MATERNAL INHERITANCE IN BARLEY

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INTRODUCTION

TWO types of inheritance, Mendelian and non-Mendelian, have been described by various workers. The majority of cases of non-Mendelian inheritance described in higher plants have dealt with variegation of one type or another. In the monocotyledons, several workers have described the occurrence of non-Mendelian inheritance in striped plants of Zea, Avena, Hordeum, Oryza and Sorghum. The present paper deals with the occurrence of maternal inheritance in a chlorina (solid color) plant obtained from Coast barley (*Hordeum vulgare*).

LITERATURE REVIEW

CHITTENDEN (1927), DEMEREC (1927), and SHARP (1934) have reviewed the work of CORRENS, BAUR and SHULL on maternal inheritance of variegation in Mirabilis, Antirrhinum and Melandrium and discuss the various theories offered to explain the phenomena. DEMEREC (1927) describes a case of maternal inheritance in maize. In his experiment, variegation (striping) was inherited only through the female gametes and the male gametes had no influence either in its transmission or its expression. All attempts made to transmit the variegation asexually were unsuccessful. He assumes that the variegation is determined by a dominant mutable gene which has a highly increased frequency of mutation when it comes in contact with other than the parent cytoplasm. Striping of the leaves, similar to the cases above, has been discussed by ANDERSON (1923) in maize, ROBB (1934) in oats, IMAI (1928) in barley and rice, KARPER and CONNER (1931) in sorghum. RHOADES (1933) found a type of male sterility which was inherited maternally. Male sterile plants were crossed to normal linkage testers having several genes located at various distances apart on the chromosomes. The F_1 plants were crossed on plants bearing all of the factors under test in the recessive condition. The backcross data were analyzed for the characters and their relationship to male sterility. The results indicate that the genetic complex plays no part in the expression of the male sterile character. In his summary, he states that there was no indication of male sterility being caused by a virus disease.

MATERIAL AND METHODS

Coast V was selected in a plot of normal Coast barley in 1926. The plant is chlorophyll deficient, the seedling color being "absinthe green." (Plate 31, RIDGEWAY 1912.)

The color of normal Coast seedlings is "cress green." (Plate 31, RIDGEWAY.) The color in Coast V remains constant until after heading when it darkens before ripening. The plants are slightly smaller than the normal Coast plants.

Several chlorophyll deficient "chlorina" plants have been previously described by ROBERTSON (1932 and 1933) and NILSSON-EHLE (1922). Their behavior when crossed with normal green plants has shown them to be normal Mendelian recessives. For this reason, no particular attention was paid to Coast V until it was found that reciprocal crosses did not behave according to simple Mendelian expectancy.

In order to determine if the Coast V plants were homozygous chlorinas, reciprocal crosses were made in which the same plants were used as male parents and as female parents, respectively.

RESULTS

TABLE 1

Results of reciprocal crosses in which both plants were used as male and female parents.

CROSS NO.	FEMALE PARENT	MALE PARENT	COLOR OF F_1 PLANT	NO. SEEDS SET
II-31-141	Coast V	28–3398	Chlorina	6 seeds
II-31-144	28–3398	Coast V	Green	4 seeds
II-31-142	Coast V	28–3398	Chlorina	7 seeds
II-31-145	28–3398	Coast V	Green	5 seeds
II-31-143	Coast V	28–3398	Chlorina	10 seeds
II-31-146	28–3398	Coast V	Green	18 seeds
II-31-147	Coast V	Colsess V	Chlorina	3 seeds
II-31-150	Colsess V	Coast V	Green	3 seeds

Description of F_1 plants

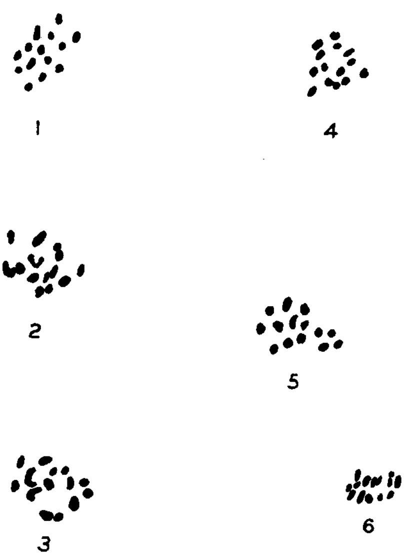
The F_1 plants of crosses No. 141, 144, 142, 145, 143 and 146 were rough-awned six-rowed, covered, and had long-haired rachillas.

