THE LINKAGE RELATIONS BETWEEN THE FACTORS FOR TUNICATE EAR AND STARCHY-SUGARY ENDOSPERM IN MAIZE¹

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Received December 10, 1920

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INTRODUCTION

At the time the present study was begun more than thirty mutant factors in the corn plant were being investigated, but a surprisingly small number of groups of linked factors had been found. It was, therefore, decided to make a systematic search for linkages by testing each factor in relation to all of the other factors. In this paper are given the results of tests made with tunicate ear, $T_u t_u$, which was chosen as being especially adapted for such a linkage study. In using tunicate ear, a dominant character, it is not necessary to grow F_2 populations to get the recessives to be used in back-crossing the F_1 plants, as any non-tunicate plant recessive for one or more of the other factors involved in the original cross is a double, triple, or multiple recessive.

The original purpose of this investigation was to establish the linkage relations between the factor pair for tunicate ear, $T_u t_u$, and other mutant factors in maize. Later, when it was shown by JONES and GALLASTEGUI

¹ Paper number 85, Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, New York.

(1919) that the factor pair for sugary endosperm, $S_u s_u$, is linked with the factor pair for tunicate ear, $T_u t_u$, this study was extended to include linkage tests involving sugary endosperm and the other mutant characters. At that time all of the material in the cultures of Dr. R. A. EMERSON and Dr. E. G. ANDERSON that was concerned with the linkage relations of sugary endosperm was transferred to the writer. Some of the tests were made by them and the data are entirely theirs. This fact will be indicated as the data are presented.

PREVIOUS LINKAGE STUDIES IN MAIZE

COLLINS and KEMPTON (1912) were the first to record a case of linkage in maize. They presented data which show a linkage between waxy endosperm and aleurone color, although they did not determine which of the aleurone color factors is concerned. BREGGER (1918) reported further evidence on this linkage and showed clearly that it is the C aleurone color factor (EAST and HAYES 1911; EMERSON 1918) that is linked with waxy endosperm. More recently KEMPTON (1919) published data which give additional evidence of the linkage between waxy endosperm and aleurone color. HUTCHISON (1921) has shown that a recessive factor for shrunken endosperm, s_h , and the dominant aleurone color inhibitor, I , are also members of this linkage group.

LINDSTROM (1917) reported the second linkage in maize. He found that the factor pair for golden plant, $G g$, is linked with the $R r$ aleurone factor pair. In a later paper LINDSTROM (1918) presented additional data on this linkage and gave evidence that a second chlorophyll factor pair, $L l$, which produces yellow seedlings when recessive, is also linked with the $R r$ factor pair.

The third linkage recorded in maize was discovered by JONES and GAL-
LASTEGUI (1919) who observed that, when the seeds with starchy and sugary endosperm from a self-pollinated plant heterozygous for both tunicate ear and sugary endosperm were planted separately, the starchy seeds produced a great excess of tunicate plants while the sugary seeds, on the other hand, produced an excess of non-tunicate plants.

It has long been known by EMERSON (1921) that one of the factor pairs for yellow endosperm is linked with the factor pair concerned in the production of purple anthers, $P_1 p_1$.

The factor pair concerned in the production of sun-red plants, $B b$, has been shown by EMERSON (1921) to be linked with the factor pair for liguleless leaf, $L_g l_g$. More recently EMERSON (1920) found that another mutant

factor pair, $T_e t_e$, which produces a wholly pistillate plant when recessive, is linked with the factors for sun-red plant color and liguleless leaf. This type of pistillate plant is known as tassel ear.

EMERSON (1920) has found a second type of pistillate plant which he calls tassel seed ($T_s t_s$). He has shown that tassel seed is wholly different from tassel ear and that it is inherited independently of it. Tassel seed is closely linked with the factor pair for pericarp color, $P p$.

MATERIALS AND METHODS

The pedigree cultures with which this study was begun were kindly furnished by Dr. R. A. EMERSON. Some of the original crosses were made by him in the summer of 1916. These, together with additional material, were transferred to the writer in the spring of 1917. In the course of this study Dr. EMERSON was exceedingly liberal in furnishing material and gave many valuable criticisms and suggestions so that I am especially indebted to him. My constant association with Dr. ANDERSON was also extremely helpful. Both EMERSON and ANDERSON placed freely at my disposal pedigreed plants involving a number of mutant factors, thus making it possible to get a large amount of linkage data from a minimum number of plants. Data on the linkage relations of sugary endosperm with other mutant factors that are from the notes of EMERSON and ANDERSON will be indicated in the tables by prefixing to the pedigree numbers a distinguishing letter. The letter "E" signifies that the data are from the notes of Dr. EMERSON, and the letter "A" refers in like manner to Dr. ANDERSON.

Ordinary cultural methods were used in growing the plants. The seeds were planted in rows with one seed at a place so that notes could be taken on individual plants. In noting the tunicate character although it is nearly always possible to identify the plants by the long glumes and thick tassels, in every case the husks were torn back and the ear examined for the tunicate character.

Back-cross data are used in every test except for the factor pairs for white seedling, $W w$, which is lethal when homozygous recessive, and virescent-white seedling, $V v$, which produces white to yellowish-white seedlings when recessive. A few of the virescent-white seedlings become green and survive, but most of them die in the seedling stage (LINDSTROM 1918).

The probable errors of the ratios were read directly from probable error tables available in the laboratories of the Department of Plant Breeding, CORNELL UNIVERSITY. The probable significance of the deviations in

relation to their probable errors are from the table of PEARL and MINER (1914).

TERMINOLOGY

The following factors were used in the linkage tests reported in this paper:

- A a*, factor pair for anthocyanin pigmentation in the leaves, sheathes, and husks, and for colored aleurone (EMERSON 1918, 1921).
- A_n a_n*, factor pair for semi-dwarf plant with anthers on the ears.
- B b*, factor pair for brown plant color (EMERSON 1921).
- B_l b_l*, factor pair for brown blotches on the leaves.
- C c*, factor pair for colored aleurone (EAST and HAYES 1911; EMERSON 1918).
- C_r c_r*, factor pair which produces a crinkling of the leaves.
- D d*, factor pair for dwarf plant.
- F f*, factor pair for a fine striping in the leaves (LINDSTROM 1918).
- F_l f_l*, factor pair for floury endosperm (EAST and HAYES 1915).
- G g*, factor pair for golden plant (LINDSTROM 1918).
- G_s g_s*, factor pair for green striping of the leaves (LINDSTROM 1918).²
- I i*, factor pair which inhibits the production of aleurone color (EAST and HAYES 1911; EMERSON 1918).
- J j*, factor pair for *japonica* striping of the leaves (LINDSTROM 1918).
- L l*, factor pair for yellow seedling (LINDSTROM 1918).
- L_o l_o*, factor pair for leaves without ligules (EMERSON 1912).
- P p*, factor pair for colored pericarp (EMERSON 1911).
- P_l p_l*, factor pair for purple anthers (EMERSON 1921).
- P_r p_r*, factor pair which produces purple aleurone in the presence of the other aleurone factor pairs (EMERSON 1918).
- R r*, factor pair for red aleurone (EAST and HAYES 1911; EMERSON 1918, 1921).
- R_a r_a*, factor pair for *ramosa* ear (GERNERT 1912).
- S_h s_h*, factor pair for shrunken endosperm (HUTCHISON 1921).
- S_u s_u*, factor pair for sugary endosperm (CORRENS 1901; EAST and HAYES 1911).
- T_e t_e*, factor pair for pistillate plant, tassel ear (EMERSON 1920).
- T_s t_s*, factor pair for pistillate plant, tassel seed (EMERSON 1920).

