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# A Diallelic Study of Six Chaff Variations in Wheat

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# A DIALLELIC STUDY OF SIX CHAFF VARIATIONS IN WHEAT

by

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Royal Jay Swenson

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# INTRODUCTION

The colors of the glumes on wheat have been described as being white, yellow, brown, or black. The white actually ranges from cream or pale straw-yellow to dark yellow. Some varieties have white or yellow glumes with brown or black nerves.

Yellow chaff color may range from a buff to a bronze. Brown chaff color ranges from light brown to dark brown and bluish brown. In some varieties, there is a reddish or mahogany tinge. Black-glumed wheats are rare in America. No common varieties are known that possess black glumes. Under dry conditions, they may only be tinged and may be more of a blue than a black (Clark, Martin, and Ball, 1922).

Although genetic studies involving chaff color in wheat are quite common, little information is available on the interrelationships and inheritance patterns of the six chaff color combinations used in this study. Such information is useful to the plant breeder by adding to his knowledge of the breeding behavior of wheat.

This study is a genetic investigation of six chaff color variants crossed in all 15 possible combinations. The purpose was to gain information pertaining to the interrelationships and inheritance of chaff color in wheat.

## REVIEW OF LITERATURE

The inheritance of chaff color in wheat has been reported by numerous investigators. Some of the classifications reported are: white, yellow, light bronze, bronze, dark bronze, buff, grey, mouse-grey, black, light brown, medium brown, dark brown, mahogany, and red.

Dr. Spillman, Washington State College, studied chaff color inheritance from 1899-1901. Without knowledge of Mendel's Laws of Inheritance, Dr. Spillman made 14 crosses and studied the $F_1$ and $F_2$ generations. In crossing brown and white chaffed varieties, he noticed in the $F_1$ that they were all brown. In the $F_2$ generation, he reported that brown chaff and light chaff color segregated into a 3:1 ratio, brown being dominant over white. He also reported a 1:2:1 ratio of one brown parental type, two intermediate browns, and one white parental type (Johnson, 1948).

Biffen (1905) in Cambridge, England, found brown dominant over white in the ratio of three brown to one white. Clark (1924) reported the results of a cross between brown chaff color and white chaff color. When Hard Federation (brown chaff) was used as the female parent and Kota (white chaff) as the male, a very close three brown to one white, simple Mendelian ratio, was obtained. When the reciprocal cross was made, the ratio was two brown to one white. Other investigators reported monogenic inheritance of brown versus white chaff color, resulting in a ratio of three brown to one white (Hayes, 1918; Clark and Hooker, 1926; and Worzella, 1942).

Fultz Mediterranean (white chaff), when crossed with Harvest King (red chaff), gave red dominant, the $F_2$ segregating into a 3:1 ratio. When Turkey Red (white chaff) was crossed with Harvest King, the $F_1$ generation was an intermediate. The $F_2$ gave one red, two intermediates, and one white. Reciprocal crosses gave similar results. In a cross involving Black Winter Emmer (black chaff) and Fultz Mediterranean, the $F_1$ gave an intermediate mulatto black. Segregation in the $F_2$ was somewhat varied. Red and brown chaff appeared, neither color having been visible in either of the parents. Considering colored and non-colored only, segregation approached a 3:1 ratio (Kezer and Boyack, 1918). Similar results were reported by Spillman (1902), Harrington (1922), and Tingey, Woodward, and Stewart (1934).

Tingey (1924) studied Dicklow (white chaff) crossed with Hard Federation (bronze chaff). All plants displaying any tinge of reddish-brown made up the group called "bronze." All plants lacking this color were called "white." In $F_3$ he got a 3:1 ratio, bronze being dominant over white glume color. Dhesi (1950) studied the $F_2$ and $F_3$ of a cross involving bronze versus white chaff color. In the $F_2$ both parental types were recovered as well as an intermediate group. The intermediate group in the $F_3$ was segregated into three types—the parental bronze type, the parental white type, and an intermediate type. Stewart and Tingey (1928) and Dewey (1956) also studied bronze versus white chaff color and reported a 3:1 ratio, bronze being dominant over white.

Biffen (1916) studied Rivet Wheat (mouse-grey chaff color) X a white chaffed common wheat and got a 3:1 ratio, grey being dominant over white. When Rivet was crossed with another grey chaffed wheat, the $F_2$ showed grey, black, and white chaffed plants. No ratio was mentioned.

