GENETIC RELATIONS OF CHLOROPHYLL AND ANTHOCYANIN SEEDLING CHARACTERS IN MAIZE¹

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INTRODUCTION

During the last decade almost a hundred genetic factors have been discovered in maize. These factors in most cases form interesting and interrelating series with one another. In particular the pericarp color, the aleurone color, the silk color, the anthocyanin color, and the seedling chlorophyll color series are the ones most commonly known. These involve many factors, some of which are found in two or more series.

One of the most interesting of the series of factors named above is that of seedling chlorophyll. This subject has been reviewed and discussed by LINDSTROM (1918, 1921).

Another prominent series is that of anthocyanin. The complicated genetic relations of this series have been discussed by EMERSON (1921).

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As we already have many of the facts of chlorophyll and anthocyanin inheritance at our command, it is desired to show in this report the genetic relations of the anthocyanin and the chlorophyll seedling characters in maize. Although the relations between the anthocyanin and the chlorophyll characters are shown by seedling characters, the factors, as far as the anthocyanin is concerned, are identical with those dealt with by EMERSON (1921) in his results on the mature-plant pigment types.

It was first desired to test the relation of each factor in the ABP_i anthocyanin series (EMERSON 1921) with the w and v chlorophyll factors (LINDSTROM 1918) with special reference to possible linkage or independence. Results of this test have been obtained on all of these relations with the exception of the B with the w or the v factors. As the results indicate a placing of the W_1 and V_1 factors each in one of the linkage groups, it is not necessary to have their relation with the B factor at this time.

NOMENCLATURE AND DESCRIPTIONS

Red- and non-red-stem seedlings are terms which will be applied herein to the presence and absence, respectively, of anthocyanin pigment in the seedlings. This color generally develops more intensely on the first leaf sheath. On some seedlings it develops well up into the leaf, and in most red seedlings the tip is brightly colored. In some cases, the red develops first on the stem proper, while in others the color may develop first at the tip. In some red-stem seedlings only traces of red are found; these traces of red may be found at the tip, on the first leaf sheath, at the basal node, or on the stem proper. The presence of red shows the presence of the A factor. Non-red-stem seedlings are those seedlings having no trace of red that can be detected by the naked eye or even by the use of a hand lens.

A description of each of the factors concerned in obtaining these relations is given below:

$W_1 w_1$, a factor pair for green chlorophyll and white or albino seedlings (LINDSTROM 1918). The recessive condition has the effect of inhibiting the development of any chlorophyll pigment, and, of course, the seedlings carrying this factor die when the endosperm of the seed is used up.

$W_2 w_2$, another factor pair for albino seedlings. This factor pair has not heretofore been described. It first appeared in material received by Doctor LINDSTROM from Doctor W. E. CASTLE. The characters are identical with those which are associated with the $W_1 w_1$ factor pair and it is impossible to distinguish, phenotypically, seedling characters caused

by W_2w_2 from those caused by W_1w_1 . It may be proved later that these are identical factors, but observations thus far indicate that they are two entirely different factor pairs. Further discussion of w_2 , together with a discussion of a red- and a non-red-stem character with which the w_2 is linked, will be given in another section of this paper.

V_1v_1 , a factor pair for green chlorophyll and the virescent character found in the seedling stage (LINDSTROM 1918). The v_1v_1 condition prevents the development of the green chlorophyll only for a time. When the seedlings first come up they have a slight trace of green at the tips of the leaves, then they gradually turn green and may even grow to maturity and produce ears.

Aa , a factor pair for the development of anthocyanin pigment in the mature plant, in aleurone cells, pericarp, silks, etc. (EMERSON 1918, 1921; ANDERSON 1921).

EMERSON has shown the relations of this factor very definitely so far as mature-plant colors and aleurone are concerned, and his papers bring out the fact that those types having A present, develop red in the seedling stage, while those having aa are devoid of anthocyanin.

At the beginning of the work reported herein, a number of seedlings were grown from each ear in the several mature plant types available. Then, during the summer, plants were observed in the field to note possible segregation there. It was found that in the presence of A the seedlings were red while in the absence of A the seedlings were non-red.

Bb , a factor pair for brown pigment in the mature plant and an intensifier of A (EMERSON 1921). EMERSON has pointed out that it is not possible to distinguish seedlings involving this factor pair; that is, he could not distinguish in the seedling stage the sun-reds (ABp_l) from the dilute-sun-reds, (Abp_l) which differ only in the B factor.² As far as the present observations go this has been the case, although families have been observed which segregate rather distinctly into intense-red stems and light-red stems. This has occurred in sun-red families and although the two classes can not be absolutely differentiated, fairly definite classes can be made. Whether this is due to the presence and absence of the B factor remains to be tested. While this has been found in some families there are other families in which dilute-sun-red seedlings are just as intense if not more so than seedlings from sun-red plants.

P_1p_1 , a factor pair for purple anthocyanin pigment in the mature plant (EMERSON 1921). This factor pair occurs in the same linkage group with

² An exception to this occurs when R_g or r^g is homozygous in progenies heterozygous for the B factor (EMERSON and HUTCHISON 1921).

$Y y$, a factor pair for yellow and white endosperm, and $S_m s_m$ a factor pair responsible for salmon-colored silks (ANDERSON 1921).

$Y y$, a factor pair for yellow and white endosperm (EAST and HAYES 1911; EMERSON 1921). As previously stated this factor pair occurs in the same linkage group as the $P_l p_l$ and $S_m s_m$ factor pairs (EMERSON 1921, ANDERSON 1921).

r^+r^g , a factor pair wherein the recessive $r^g r^g$, when B is not present, prevents the expression of A in the foliage. R^+R^g , R^+r^g , and r^+R^g will apply the same as r^+r^g (EMERSON 1921).

MATERIAL

The work herein reported was started in the spring of 1920 at the UNIVERSITY OF WISCONSIN, with material kindly furnished by Doctor E. W. LINDSTROM. Some of this material originally came from Doctor W. E. CASTLE of HARVARD UNIVERSITY, while some F_1 's came from Doctor E. G. ANDERSON, then of CORNELL UNIVERSITY. All the work reported here was carried on in conjunction with the Genetics Department of the UNIVERSITY OF WISCONSIN.

The writer wishes to express his sincere gratitude to Doctor LINDSTROM, who, at all times throughout these studies, not only put his material at the disposal of the writer, but also tendered valuable aid, encouragement, inspiration and advice; and by such generosity and aid made possible these studies.

Grateful acknowledgment is made also to Prof. L. J. COLE, for encouragement and criticisms.

Some of the data were taken directly from the records of Doctor LINDSTROM and wherever this was done reference will be noted in this paper. The source of the material will be designated by prefixing to the pedigree number the letter "L" when from Doctor LINDSTROM, and "A" when the material is from Doctor ANDERSON.

METHODS

Individual notes were taken at flowering time on all the material.

In calculating closeness of fit, the method reported by ELDERTON (1901) was used. The crossover values were calculated by HALDANE's method for the determination of percentage of crossing over from the F_2 population (HALDANE 1919).

Wherever it was necessary to use the probable-error method, the general formula, $P. E. = .6745 \sqrt{p \times q \times n}$ was used, the letters p and q being

the elements of the ratio, and n the number of individuals in the population.