² LINDSTROM used the symbol *S_l* for this factor but *G_s* is now being used by him and other workers in corn as being the more significant symbol.

$T_u t_u$, factor pair for tunicate ear (COLLINS 1917).

$W w$, factor pair for white seedling (LINDSTROM 1918).

$W_x w_x$, factor pair for waxy endosperm (COLLINS and KEMPTON 1913; BREGGER 1918; KEMPTON 1919).

$Y y$, one of the factor pairs concerned in the production of yellow endosperm (EAST and HAYES 1911; EMERSON 1921).

TUNICATE CHARACTER

The tunicate plants used in this study were all from a common source, having been obtained by Dr. EMERSON from the Department of Farm Crops, CORNELL UNIVERSITY. The plants resembled sufficiently the strain of tunicate plants described and illustrated by COLLINS (1917) as to make a detailed description here unnecessary. The most important characteristic of tunicate plants is that the glumes of the ear develop to such an extent that each kernel is entirely enclosed. The tassel glumes are also longer than those of non-tunicate plants and this gives the tassels a thickened appearance. It is possible to identify tunicate plants by their thickened tassels.

COLLINS (1917) found that the homozygous tunicate plants are sterile and that the ordinary type of tunicate plants is a case of imperfect dominance somewhat analogous to the blue Andalusian fowl. JONES and GALLASTEGUI (1919) reported observations on the inheritance of the tunicate character which confirm the conclusions of COLLINS.

A summary of the back-crosses made in the course of this study shows that of the 12,324 plants noted, 6113 were tunicate and 6211 were non-tunicate. This is a deviation from the 1:1 ratio expected, of 49.0 ± 37.4 plants. A deviation as large as this would be expected to occur about 38 times out of every 100 trials due to the errors of random sampling. These data give further evidence of COLLINS's interpretation.

LINKAGE BETWEEN TUNICATE EAR AND SUGARY ENDOSPERM FACTORS

Attention has already been called to the paper by JONES and GALLASTEGUI (1919) in which it is shown that the factor pair for tunicate ear, $T_u t_u$, is linked with the factor pair for sugary endosperm, $S_u s_u$. The numbers from which this observation was made are small, yet the distribution is clearly different from the ordinary dihybrid ratio which would obtain if the factors assorted independently.

A number of crosses were made between heterozygous tunicate plants with homozygous starchy endosperm and non-tunicate plants with sugary

endosperm. The resulting seeds were all starchy. A small planting was made from each cross and the progenies consisted of tunicate plants and non-tunicate plants in approximately equal numbers. Tunicate plants of these progenies, which had the genetic constitution $T_u t_u S_u s_u$, were back-crossed reciprocally with non-tunicate plants homozygous for sugary endosperm. The results of these back-crosses are given in table 1. The starchy and sugary seeds from these back-crossed ears were planted separately. The starchy seeds in every instance produced an excess of tunicate plants and the sugary seeds produced an excess of normal plants. The parental combinations of these factors tend to be inherited together with a recombination occurring in about 27 percent of the cases in the megasporocytes, and approximately 35 percent in the microsporocytes. The tendency of

TABLE 1
Progenies from back-crosses involving tunicate ear and sugary endosperm.

PEDIGREE NUMBERS	$S_u T_u$	$S_u t_u$	$s_u T_u$	$s_u t_u$	PERCENT CROSSING OVER
$T_u t_u S_u s_u \times t_u t_u S_u s_u$					
196-10 $\times$ 192-4.....	89	19	31	98	21.10
198-9 $\times$ 192-3.....	147	57	63	127	30.46
140-4 $\times$ E7595-11.....	90	35	24	70	26.94
Totals.....	326	111	118	295	26.94
$t_u t_u s_u s_u \times T_u t_u S_u s_u$					
E7595-11 $\times$ 140-4.....	26	8	19	25	34.62
E8575-4 $\times$ 201-7.....	78	56	32	86	34.92
Totals.....	104	64	51	111	34.85

these factors to remain together in inheritance can be explained by assuming that they are located in the same chromosome and that the recombinations are the result of crossing over. In megasporogenesis the amount of crossing over in the plants tested varied from 21.1 to 30.5 percent while in microsporogenesis the amount of crossing over in both plants tested was approximately the same, though about 8 percent higher than in megasporogenesis.

The data reported by JONES and GALLASTEGUI (1919), with only about 8 percent of crossing over, indicate a much closer linkage between the factors for tunicate ear and sugary endosperm than is shown by any of the back-cross data here presented. These investigators call attention to the fact that the plants from which their data were taken were grown in hills, and that when classifying them it was not always possible to tell which was plant and which was sucker as the plants suckered profusely. It is not

impossible that the same plants may have been counted more than once. Whether this source of error together with the small number of F_2 plants grown by them is sufficient to account for the difference between their results and the results of this study, or whether this wide variation in linkage is due to other causes, is not known.

VARIATION IN LINKAGE

These data indicate that crossing over is not absolutely fixed in amount, but varies, due apparently to fluctuations in environmental conditions, or to internal changes in the mechanism of crossing over itself. MORGAN (1919) has recently given a summary of the variation in crossing over in *Drosophila melanogaster*. It has been found that in this organism crossing over is affected both by environmental conditions and genetical factors carried by the chromosomes themselves. In plants crossing over occurs in the production of both megaspores and microspores and apparently more frequently in the latter.

TABLE 2
Statistical study of Altenburg's data on Primula sinensis. After GOWEN (1919).

	MALE HETERO- ZYGOUS	FEMALE HETERO- ZYGOUS	MALE PERCENT	FEMALE PERCENT	DIFFERENCE	DIFF P. E. Diff.
Non-crossovers.....	1829	266	55.56	67.81	12.30 ± 1.7	7.2
First single.....	1053	107	31.97	27.30	4.69 ± 1.4	3.2
Second single.....	325	11	9.87	2.81	7.07 ± 0.9	7.4
Double.....	85	8				

ALTENBURG (1916) published back-cross data on factor linkages in *Primula sinensis*, which indicate that crossing over in microsporogenesis is consistently higher than in megasporogenesis. GOWEN (1919) made a statistical study of ALTENBURG's data, a summary of which is given in table 2. The deviations range from 3.2 to 7.4 times as large as their probable errors. GOWEN points out that deviations as large as these are not without significance.

The writer has made a similar statistical study of differences in the amount of crossing over in the microsporocytes and megasporocytes in maize with the results shown in table 3. The data reported in this paper on the relation between tunicate ear and sugary endosperm indicate that the average amount of crossing over in the microsporocytes is 7.9 ± 2.0 percent higher than in the megasporocytes. The odds against a deviation as great as this being due to the errors of random sampling are about 135 to 1, and may be considered significant. A summary of BREGGER's (1918)

data on the linkage between waxy endosperm and the *C* aleurone factor shows that crossing over was 2.46 ± 1.11 percent higher in microsporogenesis than in megasporogenesis. In this case the deviation is approximately twice as large as the probable error. A difference of this magnitude would be expected about once in five trials due to errors of random sampling and is usually considered not significant. It is important to note, however, that it is in microsporogenesis that the higher percentage of crossing over occurs. The plants heterozygous for waxy endosperm and the *C* aleurone factor were grown by BREGGER in the summer of 1916 while the plants heterozygous for tunicate ear and sugary endosperm were grown in the summer of 1918, and in a different part of the garden. It

TABLE 3
Variation in linkage in maize.

