INHERITANCE OF WHITE SEEDLINGS IN MAIZE[1]

M. DEMEREC

Station for Experimental Evolution, Cold Spring Harbor, New York

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INTRODUCTION

White seedlings are characterized by the lack of chlorophyll. Under ordinary conditions, they die in the early seedling stage soon after the reserve food of the seed is exhausted. In color they vary from pure white to more or less creamy yellowish. Occasionally, individual plants have small amounts of yellowish-green tissue.

White seedlings are observed frequently in the higher plants. Most of those studied have been found to be simple recessives to the normal green. NILSSON-EHLE (1922) reported three independent factors for white seedlings which were found in different varieties of barley, and TROW (1916) showed that the white phenotype in *Senecio vulgaris* L. is determined by duplicate genes.

HALSTED and KELSEY (1904) described white seedlings in maize. Later, EMERSON (1912) and GERNERT (1912) presented evidence that the albinism studied is determined by a factor which is a simple Mendelian recessive to green. MILES (1915) furnished additional data on the inheritance of white seedlings, and made a cytological study of the albinos. He concluded that plastids are entirely absent in white plants. LINDSTROM (1918, 1920, 1921) studied the relations between white seedlings and some other chlorophyll types. RANDOLPH (1922) studied white seedlings cytologically and found plastid primordia present in all cells which normally would be green. In the extreme tip of the leaf he observed a limited region in which the cells contained green chloroplasts. He concluded that in the case of white seedlings "failure of the plant to become green is not to be explained as the result of an absence of plastids or plastid primordia."

White seedlings occur very frequently in corn; they can be observed in practically every corn field. Interesting data were obtained by HUTCHISON (1922)[2] on the presence of white seedlings in commercial varieties of corn. From 419 lots of seed collected from the northern experiment stations and seed companies, 1814 selfed ears were tested in the greenhouse; 144 of them, representing 22.4 percent of the lots, were found to throw white seedlings. The percentage might have been still higher if more ears had been selfed in certain lots. In 24 percent of the lots one ear only was selfed and in 16 percent of all the lots two ears; this lowered the chance of detecting white seedlings.

[2] With permission of Director C. B. HUTCHISON, original data are used and arranged in such a way that the frequency of occurrence of white seedlings can be shown.

MATERIAL AND METHODS

This study was taken up as the result of a need felt by workers on maize for more endosperm and seedling characters for use in linkage tests. A systematic search for seedling characters was begun during the winter of 1919–1920, a sample of seed being planted for this purpose from each available self-pollinated ear. To facilitate this search Professor R. A. EMERSON and Dr. E. G. ANDERSON made available to the writer all the selfed ears accumulated in the course of their studies on maize.[3] Many distinct variations were found, the majority affecting the development of chlorophyll. Among the ears tested, 15 were segregating for white seedlings. Twelve of them came from unrelated families. Progenies in these ears gave the material for the beginning of this investigation.

Some additional material was obtained in the spring of 1921 and 1922 from Professor C. B. HUTCHISON.

An effort was made to determine the relation of these white seedling characters to each other by intercrossing. This is rendered rather difficult by the lethal nature of the white seedling character. Heterozygous green plants must be used in crossing. These are not visibly different from their homozygous green sibs. In any selfed family throwing white seedlings, two-thirds of the green plants are expected to be heterozygous, and of random intercrosses between plants of such families, four-ninths are expected to be crosses between two heterozygous plants. But in order to be dependable both parents of the cross must be selfed. This was often impossible because most of the plants produced only one ear. Where the lines to be crossed differed by some aleurone or endosperm character, this difficulty was more easily overcome. The dominant parent was selfed while the recessive parent was pollinated by a mixture of its own pollen with pollen from the dominant parent. The crossed seeds were indicated by xenia.

In the cases where the white seedling character is dependent upon more than one Mendelian factor the chances for successful crosses are lower.

Linkage tests with other factors have been made, but these are as yet far from complete. In a few cases they have proved valuable in identifying the factors involved.

[3] The writer is greatly indebted to Professor R. A. EMERSON, under whose direction the work was carried out, and to Dr. E. G. ANDERSON, for suggestions and help rendered during the investigations.

EXPERIMENTAL RESULTS

Intercrosses

Experiments with white seedlings were begun in the spring of 1920. A few intercrosses were made in the summer of the same year, and a few more the next summer. It was not until the summer of 1922 that the intensive work was begun.

Up to this time, twenty-nine different intercrosses have been made between heterozygous plants of eighteen different stocks. The intercrosses between stocks which have genetically the same white seedling should segregate white in F_1. Contrary to expectation, all F_1 plants of the great majority of these intercrosses were green. In three cases only, the F_1 generation segregated white seedlings. In one of these cases the F_2 generation showed that the intercrossed stocks differed in their genetic constitution with respect to white seedling. In this cross three factors for white seedlings were present. The other two intercrosses were not carried farther than F_1.

These results indicate that the white phenotype in maize may be determined by many different factors. How many there are in the available material can be determined only by further investigations. At present, intercrosses are complete enough to show the presence of seven factors, and only one intercross is lacking to complete the test with another one.

The following table shows the stocks between which intercrosses were made and the F_1 seedlings found to be green (table 1.) The individuals used in each cross were selfed and shown to be heterozygous.

TABLE 1

STOCK NUMBER	1	2	3	8	11
1		x	x	x	x
2	x		x	–	x
3	x	x		x	x
8	x	–	x		x
11	x	x	x	x	

All the possible intercrosses except 2×8 were obtained. That these stocks were genetically different, however, may be inferred from the fact that the white phenotype occurring in stock 8 is determined by duplicate genes, while the white phenotype which is isolated from stock 2 is, as far as known, a simple Mendelian recessive.

Stock 4 has been intercrossed with stocks 1 and 2 only. In both cases the F_1 was green. From the cross 2×4 the F_2 generation was grown and found to give green and white seedlings in a 9 : 7 ratio, showing that two factors were involved. That white seedling in stock 4 is genetically different from that in stock 11 may be inferred from the fact that white seedling in stock 11 shows linkage with white endosperm (table 38, appendix), while white seedling in stock 4 does not show such a linkage (table 33). As far as known, the white phenotype in stock 4 is a simple Mendelian recessive and that in stock 8 is determined by duplicate genes. This fact makes it probable that white seedlings in stocks 4 and 8 are genetically different. Nothing is known about the relation between white seedlings in stocks 3 and 4. Cross 3×4 would show whether seven or eight factors for white seedlings were present in the stocks discussed.

Up to this time it has been possible to grow F_2 generations from three intercrosses between stocks 1, 2, 3, 8 and 11. Segregation in the F_2 generation (tables 28, 36 and 38) shows that white seedlings in these stocks are genetically different. From the other six intercrosses only the F_1 generation was grown. All the F_1 seedlings tested were green, however, which is possible only if the parents differ in their genetical constitution for white seedlings. To complete the test, it is necessary to grow the F_2 generation. It is considered, however, that the evidence presented may warrant the preliminary conclusion that the white phenotypes in stocks 1, 2, 3, 8 and 11 are determined by different genes. In stocks 1, 2 and 3 white seedling is a simple Mendelian recessive; therefore, in each case one gene is involved. For the expression of white seedling in stocks 8 and 11 duplicate genes are necessary.