DATA AND RESULTS

In the preceding sections of this paper the characters to be discussed are given along with their specific factors. The source of material and the methods used in these studies, also, are given.

In the following pages are found the data and result of the genetic relations of the chlorophyll and the anthocyanin types.

It is desired to show, first, the relation of the W_1 factor with the $A B P_1$ factor series. Then, to show the relation of the V factor with the same anthocyanin series, and, finally, to show the relation of W_2 , another factor for albino seedlings, with an anthocyanin factor where this anthocyanin factor is not known, thus far, with certainty.

INDEPENDENT RELATIONSHIP OF THE FACTOR PAIRS W_1w_1 AND Aa

Before the linkage relations of W_1w_1 and Yy and V_1v_1 and Aa were obtained, many data had accumulated on the relationship of the W_1w_1 and Aa factor pairs. Most of these data came from self-pollinating dilute-sun-reds in families which were segregating for dilute-sun-reds, $A b p_1$, and full greens, $a b p_1$. The fact that they were segregating for dilute-sun-red and green or non-red was enough to show that within such families two-thirds of all dilute-sun-reds would be heterozygous for the A factor or of the composition $Aa bb p_1p_1$. The testing of W_1w_1 and Aa was accomplished in the greenhouse with seedling characters by planting the seed of dilute-sun-reds. It was found that non-red seedlings were produced in the greenhouse in the absence of A . That is to say, all full greens or non-reds gave only non-red-stem seedlings the following winter in the greenhouse, while among dilute-sun-reds red-stem seedlings were found.

Progenies totaling 114 were tested for the relation of these two factor pairs. The total number of seedlings counted in obtaining this relation amounted to 9736.

The sum of all the seedling counts of those progenies segregating for the four classes of characters, namely, green, red stem, green non-red stem, white red stem, and white non-red stem, or factorially W_1A , W_1a , w_1A , w_1a , respectively, are shown in table 1.

It is obvious that the above relation of calculated to observed does not give a good fit when all four classes are taken into consideration. It is noticed that the poorness of fit appears in the green chlorophyll classes.

The non-red-stem class is considerably higher and the red-stem class is lower than the expected. This is due no doubt to the fact that within the greens the classification of red- and non-red-stems is sometimes difficult. The red, although it may be present, may pass unnoticed, being

TABLE 1

	GREENS		WHITES		TOTAL
	Red-stem W_1A	Non-red-stem W_1a	Red-stem w_1A	Non-red-stem w_1a	
Observed.....	5364	1930	1842	600	9736
Calculated, 9 : 3 : 3 : 1.....	5476	1826	1826	608	9736
o-c	-112	+104	+16	-8	

$$P=0.038$$

masked by the green. A few such errors in 99 progenies would be more than enough to account for the poorness of fit within these two classes.

Taking the relation of the red- and non-red-stems within the white class only, we have the situation shown in table 2.

TABLE 2

	RED-STEM	NON-RED-STEM	TOTAL
Observed.....	1842	600	2442
Calculated, 3 : 1 ratio.....	1832	610	2442

$$\frac{\text{Dev.}}{\text{P.E.}} = \frac{10.0}{14.7} = 0.69$$

Here the deviation divided by the probable error is less than one, which shows an excellent agreement of theoretical and observed facts.

The progeny test was computed for the four genotypic classes within the phenotype W_1A class, namely, W_1W_1AA , W_1W_1Aa , W_1w_1AA , W_1w_1Aa . The reason for this was that the whites w_1w_1 always die in the seedling stage and the full greens (aa) were discriminated against in the field due to the fact that they were known not to give the desired four-class segregation.

The results of the progeny test are as given in table 3. The fit here is very poor. The chances are only 1:22 that the deviations here are due to random sampling.

It is possible that W_1 and A may be loosely linked. If this were the case some of these progenies would show repulsion and others coupling.

Therefore in order to test this possibility the percentage recombination was figured on *each* progeny under consideration, which was segregating for the four classes. Attention is called to the fact that these calculations were made on F_3 progenies and the parental combinations were not known. Accordingly, the crossover classes are shown by calculating the percentage of recombination by the use of HALDANE's method, as noted in a previous

TABLE 3

RATIO	GENOTYPES	OBSERVED	CALCULATED	O-C	(O-C) ²	$\frac{(O-C)^2}{C}$
1	W_1W_1AA	10	13	3	9	0.69
2	W_1W_1Aa	18	25	7	49	1.96
2	W_1w_1AA	22	25	3	9	0.36
4	W_1w_1Aa	64	51	13	169	3.31
9	Total	114				6.32

$$\chi^2 = 6.32; \quad P = 0.044.$$

section of this paper. In using this method the results show directly whether the factors are together in form of coupling or in the form of repulsion. The curve showing the distribution of the percentages of recombination is given in figure 1, as also is the mean and standard

FIGURE 1.—Curve showing frequency of the percentage crossing over in 63 progenies which were heterozygous for W and A . Mean, $47.1 \pm .80$; standard deviation, $9.38 \pm .84$; coefficient of variability, $19.9 \pm .01$.

deviation. This curve is one of normal frequency, and although it has a wide distribution it seems as though W_1 and A are independent of each other. Nevertheless, it is possible from these data, alone, that W_1 and

A might be in the same linkage group but about 47 units apart. At any rate, if there is a linkage here it still remains unproven.

LINKAGE INVOLVING THE W_1w_1 AND P_1p_1 FACTOR PAIRS

In order to test the P_1p_1 factor pair with W_1w_1 and V_1v_1 , plantings of ears heterozygous for P_1 and W_1 , as well as heterozygous for P_1 and V_1 were made in the dark-room. When planted in the light the kernels from the ears used in this dark-room gave only red-stem seedlings, and as far as the writer could see all the red stems were of the same intensity, that is, no definite classes of different intensities could be made.

The seedlings were grown first in the dark in order to allow the anthocyanin produced by the P_1 factor to develop, then those seedlings showing red were marked and placed in the light so as to determine the chlorophyll characters. The purple plant pigment develops in the absence of light as well as in the presence of light (EMERSON 1921). The other anthocyanin pigments of the $A B P_1$ series are produced only in the presence of light. For instance the sun-red $A B p_1$, and dilute-sun-red type $A b p_1$ develop in the light only, while purples and dilute-purples, $A B P_1$ and $A b P_1$, respectively, develop some anthocyanin in the dark (EMERSON 1921). This was also found to be the case with seedling characters. The different plant-color types were grown in the dark as a check and the only ones to develop any color in the absence of light were those having $A P_1$ factors. Accordingly, this development of anthocyanin in the dark was attributed to the P_1 factor.

The numbers which show the linkage of P_1 and W_1 are very small. Doctor LINDSTROM's cultures which produced whites, practically all lacked the P_1 factor. In one cross of dilute-purple, ($A b P_1$) W_1W_1 , with a sun-red, ($A B p_1$) W_1w_1 three ears were found in F_2 which segregated for both P_1p_1 and the W_1w_1 factor pairs. From another cross, a dilute-sun-red, ($A b p_1$) W_1w_1 , with a purple, ($A B P_1$) W_1W_1 , one F_2 ear also was found to segregate for the two factor pairs, $W_1w_1P_1p_1$.