Variations from the normal 3:1 ratio have been reported. Mortenson (1922), after a study of three crosses, reports a nine bronze to seven white ratio in the $F_2$ generation. Separating the $F_2$ generation into dark bronze, medium-bronze, light bronze, and white from a white X bronze cross, Beach (1923) reports a 9:3:3:1 ratio.

In crossing a wild type Emmer wheat with a Durum wheat, Love and Craig (1919) reported a 15:1 ratio for brown over white. In this cross, two plants characteristic of the wild type appeared in the $F_2$ segregates. Seed from these two plants was sown, and one plant produced progeny that segregated approximately 3:1 for brown and white. It was assumed that two genes, $R_1$ and $R_2$, produced the brown color. When acting together, they have a cumulative effect with $R_1$ being a darker brown than $R_2$.

Matsuura (1929) summarized the work done by 24 investigators on chaff color inheritance. He described the glumes of wheat as being black, brown, or yellow. The black included various shades from black to grey, the brown included shades of brown to red, and the yellow included shades of dark yellow to white.

Fifteen of the 24 authors, each studying brown chaff color crossed with white chaff color, concluded that the difference between brown and yellow is monogenic, brown being dominant. However, two other authors reported a 15:1 ratio, brown being dominant over white in the $F_2$ generation when Spelta was crossed with Brown Vulgare and Yellow Durum was crossed with Brown Vulgare.

In a study of white chaff X brown chaff by Kressling and Lindhart, reported by Matsuura (1929), several instances were found where the inheritance of brown chaff color did not follow the ordinary Mendelian rules. The white plants often gave some brown plants in a complicated ratio.

Five of the 24 authors reported studies involving yellow chaff X black chaff color. When Black Turgidum was crossed with Yellow Vulgare, and Black Emmer crossed with White Vulgare, the ratios were three black or nearly black to one yellow. However, when Black Emmer (Dicoccum) was crossed with a yellow chaffed Sphaerococcum, the $F_2$ gave black, brown, and yellow chaff and chaff with tints of these colors in the outer margins. Black proved to be dominant to brown and white.

Matsuura (1929) also reported work by Vavilov and Jakushkina in which they experimented with a series of crosses between a black Persian wheat and several yellow and brown chaff colors. They showed that black differs from brown or red by a single gene. In the $F_2$ from a black Persian X Red Dicoccum cross they obtained black, brown, and yellow in a dihybrid ratio of 12:3:1. The gene for black pigment proved epistatic to the gene for red; the absence of both black and red resulted in white chaff color.

Three of the 24 authors reviewed a cross between Polish wheat (white chaff) X grey chaffed Turgidum and found white dominant to grey.

# MATERIALS AND METHODS

The crosses used in this study were made at Logan in the spring of 1957. Six selections exhibiting different chaff color combinations were used as parents. All of the six, with the exception of Brevor, were selected from genetic stocks and are fully awned.

Crosses were made in all combinations among six chaff color variants: white, bronze, and types designated as light bronze-white, brown-white, black-white, and black-bronze. Two rather distinct color series were noted on the same head--one affecting color expression in the outer florets of each spikelet and the other determining the color of the central florets. Color expression in the outer chaff ranged from black through white, including such intermediates as brown, bronze, and light bronze. Color expression in the central florets was limited to either bronze or white.

In referring to the chaff color combinations used in this study, the first word always refers to the color exhibited in the outer florets of each spikelet, or the outer chaff color. The second word always signifies the color expressed by the inner florets, or the inner chaff color. The bronze and white parents have only a single word description since no difference could be detected between outer and inner chaff color.

Brevor wheat, a standard variety of the area, was chosen as one of the parents. It possesses yellowish-white outer and inner chaff color. No color difference can be detected between the outer and inner florets. This variety is considered the white parent in this study.

The selection 217-19-5, one of the parental selections, possesses yellowish-tan outer chaff color and white inner chaff color, with a rather distinct color break between the two colors. This selection is referred to hereafter as the light bronze-white parent.

The selection 193a-465-1-2 has a dark bronze color in both outer and inner florets. No color separation can be seen between the outer and inner florets.

