A GENETIC STUDY OF CERTAIN CHLOROPHYLL DEFICIENCIES IN MAIZE¹

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INTRODUCTION

The plant pigment, chlorophyll, is without doubt the most important of all known organic substances, for upon chlorophyll depends the life of the plant containing it and consequently the existence of other forms of life which do not have the power of photosynthesis. It appears, therefore, that a fuller knowledge of chlorophyll inheritance, aside from its immediate biological interest, might lead to useful applications in the way of plant improvement.

The present paper is concerned with the genetic relations between several chlorophyll defects and certain other plant and kernel characters in maize, with the view of adding to our knowledge of the germinal constitution in that species.

MATERIAL AND METHODS

These studies have been carried on with material which was kindly furnished by Dr. E. W. LINDSTROM, Dr. G. N. STROMAN, formerly of the

¹ Contribution from the Department of Genetics, AGRICULTURAL EXPERIMENT STATION, IOWA STATE COLLEGE, No. 34.

TEXAS EXPERIMENT STATION, and Mr. M. T. JENKINS of the IOWA EXPERIMENT STATION. The letters L, S, and J, respectively, will be used before the pedigree numbers of such material. The investigations were begun at the UNIVERSITY OF WISCONSIN and completed at IOWA STATE COLLEGE. The writer wishes to acknowledge at this time his indebtedness to Dr. E. W. LINDSTROM, under whose direction these studies have been made; to Dr. L. J. COLE of the UNIVERSITY OF WISCONSIN for his counsel and encouragement during the first year of this work; and to Dr. G. N. STROMAN and Mr. M. T. JENKINS for helpful suggestions and information concerning the origin of certain characters reported herein.

The degrees of linkage in simple dihybrid segregations were calculated by the method described by EMERSON (1916). For the trihybrid ratios in which there were two complementary genes, one being linked to a third gene, the formulae given by BRUNSON (1924) were used for finding the gametic ratio. The formulae are as follows:

$$r = \sqrt{\frac{(AB + 3ab) - (Ab + aB)}{18}}$$

$$s = \frac{1}{4}\sqrt{AB + Ab + aB + ab - r}$$

The F_2 theoretical ratio was calculated by substituting the found values of r and s in the formulae adopted from EMERSON as follows:

AB	$9 r^2 + 6(2 rs + s^2)$
Ab	$3 r^2 + 6(2 rs + s^2)$
aB	$3(2 rs + s^2)$
ab	$4 r^2 + (2 rs + s^2)$

For ratios expressing linkage between the factors concerned, the closeness of fit (P) was calculated by ELDERTON'S (1901) method supplemented by PEARSON'S (1924) tables. The values of P may range from 0 to 1, measuring the probability of the deviations from the theoretical frequencies being due to errors of random sampling (HARRIS, 1912).

In dihybrid and trihybrid ratios showing independent inheritance of the factors concerned, the parental and non-parental classes were often grouped against one another and the probable error calculated from these two classes. The general formula used was:

$$P.E. = 0.6745\sqrt{p q n}$$

in which p and q are the two elements of the ratios as, 10:6 or 9:7, and n is the total number of individuals in the experiment.

The crosses

For the convenience of the reader, the crosses whose progenies form the basis of these studies are given here and also in the body of the paper.

The factor *v* occurring in the genotype of most of the crosses represents a seedling chlorophyll deficiency known as virescent in which the chlorophyll development is delayed for a time.

The virescents which are not known to be different from those previously described (DEMEREK 1924) are written without an Arabic numeral. In the following discussion, these characters shall be distinguished only by reference to their origin. It will be seen in cross No. 5 that two virescent factors have been assigned numerals. Evidence is given in the discussion for believing that these factors are different from those reported by DEMEREK.

The crosses may be represented as follows:

Cross No. 1, L 4992-23 × S 899-7

AA Cc Rr S_u s_u Yy W_l W_l VV S_c S_c ×
AA Cc rr S_u S_u Y Y w_l w_l Vv S_c S_c.

Cross No. 2, L 4992-26 × S 899-10

AA Cc Rr S_u s_u W_l W_l VV ×
AA CC rr S_u S_u w_l w_l Vv.

Cross No. 3, L 4254-38 × L 4260-7

S_u S_u L_g l_g R_o R_o ×
s_u s_u L_g L_g R_o r_o

Cross No. 4, L 4263-3 × 4260-4

S_u S_u Vv A_n a_n R_o R_o ×
s_u s_u VV A_n A_n R_o r_o

Cross No. 5, 232-11 × 230-1

YY V₇ V₇ VV V₆ v₆ ×
y y v₇ v₇ Vv V₆ V₆

The different characters symbolized in the above crosses are given in the discussion of types or in that part of the paper which describes the F₂ results.

Those characters not heretofore described are rolled (*r_o*) seedlings and several new types of virescent (*v*) seedlings.

DESCRIPTION OF CHARACTERS

Yellowish virescent. One virescent which appeared in the F₂ generation of crosses No. 1 and No. 2 has a distinct yellow color when it first emerges from the soil. Chlorophyll development in this virescent type is similar to that described by LINDSTROM (1918). The young leaves gradually

become green, beginning at the leaf tips. The yellow color can be observed in the leaves and stems until it is hidden by chlorophyll. When the plant is about three weeks old, the first leaf is usually solid green. Newly unfolded seedling leaves gradually become green from their tips downward. When grown under field conditions during the summer of 1924, about one-third of the plants matured. Most of these produced pollen, although no ears were formed. Mature virescent plants were about one-half as tall as their normal sister plants but were nearly full green.

Light virescent ($v_6 v_6$)

Plants of this type emerge from the soil practically devoid of chlorophyll. Their leaves are about one-half as broad and their stems are noticeably shorter than those of normal sister plants. Some plants develop only a slight amount of chlorophyll on their leaf tips; others may develop one or two streaks of chlorophyll about one-eighth of an inch in width running the entire length of the leaf. Still other plants have considerable chlorophyll, but have chlorophyll deficient streaks on the leaf borders. Pure virescent plants are not able to live beyond the three-leaf stage.

Two medium green virescents ($v_7 v_7$ and an associated virescent)

These two types trace back to ear J 121-4 of U. S. Selection 133. The two virescents are very similar in appearance, being typical virescent types. The type v_7 seems to have slightly more chlorophyll than its associate. Both virescents have a pale green color when emerging from the soil. Under favorable conditions for growth they become green very rapidly, making their classification difficult. Pure virescent plants are able to mature a small ear and produce an abundance of pollen.