In the dark-room test it was impossible to obtain four classes, as the classification between red- and non-red-stem in the dark was somewhat uncertain. It probably takes longer for some individuals to develop red than it takes others. At least, the red does not develop very uniformly, and as the seedlings cannot be left in the dark for more than a week, it is possible that some of the seedlings carrying the P_1 factor do not develop the red in this length of time. But, according to the law of chance, one probably should get the same ratio of normal greens to whites among those found with red in the dark at this time, as if one could have obtained

all the individuals carrying the P_1 factor. The seedlings cannot be left in the dark for much over a week for the reason that they become so rank in growth that it is nearly impossible to handle them; also, if left too long in the dark their vigor is impaired, and it is difficult for those which are genetically green to normally develop the chlorophyll.

The four ears mentioned in the preceding paragraph, all of which were of the genetic composition $W_1w_1 P_1p_1$, were grown in the dark and the data which were obtained are presented in table 4.

TABLE 4

PEDIGREE NUMBER	SEEDLING TYPE AS TO CHLOROPHYLL (ALL RED-STEMMED IN THE DARK)		TOTAL
	Green	White	
361-2	110	22	
361-7	74	14	
361-10	82	10	
366-2	24	2	
Total	290	48	338
Calculated, 3 : 1....	254	84	338
Deviation	36	36	

Dev. ÷ P. E. = 6.6

Obviously this is not a normal, independent relationship, since deviation as great as this would be expected to occur only once in about one-fourth of a million trials.

Now, if these two factors do not segregate independently, have they a linkage value?

The results of the above data fitted to 25 percent crossing over are as shown in table 5.

TABLE 5

	SEEDLING TYPE AS TO CHLOROPHYLL (ALL RED-STEMMED IN THE DARK)		TOTAL
	Green	White	
Observed	290	48	338
Calculated, 25 per cent crossing over..	289	49	338

Dev. ÷ P. E. = $1 \div 4.37 = 0.2$

Evidently the data show approximately 25 percent crossing over, and since they fail to give a good fit for independent inheritance, it seems as

if these data are worth considering very seriously as indicating a fairly close linkage relationship between the W_1 and P_l factors.

A field test was made in 1922 to check these data. This test consisted of planting F_2 seed from the same ears as those used in the dark-room test. The white or albino seedlings were removed and at maturity notes were taken on the greens as to their type of anthocyanin.

The results are given in table 6.

TABLE 6

	GREENS	
	P_l	p_l
Observed	61	6
Calculated, 25 percent crossing over....	57	10
Deviation	4	4

Dev. + P. E. = 1.67

The data here show less than 25 percent crossing over and therefore support the hypothesis that W_1 and P_l are closely linked. Data follow which will substantiate the results obtained here.

LINKAGE OF W_1w_1 AND Yy FACTORS

Realizing that the dark-room test was not an absolute test, especially since the numbers of plants were small, it was deemed necessary to test the relationship of the P_l and W_1 by other means. A good test would be one in which another factor lying in the same linkage group with P_l was involved. Indications of such a linkage became apparent when data involving Yy and W_1w_1 were scrutinized carefully. Some earlier work by KEMPTON seems to be best explained on this basis.

KEMPTON (1907) pointed out a correlation between endosperm color and chlorophyll seedling color. From a cross between *Zea tunicata* and *Zea ramosa*, one ear was obtained from selfing an F_1 plant which segregated for endosperm color and green and albino seedlings. His results are given in table 7.

TABLE 7

	NORMAL	ALBINO	TOTAL
Yellow seeds.....	57	13	70
White seeds.....	6	12	18
Total.....	63	25	88

It seems clear from the data pointed out in the succeeding paragraphs that KEMPTON was dealing with W_1w_1Yy factor pairs. This linkage was not known to be related to the W_1w_1 factor pair in question until the W_1w_1 and P_i linkage was observed.

It was shown that the Yy factor pair for yellow and white endosperm is linked with the P_ip_i factor pair for purple anthocyanin plant pigment (EMERSON 1921). It is understood that there are two or more independent factor pairs for the presence of yellow and white endosperm. Accordingly, if P_i and W_1 are linked, one of the yellow and white endosperm factors (Yy) is linked with W_1 , the others should be independent.

The factor pair for yellow and white endosperm dealt with here is presumably the same (Yy) as that reported and used by EMERSON (1921) and ANDERSON (1921), since no case was found in this work which shows independent inheritance between W_1 and Y .

The linkage data reported herein indicate about 42 percent of crossing over between Yy and W_1w_1 . This linkage was found in several families, the first being the family L4144.

Family L4144 is the progeny of a cross, L3360-28 W_1W_1YY with L3349-7 W_1w_1yy , which was made and grown by Doctor LINDSTROM. The seedling counts were made by the writer. The distribution of the progeny of the heterozygous (W_1w_1) F_1 plants in the F_2 generation of this cross is shown in table 27 (see appendix).

A summary of the results of this cross is shown in table 8.

TABLE 8

	YELLOW SEED		WHITE SEED		TOTALS
	Green	White	Green	White	
Observed.....	727	209	223	116	1275
Calculated, 42 percent crossing over.....	732	217	217	109	1275

$$\chi^2=0.943$$

In another family, L3348, (F_3) which was turned over to me, the linkage of W_1 and Y was also found. LINDSTROM's 3348 came from yellow seeds in a family segregating for yellow and white endosperm color. Some of the ears of L3348 were segregating for yellow and white endosperm and from these nine ears were obtained which were segregating for the four classes of characters concerned. This family had been inbred for three generations and came originally from a cross, L937-14 $\times$ L812-1, made by Doctor LINDSTROM.

Within the progenies of this family it was expected that both the repulsion and coupling phases would occur, as some plants should have the arrangement $\widehat{YW}_1 \widehat{yw}_1$ and others $\widehat{yW}_1 \widehat{Yw}_1$, where both would segregate for the four classes of characters. The plants which contained the former would make up the coupling phase and those having the latter would produce the repulsion phase. In no case was there a doubt of the placing of a progeny in one phase or the other.

The progenies of this family are listed in table 28. The summary of results where both factors are involved is given in table 9.

TABLE 9

1. *Coupling phase: (progeny numbers L3348-1, 8, 10, 24, and 21)*

	YELLOW SEEDS		WHITE SEEDS		TOTAL	χ^2
	Green YW_1	White Yw_1	Green yW_1	White yw_1		
Observed.....	405	112	124	59	700	0.66
Calculated, 42 percent crossing over..	402	119	119	60	700	
(o-c)	3	7	5	1		

2. *Repulsion phase: (progeny numbers L3348-14, 28 and 32)*

Observed.....	456	181	186	41	864	0.538
Calculated, 42 percent crossing over..	460	184	184	37	865	
(o-c).....	4	3	2	4		

The goodness of fit here is very significant, as it closely approaches perfection.

To test this family further, the progeny test was computed. The parent ear of L3348, namely, L2205-10, was segregating for the four characters under consideration, namely, yellow and white endosperm color and green and white chlorophyll seedling characters. The distribution of the classes in this parent ear is found at the bottom of table 28. The progeny test was calculated for the repulsion phase, as the parent ear, L2205-10, exhibited this phase, though not so distinctly as its progeny. There was a small deficiency of white seedlings from this ear and in order to check this in the next generation of this family, green and white seedlings of heterozygous individuals were totaled. The result of this showed a definite 3 : 1 relationship between the two.

