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INHERITANCE OF WAXY ENDOSPERM IN MAIZE.

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ENDOSPERM TEXTURE IN MAIZE.

In 1908 Mr. G. N. Collins found in a variety of maize imported from China a new type of endosperm which was entirely unlike the endosperms of any other varieties previously known, being neither horny, starchy, nor sweet. This new texture of the endosperm was designated cereous or waxy, which well describes its appearance, the cut surface of the seed resembling a hard wax (3).[1]

[1] Serial numbers in parentheses refer to "Literature cited," page 99.

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In subsequent breeding work this waxy endosperm was found to be alternative to horny endosperm, behaving as a recessive character when crossed with American flint and dent varieties. The new endosperm character has proved to be adapted for investigation of some of the problems of heredity in maize. The inheritance is definitely alternative, no blending or intermediate stages having been found. This absence of intergradations between the new waxy endosperm and the other endosperm textures simplifies the classification of material and renders the numerical relations of this character more definite and hence of more significance than those observed with other Mendelian characters of maize thus far studied where intermediates are comparatively common.

In the first crosses that were made the behavior of the waxy endosperm was very similar to that of a Mendelian unit character, the approximation being so close that the deviations were at first considered accidental. But with the progress of the investigation and the accumulation of larger numbers of individuals it became apparent that the deviations from the theoretical Mendelian ratios, though never large, were too definite to be ascribed to chance. It further developed that a correlation existed between the waxy texture of the endosperm and the red and blue colors in the aleurone cells of the Chinese maize in crosses with other varieties.

This bulletin reports the results of a series of crosses between the Chinese variety and an African pop corn made for the further study of the correlation between the endosperm texture and the color of the aleurone. In these experiments large numbers of seeds were classified with respect to the endosperm and aleurone characters. While the results are in the main similar to those previously reported, the experiments now comprise such large numbers of individuals as to place the deviations from the expected ratios beyond question and also to establish more definitely the existence of the correlation between endosperm texture and aleurone color.

The subject became somewhat involved when it was found that the aleurone color had to be resolved into two factors, and it became necessary to analyze the behavior of correlated characters where the correlations are between factors. In attempting to understand the correlations of the characters, both the theory of reduplication (1) and the linkage theory (11) have been kept in mind.

The experiments have yielded a body of evidence that should be of value in testing the general applicability of current theories of the segregation or alternative inheritance of characters and also in testing explanations that may be advanced in the future. To be of value in this connection, it is necessary that the data should be placed on record in the most complete and available form. An effort has been made to tabulate the results in such a way that pedigrees can be traced readily, and it is hoped that the data may have a value apart from the explanations that are suggested or considered in the body of the bulletin.

CROSSES BETWEEN THE ALGERIA AND A CHINESE VARIETY.

FIRST GENERATION.

In 1911, pollen of a plant of the white Chinese variety with waxy endosperm, was used on a plant of a colored variety of pop corn that has been grown under the name Algeria.[1] The resulting ear was indistinguishable from pure seed ears of the Algeria, both the aleurone color and the horny texture of the endosperm of the latter showing complete dominance. This hybrid ear received the number Dh 237.

The same year a cross was made, using the white waxy Chinese variety as the female parent and the Algeria as the male parent. This hybrid ear received the designation Dh 234.

SECOND GENERATION.

Seeds from Dh 234 and Dh 237 were grown in 1912 and in 1913, and 96 hand-pollinated ears were produced. These 96 ears bore four classes of seeds: Colored waxy, white waxy, colored horny, and white horny. The color of the aleurone is discussed later and may therefore be disregarded in analyzing the inheritance of the endosperm texture. The numerical results are presented in Table I.

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[1] The original seed of this variety was obtained from Dr. Trabut in Algeria by Mr. W. T. Swingle. Dr. Trabut has recently informed Mr. Swingle that the variety is not an Algerian variety, having been introduced into Algeria from Morocco.

TABLE I.—*Inheritance of endosperm texture in 96 ears of maize, the progeny of the two hybrids Dh 234 and Dh 237.*

[Lines bracketed together in pairs indicate ears borne on the same plant; ears selected for planting are designated by an asterisk (*).]

HYBRID DH 234, CHINESE VARIETY × ALGERIA.

Pedigree No. of—		Number of seeds.				D. ÷ E.	Percentage of waxy.
Progeny ear.	Self-pollinated ♂.	Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8
1099*	1106	657	160	164	— 4	0.5	24.3
1100	1103	599	167	149	18	2.5	28.2
1101	1103	533	146	133	13	1.9	27.3
1102	Self	517	129	129	....	....	24.9
1103	...do	272	80	68	12	1.4	29.4
1104	1108	573	136	143	— 7	1.0	23.7
1105	Self	609	161	152	9	1.2	26.4
1106	...do	690	182	172	10	1.3	26.3
1108	...do	691	183	172	11	1.4	26.4
1109	1112	402	86	100	— 14	2.3	21.3
1110*	1132	745	204	186	18	2.2	27.5
1111*	Self	747	165	186	— 21	2.6	22.2
1112	...do	733	201	183	18	2.2	27.4
1113	1118	643	181	160	21	2.8	28.1
1114	1118	428	120	107	13	2.1	28.0
1115	1112	508	137	127	10	1.5	27.9
1116	1118	322	83	80	3	.5	26.0
1117	Self	564	137	141	— 4	.5	24.2
1118	...do	623	137	155	— 18	2.4	21.9
1119	1108	414	107	103	4	.6	25.8
1120	1117	655	145	163	— 18	2.4	22.1
1121	Self	687	152	172	— 20	2.6	22.5
1515	...do	555	139	139	....	....	25.0
1518	1726	510	110	127	— 17	2.6	21.5
1519	Self	605	143	151	— 8	1.1	23.8
1522	1732	275	63	69	— 6	1.2	22.9
1523	Self	571	119	143	— 24	3.4	20.8
1524	1724	773	166	193	— 27	3.3	21.5
1525	Self	212	45	53	— 8	1.9	21.3
1526	1744	522	140	130	10	1.5	26.8
1527	Self	614	143	153	— 10	1.4	23.3
1529	...do	334	71	83	— 12	2.3	21.2
1530	1733	676	133	169	— 36	4.7	19.7
1531	Self	659	149	165	— 16	2.1	22.6
1532	1729	707	151	177	— 26	3.4	21.4
1533	Self	679	154	170	— 16	2.1	22.7
1534	...do	492	107	123	— 16	2.5	21.7
1535	1742	440	100	110	— 10	1.6	22.7
1536	1731	725	172	181	— 9	1.1	23.7
1537	Self	592	136	148	— 12	1.7	22.9
1538	1733	609	150	152	— 2	.3	24.6
1539	Self	626	146	156	— 10	1.4	23.3
1540	1736	679	152	170	— 18	2.4	22.4
1541	1736	631	159	158	1	.1	25.2
1542	1723	515	120	129	— 9	1.4	23.3
1543	Self	570	119	142	— 33	4.7	20.9
1544	....	491	111	123	— 12	1.9	22.6
1545	Self	417	101	104	— 3	.5	24.2
1546	1747	800	205	200	5	.7	25.0
1547	1537	633	140	158	— 18	2.5	22.2
1548	1748	607	146	152	— 6	.8	24.0
1549	Self	479	118	120	— 2	.3	24.6
1550	1740	383	79	96	— 17	3.0	20.6
1551	Self	578	123	144	— 21	3.0	21.2
Total	....	30,571	7,309	7,643	—334	7.5	23.9

TABLE I.—*Inheritance of endosperm texture in 96 ears of maize, the progeny of the two hybrids Dh 234 and Dh 237*—Continued.

HYBRID DH 237, ALGERIA × CHINESE VARIETY.

Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of waxy.
Progeny ear.	Self-pollinated ♂.	Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8
1122		648	139	162	− 23	3.7	21.4
1124		672	157	168	− 11	1.5	23.3
1125	Self	837	201	209	− 8	.9	24.0
{1127	1125	723	177	181	− 4	.5	24.4
{1128	Self	319	80	80			25.0
{1129*	...do	747	180	187	− 7	.8	24.1
{1130*	1135	741	155	185	− 30	3.7	21.0
{1131*	1117	584	134	146	− 12	1.7	22.9
{1132	Self	575	134	144	− 10	1.4	23.3
{1133	...do	758	187	189	− 2	.2	24.6
{1134*	1118	446	73	111	− 38	6.1	16.4
{1135	Self	627	135	157	− 22	3.0	21.5
{1136	1137	615	176	154	22	3.0	28.6
{1137	Self	740	193	185	8	1.0	26.0
{1138	1135	548	140	137	3	.4	25.1
{1720	1515	459	141	115	26	4.2	30.7
{1721	Self	712	165	178	− 13	1.7	23.2
{1722	1543	677	162	169	− 7	.9	23.9
{1723	Self	664	136	166	− 30	4.0	21.0
1724	1523	374	119	93	26	4.5	31.8
{1725	1519	472	114	118	− 4	.6	24.2
{1726	Self	560	122	140	− 18	2.6	21.6
{1727	1926	503	110	126	− 16	2.4	21.9
{1729	1533	613	169	153	16	2.2	27.1
1730	1539	401	92	100	− 8	1.4	22.9
{1731	1536	532	126	133	− 7	1.0	23.7
{1732	1522	419	95	105	− 10	1.7	22.7
{1733	1741	634	161	158	3	.4	25.4
{1734	1531	516	119	129	− 10	1.5	23.1
{1735	1540	458	102	114	− 12	1.9	22.3
{1736	Self	595	138	149	− 11	1.5	23.2
1738..e	...do	472	119	118	1	.2	25.2
{1740	1550	630	161	157	4	.6	25.6
{1741	Self	485	110	121	− 11	1.7	22.7
{1742	1535	559	119	140	− 21	3.0	21.3
{1743	Self	575	118	144	− 26	3.7	20.5
{1744	1526	512	133	128	5	.8	26.0
{1745	Self	625	149	156	− 7	1.0	23.8
{1746	1547	621	162	155	7	1.0	26.1
{1747	Self	658	147	164	− 17	2.3	22.7
{1748	1548	538	139	134	5	.7	25.8
{1749	Self	342	90	85	5	.9	26.3
Total		24,186	5,779	6,047	−268	5.9	23.9
Total for both hybrids		54,759	13,088	13,690	−602	8.8	23.9

EXPLANATION OF TABLE I.

In column 1 of Table I is found the pedigree number of the individual ears. When it so happened that two ears borne on the same plant were pollinated in such a way that they both appear in the same table, they are bracketed together, thus facilitating a comparison of the behavior of two crosses having the same female parent and different male parents.

Column 2 gives the pedigree number of the ear that resulted from self-pollinating the plant that served as the male parent of the ear in column 1.

Thus, for example, the first two ears were borne on the same plant but were fertilized with pollen secured from different plants. The male parent of ear No. 1099 bore the self-pollinated ear No. 1106, while the male parent of ear No. 1100 bore the self-pollinated ear No. 1103. The seed classes of these self-pollinated ears can be found by referring to Nos. 1106 and 1103, where they occur in their numerical places in column 1.

In column 2 the word "Self" indicates that the ear represented in column 1 is the result of self-pollination.

As a further example, Nos. 1104 and 1105 may be taken. It is here possible to compare the result of crossing with a sister plant, the behavior of which, when self-pollinated, is shown under No. 1108, with the result of self-fertilizing the same plant.

Columns 3, 4, and 5 are self-explanatory. Column 6 gives the deviation of the observed from the expected number of seeds, on the assumption that horny and waxy were approximating a 3 to 1 ratio.

Column 7 (headed D÷E) gives the number of times the observed deviation (D) exceeds the probable error (E), and affords a basis for judging whether the difference between the observed and expected is a real or chance deviation. To facilitate the translating of D÷E into probabilities, reference may be made to Table II, which shows the values copied without recalculation from Pearl and Miner (12). It was not thought necessary in Table I to include the probable errors, which were calculated by the formula

$$0.6745\sqrt{0.25\times0.75}\times\sqrt{\text{total seeds}},$$

since their only present use is in comparison with the deviations.

The 96 ears shown in Table I were the results of self-pollinations, crosses between sister plants, or crosses between the two hybrids. In all cases the expected percentage of waxy seeds was 25. The progeny of the two hybrids have been examined and tabulated separately, but as no significant differences were found between them, it will save space to consider them as a single group.

The 96 ears produced a total of 54,759 seeds, of which 23.9 per cent were waxy. This deviation of 1.1 per cent from the expected

25 per cent, though seemingly small, is nevertheless 8.8 times the probable error and could be expected to occur as the result of chance only once in over a billion times. The percentage of the individual ears ranged from 16 to 32.

Table II.—*Probability of occurrence of statistical deviations of different magnitudes relative to the probable error.*[1]

Deviation (probable error).	Odds against the occurrence of a deviation as great as or greater than the designated one.	Deviation (probable error).	Odds against the occurrence of a deviation as great as or greater than the designated one.	Deviation (probable error).	Odds against the occurrence of a deviation as great as or greater than the designated one.
1.0	1.00 to 1.	2.5	9.89 to 1.	4.0	142.26 to 1.
1.1	1.18 to 1.	2.6	11.58 to 1.	4.1	174.75 to 1.
1.2	1.39 to 1.	2.7	13.58 to 1.	4.2	215.92 to 1.
1.3	1.63 to 1.	2.8	15.95 to 1.	4.3	267.10 to 1.
1.4	1.90 to 1.	2.9	18.80 to 1.	4.4	332.33 to 1.
1.5	2.21 to 1.	3.0	22.26 to 1.	4.5	415.67 to 1.
1.6	2.57 to 1.	3.1	26.40 to 1.	4.6	519.83 to 1.
1.7	2.98 to 1.	3.2	31.36 to 1.	4.7	656.89 to 1.
1.8	3.45 to 1.	3.3	37.46 to 1.	4.8	825.45 to 1.
1.9	4.00 to 1.	3.4	44.87 to 1.	4.9	1051.63 to 1.
2.0	4.64 to 1.	3.5	53.95 to 1.	5.0	1350.35 to 1.
2.1	5.38 to 1.	3.6	64.79 to 1.	6.0	19,230 to 1.
2.2	6.26 to 1.	3.7	78.37 to 1.	7.0	434,782 to 1.
2.3	7.28 to 1.	3.8	95.15 to 1.	8.0	Over a billion.
2.4	8.48 to 1.	3.9	116.23 to 1.		

[1] Copied without recalculation from Pearl and Miner (12).

One ear deviated below the expected by 6.1 times the probable error, but with 96 individuals the odds against a deviation of this magnitude would be about 190 to 1.

A similar shortage of waxy seeds has been observed throughout the experiments with this character.

In a previous publication (7) 45 ears were reported, representing many different crosses and having 22,339 seeds with 23.1 per cent waxy, the deviation from the expected 25 per cent being 9.24 times the probable error. Adding this group to the results obtained from the second generation of the two hybrids Dh 234 and Dh 237, there is a total of 77,098 seeds, 18,267 of which are waxy, while the expected is 19,274 waxy seeds, a shortage of 1,007±81 seeds, a deviation of 12.4 times the probable error. A deviation of this magnitude would be expected to occur as the result of chance only once in well over a billion times.

The approximation of the observed percentage of waxy seeds to the theoretical 25 per cent is very close for the individual ears of the hybrids Dh 234 and Dh 237, only two of the ears deviating by larger amounts than could be reasonably ascribed to chance, and of these one was below and the other above the expected percentage. The large number of individuals involved has made it possible to accurately measure small differences which ordinarily would escape unchallenged as very good approximations of actual observation to theory.

The percentages of waxy seeds shown by the individual ears for the first-generation hybrids and those previously reported (7) have been plotted in figure 1, which shows that the deviation from 25 per cent is not the result of a few aberrant ears. It readily can be seen that while the mode and mean are considerably below the expected 25 per cent, the curve very closely approximates the normal probability curve.

Although the graph (fig. 1) bears a striking resemblance to the normal probability curve, there is reason for believing that the indi-

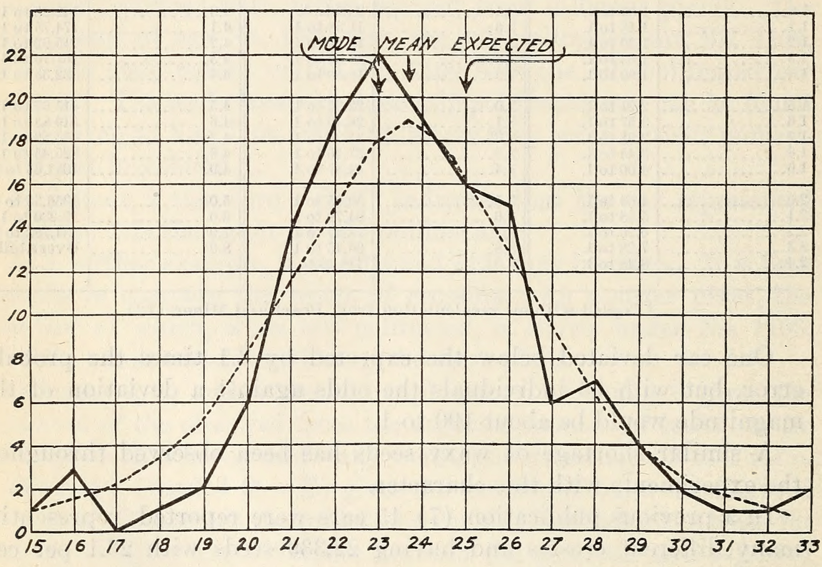

FIG. 1.—Diagram showing the percentage of waxy seeds on 141 ears obtained from the second generation of the hybrids Dh 234 and Dh 237 and the ears previously reported. The dotted line shows the probability curve for this population of 141 ears, the mean and standard deviations being the same.

viduals do not form a homogenous group deviating from a common mean.

As a means of determining whether the varying percentages of the individual ears are chance deviation from the mean of the entire group, a method has been proposed by Yule (16) by which a theoretical standard deviation is calculated, based on the harmonic mean of the observed individual ears.

The "goodness of fit" of the observed standard deviation to the calculated standard deviation is measured by the probable error of the former.

For the ears in the accompanying graph the calculated standard deviation is 1.95, and the observed standard deviation is 3.11. The difference is 8.5 times the probable error.

Since 45 of the individual ears represent crosses between the Chinese variety and horny varieties other than the Algeria, it may be well to examine the curve without these ears. Omitting these 45 ears, the standard deviation is reduced to 2.5, the mean remaining unchanged at 23.9. The theoretical standard deviation is also slightly reduced. The difference is now 5.2 times the probable error, a difference still too large to be ascribed to chance.

Thus while the mean percentage of waxy seeds reappearing in the second generation of waxy × horny hybrids is 23.9, which is too large a deviation from 25 per cent to be ascribed to chance, the individual ear approximations are not sufficiently close to the observed mean to be considered as chance departures from it. The explanation that at once presents itself is that through mistakes in classification a varying number of waxy seeds were being included in the horny group.

Endosperm texture is not subject to the minute spotting encountered in the aleurone color, and in the series of crosses here reported the classes were unusually good, owing to the fact that the Algeria parent was a pop corn and had a minimum of soft starch. Two instances where the endosperm was part horny and part waxy have been reported (5) and four additional seeds have since been found. When these mosaic seeds were planted and self-pollinated, they behaved as normal seeds heterozygous for horny endosperm.

Since mosaic endosperms are known to occur, it is of course conceivable that the horny or waxy portion of the seeds may be so reduced as to escape detection, but since such seeds are heterozygous, the only result could be to erroneously class heterozygous seeds as waxy, but this would increase rather than diminish the number of seeds classed as waxy.

A deficiency in the number of individuals with the recessive character does not readily admit of the explanation that the deviation is due to mistakes in classification. Such an explanation would require that some of the individuals exhibiting the dominant character were in reality homozygous recessives. Where a deficiency in the number of individuals with the dominant character occurs, such deviation could be the result of mistakes in classification, since it is conceivable that a failure or a partial failure of dominance results in some individuals exhibiting the dominant character to such a slight degree as to pass for homozygous recessives. If waxy seeds were being included in the horny group, some all-waxy ears would be secured in self-pollinating plants grown from the horny seeds.

Since the deviation observed was approximately 1 per cent, only one ear of every hundred would be expected to be all waxy. Several hundred ears, the result of self-pollinating plants grown from the horny seeds of waxy × horny hybrids, have been secured, but no all-waxy ears have been found.

The shortage of waxy seeds not only occurs where the expected ratio of horny to waxy is 3 to 1, but was also observed in crosses between waxy endosperm and sweet endosperm where the Mendelian dihybrid ratio was expected (8). Here the deviation was 1 per cent below the expected 18.75, and it should not occur as the result of chance oftener than once in 15,000 times.

THIRD GENERATION OF THE HYBRID DH 234.

Three ears were selected for planting from the hybrid Dh 234. These three ears are Nos. 1099, 1110, and 1111 in Table I. The last two ears were borne on the same plant. Ear No. 1110 represents a cross between the two hybrids and is discussed later, with the results from a similar ear taken from the hybrid Dh 237.

One of the two ears remaining, No. 1111, was self-pollinated, while No. 1099 was the result of pollen from another plant of the same hybrid. Both of these ears were close approximations of the expected 25 per cent waxy, as was also a self-pollinated ear secured from the male parent of No. 1099.

There were four classes of seeds on Nos. 1099 and 1111, colored and white horny and colored and white waxy. These classes were planted separately, and reciprocal crosses were made between white waxy and colored horny and colored waxy and white horny plants. Wherever possible, self-pollinated ears were secured from all the classes, but since the self-pollinated plants grown from waxy seeds resulted in ears all the seeds of which were waxy, these ears do not appear in the tables.

To avoid unnecessary complications, the inheritance of aleurone color is discussed separately from the behavior of the texture of the endosperm. The color of the aleurone appeared not to affect the behavior of the waxy endosperm as far as the percentage of waxy seeds was concerned. The progenies were examined with this point in mind, but since no differences were found it was not thought necessary to discuss the behavior of the colored seeds separately from the behavior of the white seeds.

The results obtained from the progeny of ears Nos. 1099 and 1111 were also examined separately, but presented no significant difference in their behavior, and to avoid unnecessary repetition the progeny of these two ears will be considered together. The progenies of the four classes of seeds from the two ears are separately indicated in Tables III and IV.

WAXY × HORNY.

The ears resulting from pollinating the plants grown from the waxy seeds of pedigree Nos. 1099 and 1111 with plants grown from the horny seeds of these same ears are shown in Table III. Column 1 of Table III gives the pedigree number of the progeny ear of Dh 234 from which the plants that produced the ears in that section of the table were grown. In this same column will be found symbol letters which indicate the character of the seeds from which the plants that produced the ears in the table were grown. The letters *W* and *C* indicate white or colored aleurone. The symbol used for waxy endosperm is *X* and for horny endosperm *H*.

The symbols given first indicate the character of the seeds from which the female parent of the ears in the table were grown. For

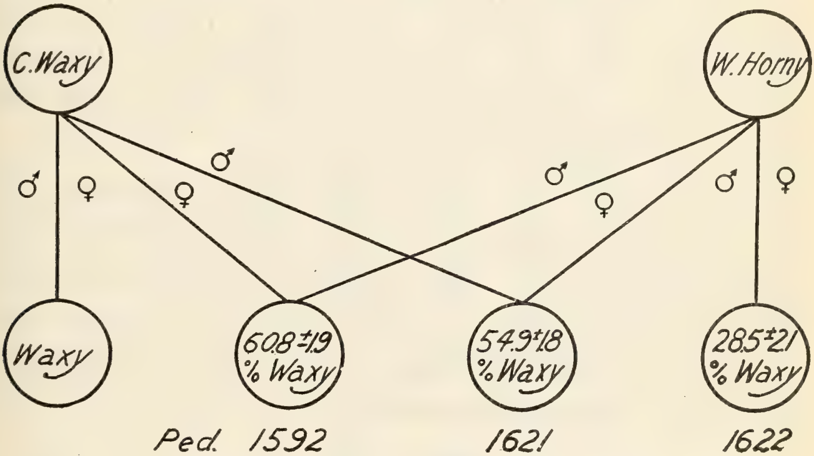

FIG. 2.—Diagram showing the relations of ears Nos. 1592, 1621, and 1622.

example, the first group of five ears which are separated from the following ears by a total are the result of crossing plants grown from the white waxy (*WX*) seeds with plants grown from the colored horny (*CH*) seeds of ear No. 1099. In this group the white waxy plants were used as the female parents. Column 3 in Table III gives the pedigree numbers of the ears representing the reciprocal cross. The classes of seeds produced by the reciprocals are found in Table IV.

There were 11,724 seeds on the 27 ears shown in Table III. The expectation of waxy seeds was 50 per cent, and the observed percentage was 49.5. The deviation of 60 seeds is 1.65 times the probable error and can, of course, be ascribed to chance. Three ears deviated from the expected percentage by more than 3 times the probable error, and one ear, No. 1592, showed a deviation above the expectation of 5.7 times the probable error.

The reciprocal of ear No. 1592 is No. 1621 (Table IV). There was also a self-pollinated ear from the male parent of No. 1592, No. 1622 (Table IV). The relations of these two ears are shown in figure 2.

The difference between the two reciprocal ears is 5.9 ± 2.62 per cent. The self-pollinated ear obtained from the horny parent does not show a significant deviation from 25 per cent. The plant which bore ears Nos. 1621 and 1622 is shown by the cross with waxy to have 60.8 per cent of the male gametes bearing the waxy character and 54.9 per cent of the female gametes with this character.

The expected result of self-pollinating a plant with such a gametic series would be an ear with 33.4 per cent waxy, from which ear No. 1622 with 28.5 per cent deviates 4.9 ± 2.1, a deviation which is not significant. The plant, then, which bore ears Nos. 1621 and 1622 produced an excess of gametes bearing the waxy character, this excess being greater in the male gametes. An excess of male gametes bearing the waxy character is contrary to the results obtained with most of the ears where it was found that the waxy gametes were below instead of above the expected percentage.

The observed excess of waxy seeds on ear No. 1592 might be explained by the assumption that a failure of the dominance of the horny endosperm resulted in some of the heterozygous horny seeds being classified as waxy. Another generation grown from the waxy seeds would throw light on this matter, since if the observed deviation was due to a failure of dominance 10 of every 100 plants grown from the waxy seeds, when self-pollinated, would be expected to result in ears with some horny seeds.

HORNY × WAXY.

As the result of pollinating plants grown from the horny seeds with plants grown from the waxy seeds of ears Nos. 1099 and 1111, 39 ears were obtained (Table IV). In this same table are also shown the ears resulting from self-pollinating the heterozygous horny plants. These ears will be discussed later, but it was thought advisable to include them in Table IV, since it makes possible the comparison of the behavior of the horny plants when self-pollinated with their behavior when pollinated with homozygous waxy. Although only 2 of the 29 ears deviated from the expected percentage in excess of three times the probable error, the deviation for the total number of seeds is 3.9 times the probable error.

TABLE III.—*Inheritance of endosperm texture in 27 ears of maize, the waxy × horny progeny of the two ears Nos. 1099 and 1111, the progeny of hybrid Dh 234.*

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Number of seeds.				D÷E.	Percentage of waxy.
	Self-pollinated ♂.	Reciprocal cross.	Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8	9
Ear No. 1099, *WX×CH:*								
1552	1644	1643	506	227	253	−26	3.4	44.8
1555	1705	None	230	120	115	5	.98	52.2
1563	None	...do	257	109	128	−19	3.51	42.4
1564	...do	...do	438	220	219	1	.14	50.2
1565	1633	1632	114	56	57	− 1	.27	49.1
Total			1,545	732	772	−40	3.02	47.4
Ear No. 1111, *WX×CH:*								
1648	1696	None	712	381	356	25	2.77	53.5
1651	1644	...do	286	139	143	− 4	.62	48.6
1652	1700	...do	611	302	305	− 3	.36	49.4
1654	1705	...do	387	202	193	9	1.3	52.2
1660	None	...do	600	283	300	−17	2.06	47.2
Total			2,596	1,307	1,298	9	.52	50.4
Ear No. 1099, *CX×WH:*								
1567		1596	537	283	268	15	1.92	52.7
1569	None	None	404	204	202	2	.29	50.1
1572	1605	1604	127	53	63	−10	2.63	41.7
1574	None	None	645	327	322	5	.58	50.6
1576	1618	1617	519	253	259	− 6	.78	48.8
1579		1610	468	221	234	−13	1.78	47.2
1583	1612	None	503	246	251	− 5	.66	49.0
1584		1623	406	195	203	− 8	1.17	47.8
1590	1620	1619	580	291	290	1	.12	50.2
1592	1622	1621	307	187	153	34	5.7	60.8
1594	1612	1611	764	377	382	− 5	.53	49.4
Total			5,260	2,637	2,630	7	.28	50.1
Ear No. 1111, *CH×WH:*								
1663	None	1684	658	329	329			50.0
1665	1687	1686	403	205	201	4	.59	50.9
1667	None	None	87	45	43	2	.63	51.7
1671	...do	...do	352	170	176	− 6	1.0	48.3
1674	1612	...do	342	153	171	−18	2.89	44.7
1676	None	1690	481	224	240	−16	2.16	46.6
Total			2,323	1,126	1,161	−35	2.15	48.5
Total of the above four groups			11,724	5,802	5,862	−60	1.65	49.6

From an examination of the crosses shown in Tables III and IV it is possible to determine whether the male and female gametes bearing waxy endosperm are produced in equal numbers. All the female gametes in Table III were bearing waxy endosperm, so that the results obtained are the ratios prevailing in the male gametes. In Table IV all the male gametes were bearing waxy endosperm, so that the ratios here represent the proportion prevailing in the female gametes.