Rolled

In the second generation of crosses No. 3 and No. 4 which combined several plant characters, a semi-lethal seedling type occurred. The young plant of this type seems perfectly normal in every respect until the third leaf appears. This leaf has a pale chlorophyll-deficient appearance and remains for a time rather closely rolled. Simultaneously with the appearance of the third leaf, the first and second leaves become pale, slightly corrugated cross-wise, thickened, and rolled upward at the borders. At this stage, in extreme types, all three leaves die, become blackened and fall from the plant, leaving the stem apparently unaffected. Some plants may recover and be indistinguishable from the normal if growing conditions are favorable. In fact, during the summer of 1924 the character did not appear in the expected proportion of three normal plants to one rolled.

Some evidently recovered so quickly that they escaped notice, and a large proportion of them survived throughout the season. Genetically rolled plants were obviously weak, for none of these plants were chosen for self-pollinating.

The rolled plant deviates from the normal in still other features. The primary root of the rolled seedling is larger in diameter and more turgid than that of normal sister plants. There is also an abnormality of the kernel associated with extreme types of the rolled character. The scutellum and adjacent part of the radicle become dark and woody in structure, and the kernel appears as though it were diseased. Seeds from a segregating ear were sterilized with chlorinated lime and grown with sterilized soil and water. With this treatment 51 normal to 19 rolled plants were produced in an F_2 family. HOLBERT, et al (1924), describe a diseased condition of the maize kernel called scutellum rot, which appears to be similar to the kernel condition associated with rolled seedlings. Seed from an ear segregating for rolled was sent to Mr. HOLBERT to be examined. He found that rolled was phenotypically different from scutellum rot.

White-base-leaf.

As previously stated by STROMAN (1924 b), the white-base-leaf character ww_1 is very variable in the amount of chlorophyll developed and the pattern in which it occurs over the plant.¹ The nature of chlorophyll dispersion in the chlorophyll deficient areas is one quality which is constant in the material studied by the writer. In the areas where the chlorophyll is sparse, it occurs in broken streaks between the leaf veins, giving a streaked or finely dappled appearance to those regions. The same characteristic dispersion occurs on the stems in a less pronounced fashion. Based on the location of chlorophyll deficient areas, the white-base-leaf character may be roughly divided into two types. In one type, the deficiency is primarily at the base of the leaves. In the other type, seedling plants have nearly pure white areas about one-half inch in length covering their leaf tips. Some of these plants assume a zebra-like appearance when half mature. The latter are probably modifications of the zebra seedling character which was described by STROMAN.

Scarred endosperm

The scarred endosperm type (figure 1) which occurred in the second generation from cross No. 1 is similar in general to the scarred endosperm character described by EYSTER (1922). The greatest difference lies in

¹ The present writer referred to this character as brindled in Iowa Acad. Sci. Proc., 31 (1924), p. 129.

the amount of endosperm developed and the deepness of scarring. In the present material, for example, the crown endosperm is very scant in some kernels; consequently, a more extreme wedge shape is assumed by the upper portion, due to the pressure from adjoining kernels. The bases of such kernels are as large as those of the normal. In length, they are about one-third less. The scars themselves are not so deep as those described by EYSTER. But they are more numerous, occurring on all sides

FIGURE 1.—Showing the relation between scarred endosperm and sectoried plants. Two normal kernels and plants are shown on the left.

in a minority of the kernels and appear as fine, slightly indented and branched stripes often extending to the kernel base.

INHERITANCE OF CHARACTERS

White-base-leaf

The white-base-leaf character was shown by STROMAN (1924 b) to behave as a recessive character in inheritance. In addition to his counts, the following results have been obtained by self-pollinating F_1 and F_2 green plants heterozygous for white-base-leaf: green seedlings, 2860(2902): white-base-leaf seedlings, 1009(967). The calculated numbers are placed in parentheses. These data support the hypothesis that white-base-leaf occurs as a recessive in a simple 3:1 ratio, (Dev./P.E. = 2.31). This simple relationship is also borne out by two backcrosses which gave 189 green to 161 white-base-leaf plants. The deviation was 14 ± 6.31 .

Scarred endosperm and sectorial plants

Scarred endosperm (figure 1) was found by EYSTER (1922) to be a simple Mendelian recessive character. The classification of normal and scarred endosperm in the present material was rather difficult to make; consequently the exact mode of inheritance of this particular scarred endosperm character cannot be ascertained at the present time. The number of F_1 ears showing the scarred endosperm segregation (15) to those which were homozygous normal (11) agrees fairly well with the assumption that the character is determined by a single genetic factor. However, the closest possible classification of the F_2 kernels shows a great deficiency of scarred kernels from the expected number, assuming a monohybrid relationship. The total counts are given in table 15. It is seen that the observed ratio agrees better with a duplicate factor hypothesis, although the deviation then is 3.30 times the probable error.

A very interesting relationship exists between scarred endosperm and a japonica-like seedling type which has been called sectored. The sectored character is evidently linked to scarred endosperm. However, difficult classification of endosperm makes this point uncertain. More will be said concerning this relationship in a later section.

Rolled

The rolled character has proven to be a simple Mendelian recessive to the normal condition. The ratio of non-rolled to rolled plants may be secured from the F_2 tables 3, 4, 5 and 6. The ratio found by summing the counts in these tables is as follows: normal seedlings, 3306 (3272); rolled seedlings, 1057 (1091). The deviation from a 3:1 ratio is 34 ± 19.3 .

An F_3 progeny test of 48 ears from normal F_2 plants furnishes further evidence as to the simple monohybrid relationship of the rolled character. On the basis of a unit factor difference between normal and rolled, a 1:2 ratio of pure and segregating families is expected. The two types of F_3 progenies occurred in exactly the expected proportions. Of the 48 progenies, 16 bred true for normal seedlings and 32 segregated for rolled. These data prove conclusively that rolled is a simple Mendelian recessive to the normal type of plant.