In calculating the agreement of the progenies of the parent ear L2205-10 only the yellow seeds were used.

The results of the progeny test are as shown in table 10.

TABLE 10

GENOTYPES	EXPECTED RATIO FOR 42 PERCENT CROSSING OVER REPULSION PHASE	OBSERVED	CALCULATED
YYW_1W_1	1.0	2.0	2.4
YYW_1w_1	2.8	7.0	6.7
YyW_1W_1	2.8	5.0	6.7
YyW_1w_1	5.92	16.0	14.2
Total	12.52	30.0	30.0

$$\chi^2=0.738$$

The result of the progeny test further proved that the parent ear was of the constitution $\widehat{Yw_1.yW_1}$, since, when the calculated was computed with 42 percent crossing over between Y and w_1 and y and W_1 , there was found to be a good agreement between calculated and observed, χ^2 being less than 1.

THE CHROMOSOME MAP

The 30 percent crossing over between Y and P_l was reported in 1921 (EMERSON 1921), as was also the 37 percent crossing over between Y and S_m , and the 10 percent crossing over between P_l and S_m (ANDERSON 1921). The relationship of W_1 in this group has been reported in a preceding section of this paper. Even though the 42 percent crossing over between W_1 and Y will have to be checked by determining its relation with other factors between these two points, there seems to be no doubt at this time that the W_1 factor should be placed in this group along with Y , P_l and S_m , and in the relative position shown in figure 2.

FIGURE 2.—The chromosome map with the relative distances plotted in percentages of crossing over.

Figure 2 gives the map of the chromosome under consideration as it now stands and as the work reported herein seems to indicate.

LINKAGE INVOLVING THE V_1v_1 AND Aa FACTOR PAIRS

The data gathered on the relation between these two factor pairs indicate a very loose linkage. Such a loose linkage is apt to be overlooked

because 45 percent crossing over, which apparently prevails, approaches independent inheritance.

Evidence of linkage between the Aa and V_1v_1 factor pairs was found in the progeny of three separate crosses of a dilute-purple plant, $\widehat{AV_1} \widehat{av_1} \widehat{bb} P_1 p_1$, by a dilute-sun-red $\widehat{AV_1} \widehat{AV_1} \widehat{bb} p_1 p_1$. One ear from each cross was obtained in F_2 which gave the coupling-phase segregation for the four seedling characters, namely, green red-stem, green non-red-stem, virescent red-stem, and virescent non-red-stem. The results are given in table 11.

TABLE 11

PEDIGREE NUMBER	GREENS		VIRESCENTS		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
	V_1A	V_1a	v_1A	v_1a	
368-8.....	271	89	86	40	
370-3.....	115	28	49	11	
373-4.....	161	44	53	23	
Observed total.....	547	161	188	74	970
Calculated, 45 percent crossing over.....	558	170	170	72	970

$$\chi^2 = 2.64 \quad P = 0.46$$

Here, P indicates a good agreement between the observed and calculated on a basis of 45 percent crossing over, although these data also fit, fairly well, an independent segregation.

From a cross, $A \ 1958 \ \widehat{V_1a} \ \widehat{v_1A} \times A \ 1136-4 \ \widehat{V_1a} \ \widehat{V_1a}$, three plants were self-pollinated. In the F_2 of this cross the mature plants showed the segregation of the Aa factor pair, although the ratio of 3 : 1 was not closely approximated. This was probably due to small numbers. In F_3 the segregation of the Aa factor pair gave a good 3 : 1 ratio.

Among the progenies from one F_2 family, seven were heterozygous for both factor pairs, and only two were found that were not heterozygous for both. In the other two F_2 families not a single F_3 progeny was found that showed a segregation for both factors. According to the F_3 data of the three families, noted above, there were five F_2 individuals having red stems and not segregating for the four classes, that is, not heterozygous for both factor pairs, or a ratio among those having red stems of five not segregating for the four classes to seven which did segregate for the four classes. The ratio expected with independent inheritance is 5 to 4 for all individuals of the AV_1 phenotype. Although this is not very close agree-

ment between expected and observed, with such small numbers we can say that such deviation might be expected occasionally with independent inheritance. The progeny test, however, verifies the hypothesis.

The three F_1 individuals selfed gave in F_2 the repulsion phase of linkage. In F_3 , five out of seven progenies giving segregation for the four classes showed repulsion, the others exhibited the coupling phase.

The results of the F_2 and the F_3 repulsion phase are given in table 12 (progeny numbers from table 29, 54-3, 4, 5, and 371-7, 9, 10, 14 and 15).

TABLE 12

	GREENS		VIRESCENTS		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed.....	692	189	227	52	1160
Calculated, 45 percent crossing over.....	640	230	230	60	1160

For the four classes a close agreement with theory is impossible due to the fact that there is an excess of red-stemmed individuals especially within the green chlorophyll classes. Under some conditions it is very difficult to classify non-red and red-stem seedlings. Especially is this true within the green classes. Generally speaking it is comparatively easy to classify stem color within the virescent classes. Considering the two virescent classes alone, on a ratio of 3.84 to 1, the ratio expected for 45 percent crossing over (of virescent red-stem to virescent non-red-stem) the deviation is 6; the P. E. = 4.9. Accordingly, deviation divided by probable error is $6 \div 4.9 = 1.22$, which shows a fairly close agreement in these two classes.

The results of the coupling phase in F_3 are given in table 13 (progeny numbers from table 29, 371-3; 371-13).

TABLE 13

	GREENS		VIRESCENTS		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed.....	208	63	70	28	369
Calculated, 45 percent crossing over.....	212	65	65	28	370

$$\chi^2 = 0.521, \quad P = 0.87$$

Here P shows an excellent fit of the observed and calculated. The seedlings in this case were grown later in the season when there was more sunlight.

Progeny of the three F_2 's whose segregation appears at the top of table 29, showed in F_3 the distribution with respect to genotypes indicated in table 14.

TABLE 14

GENOTYPES	OBSERVED	CALCULATED, 45 PERCENT CROSSING OVER
V_1V_1AA	3	1.4
V_1V_1Aa	2	2.9
V_1v_1AA	1	2.9
V_1v_1Aa	7	5.8
Total	13	13.0

$$\chi^2 = 3.601, \quad P = 0.31$$

In this progeny test, P shows that there is some agreement between the calculated and observed classes.

Further evidence of the linkage of V_1 and A is found in another series of related families. The families L2281, L2282, L2283 from one ear; L2284, L2285, L2286 from another ear; and both original ears are from an old family of Dr. LINDSTROM'S, namely, L882; and family L2303 is the product of a cross in which one individual of L882 was the female parent. In the progenies involved here there is a distinct segregation of the Aa factor pair which is shown by the fact that in these families there appeared plant color types with the A factor as well as those not carrying the A factor. A total of all individuals from heterozygous parents gave a good 3 : 1 ratio with reference to this factor, that is, 232 : 75. If R^rR^q , R^rR^q or R^qR^r had been involved, then a ratio of 15 anthocyanin types to 1 green or non-anthocyanin type would have been expected, as the families were segregating for the Bb factor pair as well (ABR^r =anthocyanin, ABR^q =anthocyanin, AbR^r =anthocyanin, while AbR^q =full green or non-red). That R^q was not involved is also shown by the fact that there appeared no non-red-stemmed seedlings in the colored aleurone classes nor any full green (or non-red) plants in the colored aleurone classes even in the field. From all angles it seems that it is the Aa factor pair which is involved in the linkage shown with the V_1v_1 factor pair.

