeds of maize were irradiated with different dosages of X-rays or thermal neutrons at the Brookhaven National Laboratory in the spring of 1952. Field plantings of 250 seeds per treatment were made at Lincoln, with two replications per treatment for each of two planting dates. The dosages of X-rays and thermal neutrons used are shown in Table 1.

Table 1. Percentages of chlorophyll chimeras, leaf slashes and twin stalks in maize for various dosages of X-rays and thermal neutrons, including two planting dates and four replications.

Treatments	Chimeras	Leaf slashes	Twin stalks	Number of plants
Control	2.4	1.7	0	803
X-rays				
4,000 r	11.9	28.1	0	797
8,000 r	15.9	24.3	1.8	490
16,000 r	13.0	20.7	0	92
24,000 r	15.4	19.2	3.8	26
32,000 r	21.1	31.6	0	19
Thermal neutrons (Nth/cm <sup>2</sup> /sec.)				
5.8 x 10 <sup>12</sup>	10.4	26.0	0	404
10.4 x 10 <sup>12</sup>	18.0	30.0	0	440
10.7 x 10 <sup>12</sup>	17.6	31.3	0	386
17.3 x 10 <sup>12</sup>	13.2	30.9	.8	385
18.7 x 10 <sup>12</sup>	18.1	36.6	4.4	432
24.8 x 10 <sup>12</sup>	21.2	41.2	3.3	306
32.1 x 10 <sup>12</sup>	18.5	17.3	5.2	173
41.7 x 10 <sup>12</sup>	26.4	48.4	6.6	91

Survival from irradiation effects could not be determined accurately in the field since plants heavily injured by irradiation, which would have survived under greenhouse conditions, were killed by adverse environmental factors, such as a dry surface crust at the time of emergence or a prevalence of smut spores which gained access through the necrotic streaks in the leaves. However, it was apparent that plant stands were severely reduced by X-ray doses of 16,000 r and higher, and by the highest thermal neutron treatment.

Notes were taken on the growing plants for chlorophyll chimeras, slashing of leaf margins and twin stalks. The chimeras included chlorophyll

changes to white, cream, various shades of yellow and green, and, in a few cases, a mottled effect of dark spots upon a light background. In some cases the same chimera occurred in an identical area on both leaf surfaces. A few instances were noted in which adjacent stripes or bands of different colors formed multiple chimeras. Leaf slashes occurred as longitudinal cuts in the margins, either on one side of the midrib or on both sides in identical areas. The slashes were distinctive from the streaking of seedling leaves which later formed necrotic tissue with consequent shredding.

The frequencies of chimeras, leaf slashes and twin stalks for all replications of both plantings are presented in Table 1. Whereas chimeras and leaf slashes were observed in the untreated series, it is evident that both X-rays and thermal neutrons caused a considerable increase in their frequencies, with a tendency toward relationship with dosage. The occurrence of twin stalks was confined to the higher radiation dosages and also showed some relationship with dosage. In most of the cases of twin stalks observed each stalk formed its own tassel and ear shoot.

Microsporocyte, pollen and ear samples were taken from all treatments for studies of chromosomal aberrations, pollen abnormalities, and ear sterilities, respectively. These studies are in progress.

Rosalind Morris and E. F. Frolik

## 2. Greenhouse studies of X-ray and thermal neutron effects on crop seedlings.

An attempt is being made to determine the effective dosage range of irradiation of dormant seeds for a number of crop species with X-ray and thermal neutrons and to find species which are differentially susceptible to the two types of irradiations.

Five types of corn are included in the 15 crops tested. These are: dent, flint, sweet, pop and waxy. Single cross foundation seed was used to insure uniformity. The limited data available indicate that all types of corn are approximately equally resistant to irradiation. More extensive tests have been made with dent corn and barley than with any of the other crops studied. The single cross L289 x I205 dent corn and Himalaya barley have been used. Dormant seeds were irradiated with X-rays and thermal neutrons at dosages shown in Table 2. The 100 seeds per treatment were planted in flats in a randomized block design consisting of 4 replications.

Plant height has been used as a measure of the injury due to irradiation. Measurements have been taken at 7 day intervals for a maximum of 35 days after planting the seeds. From preliminary statistical analysis of the data it appears that measurements on the fourteenth day show the greatest differences between control plants and plants from irradiated seed.

