# LINKAGE STUDIES IN BARLEY[1]

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Received May 1, 1928

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[1] A thesis presented to the faculty of the Graduate School of the UNIVERSITY OF MINNESOTA in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The writer wishes to express his appreciation to Dr. H. K. HAYES, Professor of Plant Genetics, UNIVERSITY OF MINNESOTA, under whose direction these investigations were conducted, for his many valuable suggestions. The writer is also indebted to F. J. STEVENSON, Assistant Professor of Plant Genetics, UNIVERSITY OF MINNESOTA, for helpful criticisms of the manuscript.

Practically all of the data have been obtained at the COLORADO AGRICULTURAL EXPERIMENT STATION at Fort Collins. The writer wishes to gratefully acknowledge the cooperation of Director C. P. GILLETTE and Professor ALVIN KEZER in providing facilities for this investigation. The writer is also indebted to G. W. DEMING for assistance in collecting data.



Second Printing 1968 / University of Texas Printing Division, Austin

## INTRODUCTION

The present conception of the chromosome theory of heredity is that the genes are arranged in a stable, orderly, linear manner in the chromosome; that genes in separate chromosome pairs are inherited independently and that there is the same number of groups of linked genetic factors as homologous pairs of chromosomes. The degree of linkage is in general considered to be correlated directly with the distance apart of the factors in the chromosome. *Drosophila melanogaster* has four pairs of chromosomes and some 400 factors have been located in them. Maize which has been studied more extensively than any other cereal crop has more than 35 factors located in eight of the ten pairs of chromosomes. With other cereal crops only a few isolated groups have been observed. There are a considerable number of easily distinguishable character pairs in cultivated barley and only 7 pairs of chromosomes. Barley can be grown satisfactorily under many different environmental conditions and for these reasons it appears desirable to use this organism in studies of linkage relations.

Arrangements have been made whereby the Minnesota, Colorado and Oklahoma stations are cooperating in studying linkage relations in barley. The present paper is a report of studies conducted in Colorado.

## REVIEW OF LITERATURE

A fairly extensive review of the published papers on linkage relations in barley was made by GRIFFEE (1925) and only those papers which have a direct bearing on the present studies are reviewed.

### *Chlorophyll Deficiencies*

An albino seedling is reported by WIEBE (1924) which was found in the $F_3$ head row of a cross between Nepal and a many noded dwarf. From later studies it was concluded that this Albino was due to a single recessive factor. NILSSON-EHLE (1922) describes six chlorophyll mutations. Albino Nos. 1 and 3 occurred in six rowed barleys and Albino No. 2 in a two rowed variety. Yellow No. 1 was found in a six rowed barley and Yellow No. 2 in a two rowed form. Chlorina, a pale green chlorophyll dificient type, occurred in Gold, a two rowed barley. All of the whites are recessive to green and the progeny of the selfed heterozygous green plants segregated in a simple Mendelian ratio of 3 green seedlings to 1 white. A linkage was found between Albino 3 and Chlorina. All of the other chlorophyll deficiencies were found to be independently inherited.

HALLQVIST (1926) made crosses between the following chlorophyll deficiencies: Albino 1, Albino 2, Albino 4, Xantha 1, Xantha 2, Chlorina, Superchlorina, Virescent 1, Virescent 3, Lutescens 1, and the abnormalities Dwarf and Linearis. Forty-two out of 78 possible combinations were made. In crosses involving different albinos a ratio of green to albino of 9 to 7 was obtained and in a cross between a virescent and a xantha; green, xantha, and virescent seedlings occurred in a ratio of 9:3:4. In crosses in which Dwarf 1 was used a deficiency in the number of Dwarfs was found. This was explained by the fact that the Dwarf gametes in fertilization take part in fewer numbers than the normal gametes. In one combination the obtained ratio comes very close to the calculated with a deficit of 28 percent in the Dwarf gametes. The linkage of Albino 3 and Chlorina, found by NILSSON-EHLE, was confirmed and a linkage of Albino 4 with Albino 3 and Chlorina was found. The crossover percentages were found to be 10.2 for Albino 3 and Chlorina, 3.8 between Chlorina and Albino 4 and 12.5 between Albino 3 and Albino 4. The same author (1923) observed the effect of different temperatures on the development of chlorophyll in a yellowish white seedling. At a temperature of about 5°C no chlorophyll was developed. At a temperature between 12°–15°C, the seedlings produced chlorophyll in the tips of the leaf. After several days the chlorophyll deficient seedlings died. In temperatures of about 20°C, the lack of chlorophyll could not be detected in the young seedlings. The plants that developed past the seedling stage presented a somewhat stunted appearance. In some cases ears were formed but in many cases these were abnormal.

COLLINS (1927) describes an albino which can be differentiated at temperatures lower than 45°F. When grown at temperatures above 65°F, no albino plants develop. A single recessive gene is responsible for this chlorophyll deficient type. The $F_2$ segregation from the cross six rowed albino × two rowed non-albino shows independent inheritance for the factor pairs concerned.

*Inheritance of other characters*

HAYES and GARBER (1927) summarize the literature on inheritance of the lateral florets as follows: "Two general results have been obtained from crossing two and six-rowed varieties. The most frequent result is an intermediate condition in the $F_1$ in which the lateral florets are awned, but produce little or no fruitfulness. In $F_2$ a 1:2:1 ratio of six-rowed, intermediate, and two-rowed forms are obtained. Six- and two-rowed forms breed true to these respective characters in later generations. Results of this nature can easily be explained on a single main factor difference. A cooperative study carried on at the MINNESOTA EXPERIMENT STATION has shown the probable origin of some *intermedium* forms. In a cross between Manchuria, a six-rowed barley, and Svanhals, a two-rowed variety, the $F_1$ was slightly fruitful and produced intermediate awns on the lateral florets. In $F_2$ a wide range of forms was obtained. The genetic nature of the $F_2$ plants was determined by growing seed of each in $F_3$. From the $F_3$ results it was possible to classify $F_2$ plants as follows:

1. Those that bred true for the six-rowed character.
2. Those that segregated, giving six-rowed, awned intermediate forms with very high fruitfulness of the lateral florets and *intermedium* forms in a 1:2:1 ratio.
3. *Intermedium* forms that bred true, giving few or no awns on the lateral florets and producing approximately 50 percent of barren lateral florets.
4. Those that gave all forms as in $F_2$.
5. Those that produced intermediates and two-rowed types.
6. Those that produced six-rowed, awned intermediates with little or no fruitfulness in the lateral florets and two-rowed forms in a 1:2:1 ratio.
7. Those that bred true for the two-rowed condition.

Results were explained by considering the Manchuria parent to contain two factors, one for six-rowed and one for *intermedium*, which was hypostatic to the six-rowed factor. It was thought possible that minor modifying factors were sometimes present which influenced the degree of fruitfulness of the lateral florets. Crosses between *intermedium* and six-rowed forms gave intermediates of high fruitfulness in $F_1$ and a ratio in $F_2$ which indicate a single factor difference. *Intermedium* forms crossed with two-rowed, gave awnless forms with very low fruitfulness in $F_1$ and a ratio indicating one main factor difference in $F_2$.

In a cross of *Hordeum deficiens steudelii*×Manchuria, GRIFFEE (1925) reports a single factor difference for six-rowed and *deficiens*. In another cross between Svanhals and Lion two main factor pairs were found to be responsible for fertility of the lateral florets. The conclusion was reached that the *intermedium* factor may be carried by a six-rowed variety and that the presence of this factor does not modify the expression of the factor for the six-rowed condition. Two-rowed lacks the factors for intermedium and six-rowed. Apparently the factor pairs which differentiate six-rowed *versus* two-rowed and *intermedium versus* two-rowed are independently inherited.

In a contribution to the genetics and the morphology of barley, VEIDEMAN (1927) states: "The cause of sterility or fertility of the lateral spikelets of barley lies not in the presence or absence of reproductive organs in the lateral florets, as commonly thought but in the structure of the pedicel of the lateral florets, typical for each variety. The longer and narrower the pedicel, the feebler is the development of the lateral spikelet, and the reverse. Thus the fertility is not an independent hereditary character but the physiological results of the anatomical structure and the function of the pedicel. To put it differently: there exists no "gene for fertility."

HOR (1924) concludes that deficiens, distichon and vulgare are multiple allelomorphs. TEDIN and TEDIN (1926) in discussing the type of spike in a cross between a six rowed and a two rowed barley, suggest that the lateral florets with rounded tips be classified as two rowed. Such two rowed plants may produce somewhat inflated lateral florets, but these never bear kernels. Such types breed true for the two rowed condition. When the palea was more or less pointed the plant was classified as heterozygous and has always proved to be heterozygous by the breeding test. In $F_3$ there are three distinct groups of families, namely, constant six-rowed or two-rowed and families segregating for all three types; no families segregating in typical two-rowed and *intermedium* were observed. Their *intermedium* is similar to the intermediate of HAYES and GARBER (1927).

HAYES and GARBER (1927) list the following characters as being dependent upon single factor differences: Hooded *versus* awned, rough *versus* smoth awn, black palea *versus* colorless, purple palea *versus* colorless, hulled *versus* naked, and black pericarp *versus* white pericarp.

GRIFFEE (1925) found that the characters early heading *versus* late heading and intermediate smooth *versus* smooth awn depend upon single factor differences. HOR (1924) decided that long haired rachilla and short haired rachilla differ by a single genetic factor.

*Linkage relations*

Several linkage studies have been reported recently in barley and various conflicting results obtained. HAYES and GARBER (1927) give a rather extensive summary of the published data. GRIFFEE (1925) found that resistance and susceptibility to *Helminthosporium sativum* are definitely inherited. By correlating the reaction of $F_3$ lines to this pathogen in relation to other characters in $F_2$ the inerfence is drawn that at least three factors or groups of factors are concerned in the production of resistance of the type possessed by Svanhals. One factor or group of factors for reaction to *Helminthosporium sativum* was linked with the factor for two rowed, one with the factor for rough awn, and one with the factor for white glumes.