Table 30 and table 31 give the seedling counts of those progenies segregating for four classes where the coupling and repulsion phases, respectively, are involved.

The crossover value was found to be 45 percent. The value of 45 percent crossing over gives a gametic ratio of about 1.2 to 1, with an F_2 pheno-

typic ratio for coupling, of 11.12 $AB : 3.4 Ab : 3.4 aB : 1.44 ab$, and for repulsion a phenotypic ratio of 10.68 $AB : 3.84 Ab : 3.84 aB : 1 ab$.

A summary of results for the coupling phase is presented in table 15.

TABLE 15

	GREENS		VIRESCENTS		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed	1722	511	501	220	2954
Calculated	1697	519	519	220	2955

$$\chi^2 = 1.115$$

$$P = 0.77$$

The repulsion phase is summarized in table 16.

TABLE 16

	GREENS		VIRESCENTS		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed	974	373	352	97	1796
Calculated, 45 percent crossing over	991	356	356	93	1796

$$\chi^2 = 1.322$$

$$P = 0.73$$

In both the coupling and repulsion phases the value of P is above 0.7, which indicates that there is a good agreement between the hypothesis and the facts. The deviations may, therefore, be explained as being due to random sampling.

In some families with small numbers, it was hard to draw an absolute line between the coupling and repulsion phases. Where there was doubt as to which phase a certain progeny belonged, calculations were made to fit the observed to both the coupling and the repulsion phases and the progeny was thrown into the one which gave the closest fit.

In finally testing the relation of V_1v_1 and Aa in this series of families their progenies were classified according to the hypothesis of 45 percent crossing over. Only the progenies falling into the four classes of genotypes $AA V_1V_1$, $AA V_1v_1$, $Aa V_1V_1$ and $Aa V_1v_1$, are used. The $AA v_1v_1$, $Aa v_1v_1$, and $aa v_1v_1$ are virescents and usually die in the field or else seldom produce ears (LINDSTROM 1918). The $aa V_1v_1$, and $aa V_1V_1$ genotypes are devoid of anthocyanin and only a few were self-pollinated in the field for the reason that they never give the desired four-class segregation.

The results of the progeny test are given in tables 17 and 18.

TABLE 17

Coupling phase (parents 44-6; 2303-5; 39-10; 39-18).

GENOTYPE	EXPECTED RATIO FOR 45 PERCENT CROSSING OVER	OBSERVED	CALCULATED
<i>AA V₁V₁</i>	1.44	3	3.2
<i>Aa V₁V₁</i>	2.40	8	5.3
<i>AA V₁v₁</i>	2.40	5	5.3
<i>Aa V₁v₁</i>	4.88	9	10.7
Total	11.12	25	24.5

P=0.65

TABLE 18

Repulsion phase (parents 2281-14; 44-3; 38-8).

GENOTYPES	EXPECTED RATIO FOR 45 PERCENT CROSSING OVER	OBSERVED	CALCULATED
<i>V₁V₁AA</i>	1.00	1	1.9
<i>V₁V₁Aa</i>	2.44	4	4.6
<i>V₁v₁AA</i>	2.44	2	4.6
<i>V₁v₁Aa</i>	4.80	13	9.1
Total	10.68	20	20.2

P=0.31

These results of the progeny test fit very well with the hypothesis of 45 percent crossing over, as is shown by P.

To be sure of the placing of *Aa* and *V₁v₁* factor pairs in the same linkage group, a factor or factors will have to be found which lie between the two in order to check the loose linkage which is found here. These results are only approximations of the true linkage, if they are linked, and all that can be said at this time is that the results here indicate 45 percent crossing over between the two factor pairs.

INDEPENDENCE OF *V₁v₁* AND *P₁p₁* FACTOR PAIRS

In order to have a check on the dark-room method used in testing *P₁* and *W*, results from some virescent material, tested by the dark-room method, will be given. Crosses were made involving the *V₁v₁* and *P₁p₁* factor pairs. Three ears from one cross, dilute-purple, *P₁p₁ V₁v₁*, with

dilute-sun-red, $p_1p_1 V_1V_1$, were obtained in F_3 which segregated in the dark.

The results of these three ears are given in table 19.

TABLE 19

PEDIGREE NUMBER	RED-STEM IN THE DARK		NON-RED-STEM IN THE DARK	
	Green	Virescent	Green	Virescent
373-1.....	120	48	110	24
373-5.....	45	20	23	5
373-3.....	25	8	44	18
Total.....	190	76	177	47
Calculated, (3 : 1 ratios).....	199	67	168	56
Deviation.....	9	9	9	9

$$\frac{\text{Dev.}}{\text{P.E.}} = \frac{9}{4.76} = 1.9$$

The deviation divided by the probable error shows independent inheritance of V_1 and P_1 , and that growing the plants in the dark-room did not affect the degree of linkage.

LINKAGE OF A FACTOR CAUSING ALBINO SEEDLINGS WITH A FACTOR PAIR CAUSING RED- AND NON-RED-STEM SEEDLINGS

In the spring of 1920 a part of two families which originally came from Dr. W. E. CASTLE, was turned over to the writer. These two families, CASTLE'S Nos. 8 and 224, open-pollinated yellow flint, were sent to CORNELL UNIVERSITY, where they were grown for one year by Doctor LINDSTROM, who self-pollinated many ears. He also continued a part of one (No. 8) for another year; some of this latter material also was turned over to the writer. The material actually turned over included those progenies from number 8 which indicated a linkage of albino seedlings with a red- and a non-red-stem seedling character, and an individual ear, which originally came from No. 224, which showed independent inheritance of these mentioned characters.

The albino character found here seems to be identical with that reported by LINDSTROM. No better specimens of albino seedlings could be found than these, as they are practically pure white.

The material in which W_2 (a duplicate factor for albino seedlings) appears, happens to be very early, and this was a decided disadvantage in making crosses with other types. During the first two summers that the

writer grew this material, the early parts of the seasons were very dry, especially at the time the material was flowering. This was a disadvantage in that the pollen was viable for only a short time. This made even self-fertilizations difficult. Suckers were very few in number and those that were found produced very little pollen. To overcome this difficulty two plantings were made in the summer of 1922, one early and one late. Difficulty in obtaining self-fertilizations was probably also due to a difference between the time of dehiscence of the anthers and the emergence of the silks, a difference which was noted in these families. Pollen sterility is another probable cause, but this phase will have to be left to later investigation. That pollen sterility may have been partly the cause of poor catches is shown by the fact that out of large numbers of self-pollinations made, many never produced a grain, others produced a few kernels, and altogether only a very few ears were obtained which were practically normal.