TABLE IV.—*Inheritance of endosperm texture in 39 ears of the horny × waxy and 28 ears of the horny × self progeny of the two maize ears Nos. 1099 and 1111, the progeny of hybrid Dh 234.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Horny × waxy.						Horny × self.					
	Self-pollinated ♂.	Reciprocal cross.	Number of seeds.				D ÷ E.	Percentage of waxy.	Number of seeds.				D ÷ E.	Percentage of waxy.
			Total.	Waxy.	Expected waxy.	Deviation.			Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1099, *CH × WX:*														
1625	Self	...	...	...	...	...	...	...	464	99	116	−17	2.7	21.3
1626	All waxy	...	427	227	214	13	1.86	52.9	...	...	...	...	...	...
{1627	...	...	566	307	283	24	2.99	54.2	...	...	...	...	...	...
{1628	Self	...	...	...	...	...	...	...	521	112	130	−18	2.7	21.5
{1629	All waxy	...	497	273	248	25	3.35	55.0	...	...	...	...	...	...
{1630	Self	...	...	...	...	...	...	...	457	97	114	−17	2.7	20.6
{1631	...	...	397	213	198	15	2.26	53.6	...	...	...	...	...	...
{1632	All waxy	1565	298	149	149	...	...	50.0	...	...	...	...	...	...
{1633	Self	...	...	...	...	...	...	...	318	78	79	− 1	.19	24.5
{1635	...	...	703	356	351	5	.56	50.6	...	...	...	...	...	...
{1636	Self	...	...	...	...	...	...	...	573	146	143	3	.43	25.5
{1637	All waxy	...	424	208	212	− 4	.57	49.0	...	...	...	...	...	...
{1638	Self	...	...	...	...	...	...	...	573	139	143	− 4	.57	24.3
1639	All waxy	...	123	65	61	4	1.7	52.9	...	...	...	...	...	...
{1641	...	...	396	196	198	− 2	.29	49.5	...	...	...	...	...	...
{1642	Self	...	...	...	...	...	...	...	551	144	133	11	...	26.2
{1643	All waxy	1552	511	263	256	7	.92	51.4	...	...	...	...	...	...
{1644	Self	...	...	...	...	...	...	...	652	166	163	3	.42	25.5
{1645	All waxy	1560	510	255	255	...	...	50.0	...	...	...	...	...	...
{1646	Self	...	...	...	...	...	...	...	368	86	92	− 6	1.07	23.4
{1647	All waxy	...	387	193	193	...	...	50.0	...	...	...	...	...	...
Total	...	...	5,239	2,705	2,620	85	3.48	51.6	4,477	1,067	1,119	−52	2.50	23.9
Ear No. 1099, *WH × CX:*														
1596	All waxy	1567	292	147	146	1	.17	50.1	...	...	...	...	...	...
{1600	...	...	421	186	210	−24	3.46	44.2	...	...	...	...	...	...
{1601	Self	...	...	...	...	...	...	...	270	74	67	7	1.46	27.4
{1602	All waxy	None	322	158	161	− 3	.49	49.0	...	...	...	...	...	...
{1603	Self	...	...	...	...	...	...	...	457	118	114	4	.64	25.8
{1604	All waxy	1572	171	88	85	3	.68	51.4	...	...	...	...	...	...
{1605	Self	...	...	...	...	...	...	...	365	101	91	10	1.97	27.7
{1606	All waxy	None	391	204	195	9	1.35	52.2	...	...	...	...	...	...
{1607	Self	...	...	...	...	...	...	...	257	70	64	6	1.28	27.5
1610	None	1579	303	148	151	− 3	.51	48.8	...	...	...	...	...	...
{1611	All waxy	1594	689	362	344	18	2.04	52.6	...	...	...	...	...	...
{1612	Self	...	...	...	...	...	...	...	447	137	112	25	4.40	31.1
1613	do.	...	...	...	...	...	...	...	335	80	84	− 4	.75	23.9
{1617	...	1576	416	219	208	11	1.60	52.6	...	...	...	...	...	...
{1618	Self	...	...	...	...	...	...	...	197	63	49	14	3.41	32.0
{1619	All waxy	1590	467	233	233	...	...	50.0	...	...	...	...	...	...
{1620	Self	...	...	...	...	...	...	...	506	122	126	− 4	.68	24.1

TABLE IV.—*Inheritance of endosperm texture in 39 ears of the horny × waxy and 28 ears of the horny × self progeny of the two maize ears Nos. 1099 and 1111, the progeny of hybrid Dh 234*—Continued.

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Horny × waxy.						Horny × self.					
	Self-pollinated ♂.	Reciprocal cross.	Number of seeds: Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.	Number of seeds: Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1099, *WH × CX*—Continued.														
{1621	All waxy	1592	348	191	174	17	2.7	54.9						
{1622	Self								207	59	52	7	1.44	28.5
{1623	All waxy	1584	497	263	248	15	1.99	53.0						
{1624	...do	None	67	30	33	− 3	1.09	44.8						
Total			4,384	2,229	2,192	37	1.66	50.8	3,041	824	760	64	3.9	27.1
Ear No. 1111, *WH × CX:*														
{1682	All waxy	None	448	236	224	12	1.68	52.7						
{1683	Self								383	83	96	−13	2.27	21.7
1684	All waxy	1663	485	236	242	− 6	.80	48.7						
1685		None	462	228	231	− 3	.41	49.4						
{1686	All waxy	1665	370	198	185	13	2.00	53.5						
{1687	Self								565	145	141	4	.57	25.6
1690	All waxy	1676	600	298	300	− 2	.25	49.7						
1692	Self								533	128	133	− 5	.74	24.0
Total			2,365	1,196	1,182	14	.85	50.6	1,481	356	370	−14	1.24	24.0
Ear No. 1111, *CH × WX:*														
1694	Self								578	142	144	− 2	.28	24.6
{1695	All waxy	None	393	212	196	16	2.39	53.9						
{1696	Self								373	99	93	6	1.05	26.5
1698	...do								540	129	135	− 6	.88	23.9
{1699	All waxy	None	511	245	255	−10	1.31	48.0						
{1700	Self								451	110	113	− 3	.48	24.4
1704	All waxy	None	192	100	96	4	.85	52.1						
{1708	...do	...do	248	121	124	− 3	.56	48.9						
{1709	Self								569	156	142	14	2.05	27.4
{1710	All waxy	None	458	240	229	11	1.52	52.4						
{1711	Self								415	103	104	− 1	.16	24.8
{1712	All waxy	None	181	94	90	4	.88	51.9						
{1713	...do	...do	179	94	89	5	1.10	52.5						
1714	...do	...do	561	287	280	7	.82	51.2						
1715	...do	...do	304	141	152	−11	1.86	46.4						
{1718	...do	...do	290	153	145	8	1.39	52.8						
{1719	Self								549	128	137	− 9	1.31	23.3
Total			3,317	1,687	1,658	29	1.5	50.9	3,475	867	869	− 2	.1	24.95
Total of the above four groups			15,305	7,817	7,653	164	3.9	51.0	12,474	3,114	3,118	− 4	.....	25.0

The horny × waxy crosses (Table IV) have a higher percentage of waxy seeds than the waxy × horny crosses (Table III). This difference is 1.4±0.41 per cent, a difference 3.9 times the probable error. While this difference could be expected as the result of chance once in 116 times, a more detailed examination of the material indicates that the difference observed for the totals is not thus to be explained. The four groups on Table IV are the reciprocals of the four groups on Table III. Thus the uppermost group on Table III is the reciprocal of the uppermost group on Table IV, etc.

A comparison of the four groups on Table III with the corresponding four groups on Table IV reveals the fact that in every case the groups on Table III have a lower percentage of waxy seeds. The percentages and probable errors for the four reciprocal groups are shown in Table V.

TABLE V.—*Inheritance of endosperm texture in the progeny of the two maize ears Nos. 1099 and 1111, by groups as shown in Table III and their reciprocals as shown in Table IV.*

Progeny of—	Nature of cross.	Percentage of waxy seeds.			D ÷ E.
		Table VI group.	Reciprocal cross.	Difference.	
Ear No. 1099	*WX* × *CH*	47.4±0.89	51.6±0.47	4.2 ± 1	4.2
Ear No. 1111	do	50.4± .67	50.9± .59	.5 ±0.89	.5
Ear No. 1099	*CX* × *WH*	50.1± .47	50.8± .51	.69± .69	1.0
Ear No. 1111	do	48.5± .7	50.6± .69	2.1 ± .98	2.1
Total	*X* × *H*	49.6± .31	50.6± .27	1.4 ± .41	3.9

Taking each group by itself, the only significant difference is that observed between the *WX* × *CH* and the *CH* × *WX* group from ear No. 1099. In this case the difference is 4.2 times the probable error and should occur as the result of chance but once in 217 times.

As above observed, however, the differences are uniform in that whenever the male parent is heterozygous for horny endosperm and the female parent homozygous for waxy endosperm the percentage of waxy seeds on the ears is lower than in the reciprocal group. This difference in reciprocals indicates a deficiency of effective male gametes bearing the waxy endosperm. This result could be brought about by a higher death rate for the gametes with the waxy character, or a less vigorous growth of the pollen tubes of such gametes, or a failure of the plants to form the gametes in equal numbers.

HORNY × SELF.

As the result of self-pollinating plants grown from the horny seeds of ears Nos. 1099 and 1111, 28 ears were obtained. (Table IV, columns 10 to 15.)

The ears resulting from self-pollinating the plants grown from horny seeds show a remarkably close approximation to the expected 25 per cent of waxy inheritance, the two individual ears that deviated in excess of three times the probable error being no more than could be expected in a group of 28 ears.

With 12,400 seeds the probable error for a 25 per cent ratio is 0.082 per cent. We may, therefore, feel reasonably certain that if the real ratio deviated from the expected by as much as three-tenths of 1 per cent the deviation could have been detected. Furthermore, the distribution of the percentages is as uniform as could be expected. Measured by the method proposed by Yule (16), the range is really smaller than the expected. In other and even larger groups it has been shown that there is a deviation of approximately 1 per cent; and since in these groups the deviation from the observed means was greater than the expected, it becomes almost certain that the deviations are due to the abnormal behavior of some of the individuals rather than to a small and consistent deviation. It would thus appear that the present group differed from the preceding by including none or very few of the aberrant individuals.

SUMMARY OF THE PROGENY OF DH 234.

The total number of ears representing the progeny of the hybrid Dh 234 and expected to have 50 per cent of the seeds waxy is 66. These 66 ears had 27,029 seeds with 50.4 per cent waxy, the deviation in this case being about 1.9 times the probable error.

While the observed percentage of waxy seeds for the 66 ears is a very close approximation to the expected percentage, we have seen that the two major groups, waxy × horny and horny × waxy, that make up this total, differ from each other by an amount that would be expected to occur as the result of chance but once in 116 times.

Had the crosses all been made in one direction—i. e., waxy by horny—there would have been a significant deviation below the expected number of waxy seeds. Had the crosses been confined to horny by waxy, the number of waxy seeds would have been in excess. Since the reciprocal crosses were made in approximately the same numbers, the fit of the observed percentage of waxy seeds for the total to the expected percentage appears good.

THIRD GENERATION OF THE HYBRID DH 237.

Four ears were selected for planting from the hybrid Dh 237. These four ears are Nos. 1129, 1130, 1131, and 1134 (Table I).

The last two ears represent crosses between Dh 237 and Dh 234, and their progenies are considered separately following the analysis of the progeny of ears Nos. 1129 and 1130. These last-mentioned ears were borne on the same plant. Ear No. 1129 was the result of self-pollinating a plant of Dh 237, while ear No. 1130 was the result of pollinating this same plant by another plant of the same hybrid.

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Ear No. 1129 had 24.1 per cent of waxy seeds, a close approximation to the expected 25 per cent, the deviation being less than the probable error. The deviation of ear No. 1130 was 3.7 times the probable error below 25 per cent. The plant that served as the male parent of ear No. 1130 bore ear No. 1135, the result of self-pollination. The deviation of this ear was also below the expected 25 per cent by three times the probable error. This fact would indicate that the low percentage of waxy seeds observed on ear No. 1130 was due to the male parent, since there was also a deficiency of waxy seeds when the male parent was self-pollinated.

TABLE VI.—*Inheritance of endosperm texture in 20 ears of maize, the waxy × horny progeny of the two ears Nos. 1129 and 1130, the progeny of hybrid Dh 237.*

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of waxy.
	Self-pollinated ♂.	Reciprocal cross.	Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8	9
Ear No. 1129, *WX* × *CH*:								
1750	1794	None	242	124	121	3	0.57	51.2
1754	1800	do	500	235	250	−15	1.99	47.0
1758	1800	do	439	213	219	− 6	.85	48.6
1762	1798	do	537	240	268	−28	3.58	44.7
1764	1800	1799	498	250	249	1	.13	50.2
1765	1800	None	528	249	264	−15	1.93	47.2
Total			2,744	1,311	1,372	−61	3.45	47.9
Ear No. 1130, *WX* × *CH*:								
1804	None	1838	363	166	181	−15	2.33	45.7
1806	do	None	435	237	217	20	2.84	54.5
1807	do	do	275	136	137	− 1	.17	49.5
1810	do	do	441	238	220	18	2.54	54.0
1813	1851	1850	398	211	199	12	1.78	53.0
1815	None	1849	465	237	232	5	.69	51.0
1816	1855	1854	515	280	257	23	3.00	54.3
Total			2,892	1,505	1,446	59	3.25	52.0
Ear No. 1129, *CX* × *WH*:								
1766	1774	None	432	222	216	6	.65	51.4
1768	1776	1775	144	75	72	3	.74	52.0
1770	None	1783	492	253	246	7	.93	51.4
Total			1,068	550	534	16	1.45	51.5
Ear No. 1130, *CX* × *WH*:								
1818	1828	1827	754	366	377	−11	1.70	48.6
1820	1837	None	207	104	108	− 4	.82	48.0
1822	1837	1836	542	293	271	22	2.80	53.8
1825	None	1835	584	268	292	−24	2.75	46.0
Total			2,087	1,031	1,043	−12	.78	49.5
Total of the above four groups			8,791	4,397	4,395	2		49.9

If any difference in the behavior of the progenies of Nos. 1129 and 1130 occurred, a lower percentage of waxy seeds on the progeny of ear No. 1130 would be expected. A careful analysis of the progeny with this point in mind failed to reveal any significant differences, so that the differences observed in the percentage of waxy seeds of the two ears, Nos. 1129 and 1130, must, for the present, be ascribed to chance; at least it does not appear to be hereditary. There were four classes of seeds on ears Nos. 1129 and 1130—colored and white waxy and colored and white horny. The four classes from each of these ears were planted separately and are separated in the tabulation, but since no differences appeared in the percentage of seeds with waxy endosperm from the colored and white seeds, they are discussed together. To avoid repetition, the progeny of the two ears are considered together, since the differences found between them were slight. The ears secured from the progeny of ears Nos. 1129 and 1130 are shown in Tables VI and VII. There were no ears with aberrant ratios larger than might be due to chance.

TABLE VII.—*Inheritance of endosperm texture in 26 ears of the horny × waxy and 17 ears of the horny × self progeny of the two maize ears Nos. 1129 and 1130, the progeny of hybrid Dh 237.*

[Lines bracketed together in pairs indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Horny × waxy.						Horny × self.					
			Number of seeds.						Number of seeds.					
	Self-pollinated ♂.	Reciprocal cross.	Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.	Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1129, *WH × CX:*														
1772	None	None	448	209	224	− 15	2.12	46.6						
1773	do	do	613	309	306	3	.36	50.4						
1774	Self								254	63	64	− 1	0.01	24.7
1775	None	1768	533	271	261	10	1.28	50.9						
1776	Self								272	80	68	12	2.50	29.4
1777	None	None	428	209	214	− 5	.71	48.8						
1778	Self								319	64	80	−16	3.07	20.0
1779	None	None	476	234	238	− 4	.54	49.2						
1780	Self								474	114	118	− 4	.63	23.6
1781	None	None	477	233	238	− 5	.68	48.9						
1782	Self								475	118	119	− 1	.15	24.9
1783	All waxy	1770	562	271	281	− 10	1.25	48.2						
1784	None	None	591	307	295	12	1.46	52.0						
1785	Self								412	90	103	−13	2.20	21.8
1786	None	None	446	211	223	− 12	1.68	47.3						
1787	Self								450	106	112	− 6	.97	23.6
1788	None	None	386	180	193	− 13	1.81	47.2						
Total			4,960	2,434	2,480	− 46	1.89	49.1	2,656	635	664	−29	1.90	23.9
Ear No. 1130, *WH × CX:*														
1827	All waxy	1818	644	310	322	− 12	1.40	48.2						
1828	Self								404	109	101	8	1.36	27.0
1829	None	None	511	276	255	21	2.75	54.0						

TABLE VII.—*Inheritance of endosperm texture in 26 ears of the horny × waxy and 17 ears of the horny × self progeny of the two maize ears Nos. 1129 and 1130, the progeny of hybrid Dh 237*—Continued.

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Horny × waxy.						Horny × self.					
			Number of seeds.					Percentage of waxy.	Number of seeds.					Percentage of waxy.
	Self-pollinated ♂.	Reciprocal cross.	Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.		Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1130, *WH × CX*—Continued.														
1833	All waxy	do	434	216	217	− 1	.14	49.8						
1834	do	do	511	250	255	− 5	.66	49.0						
1835	do	1825	503	254	251	3	.39	50.5						
1836	do	1822	297	127	148	− 21	3.61	42.8						
1837	Self								541	126	135	− 9	1.32	23.3
Total			2,900	1,433	1,450	− 17	.94	49.5	945	235	236	− 1	.14	24.9
Ear No. 1129, *CH × WX:*														
1794	Self								634	172	158	14	1.90	27.1
1795	None	None	553	268	276	− 8	1.01	48.5						
1796	Self								296	66	74	− 8	1.59	22.3
1797	None	None	230	117	115	2	.39	50.9						
1798	Self								752	194	188	6	.75	26.2
1799	None	1764	510	262	255	7	.92	51.4						
1800	Self								755	191	189	2	.25	25.3
Total			1,293	647	647		2.6	50.0	2,437	623	609	14	.97	25.7
Ear No. 1130, *CH × WX:*														
1838	All waxy	1804	545	260	272	− 12	1.52	47.8						
1839	do	None	415	208	207	1	.14	50.1						
1840	Self								308	75	77	− 2	.39	24.3
1843	All waxy	None	537	282	268	14	1.79	52.6						
1846	do	do	621	305	310	− 5	.59	49.2						
1847	Self								721	155	180	−25	3.19	21.5
1849	All waxy	1815	581	299	290	9	1.15	51.4						
1850	do	1813	561	273	280	− 7	.87	48.7						
1851	Self								547	126	137	−11	1.61	23.0
1854	All waxy	1816	614	306	307	− 1	.12	49.8						
1855	Self								563	132	141	− 9	1.30	23.5
Total			3,874	1,933	1,937	− 4	.19	49.9	2,139	488	535	−47	3.48	22.8
Total of the above four groups			13,027	6,447	6,513	− 66	1.71	49.5	8,177	1,981	2,044	−63	2.40	24.3

The four groups in Table VII are the reciprocals of the four groups in Table VI. The first group in Table VI is *WX × CH* from ear No. 1129 and the first group in Table VII is *WH × CX* from the same ear.

Since one parent was homozygous for waxy endosperm, it becomes possible to test whether the same ratio of waxy to horny genes is found in the male gametes as in the female gametes of the heterozygous parent.

The percentage of waxy seeds in Table VI is the percentage of male gametes bearing this character, while the percentage of waxy seeds in Table VII is the percentage of female gametes bearing the waxy character.

The difference between these reciprocal groups is very small, indicating that for the progeny of the hybrid Dh 237 there is little or no difference in the percentage of male and female gametes bearing waxy endosperm.

The fact is further demonstrated when the individual groups are examined. Table VIII gives the percentage of waxy seeds for the four pairs of reciprocals, with the differences between them.

TABLE VIII.—*Inheritance of endosperm texture in the progeny of the two maize ears Nos. 1129 and 1130, by groups as shown in Table VI and their reciprocals as shown in Table VII.*

Progeny of—	Nature of cross.	Percentage of waxy seeds.			D ÷ E.
		Table VI group.	Reciprocal cross.	Difference.	
Ear No. 1129	*WX* × *CH*	47.9±0.64	50.0±0.94	2.1±1.14	1.85
Ear No. 1130	do	52.0± .63	49.9± .54	2.1± .83	2.53
Ear No. 1129	*CX* × *WH*	51.5±1.00	49.1± .68	2.1±1.21	1.73
Ear No. 1130	do	49.5± .74	49.5± .63		
Total	*X* × *H*	49.9± .36	49.5± .3	.4± .47	.85

In the first instance the percentage of waxy seeds is lower when heterozygous plants were used as male parents, but in the next two pairs of reciprocals this condition was reversed, the percentage of waxy seeds being higher when heterozygous plants were used as the male parents.

In none of the pairs of reciprocals was a significant difference found, so that the percentage of male and female gametes bearing waxy endosperm may be said to be alike for the progeny of the hybrid Dh 237.

In this regard the progeny of the two hybrids differ. The progeny of the hybrid Dh 234 showed that a significant deficiency of male gametes bearing the waxy character occurred, while no such deficiency is found on the progeny of the hybrid Dh 237.

CROSSES BETWEEN THE TWO HYBRIDS DH 234 AND DH 237.

Three of the ears that were selected for planting were the result of crossing the two hybrids Dh 234 and Dh 237. These ears are Nos. 1110, 1131, and 1134 (Table I).

As only self-pollinated ears were secured from ear No. 1131, the progeny of this ear is discussed separately from the progenies of ears Nos. 1110 and 1134.

Ear No. 1131 had 22.9 per cent waxy seeds, while self-pollinated ears secured from the male and female parents had 24.2 and 23.3 per cent waxy, respectively, as shown by the following diagram:

Hybrid Dh 237 — Self — Pedigree No. 1132 (Table I), 23.3±1.2 per cent waxy
Hybrid Dh 237 — ♀ — Hybrid Dh 234 — ♂ — Pedigree No. 1131 (Table I), 22.9±1.2 per cent waxy.
Hybrid Dh 234 — Self — Pedigree No. 1117 (Table I), 24.2±1.2 per cent waxy.

As can be seen from the diagram, neither of the parents of ear No. 1131 deviated from the expected 25 per cent by a larger percentage than could be ascribed to chance, although both parents, as well as ear No. 1131, were below the expected percentage.

As ear No. 1131 was all colored, there were only two classes of seeds, horny and waxy. These were planted separately and self-fertilized by tubing (6). The waxy seeds when self-pollinated resulted in all waxy ears. Such ears, therefore, were not tabulated.

HORNY.

Four ears that were the result of self-pollinating horny plants were secured from the horny group. These ears are shown in Table IX.

Two ears were above and two below the expected 25 per cent of waxy seeds. The deviation on all of these ears could be ascribed to chance. The four ears had a total of 1,055 seeds, with 24.3 per cent waxy, the deviation of 0.7 per cent being 0.74 times the probable error.

TABLE IX.—*Inheritance of endosperm texture in ears Nos. 1893, 1894, 1895, and 1897, the progeny of maize ear No. 1131, self-pollinated, the progeny of a cross between the hybrids Dh 234 and Dh 237.*

Pedigree.	Number of seeds.				D ÷ E.	Percentage of waxy.
	Total.	Waxy.	Expected waxy.	Deviation.		
Ear No. 1893	337	94	84	10	1.61	27.9
Ear No. 1894	261	55	65	−10	1.83	21.1
Ear No. 1895	33	11	8	3	1.55	30.0
Ear No. 1897	424	97	106	− 9	1.51	22.6
Total	1,055	257	264	− 7	.74	24.3

There are two remaining ears that represent crosses between the two hybrids Dh 234 and Dh 237. These ears are Nos. 1110 and 1134 (Table I), as shown by the following diagram:

Pedigree No. 1111 (Table I), 22.2±1.0 per cent waxy.
Hybrid Dh 234 — Self
— ♀ — Pedigree No. 1110 (Table I), 27.5±1.1 per cent waxy.
Hybrid Dh 237 — ♂
— Self — Pedigree No. 1132 (Table I), 23.3±1.2 per cent waxy.

Pedigree No. 1133 (Table I), 24.6±1.0 per cent waxy.
Hybrid Dh 237 — Self
— ♀ — Pedigree No. 1134 (Table I), 16.3±1.2 per cent waxy.
Hybrid Dh 234 — ♂
— Self — Pedigree No. 1118 (Table I), 21.9±1.1 per cent waxy.

Ear No. 1110 and the two self-pollinated ears secured from the parents are all approximations of the expected 25 per cent. This is not true of ear No. 1134. The diagram shows that the female parent of the self-pollinated ear No. 1134 was a close approximation to the expected 25 per cent, while the self-pollinated ear from the male parent was below the expected by 3.1 per cent, which is almost three times the probable error. Although both parents could reasonably be said to approximate the expected 25 per cent, ear No. 1134 is below the expected by 8.7 per cent, which is 6.1 times the probable error.

There seems to be no very good explanation of this departure, either the female gametes selected male gametes bearing the horny endosperm or a differential death rate prevailed for the zygotes with waxy endosperm.

There was no difference in the behavior of the progeny of ears Nos. 1110 and 1134. The ears secured from self-pollinating plants grown from the horny seeds of No. 1134 bore 2,277 seeds, of which 25.5 per cent were waxy, the deviation being less than the probable error. Only one ear of the five secured deviated in excess of three times the probable error, and that ear, No. 1923 (Table XI), was in excess of the expected.

The 10 ears representing the progeny of ear No. 1134 that were expected to have an equal number of waxy and horny seeds had 4,943 seeds, with 49 per cent waxy. The deviation of 1 per cent is but 2.1 times the probable error. The progeny of ear No. 1134 failed to throw any light on the observed deficiency of waxy seeds in the parent ear.

The two ears, Nos. 1110 and 1134, that represent crosses between the two hybrids had but two classes of seeds, colored horny and colored waxy. These classes were planted separately. As no significant differences were found in the behavior of the progeny of the two ears, they will be considered together. The ears secured from the progeny of Nos. 1110 and 1134 are shown in tables X and XI. The ears resulting from pollinating homozygous waxy plants with heterozygous horny plants are extremely variable. Five of the eleven ears deviated from the expected percentage in excess of three times the probable error. With the exception of the ears shown in Table X the remaining ears show no significant deviation.

TABLE X.—*Inheritance of endosperm texture in 11 ears of maize, the waxy × horny progeny of ears Nos. 1110 and 1134, the progeny of crosses between hybrids Dh 234 and Dh 237.*

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of waxy.
	Self-pollinated ♂.	Reciprocal cross.	Total.	Waxy.	Expected waxy.	Deviation.		
1	2	3	4	5	6	7	8	9
Ear No. 1110:								
1856	1878	1877	525	239	262	− 23	2.97	45.6
1860	1875	1874	649	289	324	− 35	4.07	44.6
1861	None	1871	450	204	225	− 21	2.93	45.4
1863	...do	None	679	306	339	− 33	3.76	45.0
1865	1875	...do	739	380	369	11	1.2	51.4
Total			3,042	1,418	1,521	−103	5.5	46.6
Ear No. 1134:								
1898	None	None	516	237	258	− 21	2.74	45.9
1900	1921	1920	572	261	286	− 25	3.10	45.6
1902	1918	1917	765	415	382	33	3.53	54.3
1904	None	None	443	219	221	− 2	.28	49.5
1906	1923	1922	315	158	157	1	.17	50.1
1909	1925	1924	485	217	242	− 25	3.36	44.7
Total			3,096	1,507	1,548	− 41	2.19	48.7
Total of above two groups			6,138	2,925	3,069	−144	3.3	47,7

The two groups in Table XI are the reciprocals of the two groups in Table X and since one parent is homozygous for waxy endosperm it is again possible to determine whether a difference exists in the percentage of male and female gametes bearing the waxy endosperm. The ears in Table X show the proportion of waxy to horny endosperm in the male gametes, while the ears in Table XI show the proportion of waxy to horny endosperm in the female gametes. Table XII shows the differences observed in the reciprocal groups.

Table XII shows that a difference exists between the male and female gametes in the proportion of gametes bearing waxy endosperm, the male gametes bearing the waxy character being deficient.

TABLE XI.—*Inheritance of endosperm texture in eight ears of the horny × waxy and eight ears of the horny × self progeny of the two maize ears Nos. 1110 and 1134, the progeny of crosses between hybrids Dh 234 and Dh 237.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Horny × waxy.						Horny × self.					
	Self-pollinated ♂.	Reciprocal cross.	Number of seeds. Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.	Number of seeds. Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1110:														
1871	All waxy	1861	81	33	40	−7	2.3	40.6	.....	.....	.....	.....	.....	.....
{1874	None	1860	137	71	68	3	.76	51.8	.....	.....	.....	.....	.....	.....
{1875	Self	.....	.....	.....	.....	.....	.....	.....	716	151	179	−28	3.1	21.1
{1876	None	None	377	201	188	13	2.13	53.4	.....	.....	.....	.....	.....	.....
{1877	All waxy	1856	424	226	212	14	2.01	53.3	.....	.....	.....	.....	.....	.....
{1878	Self	.....	.....	.....	.....	.....	.....	.....	496	122	124	−2	.26	24.6
1882	...do	.....	.....	.....	.....	.....	.....	.....	136	28	34	−6	1.52	20.6
Total	.....	.....	1,019	531	509	22	2.04	52.2	1,348	301	337	−36	2.91	22.3
Ear No. 1134:														
{1917	All waxy	1902	452	250	226	24	3.24	55.3	.....	.....	.....	.....	.....	.....
{1918	Self	.....	.....	.....	.....	.....	.....	.....	345	93	86	7	1.16	27.0
{1920	All waxy	1900	559	254	279	−25	3.13	45.4	.....	.....	.....	.....	.....	.....
{1921	Self	.....	.....	.....	.....	.....	.....	.....	519	133	130	3	1.5	25.6
{1922	All waxy	1906	421	208	210	−2	.29	49.4	.....	.....	.....	.....	.....	.....
{1923	Self	.....	.....	.....	.....	.....	.....	.....	399	123	100	23	3.41	30.8
{1924	All waxy	1909	415	208	207	1	.14	50.6	.....	.....	.....	.....	.....	.....
{1925	Self	.....	.....	.....	.....	.....	.....	.....	457	110	114	−4	.55	24.1
1926	...do	.....	.....	.....	.....	.....	.....	.....	557	121	139	−18	2.25	21.7
Total	.....	.....	1,847	920	923	−3	.27	49.8	2,277	580	569	11	.68	25.5
Total of above two groups			2,866	1,451	1,433	18	1.0	50.7	3,625	881	856	25	1.42	24.3

TABLE XII.—*Inheritance of endosperm texture in the progeny of the two maize ears Nos. 1110 and 1134, by groups as shown in Table X and their reciprocals as shown in Table XI.*

Progeny of—	Nature of cross.	Percentage of waxy seeds. Table X group.	Reciprocal cross.	Difference.	D ÷ E.
Ear No. 1110	*X* × *H*	46.6±0.61	52.2±1.0	5.6±1.27	4.4
Ear No. 1134	....do	48.7± .61	49.8± .79	1.1±1.18	.9
Total	.....	47.7± .43	50.7± .63	3.0± .76	3.9

Fourteen self-pollinated ears were also obtained from these same horny plants. With these data it is not only possible to determine whether a difference exists between the male and female gametes, in the proportion of gametes bearing the waxy character, but also to compare the relation of the percentage of waxy seeds on the self-pollinated ear from the heterozygous parent with the percentage of male gametes bearing the waxy character, as indicated by the percentage of waxy seeds on ears that result from crossing homozygous waxy plants with heterozygous horny plants.