The factor for early heading was found to be linked with the factor for six-rowed. The linkage intensity was very low, the crossover value being 42 percent. The linkage for susceptibility to *Helminthosporium sativum* with the factor for earliness is much more intense than that with the factor for six-rowed or else earliness in itself predisposes the plant to attacks by the pathogen. From the results of the studies, four linkage groups have been established. HOR (1924) found that the long and short haired rachilla factors are independent of the allelomorphic series for fertility of the lateral florets and hairiness of the rachilla and hulled *versus* hullless were inherited independently of each other. A linkage is shown between factors for hairy glume and naked and hulled seeds. The percentage of crossing over is calculated as $25.32 \pm 1.73$. He also concludes that the factors for black versus white glume, rough versus smooth awn, and long versus short haired rachilla are in one group. Too small a number of individuals were studied in each case to be certain of his conclusions. NEATBY (1926) concludes from studies made on quantitative characters that maturity, height and density are not very closely linked with the factor pair which differentiates two- *versus* six-rowed. TEDIN and TEDIN (1926) found a correlation between the height of plant and the two-rowed type. The two-rowed segregates from a cross between six-rowed and two-rowed were, on the average, 10 cm taller than the six-rowed type. They conclude that this correlation most likely is due to linkage between the factor for two rowedness and a plant height factor.

In a more recent paper (1927) the same authors, in a study of development of the kernel basis and its relation to density, referred to three types of bases: vernum, with a transversal nick; falsum, without a nick, but with the dorsal side bevelled; spurium, without both the nick and the bevelling. The lax-eared nutens as well as the corresponding variety with fertile lateral florets, vulgare, always belong to the falsum type. The dense-eared erectum, as well as the extremely dense-eared zeocriton and the correspondingly dense-eared six-rowed variety hexastichum were all either vernum or spurium. They found that two complementary factors $E_{r1}$ and $E_{r2}$ are necessary for the development of the falsum-basis whereas the vernum basis may develop from $E_{r_1}E_{r_1}e_{r_2}e_{r_2}$, $e_{r_1}e_{r_1}E_{r_2}E_{r_2}$ or $e_{r_1}e_{r_1}e_{r_2}e_{r_2}$. They say in conclusion "In spite of the fact that conclusive proof cannot be given, we consider it highly probable, that $E_{r_1}$ and $E_{r_2}$ are linked with one another, with a crossing over between 33 and 40 percent."

## MATERIAL AND METHODS

This paper presents a study of the inheritance of simple Mendelian factor pairs and their possible linkage relations with particular attention to the linkage of certain chlorophyll deficiencies. The following varieties have been used in crosses: Colsess, Trebi, *H. distichon nigrinudum*, Minnesota Selection 90–5, Minnesota Selection 90–8, and *H. deficiens nudideficiens*.

### *Description of parents*

#### Colsess

This is a six-rowed, hooded barley with a hulled grain of a bluish green color. The straw and glume color is light yellow. The shank of the hood is about 5 mm long and is barbed at the base. The rachis is rather tough and the head does not shatter easily. The rachilla hairs are short and the outer glume is covered with very short hairs.

#### Trebi

Trebi is described by HARLAN, MARTINI, and POPE (1925) as a pure line selection made in 1907 in the cooperative breeding experiments conducted by the U. S. DEPARTMENT OF AGRICULTURE and the MINNESOTA AGRICULTURAL EXPERIMENT STATION at St. Paul, Minn. It is a six-rowed, bearded, hulled barley with heads very similar to those of Coast. Under Colorado conditions (irrigated) the kernels are large and bluish in color. The straw is weak. In threshing the awns break off from the glume more easily than those of the Coast variety.

### *Hordeum distichon nigrinudum* (HARLAN 1918)

This is an awned, two-rowed barley, with a hullless black grain and black glumes. The naked seeds have a charred appearance. The straw color is purple which is most marked in the sheath of the leaves of the upper node. The rachilla hairs are short.

### Minnesota Selection 90–5

This is a two-rowed barley of the distichon type. It has black, smooth awns. The grain and glumes are black, the rachilla hairs are long and the central rib of the outer glume has long fine hairs.

### Minnesota Selection 90–8

This is similar to Minnesota Selection 90–5 with the exception that the head is a little more lax.

### *H. deficiens nudideficiens* (HARLAN 1918)

This variety is a rough awned, two-rowed barley with a hullless grain. The grain is colorless, the rachilla hairs are long and the rachis is tough. Under Colorado (irrigated) conditions this barley is very early.

## Methods of conducting experiments

In this study of the various differential characters particular attention has been given to certain chlorophyll deficiencies. As plants which are homozygous recessive for the chlorophyll defective seedling factors cannot be grown to maturity, plants heterozygous for genetic factors for green and white seedlings were used as one or both of the parents. When one parent was heterozygous for green and white seedlings, two types of $F_1$ plants were obtained; one being homozygous for the green seedling factors and the other heterozygous for the green and white seedling factors. In crosses in which both parents were heterozygous for different chlorophyll deficiencies four types of $F_1$ plants were obtained.

By testing seedling progeny of $F_1$ plants in the greenhouse, it was possible to determine fairly accurately their genetic nature for chlorophyll deficiencies. Particular genetic types were used to make more extensive studies in the later generations.

Studies of inheritance of botanical character differences were made for the most part in crosses where chlorophyll deficiencies were not involved.

## INHERITANCE OF SIMPLE MENDELIAN CHARACTERS

### *White seedlings in Colsess*

Head selections were made in the $F_{11}$ generation of Colsess barley in 1922. The progeny of several of the selections were noticed to contain white seedlings. These seedlings died in about a week or ten days after germination. Counts of white seedlings were made in the $F_{12}$ generation in three strains which were later numbered, Colsess I, Colsess II, and Colsess III. The observed ratios of green to white seedlings in the $F_{12}$ generation were very close to a 3 to 1 ratio. The deviation divided by the probable error[1] was 1.7 in the case of Colsess I; 0.98 in the case of Colsess II, and 2.6 in the case of Colsess III. Progeny from seed of these plants were tested for white seedlings in the greenhouse in $F_{13}$. From these studies the following conclusions were drawn. Colsess No. III agrees very well with a 3 to 1 ratio of green to white seedlings on the basis of data from the $F_{12}$ and $F_{13}$ generation. The segregation obtained from Colsess I fits closely to a 3 to 1 ratio of green to white seedlings in the $F_{12}$ and $F_{13}$ generation. Colsess No. II, while indicating a 3 to 1 ratio of green to white seedlings, later developed a strain which approaches more closely to a 9 to 7 ratio. This latter strain was not used in the linkage studies.

In the $F_1$ generation of crosses between Colsess I and Colsess III, white seedlings appeared. This indicates that these two lines are dependent upon the same genetic factors for white seedlings. In crosses between Colsess I and Colsess II and between Colsess II and Colsess III similar results were obtained. The number of homozygous and heterozygous $F_2$ lines from crosses where both parents were heterozygous for white seedlings is given in table 1. In all cases where the parent plants used in the crosses were heterozygous for white seedling factors both green and white seedlings were obtained in the $F_1$. This again indicates that the white seedlings in Colsess I, II, and III are the result of the reaction of the same factor pair. This is further borne out by studying the progeny of heterozygous $F_1$ plants.

With the exception of crosses No. 58 and 59 the fits are good to the expected 3 to 1 ratio. The number of white seedlings in cross No. 59 is low. In cross 58D, divided by P.E. was 10.86 and the number of white seedlings was much larger than expected on a 3 to 1 basis. In conclusion it can be stated that the white seedlings in all crosses involving Colsess I,

[1] Tables of probable errors of Mendelian ratios prepared by the Department of Plant Breeding of Cornell University, Ithaca, New York, were used to determine the probable errors.

II, and III, except cross No. 58, are due to the reaction of the same factor pair.

TABLE 1

*Seedling counts in the $F_1$ generation of Colsess×Colsess crosses and the number of segregating and pure green families in the $F_1$.*

| CROSS | CROSS NUMBER | $F_1$ SEGREGATION | | NUMBER OF $F_2$ SEGREGATING FAMILIES | NUMBER OF $F_2$ PURE GREEN FAMILIES |
|---|---|---|---|---|---|
| | | Green | White | | |
| Colsess I ×Col. II | 12 | 8 | 8 | 5 | 3 |
| Colses I ×Col. II | 59 | 13 | 2 | 7 | 4 |
| Colses I ×Col. III | 92 | 11 | 3 | 5 | 6 |
| Colses I ×Col. III | 91 | 10 | 6 | 7 | 3 |
| Colses I ×Col. III | 15 | 11 | 4 | 7 | 4 |
| Colsess III ×Col. II | 350 | 10 | 6 | 6 | 4 |
| Colsess III ×Col. II | 352 | 10 | 5 | 7 | 4 |
| Colsess II ×Col. III | 50 | 12 | 4 | 6 | 6 |
| Colsess II ×Col. III | 58 | 10 | 5 | 8 | 3 |
| Observed Total..... | | 95 | 43 | 58 | 37 |
| *Calculated Total.....* | | *103.5* | *34.5* | *63.34* | *31.67* |

A cooperative agreement has been reached by several workers to accept *aa* which was first used by NILSSON-EHLE to denote the genotypes of white seedlings in barley. NILSSON-EHLE subscribes his letters with the numbers 1, 2, etc., to denote genetically different whites. Until such times as the white seedlings are tested with NILSSON-EHLE's material, a letter representing the variety in which the particular whites first occurred will be used as a subscript to denote a particular white seedling. If more than one white occurs in a variety, a subscript to the letter will be used until

TABLE 2

*Segregation in $F_2$ for green and white seedlings in crosses between the different Colsess strains.*

| CROSSES | CROSS NUMBER | OBSERVED RATIO | | DEVIATION IN NUMBERS | $\frac{D}{PE}$ |
|---|---|---|---|---|---|
| | | Green | White | | |
| Colsess I ×Col. II | 12 | 80 | 26 | 0.5 | 0.17 |
| Colsess I ×Col. II | 59 | 1936 | 584 | 46.0 | 3.14 |
| Colsess I ×Col. III | 92 | 143 | 39 | 6.5 | 1.65 |
| Colsess I ×Col. III | 91 | 223 | 67 | 5.5 | 1.11 |
| Colsess I ×Col. III | 15 | 1257 | 384 | 26.25 | 2.22 |
| Colsess III ×Col. II | 350 | 94 | 37 | 4.25 | 1.27 |
| Colsess III ×Col. II | 352 | 171 | 57 | 0 | 0 |
| Colsess II ×Col.III | 50 | 801 | 272 | 3.8 | 0.40 |
| Colsess II ×Col. III | 58 | 2012 | 898 | 170.5 | 10.85 |

it is identified with a white in some other variety. Thus the factor pair for the white seedling condition in the Colsess strains is designated as $A_c a_c$.