The following symbols will be used for white seedlings:

w_3 for the gene for white seedling in stock 1
w_4 for the gene for white seedling in stock 2
w_5 for one of the duplicate genes in stock 11
w_6 for the other duplicate gene in stock 11
w_7 for the gene for white seedling in stock 3
w_8 for one of the duplicate genes in stock 8
w_9 for the other duplicate gene in stock 8

Genotype $w_3\ w_3$

$W_3\ w_3$ is the name for the gene which is responsible for the white seedling in stock 1. This white seedling is probably the one which LINDSTROM (1918) used in his studies on chlorophyll inheritance.

Results of numerous crosses (tables 30, 31, and 32) show that w_3 in the homozygous recessive condition was in every case sufficient for the expression of white phenotype.

Cross between stocks 3 and 1

Table 28 gives the F_2 data of the cross between stocks 3 and 1. Four ears segregated in a 9 : 7 ratio, giving a total of 649 green and 490 white seedlings. The calculated numbers are 640.7 green and 498.3 white, giving a deviation from expectancy of 8.3 ± 11.3. The fit is very close, and the conclusion is justified that in this cross two independent genes were present, each producing the white phenotype when homozygous recessive. Four ears segregated in the 3 : 1 ratio with a total of 1012 green and 315 white seedlings. The deviation from the calculated numbers is 16.75 ± 10.6. One ear gave green seedlings only.

Heterogeneity of the F_1 plants which is expressed in the F_2 progenies is a result of the heterozygous condition of the parents. It is supposed that the parent plants had the following genetic constitution regarding white seedlings:

♀ parent, $W_3\ W_3\ W_7\ w_7$
♂ parent, $W_3\ w_3\ W_7\ W_7$

The frequency of F_1 plants was:

TABLE 2

PROGENIES SEGREGATING IN	9 : 7	3 : 1	GREEN
Observed	4	4	1
Calculated	*2.25*	*4.5*	*2.25*
Difference	+1.75	−.5	−1.25

$\chi^2 = 2.11$, $P = .352$

The fit is reasonably close.

Cross between stocks 6 and 1

The F_2 generation grown from the cross between stocks 6 and 1 shows a few interesting points. By an examination of table 29 it can be seen that the F_1 plants were of four kinds. Three of them gave only green progeny; four segregated in the 3 : 1 ratio; one segregated in the 9 : 7 ratio, giving 129 green and 94 white seedlings with a difference from expectancy of 4.0 ± 5.0; and one segregated in the 15 : 1 ratio, giving 216 green and 16 white seedlings with a difference of 1.8 ± 2.48.

The ratios obtained in F_2 are an expression of a recombination of three different factors for white seedling. The 15 : 1 ratio indicates that two of these factors act as duplicate genes producing white seedling in the double recessive condition only. Both of these factors were brought into the cross by the parent from stock 6. This conclusion may be drawn from the fact that progenies of certain plants in stock 6 segregated in the 15 : 1 ratio.

A 9 : 7 ratio would be expected in the F_2 generation of this cross only, in case stock 1 had the recessive allelomorphs of two genes. One of these genes was w_3, which, as far as known, is sufficient in itself to produce the white phenotype when homozygous recessive. The other gene was one of the duplicate genes present in stock 6. The duplicate genes from stock 6 are not named as yet, because it is not known whether they differ from the duplicate genes $W_8\ w_8$ and $W_9\ w_9$. They will temporarily be called $W_b\ w_b$ and $W_c\ w_c$.

Frequencies of F_1-generation plants indicate that the parent plants probably had the following genetical constitution for white seedling:

♀ parent from stock 6 = $W_3\ W_3\ W_b\ w_b\ W_c\ w_c$

♂ parent from stock 1 = $W_3\ w_3\ W_b\ w_b\ W_c\ W_c$; $W_3\ w_3\ W_b\ W_b\ W_c\ w_c$
$W_3\ w_3\ W_b\ W_b\ w_c\ w_c$ or $W_3\ w_3\ w_b\ w_b\ W_c\ W_c$

The frequencies of F_1 plants are as follows (table 3):

TABLE 3

PROGENIES SEGREGATING IN	9 : 7	3 : 1	45 : 19	15 : 1	GREEN
Observed	1	4	0	1	3
Calculated, ♂ = $W_3\ w_3\ W_b\ w_b\ W_c\ W_c$	.56	3.38	1.12	1.12	2.82
Difference	+.44	+.62	−1.12	−.12	+.18

The fit is very close, χ^2 equaling 1.608 and P = .803. When the calculation is made on the other possibility, e.g., on the assumption that the male parent had the genetical constitution, $W_3\ w_3\ W_b\ W_b\ w_c\ w_c$ or $W_3\ w_3\ w_b\ w_b\ W_c\ W_c$ then $\chi^2 = 1.518$ and P = .82. The fit would be very poor if the parent plants used in the cross had any other genetical constitution than noted above. One class of plants which would give an F_2 progeny segregating in 45 : 19 ratio, was not detected. This ratio would be obtained by selfing a plant which was heterozygous for all three factors for white. The small number of plants grown may account for that deficiency.

Crosses for linkage

It is not possible to make back-crosses with white seedlings, and therefore conclusions about linkage have to be drawn from the F_2 data.

Characters which can be detected in seeds or seedlings are the best ones for testing linkage relations, and especially so when a lethal factor like the white seedling is being tested. Gene w_3 has been tested for linkage with shrunken endosperm (s_h); one of the factors for aleurone color (R); liguleless (l_g); dwarf plants (d); and the factor for purple aleurone (P_r).

TEST OF w_3-s_h. Several crosses were made between plants of the constitution $W_3\, W_3\, S_h\, S_h \times W_3\, w_3\, s_h\, s_h$. In the case of linkage, when F_2 data are used, the divergence from the expectancy in recombination classes is much larger in the coupling than in the repulsion series.

Table 30 gives the data of the above-mentioned cross. The summary appears in table 4.

TABLE 4

	Sh W₃	*Sh w₃*	*sh W₃*	*sh w₃*	TOTAL
Observed............	1822	582	511	182	3097
Calculated............	*1742.10*	*580.66*	*580.66*	*193.58*	
Difference............	+79.90	+1.34	−69.66	−11.58	

$\chi^2 = 12.718$, $P = .0054$

The fit is very poor. There are only about five chances in a thousand that the observed deviation is due to errors of random sampling. That the observed deviation is not due to the linkage between w_3 and s_h can be seen from the fact that the parental class $s_h\, w_3$ is smaller and the recombination class $S_h\, w_3$ larger than the calculated numbers on the non-linkage basis. Furthermore, if we compare the ratios between green and white seedlings in S_h and in s_h classes separately, the deviation from expectancy is very small (table 5).

TABLE 5

	Sh W₃	*Sh w₃*	*sh W₃*	*sh w₃*
Observed............	1822	582	511	182
Calculated............	*1803*	*601*	*518.75*	*174.25*
Difference............	+19±14.3		−7.75±7.69	

All this evidence shows that there is no close linkage between s_h and w_3.

A comparison of germination of S_h and s_h seed indicates that the large observed deviation from expectancy, when the four classes are considered together, may be due to the poorer germination of the shrunken seed.