These 14 ears are shown in Table XIII. Column 1 of the table gives the pedigree numbers of the ears borne on the homozygous waxy plants pollinated by heterozygous horny plants. Column 2 gives the percentage of waxy seeds observed on these ears. Column 3 gives the pedigree number of the reciprocal ears of those shown in column 1. The ears shown in column 3 were borne on heterozygous horny plants, the result of pollen from homozygous waxy plants. Column 4 gives the percentages of waxy seeds on the ears shown in column 3. Column 5 gives the difference in percentage of waxy seeds between the reciprocal ears. A minus sign is used in this column to indicate the ears that had a higher percentage of waxy seeds when the male parent was heterozygous horny than when the male parent was heterozygous waxy. Column 6 gives the number of times the difference observed exceeds the probable error. Column 7 gives the pedigree number of the ears which resulted from self-pollinating the heterozygous horny plants which bore the ears shown in column 3. Column 8 gives the percentage of waxy seeds observed on the ears shown in column 7, and column 9 shows the percentage of waxy seeds expected from the gamete classes of the parents in columns 2 and 4. Column 10 gives the number of times the deviation of the percentages in column 8 from the expected 25 per cent exceeds the probable error.

TABLE XIII.—*Inheritance of endosperm texture in 14 ears of maize, the reciprocal crosses between homozygous waxy and heterozygous horny plants.*

Waxy × horny.		Horny × waxy.				Horny × self.			
Pedigree No.	Percentage of waxy.	Pedigree No.	Percentage of waxy.	Difference in reciprocal.	D÷E.	Pedigree No.	Percentage of waxy: Observed.	Percentage of waxy: Expected.	D÷E.
1	2	3	4	5	6	7	8	9	10
1552	44.8	1643	51.4	6.6±2.1	3.1	1644	25.5	23.1	0.42
1565	49.1	1632	50.0	.9±3.7	.24	1633	24.5	24.5	.19
1572	41.7	1604	51.4	9.7±3.9	2.48	1605	27.7	21.5	1.97
1576	48.8	1617	52.6	3.8±2.2	1.72	1618	32.0	25.6	3.41
1590	50.2	1619	50.0	−.2±2.1	−.09	1620	24.1	25.1	.68
1592	60.8	1621	54.9	−5.9±2.3	−2.26	1622	28.5	33.4	1.44
1594	49.4	1611	52.6	3.2±1.8	1.81	1612	31.1	26.0	4.40
1665	50.9	1686	53.5	2.6±2.4	1.07	1687	25.6	27.2	.57
1856	45.6	1877	53.3	7.7±2.2	3.50	1878	24.6	24.3	.60
1860	44.6	1874	51.8	7.2±3.2	2.29	1875	21.4	23.2	3.00
1900	45.6	1920	45.4	−.2±2.5	−.08	1921	25.6	21.0	.50
1902	45.6	1917	55.3	9.7±2.0	4.86	1918	27.0	25.2	1.16
1906	50.2	1922	49.4	.8±2.5	−.28	1923	30.8	24.8	3.41
1909	44.7	1924	50.6	5.9±2.2	2.63	1925	24.1	22.6	.55
Total	48.8	....	51.5	2.7±.61	4.44	....	25.5	25.1	1.7
Total ♀ excess	48.0	....	52.4	4.4±.73	6.60	....	25.6	25.2	1.38
Total ♂ excess	50.6	....	49.4	1.2±1.1	1.00	....	27.0	25.0	2.69

DIFFERENCES IN RECIPROCALS.

It would appear from differences in the behavior of reciprocals in the progeny of Dh 234 and also in the progeny of crosses between the two hybrids that in the descendants of certain ears there is a significant deficiency of male gametes bearing the waxy character. This deficiency may be due to a differential death rate, a lack of vigor resulting in a slower growth of the pollen tube, or an unequal formation of gametes bearing waxy endosperm.

The difference observed is not of sufficient magnitude to account for the deficiency of waxy seeds in the perjugate generation of waxy × horny hybrids. There is evidence to show that the deficiency of waxy seeds observed in the perjugate generation of waxy × horny hybrids is not entirely due to this deficiency of effective male gametes bearing the waxy character. There were 14 pairs of reciprocal crosses between identical plants. One parent of these 28 ears was homozygous for waxy, the other parent was homozygous for horny endosperm.

Of the 14 ears shown in Table XIII, 10 indicate a difference between the male and female gametes in the percentage of gametes bearing the waxy character. In 9 of these 10 pairs the proportion of male gametes bearing the waxy character was below the expected percentage and the proportion of female gametes was above the expected, indicating that the difference between the male and female gametes was not only due to a deficiency of male gametes bearing waxy endosperm but also to an excess of female gametes bearing waxy endosperm.

The total for the 14 pairs of reciprocals shows a difference of 2.7 per cent between the male and female gametes in the number of gametes bearing the waxy character. A difference of this magnitude would be expected to occur as the result of chance but once in over 300 times. Ten of the 14 pairs show the percentage of male gametes bearing the waxy character to be lower than the percentage of female gametes bearing this character.

While the totals show dependable differences, there is but one case where the individual reciprocals differ by a significant amount. Nos. 1902 and 1917 differ by 9.7 ± 2.0, which is 4.86 times the probable error. The relations of the ears of this last pair are shown in figure 3. The difference in this case is due to both the male and female gametes. There is a deficiency of 4.4 per cent in the proportion of male gametes with waxy endosperm, while there is an excess of 5.53 per cent of female gametes bearing waxy endosperm.

Self-pollinating such an ear would be expected to result in an ear with 25.2 per cent waxy. Ear No. 1918, which is the result of self-pollinating the above heterozygous horny plant, had 27.0 per cent waxy, the deviation of 1.8 per cent from 25.2 per cent being no larger than could be ascribed to chance. As long as the deficiency in any class of gametes in one sex is made up in the other sex, the discrepancy would have to be relatively large before it could be detected in self-pollinated progeny. In an ear of 600 seeds, the deviation above and below 50 per cent would need to be as much as 38 per cent.

Summing up the inheritance of waxy endosperm for the third generation of the hybrids Dh 234 and Dh 237 and the crosses between them, we have 57 ears that are expected to have 25 per cent of the seeds waxy. The observed percentage for the total of 25,329 seeds is 24.6 per cent. The deviation from 25 per cent is 2.09 times the probable error.

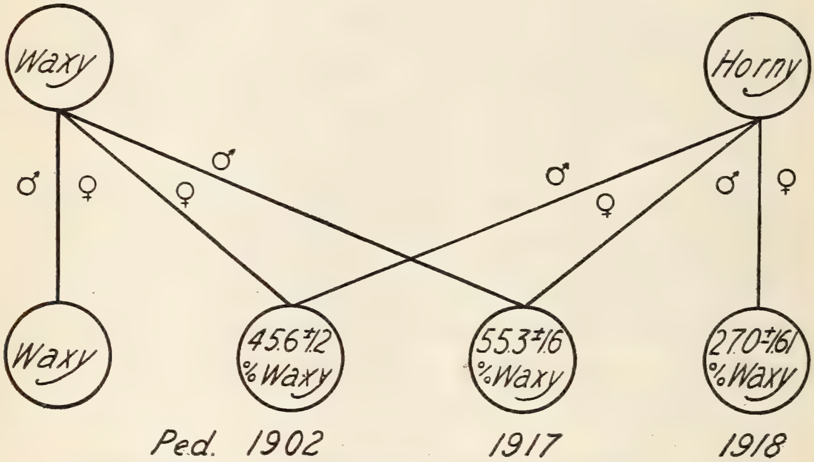

FIG. 3.—Diagram showing the relations of ears Nos. 1902, 1917, and 1918.

The second-generation ears of these bybrids, together with 45 ears previously published (7), determined the percentage of waxy seeds to be 23.7 per cent. The difference between the second and third generation ears is 0.9±0.21 per cent, which would be expected as the result of chance once in 142 times.

There were seven groups of ears that made up the total of 25,329 seeds (Table XIII). Of these seven groups, five were below and two above 25 per cent. From this we may conclude that the percentage of waxy seeds for the third generation of the hybrids was significantly below 25 per cent, but even with the 25,000 seeds involved, it is not possible to determine whether the percentage observed is approximating 23.7 per cent, the mean percentage found for the second-generation ears.

There are 131 ears of the third generation that are expected to have equal proportions of waxy and horny seeds (Table XIV). The 131 ears had 57,851 seeds, of which 49.8 per cent were waxy. The deviation of this percentage from 50 per cent is insignificant. The percentage of waxy seeds has been determined as 23.9 per cent for the 198 ears expected to have 25 per cent of the seeds waxy.

The proportion of gametes bearing the waxy character to the gametes bearing the horny character necessary to account for 23.9 per cent of waxy seeds on self-pollinated ears is 48.9 to 51.1.

The 131 ears on this basis are expected to have 48.9 per cent of waxy seeds. The deviation of the observed from this percentage would be expected to occur as the result of chance once in 25,000 times.

TABLE XIV.—*Inheritance of endosperm texture in all the maize ears.*

EARS EXPECTED TO HAVE 50 PER CENT OF THE SEEDS WAXY.

Nature of cross.	Number of ears.		Number of seeds.				D ÷ E.	Percentage of waxy.
	Observed.	Below expected.	Total.	Waxy.	Expected waxy.	Deviation.		
Progeny of hybrid Dh 234:								
Ear No. 1099	40	15	16,428	8,303	8,215	88	2.03	50.6
Ear No. 1111	26	12	10,601	5,316	5,300	16	.46	50.1
Progeny of hybrid Dh 237:								
Ear No. 1129	22	12	10,065	4,942	5,031	− 89	2.60	49.0
Ear No. 1130	24	13	11,753	5,902	5,876	26	.71	50.2
Progeny of crosses between hybrids Dh 234 and Dh 237:								
Ear No. 1110	9	5	4,061	1,949	2,030	− 81	3.76	48.0
Ear No. 1134	10	6	4,943	2,427	2,471	− 44	1.85	49.0
Total	131	63	57,853	28,839	28,925	− 86	1.05	49.8

EARS EXPECTED TO HAVE 25 PER CENT OF THE SEEDS WAXY.

Nature of cross.	Observed.	Below expected.	Total.	Waxy.	Expected waxy.	Deviation.	D ÷ E.	Percentage of waxy.
Second generation ears (Table I):								
Hybrid Dh 234	54	36	30,571	7,309	7,643	− 334	7.5	23.9
Hybrid Dh 237	42	28	24,188	5,779	6,047	− 268	5.90	23.9
Previously reported	45	29	22,339	5,179	5,585	− 406	9.24	23.1
Total	141	93	77,098	18,267	19,274	−1,007	12.4	23.7
Progeny of hybrid Dh 234:								
Ear No. 1099	18	8	7,516	1,891	1,879	12	.47	25.2
Ear No. 1111	10	7	4,956	1,223	1,239	− 16	.67	24.6
Progeny of cross between hybrids Dh 234 and Dh 237:								
Ear No. 1110	3	3	1,348	301	337	− 36	2.91	22.3
Progeny of hybrid Dh 237:								
Ear No. 1129	11	6	5,093	1,258	1,273	− 15	.62	24.7
Ear No. 1130	6	5	3,084	725	771	− 46	2.84	23.5
Progeny of cross between hybrids Dh 237 and Dh 234:								
Ear No. 1131	4	2	1,055	257	264	− 7	.74	24.3
Ear No. 1134	5	2	2,277	580	569	11	.68	25.5
Total for third-generation ears	57	33	25,329	6,235	6,332	− 97	2.09	24.6
Total for both second and third generation ears	198	126	102,427	24,502	25,607	− 105	11.82	23.9

SUMMARY OF THE INHERITANCE OF WAXY ENDOSPERM.

A large amount of data has been secured that confirms previous observations on the inheritance of the waxy endosperm which had been found to reappear in deficient numbers in the perjugate generation of crosses with horny and with sweet varieties of maize.

By adding all of the ears expected to have 25 per cent of the seeds waxy, including the 45 ears previously reported (7), there are 198 ears having 102,427 seeds. The mean percentage of waxy seeds is 23.9 and the deviation of 1.1 per cent would be expected to occur as the result of chance but once in 10 raised to the fifteenth power.

This deviation though apparently small is certainly too large to be attributed to chance. The apparently slight deviation from 25 per cent and the large number of individuals necessary to establish the significance of such small deviations suggest the possibility that such departures may not be uncommon for other character pairs which have not been subjected to such an exhaustive test.

Although the observed deviation could not reasonably be expected to occur as the result of chance, all of the individuals do not approximate the mean percentage of the whole. An analysis of the "goodness of fit" of the individual ears to their observed mean by the use of the method proposed by Yule (16) showed that the individual plants did not form a single homogeneous group with a mean percentage of waxy seeds below 25 per cent, but that many of the individual ears could not be considered as merely chance deviations.

Thus in hybrids between waxy and horny individuals the mean percentage of waxy seeds reappearing in the perjugate generation is below the expected 25 per cent by an amount too large to be due to chance. The differences between individual plants with respect to this character are also too large to be due to chance.

Reciprocal crosses clearly indicated that in some cases the percentage of male gametes bearing the waxy character was below that expected. It has not been possible thus far to determine whether this observed deficiency is due to a higher death rate, reduced vigor, or a failure of equal segregation.

The deficiency of waxy seeds can not be due to a fractionation of this character, since such a fractionation could not result in horny seeds but should give seeds that were neither horny nor waxy.

INHERITANCE OF ALEURONE COLOR.

The crosses made between the white waxy Chinese variety and the colored pop variety also produced excellent material for the study of aleurone color. The results in a very striking manner conform to the Mendelian proportions expected in monohybrid and dihybrid ratios.

In many crosses involving aleurone color the inheritance is blended rather than alternative, and classification is more or less arbitrary. In the Algeria × Chinese hybrids the classes were exceptionally good, especially in the second generation, no ears difficult of classification being found.

In the third generation, however, this crisp difference partially disappeared. Several ears were found that were so minutely spotted that an accurate classification was impossible and therefore not undertaken. The deviations in the individual ears were also somewhat wider, a few being found that could not be considered as approximations of any Mendelian ratio founded on reasonable assumptions.

In presenting the results obtained, all possible precautions have been taken to eliminate personal error. There is always room for a slight difference of opinion in the classification of aleurone color, owing to the fact that some persons detect color where others fail.

The chief object of the investigation being to study the correlation between aleurone color and endosperm texture, it was desirable to reduce all unnecessary complications. For this reason, only ears that had definitely alternative classes were considered. The conclusions, therefore, are based on ears that had very distinct classes, eliminating the chance that aberrant ratios were due to inability to properly classify the seeds. Without doubt much could be learned from a careful study of the inheritance of aleurone color in the ears that did not have definitely alternative classes. This bulletin therefore does not present a complete study of aleurone color, since only a part of the material was analyzed. It is believed that the results do afford an accurate measure of the percentage of white seeds segregating from white × colored crosses on ears with distinct classes.

The number of individuals classified is believed to be larger than in any previous experiment with aleurone color. The numerical equality of the two classes of gametes at segregation has consequently been subjected to a more searching test.

Since faintly colored ears were discarded, it is not surprising that the inheritance of aleurone color for these hybrids admits of comparatively simple explanation. That two factors are concerned in the production of aleurone color is clearly indicated by these two hybrids. Most of the ears require an explanation no more complicated, but with the partial results of the season of 1914, all the ears of which are not at present completely classified, a third factor becomes necessary, with a possible fourth.

It can easily be seen that many complications are to be expected from the recombination of these factors; hence, this phase of the problem is just touched upon in this bulletin. That these complications eventually arise in the study of aleurone color, as with many other characters, certainly limits the general application of Mendelian explanations, but should not conceal the fact that Mendelian segregation does occur with respect to aleurone color and that the numerical relations are wonderfully exact.

GAMETIC COMPOSITION OF THE TWO HYBRIDS DH 234 AND DH 237.

The percentage of white seeds obtained in the second generation of the hybrid Dh 234 showed that the aleurone color of this hybrid was behaving as a unit character, all the ears approximating 25 per cent white. The second-generation plants of the hybrid Dh 237 fell into two main groups, approximately half of the plants having a monohybrid and the other half a dihybrid ratio of white to colored seeds.

When the two hybrids were crossed, two classes of ears resulted—one group all colored, the other group having the monohybrid ratio of white to colored seeds. To explain these phenomena, it becomes necessary to assume that aleurone color is the result of two factors. The hybrid Dh 234, all the plants of which, when self-pollinated or crossed with sister plants, resulted in ears with a monohybrid ratio of white to colored seeds, must have been homozygous for one color factor and heterozygous for the other. The plants of Dh 237 which when self-pollinated produced ears with a monohybrid ratio of white seeds were also heterozygous for one color factor and homozygous for the other.

Crosses between plants of this type with plants of the hybrid Dh 234 resulted in ears all the seeds of which were colored, indicating that the factor homozygous in Dh 234 was heterozygous in Dh 237. Since one-half of the plants of the hybrid Dh 237 when self-pollinated or crossed with sister plants produced ears with a dihybrid ratio of white and colored seeds, these plants must be heterozygous for both color factors. Crosses between plants of this nature and plants of the hybrid Dh 234 resulted in ears with a monohybrid ratio of white to colored seeds.

It will be recalled that self-pollinating plants of the hybrid Dh 237 resulted in two approximately equal classes of ears, one with a monohybrid ratio of white to colored seeds and one with a dihybrid ratio of white to colored seeds. The hybrid Dh 234 when self-pollinated produced only ears with a monohybrid ratio, but when crossed with plants of the hybrid Dh 237 two classes of ears again resulted, one class having all the seeds colored, while an equal number had a monohybrid ratio of white to colored seeds.

To explain the two classes of ears resulting from self-pollinating first-generation plants of the hybrid Dh 237 and at the same time to explain the results obtained when first-generation plants of the hybrid Dh 237 were crossed with first-generation plants of the hybrid Dh 234, it is necessary to assume somewhat involved gametic formulæ.

It is assumed that in the first cross (Dh 237) the Chinese parent had the gametic combination *cR cR* and the Algeria *CR Cr*, where

C and *R* are the presence of color factors and *cr* their absence, both *C* and *R* being necessary to produce color. Were this true, wherever *cR* fertilized *CR* a colored seed would result, and this seed when planted would make the gametes *CR* and *cR*, which would give a ratio of 3 colored to 1 white, when self-pollinated.

Wherever *cR* fertilized *Cr*, a colored seed would result, which when planted would make four kinds of gametes as follows: *CR*, *Cr*, *cR*, and *cr*. Self-pollinating such a plant would result in an ear with 9 colored to 7 white seeds.

In the second cross (Dh 234) it is assumed that the Chinese parent had the gametic composition of *Cr Cr*, while the Algeria parent had the gametic combination of *CR CR*. Wherever *Cr* fertilized *CR*, a colored seed would result, which when planted would make the gametes *CR* and *Cr*. Such a plant when self-pollinated would give 3 colored seeds to 1 white. As all the seeds of the hybrid Dh 234 have the combination *CC Rr*, nothing but 3 to 1 ratios could result from self-pollinating any of the plants of this hybrid.

When the combination *CR Cr* is pollinated with the other hybrid combination of *CR cR*, an all-colored ear would be the result, but when the combination of Dh 234 *CR Cr* is pollinated by the other combination of Dh 237, *CR*, *Cr*, *cR*, or *cr*, an ear having 3 colored seeds to 1 white would be the result. This fulfills the observed conditions. Whenever an Algeria plant with the gametic composition *CR Cr* is self-pollinated, there should result an ear with 3 colored seeds to 1 white. Nothing but all-colored ears have been obtained as a result of self-pollinating Algeria plants, but there have not been more than 10 or 12 self-pollinated Algeria plants, so that the failure to obtain an ear with 3 colored seeds to 1 white calls for no comment. Two other crosses described below do afford evidence, however, that Chinese plants of the gametic composition *cR cR* and Algeria plants with the composition *CR Cr* do occur. On the other hand, whenever a Chinese plant producing *Cr* gametes was pollinated with Chinese producing *cR* gametes an all-colored ear should result. We have never obtained any colored seed in crosses between two plants of white Chinese, although a large number of such crosses have been made, a fact which makes necessary the further assumption that plants with the gametic formula ascribed to one of the Chinese parent plants must be rare.

An F_1 plant of the hybrid Dh 234 was fertilized with pollen from a white waxy Chinese plant; the resulting ear was all colored. A second ear on the Chinese plant was self-pollinated and was all white, while a second ear on the hybrid Dh 234 was self-pollinated, producing 26 per cent white. These results accord with the idea

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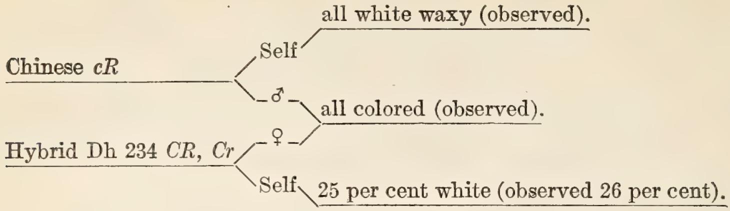
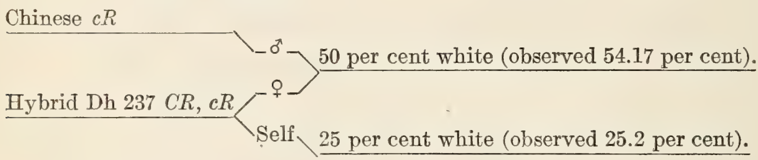
that the Chinese plant was producing gametes *cR cR*. The cross is shown by the following diagram:



An F_1 plant of the hybrid Dh 237 was pollinated with Chinese, and the resulting ear had 54.1 per cent white, while a second ear of the Dh 237 plant, when self-pollinated, had 25.2 per cent white. As Dh 237 segregating 3 colored seeds to 1 white, when self-pollinated, has been assumed to have the composition *CR cR*, a Chinese plant producing only *cR* gametes would be expected to give 50 per cent white when crossed with Dh 237 segregating 3 colored to 1 white, as in the following diagram:



COMPOSITION IN THE SECOND GENERATION OF THE HYBRID DH 234.

The hybrid Dh 234 had 46 ears, which were obtained from 31 plants, many plants having two ears. Of these 46 ears, 25 were the result of self-pollination, 12 were the result of fertilization by sister plants of the same hybrid, and 9 were the result of pollinating the hybrid Dh 234 with pollen from the hybrid Dh 237. There appeared to be no difference among these three groups as to the percentage of seeds with colored aleurone, so that they were all tabulated together and arranged numerically by pedigree numbers. Two ears from a single plant are indicated by a bracket inclosing the pedigree numbers of the ears.

The 46 ears are shown in Table XV. The total number of seeds for these ears is 26,383, with 25.8 per cent white, the expected being 25 per cent, a deviation of 0.8 per cent, which is 4.45 times the probable error. The individual ears ranged from 21.4 per cent white to 30.9 per cent white, making a continuous series. Five of the ears deviated above the expected in percentage by an excess of three times the probable error, two of these deviating by four times the probable error. Of the 46 ears, 30 had white seeds in excess of the expected number, 13 below the expected percentage, and 3 were exactly 25 per cent white.

TABLE XV.—*Inheritance of aleurone color in 46 maize ears, the second-generation progeny of the hybrid Dh 234, Chinese variety × Algeria.*

[Lines bracketed together in pairs indicate ears borne on the same plant; ears selected for planting are designated by an asterisk (*).]

Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of white.
Progeny ear.	Self-pollinated ♂	Total.	White.	Expected white.	Deviation.		
{1099*	1106	657	165	164	1	0.3	25.1
{1100	1103	599	172	149	23	3.2	28.7
1101	1103	533	165	133	32	4.7	30.9
1102	Self	517	148	129	19	2.8	28.0
1103	do	272	68	68			25.6
{1104	1108	573	151	143	8	1.0	26.3
{1105	Self	609	177	152	25	3.4	29.0
1106	do	690	178	176	2	.8	25.7
{1108	do	691	196	172	24	3.1	28.3
{1109	1112	402	113	100	13	2.2	28.0
1111*	Self	747	192	186	6	.8	25.8
{1112	do	733	215	183	32	4.0	29.3
{1113	1118	643	168	160	8	1.1	26.2
{1114	1118	428	112	107	5	.8	26.1
{1115	1112	508	134	127	7	1.1	26.3
{1116	1118	322	87	80	7	1.3	27.0
{1117	Self	564	144	141	3	.4	25.5
{1118	do	623	174	155	19	2.6	27.9
{1119	1108	414	117	103	14	2.3	28.2
{1120	1117	655	182	163	19	2.5	27.7
{1121	Self	687	191	172	19	2.5	27.8
1515	do	555	141	139	2	.3	25 4
{1518	1726	510	130	127	3	.4	24.5
{1519	Self	605	156	151	5	.7	25.8
1523	do	571	133	143	− 10	1.4	23.3
{1524	1724	773	189	193	− 4	.5	24.5
{1525	Self	212	53	53			25.0
1527	do	614	148	153	− 5	.7	24.1
1529	do	334	87	86	1	.2	26.0
{1530	1733	676	182	169	13	1.7	26.95
{1531	Self	659	176	165	11	1.4	26.7
{1532	1729	707	158	177	− 19	2.4	22.77
{1533	Self	679	175	169	6	.8	25.8
1534	do	492	127	123	4	.6	25.8
1537	do	592	148	148			25.0
{1538	1733	609	156	152	4	.5	25.6
{1539	Self	626	138	156	− 18	2.4	22.0
1540	1736	679	161	169	− 8	1.1	23.7
1541	1736	631	135	158	− 23	3.1	21.4
{1542	1723	515	114	128	− 14	2.1	22.1
{1543	Self	570	131	142	− 11	1.6	23.0
1545	do	417	109	104	5	.8	26.1
{1546	1747	800	196	200	− 4	.5	24.5
{1547	1537	633	145	158	− 13	1.8	22.8
1549	Self	479	138	119	19	2.9	28.8
1551	do	578	132	144	− 12	1.7	22.8
Total		26,383	6,807	6,596	211	4.5	25.8

The deviation of 4.45 times the probable error above the expected percentage for the total number of seeds, together with the large proportion of ears having an excess of white seeds, indicates a rather definite tendency toward a higher percentage of the recessive class than that called for by the Mendelian theory.

The inclination is to attribute such a small variation to a failure to properly classify the seeds, so that some faintly colored seeds were being included with the white seeds. The number of individuals necessary to detect such a slight error would be very large, so that the number of second-generation ears obtained is not sufficient to shed light on this matter.

COMPOSITION IN THE SECOND GENERATION OF THE HYBRID DH 237.

An examination of the zygotic formulæ for the hybrid Dh 237 will show that two equal groups of plants are to be expected in this hybrid—one group homozygous for the color factor *R* and heterozygous for the factor *C*, the other group being heterozygous for both of these factors. Representatives of both groups were obtained, 8 plants exhibiting a dihybrid and 19 plants a monohybrid ratio of white to colored seeds. Although these two ratios were expected in equal numbers, the deviation of 5 plants below the expected for the dihybrid ratio may be looked upon as a chance fluctuation.

In tabulating the plants, only 23 are shown in Tables XVI and XVII, as four plants, owing to the nature of the pollinations, produced all-colored ears only and were not tabulated. It will be recalled that all of the plants of the hybrid Dh 234 were alike in that they were homozygous for the factor *C* and heterozygous for the factor *R*.

Two groups of ears are to be expected in crossing these two hybrids: One group all colored, the result of crossing the plants of Dh 237 constituted *cC RR* with Dh 234 *CC Rr;* the other group with a monohybrid ratio of white to colored seeds, the result of crossing plants of Dh 237 constituted *Cc Rr* with Dh 234 *CC Rr*. In both cases self-pollinating plants of the hybrid Dh 234 show ears with a monohybrid ratio. In the first instance self-pollinated plants of the hybrid Dh 237 should also result in ears with monohybrid ratios and in the second instance in dihybrid ratios of white to colored seeds.

With this expectation it becomes possible to separate the plants of the hybrid Dh 237 when they were both crossed with the hybrid Dh 234 into two classes, one of which contains plants heterozygous for two color factors and the other with plants homozygous for one and heterozygous for the other factor.

Only four plants of the progeny of the hybrid Dh 237 were observed to have a dihybrid ratio of white to colored seeds. These are shown in Table XVII. However, an examination of Table XVI reveals the fact that eight plants were the result of crossing the hybrids Dh 237 and Dh 234. Since these eight plants resulted in ears with a monohybrid ratio of white to colored seeds, we must conclude from the gametic formula that had they been self-pollinated they would have given dihybrid ratios.

The four ears shown in Table XVII are the result of self-pollinating second ears borne on four of the eight plants just discussed. The plants which as the result of self-pollination produced ears Nos. 1132, 1133, 1721, 1741, 1743, and 1745 in Table XVI also produced second ears, the result of crossing Dh 237 with Dh 234. These latter ears were all colored.

Twenty-nine ears were borne on first-generation plants of the hybrid Dh 237 that may be compared with the monohybrid ratio of 3 colored to 1 white. As has been said before, some of these ears are self-pollinated, some are crosses between sister plants, and some are crosses between the hybrids Dh 237 and Dh 234. In this latter cross only plants of the hybrid Dh 237 that were heterozygous for two color factors would give a monohybrid ratio of white to colored seeds when crossed with the hybrid Dh 234.

It may not be immediately apparent that crosses between two groups of plants which when self-pollinated produce ears with 43.75 and 25 per cent, respectively, will give ears with 25 per cent white. A consideration of the gametic formulæ shows, however, that this is according to expectation. All crosses with this hybrid that resulted in other than all-colored ears approximated 25 per cent white and were therefore included with the self-pollinated and pure-seeded ears in Table XVI.

The 29 ears in Table XVI had a total of 16,947 seeds, with 25.4 per cent white, the deviation of 0.4 per cent in this case being only 1.84 times the probable error. Two of the ears deviated in excess of three times the probable error, both of these being above the expected percentage. The ears ranged from 21.6 per cent white to 28.7 per cent white, forming a well-connected series, and since the range is within four times the probable error, these ears may all be looked upon as deviations from the theoretical 25 per cent. This regularity is an exception to that encountered among most of our previous hybrids and provides an excellent opportunity to study the correlation between endosperm texture and aleurone color in crosses where the percentage of white to colored seeds is behaving in a regular manner.

The four ears resulting from self-pollinating plants of the hybrid Dh 237 that were heterozygous for two factors for color are shown in Table XVII. These four ears had a total of 2,477 seeds, with 43.3 per cent white. The deviation of 0.45 per cent from the expected percentage is less than the probable error. One ear, No. 1726, was slightly over 5 per cent in excess of the expected, the deviation in this case exceeding the probable error by 3.5 times. Another ear, No. 1747, was below the expected percentage by 3.3 times the probable error.

TABLE XVI.—*Inheritance of aleurone color in 29 maize ears, the second-generation progeny of the hybrid Dh 237, Algeria × Chinese variety (monohybrid).*

[Lines bracketed together in pairs indicate ears borne on the same plant; ears selected for planting are designated by an asterisk (*); ears borne on plants which when self-pollinated proved to be heterozygous for two color factors are indicated by a dagger (†); ears borne on plants which had they been self-pollinated would have proved to be heterozygous for two color factors are indicated by a double dagger (‡).]

Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of white.
Progeny ear.	Self-pollinated ♂.	Total.	White.	Expected white.	Deviation.		
1122	None	647	148	162	−14	1.9	22.8
1124	...do	672	171	168	3	.4	25.4
1125	Self	837	241	209	32	3.8	28.7
{1127	1125	723	190	181	9	1.1	26.2
{1128	Self	319	69	80	−11	2.1	21.6
{1129*	...do	747	189	187	2	.3	25.1
{1130*	1135	741	188	185	3	.4	25.3
1132	Self	575	160	144	16	2.3	27.8
1133	...do	758	175	189	−14	1.7	23.1
{1135	...do	627	166	157	9	1.2	26.4
{1136	1137	615	175	154	21	2.9	28.4
{1137	Self	740	205	185	20	2.5	27.7
{1138	1135	548	128	137	− 9	1.6	23.3
1721	Self	712	160	178	−18	2.3	22.5
1722†	1543	677	193	169	24	3.1	28.5
1724‡	1523	374	90	93	− 3	1.9	24.1
1725†	1519	472	125	118	7	1.1	26.5
{1728‡	1903	421	105	105	....	....	24.9
{1729‡	1533	613	148	153	− 5	.7	24.2
1730‡	1539	401	102	100	2	.3	24.9
{1733‡	1741	634	164	158	6	.9	25.9
{1734‡	1531	516	133	129	4	.6	25.8
1735†	1540	458	111	114	− 3	.5	24.2
1738	Self	472	119	118	1	.1	25.2
1741	...do	485	120	121	− 1	.1	24.7
1743	...do	575	127	144	−17	2.4	22.1
1745	...do	625	139	156	−17	2.4	22.2
1746†	1547	621	168	155	13	1.8	27.1
1749	Self	342	98	85	13	2.4	28.6
Total	....	16,947	4,307	4,237	70	1.8	25.4

TABLE XVII.—*Inheritance of aleurone color in four maize ears, the second-generation progeny of the hybrid Dh 237, Algeria × Chinese variety (dihybrid).*

Pedigree No. of—		Number of seeds.				D ÷ E.	Percentage of white.
Progeny ear.	Self-pollinated ♂.	Total.	White.	Expected white.	Deviation.		
1723	Self	664	284	290	− 6	0.7	42.75
1726	...do	560	273	245	28	3.5	48.8
1736	...do	595	256	260	− 4	.5	43.0
1747	...do	658	259	288	−29	3.3	39.4
Total	....	2,477	1,072	1,083	−11	.66	43.3

COMPOSITION IN THE THIRD GENERATION OF THE HYBRID DH 234.

Three ears were selected from the progeny of hybrid Dh 234 and planted the following season. Two of these ears are Nos. 1099 and 1111, in Table XVIII. The third ear was a cross between the two hybrids Dh 234 and Dh 237, and since it was all colored it does not appear in Table XVIII. The progeny of this last-mentioned ear are considered later in connection with two similar ears borne on plants of the hybrid Dh 237. The ear numbered 1099 was a cross between two sister plants and had almost exactly the expected percentage of white seeds. A self-pollinated ear secured from the male parent also was a close approximation to the expected 25 per cent.

The ear numbered 1111 in Table XVIII was the result of self-pollination. This ear also had white seeds, closely approximating 25 per cent. There were four classes of seeds on both the ears Nos. 1099 and 1111. These four classes were planted separately. An examination of the data failed to show any significant differences in the behavior of aleurone color due to the texture of the endosperm, making it possible to disregard the endosperm texture in analyzing the aleurone colors.

The progeny from the two ears behaved practically alike, no significant differences being found. Hand-pollinated ears to the number of 85 that had both colored and white seeds were obtained, 50 ears being from the progeny of ear No. 1099 and 35 ears from the progeny of ear No. 1111.

WHITE × COLORED.

Twenty-nine of the 85 ears obtained from the progeny of ears Nos. 1099 and 1111 were the result of crossing plants grown from the white seeds with plants grown from the colored seeds of the same ears (Table XVIII). The table is so arranged that the progeny from each of the four groups of each ear may be examined separately, if desired. In column 1 is found the number of the progeny ear from which the plants that produced the ears whose pedigree numbers are there given were grown. In this same column are also found the symbol letters for the characters. Thus the first six ears in Table XVIII, which are separated from the remaining three groups by a total, are the result of crossing plants grown from the white waxy (*WX*) seeds with plants grown from the colored horny (*CH*) seeds of ear No. 1099. The symbols mentioned first indicate the character of the seeds from which the female parents were grown. The expected proportion of white seeds is 50 per cent. The 29 ears had 11,949 seeds with 47.2 per cent white, the deviation being more than 9.4 times the probable error. A deviation of this magnitude would not be expected to occur as the result of chance more than once in over a billion times.

Two of the four groups that make up the total deviated below the expected by an amount too large to be due to chance. In one of these groups the result of crossing white horny by colored waxy seeds from ear No. 1099, the deviation of 6.9 times the error is due in a large measure to two ears, both below the expected by an amount more than eight times the probable error. One other ear, No. 1653, deviated below the expected by more than seven times the probable error, having only 39.3 per cent white. A reexamination of these ears failed to reveal errors in classification.

TABLE XVIII.—*Inheritance of aleurone color in 29 ears of maize, the white × colored progeny of the two ears Nos. 1099 and 1111, the progeny of hybrid Dh 234.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Number of seeds.				D÷E.	Per centage of white.
	Self-pollinated ♂.	Reciprocal cross.	Total.	White.	Expected white.	Deviation.		
1	2	3	4	5	6	7	8	9
Ear No. 1099, *WX × CH:*								
1552	1644	1643	506	232	253	−21	2.8	45.8
1555	1705	None	230	113	115	−2	.4	49.1
1558	None	1634	562	296	281	15	1.9	52.7
1562	do	None	415	205	207	−2	.3	49.4
1563	do	do	257	128	128			50.0
1564	do	do	438	212	219	−7	1.0	48.4
Total			2,408	1,186	1,204	−18	1.1	49.4
Ear No. 1111, *WX × CH:*								
1648	1696	None	712	345	356	−11	1.2	48.5
1651	1694	do	286	149	143	6	1.1	52.1
1652	1700	do	611	282	305	−23	2.7	46.2
1653	1703	do	502	198	251	−53	7.0	39.3
1654	1705	do	387	177	193	−16	2.4	45.7
{1658	1707	do	491	227	245	−18	2.4	46.3
{1660	None	do	600	310	300	10	1.2	51.6
Total			3,589	1,688	1,794	−106	5.0	47.0
Ear No. 1099, *WH × CX:*								
1602	1582	None	322	150	161	−11	1.8	46.6
1604	1573	1572	171	88	85	3	.7	51.5
1606	1571	None	391	196	195	1	.2	50.1
1608	1578	1577	460	215	230	−15	2.1	46.8
1610	None	1579	303	104	151	−47	8.4	34.3
1614	1589	1584	384	183	192	−9	1.4	47.6
1615	None	None	484	178	242	−64	8.7	36.8
1616	1575	do	502	259	251	8	1.1	51.6
1619	1591	1590	467	222	233	−11	1.5	47.6
1621	1593	1592	348	160	174	−14	2.2	46.0
1623	1585	1584	497	254	248	6	.8	51.5
1624	1593	None	67	36	33	3	1.1	53.8
Total			4,396	2,045	2,198	−153	6.9	46.6
Ear No. 1111, *WH × CX:*								
1678	1666	None	297	128	148	−20	3.4	43.1
1681	1670	do	441	199	220	−21	3.0	45.1
1682	None	do	448	205	224	−19	2.7	45.8
1686	1666	1665	370	179	185	−6	.9	48.4
Total			1,556	711	778	−67	5.0	45.6
Total of the above four groups			11,949	5,630	5,974	−344	9.4	47.2

The percentages for the three ears are 39.3, 34.3, and 36.8 white. These figures are closer approximations to the Mendelian dihybrid proportion of 43.75 per cent than to the expected 50 per cent white. The nature of the crosses, however, prohibits a dihybrid ratio.

Three ears, Nos. 1610, 1615, and 1653, were all borne on plants grown from white seeds and were pollinated with plants grown from colored seeds of the hybrid Dh 234. The plants grown from the white seeds could be making but one class of gametes, *Cr*, and the plants grown from the colored seeds were making two classes of gametes, *CR* and *Cr*.

A self-pollinated ear, No. 1703, was secured from the male parent of ear No. 1653. If the 39.3 per cent of white seeds on ear No. 1653 was due to the male parent being equally deficient in both male and female gametes bearing one of the two color factors the expected per-

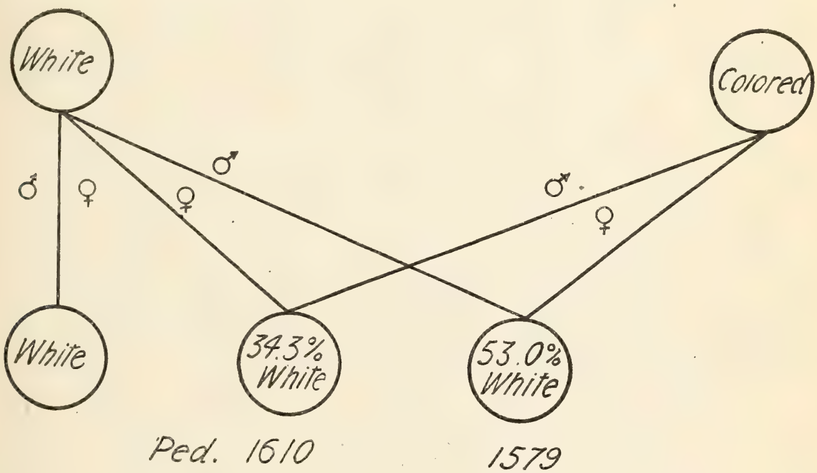


FIG. 4.—Diagram showing the relations of ears Nos. 1610 and 1579.

centage of white seeds on a self-pollinated ear would be 15.45 per cent, but since the deficiency was observed only for the male gametes a percentage of 19.65 per cent could be expected. The observed proportion on ear No. 1703 was 22.3 per cent, which is not a significant departure from the monohybrid 25 per cent or the 19.65 per cent indicated by the deficiency of colored seeds in ear No. 1653.

Further analysis is also possible for ear No. 1610, which had a reciprocal ear in No. 1579. This reciprocal ear gives a close approximation to the expected 50 per cent, while ear No. 1610 was below the expected by 8.4 times the probable error. The difference between these two reciprocals is 18.7±2.4 per cent, a difference of 7.8 times the probable error. No analysis is possible for ear No. 1615, but for the two ears numbered 1610 and 1653 there is indicated either a failure of dominance in some of the seeds or a deficiency on the part of the male parent of gametes bearing one of the color factors.

This deficiency could be due to a differential death rate, a lessened vigor resulting in a slower growth of the pollen tube, or to a failure of the plant to produce gametes in equal proportions. It will be recalled that the plants heterozygous for colored aleurone are presumed to be making two classes of gametes, *CR* and *Cr*; a deficiency of white seeds when plants of this nature are used as male parents on plants making one class of gametes (*Cr*) indicates a deficiency of gametes bearing *Cr*. The relations of those ears are shown in figures 4 and 5.

The large deviation for the total seeds of the 29 ears is due to a great extent to the three ears that deviated by more than seven times the probable error. These ears must stand as definite excep-

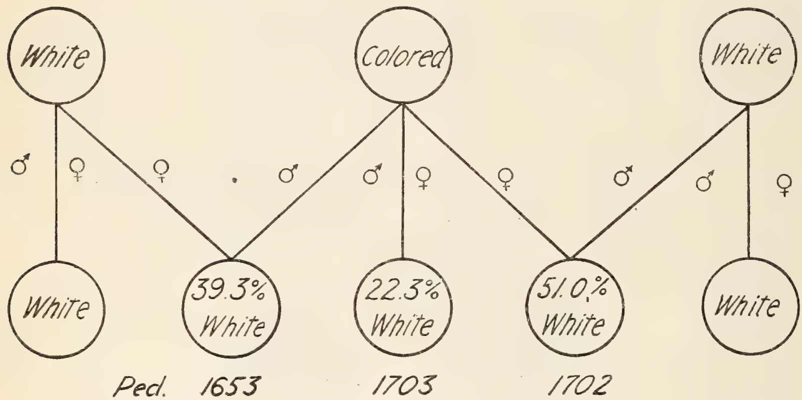


FIG. 5.—Diagram showing the relations of ears Nos. 1653, 1703, and 1702.

tions to the general agreement of the material with theory, but since they stand rather apart from the remaining ears it may be well to exclude them and then examine the totals.

Omitting the data relating to these ears from the total number of seeds for the 29 ears, the percentage of white becomes 48.5. This deviation is 4.6 times the probable error and is still too large to occur as the result of chance. That there is a tendency toward too few white seeds when heterozygous colored plants are used as male parents is demonstrated for this group, even omitting the ears with obviously aberrant ratios.

TABLE XIX.—*Inheritance of aleurone color in 31 ears of the colored × white and 24 ears of the colored × self progeny of the two maize ears Nos. 1099 and 1111, the progeny of hybrid Dh 234.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Colored × white.						Colored × self.					
	Self-pollinated ♀.	Reciprocal cross.	Number of seeds.				D ÷ E.	Percentage of white.	Number of seeds.				D ÷ E.	Percentage of white.
			Total.	White.	Expected white.	Deviation.			Seeds.	White.	Expected white.	Deviation.		
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1099, *CH × WX:*														
1625	Self	...	...	...	...	...	...	...	464	137	116	21	3.3	29.5
1626	All white	None.	427	219	214	5	0.7	51.0	...	...	...	...	...	...
1634	...do	1558	454	222	227	− 5	.7	48.9	...	...	...	...	...	...
{1635	None	None.	703	348	351	− 3	.3	49.5	...	...	...	...	...	...
{1636	Self	...	...	...	...	...	...	...	573	151	143	8	1.1	26.4
{1637	All white	None.	424	218	212	6	.9	51.4	...	...	...	...	...	...
{1638	Self	...	...	...	...	...	...	...	573	146	143	3	.4	25.5
1639	All white	None.	123	60	61	− 1	.3	48.8	...	...	...	...	...	...
{1641	None	None.	396	199	198	1	.2	50.2	...	...	...	...	...	...
{1642	Self	...	...	...	...	...	...	...	551	134	138	− 4	.6	24.6
{1643	All white	1552	511	262	256	6	.8	51.3	...	...	...	...	...	...
{1644	Self	...	...	...	...	...	...	...	652	183	163	20	2.3	28.6
{1645	All white	None.	510	236	255	−19	2.5	46.3	...	...	...	...	...	...
{1646	Self	...	...	...	...	...	...	...	368	79	92	−13	2.3	21.5
{1647	All white	None.	387	165	193	−28	4.2	42.6	...	...	...	...	...	...
Total	...	...	3,935	1,929	1,968	−39	1.8	49.0	3,181	830	795	35	2.1	26.1
Ear No. 1111, *CH × WX:*														
1694	Self	...	...	...	...	...	...	...	578	149	144	5	.7	25.8
{1695	All white	None.	393	191	196	− 5	.8	48.6	...	...	...	...	...	...
{1696	Self	...	...	...	...	...	...	...	373	89	93	− 4	.7	23.8
{1699	All white	None.	511	252	255	− 3	.4	49.3	...	...	...	...	...	...
{1700	Self	...	...	...	...	...	...	...	451	128	113	15	2.4	28.4
{1702	All white	None.	239	122	119	3	.6	51.0	...	...	...	...	...	...
{1703	Self	...	...	...	...	...	...	...	533	119	133	−14	2.1	22.3
1704	All white	None.	192	104	96	8	1.7	54.2	...	...	...	...	...	...
{1706	...do	None.	443	218	221	− 3	.4	49.2	...	...	...	...	...	...
{1707	Self	...	...	...	...	...	...	...	582	140	145	− 5	.7	24.0
{1710	All white	None.	458	220	229	− 9	1.3	48.0	...	...	...	...	...	...
{1711	Self	...	...	...	...	...	...	...	415	92	104	−12	2.7	22.2
{1712	All white	None.	181	98	90	8	1.8	54.1	...	...	...	...	...	...
{1713	...do	None.	179	98	89	9	2.0	54.7	...	...	...	...	...	...
1714	...do	None.	561	286	280	6	.8	51.0	...	...	...	...	...	...
1715	...do	None.	304	149	152	− 3	.5	49.0	...	...	...	...	...	...
{1718	...do	None.	290	150	145	5	.9	51.7	...	...	...	...	...	...
{1719	Self	...	...	...	...	...	...	...	549	137	137	...	...	25.0
Total	...	...	3,751	1,888	1,875	13	.6	50.3	3,481	854	870	−16	.9	24.5

TABLE XIX.—*Inheritance of aleurone color in 31 ears of the colored × white and 24 ears of the colored × self progeny of the two maize ears Nos. 1099 and 1111, the progeny of hybrid Dh 234*—Continued.

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Colored × white.						Colored × self.					
			Number of seeds.						Number of seeds.					
	Self-pollinated ♀.	Reciprocal cross.	Total.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.	Seeds.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1099, *CX × WH:*														
1571	Self								450	125	115	10	1.6	27.8
1572	All white	1604	127	62	63	− 1	.3	48.8						
1573	Self								379	95	95			25.0
1574	None	None.	645	317	323	− 6	.7	49.2						
1575	Self								539	149	135	14	2.1	27.6
1577	All white	1608	596	298	298			50.0						
1578	Self								557	140	139	1	.1	25.1
1579	None	1610	468	248	234	14	1.9	53.0						
1582	Self								397	106	99	7	1.2	26.7
1584	None	1623	406	214	203	11	1.6	52.4						
1585	Self								565	148	141	7	1.0	26.2
1588	None	1614	118	61	59	2	.6	51.6						
1589	Self								458	112	114	− 2	.3	24.5
1590	All white	1619	580	287	290	− 3	.4	49.4						
1591	Self								483	122	121	1	.2	25.2
1592	All white	1621	307	147	153	− 6	1.0	47.9						
1593	Self								243	61	61			25.0
Total			3,247	1,634	1,623	11	.6	50.3	4,071	1,058	1,018	40	2.1	26.0
Ear No. 1111, *CX × WH:*														
1665	All white	1686	403	206	201	5	.7	51.1						
1666	Self								494	128	121	7	1.1	25.9
1667	None	None.	87	40	43	− 3	1.0	46.0						
1668	Self								576	136	144	− 8	1.1	23.6
1669	All white	None.	768	374	384	−10	1.1	48.7						
1670	Self								743	205	186	19	2.4	27.6
Total			1,258	620	629	− 9	.8	49.3	1,813	469	453	16	1.2	25.9
Total of the above four groups			12,191	6,071	6,096	25	.7	49.8	12,546	3,211	3,136	75	2.3	25.6

COLORED × WHITE.

As the result of pollinating plants grown from the heterozygous colored seeds with pollen from plants grown from the white seeds of ears Nos. 1099 and 1111, 31 ears were obtained. These ears are shown in Table XIX. The 31 ears had 12,193 seeds with 49.8 per cent white, the deviation being 0.7 times the probable error. Fourteen ears exceeded the expected, sixteen were below the expected, and one was exactely 50 per cent white. The fit was therefore extremely good.

Only one ear, No. 1647, deviated by an excess of four times the probable error, being 8.4 per cent below the expected.

Three ears were borne on the plant that produced ear No. 1647. One ear, No. 1646, was the result of self-pollination and had 21.5 per cent white, the expected being 25 per cent. The other ear was pollinated by a homozygous white plant and had 46.3 per cent white. Although these last two ears did not deviate by a number too large to be ascribed to chance, the fact that they were both below the expected taken in conjunction with the fact that ear No. 1647 was significantly lower than the expected would seem fairly conclusive evidence that there was a deficiency of female gametes bearing white aleurone on the plant that produced these three ears.

The four groups that make up the total in Table XIX are the reciprocals of the four groups that make up the total in Table XVIII. With the exception of the first group, the families resulting from pollinating plants grown from heterozygous colored seeds with plants grown from homozygous white seeds have a higher percentage of white seeds than the reciprocal cross.

The percentages for the families and the difference between the reciprocals are shown in Table XX.

Table XX.—*Inheritance of aleurone color in the progeny of the two maize ears Nos. 1099 and 1111, by groups as shown in Table XVIII and their reciprocals as shown in Table XIX.*

[The minus sign (−) denotes a difference between reciprocal groups, the opposite of the remaining differences.]

Progeny of—	Nature of cross.	Percentage of white seeds.			
		Table XVIII group.	Reciprocal cross.	Difference.	D ÷ E.
Ear No. 1099	*WX* × *CH*	49.4±0.69	49.0±0.54	−0.4±0.87	0.46
Ear No. 1111	do	47.0± .56	50.3± .55	3.3± .78	4.25
Ear No. 1099	*WH* × *CX*	46.6± .50	50.3± .59	3.7± .78	4.77
Ear No. 1111	do	45.6± .85	49.3± .95	3.7±1.28	2.90
Total		47.2± .31	49.8± .31	2.6± .43	6.0

The difference between the reciprocal groups of 2.6 per cent should be expected to occur as the result of chance but once in more than 19,000 times. With the one exception, the groups representing crosses between homozygous white plants and heterozygous colored plants had a lower percentage of white seeds when the heterozygous colored plants were used as the male gametes. This would indicate a deficiency of male gametes bearing the colorless aleurone or an excess of the female gametes bearing colored aleurone.

In analyzing the inheritance of waxy endosperm, a deficiency of male gametes bearing the waxy character was observed for the progeny of the hybrid Dh 234. The fact that male gametes bearing colorless aleurone are below the expected would seem to indicate that the gametes bearing recessive characters are less vigorous than those bearing the dominant characters. The observed differences could also be explained by assuming the plant to be making an unequal proportion of male gametes bearing colored and colorless aleurone.

As the result of self-pollinating plants grown from the heterozygous colored seeds of ears Nos. 1099 and 1111, 24 ears were obtained. These ears are shown in Table XIX.

The expected percentage of white seeds is 25 and the observed 25.6. The deviation in this case is only 2.3 times the probable error. Only one ear deviated from the expected percentage by more than three times the probable error, all the ears showing a remarkable uniformity.

Reciprocal crosses between heterozygous colored plants and homozygous white plants showed that for the heterozygous colored plants the male gametes bearing colorless aleurone were 3 per cent below the expected proportion. These same crosses showed the female gametes to be approximately normal. From these facts it would be expected that self-pollinating these heterozygous colored plants would result in ears having approximately 23.5 per cent white. The observed percentage of 25.6 can not be considered as a chance deviation from 23.5 per cent, since the deviation of 2.1 per cent is 8.1 times the probable error.

To explain these conflicting results it is necessary to make the assumption that the gametes bearing the recessive color find a better medium for growth in the stigmas of the heterozygous plant than in those of the homozygous white plants. An adequate test of this assumption would require numbers in excess of 10,000, making it very unlikely that the hypothesis will soon be put to the test.

COMPOSITION IN THE THIRD GENERATION OF THE HYBRID DH 237.

Four ears from the hybrid Dh 237 were selected for planting. Two of the four ears are shown in Table XVII as Nos. 1129 and 1130. The other two ears were the result of crossing Dh 237 by Dh 234, and since all the seeds were colored on both these latter ears, they do not appear in Table XVI. Their progeny are discussed later with the progeny of a similar ear from the hybrid Dh 234.

Ear No. 1129, grown in 1913, was the result of self-pollinating a plant of the hybrid Dh 237. This ear had 747 seeds with 25.1 per cent white, the percentage being almost exactly the expected 25 per cent. Since this ear is demonstrated to be segregating in a normal monohybrid ratio, the progeny plants of the heterozygous seeds are expected to behave in a like manner.

Ear No. 1130 was a second ear on the same plant that bore No. 1129, but instead of being the result of self-pollination as was No. 1129, ear No. 1130 was the result of pollen from a sister plant. The plant that served as the male parent of ear No. 1130 bore a self-pollinated ear, No. 1135. This ear No. 1135, had 26.4 per cent white, the deviation only slightly exceeding the probable error.

Since we have already seen that the plant which bore ear No. 1130 was segregating in a regular Mendelian monohybrid ratio and since the male parent was also a close approximation to the monohybrid ratio, the progeny might also be expected to behave in a regular manner.

There were four classes of seeds on ears Nos. 1129 and 1130—colored and white horny and colored and white waxy. The four classes were planted separately and crosses made between plants grown from the white waxy seeds and plants grown from the colored horny seeds and also between plants grown from the white horny seeds and plants grown from the colored waxy seeds. Self-pollinated ears were obtained from all the classes, but since the self-pollinated plants grown from white seed resulted in white ears only these ears were not tabulated.

The results of the different crosses were examined separately, but since no significant differences were found in the behavior of aleurone color between waxy and horny seeds the endosperm textures may be disregarded. Further, there appeared to be no significant differences between the progeny of the two ears, so that they also may be considered together.

WHITE × COLORED.

As the result of pollinating plants grown from the white seeds with plants grown from the heterozygous colored seeds of ears Nos. 1129 and 1130 thirty ears were obtained (Table XXI). These 30 ears totaled 14,227 seeds, with 50.1 per cent white. This is a remarkably close approximation to the expected 50 per cent. Of the 30 ears, 16 were below, 13 were above, and 1 equaled the expected 50 per cent. Three ears deviated in excess of three times the probable error, all being above the expected 50 per cent. One of these ears, No. 1784, exceeded the expected proportion by 7.3 per cent, and must stand as an exception. A deviation of this magnitude would be expected to occur as the result of chance but once in more than 1,500 times.

COLORED × WHITE.

From the progeny of ears Nos. 1129 and 1130 that were the result of pollinating plants grown from the heterozygous colored seeds with plants grown from the homozygous white seeds 20 ears were obtained (Table XXII).

TABLE XXI.—*Inheritance of aleurone color in 30 ears of maize, the white × colored progeny of the two ears Nos. 1129 and 1130, the progeny of hybrid Dh 237.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Number of seeds.				D ÷ E.	Per-centage of white.
	Self-pollinated ♀.	Reciprocal cross.	Total.	White.	Expected white.	Deviation.		
1	2	3	4	5	6	7	8	9
Ear No. 1129, *WX × CH:*								
1752	1802	1801	536	255	268	−13	1.7	52.5
1754	1800	None	500	237	250	−13	1.7	47.4
1758	1800	...do...	439	216	219	− 3	.4	49.2
1762	1798	...do...	537	258	268	−10	1.3	48.0
1764	1800	1799	498	251	249	2	.3	50.4
1765	1800	None	528	251	264	−13	.9	47.6
Total			3,038	1,468	1,514	−46	2.5	48.4
Ear No. 1130, *WX × CH:*								
1804	None	1838	363	179	181	− 2	.3	49.3
1806	...do...	None	435	232	217	15	2.1	53.3
1807	...do...	...do...	275	127	137	−10	1.8	46.2
1810	...do...	...do...	441	243	220	23	3.3	55.0
1815	...do...	1849	465	224	232	− 8	1.1	48.2
1816	1855	1854	515	272	257	15	2.0	52.8
Total			2,494	1,277	1,247	30	1.8	51.2
Ear No. 1129, *WH × CX:*								
1772	None	None	448	215	224	− 9	1.7	48.0
1773	...do...	...do...	613	304	306	− 2	.2	49.6
1775	...do...	1768	533	266	266	....	....	50.0
1777	...do...	...do...	428	194	214	−20	2.9	45.3
1779	...do...	...do...	476	262	238	24	3.3	55.0
1781	...do...	...do...	477	242	238	4	.5	50.4
1784	...do...	...do...	591	339	295	44	5.4	57.3
1786	...do...	...do...	446	214	223	− 9	1.3	48.0
1788	...do...	...do...	386	189	193	− 4	.3	49.0
Total			4,398	2,225	2,199	26	.1	50.7
Ear No. 1130, *WH × CX:*								
1827	1819	1818	644	333	322	11	1.3	51.7
1829	None	None	511	262	255	7	.9	51.3
1830	1821	...do...	642	307	321	−14	1.6	47.8
1831	None	...do...	385	186	192	− 6	.9	48.3
1832	...do...	...do...	370	203	185	18	2.8	54.9
{1833	1824	...do...	435	214	217	− 3	.4	49.3
{1834	1821	...do...	511	256	255	1	.1	50.5
1835	None	1825	503	256	251	5	.7	50.9
1836	...do...	1822	297	149	148	1	.2	50.1
Total			4,298	2,166	2,148	18	.8	50.3
Total of the above four groups			14,228	7,136	7,114	22	.6	50.1

The expected percentage of white seeds is 50 and the observed 50.1. Only one ear deviated from the expected percentage by three times the probable error, the remaining ears being very close approximations of the 50 per cent. Ten ears were below, eight above, and two equaled the expected. The four groups of ears shown in this table are the reciprocals of the four groups shown in Table XXI.

There are no significant differences between the groups, all showing a remarkable uniformity, the percentage of white seeds for the totals being exactly alike. The reciprocal groups are shown in Table XXIII. This is a striking contrast with the behavior of reciprocal groups in the progeny of Dh 234, in which a deficient number of male gametes bearing colorless aleurone were found.

TABLE XXII.—*Inheritance of aleurone color in 20 ears of the colored × white and 14 ears of the colored × self progeny of the two maize ears Nos. 1129 and 1130, the progeny of hybrid Dh 237.*

[Lines bracketed together indicate ears borne on the same plant.]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Colored × white.						Colored × self.					
			Number of seeds.						Number of seeds.					
	Self-pollinated ♂.	Reciprocal cross.	Total.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.	Total.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1129, *CX × WH:*														
1766	All white.	None	432	214	216	− 2	0.3	49.6						
1767	Self								425	110	106	4	0.2	25.9
1768	All white.	1775	144	68	72	− 4	1.0	47.2						
1769	Self	None							127	31	32	− 1	.3	24.4
Total			576	282	288	−6	.1	49.2	552	141	138	3	.4	25.5
Ear No. 1130, *CX × WH:*														
{1818	All white.	1827	754	367	377	−10	1.1	48.7						
{1819	Self								568	143	142	1	.1	25.2
{1820	All white.	None	207	109	108	1	.2	49.8						
{1821	Self								619	132	155	−23	3.2	21.4
1822	All white.	1836	542	271	271			50.0						
{1823	None	None	566	307	283	24	3.0	54.2						
{1824	Self								520	133	130	3	.5	25.6
1825	None	1835	584	287	292	− 5	.6	49.2						
Total			2,653	1,341	1,326	15	.9	50.5	1,707	408	427	−19	1.6	23.9
Ear No. 1129, *CH × WX:*														
{1790	All white.	None	512	238	256	−18	2.4	46.5						
{1791	Self								296	76	74	2	.4	25.6
1792	All white.		487	228	243	−15	2.0	46.8						
{1795	None	None	553	281	276	5	.6	50.5						
{1796	Self								296	65	74	− 9	1.8	21.9
{1797	None	None	230	125	115	10	2.0	54.4						
{1798	Self								752	178	188	−10	1.3	23.7
{1799	None	1764	510	271	255	16	2.1	53.2						
{1800	Self								755	215	189	26	3.2	28.5
{1801	All white.	1752	381	190	190			49.9						
{1802	Self								247	65	62	3	.7	26.3
1803	None	None	244	130	120	10	.9	53.3						
Total			2,917	1,463	1,458	5	.3	50.2	2,346	599	586	−13	.9	25.4
Ear No. 1130, *CH × WX:*														
1838	All white.	1804	545	271	272	− 1	.1	49.8						
{1839	do	None	415	220	207	13	1.9	53.0						
{1840	Self								308	84	77	7	1.4	27.5
{1841	All white.	None	583	283	291	− 8	1.0	48.6						
{1842	Self								451	101	113	−12	1.9	22.4
{1846	All white.	None	621	299	310	−11	1.3	48.2						
{1847	Self								721	180	180			25.0
1849	All white.	1815	581	301	290	11	1.4							
{1854	do	1816	614	299	307	− 8	1.0	48.7						
{1855	Self								563	132	141	− 9	1.3	23.5
Total			3,359	1,673	1,679	− 6	.3	49.9	2,043	497	511	−14	1.1	24.6
Total of the above four groups			9,505	4,759	4,752	7	.2	50.1	6,648	1,645	1,662	−17	.7	24.6

COLORED × SELF.