FACTORS INVOLVED	FEMALE HETERO- ZYGOUS	MALE HETERO- ZYGOUS	FEMALE PERCENT	MALE PERCENT	DIFFERENCE	$\frac{\text{DIFF.}}{\text{P. E. Diff.}}$
<i>T_u-s_u</i>						
Non-crossovers.....	621	215	73.06	65.15	7.91 ± 1.99	3.97
Crossovers.....	229	115	26.94	34.85		
<i>C-w_x</i>						
Non-crossovers.....	1445	832	74.25	71.78	2.46 ± 1.11	2.22
Crossovers.....	501	327	25.75	28.22		

TABLE 4

	<i>S_u T_u</i>	<i>S_u t_u</i>	<i>s_u T_u</i>	<i>s_u t_u</i>	PERCENT CROSSEOVERS
<i>t_u t_u S_u S_u × T_u t_u S_u S_u</i>					
E8575-4 × 140-4.....	26	8	19	25	34.6 ± 3.8
<i>T_u t_u S_u S_u × t_u t_u S_u S_u</i>					
140-4 × E8575-4.....	90	35	24	70	26.9 ± 2.7
Difference.....					7.7 ± 4.4

is evident that the environmental conditions were different for these two lots of plants. Neither can the plants which were grown the same season be considered to have been exposed to identical environmental conditions, as the seeds were planted without regard to soil differences. Whether this variation in linkage is due to environmental conditions or to genes in the chromosomes themselves is at present not known.

Perhaps the best measure of the difference in the amount of crossing over in the microsporocytes and megasporocytes could be obtained by testing both the pollen and ovules of individual plants. Incidentally one plant heterozygous for tunicate ear and sugary endosperm was tested in this manner. The pedigree number of this plant is 140-4. Plant E8575-4

was of the genetic constitution $t_u t_u s_u s_u$ and was used to test the pollen and ovules of plant 140-4. The reciprocal crosses of these plants are given in table 4. It is seen that crossing over was 7.7 ± 4.4 percent higher in the microsporocytes than in the megasporocytes. Unfortunately the number of plants grown from these back-crosses is small.

LINKAGE TESTS BETWEEN THE T_u - S_u GROUP AND OTHER GROUPS OF LINKED FACTORS

Tests involving T_u and s_u with the C - w_x - s_h - I group

Factors T_u and C

Plants heterozygous for tunicate ear and sugary endosperm were back-crossed to C aleurone testers of the constitution $A A c c R R t_u t_u$. The progenies from these back-crosses are given in table 5. The deviation from the 1:1 ratio expected for independent inheritance is only 1.0 ± 10.1 plants which is a very close fit.

TABLE 5
Progeny from the back-cross $T_u t_u C c \times t_u t_u c c$.

PEDIGREE NUMBERS	$S_u T_u$	$S_u t_u$	$s_u T_u$	$s_u t_u$
362-365.....	31	32	36	36
366-367.....	67	64	83	84
368-369.....	53	53	54	58
370-371.....	54	68	60	69
Totals.....	205	217	233	247

Factors S_u and C

Extensive tests have been made by EMERSON and ANDERSON between starchy-sugary endosperm and the C aleurone factor. Heterozygous plants from the cross $S_u S_u C C \times s_u s_u c c$ were back-crossed to sugary C testers of the constitution $A A c c R R s_u s_u$. The plants grown from these back-crosses are given in table 6 under coupling series. This represents a coupling series as both dominant factors were associated in one of the parental plants. In the second part of table 6 are given the results of back-crossing heterozygous plants from the cross $S_u S_u c c \times s_u s_u C C$ to sugary C testers. As each parent contributed one of the dominant factors these data may be considered a repulsion series. In the coupling series there was a total of 2335 seeds. Of these 1185 had the parental combina-

tion and 1150 the new combinations of the factors, a deviation of 17.5 ± 16.3 from the 1:1 ratio expected. There was a total of 2067 seeds in the repulsion series of which 1027 had the parental combinations while 1040 had the factors in new combinations. This is a deviation from a 1:1 ratio of only 6.5 ± 15.3 . In both cases the fit is very close.

TABLE 6
Progeny from the back-cross $S_u s_u C c \times s_u s_u c c$.

PEDIGREE NUMBERS	$C S_u$	$C s_u$	$c S_u$	$c s_u$
Coupling series				
E7689-2 $\times$ E7509-6.....	115	82	117	84
E4734-13 $\times$ E4717-32.....	58	54	53	48
E8566-15 $\times$ E8479-1.....	91	127	101	134
E8566-7 $\times$ E8479-1.....	113	121	103	137
E7507-10 $\times$ A196-1.....	33	31	41	36
E7507-2 $\times$ A438-5.....	97	96	81	120
E8610-2 $\times$ E8567-1.....	65	72	71	54
Totals.....	572	583	567	613
Repulsion series				
E2878-1 $\times$ E2884-50.....	28	14	26	28
E2879-4 $\times$ E2884-68.....	34	23	16	24
E2881-4 $\times$ E2884-64.....	17	23	18	16
E2882-6 $\times$ E2884-43.....	96	66	74	62
E2882-9 $\times$ E2884-36.....	41	42	38	50
E2882-2 $\times$ E2884-43.....	66	39	95	28
E2883-7 $\times$ E2885-6.....	85	71	86	106
E8611-1 $\times$ E8567-1.....	88	97	85	90
E8611-3 $\times$ E8567-4.....	87	101	113	94
Totals.....	542	476	551	498

Factors T_u and W_x

A plant homozygous for waxy endosperm was crossed with a heterozygous tunicate plant with starchy endosperm. All of the resulting seeds were starchy, which, when planted produced tunicate and non-tunicate plants in approximately equal numbers. One of the tunicate plants of this progeny was back-crossed to a normal plant with waxy endosperm. The ear produced from this cross contained 104 starchy and 107 waxy seeds. These seeds were planted separately the following year but the germination was exceedingly poor. None of the waxy and only a small percentage of the starchy seeds produced plants. Of the 18 plants grown, 8 were tunicate and 10 normal.

Factors T_u and S_h

It was observed that the back-crossed ear in the tunicate-waxy test also segregated for shrunken endosperm. Of the 104 starchy seeds, 34 were noted as shrunken and 70 as normal. Of the 107 waxy seeds 80 were shrunken and only 27 were normal non-shrunken. Because of the immaturity of the seeds their separation into the various classes was not altogether satisfactory, but the numbers are distinctly different from the 1:1:1:1 ratio expected in independent inheritance. These data indicate a linkage between waxy endosperm and shrunken endosperm with about 29 percent of crossing over. The shrunken and normal seeds were planted separately. From the normal seeds there were produced 5 tunicate plants and 7 normal plants and from the shrunken seeds there were 3 tunicate plants and 3 normal plants.

Factors S_u and I

Several plants heterozygous for the factor pairs for starchy-sugary endosperm and the dominant aleurone color inhibitor were back-crossed by ANDERSON to plants having sugary endosperm and recessive for the aleurone-color inhibitor. The progenies from these back-crosses are given in table 7. There were 340 kernels with factors combined as in the parents and 310 kernels with the recombination of the factors. The deviation from a 1:1 ratio is 15.0 ± 8.6 .

TABLE 7
Progeny from the back-cross, $S_u s_u I i \times s_u s_u i i$

PEDIGREE NUMBERS	$S_u I$	$s_u I$	$S_u i$	$s_u i$
A890-8 $\times$ A889-4.....	34	14	36	29
A890-9 $\times$ A888-4.....	79	58	77	58
A891-7 $\times$ A888-2.....	75	56	69	65
Totals.....	188	128	182	152

So far as tests have been made the data indicate that the factors for tunicate ear and sugary endosperm are inherited independently of the factors belonging to the $C-W_x-S_h-I$ linkage group.