GENETIC INTERRELATIONS BETWEEN THE CHARACTERS

A virescent and W_1

An interesting relationship is exhibited between the virescent and white-base-leaf characters in the F_2 of crosses No. 1 and 2. Four types were found to occur in the proportion of 9 green:3 white-base-leaf:3 virescent:

1 albino, showing that the albino character is the result of an interaction between the factors v and w_l . A few families which show this segregation are arranged in table 1. The type called albino often develops a small amount of chlorophyll on the leaf tips, as well as other portions of the leaf. In some families, the classification between albino and white-base-leaf has been more or less arbitrary. It is a significant fact, however, that albino plants occur only in families segregating for V and W_l , never in monohybrid virescent or white-base-leaf families. The F_2 families from cross No. 1 are given in table 1 to show the interrelation between v and w_l because in those families the albino plants appear most distinct.

TABLE 1

F₂ segregation from plants having the composition $S_u S_u W_l w_l Vv$. Cross No. 1.

PEDIGREE NUMBER	GREEN	W. B. L.	VIRESCENT	ALBINO
212 (1)	161	62	44	15
863 (4)	104	25	36	12
(5)	125	37	28	10
(9)	125	51	41	11
(11)	195	69	75	17
(13)	115	39	37	17
(16)	121	48	32	18
(27)	153	55	52	15
864 (10)	170	63	51	24
(14)	161	55	42	18
(23)	48	20	25	5
Observed	1478	524	463	162
Calculated 9:3:3:1	1477	493	493	164

Deviation $\div$ probable error (10:6) = 0.06

It will be noted in table 1 that the largest deviations occur in the two mean classes. This is probably due to the fact that virescent plants were erroneously classified as white-base-leaf, although the classification appeared fairly distinct. The excellent agreement of the calculated and observed ratios when the extreme and mean classes are grouped, indicates that an error was made in classifying the white-base-leaf and virescent types only. Further evidence that the albino character is determined by the double recessive condition $w_l v$ is furnished by grouping the non-albino types (green, white-base-leaf, and virescent) against the albinos in tables 1, 12 and 13. By such grouping the following F_2 ratio is found: non-albino seedlings 7837 (7818); albino seedlings 502 (521). It is very evident that this is a 15:1 ratio (Dev./P.E. = 19/14.92 = 1.27).

A virescent factor and V

Several F_2 ears from cross No. 1 segregated for endosperm color, white-base-leaf seedlings, and virescent seedlings. It has been shown above that this particular virescent factor is independent of W_1 and that the combination $v v w_1 w_1$ produces an albino plant. Hence, the W_1 factor may be eliminated and a chlorophyll ratio secured based on the segregation of the V factor only. In order to accomplish this the green plants and white-base-leaf plants belonging to each endosperm type were added together and designated as green plants. In like manner, virescent and albino plants were grouped and designated as virescents. The F_2 segregation secured by such grouping is as follows: yellow endosperm-green plants, 180 (179); yellow endosperm-virescent plants, 61 (59); white endosperm green plants, 56 (59); and white endosperm-virescent plants, 20 (20). The calculated ratio for independent inheritance is enclosed by parentheses. The observed ratio conforms very closely to the calculated, the deviation from a 10:6 ratio of independent inheritance being only 1.00 ± 5.81 .

A virescent factor and C and R

The purple and colorless F_2 kernels from crosses No. 1 and No. 2 were planted separately and the segregates from each type of kernel noted. The F_2 results from mother ears of the composition $CRV.Crv$ are as follows: purple kernels—green plants, 634 (625.5); purple kernels—virescent plants, 205 (208.5); colorless kernels—green plants, 197 (208.5); and colorless kernels—virescent plants 76 (69.5). For a 10:6 ratio the deviation over the probable error is 1.38. The close agreement of the observed ratio with the theoretical justifies the conclusion that R and V are independently inherited.

Further evidence that this V is independent of R and also of C is furnished by F_2 data from cross No. 2. The F_2 segregation from plants of the composition $cRV.Crv$ is as follows: purple kernels—green plants, 123 (118); purple kernels—virescent plants, 33 (39); colorless kernels—green plants 95 (92); and colorless kernels—virescent plants, 28 (30). The close agreement of the observed ratio and that calculated for independent inheritance indicates that the factors C , R , and V are carried on separate chromosomes, the deviation over the probable error for a 34:30 ratio being only 0.53.

A greenish and light virescent

In the spring of 1923 a selfed ear J 45-7 of Four County, a selection from Silver King, was secured from Mr. M. T. JENKINS, of the IOWA

EXPERIMENT STATION at Ames. This ear was of interest because it contained two very distinct virescents which occurred in a good commercial variety of corn. The seed when planted in the greenhouse gave 145 green seedlings to 96 virescent seedlings, a 9:7 ratio with a deviation of 9 ± 5.19 .

In chlorophyll development, the two virescents are very similar, the only difference being that one type develops considerably more chlorophyll than the other, although neither has been found to live beyond the three-leaf stage. The two characters have been designated as greenish-virescent and light-virescent respectively. Symbols are not given to the types at present because their linkage relations and identity with other known virescents have not been determined. In a dihybrid segregation these virescents grade into one another so that they cannot be accurately classified, but in monohybrid segregations the families containing greenish and light virescents can be easily distinguished.

TABLE 2

Progenies and their seedling segregations which resulted from self-pollinating green plants in a 9:7 virescent family (J45-7 selfed).

CHARACTER OF SEGREGATION	OBSERVED	CALCULATED	SEEDLING SEGREGATES		RATIO	DEV. — P. E.
			Green	Virescent		
Pure Green.	1	1.9	95	..	..	..
Splitting for greenish virescent.	3	3.8	566	171	3:1	1.64
Splitting for light virescent.	3	3.8	542	183	3:1	.25
Splitting for both.	10	7.5	1308	1002	9:7	.56

P for progeny test = 0.67

The ratio of the progenies and a summary of their segregations are arranged in table 2. In the progeny test, the closeness of fit (P), based on an independent assortment of the two virescent factors, is 0.67. The 9:7 green and virescent families likewise show a good agreement with the calculated ratio, assuming independent inheritance between the factors for greenish and light virescent. Here the deviation over the probable error is equal to .56.

Rolled and virescent

In the spring of 1923, Doctor LINDSTROM turned over to the writer two crosses which combined the characters: anther ear dwarf (a_n), virescent (v), sugary (s_n), and liguleless (l_o). A new character which had not hitherto been observed occurred in the F_2 generation of these crosses. It has been called rolled from the characteristic rolled condition of the

seedling leaf. The character evidently originated from the family to which the male parent belonged (L 4260). It seems most logical to believe this because the F_2 segregation of hybrids involving both L 4260-4 and L 4260-7 contained rolled plants, although they were crossed on two families which were unrelated to one another. Family L 4260 came originally from Doctor C. N. COLLINS.