Cross No. 58 which deviated widely from a 3:1 ratio of green to white was studied in later generations. The different segregations of the $F_2$ plants from this cross are presented in table 3.

TABLE 3

*The observed segregation in $F_2$ compared with calculated 3:1 and 9:7 ratios of white and green seedlings in Cross No. 58.*

| FAMILY NUMBER | NUMBER SEEDLINGS | 3:1 RATIO | | | DEVIATION IN NUMBERS | D/PE |
|---|---|---|---|---|---|---|
| | | | Green | White | | |
| 1 | 104 | obs. | 80 | 24 | | |
| | | *cal.* | *78* | *26* | 2 | 0.67 |
| 2 | 272 | obs. | 200 | 72 | | |
| 3 | | *cal.* | *204* | *68* | 4 | 0.83 |
| 3 | 344 | obs. | 183 | 161 | | |
| | | *cal.* | *258* | *86* | 75.0 | 13.84 |
| 4 | 495 | obs. | 380 | 115 | | |
| | | *cal.* | *371.25* | *123.75* | 8.75 | 1.35 |
| 6 | 1106 | obs. | 843 | 263 | | |
| | | *cal.* | *829.5* | *276.5* | 13.5 | 1.38 |
| 7 | 87 | obs. | 60 | 27 | | |
| | | *cal.* | *65.25* | *21.75* | 5.25 | 1.93 |
| 10 | 502 | obs. | 266 | 236 | | |
| | | *cal.* | *376.5* | *125.5* | 110.5 | 16.90 |
| | | 9:7 ratio | | | | |
| 3 | 344 | obs. | 183 | 161 | | |
| | | *cal.* | *193.5* | *150.5* | 10.5 | 1.69 |
| 10 | 502 | obs. | 266 | 236 | | |
| | | *cal.* | *282.38* | *219.62* | 16.38 | 2.18 |

Families No. 5 and 8 were all pure green.

Five families out of nine segregated in a 3 to 1 ratio, two segregated in a 9 to 7 ratio and two were homozygous for green. This type of segregation would be obtained if one of the parents was heterozygous for two complementary factor pairs for green versus white seedlings and the other parent carried only one of these factor pairs in the heterozygous condition. In the $F_1$ a 3:1 ratio of green and white seedlings would be expected. In $F_2$ a ratio of 1 homozygous green to 3 segregating in a 3:1 ratio and two in a 9:7 ratio would be expected. The obtained ratios fit the expected very well. The segregation of the immediate progeny of the parents of cross No. 58 are of interest although the numbers are small. Colsess II gave 21 green to 17 white seedlings and Colsess III 29 green to 10 white seedlings. Colsess II fits well to a 9 to 7 ratio while Colsess III fits a 3:1 ratio.

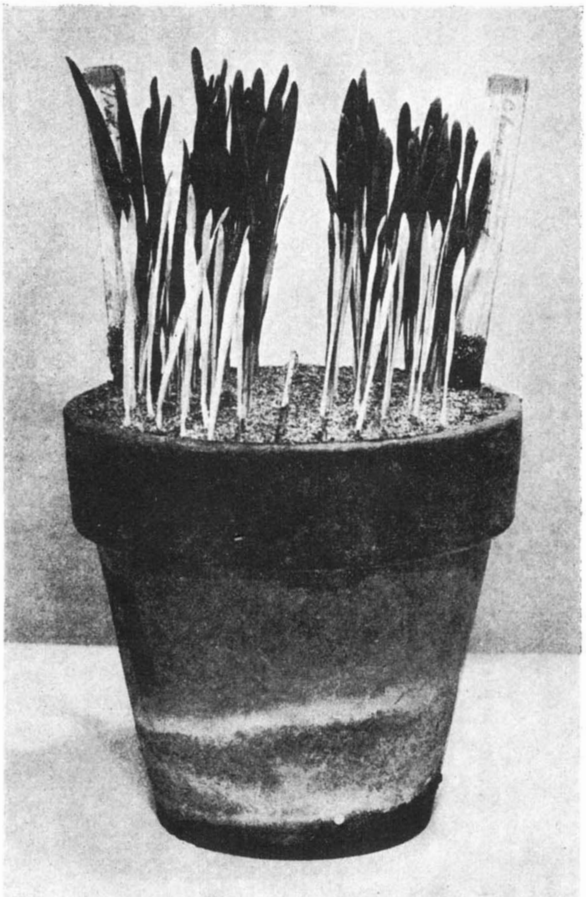

FIGURE 1.—White Seedlings in Colsess (right) and Trebi (left).

It is apparent that this strain of Colsess II carries two complementary factors for chlorophyll color. The strain will be studied more extensively for the purpose of isolating and obtaining linkage relations with the second white seedling factor.

### *White seedlings in Trebi*

These were observed originally at the MINNESOTA STATION. A plant of this strain was grown in Colorado in 1924. Progenies of this plant were later grown in 1925, 1926, and 1927. As all the Trebi plants producing white seedlings are descendants of this single individual, the counts of seedlings made in the greenhouse and field from 1925 to 1927 are summarized together. In all, 829 seedlings have been counted, from parent plants heterozygous for green and white seedling factors; of these 616 were green and 213 were white. The expected ratio on a three to one basis for the above number of individuals is 621.75 green to 207.25 white. The obtained ratio deviates 5.75 from the expected. The deviation divided by the probable error (D/PE) is less than one which indicates that a single factor pair is involved. Phenotypically the white seedlings in Colsess and in Trebi I cannot be told apart (see figure 1).

### *Xantha seedlings in Colsess*

This refers to yellow seedlings originally observed in a selection from Colsess, named Colsess IV. In the field the color is picric yellow (RIDGWAY, Plate IV). In the greenhouse the color is classified as Bright Chalcedony yellow by the use of RIDGWAY's tables (Plate XVII). This chlorophyll deficiency is modified in appearance by differences in temperature. As controlled conditions were not available, the definite thermal point for the development of chlorophyll was not learned. One plant of the xantha type was grown to maturity and the line continued for three generations. Seedling counts, of the progeny of parent plants which were heterozygous, were made both in the field and in the greenhouse. The following results were obtained:

TABLE 4

*Segregation for green versus xantha in progeny of Colsess IV.*

| GREEN | XANTHA | DEVIATION IN NUMBERS | $\frac{D}{PE}$ |
|---|---|---|---|
| 1004 | 375 | 30.25 | 2.80 |

A single factor difference is responsible for the xantha seedling in Colsess IV.

### *Black versus white glume color*

Studies were made in the following crosses: Colsess × *H. distichon nigrinudum*, Colsess × Minnesota 90–5, Colsess × Minnesota 90–8, and

Trebi×Minnesota 90–5. The results indicate that black *versus* white glume color are dependent upon a single factor pair. The following table gives the $F_2$ segregation of black and white glumed plants in the above crosses.

TABLE 5

*Segregation for black versus white glumes in the $F_2$ of crosses between black and white glumed parents.*

| CROSS | $F_2$ DATA | | DEVIATION IN NUMBERS | $\frac{D}{PE}$ |
|---|---|---|---|---|
| | Black | White | | |
| Colsess×H. dis. nig. | 3531 | 1192 | 11.25 | 0.56 |
| Colsess×Minn. 90–5 | 785 | 255 | 5.00 | 0.53 |
| Colsess×Minn. 90–8 | 224 | 88 | 10.00 | 1.94 |
| Trebi×Minn. 90–5 | 674 | 187 | 28.25 | 3.30 |

*Hoods versus awns*

Studies were made in crosses between Colsess×*H. distichon nigrinudum*, Colsess×*H. deficiens nudideficiens*, Colsess×Minnesota 90–5, and Colsess ×Minnesota 90–8. The $F_2$ segregations approach a 3 to 1 ratio, indicating that a single factor pair is responsible for the hooded and awned condition. Table 6 gives the $F_2$ segregation of hooded and awned plants.

TABLE 6

*Segregation of hooded versus awned plants in the $F_2$ of crosses between hooded and awned parents.*

| CROSS | $F_2$ DATA | | DEVIATION IN NUMBERS | $\frac{D}{PE}$ |
|---|---|---|---|---|
| | Hoods | Awns | | |
| Colsess×H. dis. nigrinudum | 3471 | 1252 | 71.25 | 3.55 |
| Colsess×H. def. nudideficiens | 2650 | 987 | 77.75 | 4.38 |
| Colsess×Minnesota 90–5 | 797 | 243 | 17.00 | 1.80 |
| Colsess×Minnesota 90–8 | 229 | 83 | 5.00 | 0.97 |

*Covered versus naked seeds*

The covered versus naked seed character pair was studied in crosses between Colsess×*H. distichon nigrinudum* and Colsess×*H. deficiens nudideficiens*. Table 7 gives the $F_2$ segregation of plants from the above crosses for the covered seed versus naked seed character pair.

From the following table it appears that the covered versus naked condition of the seed is dependent upon a single factor pair difference.

TABLE 7

*Segregation of covered versus naked seed in the $F_2$ generation of crosses between Colsess×H. deficiens nudideficiens and Colsess×H. distichon nigrinudum.*

| CROSS | $F_2$ DATA | | DEVIATION IN NUMBERS | D/PE |
|---|---|---|---|---|
| | Covered | Naked | | |
| Colsess×H. dis. nigrinudum | 3593 | 1130 | 50.75 | 2.53 |
| Colsess×H. def. nudideficiens | 2706 | 931 | 21.75 | 1.23 |

## *Long versus short haired rachilla*

Studies were made in crosses between Colsess×*H. deficiens nudideficiens*, Colsess×Minnesota 90–5, Colsess×Minnesota 90–8, and Trebi ×Minnesota 90–5. The segregation of the $F_2$ generation shows that long versus short haired rachillas differ by a single factor pair. The $F_2$ data are presented in table 8.