*Tests involving T_u and S_u with the G-R-L group*Factors T_u and G

Back-crosses involving tunicate ear and golden plant gave a total of 349 green and 314 golden plants as shown in table 8. Of the green plants

173 were tunicate and 176 non-tunicate, a fairly good 1:1 ratio. Of the golden plants 147 were tunicate and 167 non-tunicate, also a fair approximation to the equality expected. Classes one and four, which represent

TABLE 8
Progeny from the back-cross $T_u t_u G g \times t_u t_u g g$

PEDIGREE NUMBERS	$G T_u$	$G t_u$	$g T_u$	$g t_u$
406.....	47	40	39	46
407.....	31	30	15	23
408.....	74	76	62	63
90.....	21	30	31	35
Totals.....	173	176	147	167

the parental combinations of the factors, have a total of 340 plants while classes two and three, with the new combinations of the factors, have a total of 323 plants. The deviation from the 1:1 ratio expected in independent inheritance is 8.5 ± 8.6 . A deviation as large as this would be expected once in every two trials.

Factors T_u and R

A number of plants heterozygous for tunicate ear and the R aleurone factor were back-crossed to R aleurone testers of the constitution $A A C C r r t_u t_u$. The progenies of these back-crosses are given in table 9.

TABLE 9
Progeny from the back-cross $T_u t_u R r \times t_u t_u r r$

PEDIGREE NUMBERS	$R T_u$	$R t_u$	$r T_u$	$r t_u$
429-430.....	4	4	2	1
451-433.....	54	52	43	45
431-436.....	56	62	53	72
437-438.....	39	50	46	51
Totals.....	153	168	149	169

Colored and colorless seeds in approximately equal numbers were produced as expected. From the colored seeds 321 plants were grown, of which 153 were tunicate and 168 non-tunicate. The colorless seeds produced 149 tunicate and 169 non-tunicate plants. In each case the ratios are fairly close to the equality expected. Of these progenies 322 plants had the factors in the same combinations as the parents and 317 plants were the result of the new combinations of the factors involved. This is a deviation

from the 1:1 ratio expected of 2.5 ± 8.5 plants, which is an exceedingly close fit.

Factors S_u and R

A number of back-crosses involving sugary endosperm and the R aleurone factor were made by EMERSON and ANDERSON. The progenies of these back-crosses are given in table 10. The back-crossed ears produced a total of 1610 starchy and 1368 sugary seeds. The starchy seeds were

TABLE 10
Progeny from the back-cross $S_u s_u R r \times s_u s_u r r$

PEDIGREE NUMBERS	$S_u R$	$S_u r$	$s_u R$	$s_u r$
E2878-1 $\times$ E2884-50.....	21	31	46	24
E2879-4 $\times$ E2884-68.....	22	17	19	23
E2882-6 $\times$ E2884-43.....	91	76	47	66
E2882-9 $\times$ E2884-36.....	30	36	34	30
E2882-2 $\times$ E2884-43.....	68	54	13	28
E6653-2 $\times$ E6652-4.....	17	12	4	6
E6653-7 $\times$ E6652-3.....	82	75	57	69
E2883-7 $\times$ E2885-6.....	19	43	17	30
A273-7 $\times$ E7507-9.....	47	62	37	33
A273-10 $\times$ E7507-7.....	25	26	26	19
A266-4 $\times$ A273-7.....	29	29	2	3
E8483-5 $\times$ E8767-4.....	58	37	49	40
E8483-6 $\times$ E8572-4.....	42	28	32	28
E8578-1 $\times$ E8483-3.....	75	72	89	94
E8578-15 $\times$ E8483-2.....	62	64	75	71
E8611-9 $\times$ E8575-4.....	89	106	91	105
E8611-4 $\times$ E8575-4.....	28	37	27	34
Totals.....	805	805	665	703

colored and colorless in an exactly 1:1 ratio, there being 805 of each. Of the sugary seeds, 665 were colored and 703 colorless, a fairly close approximation to a 1:1 ratio. Of the total number of seeds 1508 had the factors combined as in the parents and 1470 had the factors in the new combinations. This is a deviation from the 1:1 ratio expected of only 19.0 ± 18.4 individuals. A deviation as great as this would be expected to occur once in every two trials due to the errors of random sampling.

The data from these tests give no indication of a linkage between either T_u or S_u and the members of the $G-R-L$ linkage group.

*Tests involving T_u and S_u with the $B-L_0-T_e$ group*Factors T_u and B

A number of sun-red plants of the constitution $T_u t_u B b$ were back-crossed to dilute sun-red plants with the factorial constitution $t_u t_u b b$. These back-crosses gave a total of 1405 plants as shown in table 11. Of these 692 had the parental combinations of the factors while the two new classes resulting from the recombination of factors had a total of 713 plants. This is a deviation of 10.5 ± 12.6 from a 1:1 ratio expected for factors that are inherited independently of each other.

TABLE 11
Progeny from the back-cross $T_u t_u B b \times t_u t_u b b$.

PEDIGREE NUMBERS	$B T_u$	$B t_u$	$b T_u$	$b t_u$
362-365.....	30	28	37	30
366-367.....	70	71	80	76
126.....	8	3	3	4
424-426.....	83	56	84	94
406.....	33	40	34	18
408.....	23	14	25	29
93.....	15	14	21	9
449-450.....	40	21	48	12
460-463.....	51	75	59	67
Totals.....	353	322	391	339

Factors S_u and B

Other sun-red plants known to be heterozygous for the factor pairs $B b$ and $S_u s_u$ were back-crossed by EMERSON and ANDERSON to plants having the genetic constitution $s_u s_u b b$. The results of these back-crosses are given in table 12. Starchy and sugary seeds were produced in approxi-

TABLE 12
Progeny from the back-cross $S_u s_u B b \times s_u s_u b b$.

PEDIGREE NUMBERS	$S_u B$	$S_u b$	$s_u B$	$s_u b$
F8214-E8217.....	36	39	17	17
E8218-E8221.....	45	65	34	33
E8222-E8225.....	54	36	18	15
E7347-E7348.....	69	88	57	69
A793-A796.....	75	89	61	57
Totals.....	279	317	187	191

mately equal numbers. From the table it may be seen that the sugary seeds produced only 378 plants while the starchy seeds produced 596 plants. This difference is due to the much lower percentage of germination of the sugary seeds. Both starchy and sugary seeds gave sun-red and green plants in fairly equal numbers. Of these plants 470 had the parental combinations of the factors and 504 the factors in the new combinations. This is a deviation of 17.0 ± 10.4 from equality expected for independently inherited factors.

Factors T_u and L_g

Many of the back-crosses made in the course of this study involved tunicate ear and liguleless leaf. Some of these back-cross progenies are given in table 13. There is a total of 1692 plants and for every class the

TABLE 13
Progeny from the back-cross $T_u t_u L_g l_g \times t_u t_u l_g l_g$.

PEDIGREE NUMBERS	$L_g T_u$	$L_g t_u$	$l_g T_u$	$l_g t_u$
494.....	43	49	50	35
496.....	28	20	21	19
495.....	58	59	73	61
492.....	7	10	7	6
493.....	14	16	7	13
489.....	18	33	34	32
491.....	20	25	22	14
490.....	59	45	62	67
488.....	26	48	33	41
418.....	8	11	6	16
419.....	5	4	5	3
372.....	91	75	65	76
373-374.....	17	5	9	7
375.....	34	28	31	21
Totals.....	428	428	425	411

observed number is very close to the number expected for independent inheritance. There were 839 plants with the parental combinations and 853 with the new combinations of these factors. This is a deviation of 7.0 ± 13.9 from the 1:1 ratio expected. This is a close fit and indicates that these factor pairs are not linked.