In some of this material there appears a defective endosperm character which might have some influence on the sterility or the poorness of catches, though this is, as yet only speculation. The major cause of the poorness of this material may be due in general to inbreeding.

The red- and the non-red-stem characters found here have not checked thus far with anything we know in the $A B P_i$ series. The classes of stem seedlings that were described in an earlier section of this paper will apply here. The red- and the non-red-stem classes in this material are very distinct and especially is this true in the white classes. Under some conditions it is very difficult to classify the red- and the non-red-stems within the green-chlorophyll class, and under some conditions it is even difficult among the whites. In totals of red:non-red stems there appeared numbers in the green-stem class out of proportion to a 3 : 1 ratio, but there is scarcely any doubt that this is due to the difficulty in classification within the greens as to stem color, as noted above.

Previously to the 1922 season all the mature plants of CASTLE's No. 8 in the field, were classified as dilute-reds. In the season of 1922, some full-green plants appeared. In the early part of 1923 some non-red-stem seedlings were marked and observed throughout their growing period. No red pigment was found at any stage on these marked plants. The season of 1922 was very favorable for the development of color. In the preceding two years the season was very dry, and therefore very unfavorable for proper development of color, especially for distinguishing weak dilute-sun-reds from full-greens or non-reds. If the green plants that

appeared are true full-greens, then the red and non-red character which is found in these cultures is due to either an *A* factor or the *R^g* factor.

In table 31 is found the distribution among progeny of all ears which segregated for the four classes, namely, green red-stem, green non-red-stem, white red-stem, and white non-red-stem.

The summary of the results of the coupling phase is given in table 20.

TABLE 20

	GREENS		WHITES		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed.....	1329	202	171	402	2104
Calculated, 5 : 1 gametic ratio.	1416	161	161	365	2103
o-c.....	-87	+41	+10	+37	

The results here point to about 17 percent crossing over, but the deviation of calculated from observed is so great that a good fit would be impossible. This may be due to several things. It is to be noted that within the two non-red-stem classes the deviations are plus, while in the red-stem classes one large deviation is minus. This is due probably to counts made early, before the red had a chance to develop. In a number of these progenies three counts were made of each planting and observations on the difference between these counts, taken two or three days apart, showed that there was a shifting of the non-red-stems to the red class in the second counting, while in the third the counts were practically the same as the second. This shows that if the counts were taken at an early date, an excess of non-red-stems would be obtained. At the best this coupling phase indicates about 17 percent crossing over.

In taking the distribution of stem color within the white class alone, the calculations shown in table 21 were made.

TABLE 21

	RED-STEM	NON-RED-STEM	TOTAL
Observed.....	171	402	573
Calculated, 17 percent crossing over or 5 : 1 gametic ratio.....	175	398	573
Deviation.....	-4	+4	

The deviation here is small enough to say that it is due to random sampling.

One unmistakable case of repulsion was found. The counts in this case were taken directly from Doctor LINDSTROM's records. The results are given in table 22. (The individual ear was L2258-15, and unfortunately was never used as a parent).

TABLE 22

	GREENS		WHITES		TOTAL
	Red-stem	Non-red-stem	Red-stem	Non-red-stem	
Observed.....	43	22	16	2	83
Calculated, 17 percent crossing over or 5 : 1 gametic ratio.....	42	20	20	1	83

$$\chi^2=2.0 \quad P=0.57$$

Here, although the numbers are very small, P gives a very good fit for 17 percent crossing over. There seems to have been no difficulty in classification probably because counts were made late, after pigment had developed well.

The results of the progeny test, which is the most significant test of all, are given in table 23.

TABLE 23

GENOTYPES	EXPECTED GAMETIC RATIO 5:1 OR 17 PERCENT CROSSING OVER	OBSERVED	CALCULATED
$W_2W_2R_1R_1^*$	25	6	8.5
$W_2W_2R_1r_1$	10	3	3.4
$W_2w_2R_1R_1$	10	3	3.4
$W_2w_2R_1r_1$	52	21	17.7

$$\chi^2=1.501$$

$$P=0.687$$

* R_1 and r_1 = red- and non-red-stem, respectively (arbitrarily used).

From these results W_1 and the red- and the non-red-stem factors are undoubtedly closely linked.

It was stated previously that the factors concerned here in producing red- and non-red-stem seedlings parallel what one would expect if either the A or the r^0 factor were concerned. The evidence as to which one, so far as it is available at the present time, is given below.

In a cross, 287 (14) by 305 (5), both of which were dilute-sun-reds, and the F_1 's of which were all dilute-sun-reds, there is found some evidence

which points to the r^o factor as being the one concerned in the linkage with W_2 . In the F_1 's of the cross five self-pollinations were made and all ears grown in the greenhouse. Counts were obtained on only two, the others being completely destroyed by mice. In one of these two, a 3 : 1 ratio of red-stem : non-red-stem was found, but in the other a 9 : 7 ratio of red- : non-red-stem was exhibited. The counts are given in table 24.

TABLE 24

849-3, F_2 of 287-14 $\times$ 305-5.

	RED-STEM	NON-RED-STEM
Observed	145	106
Calculated, 9 : 7 ratio	141	110
Deviation	4	4

If the factor pair for red and non-red stems concerned here was the $r^r r^o$, then from a cross $AAr^r r^o$ (287-14) with $Aar^r r^r$ we would have in F_1 four genotypes, namely, $AAr^r r^r$, $Aar^r r^r$, $AAr^r r^o$, and $Aar^r r^o$. The latter genotype would give, when selfed, a segregation of 9 red-stem : 7 non-red-stem. Now, it is known that in the 305 family the factor concerned in producing red- and non-red-stems is the A factor, as this family is derived from old stocks of Doctor LINDSTROM'S. But, in the 287 family, where the linkage of W_2 and a factor for red and non-red stems is found, the factor producing this red and non-red is not known. It is undoubtedly, as has been said, due to either A or r^o and the argument is given below. If both had been heterozygous for the same factor only 3 : 1 ratios would be obtained. But we have one here that gives us a distinct 9 : 7 ratio. We might under normal conditions get a deviation in a monohybrid which would give us a 9 : 7 where a 3 : 1 is expected, but this occurs very seldom. The result of this 9 : 7 progeny is fitted to a 3 : 1 ratio in table 25.

TABLE 25

	RED-STEM	NON-RED-STEM
Observed	145	105
Calculated, 3 : 1	188	62
Deviation	43	43

Deviation $\div$ probable error = 9.35

The odds are so great against the deviations being the result of random sampling that the former calculations will have to suffice. Had the red- and non-red-stem factor in the 287 family been the A factor, 9 : 7 ratios could never have been obtained in the cross stated above. The A which came from the 305 family, in combination with the r^o from the 287 family would be sufficient to account for the result obtained.

Accordingly, this bit of evidence points to the R instead of the A locus as being the one linked with W_2 . This checks with some of the unpublished results obtained by Doctor LINDSTROM where a W_2 is concerned. He gets 16 percent crossing over. There is about 17 percent crossing over here, which checks very closely with his results.