TABLE 8

*Segregation of long versus short haired rachilla in the $F_2$ generation.*

| CROSS | $F_2$ DATA | | DEVIATION IN NUMBERS | D/PE |
|---|---|---|---|---|
| | Long | Short | | |
| Colsess×H. def. nud. | 2736 | 901 | 8.25 | 0.47 |
| Colsess×Minn. 90–5 | 793 | 247 | 13.00 | 1.38 |
| Colsess×Minn. 90–8 | 238 | 74 | 4.00 | 0.78 |
| Trebi×Minn. 90–5 | 667 | 194 | 21.25 | 2.48 |

## INHERITANCE OF FERTILITY OF THE LATERAL FLORETS

Studies were made in a cross between Colsess and *H. deficiens nudideficiens*. The $F_1$ generation was intermediate between six- and two-rowed. (Figure 2. No. 2.) The $F_2$ generation could not be classified accurately for fertility of the lateral florets. The progeny of the $F_2$ plants were grown in the $F_3$, and the $F_2$ phenotypes were determined from the $F_3$ segregation. Seven groups were established which is a similar condition to that described by HARLAN and HAYES (1920). As six-row, two-row and deficiens have been found to be allelomorphic no attempt has been made in these studies to distinguish between two row and deficiens. The results establish the genotype of the six-rowed parent as consisting of two factor pairs for fertility of the lateral florets. Colsess is therefore represented as *vv II*. Factor *v* is similar to the *A* factor and *I* to the *B* factor of Harlan and Hayes. Similar segregations were found for the following crosses, Colsess×Minnesota 90–5 and Trebi×Minnesota 90–5. Table 9 presents the observed and the calculated segregation on the genetic hypothesis outlined. While there is a slight deviation, there is in general good agreement between the observed results and the calculated.

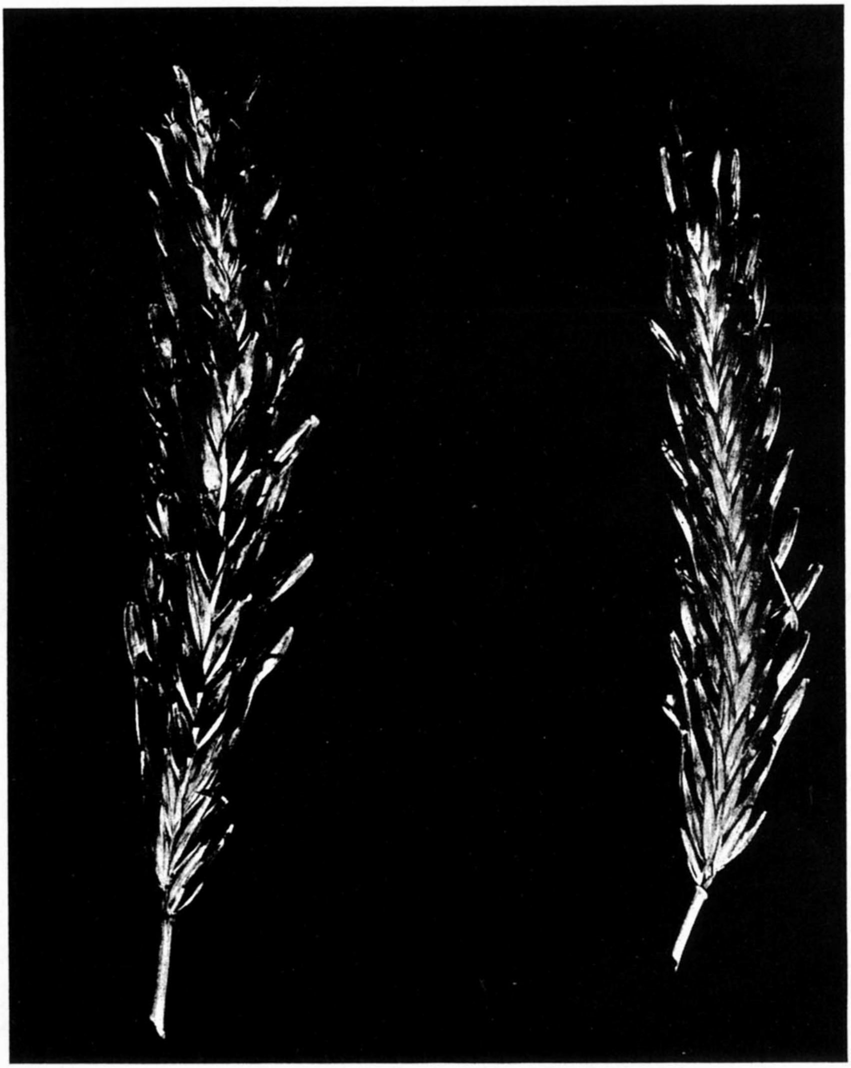

FIGURE 2.—Types of $F_1$ heads obtained from crosses between Colsess×*H. distichon nigrinudum* (left) and Colsess×*H. deficiens nudideficiens* (right).

In a cross between Colsess and *H. distichon nigrinudum* the $F_1$ plants were intermediate, figure 2, No. 1. The $F_2$ plants were classified as six-rowed and non-six-rowed. The six-rowed class includes all $F_2$ plants

TABLE 9

*Segregation in $F_2$, as determined by $F_3$ breeding behavior, for fertility of the lateral florets.*

| $F_2$ GENOTYPE | CROSSES | | | | | |
|---|---|---|---|---|---|---|
| | Colsess×H. def. nud. | | Colsess×Minnesota 90-5 | | Trebi×Minnesota 90-5 | |
| | observed | *calculated* | observed | *calculated* | observed | *calculated* |
| *vvII*<br>*vviI*<br>*vvii* | 83 | *88.7* | 148 | *123.3* | 110 | *119.2* |
| *vVIi* | 99 | *88.7* | 121 | *123.3* | 113 | *119.2* |
| *vVii* | 50 | *44.4* | 48 | *61.6* | 65 | *59.6* |
| *VVII* | 19 | *22.2* | 27 | *30.8* | 34 | *29.8* |
| *VViI* | 39 | *44.4* | 48 | *61.6* | 61 | *59.6* |
| *VvII* | 45 | *44.4* | 73 | *61.6* | 58 | *59.6* |
| *VVii* | 20 | *22.2* | 28 | *30.8* | 36 | *29.8* |
| Total | 355 | *355* | 493 | *493* | 477 | *476.9* |
| $X^2$ | | *3.51* | | *13.82* | | *3.47* |
| P | | *.7414* | | *.0320* | | *.7487* |

which produced only six rowed progeny in the $F_3$. Table 10 gives the $F_2$ segregation for non-six-rowed versus six-rowed.

TABLE 10

*Segregation for non-six-rowed and six-rowed in the $F_2$ generation of a cross between Colsess and H. distichon nigrinudum.*

| SIX-ROWED | NON-SIX-ROWED | DEVIATION IN NUMBERS | $\frac{D}{PE}$ |
|---|---|---|---|
| 125 | 412 | 9.25 | 1.37 |

The segregation observed can be explained on the basis of single factor pairs for six-rowed versus non-six-rowed. No attempt was made to study the differences in the non-six-rowed group. Since the Colsess parent has been shown by previous crosses to contain the factor pair *vv* for six-rowed; the distichon parent has the gametic constitution *VV*.

## INTERRELATIONS OF SIMPLE MENDELIAN CHARACTER PAIRS

Considerable information is already available regarding interrelations of genetic character pairs for the major botanical character differences. Consequently the interrelations for these will be presented briefly before giving the results of a study of the linkage relations of factor pairs for chlorophyll deficiencies with factor pairs for other character differences.

TABLE 11

*Pure green families and segregating families summarized on the basis of closeness of agreement with 9:7 or 3:1 ratios.*

| | | 3:1 RATIO | | | | | | 9:7 RATIO | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Observed | | *Calculated* | | Deviation in numbers | D/PE | *Calculated* | | Deviation in numbers | D/PE |
| | | Green | White | *Green* | *White* | | | *Green* | *White* | | |
| Trebi×Colsess III II-25-3 | 1 | 516 | 164 | *510* | *170* | 6 | 0.79 | | | | |
| | 2 | 465 | 117 | *436.5* | *145.5* | 28.5 | 4.04 | | | | |
| | 3 | 421 | 119 | *405* | *135* | 16. | 2.36 | | | | |
| | 5 | 464 | 161 | *468* | *156* | 5. | .68 | | | | |
| | 4 | 355 | 249 | *453* | *151* | 98 | 13.65 | *339.75* | *264.25* | 15.25 | 1.86 |
| | 8 | 533 | 335 | *651* | *217* | 118 | 13.72 | *488.25* | *379.75* | 44.75 | 4.54 |
| | 9 | 414 | 282 | *522* | *174* | 108 | 14.00 | *391.5* | *304.5* | 22.5 | 2.55 |
| | 6 | All | Green | | | | | | | | |
| | 7 | All | Green | | | | | | | | |
| Trebi×Colsess III II-25-2 | 1 | 84 | 29 | *84.75* | *28.25* | 0.75 | .23 | | | | |
| | 2 | All | Green | | | | | | | | |
| Colsess I×Trebi II-25-50 | 1 | 96 | 21 | *87.75* | *29.25* | 8.25 | 2.61 | | | | |
| | 5 | 106 | 25 | *98.25* | *32.75* | 7.75 | 2.32 | | | | |
| | 6 | 34 | 20 | *40.5* | *13.5* | 6.5 | 3.02 | | | | |
| | 11 | 177 | 48 | *168.75* | *56.25* | 8.25 | 1.88 | | | | |
| | 2 | 40 | 32 | *54.0* | *18.0* | 14.0 | 5.65 | *40.5* | *31,5* | 0.5 | 0.02 |
| | 4 | 96 | 57 | *114.0* | *38.0* | 19.0 | 5.26 | *85.5* | *66.5* | 9.5 | 2.30 |
| | 12 | 159 | 106 | *198.75* | *66.25* | 39.75 | 8.16 | *149.0* | *116.0* | 10.0 | 1.83 |
| | 13 | 146 | 87 | *174.75* | *58.25* | 28.75 | 6.45 | *131.0* | *102.0* | 15.0 | 2.94 |
| | 3 | All | Green | | | | | | | | |
| | 10 | All | Green | | | | | | | | |
| | 14 | All | Green | | | | | | | | |

## INTERRELATIONS OF CHLOROPHYLL DEFICIENCIES

### *White seedlings in Colsess and Trebi*

Crosses were made between Trebi which was segregating for green and white seedling $A_t a_t$ and the heterozygous Colsess line called $A_c a_c$. Only those crosses were considered where the parent plants by progeny tests were known to be heterozygous for factor pairs for green and white seedlings. Three separate crosses of this kind were available. The number of $F_1$ plants was 9, 2, and 11, respectively, and all were green, which indicates that the factor pair in Trebi for green and white seedlings is different from the $A_c a_c$ factor pair of Colsess. If the factor pairs are independently inherited, the calculated breeding behavior in $F_2$ is 1 pure green line, 2 heterozygous giving a ratio of 3 green:1 white and 1 segregating in a 9:7 ratio. The detailed results are given in table 11.