Factors S_u and L_g

Several tests between the factor pairs $S_u s_u$ and $L_g l_g$ were made by EMERSON and ANDERSON. The progenies of these back-crosses are listed in

table 14. The starchy seeds produced 683 plants with normal leaves and 652 plants with leaves without ligules. The sugary seeds produced 376 plants with normal leaves and 379 plants with liguleless leaves. In each case the numbers closely approach the 1:1 ratio expected. Of the total number of plants 1062 had the same combinations of these factors as the parents and 1028 were the result of the new combinations of factors. This is a deviation of only 17.0 ± 15.4 from equality and apparently the factors for sugary endosperm and liguleless leaf are not linked.

TABLE 14
Progeny from the back-cross $S_u s_u L_g l_g \times s_u s_u l_g l_g$.

PEDIGREE NUMBERS	$S_u L_g$	$S_u l_g$	$s_u L_g$	$s_u l_g$
A395-1 $\times$ E7317-6.....	90	77	61	70
A395-8 $\times$ E7317-2.....	20	25	27	21
A395-9 $\times$ E7317-5.....	111	95	89	79
E7317-6 $\times$ E7318-4.....	61	63	40	40
E7318-4 $\times$ E7317-6.....	84	81	56	47
E7318-1 $\times$ E7317-4.....	63	58	36	38
E7316-4 $\times$ E7317-5.....	30	28	9	6
E7316-5 $\times$ E7317-5.....	32	25	7	13
E7316-6 $\times$ E7317-5.....	65	52	15	26
E7316-6 $\times$ E7322-4.....	34	44	7	7
E7322-4 $\times$ E7317-6.....	30	32	5	4
E7322-3 $\times$ E7317-4.....	63	72	24	28
Totals.....	683	652	376	379

The data from these tests indicate that tunicate ear and sugary endosperm are inherited independently of the $B-L_g-T_e$ linkage group.

Tests involving T_u and S_u with the $P-T_e$ group

Factors S_u and P

Several plants heterozygous for starchy-sugary endosperm and pericarp color from the cross $S_u S_u P P \times s_u s_u p p$ were back-crossed by EMERSON and ANDERSON to plants with sugary endosperm and colorless pericarp. The progenies of these back-crosses are given in table 15. From the starchy seeds were grown 417 plants. Of these 205 had colored and 212 colorless pericarp which approaches closely a 1:1 ratio. Of the 289 plants grown from the sugary seeds 144 had colored and 145 colorless pericarp which is almost exactly a 1:1 ratio. There was a total of 350 individuals with the parental factor combinations and 356 with the factors in new combinations. This is a deviation of only 3.0 ± 9.0 from equality and indicates that these factor pairs are inherited independently.

TABLE 15
Progeny from the back-cross $S_u s_u P p \times s_u s_u p p$.

PEDIGREE NUMBERS	$S_u P$	$S_u p$	$s_u P$	$s_u p$
E6653-2 $\times$ E6652-4.....	15	12	6	3
A395-1 $\times$ E7317-60.....	75	78	56	72
A395-8 $\times$ E7317-2.....	25	20	20	28
A395-9 $\times$ E7317-5.....	90	102	62	42
Totals.....	205	212	144	145

Factors T_u and P

A number of crosses made for other tests involved tunicate ear and variegated pericarp color and a few of such heterozygous plants were back-crossed with non-tunicate plants having colorless pericarp. From these back-crossed ears were grown 1194 plants and of these 582 were tunicate and 612 non-tunicate, as shown in table 16. The tunicate plants were not noted for pericarp color as the variegation is sometimes limited to a few seeds, or even a single seed, and it would have been necessary

TABLE 16
Progeny from the back-cross $T_u t_u P p \times t_u t_u p p$.

PEDIGREE NUMBERS	$T_u P + T_u p$	$t_u P$	$t_u p$
488.....	59	35	50
489.....	52	21	45
490.....	121	64	58
491.....	42	23	22
492.....	14	5	10
493.....	21	21	12
494.....	93	38	48
495.....	131	56	64
496.....	49	13	27
Totals.....	582	276	336

to husk out and examine every seed to make sure that a given ear had colorless and not variegated pericarp. Of the non-tunicate plants 276 were noted as having pericarp color and 336 as having colorless pericarp. This is a deviation of 30.0 ± 8.3 from equality. The separation of the non-tunicate plants into classes with and without pericarp color was made on the plants in the field on a very cold day and it is possible that this wide deviation is due to having noted some of the exceedingly light variegated ears as colorless.

No tests have yet been made involving tunicate ear and sugary endosperm with tassel seed.

Tests involving T_u and S_u with the S_m - Y - P_l group

Factors T_u and P_l

Several plants heterozygous for tunicate ear and the plant-color factor pair, $P_l p_l$, were back-crossed to non-tunicate sun-red plants of the genetic constitution $t_u t_u p_l p_l$. The progenies of these back-crosses are given in table 17. The classes representing the parental combinations of these factors include 172 plants, while in the two classes with the new combinations of the factors there are 181 individuals. This is a deviation of only 4.5 ± 6.2 from a 1:1 ratio and indicates the independence of these factor pairs.

TABLE 17
Progeny from the back-cross $T_u t_u P_l p_l \times t_u t_u p_l p_l$.

PEDIGREE NUMBERS	$T_u P_l$	$t_u P_l$	$T_u p_l$	$t_u p_l$
397-398.....	9	14	16	14
421.....	46	64	59	76
422-423.....	11	11	11	11
429-430.....	2	4	2	3
Totals.....	68	93	88	104

Factors S_u and P_l

A number of plants heterozygous for starchy-sugary endosperm and the purpling plant-color factor pair, $P_l p_l$, were back-crossed by EMERSON and ANDERSON to dilute sun-red plants with sugary endosperm. The progenies of these back-crosses consisted of 557 dilute purple and 555

TABLE 18
Progeny from the back-cross $S_u s_u P_l p_l \times s_u s_u p_l p_l$.

PEDIGREE NUMBERS	$S_u P_l$	$S_u p_l$	$s_u P_l$	$s_u p_l$
E7317-6 $\times$ E7322-4.....	16	19	2	3
E7322-4 $\times$ E7317-6.....	19	16	4	4
E7322-5 $\times$ E7317-4.....	28	35	19	18
A273-7 $\times$ E7507-9.....	110	105	70	69
A273-10 $\times$ E7507-7.....	55	48	66	70
E7507-2 $\times$ A438-5.....	69	67	71	65
E7509-25 $\times$ A273-2.....	16	17	12	19
Totals.....	313	307	244	248

dilute sun-red plants. Of these plants 561 had the parental combinations and 551 had the recombinations of the factor pairs involved. This is a deviation of 5.0 ± 11.2 from equality that obtains when the factor pairs are inherited independently. These results are given in table 18.

Tests involving T_u and S_u with the A a factor pair

The factor pair for anthocyanin pigment, A a , is concerned in the production of color in the leaves and stem of the corn plant, and also in the production of color in the aleurone grains of its seeds, as shown by EMERSON (1918, 1921). EMERSON and ANDERSON have tested this factor pair with the other groups of linked factors and it seems to be independent of them.

Factors T_u and A

A sun-red plant of the genetic constitution $T_u t_u A A$ was crossed with a brown plant which had the constitution $t_u t_u a a$ (EMERSON 1921). The F_1 plants were all purple as expected. One of these purple plants, heterozygous for tunicate ear and the anthocyanin factor, was back-crossed with a brown non-tunicate plant. In the progeny there were 35 tunicate plants and 39 non-tunicate plants. Eighteen of the tunicate plants were purple and 17 were brown, and of the non-tunicate plants 23 were purple and 16 brown. The numbers are small but they suggest the 1:1 ratio expected for factors that are inherited independently.