There appears to be a differential susceptibility of dent corn and barley to the two radiations. As shown in table 2 corn seems to be more susceptible to X-rays than the barley especially if number of surviving plants is considered. On the other hand corn is more resistant to thermal neutrons than barley.



Table 2. The effects of X-ray and thermal neutron radiation on dormant seeds of barley and corn as measured by plant height 14 days after planting.

	No. plants	Average Height		No. plants	Average Height	
		cm.	% of control		cm.	% of control
Control	94	37.7	100	97	23.2	100
X-ray						
4000r	93	33.7	89.4	94	20.6	88.4
8000r	96	25.6	67.9	97	20.7	89.0
16000r	54	12.6	33.4	89	18.4	79.1
24000r	8	4.9	12.9	88	16.0	69.0
32000r	7	12.3	32.5	86	9.6	41.5
Nth						
4.7 x 10 <sup>12</sup>				97	19.4	83.7
7.2 x 10 <sup>12</sup>				99	16.7	72.0
10.2 x 10 <sup>12</sup>	98	32.5	86.1			
11.6 x 10 <sup>12</sup>				99	9.6	41.1
17.2 x 10 <sup>12</sup>				99	3.5	14.9
21.6 x 10 <sup>12</sup>	92	26.7	70.7			
25.2 x 10 <sup>12</sup>	95	17.3	45.9			

Banjamin H. Beard  
E. F. Frolik

UNIVERSITY OF THE PHILIPPINES  
The Corn Improvement at the Central Experiment  
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In Cooperation with Cornell University

1. The Maize Project.

Corn pollination has occupied our attention during the last few weeks. The material is a part of the breeding program of Dr. Dioscoro L. Umali, Cornell Ph.D.'49, who is in-charge of the Division of Plant Breeding in the Department of Agronomy.

In addition to Doctor Umali's material, a considerable collection of varieties, inbreds, and crosses was received through the kindness of Dr. Sterling Wortman, In-charge of corn improvement for the Rockefeller Foundation at Mexico City, Mexico, and from Dr. Lewis M. Roberts, Director of the Rockefeller Foundation Agricultural Program in Columbia, Medellin, Colombia, S.A. This introduced material is now approaching the tasseling stage as it was planted somewhat later than Doctor Umali's material. A collection of inbreds and hybrids was received also through the help of Dr. F. D. Richey, Coordinator of the Southern Corn Improvement Program in United States.

A brief description of the status of Doctor Umali's breeding program may be of interest to corn workers and to other corn breeders. Doctor Umali's material consist of inbred lines produced from four different flint varieties. These are called College Yellow Flint, Cuban Yellow Flint, College White Flint, and Bicol White Flint.

The two Yellow Flint varieties are distinctly of different genetic origin and that, probably, is true also of the two White Flint varieties. Previous to this crop season, Doctor Umali has tested the combining ability of a considerable number of Flint inbreds from each of the varieties. With the Yellow Flint material the combining ability of the College Yellow inbreds was determined by top crossing these with Cuban. The Cuban inbreds were tested in top crosses with College Yellow. The inbreds of the two White varieties have been tested in a similar manner.

During the present crop season the following procedures have been carried out. Five to ten inbreds of good combining ability were selected from previous yield trials from each of the four varieties. Recently, we have completed producing the following types of single crosses: (1) Intercrosses between inbreds of College Yellow, (2) intercrosses between Cuban inbreds, and (3) all possible crosses between each inbred of Cuban with each inbred of College Yellow.

We are looking forward with a great deal of interest to the yielding ability and other characteristics of these crosses as determined from rather extensive yield trials which we propose to make during the next season's crop. As two crops of corn can be grown for a year here, the program is almost a continuous one. We also hope to make some combinations between introduced material from Mexico, Columbia, and southern United States with inbred lines obtained from the local varieties here.

H. K. Hayes

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1. Utilization of American Inbreds in the South African Breeding Program.

Only a few American lines per se can be used in this country due to poor adaptation. An attempt to utilize the reportedly high combining ability of certain American lines was made by backcrossing for two generations to adapted South African lines as the recurrent parents. All comparisons were then made after crossing to a common tester.