The crosses involving rolled (r_o) may be represented factorially as follows:

Cross No. 3 L 4254-38 ($S_u S_u L_g l_g R_o R_o$) $\times$ L 4260-7 ($s_u s_u L_g L_g R_o r_o$)

Cross No. 4 L 4263-3 ($S_u S_u Vv A_n a_n R_o R_o$) $\times$ L 4260-4 ($s_u s_u VV A_n A_n R_o r_o$)

In the second generation of cross No. 4, three families segregated for both rolled and virescent. A summary of these families is given in table 3.

TABLE 3

F_2 seedling segregation of rolled and virescent. Cross No. 5.

PEDIGREE NUMBERS	NORMAL SEEDLINGS		ROLLED SEEDLINGS	
	Green	Virescent	Green	Virescent
888 (3)	107	35	27	15
(9)	166	48	44	9
(20)	170	60	61	18
Observed	443	143	132	42
Calculated 9:3:3:1	427	143	143	47

Deviation $\div$ probable error (10:6) = 1.22

If the factors for rolled and virescent were linked in inheritance, an excess of plants would be expected to occur in the mean F_2 classes. But a small excess occurs in the extreme classes when the ratio is calculated for independent inheritance and the mean classes grouped against the extreme classes. An equal deviation is expected to occur in 41 percent of the trials due only to errors of random sampling, the deviation over the probable error being equal to 1.22. Hence, it is safe to conclude that the factors R_o and V are inherited independently.

Liguleless and rolled.

Very little difficulty was experienced in classifying the rolled plants as to the ligule condition, provided only that the plants were noted before the leaves blackened and fell from the plant stem. It might be stated again, however, that only a small proportion of the rolled plants are lethal to this extent.

Three F_2 families from cross No. 3 segregated for liguleless and rolled. The data are given in table 4. The agreement of the observed ratio with the calculated, assuming independent inheritance between L_g and R_o , is

TABLE 4
Showing the F_2 families from Cross No. 4 which segregated for liguleless and rolled.

PEDIGREE NUMBER	NORMAL		ROLLED	
	Liguled	Liguleless	Liguled	Liguleless
889 (31)	63	23	22	6
(40)	72	24	20	11
L5527 (17)	121	44	35	11
Observed	256	91	77	28
Calculated 9:3:3:1	254	85	85	28

Deviation $\div$ probable error (10:6) = 0.29

TABLE 5
Showing the F_2 families from Cross No. 4 which segregated for sugary and rolled.

PEDIGREE NUMBER	STARCHY KERNELS		SUGARY KERNELS	
	Normal	Rolled	Normal	Rolled
291 (4)	107	38	49	13
(7)	244	77	83	24
889 (1)	32	9	5	3
(8)	80	23	25	7
(28)	114	51	22	8
(31)	66	24	20	4
(35)	101	29	19	6
(36)	87	32	11	3
(40)	73	22	23	9
L5527 (1)	68	30	44	7
(2)	120	37	40	13
(13)	129	45	59	17
(16)	120	53	49	11
(17)	131	35	34	11
Observed	1472	505	483	136
Calculated 9:3:3:1	1460	487	487	162

Deviation $\div$ probable error (10:6) = 0.84

very close. The deviation over the probable error based on a 10:6 ratio is only 0.29. These results prove that L_g and R_o are inherited independently.

Sugary and rolled

The F_2 progenies from cross No. 4 which segregated for sugary and rolled are given in table 5. The composition of the parent plants as regards

sugary and rolled may be represented factorially as $S_u R_o \cdot s_u r_o$. It will be noted in the table that the deviations from an independent segregation of the two characters are rather small, and that the mean classes are in excess of the expected numbers. If R_o and S_u were linked, the excess would have occurred in the extreme classes. When calculated for independent inheritance with a 10:6 grouping, the deviation is only 14 ± 16.6 . It is very evident from these results that the factors for sugary and rolled are independent in inheritance.

Rolled and anther ear dwarf

The different F_2 classes in the segregation of rolled and anther ear dwarf, from cross No. 4, were fairly distinct. However, there was sometimes an uncertainty as to the classification of dwarf-rolled plants when they were observed in the early three-leaf stage. This was due to the fact that dwarf plants have shorter, broader and slightly thicker leaves than do normal plants, consequently the rolling of the leaves is less definite. The dwarf-rolled types could be identified with more certainty if the plants were allowed to grow four or five days longer than the tall rolled plants.

TABLE 6
F₂ seedling segregation of rolled and anther ear dwarf. Cross No. 4.

PEDIGREE NUMBER	NORMAL PLANTS		ROLLED PLANTS	
	Tall	Dwarf	Tall	Dwarf
888 (7)	174	51	50	13
(34)	75	22	26	6
(49)	74	24	30	12
Observed	321	97	106	31
Calculated 9:3:3:1	312	104	104	35

Deviation $\pm$ probable error (10:6) = 0.65

Three F_2 families which segregated for rolled and dwarf are given in table 6. The agreement of the observed and calculated ratios with independent inheritance is unusually close, the deviation from a 10:6 ratio being only 5 ± 7.7 . Evidently the factors R_o and A_n are inherited independently.

LINKAGE RELATIONS

Factors V_6 , V_7 and Y

The first linkage data involving the Y (yellow endosperm) factor and establishing the Y linkage group was reported by EMERSON (1921), Y being linked to P_i , the factor for purple plant color.

The reasons for designating the virescents reported herein as v_6 and v_7 are given in the discussion. In the spring of 1923 a cross was made between two virescent-carrying strains of commercial corn: J 136-5 from U.S. selection 133, a yellow dent corn, and J 121-4 from Silver King. The strains were planted under field numbers 232 and 230 respectively. The family 230 carried two very similar medium virescent types, one of which has been designated v_7 . These two virescents are either independent or loosely linked as indicated by their linkage relations with Y and their F_2 green-virescent ratio. When V_7 alone was segregating, the crossing over percentage with Y was found to 41.5. When both virescent factors were segregating and the independence of the second virescent was assumed, a crossing over percentage of 35.5 was found. Chance alone could cause an equally large difference in the crossing over percentage. Again, when the green-virescent segregates of table 8 are calculated for independent inheritance a deficiency of 20 virescents was found, the deviation over the probable error being 2.23. The deficiency may have been caused in part by the difficulty in classifying the virescent and green plants. Further tests would be necessary to definitely determine the genetic relation of these two virescents.