Factors S_u and A

A plant heterozygous for both sugary endosperm and the A a plant- and aleurone-color factor pair was back-crossed by EMERSON to a plant recessive for these factors. The resulting ear contained 149 starchy and 165 sugary seeds. Of the starchy seeds 79 were colored, that is, they carried the A factor, and 70 lacked this factor but carried its allelomorph, a , and were colorless. In like manner 87 of the sugary seeds were colored and 78 were colorless. There are just as many seeds with the parental combinations of the factors as there are with the factors in the new combinations. It is quite probable that these factors are inherited independently.

LINKAGE TESTS BETWEEN THE T_u - S_u LINKAGE GROUP AND FACTORS WHOSE
LINKAGE RELATIONS ARE NOT YET DEFINITELY ESTABLISHED

Tests involving T_u and S_u with anther ear, $A_n a_n$

Factors T_u and A_n

Several plants heterozygous for tunicate ear and anther ear were back-crossed to non-tunicate anther-ear plants. The progenies of these back-crosses are given in table 19. Of the 464 plants grown, 217 had the parental

TABLE 19
Progeny from the back-cross $T_u t_u A_n a_n \times t_u t_u a_n a_n$.

PEDIGREE NUMBERS	$A_n T_u$	$A_n t_u$	$a_n T_u$	$a_n t_u$
358.....	61	92	70	77
359.....	43	48	29	27
361.....	5	4	4	4
Totals.....	109	144	103	108

combinations of the factors, while 247 resulted from the recombinations of the factors. This is a deviation from equality of 15.0 ± 7.3 plants and makes it appear that these factor pairs are inherited independently.

Tests involving T_u and S_u with blotched leaf, $B_l b_l$

Factors S_u and B_l

Two plants heterozygous for starchy-sugary endosperm and blotched leaf were back-crossed with plants homozygous for sugary endosperm and blotched leaf. As may be seen in table 20 there were 161 plants with the

TABLE 20
Progeny from the back-cross $S_u s_u B_l b_l \times s_u s_u b_l b_l$.

PEDIGREE NUMBERS	$S_u B_l$	$S_u b_l$	$s_u B_l$	$s_u b_l$
E6653-2 $\times$ E6652-4.....	19	10	5	5
E6653-7 $\times$ E6652-3.....	82	75	71	55
Totals.....	101	85	76	60

parental combinations and the same number of plants with the factors concerned in the new combinations. These data indicate that these factors are inherited independently. No tests were made involving tunicate ear and blotched leaf.

Tests involving T_u and S_u with crinkly leaf, C_r c_r Factors T_u and C_r

A number of plants heterozygous for tunicate ear and crinkly leaf were back-crossed to non-tunicate plants with crinkly leaves. The progenies of these back-crosses are given in table 21 where it will be seen that more plants were noted as non-crinkly than as crinkly. This is doubtless due to the fact that often the crinkly character is not very distinct and conse-

TABLE 21
Progeny from the back-cross $T_u t_u C_r c_r \times t_u t_u c_r c_r$.

PEDIGREE NUMBERS	$C_r T_u$	$C_r t_u$	$t_r T_u$	$c_r t_u$
372.....	93	82	63	68
375.....	45	38	20	11
Totals.....	138	120	83	79

quently some crinkly plants are classed as normal plants. Of the plants classed as normal, 138 were tunicate and 120 non-tunicate. Of those classed as crinkly 83 were tunicate and 79 non-tunicate. In each case the numbers approach a 1:1 ratio. Of the total progeny 217 were noted as having the parental combinations of the factors and 203 as the result of the recombinations of factors. The deviation from equality, which obtains or is approached when factors are independent, is 7.0 ± 6.9 and is considered a good fit.

Factors S_u and C_r

Tests were also made between sugary endosperm and crinkly leaves by EMERSON and the writer. Plants heterozygous for both of these factors were back-crossed with crinkly plants grown from sugary seeds. The progenies of these back-crosses are given in table 22. Fewer plants were classed as crinkly than as normal. Of the 392 plants grown from starchy

TABLE 22
Progeny from the back-cross $S_u s_u C_r c_r \times s_u s_u c_r c_r$.

PEDIGREE NUMBERS	$S_u C_r$	$S_u c_r$	$s_u C_r$	$s_u c_r$
501-504.....	50	40	33	25
525-528.....	64	60	64	34
529-532.....	96	82	91	66
Totals.....	210	182	188	125

seeds 210 were noted as normal and 182 as crinkly. The sugary seeds produced 313 plants of which 188 were noted as normal and 125 as crinkly. The total progeny consisted of 705 plants and 335 of them had the parental combination of factors while 370 were noted as having the factors in the new combinations. This is a deviation from equality of 17.5 ± 9.0 and may be considered a good fit. In these tests the data indicate that the factor pair for crinkly leaf does not belong to the T_u - S_u linkage group.

Tests involving T_u and S_u with dwarf plant, $D d$

Factors T_u and D

A number of back-crosses involving tunicate ear and the plant character called dwarf, $D d$, gave the progenies listed in table 23. Of the 485 plants

TABLE 23
Progeny from the back-cross $T_u t_u D d \times t_u t_u d d$.

PEDIGREE NUMBERS	$D T_u$	$D t_u$	$d T_u$	$d t_u$
376.....	6	10	14	9
377.....	4	2	1	1
378.....	6	6	2	2
379.....	6	8	6	1
380-381.....	63	53	34	24
382-383.....	14	18	10	11
384-385.....	26	21	11	7
388.....	13	15	7	7
389-390.....	17	10	2	8
391.....	6	10	2	2
Totals.....	161	153	89	72

in these progenies 314 were normal and 171 were dwarf. This very wide deviation from a 1:1 ratio is due to the failure of many dwarf plants to grow to maturity under field conditions. Only under the most favorable conditions is it possible to grow all of the dwarf plants to maturity. The normal plants were tunicate and non-tunicate in approximately equal numbers, there being 161 of the former and 153 of the latter. Of the dwarf plants 89 were tunicate and 72 non-tunicate. This is a rather wide deviation from a 1:1 ratio but the numbers are small. There were 233 plants with the parental combinations and 242 with the recombinations of these factor pairs. This is a deviation of only 4.5 ± 7.3 from a 1:1 ratio, and indicates that the factor pairs for tunicate ear and dwarf plant are not linked.

Tests were also made involving sugary endosperm and dwarf plant but these data are not available at present. The data indicate, however, that sugary endosperm and dwarf plant are inherited independently.

Tests involving T_u and S_u with fine striping, $F f$

Factors T_u and F

Back-crosses involving tunicate ear and the chlorophyll pattern called fine striping gave the progenies listed in table 24. There was a total of

TABLE 24
Progeny from the back-cross $T_u t_u F f \times t_u t_u f f$.

PEDIGREE NUMBERS	$F T_u$	$F t_u$	$f T_u$	$f t_u$
391a.....	29	34	33	17
391b.....	24	33	24	19
392.....	61	48	53	35
393.....	64	41	55	65
394-395.....	34	20	23	21
Totals.....	212.	176	188	157

369 plants with the parental combinations and 364 with the recombinations of these factor pairs. This is a deviation of only 2.5 ± 9.1 from the equality expected when the factors tested are not linked.

No tests were made involving sugary endosperm with fine striping.

Tests involving T_u and S_u with floury endosperm, $F_1 f_1$

Factors T_u and F_1

A number of back-crosses involving tunicate ear and floury endosperm gave the results shown in table 25. Both horny and floury seeds were

TABLE 25
Progeny from the back-cross $T_u t_u F_1 f_1 \times t_u t_u F_1 f_1$.