In the S_h class, 93.28 percent of planted seeds produced seedlings and in the s_h class 80.68 percent only. When a correction is made for the low germination of the s_h seeds the comparison is as follows (table 6):

TABLE 6

	$S_h W_3$	$S_h w_3$	$s_h W_3$	$s_h w_3$	TOTAL
Corrected	1822	582	590.87	210.44	3205.31
Calculated	*1802.99*	*600.99*	*600.99*	*200.34*	
Difference	+19.01	−18.99	−10.12	+10.10	

The fit is very close, χ^2 equaling 1.479 and P = .693, which is another confirmation of the assumption that no close correlation between s_h and w_3 exists.

TEST OF w_3-l_g. In table 31 are arranged the F_2 data obtained from the cross $R\ l_g\ d\ W_3 \times r\ L_g\ D\ W_3\ w_3$ from which the linkage relation between w_3 and l_g, r and d can be studied. The data on the relation of w_3 and l_g can be summarized as in table 7.

TABLE 7

	$Lg\ W_3$	$Lg\ w_3$	$lg\ W_3$	$lg\ w_3$	TOTAL
Observed	515	155	184	72	926
Calculated	*520.9*	*173.6*	*173.6*	*57.9*	
Difference	−5.9	−18.6	+10.4	+14.1	

The fit is fairly close, χ^2 being 6.116 and P = .107. The observed deviation is larger than it would be otherwise, since the separation into classes was made too early, and probably too many plants were classified as liguleless. Still the fit is close enough to warrant the conclusion that no appreciable linkage exists between l_g and w_3.

TEST OF w_3-r. The data concerning the relation between w_3 and the r factor for the color of the aleurone are to be found in tables 31 and 32, summarized in table 8.

TABLE 8

	$R\ W_3$	$R\ w_3$	$r\ W_3$	$r\ w_3$	TOTAL
Pedigree 13 (table 32)	712	234	247	102	1295
Pedigree 15 (table 31)	1081	343	334	102	1860
Total	1793	577	581	204	3155
Calculated	*1777*	*592.3*	*592.3*	*197.4*	
Difference	+16	−15.3	−11.3	+6.6	

The fit is very close, χ^2 equaling .983 and P > .80, so that the conclusion is justified that w_3 and r are not closely linked.

TEST OF w_3-d. Table 31 gives the data on the relation between w_3 and the factor d for dwarfness. The summary is given in table 9.

TABLE 9

	$D\ W_3$	$D\ w_3$	$d\ W_3$	$d\ w_3$	TOTAL
Observed	362	100	109	35	606
Calculated	*340.9*	*113.6*	*113.6*	*37.9*	
Difference	+21.1	−13.6	−4.6	−2.9	

The fit is close enough, χ^2 equaling 3.34 and P = .347, indicating no close relation between w_3 and d.

TEST OF w_3-p_r. A summary of the data from table 32 is given in table 10.

TABLE 10

	$P_r\ W_3$	$P_r\ w_3$	$p_r\ W_3$	$p_r\ w_3$	TOTAL
Observed	207	64	67	24	362
Calculated	*203.6*	*67.9*	*67.9*	*22.6*	
Difference	+3.4	−3.9	−.9	+1.4	

The fit is very close, χ^2 being .3897 and P larger than .80. The conclusion is warranted that no close linkage exists between w_3 and p_r.

Genotype $w_4\ w_4$

The stock carrying the recessive factor w_4 was derived from a plant of Howling Mob sweet corn grown by Doctor ANDERSON as a sample of pseudo-starchy endosperm. All selfed plants which were used in intercrosses segregated white seedling in a 3 : 1 ratio. This stock was extensively used in intercrosses with the other stocks, because it had sugary endosperm.

Cross between stocks 2 and 4

The cross between stocks 2 and 4 gave a green F_1 generation and segregated in the F_2 generation in a 9 : 7 ratio.

Parent plants used in the cross were heterozygous for the white seedling. From the selfed seed of the female parent (No. 10–1) 18 green and 7 white seedlings were obtained and from the selfed seed of the male parent 30 green and 10 white seedlings. All the tests gave green seedlings in F_1.

Table 33 gives the F_2 data of this cross. The progenies from three selfed F_1 ears segregated into 3 : 1 ratios with a total of 742 green and 231 white seedlings, the difference from the expectancy being 12.25 ± 9.11. The progenies from the other three ears segregated into 9 : 7 ratios, having a total of 391 green and 285 white seedlings. The difference from expectancy is 10.75 ± 8.7. Three ears had green progenies only.

The F_2 data show conclusively that in this cross two independent factors for the white phenotype were present. They were brought into the cross one by each parent. Presumably the parents had the following genetical constitution regarding white seedlings: $W_4\, w_4\, W_a\, W_a \times W_4\, W_4\, W_a\, w_a$.[4] The frequencies of F_1 plants support that assumption (table 11.)

TABLE 11

PROGENIES SEGREGATING IN	9 : 7	3 : 1	GREEN	TOTAL
Observed	3	3	3	9
Calculated	*2.25*	*4.5*	*2.25*	
Difference	+.75	−1.5	+.75	

$\chi^2 = .91$, $P > .606$

The F_3 generation was grown from four F_2 ears. Three of these ears segregated in a 9 : 7 ratio and one in a 3 : 1 ratio. Table 34 gives the F_3 data. The F_2 plants grown from 9 : 7 ears were as follows (table 12):

TABLE 12

PROGENIES SEGREGATING IN	9 : 7	3 : 1	GREEN	TOTAL
Observed	6	4	2	12
Calculated	*5.3*	*5.3*	*1.4*	
Difference	+.7	−1.3	+.6	

$\chi^2 = .44$, $P > .606$

Selfed plants grown from the seed taken from the 3 : 1 ear (pedigree 797) gave two kinds of progenies; i.e., green ones and others segregating into a 3 : 1 ratio, just as was expected.

Linkage relations

With w_4 no special crosses for linkage were made. Parent plants, however, used in the cross between stocks 2 and 4 differed in their genetical

[4] The relation between established genes for white seedlings and the gene for albinism which is present in stock 4 is not known. The symbol $W_a\, w_a$ will be used in this chapter as a name for the gene from stock 4.

constitution for endosperm, and the result was that the F_2 generation segregated for endosperm characters also. Seeds differing in endosperm were planted separately and notes on white seedlings taken. From the data obtained, conclusions may be drawn on linkage relations between w_4, w_a, and s_u, y, and y_p, which factors were involved in the cross. As far as was noted, the parents had the following genetical constitution:

♀ parent 10–1 $s_u\ y\ y_p\ W_4\ w_4\ W_a\ W_a$

♂ parent 6–9 $= S_u\ Y\ Y_p\ W_4\ W_4\ W_a\ w_a$

The F_1 plants differed in genetical constitution for white seedling. This difference was best expressed on the segregation of their progenies. Some of them segregated for white seedlings in a 3 : 1 ratio, indicating that they were heterozygous for one of the factors for white. Theoretically the progeny of half of the plants should segregate $w_4\ w_4$ and the other half $w_a\ w_a$. But there is no way of differentiating between the two genotypes other than by later breeding tests. If linkage between either of them and any of the involved endosperm factors existed, they could be separated because of the fact that in the case of w_4 there would be a coupling, and in the case of w_a a repulsion relation. White seedlings segregated from the progenies of part of the F_1 plants in a 9 : 7 ratio, indicating the presence of both of the factors for white seedling. If reasonably close linkage existed between either of them and any of the factors for endosperm that were involved, it would have been detected in spite of the fact that the 9 : 7 ratio is not favorable for the expression of linkage.