The female parent (Coast V) in crosses No. 141, 142, and 143 has a short-haired rachilla, so that if the offspring were hybrids they should have had long-haired rachillas. The female parent (28–3398) in crosses No. 144, 145, and 146 had smooth awns. The F_1 from the crosses should have had rough awns. The data show clearly that the F_1 plants were hybrids and were not the result of self-pollination.

The F_1 plants of cross 147 were hooded, indicating that they were hybrids. Cross 150 could not be determined in F_1 since all of the dominant characters are found in the Colsess parent. However, Colsess V is described by ROBERTSON and DEMING (1930) as a dull green-yellow. Since the F_1 was normal green, evidently the factor for green was carried over from the Coast V parent.

Pedigreed cultures

Pedigreed cultures of Coast V were grown for eight generations and no normal green plants have been found. The pedigreed cultures were made



FIGURES—1, 2 and 3 are from normal green plants.

FIGURES—4, 5 and 6 are from chlorina plants.

by selecting individual plants from Coast V rows each year. Reselections of this type have been made for eight generations.

Backcross

In order to determine if the chlorina color could be affected by continued doses of normal green genes, backcrosses to normal green plants were started in 1933. The following family histories of the backcrosses are given.

Coast V (chlorina) was crossed with normal green Coast III in 1933. The F_1 plants were crossed to *H. def. nudideficiens* in 1934. The double cross was again crossed to *H. def. nudideficiens* in 1935. The progeny of the 1935 cross were chlorina in color in 1936.

A similar condition was found when *H. dis. nigrinudum* was used as the male parent in place of *H. def. nudideficiens*. The progeny from the *nigrinudum* crosses were high fertility intermediate, awned, black glumed and covered with short-haired rachillas, showing clearly that the plants were hybrids. The *H. dis. nigrinudum* parent is two-rowed, awned, and black glumed, with a naked caryopsis and short-haired rachilla.

When Minnesota 72–8, a six-rowed, white glumed, awned plant with a covered caryopsis and long-haired rachilla was used as the male parent, the F_1 plants were six-rowed, white glumed, covered with long-haired rachillas; again indicating a hybrid. The third backcross to green has not developed far enough to describe plant characters, but, as has been stated already, it is still chlorina in color.

Inoculation studies

In order to determine if a virus disease might be the cause of the chlorina condition in the Coast V female parent, inoculations were made by applying sap obtained by grinding plants of Coast V to lacerations on normal green plants in the greenhouse. All of the normal green plants remained normal, and seedlings from the seed of these plants were normal green in the field in the spring of 1936. The results indicate that evidently the chlorina condition is not due to a virus disease which is easily transmitted to other barley plants.

*Chromosome counts**

Root tips from both Coast V and normal Coast plants were fixed in formaline-acetic alcohol and carried through in the customary manner. The sections were stained with Heidenhain's iron-alum haematoxylin or safranin-light green. Several slides of each type were examined and camera-lucida drawings of typical cells from both Coast V (chlorina) plants and normal green Coast III plants were made. The cells showed fourteen chromosomes in each case indicating no abnormalities in chromosome numbers. (Figs. 1–6.)

THE REACTION OF FACTOR PAIRS IN THE VARIOUS LINKAGE GROUPS TO CHLORINA AND NORMAL GREEN PLANT COLOR

Coast V was crossed with various barleys to test the possibility of linkage of the chlorina character with other characters which have been located in different linkage groups. The following characters were used:

* Dr. L. R. Bryant kindly supervised the preparation of the stained material.