Of the 22 lines 6 were homozygous green, 9 agreed fairly well with a 3:1 ratio and 7 with a 9:7 ratio. In the 3:1 segregating lines there was a tendency for too few white seedlings. If there was linkage of the factor pairs for green versus white seedlings in Colsess and Trebi, it could be studied only in the lines where both factor pairs are involved. There is a consistent tendency for too few white seedlings in these lines, for linkage in the repulsion phase. The breeding behavior of the 22 $F_2$ lines is summarized in table 12. The agreement between observed and calculated for independent inheritance is good.

TABLE 12

*The number of lines segregating in a 9:7 or a 3:1 ratio of green to white seedlings or producing only pure green seedlings.*

| | SEGREGATING LINES | | PURE GREEN LINES |
|---|---|---|---|
| | 9:7 ratio | 3:1 ratio | |
| Number of lines | 7 | 9 | 6 |
| *Calculated* | *5.5* | *11* | *5.5* |

It may be concluded, therefore, that the white seedlings in Trebi I are caused by the reaction of a different factor pair than $A_c a_c$ which is responsible for the white seedlings in Colsess. The factor pair for green and white seedlings of Trebi I will be represented as $A_t a_t$.

### *White seedlings and xantha seedlings in Colsess*

Crosses were made between lines which were heterozygous for the factor pairs $A_c a_c$ green versus white and $X_c x_c$ green versus xantha seedling.

Only those crosses were considered where both parent plants used proved to be heterozygous for the chlorophyll deficiencies which were being studied. In accordance with the factorial method used, $A_ca_cX_cX_c$ was crossed with $A_cA_cX_cx_c$. The $F_1$ seedlings were all green indicating that the factors causing white and xantha seedlings in Colsess are not allelomorphic. The $F_1$ plants should be of four different genotypes $A_cA_cX_cX_c$ producing only green seedlings in the $F_2$; $A_cA_cX_cx_c$ producing green and xantha seedlings in the proportion of 3:1; $A_ca_cX_cX_c$ producing seedlings in the ratio of 3 green to 1 white and $A_ca_cX_cx_c$ producing all three types of seedlings green, xantha, and white.

Forty-nine $F_1$ plants from crosses where both parents were heterozygous were obtained. The segregation for chlorophyll deficiencies was studied in $F_2$. On the basis of the breeding behavior in $F_2$, 13 $F_1$ plants proved homozygous for factors for green seedlings, 12 gave $F_2$ progeny segregating for green and xantha, 13 gave $F_2$ progeny segregating for green and white and 13 proved to be heterozygous for both the green versus xantha and green versus white factor pairs. This latter group gave an opportunity to study linkage relations of the two types of chlorophyll deficiencies. Because of the relatively few plants in the $F_2$ progenies it was necessary to make the study in $F_3$. The study was made by growing the progenies of $F_2$ green plants from $F_2$ lines segregating for green, xantha and white seedlings.

The calculated segregation on the basis of independent inheritance of the factor pairs concerned is as follows: One plant out of every 9 should be homozygous for both dominant factor pairs and should breed true for green seedlings. Four plants would be heterozygous for 1 factor pair and homozygous for the other factor pair. Green and xantha seedlings would be produced by the progeny of two of these plants and green and white seedlings would be produced by the progeny of the other two. The four remaining plants would be heterozygous for both factors and would give progeny consisting of green, xantha, and white seedlings. There were 47 $F_2$ plants which matured in lines which in $F_2$ segregated for green, xantha and white seedlings. The genetic nature of these was determined by their $F_3$ breeding behavior. The calculated ratio for independent inheritance and for the four classes of plants described above is 5.22:10.44:10.44:20.88. If the factor pair $X_cx_c$ is inherited independently of the factor pair $A_ca_c$ only 21 of the 47 plants tested should give green, xantha and white seedlings.

The progeny of all 47 plants, however, gave green, xantha and white seedlings. This indicates a possible linkage of factors for xantha ($x_c$) and white ($a_c$). An attempt was made to determine the crossover value from the $F_3$ seedling counts from the 47 $F_2$ plants.

All of the $F_3$ segregations were in the repulsion phase so the $F_3$ seedling counts of the 47 $F_2$ plants were summarized.

A short method has been derived to determine the expected number of lines which would give the coupling type of linkage in the $F_3$ generation if the repulsion type was obtained in the $F_2$ generation. By the use of Emerson's gametic ratio represented by $r$:$s$ these calculations can be made. In the case of repulsion $s$ would be higher than $r$. By squaring $r$ and $s$ the expected number of $F_3$ lines showing repulsion and coupling would be obtained. The same method can be used to determine the number of lines which will show repulsion in the $F_3$ when coupling is obtained in the $F_2$ generation. An example is given below with 10 percent crossing over and repulsion: $r=1$, $s=9$; therefore 1 line would segregate in the coupling phase to 81 lines segregating in the repulsion phase.

Table 13 gives the summary of the segregations of the $F_3$ progeny of 47 green $F_2$ plants from the families heterozygous for both factors in the $F_2$.

TABLE 13

*The $F_3$ seedling counts of 47 green plants from the $F_2$ families heterozygous for both xantha and white seedlings from crosses between Colsess and Colsess IV.*

| CROSS | NO. OF $F_2$ GREEN PLANTS | SEEDLING RATIO | | | | |
|---|---|---|---|---|---|---|
| | | Green | Xantha | White | Total | $X^2$ |
| Colsess × Colsess IV | 35 | 8314 | 4120 | 3995 | 16531 | |
| Colsess IV × Colsess | 12 | 2869 | 1379 | 1460 | 5773 | |
| Total | 47 | 11183 | 5499 | 5455 | | |
| Observed ratio | | 11183 | 5499 | 5455 | 22304 | |
| *Calculated ratio* | | *12546* | *4182* | *5576* | *22304* | *565.4* |

By examining the data in table 13, it will be seen that the xantha class has a larger number of individuals than the white class. This brings up the question: where do the double recessives belong? In a cross in which the same factor pair $X_cx_c$ was studied in relation to green versus white seedlings in Trebi $A_ta_t$ the white class undoubtedly contained the double recessives. When a close examination of the individual lines in the Colsess crosses was made a variation was noticed in the number of xantha and white plants. Some lines were higher in white seedlings and others were higher in xantha seedlings. When all lines are grouped a difference of 44 seedlings in favor of the xantha class out of a total of 10954 white and xantha seedlings was found. In the determination of the agreement between the calculated and observed ratios the double recessives have been considered as being included in the white class. It will be noted from table 13 that the fit of the observed ratio to the calculated 9:3:4 ratio is poor. $X^2 = 565.44$. Since the double recessive group cannot be separated from the white seedlings of the genetic constitution $a_c a_c X_c X_c$ and $a_c a_c X_c x_c$ it is not possible to use a formulae based on the double recessive group to determine the linkage value. Various crossover values were calculated and the different ratios compared with the observed. From the calculation it was found that the white class which contained the double recessive chlorophyll classes and simple recessive white group remained uniform for all degrees of linkage postulated. The $X^2$ method was used to determine the goodness of fit and good fits were obtained for crossover values between 12.5 and 4 percent.

TABLE 14

*The observed and calculated ratio for various crossover percentages.*

| | CROSSOVER PER CENT | GREEN | XANTHA | ALBINO | $X^2$ | P |
|---|---|---|---|---|---|---|
| Observed | | 11183 | 5499 | 5455 | | |
| *Calculated* | *50* | *12546* | *4182* | *5576* | *565.44* | *.0000* |
| " | *20* | *11375.0* | *5352.96* | *5576* | *9.8520* | *.0074* |
| " | *12.5* | *11239.12* | *5488.87* | *5576* | *2.9232* | *.2343* |
| " | *12* | *11232.33* | *5495.63* | *5576* | *2.8458* | *.2455* |
| " | *11.1* | *11220.92* | *5507.20* | *5576* | *2.7550* | *.2587* |
| " | *10* | *11207.76* | *5520.24* | *5576* | *2.7621* | *.2576* |
| " | *9.1* | *11198.08* | *5529.29* | *5576* | *2.8189* | *.2494* |
| " | *8.3* | *11190.66* | *5537.24* | *5576* | *2.8938* | *.2386* |
| " | *4.76* | *11164.65* | *5563.36* | *5576* | *3.3738* | *.1903* |
| " | *4.* | *11160.92* | *5567.08* | *5576* | *3.4602* | *.1827* |

Further studies were made using the formulae presented by Collins (1) for use when there is difficulty in distinguishing any two classes. The formulae used were $p = \sqrt{\frac{AB - 2Ab}{AB + Ab}}$ and $p = \sqrt{\frac{4AB - 2n}{n}}$. When p is calculated from the ratio of AB to Ab[1] its value is 0.1053. When p is calculated from the ratio of AB to the total it equals 0.0745. When the above

[1] AB, Ab, aB, ab = the number of individuals in each of the four zygotic classes in a hybrid involving two character pairs Aa and Bb.

results are considered as crossover percentages values of 10.53 and 7.45 are obtained.