TEST OF w_4-w_a-s_u. A summary of data from progenies of the plants which segregated in a 3 : 1 ratio is given in table 13.

TABLE 13

PEDIGREE NUMBER		*Su W*	*Su w*	*su W*	*su w*	TOTAL	GOODNESS OF FIT
332–1	Observed	193	49	54	17	313	$\chi^2=3.92$
	Calculated	*176.1*	*58.7*	*58.7*	*19.5*		P= .27
	Difference	+16.9	−9.7	−4.7	−2.5		
332–7	Observed	150	48	42	16	256	$\chi^2=1.00$
	Calculated	*144*	*48*	*48*	*16*		P= .80
	Difference	+6	0	−6	0		
332–8	Observed	127	49	45	13	234	$\chi^2=.883$
	Calculated	*131.6*	*43.9*	*43.9*	*14.6*		P>.80
	Difference	−4.6	+5.1	+1.1	−1.6		

The following are the data on the progenies from plants segregating in a 9 : 7 ratio (table 14):

TABLE 14

	Su W	*Su w*	*su W*	*su w*	TOTAL
Observed	282	198	75	56	611
Calculated	*258*	*201*	*85.5*	*66.5*	
Difference	+24	−3	−10.5	−10.5	

$\chi^2=6.229$, P = .103

The fit would be still better if it were not for the low germination of the sugary classes.

The only conclusion that can be made from the above data is that no close linkage exists between sugary endosperm and either w_4 or w_a.

TEST OF w_4-w_a-y. Data relating to the progenies of the plants which segregate into a 3 : 1 ratio are given in table 15.

TABLE 15

PEDIGREE NUMBER		*YW*	*Yw*	*yW*	*y w*	TOTAL	GOODNESS OF FIT
322–1	Observed	146	34	47	15	242	
	Calculated	*136.1*	*45.4*	*45.4*	*15.1*		$\chi^2=3.537$ P = .338
	Difference	+9.9	−11.4	+1.6	−.1		
332–7	Observed	111	35	39	13	198	
	Calculated	*111.4*	*37.1*	*37.1*	*12.4*		$\chi^2=.25$ P > .80
	Difference	−.4	−2.1	+1.9	+.6		
332–8	Observed	97	37	33	12	179	
	Calculated	*100.8*	*33.5*	*33.5*	*11.2*		$\chi^2=.578$ P > .80
	Difference	−3.8	+3.5	−.5	+.8		

The data of 9 : 7 families are summarized in table 16.

TABLE 16

	Y W	*Y w*	*y W*	*y w*	TOTAL
Observed	200	160	72	48	480
Calculated	*202.5*	*157.5*	*67.5*	*52.5*	
Difference	−2.5	+2.5	+4.5	−4.5	

$\chi^2=.76$ P > .80

In all the cases the fit is very close and the conclusion that there is no close linkage between w_4, w_a and y is justifiable.

TEST OF w_4-w_a-y_p. A summary of the data is given in table 17.

TABLE 17

PEDIGREE NUMBER		$Y W$	$Y w$	$y W$	$y w$	TOTAL	GOODNESS OF FIT
332–1	Observed	35	12	12	3	62	
	Calculated	*34.9*	*11.6*	*11.6*	*3.9*		$\chi^2 = .232$ P>.80
	Difference	+.1	+.4	+.4	−.9		
332–7	Observed	30	11	9	2	52	
	Calculated	*29.25*	*9.75*	*9.75*	*3.25*		$\chi^2 = .719$ P>.80
	Difference	+.75	+1.25	−.75	−1.25		
332–8	Observed	24	10	9	2	45	
	Calculated	*25.4*	*8.4*	*8.4*	*2.8*		$\chi^2 = .654$ P>.80
	Difference	−1.4	+1.6	+.6	−.8		

The data of 9 : 7 families are shown in table 18.

TABLE 18

	$Y W$	$Y w$	$y W$	$y w$	TOTAL
Observed	60	36	22	12	130
Calculated	*54.8*	*42.7*	*18.3*	*14.2*	
Difference	+5.2	−6.7	+3.7	−2.2	

$\chi^2 = 2.64$ P>.457

The numbers are not very large, but in each case the fit is very close, and the conclusion may be drawn that there is no linkage between w_4, w_a, and the factor for the pale yellow endosperm.

Cross between stocks 6 and 2

The progeny of the female parent from stock 6 segregated in a 15 : 1 ratio, giving 70 green and 6 white seedlings with a deviation from expectancy of 1.0 ± 1.42. The male parent from stock 2 produced green and white seedlings in a 3 : 1 ratio. All the F_1 seedlings of the cross 6×2 were green, indicating that the white seedlings involved in the parent stocks were genetically different. Table 35 gives the F_2 data.

From the table it can be seen that two pedigrees segregated in a 63 : 1 ratio with a total of 196 green and 5 white seedlings, the deviation from expectancy being only 1.86 ± 1.19. Two other pedigrees segregated into a 15 : 1 ratio, having a total of 180 green and 11 white seedlings, with a difference from expectancy of $.94 \pm 2.26$. Two pedigrees segregated in a 3 : 1 ratio, and the last two gave green seedlings only. Segregation in a 63 : 1 ratio shows that three homozygous recessive genes were necessary for the expression of the white seedling in question. A 15 : 1 ratio is a result of a recombination of these three genes.

The segregation of progenies from the selfed parent plants together with the frequencies of the F_1 plants indicates that the genetic constitution of the parent was as follows:

♀ parent from stock 6 = $W_4\ W_4\ W_b\ w_b\ W_c\ w_c\ w_d\ w_d$[5]

♂ parent from stock 2 = $W_4\ w_4\ w_b\ w_b\ W_c\ W_c\ W_d\ W_d$

A comparison follows (table 19):

TABLE 19

PROGENIES SEGREGATING IN	3 : 1	15 : 1	45 : 19	63 : 1	GREEN
Observed	2	2	0	2	2
Calculated	*3*	*1*	*1*	*1*	*2*
Difference	−1	+1	−1	+1	0

$\chi^2 = 3.33$ P = .507

The numbers were small, which probably accounts for the fact that not all expected classes have been detected.

Genotypes $w_5\ w_5$ and $w_6\ w_6$

The origin of stock 11, carrying recessive factors w_5 and w_6, was an ear of dent corn No. 1975–2 taken from the cultures of Doctor ANDERSON.

The data on the progenies of selfed plants which are segregating white seedlings may be found in table 37. In spite of the fact that the numbers are very small, it can be seen that the segregation is very irregular and that probably more than one factor is necessary for the expression of the white phenotype.

Cross between stocks 11 and 3

A cross between stocks 11 and 3 gave the most interesting F_2 data of all the crosses reported in this paper. All plants of the F_1 generation were green. Table 38 presents the F_2 data.

[5] $w_b\ w_c\ w_d$ are symbols used in this chapter only to indicate genes for white seedling from stock 6.

LINKAGE BETWEEN w_5 AND y. The female parent from stock 11 had white endosperm and the male parent from stock 3 had yellow endosperm. The F_2 seed was separated according to the endosperm color, and each class planted separately. From the data in table 38 it may be noted that in certain pedigrees a definite correlation exists between white seedlings and white color of endosperm. The pedigrees which segregate white seedlings in a 3 : 1 ratio are the best to be used for the determination of linkage. The data are given in table 20.