The unadapted American lines flowered later yet matured earlier than South African lines or backcrossed generations while F<sub>1</sub>'s were intermediate.

Greater stalk breakage in crosses was associated with the American lines used and this character proved to be additive in inheritance; as was also the case with shelling percentage.

The test cross yields of the American lines were only average or below average. Only a few high combining selections were obtained in any of the backcrossed generations and these were considered to be new recombinations, with a more favorable gene dosage than either parent. Combining ability under South African conditions is apparently due largely to adaptation to variable moisture conditions. Selection for adaptability while backcrossing to the American lines to retain combining ability should prove more useful.

B. Stead

## 2. A Quantitative Approach to Flint-Dent Contrasts

On grinding in a burr mill, the soft starch of the dent corns pulverises to a meal, while the flinty portion tends to granulate. Separation by an appropriate sieving method gave a quantitative measure of flint-dent gradation. An empirical scale of nine grades of indentation, significantly different in soft starch yields, could be set up, on which the segregates of a wide array of crosses between inbreds could be accommodated on a quantitative basis.

Data from a preliminary study with this method indicates:-

1. That a degree of dominance exists in respect to the dent character.
2. Flintiness seems to be associated with some mechanism of preferential fertilization. Whether this advantage of the flint genotype is gametic or merely one of time of pollination, was not established.
3. A probable cytoplasmic influence was apparent and the phenotype of a double cross hybrid is determined not only by the parental genotypes involved, but also by their position in the cross.

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## 1. Variegated pericarp studies

It has been shown that when variegated pericarp of "medium" grade mutates to the stable self-colored (self-red) type another mutant showing a distinctly lighter type of variegation frequently is formed as a co-twin (Brink and Nilan, GENETICS: 37:519-544). On the basis of limited data it was suggested that the mutant co-twin to self-color is identical with "light" variegated, a phenotype which regularly occurs with a somewhat variable and usually low, frequency among the offspring of all medium variegated plants in this stock. Additional data obtained in 1952 and based upon twin spots occurring on two ears confirm the identity.

Both the ears upon which twin spots appeared were heterozygous for colorless pericarp. They were pollinated by colorless pericarp. The three classes of kernels (medium variegated, as the "control", and the two components

of the twin spots, namely, self-red and light variegated) were grown out. Pollen from several of the resulting plants was then applied to a closely related colorless pericarp stock. The colored offspring from self-red mutant kernels are regularly self-red, and are omitted from the summary. The distributions of offspring of the heterozygous plants tracing to the medium and light variegated kernels on the original twin-spot ears are tabulated below.

## Ear No. 1

Family	Distribution of offspring			
	Colorless	Self-red	Light var.	Med. var.
	(Descended from light var. twin-spot kernels)			
63-377	32	2	18	17
-380	35	0	12	15
-381	35	4	17	13
-382	<u>26</u>	<u>3</u>	<u>18</u>	<u>19</u>
Totals	128	9	65	64
	(Descended from medium var. "control" kernels)			
63-393	41	7	6	12
-394	31	13	5	27
-396	<u>34</u>	<u>6</u>	<u>8</u>	<u>28</u>
Totals	106	26	19	67

## Ear No. 2

Family	Distribution of offspring			
	Colorless	Self-red	Light var.	Med. var.
	(Descended from light var. twin-spot kernels)			
63-132	23	1	29	3
-134	35	1	25	2
-135	<u>18</u>	<u>0</u>	<u>32</u>	<u>2</u>
Totals	76	2	86	7
	(Descended from medium var. "control" kernels)			
63-148	17	3	2	14
-149	27	2	5	26
-150	33	4	4	13
-151	25	7	4	20
-152	<u>13</u>	<u>5</u>	<u>2</u>	<u>9</u>
Totals	115	21	17	82

The light variegated segregates in the families descended from the light variegated kernels in the twin-spot sectors were identical in appearance with the light variegateds appearing among the descendants of the kernels on the medium variegated portions of the same ears. It may be concluded that they represent a single genetic class of variegated pericarp.