GROUP	CHARACTER PAIR	FACTOR PAIRS
I	6-row vs. non-6-row	*Vv*
	Chlorina vs. normal plant color (Minn. 84–7)	*Ff*
II	Black vs. white glume color	*Bb*
III	Covered vs. naked caryopsis	*Nn*
IV	Hoods vs. awns	*Kk*
	Intermedium vs. non-intermedium	*Ii*
V	Rough vs. smooth awn	*Rr*
	Long vs. short-haired rachillas	*Ss*
VI	Green vs. white seedlings (Colsess I)	A_ca_c
VII	Green vs. chlorina seedlings (Colsess V)	F_cf_c
	Green vs. virescent seedlings (Coast III)	Y_cy_c

Group I. The factor pair *Vv* for 6-row vs. non-6-row is linked with *Ff* (green vs. chlorina seedlings) in Minnesota 84–7. The progeny of both F_1 chlorina and F_1 green plants from Coast V crosses were tested for the segregation of *Vv* and *Ff*. The results are given in table 2. The numbers of plants segregating in the dominant and in the recessive classes are given in the columns headed A and a. Table 3 gives the number of plants in the dif-

TABLE 2

Segregation of factor pairs in crosses in which Coast V was used as both male and female parent.

CROSS	FACTOR PAIR	GROUP	PLANT COLOR F_1	A*	a	D/PE
Coast V×Minn. 84–7	*Ff*	I	Chlorina	3880	1380	3.06
Minn. 84–7×Coast V	*Ff*	I	Green	4823	1454	4.98
Coast V×*H. dis. nigrinudum*	*Bb*	II	Chlorina	1756	624	2.04
H. dis. nigrinudum×Coast V	*Bb*	II	Green	1076	354	0.32
Coast V×*H. dis. nigrinudum*	*Nn*	III	Chlorina	1775	605	0.70
H. dis. nigrinudum×Coast V	*Nn*	III	Green	1071	359	0.14
Coast V×Colsess	*Kk*	IV	Chlorina	402	141	0.77
Colsess×Coast V	*Kk*	IV	Green	661	208	1.07
Coast V×Smyrna I	*Ss*	V	Chlorina	400	117	1.84
Coast V×Minn. 84–7	*Ss*	V	Chlorina	412	150	1.37
Smyrna I×Coast V	*Ss*	V	Green	852	269	1.15
Minn. 84–7×Coast V	*Ss*	V	Green	510	166	0.39
Coast V×28–3398	*Rr*	V	Chlorina	404	129	0.63
28–3398×Coast V	*Rr*	V	Green	354	114	0.47
Coast V×Colsess I	A_ca_c	VI	Chlorina	369	111	1.41
Colsess I×Coast V	A_ca_c	VI	Green	358	101	2.20
Colsess V×Coast V	F_cf_c	VII	Green	605	209	0.66
Coast III×Coast V	Y_cy_c	VII	Green	1272	395	1.85

* A—indicates the dominant classes; a—the recessive.

ferent genotypes as determined by F_3 segregations of the different F_2 plants. Column AA gives the double dominants, Aa the heterozygous dominants, and aa the double recessives.

The F_2 segregation of the factor pair *Ff* for green or chlorina seedlings gives a poor fit to a 3 to 1 ratio in the green families. However, the genetic constitution as determined from F_3 seedling counts in both cases is good. The number of chlorina plants is low in the green families.

The segregation of *Vv* for 6-row or non-6-row indicates a normal 1:2:1 ratio, found when incomplete dominance allows one to distinguish the (AA) and (Aa) classes.

TABLE 3

Number of F_2 plants of different genotypes as determined by F_3 segregations.