Fourteen self-pollinated ears were obtained that were expected to have 25 per cent white. These ears are also shown in Table XXII, columns 10 to 15. Two ears deviated slightly in excess of three times the probable error, but the remaining ears were very close approximations to the expected 25 per cent. Seven ears were above, six below, and one equaled the expected percentage.

TABLE XXIII.—*Inheritance of aelurone color in the progeny of the two maize ears Nos. 1129 and 1130, by groups as shown in Table XXI and other reciprocals as shown in Table XXII.*

[The minus sign (—) denotes a difference between reciprocal groups, the opposite of the remaining differences.]

Progeny of—	Nature of cross.	Percentage of white seeds.			
		Table XXI group.	Reciprocal cross.	Difference.	D÷E.
Ear No. 1129	*WX* × *CH*	48.4±0.61	49.2±1.4	0.8±1.53	0.5
Ear No. 1130	do	51.2± .68	50.5± .66	— .7± .94	.75
Ear No. 1129	*WH* × *CX*	50.7± .51	50.2± .63	— .5± .81	.62
Ear No. 1130	do	50.5± .52	49.9± .58	— .6± .78	.77
Total	*W* × *C*	50.1± .28	50.1± .34	0	

SUMMARY OF THE HYBRID DH 237.

From the progeny of the hybrid Dh 237 there were in all 48 plants that produced 64 ears. Of these, 32 ears were below, 28 above, and 4 equaled the expected percentages. There were only 6 ears that must be considered exceptions. While the ratios on these 6 ears can not be brought into accord with the other results, the progeny of hybrid Dh 237 is strikingly uniform as compared with the sister hybrid Dh 234.

PROGENY OF THE CROSSES BETWEEN THE TWO HYBRIDS DH 234 AND DH 237.

EARS NOS. 1110, 1131, AND 1134.

Three ears representing crosses between the two hybrids Dh 234 and Dh 237 were selected for planting. These three ears were all colored and therefore do not appear in the second-generation tables. The ear numbered 1110 was borne on a plant of the hybrid Dh 234, which, when self-pollinated, produced ear No. 1111, the progeny of which have been considered on pages 39 to 46.

The ears are shown in the following diagram:

Hybrid Dh 234 *CC Rr* — Self — Pedigree No. 1111, 25.8 per cent. white.
Hybrid Dh 234 *CC Rr* — ♀ × Hybrid Dh 237 *Cc RR* — ♂ — Pedigree No. 1110, all colored.
Hybrid Dh 237 *Cc RR* — Self — Pedigree No. 1132, 27.8 per cent. white.

Hybrid Dh 237 *Cc RR* — Self — Pedigree No. 1132, 27.8 per cent. white.
Hybrid Dh 237 *Cc RR* — ♀ × Hybrid Dh 234 *CC Rr* — ♂ — Pedigree No. 1131, all colored.
Hybrid Dh 234 *CC Rr* — Self — Pedigree No. 1117, 25.5 per cent. white.

Hybrid Dh 237 *Cc RR* — Self — Pedigree No. 1133, 23.1 per cent. white.
Hybrid Dh 237 *Cc RR* — ♀ × Hybrid Dh 234 *CC Rr* — ♂ — Pedigree No. 1134, all colored.
Hybrid Dh 234 *CC Rr* — Self — Pedigree No. 1118, 27.9 per cent. white.

The same explanation will apply to all three ears, Nos. 1110, 1131, and 1134. Self-pollinated ears were obtained from the male and female parents of each of the ears, and the results showed all of the plants to be segregating in a regular manner, producing the unit character ratio of 3 colored to 1 white.

It has been assumed that the hybrid Dh 234 was producing gametes *CR Cr*, and that the hybrid Dh 237 was producing gametes *CR cR*. Either hybrid, self-pollinated, would result in a monohybrid ratio, while if crossed it would result in ears with all of the seeds colored. If this assumption is correct the expected result of planting the seeds from a cross between two such plants and self-pollinating them would be one ear all colored, two having 3 colored seeds to 1 white, and one having 9 colored seeds to 1 white.

PROGENY OF EAR NO. 1131.

As only self-pollinated ears were obtained from the progency of ear No. 1131, these ears will be discussed separately.

There were two classes of seeds on ear No. 1131, colored horny and colored waxy. These two classes were planted separately. The ears obtained from both classes are shown in Table XXIV. The upper group of four ears was obtained from self-pollinating plants grown from the waxy seeds, and the lower group is the result of self-pollinating plants grown from the horny seeds. The 10 ears do not afford a sufficient number to determine whether 1 all-colored ear, 2 ears segregating 3 colored to 1 white, and 1 ear segregating 9 colored to 7 white are obtained.

No all-colored ears were obtained. Nine of the 10 ears are approximating 25 per cent white, while the remaining ear, No. 1892, approximates the Mendelian dihybrid ratio. The total number of seeds for the nine monohybrid ears is 2,158, with 24.7 per cent white, the deviation being less than the probable error. None of the ears deviated in excess of three times the probable error, 5 were below, and 4 above the expected.

TABLE XXIV.—*Inheritance of aleurone color in 10 ears of the colored × self progeny of maize ear No. 1131, the progeny of a cross between hybrids Dh 234 and Dh 237.*

Character of cross and pedigree No. of progeny.	Number of seeds.				D ÷ E.	Percentage of white.
	Total.	White.	Expected white.	Deviation.		
Colored waxy × self:						
1887	269	69	67	2	0.4	25.6
1888	279	75	69	6	1.2	26.9
1889	257	58	64	− 6	1.3	22.5
1890	47	10	12	− 2	1.0	21.3
Total	852	212	213	− 1	.1	24.9
Colored horny × self:						
[a]1892	36	18	15	3	1.5	50.0
1893	337	69	84	−15	2.8	20.5
1894	261	69	65	4	.9	26.4
1895	33	5	8	− 3	1.8	15.1
1896	251	75	63	12	2.6	29.8
1897	424	105	106	− 1	.2	24.8
Total	1,306	323	326	− 3	.4	24.7
Total for both groups	2,158	535	539	− 4	.29	24.7

[a] Ear No. 1892 is assumed to be approximating 43.75 per cent white and is not included in the totals.

PROGENY OF EARS NOS. 1110 AND 1134.

There were also two classes of seeds on ears Nos. 1110 and 1134, colored horny and colored waxy. These two classes were planted separately, and crosses were made between them. Self-pollinated ears were also secured from each class.

The progeny of the two ears were examined separately, but no significant differences were found, so the progeny are tabulated together.

COLORED × COLORED.

As the result of crossing plants grown from the colored horny seeds with the plants grown from the colored waxy seeds of ears Nos. 1110 and 1134, 24 ears were obtained (Table XXV). The crosses were made using the waxy plants as both male and female parents, but as no significant differences were found the endosperm textures may be disregarded. Five all-colored ears were obtained that are not tabulated. The 25 ears tabulated were borne on 23 plants.

The expected proportions for these 28 individual plants is 15.75 plants all colored, 10.5 plants with a monohybrid ratio, and 1.75 plants with a dihybrid ratio. The observed plants fell into two groups only, 5 ears all colored and 23 with a monohybrid ratio. The deviation, though too large to be ascribed to chance, may, nevertheless, be the result of accident.

The observed deviation would be expected to occur as the result of chance but once in 500 times. Although this deviation would seem significant, it is, in fact, merely accidental. Self-pollinating these plants proved that they were in the expected proportion of 1 homozygous for both color factors, 2 heterozygous for one and homozygous for the other, and 1 heterozygous for both factors. The deviations noted from this grouping would be expected to occur as the result of chance eight times in a hundred.

The large deviation from the expected grouping for the crosses between sister plants was probably the result of an unconscious selection of the male parents, since we have seen that the plants were present in the expected proportions. Seven of these 23 ears were borne on plants that were shown by means of self-pollinated ears to be heterozygous for two color factors. But since these seven ears were all the result of pollen from plants that were homozygous for one color factor and heterozygous for the other, they had approximately 25 per cent of the seeds white.

One of the four groups that comprise the total deviated in excess of the expected percentage by 3.7 times the probable error. The deviation in this group is due to an excess of white seeds on ear No. 1876. This ear had 32.4 per cent of the seeds white. The deviation of 7.4 per cent above the expected 25 per cent is 4.9 times the probable error. The plant that produced the ear in question bore two other ears, Nos. 1874 and 1875. No. 1874, like 1876, was the result of pollen secured from a plant grown from the colored waxy seeds of ear No. 1110. The third ear, No. 1875, was the result of self-pollinating the female parent of ears Nos. 1874 and 1876. The self-pollinated ear No. 1875 had 41.6 per cent white, demonstrating the female parent of these three ears to be heterozygous for the two factors for color. Unfortunately, an ear was not secured from the male parent of No. 1876, so the gametic constitution of this plant can not be definitely determined. Ear No. 1876, however, with 32.4 per cent white, is closer to a monohybrid ratio than a dihybrid ratio, but it stands almost midway between the two ratios and can scarcely be referred to either. The relations of these ears are shown in figure 6.

TABLE XXV.—*Inheritance of aleurone color in 24 ears of the colored waxy × colored horny and 28 ears of the colored waxy × self progeny of the two maize ears Nos. 1110 and 1134, the progeny of crosses between hybrids Dh 234 and Dh 237.*

[Lines bracketed together indicate ears borne on the same plant; ears that were considered as approximations of 43.75 per cent white are marked with an asterisk (*); ears that were pollinated by sister plants are marked with a dagger (†).]

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Colored waxy × colored horny.						Colored waxy × self.					
	Self-pollinated ♂.	Reciprocal cross.	Number of seeds: Total.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.	Number of seeds: Total.	White.	Expected white.	Deviation.	D ÷ E.	Percentage of white.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1110, *CX × CH:*														
1856	1878	1877	525	143	131	12	1.8	25.4						
1857	Self								433	91	108	−17	2.4	21.0
1858	1880	None	491	121	123	− 2	.3	24.7						
1859	Self								*477	207	208	− 1	.1	43.4
1860	1875	1874	649	164	162	2	.3	25.3						
1861	None	1871	450	109	112	− 3	.5	24.2						
1862	Self								*532	193	233	−40	5.2	36.3
1863	None	None	679	174	170	4	.5	25.6						
1864	Self								*556	253	244	9	1.1	45.5
1865	1875	None	739	181	185	− 4	.5	24.5						
1866	Self								676	158	169	−11	1.3	23.4
1867	do								69	22	17	5	2.4	31.9
1868	do								95	21	24	− 3	1.1	22.1
1869	do								*135	60	57	3	1.2	44.4
1870	do								*51	18	22	− 4	1.7	35.3
Total			3,533	892	883	9	.5	25.2	1,273	292	318	−26	2.5	23.0
Total, marked ears									*1,751	731	765	−34	2.4	41.7
Ear No. 1134, *CX × CH:*														
1899									*695	284	304	−20	2.3	40.9
1902	1918	1917	765	215	191	24	2.9	28.1						
1903	Self								55	9	14	− 5	2.3	16.3
1904	None	None	443	115	111	4	.7	26.0						
1905	1934	1935	366	82	91	− 9	1.6	22.4						
1906	1923	1922	315	87	79	8	1.5	27.6						
1907†									560	143	140	3	.4	25.5
1909	1925	1924	485	103	121	−18	2.8	21.3						
1910	Self								*502	211	219	− 8	1.1	42.0
1911	1934	1933	484	129	121	8	1.3	26.6						
1912	Self								562	134	140	− 6	.9	249.
1913†	1912								619	144	155	−11	1.5	23.3
1914	Self								*513	272	220	52	6.5	53.0
1905	do								525	133	131	2	.3	25.3
Total			2,858	731	712	19	1.2	25.6	2,321	563	580	−17	1.2	24.2
Total, marked ears									*1,710	767	748	19	1.3	44.8
Total, two *X* × *H* groups			6,391	1,623	1,598	25	1.1	25.4	3,594	855	898	−43	2.4	23.8
Total, marked ears									*3,461	1,498	1,513	−15	.7	43.3

TABLE XXV.—*Inheritance of aleurone color in 24 ears of the colored waxy × colored horny and 28 ears of the colored waxy × self progeny of the two maize ears Nos. 1110 and 1134, the progeny of crosses between hybrids Dh 234 and Dh 237*—Continued.

Parent ear and pedigree No. of progeny.	Pedigree No. of—		Colored waxy × colored horny.						Colored waxy × self.					
	Self-pollinated ♂.	Reciprocal cross.	Number of seeds. Total.	Number of seeds. White.	Number of seeds. Expected white.	Number of seeds. Deviation.	D ÷ E.	Percentage of white.	Number of seeds. Total.	Number of seeds. White.	Number of seeds. Expected white.	Number of seeds. Deviation.	D ÷ E.	Percentage of white.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ear No. 1110, *CH* × *CX*:														
1871	1862	1861	81	21	20	− 1	.4	25.9						
1872	1862	None	538	144	134	10	1.5	26.8						
1873	Self								73	19	18	1	.4	26.0
1874	None	1860	137	41	34	7	2.1	29.9						
1875	Self								*716	298	306	− 8	1.0	41.6
1876	None	None	377	122	94	28	4.9	32.4						
1877	1857	1856	424	101	106	− 5	.8	23.9						
1878	Self								496	136	124	12	1.8	27.4
1880	do								371	87	93	− 6	1.1	23.4
1882	do								*136	61	58	3	.8	44.8
Total			1,557	429	387	42	3.7	27.5	940	242	235	7	.8	25.8
Total, marked ears									*852	359	372	−13	1.3	42.2
Ear No. 1134, *CH* × *CX*:														
1917	1903	1902	452	120	113	7	1.1	26.5						
1918	Self								345	92	86	6	1.1	26.6
1922	None	1906	421	109	105	4	.7	26.6						
1923	Self								399	113	100	13	2.2	28.3
1924	1910	1909	415	108	104	4	.7	26.9						
1925	Self								457	111	114	− 3	.5	24.3
1928	do								397	88	99	−11	1.9	22.1
1929	None	None	332	88	83	5	.9	26.5						
1932	1912	do	477	112	119	− 7	1.1	23.5						
1933	1912	1911	324	101	81	20	3.8	31.2						
1934	Self								*346	161	151	10	1.6	46.6
1935	1912	1911	222	66	55	11	2.5	29.7						
1937	Self								*443	188	194	− 6	.9	42.4
Total			2,643	704	661	43	2.9	26.6	1,598	404	400	4	.3	25.3
Total, marked ears									*789	349	345	4	.4	44.3
Total, two *H* × *X* groups			4,200	1,113	1,050	63	3.3	26.5	2,538	646	635	11	.8	25.4
Total, two groups, marked ears									*1,641	708	718	−10	.7	43.1
Total, four *C* × *C* groups			10,591	2,736	2,648	88	2.9	25.8	6,132	1,501	1,533	−32	1.4	24.5
Total, four groups, marked ears									*5,102	2,206	2,230	−24	1.0	43.2

The probable error is so high on ear No. 1874 that the deviation from 25 per cent is insignificant, although the percentage of white seeds on this ear approximates the percentage observed on ear No. 1876 more closely than that observed on the reciprocal ear, No. 1860; the deviation from either is insignificant.

It becomes of interest to note that there is one other case where a plant heterozygous for two color factors when pollinated with pollen from a plant heterozygous for one color factor and homozygous for the other has a percentage of white seeds intermediate between 25 and 43.75. The ears are Nos. 1933 and 1935, Table XXV. The plant that bore these ears also bore ear No. 1934. The ear numbered 1935 had for a male parent the same plant which served as the male parent of No. 1933. Both of these ears had white seeds in excess of the expected. Ear No. 1934 was the result of self-pollinating the female parent of ears Nos. 1933 and 1935. This self-pollinated ear had 46.6 per cent of its seeds white, demonstrating the plant to be heterozygous for two color factors.

The male parent of ears Nos. 1933 and 1935 produced an ear the result of self-pollination, No. 1912. This ear had 24.9 per cent of its

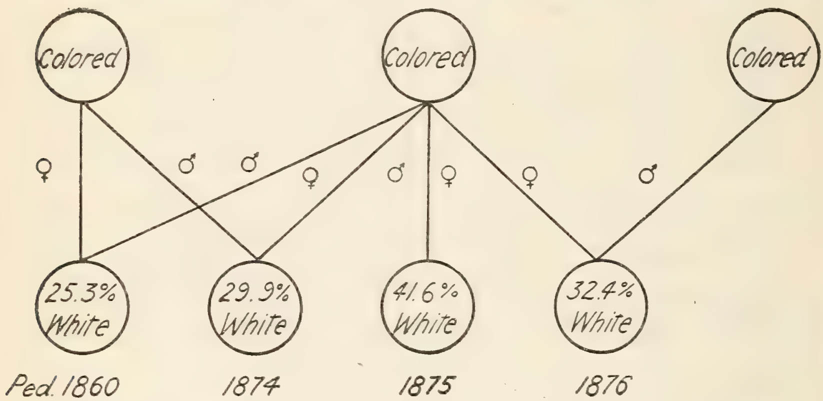


FIG. 6.—Diagram showing the relations of ears Nos. 1860, 1874, 1875, and 1876.

seeds white, demonstrating the male parent to be approximating the percentage expected if the plant were heterozygous for one color factor and homozygous for the other.

A reciprocal cross was also made between the plant which produced ears Nos. 1933, 1934, and 1935 and the plant which produced ear No. 1912. The ear representing the reciprocal cross of ears Nos. 1933 and 1935 is No. 1911. This latter ear had 26.6 per cent of its seeds white, the deviation from 25 per cent being only slightly in excess of the probable error. The difference between the reciprocal ears (averaging Nos. 1933 and 1935) is 4.1 per cent, a difference that would be expected as the result of chance once in six times. The relations of these ears are shown in figure 7 .

The seeds from three ears, Nos. 1876, 1933, and 1935, were reexamined and the classification was found to be correct. The distinction between white and colored seeds was very good, no doubtful seeds being encountered. Ears Nos. 1876, 1933, and 1935 indicate that the deviation is constitutional, as all the ears are near enough to the same ratio to be placed in a single group. This affords evidence that one of the factors for color is varying, and the rather definite deviation indicates that the change is in the nature of fractionation.

If definite segregation of hereditary units is a fact, then the number of white seeds reappearing in the second generation of white × colored crosses will approximate certain percentages. If these percentages are not approximated, two explanations are possible on the basis of equal segregation:

(1) The predication of additional factors, inhibitors, and assumptions. By this method any percentage is possible, though when more than three factors are required it is seldom possible to test the explanation, since the number of individuals necessary to measure accurately small differences is extremely large. Immediate percentages may be explained by the use of additional fac-

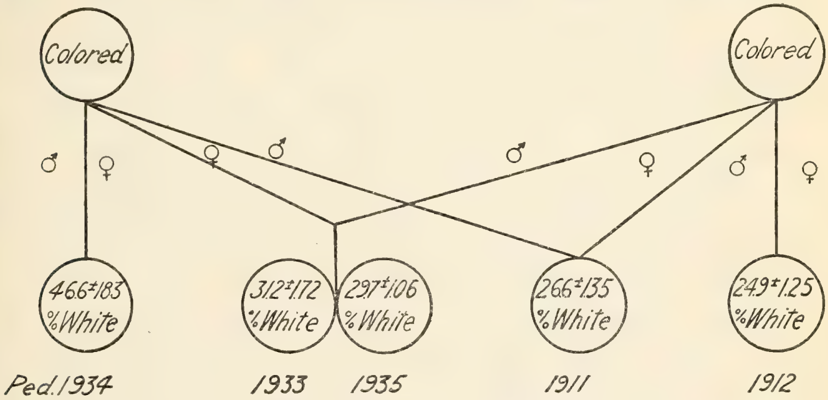


FIG. 7.—Diagram showing the relations of ears Nos. 1934, 1933, 1935, 1911, and 1912.

tors, but in most cases it becomes impossible to reconcile the explanation with the behavior of the same individual in other combinations. Not infrequently individual ears of maize are found that seem to fulfill certain comparatively simple explanations, but when the related pedigrees are analyzed a frequent result is to find incompatible individuals.

(2) "Failure of dominance" is the term often used to explain an excess of the recessive character, but this explanation will not serve when the recessive character is deficient. If the fact that hereditary units undergo change during hybridization requires any further evidence than that presented by Castle and Phillips (2) this frequent "failure of dominance" in generations succeeding the first would seem to furnish this evidence. If in a cross between a colored and a white plant the color proves to be dominant in the first generation, but in subsequent generations this complete dominance partially disappears, as it actually does, it seems natural to assume that either the color or the white, or both, have undergone some change, so that they do not stand as unalterably opposed as at first. In other words, a partial blend has taken place. Such a theory without doubt "strikes at the very heart of Mendelism," but the facts as they are must be acknowledged.

In demonstrating that an excess of white seeds is due to a failure of dominance the seeds bearing this character are planted, and upon the appearance of some seeds with the dominant character the "failure of dominance" is considered demonstrated. This is all very well, but it is also just what would be expected if segregation were not definite or complete. The finding of some seeds bearing the dominant character on plants grown from the suspected seeds does not explain the discrepancies observed in the parent stock unless the proper proportion of plants show the dominant character. In most cases the actual number of plants necessary to determine whether this proportion is as expected is so large that investigators have been content when some of the plants exhibited the expected dominant character.

COLORED × SELF.

Twenty-eight ears were obtained from self-pollinating plants grown from the heterozygous colored seeds of ears Nos. 1110 and 1134. Of these 28 ears, 17 were considered as approximations of the monohybrid ratio of 3 colored to 1 white. The total number of seeds secured from these 17 ears was 6,132, with 25 per cent white.

The individual ears are also shown in Table XXV. The ears marked with a star are those considered as approximations of some percentage other than 25 per cent. Of the 17 ears, none deviated from the 25 per cent in excess of three times the probable error. The remaining 11 ears with two exceptions were close approximations to the dihybrid percentage of 43.75 per cent white. The total number of seeds obtained from the 11 ears was 5,102, with 43.2 per cent white. The deviation of 0.55 per cent below the expected just equals the probable error. With the exception of ears Nos. 1914 and 1862 none of the 11 ears deviated from the 43.75 per cent white in excess of three times the probable error. The deviations noted on ears Nos. 1914 and 1862 practically balance each other. No. 1862 being 5.2 times the probable error below the expected and No. 1914 being 6.5 times above the expected ratio.

Ear No. 1862 has a percentage of white seeds 11.3 per cent above the 25 per cent expected ratio for a monohybrid and 7.45 per cent below the 43.75 per cent expected on a dihybrid ratio. The probable error is ±1.4 and the deviation is 5.3 times the probable error from the dihybrid percentage, which the ear more nearly approximates.

The same plant which produced ear No. 1862 also produced ear No. 1861, which was the result of pollen from the plant which produced ear No. 1871. These ears, Nos. 1861 and 1871, are reciprocals, and are very close approximations to the monohybrid percentage of 25. If the plant which produced ear No. 1862 was heterozygous for two color factors, pollinating this plant with one homozygous for one color factor and heterozygous for the other would result in an ear with 25 per cent of its seeds white. This same percentage of white seeds would of course be the result if both the plants in question were homozygous for the same color factor and heterozygous for the other. The percentage of white seeds is a fairly close approximation of 31.25 per cent expected on a 11 to 5 ratio, but the assumptions necessary to account for this ratio on ears that result from self-pollination are too absurd to permit such an explanation. The relations of these ears are shown in figure 8.

Here again we have evidence of a change in the effect produced by the factors, but since the same plant behaved normally when crossed with a sister plant in respect to both male and female gametes we must assume that whatever the change it was not sufficient to affect the results except where the changed gamete was received from both parents.

If we look upon ear No. 1862 as being a deviation from a dihybrid ratio, there is an excess of colored seeds. If the assumption

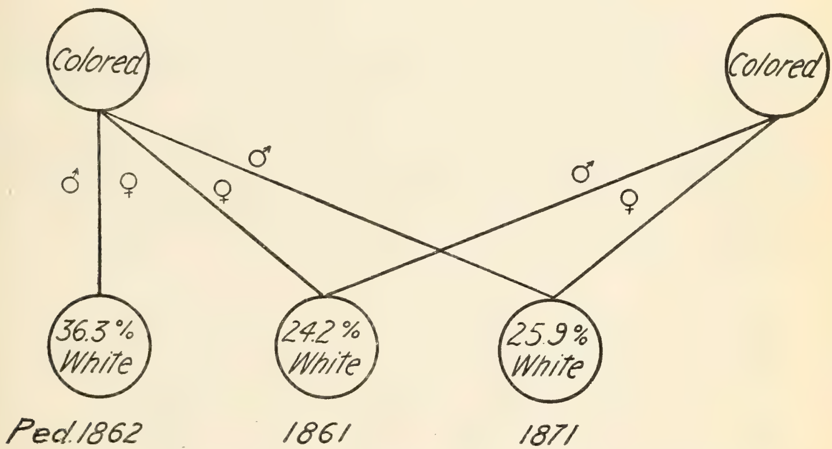


FIG. 8.—Diagram showing the relations of ears Nos. 1862, 1861, and 1871.

is made that this excess is due to a fractionation of one of the factors, this altered factor must be the one for which the plant which bore No. 1871 was homozygous.

Thus the plant which bore ear No. 1862 was forming gametes *CR*, *Cr*, *cR*, and *cr*. If we assume that a sufficient amount of the factor *R* was included in the gamete *Cr′* to make the union of the two gametes *Cr′* result in a colored zygote the ratio of white to colored seeds would be altered and the percentage would be 39.06 white, a percentage closely approximated by ear No. 1862. (See Table XXVI.) This change, however, was not sufficient to produce color when combined with a pure *Cr* gamete obtained from the sister plant, as is shown by ears Nos. 1861 and 1871.

TABLE XXVI.—*Possible effect of self-fertilizing a plant in which the color factor has become fractionated in such a way as to make the union of the gametes result in a colored zygote.*

[The percentage of white seeds is 39.06.]

Gametes.	CR.	CR′.	Cr′.	Cr.	cR.	cR′.	cr′.	cr.
CR	Colored	Colored	Colored	Colored	Colored	Colored	Colored	Colored.
CR′	do	do	do	do	do	do	do	Do.
Cr′	do	do	do	White	do	do	do	White.
Cr	do	do	White	do	do	do	White	Do.
cR	do	do	Colored	Colored	White	White	do	Do.
cR′	do	do	do	do	do	do	do	Do.
cr′	do	do	do	White	do	do	do	Do.
cr	do	do	White	do	do	do	do	Do.

The other aberrant ear, No. 1914, which is shown in figure 9, is a very close approximation of the 1 to 1 ratio, the deviation being but slightly in excess of two times the probable error. The deviation is also insignificant from the 56.25 per cent white expected on a 7 to 9 ratio, while the expected ratio was 9 to 7 or 43.75 per cent white. Here again we may be dealing with a fractionation of the factor *R* in such a way perhaps that enough has been separated from the factor *R* to occasionally prevent the normal color reaction with the

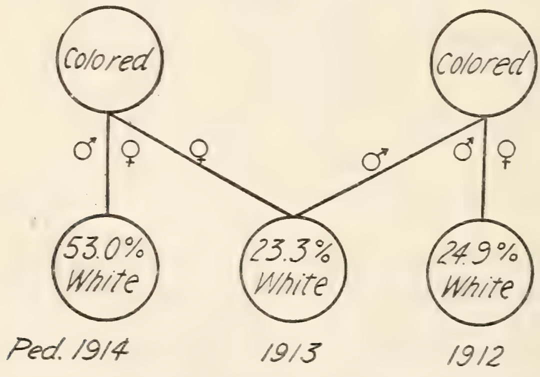


FIG. 9.—Diagram showing the relations of ears Nos. 1914, 1913, and 1912.

factor *C*. (See Table XXVII.) If this assumption is made, the expected percentage of white seeds is 53.1, which is indeed a very close approximation to the observed 53 per cent.

With the assumption that the plant which bore ear No. 1914 was of the type indicated in Table XXVII, such a plant if crossed with one heterozygous for the factor *C* and homozygous for the normal *R* factor would give an ear with the monohybrid ratio of white to colored seeds which fits the observed results, as is shown in figure 9.

TABLE XXVII.—*Possible effect of self-fertilizing a plant in which the color factor has become fractionated in such a way as to prevent the normal reaction.*

[The percentage of white seeds is 53.125.]

Gametes.	CR.	CR′.	Cr′.	Cr.	cR.	cR′.	cr′.	cr.
CR	Colored	Colored	Colored	Colored	Colored	Colored	Colored	Colored.
CR′	do	do	do	White	do	do	do	White.
Cr′	do	do	White	do	do	do	White	Do.
Cr	do	White	do	do	do	White	do	Do.
cR	do	Colored	Colored	Colored	White	do	do	Do.
cR′	do	do	do	White	do	do	do	Do.
cr′	do	do	White	do	do	do	do	Do.
cr	do	White	do	do	do	do	do	Do.

SUMMARY OF THE INHERITANCE OF ALEURONE COLOR.

The total number of ears expected to have 25 per cent of their seeds white was 163. This number includes both the second and the third generation of the two hybrids. The groups are shown in Table XXVIII. The 163 ears had a total of 81,336 seeds, with 25.5 per cent white. This percentage is misleading, for, while it is only

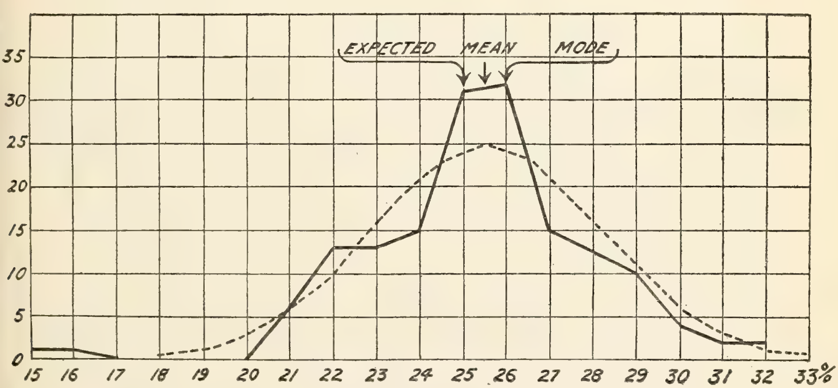


FIG. 10.—Diagram showing the percentages of white seeds on 163 ears expected to have 25 per cent of the seeds white compared with the normal probability curve.