To further test the linkage relationship, the number of differently breeding $F_3$ lines which would be expected from the green plants of the $F_2$ families which segregated into green, xantha and white seedlings was calculated for independent inheritance and various degrees of linkage and compared with the observed ratio. The calculations were made from the following relationships based on Emerson's gametic ratio r:s

$$\begin{aligned} AA\ BB &= r^2 \\ AA\ Bb &= 2rs \\ Aa\ BB &= 2rs \\ Aa\ Bb &= 2s^2+2r^2 \end{aligned}$$

The calculated ratio of $F_2$ plants in each of the 4 genotypic groups AA BB, AA Bb, Aa BB, and Aa Bb on the basis of independent inheritance is 1:2:2:4; for 10 percent crossing over 1:18:18:164 and for 4 percent crossing over 1:48:48:1154. Considering each of the middle classes as one, the ratios become: 0.5:1:1:2; 0.055:1:1:9.1; 0.0:1:1:24.04. When we compare the above ratios with the observed breeding behavior of $F_3$ families all 47 of which segregated for green, xantha, and white, it appears that the crossover value is less than 4 percent. In order to determine the value more accurately, larger numbers are needed. The above method seems to offer possibilities for testing the crossover percentage for crosses in which the double recessive cannot be separated and where the recessive and double recessive plants are lost before maturity. It appears very probable, however, that the factor pair $X_cx_c$ for green vs. xantha seedlings in Colsess is closely linked to the factor pair $A_ca_c$ for green versus white seedlings in Colsess. The crossover percentage is low.

### *White seedlings in Trebi with xantha seedlings in Colsess*

Crosses were made between Trebi I which carries the factor pair $A_ta_t$ and Colsess IV which carries a factor pair for xantha seedlings $X_cx_c$. In the $F_1$ generation 31 seedling plants were pure green from crosses where both parents were known to be heterozygous for their respective chlorophyll deficient seedling factors indicating that white seedlings in Trebi and xantha seedlings in Colsess IV are caused by the interaction of genetic factors which are not allelomorphic. The progeny of twenty-nine $F_1$ plants were studied. Seven segregated for green, xantha, and white seedlings; 9 segregated for green and xantha seedlings; 5 segregated for green and white seedlings and 8 bred true for pure green seedlings. The $F_1$ plants were very small and only a few seeds were obtained from each. In order to study the segregations with a larger number of seedlings, the progeny from the green plants from lines which segregated in $F_2$ for three types of seedlings were grown in $F_3$. The breeding behavior of the progeny of 32 $F_2$ plants is given in table 15.

TABLE 15

*$F_3$ breeding behavior of the progeny of the green plants from the $F_2$ families segregating in a 9:3:4 ratio*

*13 Lines segregating in a 9:3:4 ratio*

| OBSERVED RATIO | | | *Calculated Ratio* | | | $X^2$ |
|---|---|---|---|---|---|---|
| Green | Xantha | White | *Green* | *Xantha* | *White* | |
| 2872 | 848 | 1065 | *2691.6* | *897.2* | *1196.2* | *29.18* |

*7 Lines segregating in a 3:1 ratio of green to xantha*

| OBSERVED RATIO | | *Calculated Ratio* | | DEV. IN NUMBERS | D/PE |
|---|---|---|---|---|---|
| Green | Xantha | *Green* | *Xantha* | | |
| 1730 | 560 | *1717.5* | *572.5* | 12.5 | 0.89 |

*6 Lines segregating in a 3:1 ratio of green to white*

| OBSERVED RATIO | | *Calculated Ratio* | | DEV. IN NUMBERS | D/PE |
|---|---|---|---|---|---|
| Green | White | *Green* | *White* | | |
| 1910 | 631 | *1905.75* | *635.25* | 4.25 | 0.29 |

*6 lines produced only pure green seedlings*

Any linkage, if present, would be studied in the 13 lines segregating for green, xantha, and white seedlings. If linkage were present it would be of the repulsion phase as in the previous cross. With linkage in the repulsion phase, the number of individuals in the middle or phenotypic classes Ab and aB would be high and the extreme classes or AB and ab would be low. In this cross the AB class is represented by the green seedlings and the Ab class by the xantha seedlings. The aB and ab classes or white seedlings are grouped and cannot be differentiated. Therefore with linkage in the repulsion phase the xantha seedlings should be higher than for independent inheritance and the green seedlings lower than calculated for independent inheritance. As this is not the case, however, as shown by the results given in table 15 it may safely be concluded that the factor pairs $A_ta_t$ and $X_cx_c$ are inherited independently. The agreement with a 9:3:4 ratio calculated for independent inheritance is not good. The number of chlorophyll deficient seedlings of both types are lower than the calculated. A certain amount of elimination of the seedlings which are recessive for chlorophyll deficiencies might explain this condition.

Further tests were made with the lines segregating in $F_2$ for green versus xantha and those segregating for green versus white seedlings. Progeny from heterozygous $F_2$ plants were grown in the $F_3$ and seedling counts made. The data are given in table 16.

TABLE 16

*Summary of segregation for xantha and white seedlings in lines heterozygous for a single factor pair.*

| SEGREGATING FOR | OBSERVED | | *Calculated* | | DEVIATION IN NUMBERS | D/PE |
|---|---|---|---|---|---|---|
| | Green | Chlorophyll defective | *Green* | *Chlorophyll defective* | | |
| $C_cx_c$ | 1353 | 366 | *1289.25* | *429.75* | 63.75 | 5.28 |
| $A_ta_t$ | 3126 | 973 | *3074.25* | *1024.75* | 51.75 | 2.77 |

The number of xantha seedlings is lower than the calculated with a value of D/PE of 5.28.

## INTERRELATIONS OF CHARACTER PAIRS FOR OTHER BOTANICAL CHARACTER DIFFERENCES

### *Black versus white glume color (Bb) and hoods versus awns (Kk)*

Studies were made in crosses between Colsess×*H. distichon nigrinudum*, Colsess×Minnesota 90–5, and Colsess×Minnesota 90–8. The segregations obtained in the $F_2$ generation are given in table 17.

TABLE 17

*Segregation in $F_2$ for black versus white glumes (Bb) and hoods versus awns (Kk) in crosses between Colsess ×H. distichon nigrinudum, Colsess×Minnesota 90–5 and Colsess×Minnesota 90–8.*

| CROSS | | *BK* | *Bk* | *bK* | *bk* | $X^2$ | *P* |
|---|---|---|---|---|---|---|---|
| Colsess×*H. dis. nig.* | obs. | 2611 | 920 | 860 | 332 | 7.45 | .0602 |
| | *cal.* | *2657* | *886* | *886* | *295* | | |
| Colsess×Minn. 90–5 | obs. | 603 | 182 | 194 | 61 | 1.67 | .6479 |
| | *cal.* | *585* | *195* | *195* | *65* | | |
| Colsess×Minn. 90–8 | obs. | 166 | 58 | 63 | 25 | 2.41 | .4983 |
| | *cal.* | *175.5* | *58.5* | *58.5* | *19.5* | | |

In the cross between Colsess×*H. distichon nigrinudum* the number of awned plants in both the black and white glumed classes is higher than calculated on a 3:1 basis which explains the $X^2$ value of 7.45 with a P value of .0602. The chances that a deviation as high or higher may occur due to random sampling are 602 in 10000 trials or about 1 in 17. The other two crosses fit the expected ratio for independent inheritance very well. It can safely be concluded from the above data that black versus white glume color is caused by a factor pair inherited independently of the factor pair for hoods *versus* awns.

*Black versus white glume color (Bb) and long versus short haired rachillas (Ss)*

The results of three crosses, Colsess×Minnesota 90–5, Colsess×Minnesota 90–8, and Trebi×Minnesota 90–8 are given in table 18.

TABLE 18

*Segregation in $F_2$ for black versus white glumes (Bb) and long versus short haired rachillas (Ss).*

| CROSS | | *BS* | *Bs* | *bS* | *bs* | $X^2$ | *P* |
|---|---|---|---|---|---|---|---|
| Colsess×Minn. 90–5 | obs. | 592 | 193 | 201 | 54 | 2.14 | .5471 |
| | *cal.* | *585* | *195* | *195* | *65* | | |
| Colsess×Minn. 90-8 | obs. | 164 | 60 | 74 | 14 | 6.45 | .0937 |
| | *cal.* | *175.5* | *58.5* | *58.5* | *19.5* | | |
| Trebi×Minn. 90–5 | obs. | 520 | 154 | 147 | 48 | 4.88 | .1826 |
| | *cal.* | *484.3* | *161.4* | *161.4* | *53.8* | | |

From the above data it is concluded that the factor pair for black and white glume is inherited independently of the factor pair which differentiates long *versus* short haired rachillas.

*Black versus white glume color (Bb) and covered versus naked seed (Nn)*

The factor pairs concerned were *Bb* and *Nn*. The results are given in table 19.

TABLE 19

*Segregation in $F_2$ for black versus white glumes (Bb) and covered versus naked seed (Nn) in a cross between Colsess and H. distichon nigrinudum.*

| | *BN* | *Bn* | *bN* | *bn* | $X^2$ | *P* |
|---|---|---|---|---|---|---|
| Observed | 2679 | 852 | 914 | 279 | 3.26 | .3578 |
| *Calculated* | *2657* | *886* | *886* | *295* | | |

These data indicate that the factor pair for black *versus* white glume color is inherited independently of the factor pair for covered *versus* naked seed.

*Black versus white glume color (Bb) and non-six-rowed versus six-rowed (Vv)*

Studies were made of the factor pairs *Bb* and *Vv* in a cross between Colsess and *H. distichon nigrinudum*. The $F_2$ plants were classified as six-rowed and non-six-rowed. Table 20 presents the data obtained in $F_2$.

TABLE 20

*Segregation in $F_2$ for non-six-rowed versus six-rowed (Vv) and black versus white glume color (Bb).*

| | *BV* | *bV* | *Bv* | *bv* | $X^2$ | *P* |
|---|---|---|---|---|---|---|
| Observed | 304 | 108 | 88 | 37 | | |
| *Calculated* | *302* | *100.7* | *100.7* | *33.6* | 2.48 | .4856 |

*BV* = Black glume non-six-rowed
*bV* = White glume non-six-rowed
*Bv* = Black glume six-rowed
*bv* = White glume six-rowed

From the above data it may be concluded that the factor pair *Bb* for black *versus* white glume is inherited independently of the factor pair *Vv* for non-six-rowed *versus* six-rowed.