CROSS	FACTOR PAIRS	GROUP	PLANT COLOR F_1 AND F_2	AA	Aa	aa	χ^2	P
Coast V×Minn. 84–7	*Ff*	I	Chlorina	96	192	113	2.1620	0.3444
Minn. 84–7×Coast V	*Ff*	I	Green	99	196	83	1.8731	0.3982
Coast V×*H. dis. nigrinudum*	*Vv*	I	Chlorina	598	1192	590	0.0607	Large
H. dis. nigrinudum×Coast V	*Vv*	I	Green	347	745	338	2.6307	0.2766
Coast V×*H. dis. nigrinudum*	*Bb*	II	Chlorina	248	476	260	1.3333	0.5270
Coast V×*H. dis. nigrinudum*	*Nn*	III	Chlorina	233	489	262	1.7460	0.4285
Coast V×Colsess	*Kk*	IV	Chlorina	113	282	139	4.2172	0.1238
Colsess×Coast V	*Kk*	IV	Green	209	449	208	1.1847	0.5625
Coast V×*H. dis. nigrinudum*	*Ii*	IV	Chlorina	88	155	101	4.3430	0.1171
H. dis. nigrinudum×Coast V	*Ii*	IV	Green	190	364	214	3.5833	0.1719
Coast V×Colsess I	A_ca_c	VI	Chlorina	80	176	83	0.5516	V. large
Colsess I×Coast V	A_ca_c	VI	Green	128	230	101	3.0611	0.2177
Coast III×Coast V	Y_cy_c	VII	Green	354	619	326	4.0716	0.1315

A further test was made in the families involving crosses between Coast V and Minnesota 84–7. Coast V is chlorina and 6-rowed and evidently carries *FF* for green which is suppressed by the maternal chlorina condition. Minnesota 84–7 is 2-rowed and carries *ff* for chlorina.

The segregations of *Ff* and *Vv* are given in table 4 for the chlorina families obtained when Coast V is used as the female parent.

The data in both the chlorina and green F_2 families show linkage values of 36.31 ± 0.85 and 38.57 ± 1.005, respectively. The probable error of the difference is 1.32 percent, indicating it is probably not significant. However, the percentages are significantly higher than previous determinations, ROBERTSON et al (1932). Since the linkage values in both green and chlorina families are similar, there is evidently no differential influence of the green or chlorina condition in the families studied.

Group II. The factor pair (*Bb*) for black versus white glume color is located in Group II. This is linked with $A_t a_t$ (green versus white seedlings) in Trebi I. Several crosses were made in which Coast V was crossed with varieties having black glumes. The segregations of the F_2 families having all the plants chlorina in color and in F_2 families having all of the plants normal green in color are given in tables 2 and 3.

The segregation of black versus white glume color fits the calculated 3:1 ratio very well in both the pure chlorina families and the normal green families.

The F_2 genotypes as determined from the F_3 segregations, table 3, again indicate a normal 1:2:1 ratio in the chlorina families.

TABLE 4

Linkage relationship of Vv and Ff in families from F_1 chlorina plants.

	COAST V CHLORINA		MINN. 84-7 CHLORINA		χ^2	P
	NON-2-ROW	2-ROW	NON-2-ROW	2-ROW		
Observed	1504	388	358	255		
Calculated 9:3:3:1	1409.06	469.69	469.69	156.56	109.06	V. small
Calculated 36.31% crossing over	1506.51	372.24	372.24	254.01	1.2201	0.7509

Group III. The factor pair *Nn* (covered versus naked caryopsis) has been placed in Group III. Crosses involving *Nn* were made with Coast V which has a covered caryopsis. The F_2 segregations for normal green families and chlorina families are given in table 2. The F_2 and F_3 behavior of the chlorina families indicates that the segregation is similar to that found in green plants of the reciprocal cross.

Group IV. In Group IV are *Kk* (hoods versus awns) and *Ii* (non-intermedium versus intermedium). Both factors unfortunately were not located in a single parent used in the studies. The results of crossing Coast (awned) with Colsess (hooded) are given in table 2. The data show that the segregation is similar in both chlorina and green families indicating that there is no influence of the Coast chlorina on *Kk*.

The genetic constitution of the F_2 plants in chlorina or green families segregating for *Ii* was determined by the segregation of the F_3 families, table 3. The number of plants of the different genetic constitution again indicates independent inheritance. The factor pairs *Kk* and *Ii* have previously been shown to be linked with about 15.12 ± 0.65 percent crossing over (ROBERTSON 1933).

Group V. The factor pairs *Ss* and *Rr* from short versus long haired rachilla and rough versus smooth awns are in Group V. The behavior of *Ss* was studied in crosses with Coast V which has a short-haired rachilla. The F_2 segregation again shows a 3:1 segregation in both chlorina and green families, indicating that *Ss* reacts independently of the chlorina condition found in Coast V. The behavior of the main factor pair *Rr* for rough versus smooth awn is given in table 2. The segregation of *Rr* also indicated no interaction with the chlorina condition.