0.5 per cent above the expected ratio, the deviation for the number of seeds involved is almost five times the probable error.

A deviation of this magnitude should not occur as the result of chance oftener than once in 666 times. The deviation, then, demands an explanation. That this deviation is not the result of a few aberrant ears is shown by the curves in figure 10. Only 11 of the 163 ears deviated in excess of three times the probable error, and only 3 exceeded four times the probable error, although with 163 ears we would expect 8 to deviate in excess of three times the probable error. There is undoubtedly a tendency to produce an excess of white seeds among most of the groups expected to segregate in a normal Mendelian monohybrid ratio. This tendency to produce an excess of white seeds is more evident in the hybrid Dh 234 and its progeny than in the hybrid Dh 237.

TABLE XXVIII.—*Inheritance of aleurone color in all the maize ears expected to have 25 per cent of the seeds white.*

Nature of cross.	Number of ears—		Number of seeds.				D÷E.	Percentage of white.
	Observed.	Below expected.	Total.	White.	Expected white.	Deviation.		
Progeny of hybrid Dh 234:								
Ear No. 1099	15	3	7,252	1,888	1,813	75	3.01	26.0
Ear No. 1111	10	5	5,294	1,323	1,323			25.0
Progeny of hybrid Dh 237:								
Ear No. 1129	7	3	2,898	740	724	16	1.02	25.5
Ear No. 1130	7	3	3,750	905	937	−32	1.79	24.1
Progeny of Dh 234 × Dh 237:								
Ear No. 1110	18	9	7,234	1,833	1,808	25	1.00	25.3
Progeny of Dh 237 × Dh 234:								
Ear No. 1131	9	5	2,158	535	539	−4	.29	24.7
Ear No. 1134	22	7	9,420	2,402	2,355	47	1.66	25.5
Second generation:								
Hybrid Dh 234	46	13	26,383	6,807	6,596	211	4.45	25.8
Hybrid Dh 237	29	11	16,947	4,307	4,237	70	1.84	25.4
Total	163	59	81,336	20,740	20,334	406	4.88	25.5

One explanation of this deviation would be that through mistakes in classification colored seeds were being included among the white. If this were the case, the white seeds planted and self-pollinated would be expected to result in some ears having colored seeds. The deviation is so small, however, that only one such ear could be expected in growing and self-pollinating 200 of the so-called white seeds.

If seeds bearing color had been classified as white, crosses between plants grown from the white seeds with plants grown from the colored seeds would be expected to result in some ears with a monohybrid ratio of white to colored seeds, instead of equal numbers of white and colored seeds. Several hundred ears representing the above crosses were obtained without finding any ears with a monohybrid ratio.

The possibility, then, that some of the seeds classified as white were in reality colored is remote. In hybrids involving endosperm texture the significant deviations observed have been with the recessive class below the expected (5, 7, and 8).

This significant departure above the expected number of recessives is not supported by the remainder of the progeny expected by the nature of the crosses to have equal numbers of white and colored seeds (Table XXIX).

There were 110 ears of the progeny of both the hybrids that were expected to be segregating in a 1 to 1 ratio. These ears had 47,872 seeds, with 49.2 per cent white. Here again the seemingly close approximation of the observed percentage to that expected by theory is misleading. The deviation of 0.8 per cent is 5.10 times the probable error and is evidently too large to be ascribed to chance. Only 4 of the 110 ears deviated from the expected percentage in excess of three times the probable error, and with 110 ears 5 such ears would be expected.

The deviation in this case can not be explained by assuming that colored seeds are being classified as white, as the colored seeds are in excess. It is hardly reasonable to assume that white seeds were being included in the colored class. The second-generation plants from the colored groups failed to produce any all-white ears, which would be the case if the excess of colored seeds resulted from mistakes in classification.

TABLE XXIX.—*Inheritance of aleurone color in all the maize ears expected to have 50 per cent of the seeds white.*

Nature of cross.	Number of ears.		Number of seeds.				D÷E.	Percentage of white.
	Observed.	Below expected.	Total.	White.	Expected white.	Deviation.		
Progeny of hybrid Dh 234:								
Ear No. 1099	35	20	13,986	6,794	6,994	−200	5.01	48.6
Ear No. 1111	25	16	10,154	4,907	5,077	−170	5.00	48.3
Progeny of hybrid Dh 237:								
Ear No. 1129	24	14	10,929	5,438	5,463	− 25	.71	49.7
Ear No. 1130	26	12	12,803	6,457	6,401	56	1.46	50.4
Total	110	62	47,872	23,596	23,937	−341	5.10	49.2

One parent of each of the ears having equal numbers of white and colored seeds must be homozygous for white aleurone, and is, therefore, making white gametes only. When these gametes unite with gametes produced by plants heterozygous for colored aleurone, the resulting seeds are expected to be white and colored in equal proportions, but this has not proved to be the case. A deficit too large to be due to chance occurs in the number of white seeds. It becomes of interest to note that the largest deviations below the expected percentage occur in the progeny of the hybrid Dh 234. This is all the more remarkable, since the hybrid in question has been shown to be producing an excess of white seeds on the first-generation ears as well as on the second-generation ears, expected to have but 25 per cent of their seeds white.

Since the variation in the percentage of white seeds, noted for the 47,872 seeds forming the total for the 110 ears which were expected to have equal numbers of white and colored seeds, was of necessity confined to one parent, it became of interest to know whether that parent was defaulting equally in the number of male and female gametes carrying white aleurone. The progeny of ear No. 1099 had 6,804 seeds born on homozygous white plants, but pollinated with pollen from heterozygous colored plants. The percentage of these white seeds was 47.5. The heterozygous colored plants grown from seeds of ear No. 1099 bore 7,182 seeds that were the result of pollen from the homozygous white plants. The percentage of these white seeds was 49.6.

The difference between the white plants pollinated with pollen from the colored plants and the colored plants pollinated with pollen from the white plants is 2.1 ± 0.571 per cent. This difference is 3.67 times the probable error and would seem to indicate that the heterozygous colored plants were making the expected proportions of female gametes with the observed shortage occurring in the male gametes.

A similar analysis of the progeny of ear No. 1111 shows the percentage of male gametes bearing white aleurone to be below the expected by 5.2 times the probable error.

The homozygous white plants of ear No. 1129 bore 7,434 seeds that were the result of pollen from heterozygous colored plants of this same progeny. The observed percentage of white seeds is 49.7. The heterozygous colored plants bore 3,493 seeds that were the result of pollen from the homozygous white plants. The observed percentage was 50. The difference between these two groups is but 0.3 per cent and can not be considered significant, though the variation is in the same direction as the cases previously considered.

The progeny of ear No. 1130, progeny of the hybrid Dh 237, varied slightly in the other direction, the male parents proving to have a higher percentage of white than of colored gametes, and while the white female gametes also were in excess, the excess of white male gametes exceeded that of the white female gametes by 0.5 per cent, which is not significant.

Combining the progeny considered above, there were 26,174 seeds which were borne on homozygous white plants, but the result of pollen from heterozygous colored plants. The observed proportion of white seeds in these was 48.8 per cent.

The heterozygous colored plants which were the result of pollen from homozygous white plants bore 21,698 seeds. The observed percentage of white seeds in these is 50. The difference between these two groups is 1.2 ± 0.31 per cent. This difference is 3.87 times the probable error, which is a rather large difference to be ascribed to chance.

The hybrid Dh 237 seems to be much more regular in behavior, at least as regards the proportions of white and colored seeds, though this hybrid produced ears segregating in a dihybrid ratio, as well as ears approximating a monohybrid ratio; usually in dealing with two color factors it is found that the inheritance of color is most irregular, the ratios often exhibiting a great range of variation.

Fifteen ears that were assumed to be segregating approximately 9 colored to 7 white are shown in Table XXX. These 15 ears had 6,519 seeds with 43.0 per cent white, the deviation of 0.75 per cent being 1.55 times the probable error and no larger than can be reasonably ascribed to chance.

TABLE XXX.—*Inheritance of aleurone color in all the maize ears expected to have 43.75 per cent of the seeds white.*

Nature of cross.	Number of ears.		Number of seeds.				D÷E.	Percentage of white.
	Observed.	Below expected.	Total.	White.	Expected white.	Deviation.		
Hybrid Dh 237, Algeria × Chinese variety:								
Second generation	4	2	2,477	1,072	1,083	−11	0.66	43.3
Hybrid Dh 234 × Dh 237:								
Progeny of ear No. 1110	6	3	2,020	879	854	25	1.65	43.5
Hybrid Dh 237 × Dh 234:								
Progeny of ear No. 1131	1	....	36	18	15	3	1.50	50.0
Progeny of ear No. 1134	4	3	1,986	839	868	−29	1.95	42.2
Total	15	8	6,519	2,808	2,850	−42	1.55	43.0

CORRELATION BETWEEN ENDOSPERM TEXTURE AND ALEURONE COLOR.

In several hundred crosses between American varieties of maize with horny endosperm and the Chinese variety with waxy endosperm a correlation has always been found to exist between the texture of the endosperm and the color of the aleurone. The results of a number of these crosses have been previously reported (7 and 4).

The study of correlation which had been relegated to the background upon the appearance of Mendelism with its theory of independent units received fresh impetus with the announcement of Bateson and Punnett that the mathematical regularity common in Mendelism was also to be found in the relationships between characters. These authors found that correlations were gametic, the parental combinations being found to occur in the gametes more frequently together than separated. To account for this difference in the gametic ratios they have assumed that the cells bearing the parental characters divide or reduplicate more frequently than the cells bearing the characters derived from different parents. For some inexplicable reason they assumed that the ratio between the number of gametes in which the parental combinations occurred together to the number in which they were separated would fit a definite series composed of the familiar Mendelian ratios of 3 to 1, 7 to 1, 15 to 1, etc. From this arbitrary series they have evolved an elaborate system of cell division to account for the gametic associations.

As higher couplings were secured these authors came to the realization that an insufficient number of cell divisions occurred between synapsis and the formation of the gametes to give these higher ratios. As a consequence they have assumed that segregation takes place earlier in the life history of the organism.

Working on the same problem, Morgan came to the conclusion that correlations were due to the fact that the correlated characters were located on the same chromosome (11). At synapsis the chromosomes derived from one parent pair with those from the other parent and presumably twist around each other. At the maturation division these pairs of twisted chromosomes split, resulting in the genes that are located close together along the chromosome falling together more often than apart. The degree of correlation depends upon the distance separating the character determiners, or genes. This distance is determined by the percentage of gametes bearing the characters derived from opposite parents which are called "crossovers." Thus the adherents of this theory would explain a gametic ratio of 3–1–1–3 as the result of the correlated characters lying 25 units apart on the chromosome.

Morgan and his coworkers, unhampered by an arbitrary gametic series and in fact working with material very unsuited for such an analysis owing to differential death rates, have amassed a wealth of material which has certainly served to put the linkage theory in an exceptionally strong position.

These authors claim no definite gametic series, and in the present status of the theory such a series would be meaningless, but while the theory makes little provision for such a series, it does not preclude it.

Once having established the number of units separating the correlated characters, deviations too large to be ascribed to chance are looked upon as the mutation of the locus of one or both of the characters, the value of the theory resting upon the infrequency of such departures. Whether we look upon a given gametic series as the result of unequal cell division or whether we assume that the gametic ratios are the result of the correlated characters lying a certain distance apart on the same chromosome, the question arises, Is the correlation of the same intensity between two characters for the individual ears of a given family? Both theories require that this be true and that the correlation between any given pair of characters remain constant.

In this bulletin there is evidence to show that at least in the second generation the correlations observed are for the most part explained by assuming a gametic series of 3–1–1–3.

METHOD OF MEASURING CORRELATIONS.

It has been the common practice to test the "goodness of fit" of couplings by contrasting the observed series with the calculated series and trusting to the eye to detect the agreement.

The danger of this method has been effectively pointed out by Collins (4), who proposed using Yule's coefficient of association with its probable error as a quantitative method of making the comparisons. For the higher degrees of coupling the coefficient of association with its probable error does not afford a satisfactory method of comparison, since the differences between the higher couplings, when measured by the coefficient of association, are extremely small.

With couplings of this nature and where more than two coupled characters occur, a method proposed by Pearson (13) can be used. By the use of Elderton's tables (9) the method is very simple. Caution, however, should be observed in applying this method as a measure of correlation where the characters are departing from the Mendelian expected ratios. This method does not distinguish between departures from the Mendelian proportions and differences in the way the characters are combined. Since the behavior of the individual characters from a Mendelian standpoint need not affect their association with each other, we are not concerned with any discrepancies between the observed and expected percentages of these characters, desiring only to know whether the characters under discussion are correlated or associated in a given proportion. It is obvious, then, that to measure the "goodness of fit" of the observed association to the theoretical association by the use of Pearson's formula (13) and Elderton's tables we must first eliminate any differences between the observed proportion of the individual characters and the Mendelian expected ratios, otherwise an injustice will be done to the agreement of the observed with the theoretical association.

Mr. G. Udney Yule has recognized this difficulty in applying Pearson's formula to testing the "goodness of fit" of a coupling ratio where the Mendelian ratios of the characters are skew, and in a letter to Mr. Collins suggested another method (15, pp. 585–590).

This method very satisfactorily corrects the material to the proper Mendelian proportions without altering the degree of association, but it seems to offer little advantage in cases of a low degree of coupling over Yule's coefficient of association, which is not affected by the Mendelian proportions of the characters.

As all our observed associations more nearly approximate the lower coupling series of 3–1–1–3 than any of the others proposed, the degree of association has been measured by Yule's coefficient of association (14), which has proved very satisfactory except in cases where one class is unusually low. This method has the advantage of being easily executed and comparatively rapid, which is no small item in figuring the association for hundreds of individuals, though its general application has been challenged by Heron (10).

As we are primarily concerned with comparing observed correlation with theoretical expectation rather than accurately measuring the degree of correlation, there can be no real objection to the formula proposed by Yule, which has been used throughout in comparing individuals with a common ancestry.

GAMETIC CORRELATIONS IN THE TWO HYBRID DH 234 AND DH 237.

In all the early crosses between the Chinese variety with waxy endosperm and American horny varieties the second-generation seed showed a correlation between the color of the aleurone and the texture of the endosperm. The first exception occurred in the hybrid Dh 234. The reciprocal hybrid Dh 237 had, however, the usual correlation between colored aleurone and horny endosperm.

The gametic formulas for the aleurone color have already been considered on pages 32 and 33, where the hypothesis was adopted that in the hybrid Dh 237 the gametic composition of the Chinese parent was *cR cR* and of the Algeria parent *Cr cr*. Adding the symbol *H* for horny endosperm texture and *h* for the waxy texture, we have for the Chinese *cRh cRh* and for the Algeria *CRH CrH*.

In crossing *cRh* and *CRH* a colored horny seed would result which when planted would make gametes *CRH*, *CHh*, *cRH*, and *cRh*, and when self-pollinated would result in ears having 3 colored seeds to 1 white and 3 horny seeds to 1 waxy. Wherever *cRh* and *CrH* are crossed, a colored horny seed would result, which when planted would make eight classes of gametes, *CRH*, *CRh*, *CrH*, *Crh*, *cRH*, *cRh*, *crH*, and *crh*, and when self-pollinated would result in an ear having 9 colored seeds to 7 white and 3 horny seeds to 1 waxy. This has been found to be true with respect to this hybrid, with the additional fact that a correlation exists between endosperm texture and aleurone color.

The Chinese parent of the second hybrid Dh 234 was assumed to have the gametic composition *Crh Crh*, while the gametic composition of the Algeria parent was assumed to be *CRH CRH*. All the seeds of a cross between the Chinese variety and Algeria would be colored horny. These seeds would all produce four classes of gametes, *CRH*, *CRh*, *CrH*, and *Crh*, resulting in ears with 3 colored seeds to 1 white and 3 horny seeds to 1 waxy when self-pollinated. This was found to be the case for all the ears secured, but no correlation was found between endosperm texture and aleurone color.

Since the aleurone color of the hybrids Dh 234 and Dh 237 is shown to be the result of two independent factors, it becomes apparent at once that the correlation previously reported as between aleurone color and endosperm texture must be looked upon as a correlation between endosperm texture and one of the factors for aleurone color.

CORRELATION IN THE SECOND GENERATION OF THE HYBRID DH 234.

The homozygous color factor in the hybrid Dh 234 was designated *C* and the heterozygous factor was called *R*. Second-generation seed from this hybrid produced 37 ears, the result of self-fertilization or of crosses between sister plants in the same hybrid. (Table XXXI.)

If the association were between the endosperm texture and the factor for color *R*, these ears would show a correlation, but should the association be between the color factor *C* and the horny endosperm texture the 37 ears obtained would exhibit no correlation, since all the gametes are homozygous for this factor. The correlation between aleurone color and horny endosperm texture for the 20,483 seeds borne on the 37 ears was 0.004 ± 0.013, which is less than the probable error. Two individuals among these 37 ears showed correlations more than four times the probable error.

Two correlations, however, exceeding the probable error by 4.6 and 4.1 times would be expected to occur as the result of chance in 37 observations once in about 19 times. As this chance is small, these correlations may be considered as the result of chance. The remaining ears showed no significant correlations; 16 of the 37 ears had negative and the remainder positive correlations between colored aleurone and horny endosperm.

The results from the self-pollinated ears of the hybrid Dh 234 would indicate that there is no correlation between endosperm texture and the color factor which is heterozygous in this maize hybrid. This factor has been designated *R*.

TABLE XXXI.—*Correlation between the endosperm texture and the aleurone color of self-pollinated and pure-seeded ears of maize in the second generation of the hybrid Dh 234.*

[Lines bracketed together in pairs indicate ears borne on the same plant; ears selected for planting are designated by an asterisk (*).]

Pedigree No. of—		Total.	Number of seeds.				Correlation, W+X.	Probable error.	Percentage of—	
Progeny ear.	Self-pollinated ♂.		*WX.*	*WH.*	*CX.*	*CH.*			Waxy.	White.
1	2	3	4	5	6	7	8	9	10	11
1099*	1106	657	38	127	122	370	−0.019	0.071	24.3	25.1
1100	1103	599	43	129	124	303	.102	.068	28.2	28.7
1101	1103	533	39	126	107	261	.139	.072	27.3	30.9
1102	Self	517	41	107	88	281	.105	.074	24.9	28.6
1103	...do	272	19	49	61	143	− .047	.103	29.4	25.0
1104	1108	573	30	121	106	316	− .149	.077	23.7	26.3
1105	Self	609	44	133	117	315	− .057	.069	26.4	29.0
1106	...do	690	46	132	136	376	− .019	.075	26.3	25.7
1108	...do	691	44	152	139	356	− .124	.063	26.4	28.3
1109	1112	402	17	96	69	220	− .277	.093	21.3	28.0
1111*	Self	747	43	149	122	433	− .256	.065	22.2	25.8
1112	...do	733	70	145	131	387	.201	.057	27.4	29.3
1113	1118	643	48	120	133	342	.014	.068	28.1	26.2
1114	1118	428	34	78	86	230	.070	.081	28.0	26.1
1115	1112	508	41	93	96	278	.121	.074	27.9	26.3
1116	1118	322	22	65	61	174	.017	.096	26.0	27.0
1117	Self	564	42	102	95	325	.122	.072	24.2	25.5
1118	...do	623	40	134	97	352	.076	.071	21.9	27.9
1119	1108	414	31	86	76	221	.023	.084	25.8	28.2
1120	1117	655	39	143	106	367	− .064	.072	22.1	27.7
1121	Self	687	45	146	107	389	.056	.068	20.5	24.2
1515	...do	555	37	104	102	312	− .003	.075	25.0	25.4
1519	...do	605	33	123	110	339	− .095	.075	23.8	25.8
1523	...do	571	28	105	91	347	.008	.082	20.8	23.3
1525	...do	212	12	41	33	126	.055	.088	21.3	25.0
1527	...do	614	35	113	108	358	.014	.075	23.3	24.1
1529	...do	334	22	65	49	198	.156	.097	21.2	26.0
1531	...do	659	26	150	123	360	− .327	.071	22.6	26.7
1533	...do	679	40	135	114	390	.007	.071	22.7	25.7
1534	...do	492	28	99	79	286	.059	.083	21.7	25.7
1537	...do	592	32	116	104	340	− .052	.075	22.9	25.0
1539	...do	626	30	108	116	372	− .057	.078	23.3	22.0
1543	...do	570	27	104	92	347	− .008	.082	20.9	23.0
1545	...do	417	32	77	69	239	.180	.082	24.2	26.1
1547	1537	633	37	108	103	385	.123	.073	22.2	22.8
1549	Self	479	30	108	88	253	− .112	.079	24.6	28.8
1551	...do	578	30	102	93	353	.054	.062	21.2	22.8
Total		20,483	1,295	4,091	3,653	11,444	− .004	.0125	24.2	26.3

CORRELATION IN THE SECOND GENERATION OF THE HYBRID DH 237.

If the correlation is between the color factor *C* and horny endosperm, the self-pollinated ears of the hybrid Dh 237 should exhibit a correlation between aleurone color and endosperm texture, since this hybrid has been assumed to be heterozygous for the factor *C*. From this hybrid 20 ears were obtained that had approximately 25 per cent of the seeds white, indicating that these plants were homozygous for the color factor *R* (Table XXXII). These 20 ears had a total of 12,394 seeds with a correlation of 0.769±0.006 between colored aleurone and horny endosperm. The lowest correlation secured in any individual ear was 0.697±0.35, which is certainly a significant correlation.

The correlation for the combined seeds of these 20 ears was a very close approximation of the 0.766 expected on the assumption that the correlation is the result of a 3–1–1–3 reduplication in the gametes. One ear, No. 1128, has a correlation exceeding the expected 0.766 by 3.8 times the probable error, but the remaining ears are exceptionally close approximations of the 3–1–1–3 coupling, and with 20 ears one such deviation is not surprising.

TABLE XXXII.—*Correlation between the endosperm texture and the aleurone color of self-pollinated and pure-seeded ears of maize having approximately 25 per cent of the seeds white in the second generation of the hybrid Dh 237.*

[Lines bracketed together in pairs indicate ears borne on the same plant; ears selected for planting are designated by an asterisk (*).]

Pedigree No. of—		Number of seeds.					Correlation, $W+X$.	Probable error.	Percentage of—	
Progeny ear.	Self-pollinated ♂.	Total.	*WX.*	*WH.*	*CX.*	*CH.*			Waxy.	White.
1	2	3	4	5	6	7	8	9	10	11
1122	None	647	74	74	65	434	0.741	0.032	21.4	22.8
1124	do	672	94	77	63	438	.789	.026	23.3	25.4
1125	Self	837	129	112	72	524	.786	.023	24.0	28.7
{1127	1125	723	102	88	75	458	.751	.027	24.4	26.2
{1128	Self	319	46	23	34	216	.868	.027	25.0	21.6
{1129*	do	747	102	87	78	480	.766	.026	24.1	25.1
{1130*	1135	741	96	92	59	494	.794	.025	21.0	25.3
1132	Self	575	80	80	54	361	.739	.033	23.3	27.8
1133	do	758	104	71	83	500	.798	.024	24.6	23.0
{1135	do	627	83	83	52	409	.774	.029	21.5	26.4
{1136	1137	615	104	71	72	368	.764	.028	28.6	28.4
{1137	Self	740	125	80	68	467	.829	.023	26.0	27.7
{1138		548	70	58	70	350	.715	.037	25.1	23.3
1721	Self	712	89	71	76	476	.774	.027	23.2	22.5
1733	1741	634	85	79	76	394	.697	.035	25.4	25.9
1738	Self	472	60	59	45	308	.749	.036	25.2	25.2
1741	do	485	63	57	47	318	.759	.036	23.6	24.7
1743	do	575	59	68	59	389	.702	.039	20.5	22.1
1745	do	625	82	57	67	419	.799	.030	23.8	22.2
1749	do	342	58	40	32	212	.818	.031	26.3	28.6
Total		12,394	1,705	1,427	1,247	8,015	.769	.0064	23.8	25.3

Since the hybrid Dh 234 with the gametic composition *Crh CRH* did not show a correlation between endosperm texture and aleurone color and the hybrid Dh 237 with the gametic composition *cRh CRH* did show a correlation, we can assume that the correlation is between the color factor *C* and endosperm texture. Additional evidence that the correlation is between a factor for color and endosperm texture is obtained from the self-pollinated ears of the hybrid Dh 237 that had approximately 43.75 per cent white seeds, indicating that the plants in question were heterozygous for both color factors *C* and *R*.

If the correlations were independent of the gametic composition, we might expect no consistent differences in the degree of correlation between the monohybrid and dihybrid ears; but if, on the contrary, the correlation is between a factor for color and endosperm texture, the correlation should be reduced in a definite degree on the dihybrid ears. The reason for this reduction in the degree of correlation follows.

A plant which when self-pollinated produces an ear with a dihybrid ratio of colored to white seeds and a monohybrid ratio of horny to waxy seeds must be heterozygous for both color factors and endosperm texture.

If we assume that the association is between a color factor *C* and horny endosperm *H*, and if we further assume that the association results in the combination *CH* being formed three times as often as the combination *Ch*, we then have the above plant making the following gametic classes: 3 *CRH*, 1 *CRh*, 3 *CrH*, 1 *Crh*, 1 *cRH*, 3 *cRh*, 1 *crH*, and 3 *crh*.

The union of the gametes *CrH* and *crh* will result in a white horny zygote; and since *C* and *H* are the associated factors, these seeds will be produced in relatively large numbers, resulting in a reduction in the degree of correlation between colored aleurone and horny endosperm.

A plant which when self-pollinated produces an ear with a monohybrid ratio of white to colored seeds, as well as a monohybrid ratio of horny to waxy seeds, must be homozygous for one color factor and heterozygous for the other color factor as well as endosperm texture. If we assume the heterozygous color factor to be the one which is associated with endosperm texture, we have the above plant making the following gametic classes: 3 *CRH*, 1 *CRh*, 1 *cRH*, and 3 *cRh*. The union of gametes *CRH* with *cRH* results in a colored horny zygote.

Thus every gamete carrying the color factor *C* results in a colored zygote, and the correlation is the same as if it were between color and texture rather than a factor for color and texture, and the normal 41–7–7–9 zygotic grouping is expected, and the correlation between colored aleurone and horny endosperm is 0.766.

When the dihybrid ratio of white to colored seeds is obtained, all of the gametes bearing the factor for color *C* do not result in colored seeds, and the zygotic classes are altered from the above 41–7–7–9 to 123–21–69–43 and the correlation is reduced from 0.766 to 0.570.

From the hybrid Dh 237 four self-pollinated ears were obtained that had the percentage of white seeds closely approximating 43.75, the expected ratio where two independent factors are required to produced a colored seed (Table XXXIII).

TABLE XXXIII.—*Correlation between the endosperm texture and the aleurone color of self-pollinated ears of maize having approximately 43.75 per cent of the seeds white in the second generation of the hybrid Dh 237.*

Pedigree No. of—		Number of seeds.					Correlation, *W*+*X*.	Probable error.	Percentage of—	
Progeny ear.	Self-pollinated ♂.	Total.	*WX.*	*WH.*	*CX.*	*CH.*			Waxy.	White.
1	2	3	4	5	6	7	8	9	10	11
1723	Self	664	94	190	42	338	0.60	0.045	21.0	42.75
1726	...do	560	94	179	28	259	.653	.046	21.6	48.2
1736	...do	595	93	163	45	294	.577	.046	23.2	43.0
1747	...do	658	96	163	51	348	.601	.033	22.3	39.3
Total		2,477	377	695	166	1,239	.603	.023	21.9	43.2

The total number of seeds for the four ears are grouped as follows:

Class.	Number of seeds.				Correlation.
	CH.	*CX.*	*WH.*	*WX.*	
Observed	1,239	166	695	377	0.603±0.0229
Expected	1,190	203	668	416	.570

The agreement is very close, the deviation of 0.033 being but slightly larger than the probable error, and none of the four ears comprising the group deviated in excess of twice the probable error.

CORRELATION IN CROSSES BETWEEN THE TWO HYBRIDS DH 234 AND DH 237.

If the above explanation is correct and the association is between the factor for color C and horny endosperm H, a cross between the two first-generation hybrids should result in two groups of ears, one group all colored, the other group with four classes of seeds, but no correlation. Both these groups were obtained; the all-colored group has been previously discussed under aleurone color, and the progeny of three such ears are considered from the standpoint of correlations on pages 88 to 95.

Nine ears were obtained with the hybrid Dh 234 as the female parent and eight ears were secured with the same hybrid used as the male parent. These 17 ears showed four classes of seeds, indicating that the plants of the hybrid Dh 237 were heterozygous for the color factor C as well as endosperm texture. None of the correlations are above 0.1, 9 being plus and 7 minus correlations. The two groups are shown in Table XXXIV. Together they aggregate 10,032 individuals with a correlation of 0.0149±0.0166.

TABLE XXXIV.—*Correlation between the endosperm texture and the aleurone color of ears of maize, crosses between the hybrids Dh 234 and Dh 237, using each as the male and as the female parent.*

CROSSES BETWEEN HYBRIDS DH 234 × DH 237.

Pedigree No. of—				Number of seeds.					Correlation, W + X.	Probable error.	Percentage of—	
Progeny ear.	Self-pollinated. ♂	Self-pollinated. ♀	Reciprocal cross.	Total.	*WX.*	*WH.*	*CX.*	*CH.*			Waxy.	White.
1	2	3	4	5	6	7	8	9	10	11	12	13
1518	1726	1519	1725	510	28	102	82	298	0.014	0.083	21.5	24.5
1524	None	1525	None	773	40	149	126	458	−.012	.069	21.5	24.5
1530	1733	1531	1734	676	36	146	97	397	.005	.073	19.7	26.9
1532	None	1533	1729	707	35	123	116	433	.033	.073	21.4	22.4
1538	...do	1539	None	609	33	123	117	336	−.107	.075	24.6	25.6
1540	1736	None	1735	679	37	124	115	403	.023	.072	22.4	23.7
1541	None	...do	None	631	36	99	123	373	.048	.074	25.2	21.4
1542	1723	1543	1722	515	24	90	96	305	−.028	.087	23.3	22.1
1546	1747	1547	1746	800	42	154	163	441	−.151	.066	25.0	24.5
Total				5,900	311	1,110	1,035	3,444	−.035	.024	22.8	24.1

CROSSES BETWEEN HYBRIDS DH 237 × DH 234.