Further evidence which points to R^o or r^o as being the factor concerned here in linkage with W_2 comes from a cross of 377-1 $W_1W_1 W_2w_2$ ($AA r^r r^o?$) dilute-sun-red, with 325-22 $W_1W_1 W_2w_2$ ($aa r^r r^r$) full-green or non-red. In the F_1 generation, all the mature plants were dilute-sun-reds, showing that the A factor was present. If 377-1 had contained AA we should have expected this to be the case and then in F_2 all the ears would have segregated, upon planting, into 3 reds to 1 non-red. If 377-1 had contained Aa , then we would have expected in F_1 a 1 : 1 ratio of red : non-red. The facts of the case are that in F_1 no segregation took place and in F_2 all progenies segregated for reds and non-reds. The segregation was of two kinds, one giving a 3 : 1 ratio, and the other kind an approximation to a 9 : 7 ratio. If the constitution of 377-1 was $AA R^r R^o$ and 325-22, $aa R^r R^r$, the results obtained are what one would expect. In such a case there would be two kinds of F_1 's, namely, $Aa R^r R^r$ and $Aa R^r R^o$. In F_2 the former would give a 3 : 1 ratio of red- : non-red-stems and the latter a 9 : 7 ratio of the same characters.

The results are shown in table 26.

TABLE 26

PEDIGREE NUMBER	RED-STEM	NON-RED-STEM	APPROXIMATE RATIO
52 (1)	10		9 : 7
(3)	85	77	9 : 7
(4)	142	66	3 : 1
(5)	18	16	9 : 7
(6)	13	17	9 : 7
(7)	12	12	9 : 7
(8)	14	56	3 : 1
(9)	9	9	9 : 7

Most of these eight progenies have small numbers, and it is hard to identify some of them with 3 : 1 or a 9 : 7 ratio; among the others there is no doubt as to some being 3 : 1 and others 9 : 7.

A significant fact is brought out by the following relation. In a cross of the 377 family wherein the linkage of W_2 and a factor for red- and non-red-stem seedlings is concerned (it also gave a 3 : 1 ratio of red- : non-red-stem seedlings) with another family (325) where the A factor is known to be concerned in producing 3 red- : 1 non-red-stem seedlings, there are obtained 9 red- : 7 non-red-stem seedlings. Accordingly, if factors which were producing 3 : 1 ratios in their respective lines gave on combination 9 : 7 ratios, the only logical conclusion is that these factors are different. It follows, then, that if one is known to be A the other is presumably r^q , since only these two factors are at present known to be responsible for red- and non-red-stem plants.

This, then, seems to show that the R^q is present here and responsible for the red- and non-red-stem character concerned in the linkage with W_2w_2 . This is contradictory to the evidence pointed out where CASTLE's other line is considered. This other line, CASTLE's No. 224, although there is no direct heritable connection of it with No. 8 (the line considered above in the linkage of W_2 and red and non-red stem) was supposed to contain the same W , but from this it seems to be certain that these two factors for albino seedlings are different.

A brief account will be given of CASTLE's No. 224 which shows an independence of a W with a factor causing red- and non-red-stem seedlings.

The segregation of the progeny and the results are given in table 33. The value of P is 0.19, which is not a very good fit, although within the white class the deviation divided by the probable error equals 1.5. Judging from the data of the white class, it is reasonable to say that the two factors concerned here are independent of each other.

To test the presence and absence of A , crosses were made between one family, 290 (from 35-1), which was composed of all full-greens, with brown plants, aBP_1 . With such a cross if A were present we would expect full-anthocyanin plants in the next generation (EMERSON 1921), but if A were absent only plants with the absence of any red pigment would appear. Crosses, 290-31 E gr.³ with 372-10 brown, and 290-32 E gr. with 372-10 brown, were made, and their progeny grown in the greenhouse the following winter. In every case the entire progeny had red stems while not a red-stem plant appeared in the selfed plants of No. 290. Family 290 was

³ E gr. = full-green plant.

selected for the test of this stem character, as it was composed of only full-greens or non-red plants.

Also the crosses, 290-22 E gr. with 384-12 E gr.; 290-25 E gr. with 285-4 E gr.; 290-48 E gr. with 303-14 E gr.; gave only red-stem progeny.

A cross 290-45 E gr. with L4247-1 D gr.⁴ *R* tester, gave only colorless kernels, showing that the *r* was present here and not *R*.

From the above data of progenies of CASTLE'S 224 it seems certain, then, that the factor concerned in causing red- and non-red-stem seedlings here is the *r*^o factor. At least it parallels the results that one would expect if *r*^o were present, and according to EMERSON (1921) the test with browns and greens is the logical test for *r*^o. So we can conclude that the *W* concerned here is independent of *R*.

From these data it is not absolutely safe to draw definite conclusions as to the factors concerned for albinos and red- and non-red-stem seedlings reported above. The evidence, however, seems to point to one factor for red- and non-red-stem seedlings, the *r*^o, and two factors for albino seedlings. The albino factor in CASTLE'S No. 8 (*W*₂) is definitely linked to a factor for red- and non-red-stem seedlings and evidence is brought forward, to show that this factor is *r*^o. Then, if this is true, the albino factor in CASTLE'S 224 is an entirely different factor from *W*₂, as it is independent of the *r*^o.

SUMMARY

The independent relationship of *W*₁ and *A* is reported. The possibility of a very loose linkage relationship between these two factors is also presented.

By means of a dark-room test the factors *P*₁ for plant color and *W*₁ for albino seedlings were found to be linked. The crossover value approximated 25 percent.

A loose linkage was found between *Y* and *W*₁ with a crossover value of 42 percent.

The arrangement of the three above linked factors is *Y-P*₁-*W*₁. The chromosome map of this group is shown, including the *S*_m factor for silk color.

The *Aa* factor pair for aleurone and plant color was found to be loosely linked with the *V*₁*v*₁ factor pair for green-virescent seedlings. The amount of crossing over was 45 percent.

By means of the dark-room test an independent relationship was found between *P*₁ and *V*₁.

⁴ D gr. = dilute-sun-red.

A linkage is reported which involves a factor causing albino seedlings, W_2 , with a factor pair causing red- and non-red-stem seedlings ($r^e?$). The crossover value was found to be about 17 percent.

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APPENDIX—Tables 27 to 33

TABLE 27

*F*₂ dihybrid segregation of the cross L3360-28×L3349-7 exhibiting 42 percent crossing over between Y and W₁.

PEDIGREE Numbers	YELLOW SEED		WHITE SEED		SEED PLANTED		TOTAL CHLOROPHYLL	
	Green	White	Green	White	Yellow	White	Green	White
L4144-2	110	35	30	19	150	50	140	54
L4144-13	64	19	21	6	115	41	85	25
L4144-14	108	38	38	12	150	50	146	50
L4144-16	118	27	34	14	150	50	152	41
L4144-20	119	32	32	15	150	50	151	47
L4144-21	84	24	30	24	150	50	114	48
L4144-23	124	34	38	26	158	65	162	60
Total	727	209	223	116	1023	356	950	325

TABLE 28

Segregation of the progenies from yellow seed of L2205-10, W₁w₁Yy.