TABLE 20

PEDIGREE NUMBER	*Y W*	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
803–7	86	23	13	18		
–9	164	14	22	36		
Observed	250	37	35	54	376	
Calculated (without linkage)	*211.5*	*70.5*	*70.5*	*23.5*		
Difference	+38.5	−33.5	−35.5	+30.5		$\chi^2=71.5$ $P<10^{-6}$
Calculated (with linkage and 24.3 percent crossing over)	*242.2*	*39.9*	*39.9*	*54*		
Difference	+7.8	−2.9	−4.9	0		$\chi^2=1.065$ $P=.7864$

From the comparison made above it can be seen that when the calculations are made on the basis of a free segregation of factors, the chances are exceedingly low that the observed deviation from expectancy may be due to errors of random sampling. On the contrary, the fit is very close if calculations are made with the assumption of linkage and the conclusion is warranted that the linkage between the factor for white seedling and that for white endosperm exists. From the data obtained the percentage of crossing over is computed by EMERSON'S (1916) formulae to be 24.3.

Since the data in question represents the coupling series it can be seen that the linked factor for white seedling must have come from the female parent which carried the factor for white endosperm.

KEMPTON (1917) made a preliminary report on a case of linkage between white seedling and white endosperm. Intercrosses between his white seedling and the one used in this investigation have not been made as yet. The data presented by KEMPTON, owing to the complexity of the case, were not satisfactory for the calculation of percentage of crossovers, which fact makes an indirect check impossible.

Free segregation between w_7 and y. The recessive gene w_7 was brought into the cross by the male parent. The white seedling, which does not show linkage with white endosperm, and is found in pedigrees which segregate in a 3 : 1 ratio, is determined by w_7. The relation between w_7 and endosperm color may be seen from the following summary of the data (table 21):

Table 21

	Y W	*Y w*	*y W*	*y w*	TOTAL
Observed	328	91	111	25	555
Calculated	*312.75*	*103.75*	*103.75*	*34.75*	
Difference	+15.25	−12.75	+7.25	−9.75	

The fit is fairly close, χ^2 being 5.57 and P = .1376, and the conclusion may be drawn that no close linkage between w_7 and y exists.

A 9 : 1 ratio. From table 38 it can be seen that in three pedigrees white seedlings segregated in almost exactly a 9 : 1 ratio. The repeated occurrence of a ratio very close to 9 : 1 suggests that this ratio could hardly be attributed to deviations from other ratios, due entirely to errors of random sampling. The only simple ratio which is close enough to 9 : 1 to be considered is the 15 : 1 ratio.

The following is a summary of the data of pedigree 801–3, 802–2, and 803–13 which segregated in a 9 : 1 ratio (table 22):

Table 22

SEEDLINGS	*W*	*w*	TOTAL
Observed	409	45	454
Calculated (15 : 1)	*425.6*	*28.4*	
Difference	−16.6±3.48		

The deviation from the expectancy is 4.8 times its probable error, and the chance that the observed difference is due to errors of random sampling is about one in a thousand. The probability is much too low to support the conclusion that in the given case 15 : 1 was the expected ratio.

The 9 : 1 ratio, however, could be a modified 15 : 1 ratio. This modification may be due to linkage of duplicate genes. Coupling between two duplicate genes would tend to make the ratio smaller. The ratio may be modified between the limits of 15 : 1 and 3 : 1 according to the closeness of linkage. On the contrary, repulsion between the two duplicate genes would tend to increase the ratio between the limits of 15 : 1 and 1 : 0.

It is assumed that the 9 : 1 ratio observed in the cross 11×3 is caused by coupling between two duplicate genes with about 36.9 percent of crossing over between them.

LINKAGE WITH ENDOSPERM COLOR. The data from pedigrees which segregate in a 9 : 1 ratio show coupling between white seedling and white endosperm. This linkage relation is a good check of the assumption that linked duplicate genes are involved in the cross.

If the above assumption be correct, then the observed classes are a product of a recombination of three linked genes, i.e., two duplicate genes for white seedling and one for the color of endosperm. If calculations made on that basis agree with the observed data, this is another strong support of the hypothesis.

As shown before, about 24.3 percent of crossovers occur between the gene y for endosperm color and w_5 one of the duplicate genes for white seedling. The percentage of crossovers between w_5 and w_6 is about 36.9. There are two possibilities with respect to the order of these three linked genes. The order may be Y-W_5-W_6 or W_5-Y-W_6. The possibility of its being W_5-W_6-Y is eliminated by the fact that the percentage of crossing over between W_5-W_6 is larger than that between W_5-Y.

To determine which was the probable order of the genes in the given case, both possibilities are tried out in the calculations.

The formulae for the calculation of frequencies of different classes are developed on the same principle as used by EMERSON (1916). They are as follows:

The frequency for the class with:

Yellow endosperm and green seedlings $= 3a^2+4ab+6ac+6ad+6bc+6bd+2b^2+3c^2+6cd+3d^2$

Yellow endosperm and white seedlings $=2ab+b^2$

White endosperm and green seedlings $=2ab+b^2+2ac+2bc+c^2+2ad+2bd+2cd+d^2$

White endosperm and white seedlings $=a^2$

When it is assumed that the order of the genes is Y-W_5-W_6, then,
a stands for the frequency of non-crossovers;
b stands for the frequency of single crossovers in region Y-W_5;
c stands for the frequency of single crossovers in region W_5-W_6;
d stands for the frequency of double crossovers.

The value of d is computed indirectly from the theoretical formula: $\frac{(b+d)\ (c+d)}{100}=d$, the interference not being taken into account.

When it is assumed that the order of the genes is W_5-Y-W_6, then,
a stands for the frequency of non-crossovers;
b stands for the frequency of double crossovers;
c stands for the frequency of single crossovers in region Y-W_6;
d stands for the frequency of single crossovers in region W_5-Y.

Then the values for a, b, c and d are calculated as follows:

$$d+c=36.9$$
$$d+b=24.3$$
$$b=\frac{24.3\times(b+c)}{100}$$

A comparison of the two possibilities is made in (table 23).

TABLE 23

PEDIGREE NUMBER		*Y W*	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
801–3		125	3	13	12		
802–2		125	5	28	12		
803–13		99	4	19	9		
	Observed.............	349	12	60	33	454	
	Calculated (Y-W_5-W_6....	*320*	*19.2*	*88.8*	*26*		
	Difference.............	+29	−7.2	−28.8	+7		$\chi^2=16.56$ P=.000752
	Calculated (W_5-Y-W_6....	*332.5*	*8.1*	*76.5*	*36.9*		
	Difference.............	+16.5	+3.9	−16.5	−3.9		$\chi^2=6.662$ P=.0854

The possibility that the order of the genes was Y-W_5-W_6 is practically eliminated by the very poor fit between observed and calculated data. The chances that the observed deviation is due to the errors of random sampling are about 7.5 in ten thousand.

On the other hand, a satisfactory fit supports the possibility that the order of the genes is W_5-Y-W_6. The fit would be still closer if it were not for the low germination of classes with white endosperm in pedigree No. 801–3. The germination of yellow seeds was 75 percent and white ones 45.5 percent only. This poorer germination of white seed does not appreciably change the ratio between green and white seedlings but makes the classes with white endosperm lower. This is very clearly indicated in deviations from expectancy which are minus for both of the white-endosperm classes. If pedigree No. 801–3 is disregarded and No. 802–2 and No. 803–13 only taken into account, the fit is very close, χ^2 being 3.3057 and P=.3518.