Progeny ear.	Self-pollinated. ♂	Self-pollinated. ♀	Reciprocal cross.	Total.	*WX.*	*WH.*	*CX.*	*CH.*	Correlation, W + X.	Probable error.	Waxy.	White.
1725	1519	1726	1518	472	34	91	80	267	.109	.079	24.2	26.5
1734	1531	1733	1530	516	27	106	92	291	−.124	.082	23.1	25.8
1729	1533	None	1532	613	40	108	129	336	−.019	.071	27.1	24.2
1735	None	1736	1540	458	25	86	77	270	.010	.088	22.3	24.2
1722	1543	1723	1542	677	41	152	121	363	−.106	.068	23.9	28.5
1746	1547	1747	1546	621	47	121	115	338	−.069	.068	26.1	27.1
1730	None	None	None	401	27	75	65	234	.129	.088	22.9	24.9
1724	...do	...do	...do	374	30	60	89	195	.041	.087	31.8	24.1
Total				4,132	271	799	768	2,294	.015	.027	25.1	26.0

With an association between one of two factors for color and endosperm texture, a variety of zygotic ratios may be obtained, even though the assumption is made that the gametic reduplication is only of the series 3–1–1–3. Table XXXV gives the degrees of correlation expected between endosperm texture and aleurone color where the assumption is made that the reduplication in the gametes between endosperm texture and a factor for color (*C*) is of the series 3–1–1–3. The minus sign is used to indicate a correlation between colored aleurone and waxy endosperm; the other correlations are between colored aleurone and horny endosperm. Column 4 gives the gametic composition of the two parents which, when crossed, give the zygotic classes shown in column 5 and the correlations shown in column 1. The letters *C* and *R* represent color factors. *H* represents the dominant character, horny endosperm, and *h* waxy endosperm.

TABLE XXXV.—*Possible degree of correlation between aleurone color and endosperm texture, the gametic reduplication being 3–1–1–3.*

[A correlation between colored aleurone and waxy endosperm is indicated by the minus sign in column 1; the other correlations are between colored aleurone and horny endosperm.]

Degree of correlation.	Percentage of— White.	Percentage of— Waxy.	Gametic composition of parents.	Zygotic classes.[1]
1	2	3	4	5
0.800	50	50	*CcRrHh CcRRhh*	3- 1- 1- 3
—.800	50	50	*CcRrHh CcRRhh*	1- 3- 3- 1
.766	25	25	*CcRRHh CcRRHh*	41- 7- 7- 9
—.744	25	25	*CcRRHh CcRRHh*	33-15-15- 1
.615	25	50	*CcRRHh CcRrhh*	7- 5- 1- 3
—.615	25	50	*CcRRHh CcRrhh*	5- 7- 3- 1
.615	50	25	*CcRRHh ccRRHh*	7- 5- 1- 3
—.615	50	25	*CcR RHh ccRRHh*	5- 7- 1- 3
.570	43.75	25	*CcRrHh CcRrHh*	123-21-69-43
—.380	43.75	25	*CcRrHh CcRrHh*	99-45-93-19
.270	43.75	50	*CcRrHh CcRrhh*	21-15-11-17
—.270	43.75	50	*CcRrHh CcRrhh*	15-21-17-11
0	50	50	*CcRrhh ccRRHh*	1- 1- 1- 1
0	50	25	*CCrrHh ccRrHh*	3- 1- 3- 1

[1] The first figure in column 5 is the colored horny, followed by the colored waxy, the white horny, and the white waxy zygotes, respectively.

CORRELATION IN THE THIRD GENERATION OF THE HYBRID DH 234.

Two ears from each of the two first-generation hybrids were selected for planting. The four classes of seeds from each ear were planted in separate rows. Crosses were made between plants from the white waxy and colored horny seeds and between plants from the colored waxy and white horny seeds. Self-pollinated ears were also obtained from all the classes, but the ears resulting from self-pollinating the colored horny seeds are the only self-pollinated ears that exhibit four classes of seeds.

The two ears grown from the hybrid Dh 234 are shown in Table XXXI as pedigree Nos. 1099 and 1111. Ear No. 1099 was the result of pollinating a plant of the hybrid Dh 234 with pollen from a plant of the same hybrid which when self-pollinated produced ear No. 1106. Both these ears curiously enough have exactly the same degree of association, or, rather, lack of association, -0.019 ± 0.07.

The other ear, No. 1111, was the result of self-pollinating a plant of hybrid Dh 234 and had a correlation of -0.256 ± 0.063, heretofore referred to as one of the two ears that might be held to show a significant correlation.

TABLE XXXVI.—*Correlation between the endosperm texture and the aleurone color of 32 ears of maize, the progeny of ear No. 1099 of the third generation of the hybrid Dh 234.*

Progeny ear.	Pedigree No. of— Self-pollinated. ♂	Pedigree No. of— Self-pollinated. ♀	Pedigree No. of— Reciprocal cross.	Number of seeds. Total.	Number of seeds. *WX.*	Number of seeds. *WH.*	Number of seeds. *CX.*	Number of seeds. *CH.*	Correlation, W+X.	Probable error.	Percentage of— Waxy.	Percentage of— White.
1	2	3	4	5	6	7	8	9	10	11	12	13
WHITE WAXY × COLORED HORNY.												
1552	1644	All white waxy.	1643	506	113	119	114	160	0.145	0.061	44.8	45.8
1555	1705	...do	None	230	60	53	60	57	0.036	0.088	52.2	49.1
1563	None	None	...do	257	56	72	53	76	.045	.085	43.4	51.0
1564	...do	...do	...do	438	92	120	128	98	−.260	.061	50.2	48.4
Total				1,431	321	364	355	391	−.102	.035	47.2	47.8
COLORED WAXY × WHITE HORNY.												
1572	All white	1573	1604	127	22	40	31	34	−.247	.115	41.7	48.8
1574	None	1575	None	645	166	151	161	167	.067	.053	50.6	49.2
1579	...do	None	1610	468	114	134	107	113	−.054	.062	47.2	53.0
1584	...do	1585	1623	406	111	103	84	108	.162	.065	47.8	52.4
1590	All white	1591	1619	580	145	142	146	147	.014	.056	50.2	49.4
1592	...do	1593	1621	307	86	61	101	59	−.104	.078	60.8	47.9
Total				2,533	644	631	630	628	.009	.027	50.7	50.7
WHITE HORNY × COLORED WAXY.												
1602	All waxy	1603	None	322	76	74	82	90	.018	.075	49.0	46.6
1604	...do	1605	1572	171	46	42	42	41	.046	.103	51.4	51.5
1606	...do	1607	None	391	95	101	109	86	−.148	.069	52.2	50.1
1610	None	None	1579	303	44	60	104	95	−.197	.079	48.8	31.5
1619	All waxy	1620	1590	467	110	112	123	122	−.013	.062	50.0	47.6
1621	...do	1622	1592	348	86	74	105	83	−.042	.072	54.9	46.0
1623	...do	None	1584	497	134	120	129	114	−.044	.062	53.0	51.5
1624	...do	...do	None	67	17	19	13	18	.108	.054	44.8	53.7
Total				2,566	608	602	707	649	−.037	.027	51.3	47.2
COLORED HORNY × WHITE WAXY.												
1626	All waxy	None	None	427	112	107	115	93	.068	.088	51.0	52.9
1635	None	1636	...do	703	179	169	177	178	.032	.051	49.5	50.6
1637	All waxy	1638	...do	424	109	109	99	107	.042	.088	51.4	49.0
1639	...do	None	...do	123	32	28	33	30	.019	.121	48.8	52.9
1641	None	1642	...do	396	106	93	90	107	.151	.066	50.2	49 5
1643	All waxy	1644	1552	511	133	129	130	119	.044	.059	51.3	51.4
1645	...do	1646	1560	510	120	116	135	139	.034	.060	46.3	50.0
1647	...do	None	None	387	80	85	113	109	.047	.070	42.6	50.0
Total				3,481	871	836	892	882	.014	.023	50.5	49.0
COLORED HORNY × SELF.												
1625	Self	Self		464	27	110	72	255	−.068	.059	29.5	21.3
1636	...do	...do		573	49	102	97	325	.239	.066	26.4	25.5
1638	...do	...do		573	34	112	105	322	.030	.076	25.5	24.3
1642	...do	...do		551	31	103	113	304	−.152	.076	24.6	26.2
1644	...do	...do		652	45	138	121	348	.009	.067	28.1	25.5
1646	...do	...do		368	21	58	65	224	.195	.095	21.5	23.4
Total				3,181	207	623	573	1,778	.0152	.031	26.1	24.5

TABLE XXXVII.—*Correlation between the endosperm texture and the aleurone color of 23 ears of maize, the progeny of ear No. 1111 of the third generation of the hybrid Dh 234.*

WHITE WAXY × COLORED HORNY.

Pedigree No. of—			Number of seeds.					Correlation, W+X	Probable error.
Progeny ear.	Self-pollinated ♂.	Reciprocal cross.	Total.	WX.	WH.	CX.	CH.		
1	2	3	4	5	6	7	8	9	10
1648	1696	None	712	179	166	202	165	−0.062	0.049
1651	1694	...do	286	77	72	62	75	.128	.078
1652	1700	...do	611	142	140	160	169	.035	.068
1654	1705	...do	387	97	80	105	105	.098	.068
1660	None	...do	600	155	155	128	162	.119	.055
Total			2,596	650	613	657	676	.044	.026

COLORED WAXY × WHITE HORNY.

1665	1687	1686	403	105	101	100	97	0.005	0.067
1667	None	None	87	20	20	25	22	− .064	.144
Total			490	125	121	125	119	− .009	.061

WHITE HORNY × COLORED WAXY.

1682	All waxy	None	448	110	95	126	117	0.040	0.064
1686	...do	1665	370	90	89	108	83	− .125	.071
Total			818	200	184	234	200	− .036	.047

COLORED HORNY × WHITE WAXY.

1695	All waxy	None	393	95	96	117	85	−0.164	0.067
1699	...do	...do	511	126	126	119	140	.081	.060
1704	...do	...do	192	51	53	49	39	− .350	.078
1710	...do	...do	458	114	106	126	112	− .022	.085
1712	...do	...do	181	56	42	38	45	.223	.096
1713	...do	...do	179	57	41	37	44	− .246	.096
1714	...do	...do	561	36	150	151	124	.147	.056
1715	...do	...do	304	168	81	73	82	− .029	.077
1718	...do	...do	290	77	73	76	64	− .060	.079
Total			3,069	780	768	786	735	− .024	.024

COLORED HORNY × SELF.

1694	Self		578	39	110	103	326	0.057	0.073
1696	...do		373	23	66	76	208	− .025	.092
1700	...do		451	31	97	79	244	− .007	.081
1711	...do		415	26	66	77	246	.115	.089
1719	...do		549	35	102	93	319	.081	.076
Total			2,366	154	441	428	1,343	.050	.036

As no correlation was found on the second-generation ears of this hybrid, none was to be expected on the third-generation ears. Fifty-five ears were obtained, representing many combinations. With the possible exception of two ears, Nos. 1564 (Table XXXVI) and 1704 (Table XXXVII), no correlations were obtained. The individual ears shown in these tables are so arranged that the ears resulting from the same cross may be readily compared. Ear No. 1564 had a correlation of 0.260±0.06. A correlation of this magnitude would be expected to occur as the result of chance once in 267 times, but since it occurs in a group of four, it would be expected as the result of chance once in 67 times.

Ear No. 1704 had a correlation of 0.350±0.078, which is 4.5 times the probable error, and should occur as the result of chance once in 415 times, but since it is but 1 in a group of 10 individuals, the odds against its chance occurrence are 42 to 1. We may with some propriety conclude that the correlations found on these two ears are accidental. The results, then, as shown by the third-generation ears support the assumption that this hybrid is homozygous for the color factor *C*.

CORRELATION IN THE THIRD GENERATION OF THE HYBRID DH 237.

Two ears were selected and grown from the hybrid Dh 237. These two ears are shown in Table XXXII, pedigree Nos. 1129 and 1130. Ear No. 1129 was the result of self-pollinating a plant of the hybrid Dh 237, and ear No. 1130 is a second ear from this same plant. The male parent of this latter ear, when self-pollinated, produced ear No. 1135. Ear No. 1129 had the exact degree of correlation which is expected on a 3–1–1–3 coupling, 0.766±0.026, while the second ear of the same plant, No. 1130, had a correlation of 0.794 ±0.025. The male parent of ear No. 1130 had a correlation of 0.774 ±0.029. These two ears are very close approximations of the 0.766 correlation which is expected on a 3–1–1–3 coupling. There were, of course, four classes of seeds on each of these two ears. The different classes were planted separately.

Crosses were made between plants from the white waxy seeds and plants from the colored horny seeds from the same ear. These crosses were made, using white waxy plants as the female parent, and also as the male parent. Self-pollinated ears were also secured from all the plants to make sure that they were of the type expected. The self-pollinated colored horny ears, however, are the only self-pollinated ears that would have all four classes of seeds. The three ears obtained from self-pollinated plants grown from colored horny seeds of ear No. 1129 are shown in Table XXXVIII.

The correlation for these three ears is 0.770±0.017. This correlation is certainly a close approximation of the expected 0.766, but upon examining the three ears that make up the total we find the difference between the extremes to be 0.384±0.06, a difference of more than six times the probable error, which can hardly be ascribed to chance fluctuation. The ear with the lowest correlation (No. 1796, correlation 0.450±0.063) deviates from the expected 0.766 by

0.316, which is slightly in excess of five times the probable error. The correlation of 0.45 is rather close to the expected 0.57 where a plant heterozygous for two color factors is self-pollinated, but the percentage of white seeds, 21.9, precludes this explanation.

Fortunately another ear borne on the same plant was pollinated by a plant grown from a homozygous white waxy seed. If ear No. 1796, deviating from the expected correlation of 0.766 by five times the probable error, represents but a chance fluctuation from this correlation, then the first ear of this same plant should, when crossed with white waxy, produce an ear with a correlation approximating 0.8. The ear representing this cross is ear No. 1795. (Table XXXIX.) The correlation found was 0.387±0.05, certainly not an approximation of 0.8. These correlations show that the two ears of the plant were producing the same excess of gametes bearing colored waxy and white horny genes. The relations of these ears are shown in figure 11.

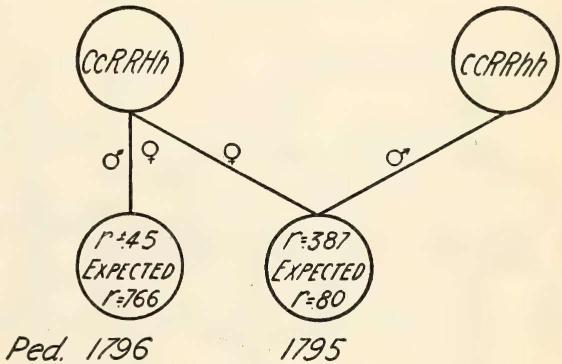


FIG. 11.—Diagram showing the relations of ears Nos. 1796 and 1795.

Since the male parent of ear No. 1795 was a homozygous recessive, the zygotic ratio observed on this ear is also the gametic ratio of the female gametes within the range of chance fluctuation.

To determine the gametic ratio of this ear as accurately as possible the sum of the two reduplicated groups was divided by the sum of the nonreduplicated groups and the gametic ratio found to be 1.5 to 1, or 3 to 2. The expected correlation on an ear the result of self-pollinating a plant with the gametic ratio of 3–2–2–3 is 0.517. Ear No. 1796 is the result of self-pollinating the plant which bore ear No. 1795 with the above gametic ratio. The observed correlation on ear No. 1796 is 0.45, which deviates from a 0.517 correlation by 0.067±0.063, the deviation being insignificant. The plant, then, which produced ears Nos. 1795 and 1796 may with propriety be considered as having formed gametes in the proportion of 3–2–2–3, while the majority of ears with a correlation have been shown to approximate the gametic series 3–1–1–3.

The adherents of the linkage theory would look upon this departure from the expected as a mutation of the locus of one or both of the characters, resulting in the distance separating them being widened from 25 to 40 units. To explain this gametic ratio on the reduplication theory requires but a simple alteration of the series of cell division, assumed to account for 3–1–1–3 couplings.

The 3–1–1–3 gametic ratio is assumed to be the result of the type of cell division shown in figure 12, and the 3–2–2–3 coupling merely requires that the cells *Ab* and *aB* divide once while the cells *AB*, *ab* are undergoing two divisions. (Fig. 13.)

The fact that both of these ears had approximately the expected percentage of both white and waxy seeds demonstrates beyond doubt that the distributions observed are not due to a failure to properly classify the material or to the presence of other factors that would influence the expected proportions. If these correlations are to be

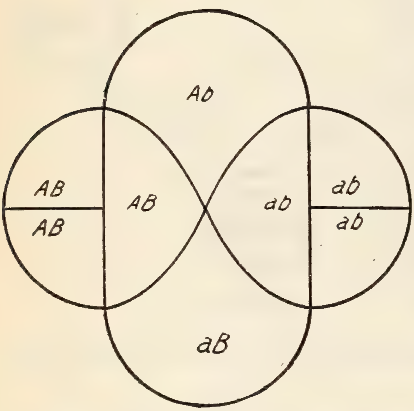


FIG. 12.—Diagram showing the type of cell division proposed by Punnett to explain a 3–1–1–3 gametic coupling.

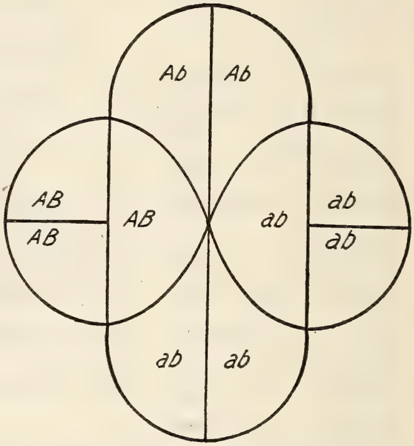


FIG. 13.—Diagram showing a possible modification of figure 12 to account for a 3–2–2–3 coupling.

looked upon as the result of reduplication the only explanation is to admit other series than those proposed. The remaining two ears of the three self-pollinated horny plants are sufficiently close approximations of the expected 0.766.

Five ears were secured from plants grown from the white waxy seeds of pedigree No. 1129 that were the result of pollinating these plants with plants grown from the colored horny seeds of the same ear. Three ears were also obtained where the parentage was reversed. These eight ears are shown in Table XXXIX.

The first group had a correlation 0.806±0.017 between colored and horny, the expected being 0.8. Of the individual ears only one deviated in excess of four times the probable error, that one—No. 1764—deviating by eight times the probable error. The correlation of 0.91, observed on this ear, is intermediate between the 0.8 expected on a 3–1 coupling and the 0.96 expected on a 7–1 coupling, though it is a closer approximation of the latter. The deviation of 0.06±0.013 from the 7–1 coupling is, however, 4.6 times the probable error.

Ear No. 1764 has a reciprocal ear in No. 1799. This ear had a correlation of 0.7, a deviation of 0.1±0.03 from the expected 0.8, and differing from No. 1764 by 0.21±0.048, which is almost 4.5 times the probable error. A self-pollinated ear was obtained from the same plant that bore ear No. 1799. This self-pollinated ear is No. 1800 (Table XXXVIII). The correlation of 0.834 observed on this ear is higher than the expected 0.766. The deviation of 0.068±0.02 from 0.766 is 3.4 times the probable error, which is rather large to be attributed to chance. The relations of these ears are shown in figure 14.

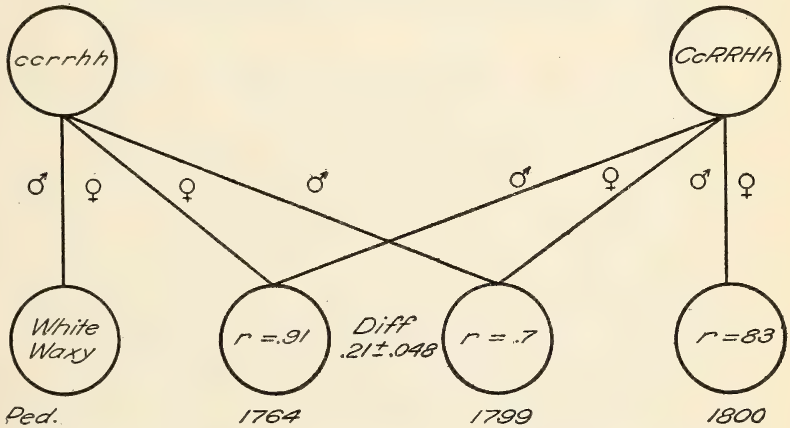


FIG. 14.—Diagram showing the relations of ears Nos. 1764, 1799, and 1800.

Since the female parent of ear No. 1764 was homozygous for waxy endosperm texture, the correlation of 0.91 represents the reduplication in the gametes of the male parent. This reduplication is higher than the expected, the degree of correlation indicating the reduplication to be closer to a 7–1 than a 3–1; in reality the series very closely approximates 4.5–1. The reciprocal ear of No. 1764—No. 1799—has a lower reduplication series than 3–1–1–3, being in reality 2.4–1.

The correlation of 0.834 on ear No. 1800, the self-pollinated ear of the heterozygous colored horny parent, indicates a gametic series intermediate between the 4.5–1 and 2.4–1.

The expected correlation in self-pollinating a plant with a male gametic series of 203–44–45–206 and a female gametic series of 168–71–80–191 is 0.788. Ear No. 1800, which represents such a self-pollinated ear, has a correlation of 0.834±0.02, the deviation of 0.046 from 0.788 being no larger than is to be expected.

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This difference between the male and female gametes in the degree of reduplication could be brought about by a higher death rate prevailing in the pollen grains carrying white horny and colored waxy, the combinations that came from opposite parents. It might be urged that these combinations reacted in an unfavorable way, lessening the life of the pollen grain or so reducing it in vigor as to have a larger proportion of the ovaries fertilized by the parental, white waxy and colored horny combinations.

It would be necessary that the death rate be alike for the two combinations, colored waxy and white horny, or the percentages of white and waxy would be found deficient. This is in itself an argument against this explanation, since it seems improbable that *CX* and *WH* should happen to be equally weak. The percentages of white to waxy seeds for the three ears are sufficiently close approximations to the expected to indicate that the two combinations were retarded about equally.

Ear No. 1764 had 50.2 per cent waxy and 50.4 per cent white seeds, certainly very close to the expected 50 per cent. The reciprocal ear, No. 1799, had 51.4 per cent waxy and 53.2 per cent white seeds. The differences between white and waxy percentages of these two reciprocals are not significant. The percentage of waxy seeds on the self-pollinated ear (No. 1800) is almost exactly the expected percentage, while the percentage of white seeds is in excess of the expected by more than three times the probable error. That the excess of white seeds on this ear is not brought about by a failure of the pollen grains carrying colored waxy combinations is demonstrated by the percentage of waxy seeds, which is normal. In other words, if the high percentage of white seeds is due to a high mortality of the pollen grains carrying colored aleurone, this mortality must have been equal in the pollen grains carrying colored-waxy and colored-horny combinations.

The expected grouping compared with that observed for the 755 seeds is as follows:

Class.	Number of seeds.			
	CH.	*CX.*	*WH.*	*WX.*
Expected	484	82.5	82.5	106
Observed	476	64	88	127

As can be seen, there was a failure of both colored horny and colored waxy gametes, but greater in the colored waxy than in the colored horny, while a corresponding increase is noted in both the white horny and white waxy combinations, though the increase is much larger in the latter case. The figures would seem to indicate that the higher correlation was due to the weak growth of the pollen grains carrying the odd character combinations. If this be the case, it should also be observed on ear No. 1764, but not on ear No. 1799, as the male parent of this ear was making but one kind of pollen grains—white waxy.

The grouping for ear No. 1764 is as follows:

Class.	Number of seeds.			
	CH.	*CX.*	*WH.*	*WX.*
Expected	186.7	62.3	62.3	186.7
Observed	203	44	45	206

These figures would certainly seem to indicate that the odd combinations *CX* and *WH* were in some way at a disadvantage when compared with *CH* and *WX*.

The grouping for ear No. 1799 is as follows:

Class.	Number of seeds.			
	CH.	*CX.*	*WH.*	*WX.*
Expected	191.3	63.7	63.7	191.3
Observed	168	71	80	191

The low correlation on this ear is obviously due to paucity of colored horny female gametes, a combination that would not be expected to be deficient. No question of the vigor of part of the pollen grains is concerned on this ear, since they were all alike. A shortage in the colored horny gametes was indicated on the self-pollinated ear (No. 1800), but not to the extent noted on ear No. 1799, while an increase was observed of the white waxy gametes on ear No. 1800, which was also found on ear 1764, but not in such an increased degree as would naturally be expected.

Summing up the three ears, we find ear No. 1799 indicating that the female gametes were deficient in the colored horny combination, practically the expected proportion of white waxy gametes, and a slight excess of the two odd combinations. The male gametes, as indicated on ear No. 1764, were in excess in both the colored horny and white waxy combinations and deficient in the odd combinations.

From these two ears we would expect the self-pollinated ear to be deficient in colored horny seeds, in excess in white waxy seeds. Using the zygotic ratios of the male and female parents as representing the actual gametic ratios, we find the white waxy combination in excess by 20 in the male gametes and equal in the female gametes; so we would expect an excess of about 20 in the self-pollinated ear, and we find an excess of 21.

The colored horny combination in the male gametes was in excess by 17 and deficient in the female gametes by 21; so a deficiency of 4 would be expected on the self-pollinated ear, and we find a deficiency of 8.

The colored waxy combination in the male gametes is deficient by 18; in the female gametes this same combination is in excess by 8; so a deficiency of 10 would be expected in the self-pollinated ear, and a deficiency of 18 is noted.

The white horny combination is deficient by 17 in the male gametes and in excess by 17 in the female gametes; so that they would be expected in the theoretical proportion on the self-pollinated ear, and we find an excess of 6. This agreement of evidence derived from so many different sources would indicate that the departures observed were the result of a definite and unexpected gametic series formed by the plant which bore ears Nos. 1799 and 1800, rather than fluctuations due to chance.

The three ears that were obtained when plants grown from white waxy seeds were used as the male parent had a total of 1,293 seeds with a correlation of 0.610 ± 0.025, but since one ear of the three has been shown to be of entirely different coupling this ear should not be included in the totals. Omitting, then, this one ear, No. 1795, which is outstanding and does not belong to the series, the total number of seeds then becomes 740, with a correlation of 0.737 ± 0.025—a deviation from the expected 0.8 of but 2.5 times the probable error.

Nine ears were secured from plants grown from the colored waxy seeds as the male parent, and two ears were secured from plants grown from the white horny seeds as the male. These ears are also shown in Table XXXVI. The correlation for the total number of seeds is not significant. One ear, however, No. 1781, has a negative association between C and H of 0.220 ± 0.059, a deviation from a zero correlation by 3.7 times the probable error. This ear could in all probability be looked upon as the result of chance fluctuation in sampling, though closely approximating the 0.27 expected when a plant heterozygous for the color factors C and R and horny endosperm texture with a 3–1–1–3 coupling between the factor C and waxy endosperm is crossed with a homozygous waxy plant heterozygous for the two factors for color.

As a test of the possibilities of securing a correlation when crossing two plants, one heterozygous for endosperm texture and without the factor for color C, the other homozygous for endosperm texture and heterozygous for the factor C, crosses were made between plants from white horny seeds and plants from colored waxy seeds. These crosses were made, using the colored waxy plants as the female parent and also as the male parent.

It is obvious that no coupling could occur in the gametes, but Collins (4) reported significant correlations on two ears representing a similar cross that as yet can not be explained. It would be possible, however, to obtain a correlation by crossing a plant grown from a white horny seed with a plant grown from a colored waxy seed where two factors are required to produce color, and the correlation is between one of these color factors and endosperm texture.

TABLE XXXVIII.—*Correlation between the endosperm texture and the aleurone color of 22 ears of maize, the progeny of ear No. 1129 of the third generation of the hybrid Dh 237.*

Progeny ear.	Pedigree No. of— Self-pollinated. ♂	Pedigree No. of— Self-pollinated. ♀	Pedigree No. of— Reciprocal cross.	Number of seeds. Total.	Number of seeds. *WX.*	Number of seeds. *WH.*	Number of seeds. *CX.*	Number of seeds. *CH.*	Correlation, W+X.	Probable error.	Percentage of— Waxy.	Percentage of— White.
1	2	3	4	5	6	7	8	9	10	11	12	13
COLORED HORNY × SELF.												
1796				296	24	41	42	189	0.450	0.063	23.3	21.9
1798				752	107	71	87	487	.788	.025	26.2	23.7
1800				755	127	88	64	476	.834	.020	25.3	28.5
Total				1,803	258	200	193	1,152	.770	.017		
WHITE WAXY × COLORED HORNY.												
1754	1800		None	500	178	59	67	196	0.797	0.025	47.0	47.4
1758	1800		do	439	165	51	48	175	.790	.030	48.6	49.7
1762	1798		do	537	170	88	70	209	.704	.032	44.7	48.0
1764	1800		1799	498	206	45	44	203	.910	.014	50.2	50.4
1765	1800		None	528	177	74	72	205	.705	.033	47.2	47.6
Total				2,502	896	317	301	988	.806	.017		
COLORED HORNY × WHITE WAXY.												
1795	None	1796	None	553	164	117	104	168	0.387	0.050	48.5	50.5
1797	do		do	230	93	32	24	81	.810	.036	50.9	54.4
1799	do	1800	1764	510	191	80	71	168	.700	.034	51.4	53.2
Total				1,293	448	229	199	417	.610	.025		
COLORED WAXY × WHITE HORNY.												
1766	All white		None	432	112	102	110	108	0.038	0.065	51.4	49.6
1768	do		1775	144	33	35	42	34	−.135	.112	52.0	47.2
Total				576	145	137	152	142	−.009	.056		
WHITE HORNY × COLORED WAXY.												
1772	None		None	448	95	120	114	119	−0.095	0.064	46.6	48.0
1773	do		do	613	146	158	161	148	−.082	.055	50.4	49.6
1775	do		1768	533	128	138	143	124	−.096	.058	50.8	50.0
1777	do		None	428	97	97	112	122	.043	.065	48.8	45.3
1779	do		do	476	127	135	107	107	−.036	.062	49.2	55.0
1781	do		do	477	105	137	128	107	−.220	.059	48.9	50.4
1784	do		do	591	174	165	133	119	−.029	.056	52.0	57.3
1786	do		do	446	101	113	110	122	−.004	.064	47.3	48.0
1788	do		do	386	87	102	95	102	−.044	.069	47.2	49.0
Total				4,398	1,060	1,165	1,103	1,070	−.061	.020		

The assumption can then be made that the white horny plant is producing gametes *CHr*, *Chr*, *cHr*, and *chr*, with a correlation between *C* and *H*. Such a plant, if self-pollinated, would produce an all-white ear with 3 horny seeds to 1 waxy.