PEDIGREE NUMBERS	$F_1 T_u$	$F_1 t_u$	$f_1 T_u$	$f_1 t_u$
397-398.....	20	21	3	9
399-403.....	24	24	18	20
404-405.....	12	22	21	26
Totals.....	56	67	42	55

produced on tunicate and non-tunicate plants in approximately equal numbers. The two classes having the parental combinations of these

factor pairs include 111 plants and the classes with the factor recombinations have a total of 109 plants. This is a deviation of only 1.0 ± 5.0 from a 1:1 ratio and indicates that these factor pairs are inherited independently.

No tests were made involving sugary endosperm with floury endosperm.

Tests involving T_u and S_u with japonica striping, $J j$

Factors T_u and J

A number of plants heterozygous for tunicate ear and the *japonica* chlorophyll pattern (LINDSTROM 1918) were back-crossed with non-tunicate, *japonica*-striped plants. The progenies from these back-crosses are given in table 26. Of the total 341 plants were classed as green and 234 as *japonica*-striped. This deficiency in *japonica* plants is doubtless due to the fact that in some plants the *japonica* character is so much reduced that it is represented by a mere line or splash and such plants are easily overlooked, and classed as green. It is possible that in taking these data some of the plants were inconspicuously striped and were noted as green. Both green and *japonica* plants show a good 1:1 ratio of tunicate and non-tunicate plants. Of the total progenies 293 plants had the parental combinations of the factor pairs and 282 resulted from factor recombinations. This is a deviation of 5.5 ± 8.1 from equality and indicates that tunicate ear and *japonica* striping are inherited independently.

Tests involving sugary endosperm and *japonica* striping were not made.

Tests involving T_u and S_u with purple aleurone, $P_r p_r$

Factors T_u and P_r

Two plants heterozygous for tunicate ear and purple aleurone were back-crossed with non-tunicate plants with homozygous red aleurone. Ears were produced with purple and red seeds in approximately equal numbers. From the purple seeds were grown 72 tunicate and 70 non-tunicate plants and from the red seeds 80 tunicate and 70 non-tunicate plants were produced, a good 1:1 ratio in each case. Of the total progenies 142 had the parental combination of factors and 150 the factors in recombinations. This is a deviation of 4.0 ± 5.8 from equality and indicates factor independence.

Factors S_u and P_r

A single plant heterozygous for sugary endosperm and the purple aleurone factor was back-crossed by Dr. EMERSON to a homozygous sugary plant

with red aleurone. There were produced 166 purple starchy and 188 red starchy seeds and 89 purple sugary and 88 red sugary seeds. Both the starchy and sugary seeds were purple and red in approximately equal

TABLE 26
Progeny from the back-cross $T_u t_u J j \times t_u t_u j j$.

PEDIGREE NUMBERS	$J T_u$	$J t_u$	$j T_u$	$j t_u$
412.....	15	24	8	11
413.....	13	14	10	9
414.....	11	14	6	3
415.....	32	31	27	33
416.....	15	15	6	12
417.....	55	52	40	39
418.....	10	12	4	15
419.....	8	5	2	2
420.....	9	6	6	1
Totals.....	168	173	109	125

numbers. Of the 501 seeds produced, 247 had the parental combinations and 254 the new combinations of these factor pairs. This is a deviation of only 3.5 ± 7.5 from the equality expected for factors that are inherited independently.

Tests involving T_u and S_u with ramosa ear, $R_a r_a$

Factors T_u and R_a

Several plants heterozygous for tunicate ear and *ramosa* ear were back-crossed to non-tunicate *ramosa* plants. The progenies from these back-

TABLE 27
Progeny from the back-cross $T_u t_u R_a r_a \times t_u t_u r_a r_a$.

PEDIGREE NUMBERS	$R_a T_u$	$R_a t_u$	$r_a T_u$	$r_a t_u$
439.....	73	95	93	72
441.....	10	9	7	13
442.....	20	25	16	10
440.....	26	22	33	39
Totals.....	129	151	149	134

crosses are given in table 27. There were produced 280 normal and 283 *ramosa* plants. Of the normal plants 129 were tunicate and 151 non-tunicate, and of the *ramosa* plants 149 were tunicate and 134 non-tunicate. Plants in which both the tunicate and *ramosa* characters are involved have

a much-branched, succulent and wholly sterile ear. This type of sterile ear has been referred to by COLLINS (1917) as the "cauliflower" type of inflorescence. From table 27 it may be seen that 263 plants had the parental combinations and 300 plants had the new combinations of these factor pairs. This is a deviation of 18.5 ± 8.0 from equality. A deviation as large as this would be expected about once in every eight trials, due to the errors of random sampling.

Factors S_u and R_a

A number of back-crosses involving sugary endosperm and *ramosa* plant were made by EMERSON with the results shown in table 28. Starchy

TABLE 28
Progeny from the back-cross $S_u s_u R_a r_a \times s_u s_u r_a r_a$.

PEDIGREE NUMBERS	$S_u R_a$	$S_u r_a$	$s_u R_a$	$s_u r_a$
E8024-6 $\times$ E8035-16.....	72	65	42	47
E8014-1 $\times$ E8035-14.....	57	73	44	51
E8024-1 $\times$ E8035-20.....	83	73	53	51
E8014-8 $\times$ E8035-14.....	61	62	60	60
Totals.....	273	273	199	209

and sugary seeds were produced in approximately equal numbers. The starchy seeds produced normal and *ramosa* plants in equal numbers, there being 273 of each. From the sugary seeds were grown 199 normal and 209 *ramosa* plants, a close approximation to a 1:1 ratio. There were in the total progenies 482 plants with the factorial constitution of the parents and 472 plants with these factors in new combinations. This is a deviation of 5.0 ± 10.4 from the equality expected for factors that are not linked.

These data indicate that the factor pair for *ramosa* ear does not belong to the T_u - S_u linkage group.

Tests involving T_u and S_u with green striping, G_s g_s

Factors T_u and G_s

A number of plants heterozygous for tunicate ear and the chlorophyll pattern called green striping were back-crossed to non-tunicate green-striped plants. Relatively large plantings from these back-crossed ears were made in 1918 but because of a number of unfavorable conditions, including an unusually early killing frost, it was not possible to note the green-striped plants for the tunicate character. The green plants were

noted for the tunicate character with the results given in table 29. There were 197 green plants and 201 that were green striped, a good 1:1 ratio. Of the green plants 104 were tunicate and 93 non-tunicate. This is a deviation of 5.5 ± 4.7 from equality and indicates that the factors are independent.

Tests involving sugary endosperm with the green-stripping chlorophyll pattern have not yet been made.

TABLE 29
Progeny from the back-cross $T_u t_u G_s g_s \times t_u t_u g_s g_s$.

PEDIGREE NUMBERS	$G_s T_u$	$G_s t_u$	$g_s T_u + g_s t_u$
85.....	7	11	18
86.....	18	10	25
87.....	48	47	101
88.....	7	3	5
89.....	24	22	52
Totals.....	104	93	201

Tests involving T_u and S_u with virescent-white seedling, $V v$

Factors T_u and V

A plant heterozygous for virescent-white seedling and recessive for the tunicate character was crossed with a heterozygous tunicate plant that was homozygous dominant for the virescent-white seedling factor pair. This cross may be represented factorially as $t_u t_u V v \times T_u t_u V V$. Tunicate and non-tunicate plants in approximately equal numbers were produced. Half of the tunicate as well as half of the non-tunicate plants should be heterozygous for virescent-white seedling. A number of the tunicate plants of this progeny were self-pollinated. A few seeds from each self-pollinated ear were planted in the greenhouse to determine which of the parent plants were heterozygous for virescent-white seedling. The heterozygous plants were expected to produce green and virescent-white seedlings in a 3:1 ratio. The seedlings from plant 130-7 were found to segregate in this manner. A field-planting from this ear produced 65 green plants and it was found that 46 were tunicate and 19 non-tunicate. These numbers are relatively small but suggest a 3:1 ratio which one would expect if the factor pairs are inherited independently. Theoretically there should have been produced 9 tunicate green: 3 non-tunicate green: 3 tunicate virescent-white: 1 non-tunicate virescent-white plants. Plants homozygous for

virescent-white seedling usually die shortly after germination and only plants of the constitution Vv and VV grow to maturity. Of the green plants that grew to maturity there were expected 3 tunicate: 1 non-tunicate plants in case the factor pair for tunicate ear and virescent-white seedling are independent. The observed numbers approach these expected numbers.