The cross between a normal green plant from 232 and a pure virescent plant from 230 may be represented factorially as follows:

Cross No. 5 232-11 ($YY V_7V_7 VV V_6v_6$) $\times$ 230-1 ($yy v_7v_7 Vv V_6V_6$)

The F_1 plants were all normal green, showing that different virescent factors were involved. Among seven F_2 progenies, two trihybrid green and virescent, and two dihybrid medium virescent segregating progenies occurred. One must conclude from this that the pure virescent plant 230-1 was heterozygous for a second virescent factor. The two trihybrid segregating families produced a total of 283 green seedlings to 329 virescents. The deficiency of virescents was caused largely by errors in the classification of some greenish virescents. Data from these families are not included in the linkage calculations.

One F_2 family, 921-9 segregated for one of the medium virescents, v_7 . The relation of this virescent to yellow endosperm may be seen in table 7. From the composition of the parents, the coupling phase would be expected if Y and the virescent factor were linked. An excess of 47 plants did occur in the extreme classes when based on the calculation for independent inheritance, the deviation over the probable error having the value of 4.6. A gametic ratio of 1.41:1 was found, indicating coupling linkage between Y and V_7 , with a crossing over percentage of 41.5. The

closeness of fit was fair, P being equal to 0.38. However, the difficulty in classifying some of the virescent plants lowered this value to some extent.

Two F_2 families segregated for the two medium virescents. The seedling counts from these families are given in table 8. Here again the coupling phase of linkage between the factors Y and V_7 is exhibited. The percentage of crossing over was found to be 35.5 with a value for P of 0.40.

TABLE 7

F_2 segregation from plants of the composition $YV_7 VV_6 \cdot yv_7 vV_6$. Cross No. 5.

PEDIGREE NUMBER	YELLOW ENDOSPERM		WHITE ENDOSPERM	
	Green	Virescent	Green	Virescent
921 (9)	592	149	178	79
Observed	592	149	178	79
Calculated (1.41:1 linkage)	585	164	164	85

$P=0.38$

The weighted gametic ratio from the Y and V_7 segregation shown in tables 7 and 8 is 1.61:1.00, which indicates an average crossing over percentage of 38.3.

TABLE 8

F_2 segregation from plants of the composition $YV_7 VV_6 \cdot yv_7 vV_6$. Cross No. 5.

PEDIGREE NUMBER	YELLOW ENDOSPERM		WHITE ENDOSPERM	
	Green	Virescent	Green	Virescent
921 (6)	203	130	46	44
(8)	242	147	60	72
Observed	445	277	106	116
Calculated (1.83:1 linkage)	428	280	103	133

$P=0.40$

Two other F_2 families segregated for light virescent (v_6) and medium virescent (v_7). These two families reveal a rather unusual occurrence. They furnish evidence that both virescent factors are borne on the same chromosome with the factor for yellow endosperm. The relation of the two virescents to one another may be seen in table 9. It will be noted that the inter-relation between medium virescent and light virescent is similar to that between the virescent and albino characters. The factor for light virescent dominates the factor for medium virescent, consequently

they would produce the ordinary 9:3:4 ratio if they were not linked in inheritance. There is an excess of 17 plants over the number expected with independent inheritance between the two virescent factors. This indicates repulsion linkage which is expected since the virescents entered the cross from different parents. A gametic ratio of 1:1.37, indicating a cross over percentage of 42.2 between V_6 and V_7 is shown by the F_2 data.

TABLE 9

F₂ segregation from plants of the composition $YV_7 Vv_6 \cdot yv_7 VV_6$. Cross No. 5.

PEDIGREE NUMBER	GREEN	MEDIUM VIRESCENT	LIGHT VIRESCENT
921 (1)	209	81	104
(7)	288	98	133
Observed	497	179	237
Grouping virescents	497	416	
Calculated :(1:1.37 linkage)	497	416	

Those families segregating for the factors V_6 , V_7 , and Y are given in table 10. Before calculating the linkage relations, the medium virescent plants were grouped with the green plants under both the yellow and white endosperm classes. This is legitimate because the factor for light

TABLE 10

F₂ segregation from plants of the composition $YV_7 Vv_6 \cdot yv_7 VV_6$, with classes grouped to show the relation between Y and V_6 . Cross No. 5.

PEDIGREE NUMBER	YELLOW ENDOSPERM			WHITE ENDOSPERM		
	Green	Medium Virescent	Light Virescent	Green	Medium Virescent	Light Virescent
921 (1)	146	49	95	63	32	9
(7)	211	61	130	77	37	3
Observed	357	110	225	140	69	12
Grouping		467	225		209	12
Calculated						
(1:3.5 linkage)		468	217		217	11

$\chi^2 = 0.683$ P = very good fit

virescent expresses itself in the presence as well as in the absence of the factor for medium virescent. Hence, the light virescent plants occur in undisturbed proportions among the yellow and white endosperm classes. Linkage calculations revealed 23 percent of crossing over between Y and V_6 . The closeness of fit is very good, the value of χ^2 being only 0.683.

A summary of the above linkage tests may be given in the form of a chromosome map as follows:

V_6	23.....	Y	38.....	V_7
.....42.....				

The relation of V_6 and V_7 to the other factors in the linkage group has not been determined. Therefore, the true position of V_6 and V_7 in relation to Y may be reversed from that shown in the chromosome map. It is believed that a more distinct strain of the medium virescent material (v_7) should be isolated if possible before making outcrosses for linkage tests.

Relation between the factors W_1 and S_u

STROMAN (1924b) has shown that the factor for white-base-leaf (w_1) and sugary endosperm (s_u) are linked with about 25 percent of crossing over. The writer has accumulated additional data verifying the linkage of W_1 and S_u .

During the summer of 1922 crosses were made in order to study the interrelation of kernel characters and the white-base-leaf character.