The colored waxy plant might be making gametes *CRh Crh*. A cross between a colored waxy plant of this nature and a white horny plant such as has been described would result in an ear with four classes of seeds: *CH*, 7; *CX*, 5; *WH*, 1; *WX*, 3; correlation, 0.615. In this case, however, the percentage of white seeds is but 25, and the correlation is 0.615, while in the two ears reported by Collins, one had 30.1 per cent white with a correlation of 0.373 ± 0.057, and the other had 48 per cent white and a correlation of 0.47 ± 0.056. It is at once apparent that neither of these ears could be looked upon as approximations of the above zygotic arrangement.

From the second ear of the hybrid Dh 237, No. 1130, from which the six classes of seeds were planted, three self-pollinated ears from colored horny plants were secured that had four classes of seeds (Table XXXIX). These three ears had a correlation of 0.725 ± 0.017, slightly lower than the expected 0.766. None of the three ears deviated from the expected in excess of three times the probable error, though all three were below the expected. As the result of crossing plants grown from white waxy seeds with plants grown from colored horny seeds of ear No. 1130, six ears were obtained by using the white waxy plants as the female parents, and five ears were obtained by using the white waxy plants as the male parents. These 11 ears are also shown in Table XXXIX.

The 6-ear group had a correlation of 0.809 ± 0.01, which is a very close approximation of the expected 0.8. None of the individual ears of this group deviated from the expected correlation by as much as three times the probable error.

The ears of the 5-ear group had with one exception lower correlations than the lowest obtained in the 6-ear group. The correlation for the five ears was 0.76 ± 0.01, which differs from the 0.809 correlation obtained in the reciprocal ears by 0.049 ± 0.015. None of the ears in the 5-ear group deviated by as much as three times the probable error from the expected correlation. These two groups, together with the three self-pollinated ears from the colored horny plants, are certainly very close approximations of the expected results where the coupling is of the form 3–1–1–3. The individual ears exhibit a remarkably uniform grouping of the four classes of seeds.

Crosses were also made between plants from the colored waxy seeds and plants from the white horny seeds, which should result in ears with no correlation.

TABLE XXXIX.—*Correlation between the endosperm texture and the aleurone color of 14 ears of maize, the progeny of ear No. 1130 of the third generation of the hybrid Dh 237.*

[Lines bracketed together indicate ears borne on the same plant.]

Progeny ears.	Pedigree No. of— Self-pollinated. ♂	Pedigree No. of— Self-pollinated. ♀	Pedigree No. of— Reciprocal cross.	Number of seeds. Total.	Number of seeds. *WX.*	Number of seeds. *WH.*	Number of seeds. *CX.*	Number of seeds. *CH.*	Correlation, *W+X*	Probable error.	Percentage of— Waxy.	Percentage of— White.
1	2	3	4	5	6	7	8	9	10	11	12	13
COLORED HORNY × SELF.												
1840	Self			308	38	46	37	187	0.615	0.060	24.3	27.5
1847	...do			721	83	97	72	469	.695	.084	21.5	25.0
1855	...do			563	76	56	56	375	.740	.035	23.5	23.5
Total.				1,592	197	199	165	1,031	.725	.017	22.75	24.9
COLORED HORNY × WHITE WAXY.												
1838	All waxy		1804	545	193	78	67	207	.768	.027	47.8	49.8
1839	...do	1840	None	415	153	67	55	140	.706	.037	50.1	53.0
1846	...do	1847	...do	621	219	80	86	236	.765	.025	49.2	48.2
1849	...do		1815	581	222	79	77	203	.754	.027	51.4	51.8
1854	...do	1855	1816	614	223	76	83	232	.784	.024	49.8	48.7
Total.				2,776	1,010	380	368	1,018	.760	.012	50.1	52.0
WHITE WAXY × COLORED HORNY.												
1804	None		1838	363	132	47	34	150	.850	.027	45.7	49.3
1806	...do		None	435	180	52	57	146	.799	.027	54.5	53.3
1807	...do		...do	275	95	32	41	107	.775	.037	49.5	46.2
1810	...do		...do	441	183	60	55	143	.776	.028	54.0	55.0
1815	...do		1849	465	164	60	53	188	.814	.025	51.0	48.2
1816	1855		1854	515	215	57	65	178	.824	.023	54.3	52.8
Total.				2,494	969	308	305	912	.809	.011	51.0	51.2
COLORED WAXY × WHITE HORNY.												
1818	All white		1827	754	185	182	181	206	0.074	0.049	48.6	48.7
1820	...do		None	207	57	52	47	51	.086	.095	48.0	49.8
1822	...do		1836	542	136	135	157	114	−.155	.057	53.8	50.0
1825	None		1835	584	139	148	129	168	.100	.055	46.0	49.2
Total.				2,087	517	517	514	539	.042	.029	49.6	49.4
WHITE HORNY × COLORED WAXY.												
1827	All waxy		1818	644	170	163	140	171	0.119	0.053	48.2	51.7
1829	None		None	511	134	128	142	107	−.117	.059	54.0	51.3
{1833	All waxy		...do	434	116	98	100	120	.173	.063	49.8	49.3
{1834	...do		...do	511	128	128	122	133	.043	.060	49.0	50.5
1835	...do		1825	503	125	131	129	118	−.068	.060	50.5	50.9
1836	...do		1822	297	58	91	69	79	−.156	.077	42.8	50.1
Total.				2,900	731	739	702	728	.013	.025	49.4	50.6

As the result of such crosses 10 ears were obtained, 4 with the colored waxy plants as the female parent and 6 with colored waxy plants as the male parent (Table XXXIX). The highest correlation secured was 0.173±0.063 on ear No. 1833, which can not be considered significant, being less than three times the probable error.

The results obtained from the progeny of the two ears, Nos. 1129 and 1130, of the hybrid Dh 237 were, with a few exceptions, fairly close approximations of the expected results on the assumption that the gametes were formed in a series of 3–1–1–3.

SECOND GENERATION OF THE CROSSES BETWEEN THE TWO HYBRIDS DH 234 AND DH 237.

Aside from the two first-generation hybrids between the Algeria and the Chinese varieties of maize, Dh 234 and Dh 237, and their immediate progeny, the result of self-pollination or crosses between two plants of the same hybrid there were 34 ears, the result of crossing the two first-generation hybrids. Seventeen of these ears were all colored with both horny and waxy seeds.

Three of these all-colored ears were grown the following season. One ear, resulting from using the hybrid Dh 234 as the female parent and the hybrid Dh 237 as the male parent, was renumbered cross Dh 330 and grown under that symbol. The other two ears grown were the result of using the hybrid Dh 237 as the female parent and the hybrid Dh 234 as the male parent. These two ears were known as crosses Dh 333 and Dh 334. The female parent of the cross Dh 333 was used as the male parent of the cross Dh 330.

On each of these three all-colored ears there are 16 classes of zygotes, only 6 of which will exhibit, when self-pollinated, ears with all 4 classes of seeds, colored and white horny and colored and white waxy.

All 6 of these classes of zygotes when planted and self-pollinated are expected to have horny and waxy seeds in the proportion of 3 to 1, while 4 of the 6 are expected to have colored and white in the proportion of 3 to 1. The remaining 2 classes are expected to have colored and white seeds in the proportion of 9 to 7.

For the 6 classes of zygotes, 4 very different degrees of correlation are expected, in the following proportions: Four ears with no correlation between the colored aleurone and horny endosperm, 3 ears with a correlation of 0.766 between colored aleurone and horny endosperm, one with a correlation of 0.744 between colored aleurone and waxy endosperm, and one with a correlation of 0.380 between colored aleurone and waxy endosperm. Of the 16 zygotic combinations represented on the all-colored ears, only 2 classes of seeds could be distinguished, namely, horny and waxy. These were planted separately.

When the colored horny plants are crossed with the colored waxy plants, 6 of the 16 zygotic combinations are expected to exhibit all 4 classes, and since there are three classes of waxy, 14 combinations result, as shown in Table XLII. Of these 14 ears, 12 are expected to have colored and white in the proportion of 3 to 1 and horny and waxy seeds in equal numbers, while the remaining 2 ears are expected to have colored and white seeds in the proportion of 9 to 7, with equal numbers of waxy and horny seeds. The 14 classes of ears are expected to be divided into five groups, with different degrees of correlation, as follows: Twenty ears with no correlation, 27 ears with a correlation of 0.615 between colored and horny, 9 with a correlation of 0.270 between colored and horny, 9 with a correlation of 0.615 between colored and waxy, 3 with a correlation of 0.270 between colored and waxy. The classes of zygotes are represented in Table XL.

TABLE XL.—*Classes of zygotes on the all-colored ears resulting from crossing the hybrids Dh 234 and Dh 237.*

Gametes.	Hybrid Dh 234.			
	CRH.	*CRh.*	*CrH.*	*Crh.*
Hybrid Dh 237:				
3 *CRH*	①	②	③	④
1 *CRh*	⑤	⑥	⑦	⑧
1 *cRH*	⑨	⑩	⑪	⑫
3 *cRh*	⑬	⑭	⑮	⑯

The italic letters in the column boxes of the table represent the gametic combinations formed by the hybrid Dh 234, and those in the left-hand column represent the gametic combinations formed by the hybrid Dh 237. The figures 3, 1, 1, and 3 preceding the italic letters in the left-hand column indicate the proportion in which each of these gametic combinations are formed in the hybrid Dh 237. Owing to the reduplication of certain combinations, resulting in an association of the color factor *C* and the endosperm texture *H*, there was no reduplication in the hybrid Dh 234.

Each circle in the table represents one of 16 zygotic combinations formed by crossing the two hybrids Dh 234 and Dh 237. The circles are numbered for convenience of reference. Thus, owing to the reduplication, the zygotic combinations represented by circles 1, 2, 3, and 4 are present on the ears three times as often as the combinations represented by circles 5, 6, 7, and 8. It must be borne in mind that two factors are required to produce colored seeds; these factors are represented by the letters *C* and *R*. The endosperm textures horny and waxy are represented by the letters *H* and *h*.

Table XLI shows the expected result of self-fertilizing the 16 classes of zygotes in Table XL. When horny and waxy seeds are both present on a self-pollinated ear the expected proportion is always 3 horny seeds to 1 waxy, within the range of chance fluctuation.

TABLE XLI.—*Expectation of seed classes resulting from the self-fertilization of the zygotes enumerated in Table XL.*

Circle.	Class of seeds.	Circle.	Class of seeds.
No. 1	All colored, horny.	Nos. 8 and 14	3 colored to 1 white, all waxy.
Nos. 2 and 5	All colored, horny, and waxy.	No. 11	9 colored to 7 white, all horny.
Nos. 3 and 9	3 colored to 1 white, all horny.	Nos. 12 and 15	9 colored to 7 white, horny, and waxy.
Nos. 4, 7, 10, and 13.	3 colored, 1 white, horny and waxy.	No. 16	9 colored to 7 white, all waxy.
No. 6	All colored, waxy.		

The following list shows the circles that would have four classes of seeds when self-pollinated, together with the degree of correlation expected:

Circles Nos. 4 and 7, no correlation.
Circle No. 10, correlation, colored and waxy, 0.744.
Circle No. 12, correlation, colored and waxy, 0.380.
Circle No. 13, correlation, colored and horny, 0.766.
Circle No. 15, correlation, colored and horny, 0.570.

The proportions in which the different degrees of correlation are expected are as follows:

No correlation	4 ears.
Correlation between colored and horny, 0.766	3 ears.
Correlation between colored and horny, 0.570	3 ears.
Correlation between colored and waxy, 0.744	1 ear.
Correlation between colored and waxy, 0.380	1 ear.

Table XLII shows the expected results of crossing colored horny with colored waxy plants when the ears obtained exhibit four classes of seeds, the expectation being that these ears are to have horny and waxy seeds in equal numbers.

TABLE XLII.—*Expectation of seed classes resulting from the crossing of colored horny with colored waxy maize plants whose ears exhibit four classes of seeds.*

Circle.	Color.	Texture.	Correlation.
Number 4 × 8	3 colored, 1 white	Horny and waxy	None.
Number 7 × 8	do	do	Do.
Number 12 × 8	do	do	Do.
Number 15 × 8	do	do	Do.
Number 10 × 14	do	do	Colored and waxy. 0.615.
Number 12 × 14	do	do	Do.
Number 13 × 14	do	do	Colored and horny, 0.615.
Number 15 × 14	do	do	Do.
Number 4 × 16	do	do	None.
Number 7 × 16	do	do	Do.
Number 10 × 16	do	do	Colored and waxy, 0.615.
Number 12 × 16	9 colored, 7 white	do	Colored and waxy, 0.270.
Number 13 × 16	3 colored, 1 white	do	Colored and horny, 0.615.
Number 15 × 16	9 colored, 7 white	do	Colored and horny, 0.270.

The proportions in which the different degrees of correlation are expected where colored horny is crossed with colored waxy are as follows:

No correlation	20 ears.
Correlation between colored and horny, 0.615	27 ears.
Correlation between colored and horny, 0.270	9 ears.
Correlation between colored and waxy, 0.615	9 ears.
Correlation between colored and waxy, 0.270	3 ears.

It can readily be seen that a very large number of individuals would be necessary to determine whether the ratios, together with the expected degrees of correlation, were obtained in the correct proportions. The results obtained from the cross Dh 333 can be disposed of rather easily, since only four self-pollinated ears were secured from the colored horny group (Table XLIII). With three of these ears it is not possible to accurately determine the degree of correlation to which to refer them, since the number of individuals is small. The fourth ear seems to have rather too high a degree of correlation between colored and horny to be referred to the expected 0.766, but the chances of such a deviation being due to an error in sampling are about 5.5 in 10. It can therefore be assumed that the four ears secured from the cross Dh 333 do not in any way conflict with the expected results.

The remaining crosses, Dh 330 and Dh 334, have a slightly larger number of ears with which to further test the fit of observed to theory, but it is not the number of ears, which indeed are far short of sufficient numbers to make an accurate test of proportions, but from the way in which they are related that the most interesting results are obtained.

TABLE XLIII.—*Correlation between the endosperm texture and the aleurone color in four ears of maize, the progeny of colored horny seeds of cross Dh 333 self-pollinated.*

Progeny ear.	Number of seeds.					Correlation, $W+X$.	Probable error.	Percentage of—	
	Total.	*WX.*	*WH.*	*CX.*	*CH.*			Waxy.	White.
1	2	3	4	5	6	7	8	9	10
1893	337	16	53	78	190	−0.153	0.103	27.9	20.5
1894	261	14	55	41	151	− .032	.117	21.1	26.4
1895	33	2	3	9	19	.169	.270	33.3	15.2
1897	424	58	47	39	280	.800	.031	22.9	24.7

At first glance the degrees of correlation obtained with the cross Dh 330 by pollinating the colored waxy individuals with the colored horny individuals and the reverse, together with the few self-pollinated horny plants, seem to very nearly approximate those expected on theory, as all of the correlations obtained could be referred to some of the expected degrees of association.

The first ear shown in Table XLIV, No. 1856, has an exact reciprocal in ear No. 1877, and the self-pollinated colored horny parent is ear No. 1878, both of the same table. All three of these ears show practically no correlation, and the Mendelian ratios approximate the expected proportions. This group can be said to fulfill the expected results where either circles 4, 7, 12, 15 are crossed with circle 8, or where circles 4 or 7 are crossed with circle 16 (Table XLII).

The second group consists of ear No. 1860, its exact reciprocal ear No. 1874, together with the self-pollinated colored horny parent ear No. 1875 (Table XLIV).

TABLE XLIV.—*Correlation between the endosperm texture and the aleurone color of 12 ears of maize, the progeny of the cross Dh 330.*

Progeny ear.	Pedigree No. of— Self-pollinated. ♂	Pedigree No. of— Self-pollinated. ♀	Pedigree No. of— Reciprocal cross.	Number of seeds. Total.	Number of seeds. *WX.*	Number of seeds. *WH.*	Number of seeds. *CX.*	Number of seeds. *CH.*	Correlation, *W*+*X*.	Probable error.	Percentage of— Waxy.	Percentage of— White.
1	2	3	4	5	6	7	8	9	10	11	12	13
COLORED WAXY × COLORED HORNY.												
1856	1878		1877	525	69	74	170	212	0.075	0.067	45.6	25.4
1860	1875		1874	649	119	45	170	315	.653	.039	44.6	25.3
1861	None		1871	450	51	58	153	188	.034	.074	45.4	24.2
1863	...do		None	679	72	102	234	271	−.114	.059	45.0	25.6
1865	1875		...do	739	143	38	237	321	.670	.031	51.4	24.5
COLORED HORNY × COLORED WAXY.												
1871	All waxy	None	1861	81	10	11	23	37	0.188	0.053	40.6	25.9
1874		1875	1860	137	25	16	46	50	.259	.120	51.8	29.9
1876	None	None	None	377	86	36	115	140	.491	.064	53.4	32.4
1877	All waxy	1878	1856	424	51	50	175	148	−.074	.076	53.3	23.9
COLORED HORNY × SELF.												
1875	Self			716	104	194	47	371	0.605	0.042	21.1	41.6
1878	...do			496	32	104	90	270	−.040	.080	24.6	27.4
1882	...do			136	19	42	9	66	.538	.077	20.6	44.8

Since the self-pollinated ear from the colored horny parent of the above reciprocals had approximately 9 colored to 7 white seeds with a correlation of 0.605 between C and H, it could have come only from circle 15 (Table XL). The expected correlation upon self-pollinating circle 15 is 0.570, of which 0.605±0.04 can reasonably be considered an approximation.

There are three classes of waxy seeds with which circle 15 may be crossed that will result in ears with four classes of seeds. These seeds are represented by circles 8, 14, and 16 in Table XL. Circle 8 can be eliminated, since a cross between it and circle 15 would result in an ear with no correlation. The choice lies between 14 and 16. The result of crossing circles 15 and 14 would be an ear with a correlation approximating 0.615 between *C* and *H*. This is a fairly close approximation to the 0.653±0.039 obtained with ear No. 1860, but the correlation of 0.259±0.12 obtained with the exact reciprocal of ear No. 1860, namely, No. 1874, is a very close approximation to the expected 0.270, when circles 15 and 16 are crossed. In this case, as is shown on page 90, the expected ratio of colored to white seeds is 9 to 7, while on the ear concerned, No. 1874, the colored seeds are approximately three times the number of white seeds. The correlation of 0.259 certainly can not be looked upon as a chance fluctuation from the correlation 0.615 expected when circles 15 and 14 are crossed. A case parallel to this is found in the cross Dh 334. The colored waxy parent pollinated by the colored horny is represented by ear No. 1902, the exact reciprocal is ear No. 1917, and the self-pollinated colored horny parent is ear No. 1918 (Table XLV).

TABLE XLV.—*Correlation between the endosperm texture and the aleurone color of 10 ears of maize, the progeny of the cross Dh 334.*

Progeny ear.	Pedigree No. of— Self-pollinated. ♂	Pedigree No. of— Self-pollinated. ♀	Pedigree No. of— Reciprocal cross.	Number of seeds. Total.	*WX.*	*WH.*	*CX.*	*CH.*	Correlation, W + X.	Probable error.	Percentage of— Waxy.	Percentage of— White.
1	2	3	4	5	6	7	8	9	10	11	12	13
COLORED WAXY × COLORED HORNY.												
1902	1918	1903	1917	765	166	49	249	301	0.640	0.038	54.3	28.1
1904	None	None	None	443	57	58	162	166	.002	.073	49.5	26.0
1906	1923	...do	1922	315	40	41	112	116	.076	.085	50.1	27.6
1909	1925	1910	1924	485	71	32	146	236	.563	.042	44.7	21.3
COLORED HORNY × COLORED WAXY.												
1917	All waxy	1918	1902	452	80	40	170	162	.348	.067	55.3	26.5
1922	...do	1923	1906	421	56	53	156	160	.040	.046	49.4	26.5
1924	...do	1925	1909	415	83	25	125	182	.658	.049	50.6	26.9
COLORED HORNY × SELF.												
1918	Self			345	46	46	47	206	.628	.054	27.0	26.6
1923	...do			399	42	71	81	205	.199	.077	30.8	28.3
1925	...do			457	59	52	51	295	.736	.037	24.1	24.3

The self-pollinated colored horny ear had approximately 3 colored seeds to 1 white and a correlation of 0.628±0.054 between *C* and *H*. This correlation is about midway between that expected for self-pollinating circles 13 and 15, though it is slightly closer to the latter. Self-pollinating circle 15 would have an expected ratio of 9 colored to 7 white seeds, but since the ear in question is a fairly close approximation to the ratio of 3 colored to 1 white it fits the expected proportions when circle 13 is self-pollinated.

Assuming the plant in question to be the result of planting circle 13, there are two classes of waxy seeds with which it may be crossed that will result in ears with four classes of seeds. These classes are represented by circles 14 and 16.

The ears secured by either cross would be alike, both having 3 colored seeds to 1 white and a correlation of 0.615 between *C* and *H*. Ear No. 1902, with a correlation of 0.64±0.038, is a close approximation to the expected results on this basis, but the exact reciprocal ear, No. 1917, with a correlation of 0.348±0.067, can hardly be looked upon as approximating the expected 0.615. This correlation is much closer to that expected when circles 15 and 16 are crossed, but the ratio of white to colored seeds would in that case be as 7 to 9, and the observed ratio is a close approximation to the 3 to 1 ratio. In both the cases where the reciprocals differ in the degree of correlation the lowest correlation is found where the colored horny plant served as the female parent, indicating a higher correlation in the male gametes. This tendency has been observed with ear No. 1764 (Table XXXVIII), where a significant difference was observed in reciprocals, and also with ears Nos. 1804, 1815, and 1816 (Table XXXIX), where smaller differences in this direction were observed.

This difference may be due to a higher death rate for the pollen grains bearing the character combinations resulting from different parents, or it may be that such pollen grains are less vigorous or that the male gametes are not being formed in the expected proportions.

The remaining ear of cross Dh 330 that resulted from pollinating colored horny individuals by colored waxy is ear No. 1876. There is no reciprocal of this cross nor is there a self-pollinated ear from the colored horny parent. The ratio of white to colored seeds is rather closer to a 3 to 1 than a 7 to 9, and the correlation, 0.491 ±0.064, though low, may be looked upon as an approximation of the expected 0.615, when circles 13 and 16, 13 and 14, or 15 and 14 are crossed.

Of the three self-pollinated ears of the cross Dh 330, one ear, No. 1875, has already been discussed. Ear No. 1878, having no significant correlation, could be the result of self-pollinating circles 4 or 7. Ear No. 1882, with an approximate ratio of 9 colored to 7 white seeds and a correlation of 0.538 between *C* and *H*, is a very close approximation of the expected 0.570 when circle 15 is self-pollinated. The remaining ears of the cross Dh 334 also seem to approximate the expected correlations.

Ears Nos. 1906, 1904, and 1922 are all close approximations to the expected results of crossing circles 4, 7, 12, or 15 with circle 8 or 4 or circle 7 with 16. Ears Nos. 1906 and 1922 are exact reciprocals, and as such agree as well as could be expected. The colored horny parent of these last-mentioned ears had a self-pollinated ear, No. 1923, which could have been the result of the self-pollination of circles 4 or 7, so that ears Nos. 1906 and 1922 are probably the result of crossing circles 4 or 7 with circles 8 or 16. Ears Nos. 1909 and 1924 are exact reciprocals, and with the self-pollinated ear from the colored horny parent, No. 1925, make a complete group. The self-pollinated colored horny parent is a very close approximation to the result expected when circle 13 is self-pollinated. The reciprocals, Nos. 1909 and 1924, are in fairly close agreement with each other and are close approximations to the expected result of crossing circle 13 with either circle 14 or 16.

SUMMARY OF THE CORRELATIONS BETWEEN ENDOSPERM TEXTURE AND ALEURONE COLOR.

The preceding experiments were undertaken in the spring of 1910 with the view to determining whether the previously observed coherence between endosperm texture and aleurone color could be referred to the 3–1–1–3 reduplication series of Bateson and Punnett. The intention was to obtain a number of individuals large enough to determine definitely the degree of reduplication, as well as to decide whether all plants gave the same reduplication ratio.

The experiments have now been carried to the third generation, and the degree of correlation with 17,015 seeds has been found to be 0.762 ± 0.0057. This correlation is a very close approximation to the 0.766 expected if the reduplication was of the series 3–1–1–3. Some plants have been found, however, which gave reduplications other than 3–1–1–3, and it is possible that succeeding generations of these will throw additional light on this complicated subject. In some cases the departures could be readily explained by slightly modifying the theory proposed by Punnett as to the type of cell division, which resulted in the 3–1–1–3 ratio, but in other cases an extremely complicated theory of cell divisions would be required to give an adequate explanation of the observed ratios.

To explain the aberrant cases by Morgan's linkage hypothesis, we would be forced to believe that at least one of the characters was insecurely located on the chromosome, since with the widely different correlations obtained it is necessary to assume that the mutation of the locus of at least one of the characters is of frequent occurrence.

With a new series of hybrids between these same varieties comprising some 20,000 seeds, a correlation has been obtained which more nearly approximates a 4–1–1–4 than a 3–1–1–3 gametic series. The correlation for these last hybrids differs from that obtained in the original crosses by more than eight times the probable error. From this we must conclude that the correlation between the same characters differs widely in different families, though the individuals within a family seem to approximate the same mean.

We must further conclude that the association between these two characters in maize does not always fit the arbitrary series of 3 to 1, 7 to 1, etc., proposed by Bateson, but that in some instances the couplings more nearly approximate the intermediate points of this series, such as 4 to 1, 5 to 1, etc.

It is not intended to imply that the reduplication found in the gametes is the direct result of unequal cell division, although the observed results can be explained on such a hypothesis. The assumption that for the higher coupling ratios segregation must take place before synapsis in order to permit of the proper number of cell divisions seems thus far unwarranted by any cytological evidence.

A study of the Mendelian behavior of the aleurone color has led to the realization that since characters are the result of many factors more or less independent the correlations must also be between these invisible factors rather than between the visible characters.

The fact that correlations are between factors which can be detected only when in combination with certain other factors permits of many different degrees of correlation and lessens the degree of confidence to be placed in conclusions regarding both the factorial composition and the correlations or couplings. There is danger of explaining aberrant Mendelian ratios by the predication of correlations and to explain aberrant coupling ratios by assuming changes in the factorial composition. Because of this fact, great care must be given to the analysis of correlated characters from the standpoint of their Mendelian behavior, since much depends upon the number of factors involved.

Reciprocal crosses between plants heterozygous for endosperm texture and aleurone color and plants homozygous for the recessive characters waxy endosperm and colorless aleurone have shown in many cases that certain character combinations are deficient in the male gametes. It is suggested that this deficiency may be due to a higher death rate, less vigor, or a failure of the plant to produce these odd combinations in the proper proportions.

If we can assume that correlations are the result of unequal cell division, we can further assume that the reduplicated character combinations are also the most vigorous. Thus the tubes from the pollen grains bearing the reduplicated characters may grow more rapidly than the pollen tubes from the grains bearing the odd combinations. Such a difference in the rate of growth would not occur in the female gametes, and they would be present in the theoretical proportions unless a differential death rate supervened.

It does not seem unreasonable to believe that any reaction, which causes the more rapid division of the cells bearing the correlated characters, may also cause the gametes with these same combinations to be more vigorous. In most cases when an ear is pollinated there are enough pollen grains on each stigma to insure the presence of all gametic combinations, and if any difference in the rate of growth prevailed for a certain gametic combination most of the seeds would be fertilized by that combination.

CONCLUSION.

A thorough understanding of the laws of heredity is essential in determining the most effective methods of breeding plants and animals with the special characters that are needed for purposes of commercial production under different environmental conditions. It is of general interest to practical breeders at the present time to know the extent to which it is possible to rely upon the application of the Mendelian principles of heredity. Assurance has been given by certain writers that analysis and recombination of characters of varieties by the Mendelian methods could be substituted to advantage for the methods of selection that have been considered as the most effective means of obtaining improved strains.

An adequate investigation of the current theories in regard to the laws of heredity requires the detailed analysis of results derived from the study of large numbers of individuals. In this respect the seeds of maize offer unusual opportunities. Instead of a single offspring, or a few, from 400 to 800 seeds result from a single application of pollen, and the technique of hybridization is extremely simple. In addition to the ease of manipulation and the relatively large numbers obtained, maize seeds offer the further advantage of several alternative characters which permit rapid and accurate classification. This makes possible the definite determination of questions which depend upon the regularity of the proportions in which the characters are represented in the various hybrid stocks.

With these possibilities in view, the experiments reported in this bulletin were undertaken in 1910, to analyze further the inheritance of contrasted characters and to obtain a clearer understanding of the nature of the interrelations or correlations between such characters. The characters chosen were the waxy endosperm texture found in a variety of maize from China and the colors of the aleurone cells with which this endosperm texture was known to be associated.

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The results of this analysis show that the number of seeds with the waxy endosperm reappearing in the perjugate generation of waxy × horny crosses is less than the expected for a simple Mendelian character, but this deviation, though significant, is too small to warrant the predication of additional factors. In making this determination, more than 100,000 seeds were classified, and it has been possible therefore to establish the actual percentage within 0.3 of 1 per cent.

The same material was used to test the inheritance of aleurone color, which also was found to depart from the theoretical ratios. Unlike the waxy endosperm texture, no definite trend above or below the expected ratios was observed, but many abnormal ratios were obtained which necessitated further refinements in the factorial analysis of this character.

From the results of the Mendelian analysis of aleurone color and endosperm texture it must be concluded that in many cases uniform Mendelian reactions are obtained which allow certain predictions to be made with respect to the behavior of these characters in subsequent generations. But that these predictions based upon the gametic analysis will be uniformly fulfilled must not be supposed. As we have seen, aberrant behavior is far from uncommon, increasing with the progress of investigation and the refinement of analysis. The fact is coming to be appreciated that instead of a few simple unassociated factors most characters are composed of many complex units which may no longer be considered singly but that their interrelations or correlations must be taken into account.

The present investigations show that certain of the more definitely alternative characters of maize are subject to variation or fluctuating behavior that renders these supposed Mendelian factors too irregular to justify a belief that the very definite relationship predicted in theories of gametic coupling could exist between such characters. There can be little doubt, however, that at least with several combinations of characters the gametic ratios are to a certain extent regular, but that these ratios fit any arbitrary series is not so well demonstrated.

For the breeder of crop plants where most of the desired characters are almost infinitely complex, seldom alternative, and often intangible, Mendelism seems to have little of practical value to offer, whether the attempt of some investigators to so extend the theory to embrace such characters be approved or not. While Mendelism may assist in making desired combinations, there is nothing to show that it can serve as a substitute for selection either in finding the best stocks or in preserving them from subsequent deterioration.

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