*Hoods versus awns (Kk) and long versus short haired rachilla (Ss)*

Studies were made in crosses between Colsess × *H. deficiens nudideficiens*, Colsess × Minnesota 90–5, and Colsess × Minnesota 90–8. Table 21 gives

TABLE 21

*Segregation in $F_2$ for hoods versus awns and long versus short haired rachilla.*

| CROSS | | *KS* | *Ks* | *kS* | *ks* | $X^2$ | *P* |
|---|---|---|---|---|---|---|---|
| Colsess × *H. def. nud.* | obs. | 1983 | 667 | 753 | 234 | 9.87 | .0198 |
| | *cal.* | *2046* | *682* | *682* | *227* | | |
| Colsess × Minn. 90–5 | obs. | 609 | 188 | 184 | 59 | 2.40 | .4820 |
| | *cal.* | *585* | *195* | *195* | *65* | | |
| Colsess × Minn. 90–8 | obs. | 175 | 54 | 63 | 20 | 0.71 | High |
| | *cal.* | *175.5* | *58.5* | *58.5* | *19.5* | | |

the observed and calculated ratios in the $F_2$ generation for hoods *versus* awns and long *versus* short haired rachilla. In the cross between Colsess and *H. deficiens nudideficiens* there is a wide deviation between the monohybrid observed and calculated ratio for hoods *versus* awns. The awned group is higher than calculated and $X^2$ for a 9:3:3:1 ratio is 9.87. For this cross a calculated crossover value of 48.88 percent was obtained by Yule's coefficient of association Q (1924). A crossover value as high as this cannot be distinguished from independent inheritance with any degree of certainty in an $F_2$ generation. The value for P for the two other crosses indicates independent inheritance of the factor pairs for hoods *versus* awns and long *versus* short haired rachilla.

### *Hoods versus awns (Kk) and covered versus naked seed (Nn)*

In crosses between Colsess×*H. distichon nigrinudum* and Colsess×*H. deficiens nudideficiens* a study was made of the interrelations of the factor pairs for hoods *versus* awns, Kk, and covered versus naked seed, *Nn*. Table 22 presents the $F_2$ data.

TABLE 22

*Segregation in $F_2$ for hoods versus awns and covered versus naked seeds.*

| CROSS | | *KN* | *Kn* | *kN* | *kn* | $X^2$ | *P* |
|---|---|---|---|---|---|---|---|
| Colsess×*H. dis. nig.* | obs. | 2635 | 836 | 958 | 294 | 8.88 | .0313 |
| | *cal.* | *2657* | *886* | *886* | *295* | | |
| Colsess×*H. def. nud.* | obs. | 1969 | 681 | 737 | 250 | 9.60 | .0229 |
| | *cal.* | *2056* | *682* | *682* | *227* | | |

In the above two crosses the awned plants are higher than calculated on a 3:1 basis which causes the dihybrid segregation to deviate widely from a calculated 9:3:3:1 ratio. The crossover value as obtained by the use of Q is 49.35 percent for the first cross and 49.20 percent for the second cross. The above crossover values cannot be considered as indications of linkage. However $X^2$ for the goodness of fit to a calculated 9:3:3:1 is 8.88 for the first cross and 9.50 for the second. P is .0313 and .0240 respectively. It can be concluded that the factor pair which causes the production of hoods versus awns is inherited independently of the factor pair which differentiates covered versus naked seeds.

### *Hoods versus awns (Kk) and non-six-rowed versus six-rowed (Vv)*

In a cross between Colsess and *H. distichon nigrinudum* the interrelations were studied of the factor pairs, *Kk* for hoods *versus* awns and *Vv* non-six-rowed *versus* six-rowed. The $F_2$ plants were classified as six-rowed or non-six-rowed. In table 21 the different $F_2$ phenotypes are represented by letters as follows: *KV* is hooded and non-six-rowed; *kV* is awned and non-six-rowed; *Kv* is hooded and six-rowed, and *kv* is

TABLE 23

*Segregation in $F_2$ for hoods versus awns (Kk) and six rowed versus non-six-rowed (Vv).*

| | KV | kV | Kv | kv | $X^2$ | P |
|---|---|---|---|---|---|---|
| Observed | 320 | 92 | 97 | 28 | 2.89 | .4115 |
| *Calculated* | *302* | *100.7* | *100.7* | *33.6* | | |

awned and six-rowed. The above data indicate that the factor pair for hoods *versus* awns is inherited independently of the factor pair for six-rowed *versus* non-six-rowed.

### *Long versus short haired rachilla (Ss) and covered versus naked seed (Nn)*

Studies were made of the interrelations of the factor pairs *Ss* and *Nn* in a cross between Colsess and *H. deficiens nudideficiens.* The $F_2$ data are presented in table 24.

TABLE 24

*Segregation in $F_2$ for long versus short haired rachilla and covered versus naked seed.*

| | SN | Sn | sN | sn | $X^2$ | P |
|---|---|---|---|---|---|---|
| Observed | 2061 | 675 | 645 | 256 | 5.79 | .1242 |
| *Calculated* | *2046* | *682* | *682* | *227* | | |

There is some deviation from the calculated 9:3:3:1 ratio. The genotypes of the parents of this cross were *NNss* and *nnSS*; therefore if linkage was present the *SN* and *sn* classes should have a similar number than is expected with independent inheritance which is not the case. The calculated value of $p$ by Yule's Coefficient of Association was .4730. On these bases the conclusion may be made that the factor pair *Ss* for long and short haired rachilla and the factor pair *Nn* for covered and naked seed are inherited independently.

### *Covered versus naked seed (Nn) and non-six-rowed versus six-rowed (Vv)*

The factor pairs *Nn* and *Vv* were studied in a cross between Colsess and *H. deficiens nudideficiens.* Table 25 presents the $F_2$ data for covered *versus* naked seed and non-six-rowed *versus* six-rowed.

TABLE 25

*Segregation in $F_2$ for covered versus naked seed and non-six-rowed versus six-rowed.*

| | $VN$ | $Vn$ | $vN$ | $vn$ | $X^2$ | $P$ |
|---|---|---|---|---|---|---|
| Observed | 315 | 97 | 94 | 31 | 1.35 | .7212 |
| *Calculated* | *302* | *100.7* | *100.7* | *33.6* | | |

The data in table 25 indicate that the factor pair $Nn$ is inherited independently of the factor pair $Vv$.

## INTERRELATIONS OF CHLOROPHYLL DEFICIENCIES WITH OTHER BOTANICAL CHARACTERS

### *Green versus white seedlings ($A_ta_t$) and black versus white glume color ($Bb$)*

In a cross between Trebi and Minnesota 90–5 the factor pairs studied were in the coupling phase. The Trebi parent was white glumed and carried the factor for white seedlings. The Minnesota 90–5 parent was black glumed and was homozygous for green seedlings. The $F_2$ segregation for green *versus* white seedlings and black *versus* white glumes is given in table 26.

TABEL 26

*Segregation in $F_2$ jor green versus white seedlings and black versus whte glume color.*

| | $A_tB$ | $A_tB$ | $a_tB$—$a_tb$ | $X^2$ | $P$ |
|---|---|---|---|---|---|
| Observed | 447 | 68 | 157 | 40.01 | very low |
| *Calculated* (*9:3:4*) | *378* | *126* | *168* | | |

The white seedling plants died and only the green plants survived to maturity. It will be observed that the white glumed class has fewer plants than are expected with independent inheritance and the fit to a calculated 9:3:4 ratio is very poor. Two of the classes were eliminated by the death of the white seedlings. To calculate the linkage value: Collins' formula $p=\sqrt{\frac{AB-2Ab}{AB+Ab}}$ in which the crossover value is calculated from two classes was used. The crossover percentage obtained by this method was 22.29 percent. The observed data are compared with the theoretical on the basis of a crossover value of 22.29 percent (see table 27).

TABLE 27

*Comparison of observed and calculated on the basis of a C. O. value of 22.29 per cent for the characters green versus white seedlings ($A_ta_t$) black versus white glumes in a cross between Trebi and Minnesota 90–5.*

| | $A_tB$ | $A_tb$ | $a_tB$——$a_tb$ | CALCULATED CROSSOVER PERCENT | $X^2$ | P |
|---|---|---|---|---|---|---|
| Observed | 447 | 68 | 157 | 22.29 | 1.00 | .6065 |
| *Calculated* | *436* | *68* | *168* | | | |

The agreement between observed and calculated was good and apparently the factor pair $A_ta_t$ and $Bb$ are linked.

*Green versus white seedlings ($A_ca_c$) and black versus white glume color ($Bb$)*

Crosses between Colsess×*H. distichon nigrinudum*, Colsess×Minnesota 90–5, and Colsess×Minnesota 90–8 were studied. Table 28 gives the observed and calculated ratio for the factor pairs concerned.

TABLE 28

*Segregation in $F_2$ of green versus whit seedlings $A_ca_c$ and black versus white glume color.*

| CROSS | | $A_cB$ | $A_cb$ | $a_cB$——$a_cb$ | $X^2$ | P |
|---|---|---|---|---|---|---|
| Colsess×*H. dis. nig.* | obs. | 1953 | 690 | 812 | 5.88 | .0537 |
| | *cal.* | *1943* | *648* | *864* | | |
| Colsess×Minn. 90–5 | obs. | 1283 | 408 | 518 | 3.53 | .1766 |
| | *cal.* | *1243* | *414* | *552* | | |
| Colsess×Minn. 90–8 | obs. | 434 | 178 | 181 | 7.60 | .0231 |
| | *cal.* | *446* | *149* | *198* | | |

In this case as in other crosses the number of white seedlings is lower than calculated on a 3:1 basis. As no striking deviation is found in the other two classes it is evident that the factor pair for black *versus* white glume color is inherited independent of the $A_ca_c$ factor pair for chlorophyl development. It will be remembered that the factor pair in Colsess for green *versus* white seedlings, $A_ca_c$, was independent of that in Trebi, $A_ta_t$, and that $A_ta_t$ from Trebi was linked with a factor pair ($Bb$) for black *versus* white glumes.