The crosses may be represented factorially as follows:

Cross No. 1, L 4992-23 $\times$ S 899-7

$AA \ Cc \ Rr \ S_u s_u \ Yy \ W_1 W_1 \ VV \ S_c S_c \times$

$AA \ Cc \ rr \ S_u S_u \ YY \ w_1 w_1 \ Vv \ S_c s_c$

Cross No. 2, L 4992-26 $\times$ S 899-10

$AA \ Cc \ Rr \ S_u s_u \ W_1 W_1 \ VV \times$

$AA \ CC \ rr \ S_u S_u \ w_1 w_1 \ Vv$

Family L 4992 was the F_1 of a cross between Black Mexican sweet corn and Golden Glow, a yellow dent corn. Family S 899 was a homozygous F_3 white-base-leaf family, originating from a hybrid ear (A 1222-3 $\times$ A 1315-8) made by Dr. G. N. STROMAN from material secured from Dr. E. G. ANDERSON. Ear 1222-3 was factorially $AA \ Cc \ s_u s_u$. The other ear, A 1315-8, came from CASTLE's number 123, being heterozygous for some chlorophyll deficiencies and defective seed.

In arranging the F_2 and F_3 data from crosses No. 1 and No. 2, those families which segregated for sugary and white-base-leaf only ($S_u s_u \ W_1 w_1 \ VV$) were placed in separate groups from those families which segregated for virescent in addition ($S_u s_u \ W_1 w_1 \ Vv$).

The degrees of linkage in the simple dihybrid segregations were calculated by the method described by EMERSON (1916). For those families which segregated for sugary, white-base-leaf, and virescent types, the

green plants were grouped against the non-greens, the latter class including the characters white-base-leaf, virescent and albino. The gametic ratio was then calculated by formulae suggested by BRUNSON (1924) for use with trihybrid ratios involving two complementary genes, one of which is linked to a third gene. In the present case the genes for virescent and white-base-leaf are the two complementary genes, the factor for white-base-leaf being the complementary gene which is linked to a third gene, the factor for sugary.

Those F_2 families which showed the dihybrid segregation for sugary and white-base-leaf are given in table 11. The calculated gametic ratio was found to be 1:3.2. It will be seen in the table that there is an excess

TABLE 11

F₂ segregation from plants having the composition $S_u w_1 V \cdot s_u W_1 V$. Crosses 1 and 2.

PEDIGREE NUMBER	STARCHY		SUGARY	
	Green	W. B. L.	Green	W. B. L.
211 (10)	179	85	51	2
863 (17)	110	50	51	2
(24)	113	71	50	5
(26)	193	74	83	3
864 (17)	125	78	61	0
865 (1)	135	78	68	0
(8)	175	80	79	5
(14)	176	66	78	2
(23)	115	44	45	2
(28)	108	53	60	3
866 (4)	150	41	87	0
(9)	66	43	33	1
(10)	83	31	26	1
(12)	176	66	95	5
(22)	93	46	37	1
Observed	1997	906	904	32
Calculated (1:3.2 linkage)	1974	905	905	55

P=0.02

of plants occurring in the starchy green class and a deficiency in the sugary white-base-leaf class. The deficiency of white-base-leaf plants among the sugary kernels is very significant because of the smallness of the class resulting from repulsion linkage. The deviations in the other classes are negligible. These points may be illustrated by the closeness of fit calculations for table 11 as follows:

Phenotypes	Observed	Calculated, 1:3.2 linkage	(0-C)	(0-C) ²	$\frac{(0-C)^2}{C}$
Starchy green	1997	1974	23	529	0.268
Starchy white-base-leaf	906	905	1	1	0.001
Sugary green	904	905	1	1	0.001
Sugary white-base-leaf	32	55	23	529	9.618
				$\chi^2 =$	9.888
Closeness of fit for total				P =	0.02

This does not explain the deviations, however. The excess of plants in the double dominant class might be accounted for on the basis of pure chance variation or contamination, but it is harder to account for the large proportional minus deviation in the double recessive class. The deficiency may be due partly to the poor germination of the sugary kernels

TABLE 12

F₂ segregation from plants having the composition S_a w₁v · s_a W₁V. Crosses No. 1 and 2.

PEDIGREE NUMBER	STARCHY KERNELS				SUGARY KERNELS			
	Gr.	W. B. L.	Vir.	Alb.	Gr.	W. B. L.	Vir.	Alb.
209 (8)	137	69	43	31	62	0	18	0
211 (8)	12	8	2	2	5	0	0	0
(9)	97	54	42	15	46	1	13	1
863 (2)	66	40	26	16	43	3	14	0
(3)	72	23	25	12	30	1	13	0
(6)	128	58	48	19	49	5	12	3
(14)	130	54	41	18	66	2	15	2
(31)	91	43	39	15	35	4	8	0
864 (20)	103	49	40	11	54	3	13	2
865 (4)	79	50	20	7	42	5	2	0
(6)	67	42	24	8	32	2	18	0
(7)	64	31	14	11	30	1	11	0
(20)	79	34	24	13	34	1	7	0
(24)	90	48	39	15	42	3	8	0
(32)	70	33	30	8	28	3	10	1
(33)	88	52	31	10	45	2	10	1
866 (5)	84	36	22	11	34	3	12	1
(7)	70	29	26	10	29	0	14	1
(20)	41	13	9	3	18	2	3	2
(27)	77	33	23	6	36	0	14	1
(40)	133	53	49	19	51	4	31	1
Observed	1778	852	617	260	811	45	246	16
Grouping	1778		1729		811		307	
Calculated 1:4.3 linkage	1765		1704		836		320	

P=0.63

in the double recessive class, the germination of sugary kernels being 4 percent lower than that of the starchy. Unfortunately, double recessive plants were not available for backcrossing to F_1 hybrids during the summer of 1924.

TABLE 13
Summary of the F_3 progeny test from crosses No. 1 and 2.