The conclusion that the order of the genes is W_5-Y-W_6 may also be drawn from other evidence. When the observed values for different classes are substituted in the formulae mentioned above, four equations are obtained which can be solved for a, b, c and d. The values obtained in that way are as follows: $a=5.745$, $b=.965$, $c=1.415$, $d=2.375$. The relative values of b and d are of significance for the conclusion. It will be recalled that b stands for double crossovers when the order of the genes is W_5-Y-W_6, and for single crossovers between Y-W_5 when the order is assumed to be Y-W_5-W_6. Similarly, d stands for double crossovers if the order is Y-W_5-W_6 and for single crossovers in the region W_5-Y if the order is W_5-Y-W_6. The relative value of b as obtained by calculation shows that it can be the frequency of double crossovers only, and therefore proves that the order of the genes is W_5-Y-W_6.

Y is about half way between W_5 and W_6. The percentage of crossing over between W_5 and Y is about 24.3 and between Y and W_6 about 24.5. P_l, one of the factors for the plant color, was shown to be linked with Y (EMERSON 1921, ANDERSON 1921). A cross involving all of these four factors should give more satisfactory data on the percentage of crossovers, but as yet it has not been grown.

A 28.6 : 1 RATIO. As shown before in the case of coupling between linked duplicate genes, when the percentage of crossovers is 36.9, the expected ratio of green to white seedlings will be 9 : 1. On the contrary, the expected ratio will be 28.6 : 1 in the case of repulsion between the duplicate genes, with the same percentage of crossing over. Pedigree No. 803–15 segregated in 84 green seedlings and 1 white with a deviation from the 28.6 : 1 ratio of 1.86 ± 1.1. It is not considered, however, that one white seedling is sufficient evidence for a conclusion. It may be only an accident due to error or to some unknown cause. During the work with the other seedling characters in a few instances there were observed single white seedlings in pedigrees which otherwise did not throw white. The probability is very high, however, that the deviation from the expectancy in this case is due to errors of random sampling. The F_3 generation will be necessary for a final conclusion.

A 9 : 7 OR 2.08 : 1 RATIO. From the data which are now available it is not possible to determine exactly into which ratio pedigrees 803–10, 803–17, and 803–18 segregated. There are two ratios possible, i.e., 9 : 7 and 2.08 : 1, the latter being a combination of 3 : 1 and 9 : 1 ratios. They are too close to be distinguished with numbers of individuals obtained hitherto.

A 9 : 7 ratio would occur if the parent plants were homozygous recessive for one of the duplicate genes and heterozygous for the other one and also for w_7. A 2.08 : 1 ratio would result from heterozygosity of all three genes, i.e., w_7, w_5 and w_6. In both cases linkage between white seedling and white endosperm should be evident. The two possibilities are compared in table 24.

TABLE 24

	Y W	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
Observed (803-10, -17, -18)	189	89	37	44	359	
Calculated (9 : 7)	*174*	*96.3*	*28.7*	*60*		
Difference	+15	−7.3	+8.3	−16		χ^2=8.48 P= .0425
Calculated (2.08 : 1)	*194*	*73.6*	*46.4*	*45*		
Difference	−5	+15.4	−9.4	−1		χ^2=5.262 P= .1561

The data of the F_3 generation are needed for a final conclusion.

GENETICAL CONSTITUTION OF F_1 PLANTS. The unknown parts of the genetical constitution of parents may be determined from the frequency of occurrence of the several kinds of F_2 behavior. The most probable constitutions of the parents are:

♀ parent from stock 11 = $y\ y\ W_7\ W_7\ W_5\ w_5\ W_6\ w_6$

♂ parent from stock 3 = $Y\ Y\ W_7\ w_7\ W_5\ W_5\ W_6\ w_6$

A comparison follows (table 25):

TABLE 25

SEGREGATION IN F_2	9 : 7 AND 2.08 : 1	3 : 1 WITHOUT LINKAGE	3 : 1 LINKAGE WITH *y*	9 : 1	28.6 : 1	GREEN
Observed	3	7	2	3	1	3
Calculated	*3*	*6.5*	*1.5*	*1.5*	*.87*	*5.63*
Difference	0	+.5	+.5	+1.5	+.13	−2.63

The fit is very close, χ^2 being 2.949 and P = .708.

SUMMARY OF RESULTS OF THE CROSS 11 AND 3. The F_2 data from the cross of the stocks 11 and 3 indicate the presence of linked duplicate genes. This indication is supported by:

1. The repeated occurrence of segregation in very close to a 9 : 1 ratio, which is assumed to result from coupled duplicate genes when 36.9 percent of crossing over takes place.
2. The occurrence of a 28.5 : 1 ratio, which is supposed to be the result of repulsion between duplicate genes, with 36.9 percent of crossing over. This point, however, has to be tested in the F_3 generation.
3. A satisfactory fit between observed and calculated data, when linkage between duplicate genes is used as a basis for calculations.
4. A very close fit between observed and calculated frequencies of F_1 plants giving the several kinds of segregation in F_2.

For a final conclusion, however, the F_3 data are necessary.

The F_2 data show the existence of linkage between endosperm color and white seedling which is determined by the linked duplicate genes. A reasonable fit between observed and calculated data was obtained when the calculations were made on the assumption that the order of the genes was W_5-Y-W_6, with about 25 percent of crossing over in each region.

It was shown also that white seedlings brought into the cross by different parents were genetically different.

Genotype w_7 w_7

The stock carrying the recessive factor w_7 originated from a selfed ear grown by Doctor D. F. JONES, and sent to Doctor E. G. ANDERSON for a study of its very deep orange endosperm color.

All crosses and selfings made up to this time show that w_7 in homozygous recessive condition is sufficient for the expression of the white phenotype.

Cross between stocks 8 and 3

Table 36 gives the F_2 data from a cross between stocks 8 and 3. From the table it can be noticed that in the pedigrees 800–4, –6, and –13, the deviation from the expectancy is too large to be due to errors of random sampling. It is thought that this large deviation is caused by the fact that in the same pedigrees there was present a weak morphological character called "spear" which made the classification of white seedlings very difficult.

The progenies of the F_1 plants segregated in 15 : 1, 3 : 1, 9 : 7, and 45 : 19 ratios. A 45 : 19 ratio was obtained from No. 805–5, which gave 339 green and 155 white seedlings, with a difference from expectancy of

8.4 ± 6.85. A 45 : 19 ratio is not far from the 3 : 1 ratio. In the present case 31.5 ± 6.49 would be the deviation from expectancy calculated on a 3 : 1 basis. It would mean about one chance in a thousand that the observed deviation was due to random sampling. The fit is much closer if the calculation is made on the basis of a 45 : 19 ratio. In that case the chances are about four in ten that the observed deviation is due to random sampling.

Segregation into a 45 : 19 ratio shows that the selfed plant was heterozygous for three factors determining white seedlings, two of them being duplicate genes.

The frequencies of F_1 plants are as follows (table 26):

TABLE 26

PROGENIES SEGREGATING IN	9 : 7	3 : 1	15 : 1	45 : 19	GREEN
Observed	3	4	1	1	6
Calculated	*3.75*	*3.75*	*1.87*	*1.88*	*3.75*
Difference	−.75	+.25	−.87	−.88	+2.25

$\chi^2 = 2.33$ P = .677.