PEDIGREE NUMBER	YELLOW SEED		WHITE SEED		SEED PLANTED		TOTAL CHLOROPHYLL	
	Green	White	Green	White	Yellow	White	Green	White
L3348-2	103	34	0	0	56	0	103	34
L3348-3	57	0	16	0	63	25	73	0
L3348-4	79	17	15	6	116	29	94	23
L3348-4	30	10	13	6	51	21	43	16*
L3348-5	17	0	8	0	25	10	25	0
L3348-6	25	0	10	0	27	12	35	0
L3348-7	56	0	0	0	63	0	56	0
L3348-8	78	27	19	16	124	38	97	43*
L3348-10	80	20	27	14	128	61	107	34*
L3348-12	50	14	0	0	100	0	50	14
L3348-14	145	61	78	12	220	99	223	73*
L3348-16	101	34	0	0	152	0	101	34
L3348-20	57	9	0	0	74	0	57	9
L3348-21	105	29	35	14	140	55	140	43
L3348-22	71	32	0	0	106	0	71	32
L3348-24	33	9	15	3	98	24	48	12*
L3348-26	16	0	2	0	17	3	18	0
L3348-27	80	0	0	0	88	0	80	0
L3348-28	152	62	49	16	247	81	201	78*
L3348-49	29	9	0	0	40	0	29	9
L3348-31	86	21	0	0	114	0	86	21
L3348-32	159	58	59	13	230	80	218	71*
L2205-10	165	46	59	10	245	84	224	56*

*Dr. LINDSTROM's counts included.

TABLE 29

F_2 and F_3 segregation of a cross whose F_1 was of the arrangement $\widehat{V_1a} \widehat{v_1A}$ and which shows 45 percent crossing over between V_1 and a and v_1 and A .

PARENT NUMBER	PEDIGREE NUMBER	GREENS		VIRESCENTS	
		Red-stem	Non-red-stem	Red-stem	Non-red-stem
	54-3	46	16	12	3
	54-4	50	8	12	6
	54-5	68	17	12	3
	Total F_2	164	41	36	12
54-4	371-3	83	27	39	11
	371-4	0	19	0	0
	371-5	12	0	0	0
	371-7	88	30	19	9
	371-9	48	16	20	5
	371-10	143	36	65	11
	371-12	21	7	0	0
	371-13	125	36	31	17
	371-14	116	38	48	6
54-3	371-15	133	28	39	9
	369-5	0	128	0	35
	369-8	23	0	0	0
	369-12	0	19	0	12
	369-14	23	0	0	0
54-5	372-1	9	0	6	0
	372-2	28	5	0	0
	372-5	0	20	0	9
	372-9	0	35	0	0
	372-11	0	32	0	0
	372-16	0	25	0	4

TABLE 30

Coupling-phase segregation of progenies in F_3 and later generations from parents heterozygous for V_1v_1 and Aa factor pairs and which show 45 percent crossing over.

PEDIGREE NUMBER	GREENS		VIRESCENTS	
	Red-stem	Non-red-stem	Red-stem	Non-red-stem
L2281-5	27	4	7	3
L2281-9	38	5	9	4
L2281-13	28	8	7	5
L2281-11	98	38	31	13
L2281-26	25	9	6	5
44-6	64	20	19	11
315-4	121	34	32	14
317-3	67	19	19	7
317-8	218	80	68	21
L2284-22	46	5	10	1
L2286-16	32	8	7	3
L2286-18	22	6	11	4
L2286-19	22	6	8	6
L2284-12	29	11	7	5
311-6	118	23	22	19
311-8	47	13	12	6
L2303-5	38	16	11	6
L2303-8	41	8	8	4
L2303-12	53	17	16	7
L2303-17	34	8	15	3
39-18	35	28	10	9
39-10	33	8	6	2
299-1	97	24	38	13
299-19	129	38	45	13
300-27	51	8	10	6
303-16	126	48	41	19
304-4	83	19	26	11
Total	1722	511	501	220

TABLE 31

Repulsion-phase segregation of progenies in F_3 and later generations involving V_1 and A factor pairs with 45 percent crossing over.

PEDIGREE NUMBER	GREEN		VIRESCENT	
	Red-stem	Non-red-stem	Red-stem	Non-red-stem
L2281-14	25	8	12	2
L2282-3	16	3	10	3
44-3	41	6	8	0
44-7	20	9	8	2
45-11	39	14	17	4
315-6	12	4	5	2
317-2	85	26	29	8
L2284-4	13	8	10	3
L2284-6	31	9	9	0
L2284-8	22	10	12	3
L2284-23	30	9	6	2
L2285-2	30	13	9	3
L2286-22	23	17	4	1
42-8	8	6	3	1
311-2	56	22	16	4
311-17	34	17	22	5
312-10	132	34	38	9
312-12	72	20	10	3
38-8	58	33	24	5
38-11	22	8	4	1
299-8	111	37	49	16
299-9	94	47	39	16
300-20	6	9	7	1
316-1	4	4	1	3
Total	984	373	352	97

TABLE 32

Segregation of the progenies whose parents were heterozygous for W_2 and a red- and a non-red-stem character. (From CASTLE'S No. 8).

PEDIGREE		GREEN		WHITE	
Parents	Progeny	Red-stem	Non-red-stem	Red-stem	Non-red-stem
CASTLE No. 8	L2258-5	70	0	22	0
	L2258-7	0	54	0	25
	L2258-15	43	22	16	2
	L2258-16	58	0	18	0
	L2258-32	83	16	11	24
	L2258-38	7	13	0	0
	L2258-49	16	16	0	0
	L2258-54	18	11	0	0
	L2258-32	54	3	0	10
	L3351-3	10	0	2	0
	L3351-4	0	52	0	10
	L2251-7	28	12	0	0
	L2251-13	53	10	10	12
	34-1	2	0	0	1
34-9	34-4	61	8	9	21
	34-9	32	2	7	12
	34-12	33	0	0	0
	34-10	2	0	0	0
	34-14	16	2	4	9
	34-13	39	8	3	4
	287-1	129	12	15	45
	287-4	87	20	22	60
	287-9	126	19	18	48
	287-10	133	14	12	36
	287-12	81	15	12	31
	287-13	61	5	5	13
	34-13	288-1	113	17	7
	288-2	80	18	19	20
34-13	288-3	24	7	0	0
	288-5	72	15	8	15
	288-10	31	0	0	0
	288-13	12	2	0	1
	288-15	17	3	1	1
	288-16	21	0	3	0
	288-17	16	0	0	0
	288-18	17	10	3	0
	34-14	289-3	0	0	0
	289-4	29	0	6	0
	289-6	30	0	0	0
	289-7	41	25	0	0
	L3351-13	377-3	45	0	0
	377-7	56	10	8	9
	377-8	22	3	0	2

TABLE 33

Segregation in F_3 and later generations where a W factor and a factor for red- and non-red-stem seedlings are independent. Derived from CASTLE'S number 224.

PEDIGREE		GREEN		WHITE	
Parents	Progeny	Red-stem	Non-red-stem	Red-stem	Non-red-stem
CASTLE 224	L2215-2	83	35	21	10
	L2215-22	82	32	20	7
	L2215-29	13	5	6	1*
	L2215-29	11	4	5	4
L2215-29	35-1	0	73	0	14
	35-9	35	8	0	0
	35-16	25	10	8	3
Total		214	86	60	25

*Dr. LINDSTROM'S counts.