NUMBER OF FAMILIES INCLUDED	STARCHY KERNELS				SUGARY KERNELS			
	Green	W. B. L.	Vir.	Alb.	Green	W. B. L.	Vir.	Alb.
5	382	121						
<i>Calculated (3:1)</i>	377	126						
Deviation $\div$ probable error (3:1) = 0.76								
6	258	89	88	25				
<i>Calculated (9:3:3:1)</i>	259	86	86	29				
Deviation $\div$ probable error (10:6) = 0.71								
2	304				78			
1	74		28	20		8		
<i>Calculated (9:3:3:1)</i>	73		24.5	24.5		8		
Deviation $\div$ probable error (10:6) = 0.27								
11	831	382			336	16		
<i>Calculated (1:2.48 linkage)</i>	815	359			359	32		
P = 0.01								
5	267	118	78	38	91	7	27	1
Grouping	267		234		91		35	
<i>Calculated (1:1.9 linkage)</i>	249		221		104		53	
P = 0.02								
1	130	9			12	21		
<i>Calculated (6.62:1 linkage)</i>	118	10.5			10.5	32		
P = .15								
1					12			3
7					799			

Those F_2 families which segregated for sugary, white-base-leaf, and virescent are given in table 12. Again it will be noted that there is an excess of plants over the calculated among the starchy classes and a deficiency among the sugary classes. The linkage calculations show a crossing over percentage of 18.9 between W_l and S_u . A value for P of 0.63 is shown, which is much higher than that of the former table. The method of grouping is partly responsible for the higher value of P.

An F_3 progeny test of white-base-leaf and sugary including 38 families is shown in table 13. Of these families, sixteen exhibited the repulsion phase of linkage between W_l and S_u and one exhibited the coupling phase. The 16 families were grouped into two classes, those not segregating for virescent and those segregating for it. Two groups thus classified showed repulsion linkage. The one family which exhibited linkage in the coupling phase did not segregate for virescent. The crossover percentages given by the three groups was 28.7, 34.5, and 13.1 respectively. The latter figure is based on only 172 plants. In the F_3 generation, the closeness of fit is similar to that of F_2 in being very low (as shown in table 13), the values of P for the three sets of data being 0.01, 0.02, and 0.15.

TABLE 14

Summary of F_2 genotypes as indicated by the F_3 progeny test given in table 13.

F_2 GENOTYPES AND CALCULATED RATIOS (1:4 LINKAGE)	OBSERVED NUMBER	CALCULATED NUMBERS (1:4 LINKAGE)	DEVIATIONS
1 $S_u S_u W_l W_l$	0	.51	.51
8 $S_u S_u W_l w_l$	11	4.06	6.94
8 $S_u s_u W_l W_l$	2	4.06	2.06
2 $S_u W_l s_u w_l$	1	1.01	.01
32 $S_u w_l s_u W_l$	16	16.21	.21
.. $S_u w_l$ (no selfs)	..	..	..
16 $s_u s_u W_l W_l$	8	8.10	.10
8 $s_u s_u W_l w_l$	0	4.05	4.05
.. $s_u w_l$ (no selfs)	..	..	..
Total	38	38.00	

P=0.008

A summary of the F_2 genotypes is given in table 14. It will be noted that the progeny test shows a very aberrant ratio. The F_2 genotypes occur in such fashion that it would be impractical to calculate the percentage of crossing over by the ordinary r and s method. When the calculation is based only on the number of families showing the repulsion linkage (16) and the coupling linkage (1), a crossing over percentage of 20 is found. On account of the great deviations in the other F_2 genotypes, the percent

of crossing over has little meaning. It will be noted that the largest deviations occur in the $S_u S_u W_l w_l$ and $s_u s_u W_l w_l$ classes, seven progenies more than expected occurring in the former class, and none occurring in the latter class where four were expected. Differential viability has no doubt played some part in causing the deviations, for there were many F_2 plants which did not produce an ear. Another explanation for the aberrant F_2 and F_3 seedling ratios may be that the w_l factor is unable to express itself in the presence of s_u under some conditions. It must be admitted that more study will be necessary before the S_u and W_l relationship can be satisfactorily explained.

TABLE 15

Showing the summary of fifteen F_2 families as regards scarred endosperm and sectioned plants. Cross No. 1.

PEDIGREE NUMBER	KERNELS		PLANTS FROM NORMAL KERNELS		PLANTS FROM SCARRED KERNELS	
	Normal	Scarred	Non-sectioned	Sectioned	Non-sectioned	Sectioned
Observed, fifteen ears segregating for scarred endosperm.....	3906	298	3694	2	68	97
Calculated (15:1)	3941	263				
Deviation $\div$ probable error (15:1) = 3.30			Percent of sectioned plants .05		Percent of sectioned plants 58.8	

The average weighted gametic ratio of all the F_2 and F_3 families was found to be 1:3.54 which indicates a crossing over percentage of 22 between the factors W_l and S_u . It is not known what weight should be placed on the crossover percentage (20) calculated from the F_3 progeny test. From the data given herein it seems safe to conclude that the factors S_u and W_l are about 20 or 22 units apart.

Relation between scarred endosperm (s_c) and sectioned plants

A very definite correlation between sectioned plants and scarred endosperm kernels was shown in the second generation from cross No. 1. The intensity of scarring on the endosperm is apparently not associated with a relative degree of striping on the sectioned plants, because intensely scarred kernels often produced normal green plants. Table 15 shows the summary of all the counts which were made from ears segregating for scarred endosperm. The occurrence of the two sectioned plants among normal kernels might well be the result of errors in the classification of the kernels. Due to the difficulty in classifying the scarred kernels, and to

the variation in the sectoring of the plants, it is not possible to determine the exact genetic relation of the two characters at present. However, the occurrence of 59 percent of sectoried plants among scarred endosperm kernels and of only .05 percent among the normal kernels indicates a very close relationship between the two characters.

DISCUSSION

In this paper is reported the linkage of two virescent factors V_6 and V_7 lying about 23 and 38 units respectively from the factor Y . Evidence shall here be given for believing that these virescent factors are genetically different from the factors V_1 , V_2 , V_3 , V_4 , and V_5 reported by DEMEREC (1924). He found that V_1 belongs to the $C-W_x$ linkage group, and V_4 to the $B-L_e$ group; therefore neither V_1 nor V_4 can be linked with Y to which the present genes are linked. He has also found (unpublished data) that V_2 , which is probably identical with STROMAN'S V_1 (1924a), is not linked to Y . Other data, while not entirely conclusive, furnish a rather strong indication that the factors V_3 and Y are likewise independent. His counts are as follows: yellow endosperm—green seedlings, 95 (96); yellow endosperm—virescent seedlings 29 (32); white endosperm—green seedlings 35 (32); white endosperm—virescent seedlings 11 (10). The theoretical ratio for independent inheritance is placed in parentheses. When the ratio is grouped on a 10:6 basis, the deviation is zero. Hence, it seems safe to conclude that the factor V_3 is genetically different from the writer's virescent types in that the distances of the latter from Y are about 23 and 38 units. The virescent factor V_6 was found by KVAKAN (1924) to belong to the linkage group with brown aleurone (B_n), glossy (g_l), and ramosa (r_a). Hence, it is also independent of Y . It appears, therefore, that the evidence in favor of the two present virescent genes being different from those heretofore reported is sufficient to justify assigning them the next two higher numerals in the virescent series, as V_6 and V_7 .