Light and medium variegateds occurred with equal frequency in the four families descended from the light variegated kernels from the twin-spots on Ear No. 1. The corresponding families from Ear No. 2 show a large preponderance of light variegateds. The difference is explainable on the hypothesis (Brink and Nilan, cited above) that Modulator, the genetic element which differentiates light and medium variegateds, is linked with the P locus in the Ear No. 2 group and independent of P in the families derived from Ear No. 1.

R. A. Brink

## 2. Segregations of the Cg gene in the presence of plus modifiers.

Genetic evidence has been obtained that the expression of the Cg (corn grass) gene may not only be reduced from the dominant to the recessive condition but be eliminated entirely by the accumulative effect of plus modifier genes. In some F<sub>2</sub> families the Cg gene was expressed in less than three per cent of the individuals.

The genotype of plants from F<sub>2</sub> segregations of the Cg gene at high plus modifier levels may be determined by a progeny test with F<sub>3</sub> families or by outcrosses to Connecticut 142, a prolific rice pop inbred. The progeny test is effective in determining whether the normal F<sub>2</sub> segregants are +/+ or Cg/+ because the Cg/Cg plants can be recognized as corn grass in cases where the Cg/+ plants appear normal. C142 may be used to determine the corn grass genotype because the plus modifier genes for the Cg gene are largely recessive in combination with this rice pop inbred although they are dominant in combination with most other inbreds.

The wide array of distinct pleiotropic effects of the Cg gene has made possible the interaction of many plus modifier genes and their subsequent classification.

## 3. Corn grass morphology

A classification of the effects of modifier genes on the expression of the Cg gene has entailed a morphological analysis. The structural nature of modern corn becomes more obvious in corn grass since many of the morphological peculiarities of corn grass result from the active development of parts that are normally suppressed during ontogeny.

Evidence bearing on the structure of the maize inflorescence has been studied. The gross morphology of a series of corn grass cobs seems to support the spiral fusion theory while an examination of the vascular anatomy does not support this theory. The effects of the Cg gene on the ontogeny of corn have been studied on greenhouse grown plants.

#### 4. The vestigial rachilla expression of the Vg gene

Reduction of the floral bracts in Vg corn allows for the expansion of the base of the kernel while reduction of the rachilla makes possible greater expansion in length. Although the floral bracts, of which the glume is the most prominent and lowermost, may present a "stick in the teeth" problem to connoisseurs of corn on the cob, they may be easily washed away from the cut-corn during the commercial canning process. The most valuable expression of the Vg gene now appears to be the feature of deeper kernels via the reduced rachilla. Up to two-thirds of the diameter of the normal cob may be occupied by the rachillas. The crowding of the base of the kernels on a smaller Vg cob necessitates expansion in length. Tests on 44 ears of the normal and Vg forms of one experimental hybrid showed that the Vg ears yielded 14.1% more cut off than did their normal counterparts. This increase in percentage cut off was not effected by change in the outside diameter, but by a reduction in rachilla length.

#### 5. Resistance to blasting of Vg tassels

Resistance to anther blasting is a major obstacle in the development of Vg pollen shedding inbreds. In the moist cool summer of 1951 at Madison most Vg plants with short tassel glumes were good pollen shedders. This was not the case this past summer (1952) which was comparatively hot and dry. The plus modified Vg Oh55 inbred blasted completely while other plus modified lines blasted to varying degrees.

It may be that cool damp areas will be best suited for increasing Vg inbred seed. If the Vg inbred was used as the seed parent, glumeless hybrids could still be produced in dry areas such as Idaho.

The plus modifier genes for the Vg gene are dominant and so are expressed in the  $F_1$  hybrid. Since heterosis tends to stimulate pollen shedding, we should be able to get good glumeless sweet corn hybrids if we can develop good Vg pollen shedding inbreds. The present Vg breeding program includes a series of outcrosses to the heat tolerant tropical corns on the theory that they are also resistant to tassel blasting. Outcrosses have also been made to red and purple anther lines since there is an indication that the dark anther colors aid Vg pollen shedding. This was born out by data collected on a plus modified VgC13 stock which was segregating for anther color.

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1. A heritable somatic mutation in the structure of the endosperm in  
Zea mays L.