Group VI. This group contains $A_c a_c$ (green versus white seedlings) in Colsess I. The segregation of $A_c a_c$ is given for both chlorina and green families. The data presented in tables 2 and 3 again show a similar segregation for $A_c a_c$ in both green and chlorina families.

Group VII. Group VII contains $F_c f_c$ (green versus chlorina seedlings) in Colsess V and $Y_c y_c$ (green versus virescent seedlings) in Coast III. The segregation of $F_c f_c$ is given in table 2. The reciprocal cross was chlorina in

TABLE 5

Linkage relationship of Vv and Ff in F_2 families from F_1 normal green plants.

	GREEN		MINN. 84-7 CHLORINA		χ^2	P
	NON-2-ROW	2-ROW	NON-2-ROW	2-ROW		
Observed	1178	291	273	156		
Calculated 9:3:3:1	1067.6	355.9	355.9	118.6	54.36	V. small
Calculated 38.57% crossing over	1128.08	294.42	295.42	179.08	6.9513	0.0738

F_1, but too small a number survived to make counts in F_2. The F_2 segregation in the green families shows no abnormal behavior of $F_c f_c$ in a cross where Coast V was used as the male parent.

In the studies involving $Y_c y_c$, Coast V was again used as the male parent. Since the characters, with the exception of plant color, are the same, it is necessary to check the possibility of self-fertilization taking place. If self-fertilization had taken place, one out of four F_1 plants should be virescent, and one pure green. The other two would segregate for green and virescent in F_2. If they were crossed with Coast V, which carries the $Y_c y_c$, half of the plants should be pure green and half should segregate for green and virescent in F_2. Out of eight families, none were virescent in F_1 and four segregated for green and virescent in F_2.

When Coast III was crossed with Coast V (chlorina) a normal 3:1 segregation was obtained in the green families. The F_3 data also indicated a single factor pair responsible for green versus virescent in Coast III.

DISCUSSION

Maternal inheritance in striped plants has been noted in several of the cereals. Maternal inheritance of solid plant color, however, seems to be of rarer occurrence. A chlorophyll deficient plant with very light green color was found in Coast barley and has been described as Coast V chlorina. This plant color is transmitted through the female parent and not through the pollen.

The possibility of a virus disease was considered and inoculation tests with juice extracted from chlorina seedlings were made on normal plants. No change was noted on the plants or on their progeny, indicating that the chlorina condition was not easily transmitted to normal plants. Many chlorophyll deficiencies of varying shades of green are more or less common in barley. Three of these, at least, are inherited as simple Mendelian recessives.

Unfortunately, only a few factor pairs have been located in the various linkage groups in barley, and the reaction of at least one factor pair in each linkage group to the Coast V chlorina condition was studied. The tests made indicate that the factor pairs studied reacted independently of the chlorina condition. A greater number of factor pairs would add to the value of the data, but the results obtained clearly show that Coast V chlorina is not a simple Mendelian character and that some other explanation is necessary to explain its behavior.

The results indicate that it is maternal and evidently of a similar type to that described by DEMEREC (1927) and by RHOADES (1933) in maize.

SUMMARY

Coast V is a pale green chlorophyll deficient plant. The chlorina color is Ridgeway's "absinthe green."

When Coast V is used as a female parent in crosses with other barleys the F_1, F_2 and F_3 are all chlorophyll deficient like the Coast V parent, indicating maternal inheritance of the chlorina plant color.

In crosses in which Coast V is used as the male parent, the F_1 is normal green in color. In later generations the Coast V chlorina color does not appear or segregate out when Coast V is used as the male parent. This indicates that the pollen does not carry a factor for Coast V chlorina.

Factor pairs located in all of the seven linkage groups gave simple Mendelian segregations in both chlorina (Coast V) and normal green families (reciprocal crosses).

Three generations of backcrossing to normal green did not change the Coast V parental color.

Inoculation tests with extracts from Coast V chlorina seedlings had no apparent effect on the color of normal plants.

Pedigree breeding has shown the Coast V chlorina to be constant for eight generations.

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