The yellow virescent factor which was carried by the male parent of crosses No. 1 and 2 is independent of Y . It is therefore independent of and genetically different from V_6 and V_7 . A third virescent of cross No. 5 associated with V_7 is either independent of or loosely linked to V_7 .

The two virescent types originating from a selfed ear of the variety Four County White proved to be independent of one another. Their relation to the other virescents reported herein has not been tested. The same is true in cross No. 4 of the virescent which was found to be independent of rolled seedlings, anther ear dwarf, and sugary.

In the second generation of crosses No. 3 and No. 4 there appeared a semi-lethal seedling character which has been called rolled. It answers very closely to the description of the disease scutellum rot given by HOLBERT, et al (1924). Seed from a segregating ear was sent to Mr. HOLBERT for identification. He found it to be phenotypically different from scutellum rot. Contrary to prediction, this diseased appearing condition of the seedling leaves, kernel, and roots behaved as a simple Mendelian recessive through a second and third generation.

The interaction between different chlorophyll characters in maize furnishes an interesting genetic study. The types most deficient in chlorophyll ordinarily dominate the less deficient types when their factors occur in the double recessive condition. It has been further demonstrated by DEMEREC (1924) that the phenotype of seedlings recessive for two virescent factors is lighter in color than either of the parent types. The F_2 segregation of certain virescents gave the ratio, 9 green:6 virescent:1 very light virescent. A similar ratio was given by the characters fine-striped and a virescent. One rather similar case of the interaction between two chlorophyll types is reported in the present paper. This occurs in the case of white-base-leaf and the virescent of cross No. 1. The double recessive condition of the factors for these types produces an albino plant. The double recessive type, however, often develops a small amount of chlorophyll on its leaf tips. In some families it produces slightly more chlorophyll than any of the types commonly known as pure white (*w w*).

There is a similarity between virescents and albinos with respect to their number and linkage relations as reported by different geneticists. Seven different genes for albino seedlings and indications for many more have been found (DEMEREC 1923). Four albino genes occur in two linkage groups, while six different virescent factors occur in five linkage groups. In the *Y* group three factors for albino and two for virescent have been found.

Chlorophyll is extremely variable in its expression, for example, in maize the phenotype of chlorophyll varies from an almost entire absence of green through numerous shades and patterns of greening to the full dark green color of our common commercial varieties. The large number of chlorophyll defects found in maize indicates the relative instability of the genes which determine chlorophyll, or else it indicates the presence of a very large number of such genes only a small percentage of which have mutated. However this may be, there is a close correspondence between the chemical complexity of chlorophyll and the number and diversity of the known chlorophyll mutants.

It seems that since chlorophyll is such a fundamentally important substance, nature has acted wisely in having not a few genes but many genes control it. Such an arrangement affords the greatest possible flexibility allowing ready adjustment to a changing environment.

SUMMARY

A virescent seedling type of maize having a distinct carotinoid-like appearance proved to be inherited independently of the factors Y , C , R , and W_1 .

The factor for the above virescent and for white-base-leaf (w_1) produced in the F_2 generation a ratio of 9 green seedlings, 3 white-base-leaf seedlings, 3 virescent seedlings, and 1 albino seedling, the albino being of the genotype $w_1 w_1 v v$.

The seedling type, rolled (r_o), an abnormality of the leaves and underground parts, was found to be strictly Mendelian in inheritance.

Data are presented to show that the factor for rolled (r_o) is independent of the factors A_n , S_u , L_g , and one virescent factor.

Two virescents designated as v_6 and v_7 were found to be linked to Y with a crossing over percentage of 23 and 38 respectively. A crossing over percentage between v_6 and v_7 of about 42 was found, indicating that the two virescent factors are located on opposite ends of the chromosome.

Further evidence was found in support of a linkage between the factors S_u and W_1 . The data, while highly variable, indicate between 20 and 22 percent of crossing over.

LITERATURE CITED

- BRUNSON, A. M., 1924 The inheritance of a lethal pale green seedling character in maize. Cornell Univ. Agric. Exp. Sta. Mem. 72: 1-22.
- DEMEREK, M., 1923 Inheritance of white seedlings in maize. Genetics 8: 561-585.
- 1924 Genetic relations of five factor pairs for virescent seedlings in maize. Cornell Univ. Agric. Exp. Sta. Mem. 84: 1-38.
- ELDERTON, W. PALIN, 1901 Tables for testing the goodness of fit of theory to observation. Biometrika 1: 155-163.
- EMERSON, R. A., 1916 The calculation of linkage intensities. Amer. Nat. 50: 411-420.
- 1921 The genetic relations of plant colors in maize. Cornell Univ. Agric. Exp. Sta. Mem. 39: 1-156.
- EYSTER, W. H., 1922 Scarred endosperm and size inheritance in kernels of maize. Missouri Agric. Exp. Sta. Res. Bull. 52: 1-10.
- HARRIS, J. ARTHUR, 1912 A simple test of the goodness of fit of Mendelian ratios. Amer. Nat. 46: 741-745.
- HOLBERT, JAMES R., BURLISON, W. L., KOEHLER, BENJAMIN, WOODWORTH, C. M., and DUNCAN, GEORGE H., 1924 Corn root, stalk, and ear rot diseases, and their control thru seed selection and breeding. Illinois Agric. Exp. Sta. Bull. 255: 239-478.
- KVAKAN, PAUL, 1924 The inheritance of brown aleurone in maize. Cornell Univ. Agric. Exp. Sta. Mem. 83: 1-22.

- LINDSTROM, E. W., 1918 Chlorophyll inheritance in maize. Cornell Univ. Agric. Exp. Sta. Mem. **13**: 1-68.
- PEARSON, KARL, 1924 Tables for statisticians and biometricians. London: Cambridge Univ. Press.
- STROMAN, G. N., 1924a Genetic relations of chlorophyll and anthocyanin seedling characters in maize. *Genetics* **9**: 91-123.
- 1924b The inheritance of certain chlorophyll characters in maize. *Genetics* **9**: 493-512.