No tests involving sugary endosperm and virescent-white seedling have yet been made.

Tests involving T_u and S_u with white seedling, Ww

Factors T_u and W

A plant heterozygous for tunicate ear and white seedling was self-pollinated and produced in the F_2 generation 258 mature green plants. Of these 181 were tunicate and 77 non-tunicate. Plants recessive for the white-seedling factor die in the seedling stage and only plants of the constitution Ww and WW grow to maturity. The green plants which survived and matured were expected to be tunicate and non-tunicate in a 3:1 ratio in case the factor pairs are independent. Although the numbers are small they approach this ratio closely enough, deviation 12.5 ± 4.7 , to suggest that the factors for tunicate ear and white seedling are not linked.

Tests involving sugary endosperm with white seedling were not made.

Tests involving T_u and S_u with yellow endosperm, Yy

Factors T_u and Y

A back-cross involving tunicate ear and yellow endosperm color gave progenies as shown in table 30. These back-crossed ears contained yellow

TABLE 30
Progeny from the back-cross $T_u t_u Yy \times t_u t_u yy$.

PEDIGREE NUMBERS	$Y T_u$	$Y t_u$	$y T_u$	$y t_u$
471-472.....	23	29	20	25
473-474.....	6	14	10	9
Totals.....	29	43	30	34

and white seeds in approximately equal numbers. The yellow seeds produced 29 tunicate and 43 non-tunicate plants. The white seeds produced 30 tunicate and 34 non-tunicate plants. The numbers are very small but suggest a 1:1 ratio. Of the total number of plants 63 had the parental

and 73 the new combinations of the factors involved. This is a deviation of 5.0 ± 3.9 from the 1:1 ratio expected for independent inheritance.

It was not determined which of the factors for yellow endosperm is here concerned.

No back-cross tests were made involving sugary endosperm with yellow endosperm but F_2 progenies grown by EMERSON gave no indication of linkage.

Tests involving T_u and S_u with pale-yellow endosperm

Factors T_u and pale-yellow endosperm

A back-cross involving tunicate ear and pale-yellow endosperm color gave a total of 205 plants, 109 having grown from pale-yellow seeds and 96 from white seeds. Both pale-yellow and white seeds produced tunicate and non-tunicate plants in approximately equal numbers. The yellow seeds produced 53 tunicate and 56 non-tunicate plants, while the white seeds produced 50 tunicate and 46 non-tunicate plants. Apparently these factors are inherited independently.

No tests involving sugary endosperm with pale-yellow endosperm color were made.

SUMMARY

The data from this study substantiate the conclusion of previous investigators that ordinary tunicate plants represent a case of imperfect dominance. The homozygous tunicate plants are practically sterile.

The factor pairs for tunicate ear and sugary endosperm tend to be inherited together, with a recombination of the factors occurring in about 30 percent of the cases. This may be explained by assuming that these factors are located in the same chromosome and that the recombinations are the result of crossing over.

A statistical study of the data on the linkage between the factor pairs for tunicate ear and sugary endosperm, and between waxy endosperm and the *C* aleurone factor, indicate that crossing over in corn occurs more frequently in microsporogenesis than in megasporogenesis. It has also been found by other investigators that in *Primula sinensis* crossing over apparently occurs more frequently in microsporogenesis.

A summary of the linkage tests involving the factor pairs for tunicate ear and sugary endosperm with the other groups of linked factors is given in table 31. In every test except one the deviation from a 1:1 ratio between

TABLE 31
Summary of the linkage tests between the T_u - S_u group and other linkage groups.

LINKAGE GROUPS	FACTORS INVOLVED	PARENTAL COMBINATIONS	NEW COMBINATIONS	DEVIATION FROM 1:1 RATIO	DEV. P. E. Diff.
$C-W_x-S_h-I$	$C-T_u$	452	450	1.0 ± 10.0	0.1
	$C-S_u$	2212	2190	11.0 ± 22.4	0.5
	W_x-T_u	8	10	1.0 ± 1.4	0.7
	S_h-T_u	8	10	1.0 ± 1.4	0.7
	$I-S_u$	340	310	15.0 ± 8.6	1.8
$G-R-L$	$G-T_u$	340	323	8.5 ± 8.6	1.0
	$R-T_u$	322	317	2.5 ± 8.5	0.3
	$R-S_u$	1508	1470	19.0 ± 18.4	1.0
$B-L_g-T_e$	$B-T_u$	692	713	10.5 ± 12.6	0.8
	$B-S_u$	470	504	17.0 ± 10.4	1.6
	L_g-T_u	839	853	7.0 ± 13.9	0.5
	L_g-S_u	1062	1028	17.0 ± 15.4	1.1
$P-T_e$	$P-S_u$	350	356	3.0 ± 9.0	0.3
	$P-T_u$	276	336	30.0 ± 8.3	3.6
$Y-P_l$	P_l-T_u	172	181	4.5 ± 6.2	0.7
	P_l-S_u	561	551	5.0 ± 11.2	0.4
A	$A-T_u$	34	40	3.0 ± 2.9	1.0
	$A-S_u$	157	157	0.0 ± 6.0	0.0

TABLE 32
Summary of the tests between the T_u - S_u group and other factors.

FACTORS INVOLVED	PARENTAL COMBINATIONS	NEW COMBINATIONS	DEVIATION FROM A 1:1 RATIO	DEVIATION P. E. Diff.
A_n-T_u	217	247	15.0 ± 7.3	2.0
B_l-S_u	161	161	0.0 ± 6.0	0.0
C_r-T_u	217	203	7.0 ± 6.9	1.0
C_r-S_u	335	370	17.5 ± 9.0	2.0
$D-T_u$	233	242	4.5 ± 7.3	0.6
$F-T_u$	369	364	2.5 ± 9.1	0.3
F_l-T_u	111	109	1.0 ± 5.0	0.2
$J-T_u$	293	282	5.5 ± 8.1	0.7
P_r-T_u	142	150	4.0 ± 5.8	0.7
P_r-S_u	247	254	3.5 ± 7.5	0.5
R_e-T_u	263	300	18.5 ± 8.0	2.3
R_e-S_u	482	472	5.0 ± 10.4	0.5
G_s-T_u	104	93	5.5 ± 8.1	0.7
$Y-T_u$	63	73	5.0 ± 3.9	1.3
T_u -Pale-yellow endosperm	99	106	3.5 ± 4.8	0.7

the parental combinations and new combinations is less than twice the probable error. This indicates that the T_u - S_u group is independent of the other groups that have as yet been established. In the test between T_u and P the deviation is nearly four times the probable error but this wide deviation is doubtless due to the extremely unsatisfactory material from which these data were taken, as has already been mentioned.

Linkage tests have also been made between the T_u - S_u group and other mutant factors whose linkage relations are not yet definitely established. A summary of these tests is given in table 32. The data give no evidence that any of these factors belong to the T_u - S_u linkage group. Unfortunately some of these tests were made with only one member of the T_u - S_u group. Such tests are not conclusive as factors located in the same chromosome may be far enough apart so that crossing over occurs in approximately 50 percent of the cases. This would give the same results as if the factors were in different chromosomes and assorted independently.

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