The expected numbers are calculated with the assumption that the parent plants had the following constitution:

♀ parent from stock 8 = $W_7\ W_7\ W_8\ w_8\ W_9\ w_9$

♂ parent from stock 3 = $W_7\ w_7\ W_8\ w_8\ W_9\ W_9$

or less probably

♀ parent from stock 8 = $W_7\ W_7\ W_8\ w_8\ W_9\ W_9$

♂ parent from stock 3 = $W_7\ w_7\ W_8\ w_8\ W_9\ w_9$

It is believed that one of these assumptions is correct. The F_2 data showed plainly that in the present cross three factors for white seedlings were involved, two of which are duplicate genes. The above parental combinations are the only ones which give in the F_1 generation a satisfactory fit with the data obtained.

Genotypes $w_8\ w_8$ and $w_9\ w_9$

White seedling which is determined by duplicate genes $w_8\ w_9$ was found in the selfed progenies of High Protein Strain of corn obtained from SOUTH DAKOTA EXPERIMENTAL STATION. The data which show the F_2 segregation can be found in table 36, and the discussion of the results is given on pages 582 and 583.

A 63 : 1 ratio

A cross was made between a plant heterozygous for white seedling from stock 5 and a normal green plant. The progeny of two F_1 plants segregated into a 63 : 1 ratio, and the progeny of four other plants were green. The data are given in table 27.

TABLE 27

PEDIGREE NUMBER	W		w
813–7	115		3
–8	147		5
Total	262		8
Calculated	*266.2*		*4.2*
Difference	−3.8	±	1.37

The segregation into the 63 : 1 ratio indicates that three recessive pairs of genes are required for the expression of this white seedling. A 63 : 1 ratio, however, may be a 15 : 1 ratio modified by a repulsion between duplicate genes. The F_3 generation will give the evidence for the final conclusion.

It is not known as yet if this white seedling is genetically different from the one described before, which was shown to be determined by triplicate genes.

SUMMARY

White seedlings, frequently found in the commercial varieties of maize, are determined by many genetically different factors.

The investigation is not as yet sufficiently complete to show how many factors for albinism were present in the material used in the tests. The analysis has advanced far enough to prove the existence of seven different genes for white seedlings, but indications are very strong that there are many more.

Three of these factors are single Mendelian recessives.

Two others are duplicate genes. The progeny of a selfed plant which is heterozygous for both of these genes segregates into a 15 : 1 ratio.

The remaining two factors are also duplicate genes. The indications are strong that they are linked together with about 36.9 percent of crossing over.

Segregation into a 63 : 1 ratio was observed among the progenies of two unrelated stocks. This ratio suggests the existence of triplicate genes.

The relation between these genes and those mentioned above is not known.

It was shown that w_3 is not closely linked with any one of the following: s_h, l_g, d, r and p_r.

Gene w_4 and the factor for white seedling in stock 4 are not closely linked with s_u, y and y_p.

Genes w_5 and w_6 are two duplicate genes linked together. They are also linked with endosperm color. The probable order of the genes is: W_5-Y-W_6, with about 25 percent of crossing over in each region.

Gene w_7 is not linked with y.

Genes w_8 and w_9 are two independent duplicate genes.

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APPENDIX—Tables 28 to 38

TABLE 28

F_2 data from the cross between stocks 3 and 1.

F_1 PEDIGREE NUMBERS	W	w	TOTAL	CALCULATED w	DIFFERENCE
	9 : 7 ratios				
812- 2	187	143	330	144.6	1.6 ± 6.08
- 5	120	105	225	98.4	6.6 ± 5.02
- 8	153	118	271	118.3	.3 ± 5.51
-10	189	124	313	137.0	13.0 ± 5.92
Total	649	490	1139	498.3	8.3 ±11.3
	3 : 1 ratios				
812- 4	282	78	360	90.0	12.0 ± 5.54
- 7	234	82	316	79.0	3.0 ± 5.19
-13	241	66	307	76.75	10.75± 5.12
-14	255	89	344	86.0	3.0 ± 5.42
Total	1012	315	1327	331.75	16.75±10.6
812- 3	Homozygous for green				

TABLE 29

F_2 data from the cross between stocks 6 and 1.

F_1 PEDIGREE NUMBERS	W	w	TOTAL	CALCULATED w	DIFFERENCE
	9 : 7 ratio				
815-7	129	94	223	98.0	4.0 ±5.0
	15 : 1 ratio				
815-6	215	16	231	14.2	1.8 ±2.48
	3 : 1 ratios				
815-2	90	20	110	27.5	7.5 ±3.06
-3	192	40	232	58.0	18.0 ±4.45
-4	88	27	115	28.75	1.75±3.13
-8	84	23	107	26.75	3.75±3.2
815- 5, - 9, -10	Homozygous for green				

TABLE 30

F_2 data of a cross $W_3 W_3 S_h S_h \times W_3 w_3 s_h s_h$.

PEDIGREE NUMBERS		NUMBER OF SEEDS PLANTED			NUMBER OF SEEDLINGS			
					Sh		*sh*	
F_1	Parents	*Sh*	*sh*	Total	*W*	*w*	*W*	*w*
816– 2	345– 7×334–1	191	48	239	140	43	35	6
– 4		217	79	296	160	36	57	10
– 6		226	76	302	160	47	47	23
– 8		163	56	219	112	39	27	16
– 9		157	49	206	94	33	30	13
816– 1	green							
– 5								
– 7								
817– 1	345–17×334–3	97	25	122	61	23	19	3
– 3		130	41	171	95	28	30	7
– 4		131	45	176	78	34	22	14
– 6		159	55	214	112	39	41	11
– 9		159	55	214	121	34	29	18
817– 2	green							
– 5								
– 8								
–10								
–11								
–12								
819– 4	347– 9×334–3	231	79	310	159	70	48	16
– 6		214	84	298	162	47	35	10
– 7		79	23	102	57	12	15	6
–10		231	67	298	165	52	27	13
–11		192	77	269	146	45	49	16
819– 1	green							
– 2								
– 8								
– 9								
–12								
–13								
–14								
Totals		2577	859	3436	1822	582	511	182
					2404		693	

TABLE 31

F_2 data of a cross $R\ l_g\ d\ W_3\ W_3 \times r\ L_g\ D\ W_3\ w_3$.

PEDIGREE NUMBERS	R								r							
	D				d				D				d			
	L_g		l_g		L_g		l_g		L_g		l_g		L_g		l_g	
	W	w	W	w	W	w	W	w	W	w	W	w	W	w	W	w
15- 2	177	48							40	16						
- 3	238	60							76	21						
- 4	127	65							48	8						
- 5	113	24	36	13	27	7	9	8	29	13	18	4	8	5	3	2
- 7	103	26	34	11	31	6	11	3	26	5	13	4	16	2	4	2
-18	126	51	49	21					36	16	17	4				
Total for $R\ r$	884	274	119	45	58	13	20	11	255	79	48	12	24	7	7	4
Total for $D\ d$	216	50	70	24	58	13	20	11	55	18	21	8	24	7	7	4
Total for $L_g\ l_g$	342	101	119	45					91	34	38	12				

TABLE 32

F_2 data from a cross $r\ P_r\ W_3\ w_3 \times R\ p_r\ W_3\ W_3$.