Strain No. 103 of our dent variety M-1 has been inbred for 5 years by artificial self-fertilization. In 1938 one selfed plant of inbred 103 developed two different types of kernels on its ear. The kernels appeared to be dent and flint respectively. This unusual ear was 14 cm. long and the flint type kernels were restricted to the upper 6.5 cm. while the kernels on the rest of the ear were of the parental dent type. Kernels from the middle of the flinty as well as of the denty portion of the ear were planted separately and their plants self-fertilized. On the plants which developed from the flinty kernels, ears with the flinty kernel type formed. Some of these ears developed kernels on which a small starchy circle was visible in the upper portion. In the second generation after self-fertilization, plants formed ears which showed segregations for dent and flint kernels. From the kernels of the denty part of the originally mutated ear; plants were obtained on which after selfing, only kernels of the denty type appeared.

From our investigations it follows that before or during the formation of the embryo sack cells in the mutated portion of the ear, a gene mutation from the dent to the flint type occurred. The mother cell in the embryo sack, as well as the two polar nuclei must have had genes for the flinty type of kernel while the pollen on the same plant must have had genes for the denty type of kernel.

2. Heritable proliferation of tassels and vegetative reproduction in  
Zea mays L.

In 1931 I first reported in "Der Zuchter" the occurrence of a heritable proliferation of tassels in certain plants which were offspring of plants with decussated / opposite positioned leaves. Since that time about one thousand such plants have been studied so that now it is possible to present

a short survey of the growth, morphology, and inheritance of the mentioned character. A difference between these and normal plants is detectable as soon as the fourth leaf appears due to the fact that the further growth of the abnormal plants is very slow. In the flowering stage the abnormal plants have a height of 50 to 90 cm. if the tassel, which usually hangs down, is extended. The stalk is about 20 to 40 cm. high and has 4 to 5 nodes. The leaves are about 2 to 3 cm. in width and have a length of from 30 to 50 cm. The largest leaf is at the third node below the tassel. The tassels are about 40 to 60 cm. long and have 28 to 35 nodes. On these nodes are inflorescences of a peculiar form and size. On the base of the tassels are shoots that resemble young maize plants and at the terminal part, very small spikelets are attached. These spikelets lack anthers. Directionally from the top to the base of the tassel there may be found: nearly 50 spikelets (lacking anthers) on a length of about 4 cm., next, approximately 100 spikelets with normal anthers on 5 cm., and then a part of the tassel with more than 100 abnormal spikelets and shoots respectively. In the uppermost shoots, anthers and pistils occur, but near the base of the tassel, the inflorescences in the shoots are often not developed. These shoots have a leaflike organ at the base. This organ has developed from the glume. The next leaves on such shoots show a visible sheath and blade at this stage of development.

Sometimes a scalelike organ occurs between the undifferentiated leaves and those leaves with a differentiated sheath and blade. This scalelike organ has probably developed from the lemmas and paleas. The proliferation of the staminate inflorescence has probably taken place at the time of the formation of the glumes. The glumes have changed into leaves and from the vegetation point a shoot instead of a flower has developed. The second, upper flower has not appeared. The shoots on the lower most nodes have small roots. Such shoots when transplanted to soil, grow into plants of about 120 cm. height, and develop normal tassels. However, these plants usually do not have ears. In some lower shoots of the first mentioned abnormal plants, very small ears are visible. From self-fertilization which normally takes place in such shoots, offspring may be obtained. These offspring are abnormal plants resembling the parental type. Hybridization of normal plants with the proliferating type, through the use of pollen from abnormal plants, results in an  $F_1$  with abnormal plants similar to the defective parent. The abnormal factor is dominant in action. The  $F_2$  consists of abnormal and normal plants in a segregation pattern of nearly 3:1. In spite of crosses with ten maize chromosome testers, data is lacking at this date as to the location of the gene or genes controlling proliferation. In the abnormal plants one abnormally long and one abnormally short chromosome have been found. These chromosomes are probably the product of a reciprocal translocation and are perhaps responsible for the abnormal development of the tassels on the plants described.

A. Tavcar



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IV Seed Stocks. A complete listing of stocks of genes and gene combinations available at Cornell appears in the 1952 Maize News Letter. Subsequent listings will originate from the Illinois station in accordance with the information presented under item 2 of announcements.

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