*Green versus white seedlings ($A_ca_c$) and hoods versus awns ($Kk$)*

Studies were made in crosses between Colsess×*H. distichon nigrinudum*, Colsess×Minnesota 90–5 and Colsess×Minnesota 90–8. The cross was made in the repulsion phase. If linkage is present the $a_cK$ and $A_ck$ classes would be larger than for independent inheritance. The plants having the recessive condition $a_ca_c$ would die in the seedling stage. With simple Mendelian independent inheritance and an absence of linkage a 9:3:4 ratio would be expected. Table 29 presents the expected and calculated ratios in $F_2$.

TABLE 29

*Segregation in $F_2$ for the characters green versus white seedlings and hoods versus awns.*

| | | $A_cK$ | $A_ck$ | $a_cK$——$a_ck$ | $X^2$ | P |
|---|---|---|---|---|---|---|
| Colsess×*H. dis. nig.* | obs. | 1939 | 704 | 812 | 7.98 | .0185 |
| | *cal.* | *1943* | *648* | *864* | | |
| Colsess×*H. def. nud.* | obs. | 1053 | 397 | 479 | 4.43 | .1135 |
| | *cal.* | *1085* | *362* | *482* | | |
| Colsess×Minnesota 90-5 | obs. | 1269 | 422 | 518 | 2.84 | .2463 |
| | *cal.* | *1243* | *414* | *552* | | |
| Colsess×Minnesota 90-8 | obs. | 435 | 175 | 181 | 6.43 | .0405 |
| | *cal.* | *446* | *149* | *198* | | |

The above data gives a fair fit to the calculated ratio 9:3:4. There is a slightly higher number of individuals in the green awned class and a slightly lower number in the green hooded class than is expected with independent inheritance. This slight deviation is persistent in all four crosses and suggests a linkage with a high percentage of crossing over.

TABLE 30

*$F_2$ segregations for green versus white seedlings and hoods versus awns and calculated linkage values for the different crosses.*

| CROSS | $A_cK$ | $A_ck$ | $a_cK$——$a_ck$ | Calculated Crossover Percent |
|---|---|---|---|---|
| Colsess×*H. dis. nig.* | 1939 | 704 | 812 | 44.82 |
| Colsess×*H. def. nud.* | 1053 | 397 | 479 | 42.26 |
| Colsess×Minnesota 90-5 | 1269 | 422 | 518 | 50.13 |
| Colsess×Minnesota 90-8 | 435 | 175 | 181 | 37.32 |
| Total | 4696 | 1698 | 1990 | 45.09 |

The calculated linkage value was obtained from Collins' formulae $p=\sqrt{\frac{AB-2Ab}{AB+Ab}}$ for use when there is difficulty in distinguishing any two classes. Considerable variation was found in the calculated percentage of crossing over in the different crosses. The white seedling class is lower than calculated on a 3:1 basis and there is evidently some gametic elimination of the white seedling classes. The calculated results for independent inheritance was obtained from a gametic ratio for the factors for green and white seedlings of 1.0525 to 1. This ratio was calculated from the phenotypic ratio of green to white seedlings of 3.213:1 which was obtained from these crosses. In comparing observed with theoretical on the basis of 45.09 crossing over it was considered also that the functional gametes bearing the factors for green and white seedlings were in the ratio of 1.0525 to 1. The $X^2$ value for the linkage with 45.09 percent crossing over is .01 and P is very large while the $X^2$ value for independent inheritance is 8.17 with a P value of .0042 (see table 31).

TABLE 31

*Observed and calculated ratios for independent inheritance and 45.09 percent crossing over.*

| RATIO | $A_cK$ | $A_ck$ | $a_cK$—$a_ck$ | $X^2$ | P* |
|---|---|---|---|---|---|
| Observed | 4696 | 1698 | 1990 | | |
| *Independent inheritance* | *4795* | *1599* | *1990* | 8.17 | .0042 |
| *45.09 percent crossing over* | *4692* | *1702* | *1990* | .01 | very large |

* P was obtained from table of $X^2$ where n=2.

### *Green versus white seedlings ($A_ca_c$) and long versus short haired rachilla (Ss)*

Studies were made in crosses between Colsess×*H. deficiens nudideficiens*, Colsess×Minnesota 90–5 and Colsess×Minnesota 90–8. Table 32 presents the $F_2$ segregation for green *versus* white seedlings and long *versus* short haired rachilla.

While some slight deviations from the calculated 9:3:4 ratio were found, no consistent variation was observed except for the classes of white seedlings which were lower than calculated in each case. The $X^2$ for the crosses between Colsess and the Minnesota selections was 4.02 and 5.61 with values of .1353 and .0624 respectively. In the cross between Colsess and *H. deficiens nudideficiens* the value of $X^2$ is 0.80, which gives a value of P which is very large. These data indicate that the factor pair $A_ca_c$ for green and white seedlings is inherited independently of the factor pair for long and short haired rachilla.

TABLE 32

*Segregation in $F_2$ for green versus white seedlings and long versus short haired rachillas in crosses between Colsess×H. deficiens nudideficiens, Colsess×Minnesota 90–5 and Colsess×Minnesota 90–8.*

| CROSS | | $A_cS$ | $A_cS$ | $a_cS$——$a_cs$ | $X^2$ | P |
|---|---|---|---|---|---|---|
| Colsess×*H. def. nud.* | obs. | 1073 | 377 | 479 | 0.80 | large |
| | *cal.* | *1085* | *362* | *482* | | |
| Colsess×Minn. 90–5 | obs. | 249 | 442 | 518 | 4.02 | .1353 |
| | *cal.* | *1243* | *414* | *552* | | |
| Colsess×Minn. 90–8 | obs. | 479 | 133 | 181 | 5.61 | .0624 |
| | *cal.* | *446* | *149* | *198* | | |

## *Green versus white seedlings ($A_ta_t$) and long versus short haired rachilla (Ss)*

Studies were made in a cross between Trebi and Minnesota 90–5. The results are given in table 33.

TABLE 33

*Segregation in $F_2$ for green versus white seedlings ($A_ta_t$) and long vs. short haired rachilla (Ss).*

| | $A_tS$ | $A_ts$ | $a_tS$——$a_ts$ | $X^2$ | P |
|---|---|---|---|---|---|
| Observed | 388 | 127 | 157 | 0.98 | large |
| *Calculated* | *378* | *126* | *168* | | |

The observed ratio fits the calculated 9:3:4 ratio very well, $X^2$ being 0.98. This indicates clearly that the factor pair $A_ta_t$ is inherited independently of the factor pair *Ss*.

## *Green versus white seedlings ($A_ca_c$) and covered versus naked seed (Nn)*

The inheritance of the interrelations of green *versus* white seedlings and covered *versus* naked seeds were studied in crosses between Colsess ×*H. distichon nigrinudum* and Colsess×*H. deficiens nudideficiens*. In the above crosses one parent was homozygous for the green seedling and naked seed factors and the other heterozygous for the factor pair for green *versus* white seedlings and homozygous for the covered seed factor. The $F_2$ segregation agrees well with the calculated ratio of 9:3:4, $X^2$ being 4.23 for the cross Colsess×*H. distichon nigrinudum* and 0.51 for the Colsess ×*H. deficiens nudideficiens* cross. The calculated value of P was .1231 for the former and very large for the latter cross. (See table 34.)

TABLE 34

*Segregation of $F_2$ for green versus white seedlings and cover versus naked seed.*

| CROSS | | $A_cN$ | $A_cn$ | $a_cN$—$a_cn$ | $X^2$ | P |
|---|---|---|---|---|---|---|
| Colsess×*H. dis. nig.* | obs. | 1975 | 668 | 812 | 4.23 | .1231 |
| | *cal.* | *1943* | *648* | *864* | | |
| Colsess×*H. def. nud.* | obs. | 1076 | 374 | 479 | 0.51 | large |
| | *cal.* | *1085* | *362* | *482* | | |

It is evident from the above data that the factor pair $A_ca_c$ is inherited independently of the factor pair *Nn*.

### *Green versus white seedling ($A_ca_c$) and non-six-rowed versus six-rowed (Vv)*

This study of interrelations was made in a cross between Colsess×*H. distichon nigrinudum*. Table 35 gives the $F_2$ segregation for green *versus* white seedlings and non-six-rowed *versus* six-rowed.

TABLE 35

*Segregation of $F_2$ for green versus white seedlings and non-six-rowed versus six rowed.*

| | $A_cV$ | $A_cv$ | $a_cV$—$a_cV$ | $X^2$ | P |
|---|---|---|---|---|---|
| Observed | 483 | 141 | 195 | 2.58 | .2839 |
| *Calculated (9:3:4)* | *460.7* | *153.6* | *204.8* | | |

The data presented in table 35 clearly indicate that the factor pair $A_ca_c$ is inherited independently of the factor pair *Vv*.

## SUMMARY

1. Simple Mendelian inheritance was found for the following factor pairs: black *versus* white glume color (*Bb*), hoods *versus* awns (*Kk*), covered *versus* naked seed (*Nn*), non-six-rowed *versus* six-rowed (*Vv*), long *versus* short-haired rachilla (*Ss*), green *versus* white seedlings ($A_ca_c$), green *versus* white seedlings ($A_ta_t$) and green *versus* xantha seedlings ($X_cx_c$).

2. A two-factor difference was found for fertility of the lateral florets in crosses involving Colsess, a six-rowed barley, and *H. deficiens nudideficiens*, Colsess × Minnesota 90–5. Colsess evidently has the genetic constitution *vv* II while *H. deficiens nudideficiens* and Minnesota 90–5 the genetic constitution *VV* ii.

3. Three genetically different seedling chlorophyll deficiencies are inherited as simple Mendelian recessives. These chlorophyll deficiencies are designated as follows: white $a_ta_t$, white $a_ca_c$, and xantha $x_cx_c$.

4. Two complementary factors for chlorophyll production were found in a strain of Colsess. One factor pair was found to be $A_c a_c$; further studies will be made with the other pair.

5. Independent Mendelian inheritance was found between the following character pairs: black versus white glume color, hoods versus awns, covered versus naked seed, non six-rowed versus six-rowed, and long versus short-haired rachilla.

6. Studies of the interrelation of chlorophyll deficiencies and other characters indicate two probable linkage groups:

(a) Green *versus* white seedlings $A_c a_c$, green *versus* xantha seedlings $X_c x_c$, and possibly hoods *versus* awns *Kk*.

(b) Black *versus* white glume color *Bb* and green *versus* white seedlings $A_t a_t$.

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