PEDIGREE NUMBERS	R				r		TOTAL
	Pr		pr				
	W	w	W	w	W	w	
13- 3	133	37			46	21	237
- 4	145	45			40	18	248
- 5	160	64			59	20	303
-10	116	35	32	13	49	18	203
-16	91	29	35	11	53	25	244
Total for $R\ r$	645	210	67	24	247	102	1295
Total for $P_r\ p_r$	207	64	67	24			362

TABLE 33

F_2 data from the cross between stocks 2 and 4.

F_1 PEDIGREE NUMBERS	*su*		*Su*						NOT CLASSIFIED		TOTAL		CALCULATED	DIFFERENCE
			Y		*Y_p*		*y+yp*							
	W	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*w*	
	9 : 7 ratios													
332- 2	42	25	90	80	32	14	11	4	34	21	209	144	154.5	10.5 ±6.29
- 4	20	22	50	32	14	9	5	4	30	26	89	67	68.25	1.25±4.18
-12	13	9	60	48	14	13	6	4	24	27	93	74	73.0	1.0 ±4.32
Total.....	75	56	200	160	60	36	22	12	88	74	391	285	295.75	10.75±8.7
	3 : 1 ratios													
332-1	54	17	146	34	35	12	12	3	47	11	294	77	92.75	15.75±5.63
-7	42	16	111	35	30	11	9	2	45	18	237	82	79.75	2.25±5.22
-8	45	13	94	37	24	10	9	2	39	10	211	72	70.75	1.25±4.91
Total.....	141	46	351	106	89	33	30	7	131	39	742	231	243.25	12.25±9.11
	Homozygous for green													
332-5														
-6														
-9														

TABLE 34

F_3 progenies from the cross between stocks 2 and 4.

PEDIGREE NUMBERS F_2	PEDIGREE NUMBERS F_1	W	w	TOTAL	CALCULATED w	DIFFERENCE
I. F_3 progenies from ears segregating in 9 : 7 ratios						
		9 : 7 ratios				
794–3	332– 4	69	50	119	52.1	2.1± 3.65
–5		96	92	188	82.2	9.8± 4.59
–8		16	19	35	15.4	3.6± 1.98
796–1	332–12	157	101	258	112.7	11.7± 5.37
–3		30	24	54	23.7	.3± 2.46
–5		197	126	323	141.3	14.3± 6.01
Total........		565	412	977	427.4	15.4±10.46
		3 : 1 ratios				
794–2	332– 4	176	71	247	61.8	9.2± 4.59
–4		147	43	190	47.5	4.5± 4.03
–6		207	80	287	71.7	8.3± 4.95
–7		66	12	78	19.5	7.5± 2.58
Total........		596	206	802	200.5	5.5± 8.27
	Homozygous for green					
795–10	332– 2					
796– 4	332–12					
II. F_3 progenies from ears segregating in 3 : 1 ratios						
		3 : 1 ratios				
797–4	332– 7	178	66	244	61.0	5.0± 4.56
–5		140	40	180	45.0	5.0± 3.92
–7		69	17	86	21.5	4.5± 2.71
Total........		387	123	510	127.5	4.5± 6.6
	Homozygous for green					
797–1						
–8						
332–7						

TABLE 35

F_2 data from the cross between stocks 6 and 2.

F_1 PEDIGREE NUMBERS	W	w	TOTAL	CALCULATED w	DIFFERENCE
	63 : 1 ratios				
814– 1	83	2	85	1.33	.67± .77
– 9	113	3	116	1.81	1.19± .90
Total.....	196	5	201	3.14	1.86±1.19
	15 : 1 ratios				
814–11	82	6	88	5.5	.5 ±1.53
–12	98	5	103	6.44	1.44±1.66
Total.....	180	11	191	11.94	.94±2.26
	3 : 1 ratios				
814– 8	125	28	153	38.25	10.25±3.61
–14	92	27	119	29.75	2.75±3.19
Total.....	217	55	272	68.00	13.00±4.82
814–13 –15	Homozygous for green				

TABLE 36

F_2 data from a cross between stocks 8 and 3.

F_1 PEDIGREE NUMBERS	W	w	TOTAL	CALCULATED w	DIFFERENCE
	9 : 7 ratios				
800- 4	194	110	304	133.0	23.0 ±5.83
-11	141	87	228	99.75	12.75±5.05
-12	152	97	249	109.0	12.0 ±5.28
	45 : 19 ratio				
800- 5	339	155	494	146.6	8.4 ±6.85
	15 : 1 ratio				
800- 3	183	11	194	12.1	1.1 ±2.27
	3 : 1 ratios				
800- 2	233	70	303	75.8	5.8 ±5.08
- 6	286	59	345	86.2	27.2 ±5.42
- 7	159	44	203	50.7	6.7 ±4.16
-13	274	65	339	84.8	19.8 ±5.38
	Homozygous for green				
800- 1					
- 8					
- 9					
-10					
-15					
-17					

TABLE 37

Showing the segregation in stock 11.

PEDIGREE NUMBERS		SEEDLINGS	
Offspring	Parents	W	w
82-10	A1975- 2	94	14
337- 2	82-10	60	16
- 7		38	5
784- 3	337- 7	9	1
-10		7	3
-11		24	1
-12		29	3
-13		62	3
-16		8	3

TABLE 38

F_2 data from the cross between stocks 11 and 3.

F_1 PEDIGREE NUMBERS	*Y*		*y*		TOTAL			CALCULATED *w*	DIFFERENCE
	W	*w*	*W*	*w*	*W*	*w*	Total		
	3 : 1 ratios. Linkage between *y* and *w*								
803– 7	86	23	13	18	99	41	140	35	6.00±3.46
– 9	164	14	22	36	186	50	236	59	9.00±4.49
Total.....	250	37	35	54	285	91	376	94	3.00±5.66
	3 : 1 ratios; no linkage between *y* and *w*								
802– 1	36	15	11	4	47	19	66	16.50	2.5 ±2.37
803– 3	43	7	12	3	55	10	65	16.25	6.25±2.35
– 4	10	3	3	1	13	4	17	4.25	.25±1.20
– 5	24	9	10	2	34	11	45	11.25	.25±1.96
–11	96	23	34	7	130	30	160	40.00	10.0 ±3.69
–12	71	12	19	5	90	17	107	26.75	9.75±3.02
–16	48	22	22	3	70	25	95	23.75	1.25±2.85
Total.....	328	91	111	25	439	116	555	138.75	22.75±6.88
	9 : 1 ratios								
801– 3	125	3	13	12	138	15	153	9.2 : 1	(Observed ratio)
802– 2	125	5	28	12	153	17	170	9.0 : 1	(Observed ratio)
803–13	99	4	19	9	118	13	131	9.07 : 1	(Observed ratio)
Total.....	349	12	60	33	409	45	454		
	9 : 7 or 2.08 : 1 ratios								
803–10	47	20	8	15	55	35	90	9 : 7	6.4 ±3.17
								2.08 : 1	3.8 ±3.06
–17	51	31	15	7	66	38	104	9 : 7	7.5 ±3.41
								2.08 : 1	4.2 ±3.3
–18	91	38	14	22	105	60	165	9 : 7	12.2 ±4.3
								2.08 : 1	6.4 ±4.18
Total.....	189	89	37	44	226	133	359		
	28.59 : 1 ratio								
803–15	78	..	6	1	84	1	85	2.86	1.86±1.1
	Homozygous for green								
803– 6									
– 8									
–14									