The brown parental selection exhibits dark brown outer chaff color. The brown plants used as parents appear to have been segregating for white and bronze inner chaff color. In some crosses, a brown-white plant was apparently used, and in other crosses a brown-bronze plant was involved. Both types are known to exist within this selection, and they cannot be distinguished at the time of pollination. This parent is designated as brown-white or brown-bronze, depending on the cross.

The two selections 198-7-5 and 198-4-2 both possess black outer chaff color. However, the inner florets differ in color, 198-7-5 being bronze and 198-4-2 being white. The selection 198-7-5 is referred to as the black-bronze parent and 198-4-2 is designated as the black-white parent.

Letters were assigned to each parent for purposes of abbreviation. Table 1 shows the parental selections, color combination, and letter designation of each of the six parents. Table 2 summarizes cross numbers, parental selections, and identifying symbols used in this study.

In the fall of 1957, the $F_0$ seed was space planted one foot apart to permit the production of a large number of kernels.

When the resulting $F_1$ plants were mature, each plant was harvested and threshed individually. Care was taken to assure that no mixing

Table 1. Selection numbers, color combinations, and letter designations of the six parents

| Selection | Color combination | Letter |
|---|---|---|
| Brevor | White | A |
| 217-19-5 | Light bronze-white | B |
| 193a-465-1-2 | Bronze | C |
| Brown | Brown-white or -bronze | D |
| 198-4-2 | Black-white | E |
| 198-7-5 | Black-bronze | F |

Table 2. Cross numbers, parental selections, and identifying symbols used in this study

| Cross | Parents | Color combinations of parents* | Letter symbols of crosses |
|---|---|---|---|
| 558 | 198-7-5 x brown | Black-bronze x brown-white | F x D |
| 559 | 217-19-5 x brown | L. bronze-white x brown-white | B x D |
| 561 | Brown x 198-4-2 | Brown-bronze x black-white | D x E |
| 562 | Brevor x 193a-465-1-2 | White x bronze | A x C |
| 563 | Brown x Brevor | Brown-white x white | D x A |
| 564 | Brevor x 217-19-5 | White x L. bronze-white | A x B |
| 565 | 217-19-5 x 198-4-2 | L. bronze-white x black-white | B x E |
| 566 | 193a-465-1-2 x 198-4-2 | Bronze x black-white | C x E |
| 567 | 198-4-2 x 198-7-5 | Black-white x black-bronze | E x F |
| 569 | 217-19-5 x 198-7-5 | L. bronze-white x black-bronze | B x F |
| 570 | 193a-465-1-2 x brown | Bronze x brown-white | C x D |
| 571 | 193a-465-1-2 x 198-7-5 | Bronze x black-bronze | C x F |
| 572 | 193a-465-1-2 x 217-19-5 | Bronze x l. bronze-white | C x B |
| 574 | Brevor x 198-4-2 | White x black-white | A x E |
| 575 | 198-7-5 x Brevor | Black-bronze x white | F x A |

* The first term of a hyphenated color combination refers to outer chaff and the second term to inner chaff color.

took place between seeds of different plants. This was done to detect possible self-fertilized plants and to keep $F_2$ families separate.

The $F_2$'s were planted in the fall of 1958. Each cross was planted in rows one foot apart and 400 feet in length. Each row was divided into five 80 foot sections. In most instances, a different family was planted in each section. Every third row was left unplanted to facilitate taking notes and observing the plants.

The $F_2$'s were planted with a V-belt seeder. Seeds were spaced approximately five to six inches apart in the row.

At maturity, when the color could be classified, the plants were pulled individually, bundled into families, and labeled. The plants were stored in a closed shed until classification. Identification of the characters was made during the fall of 1959. Each family was classified and recorded separately in order to check the consistency of the inheritance pattern from family to family within a cross.

Ricker mounts were made showing both parental types and a typical $F_1$ head. A color description was attached to the ricker mounts. This was done so that a good visual example, plus a written description, would be available for comparison with the $F_2$ plants during classification.

Plants from the crosses involving the awnless parent, Brevor, were classified as awned or awnless. All crosses were classified on the basis of outer and inner chaff color. Natural sunlight was used in making the classifications. As each cross was recorded, the appropriate ricker mount was in view.

The data presented in this thesis were obtained from a study of the $F_2$ generation. Analysis of the data consisted of chi-square calculations for goodness of fit to hypothesized ratios. Individual chi-squares were calculated for each family, and a total chi-square was computed on each cross. A chi-square was also computed on the pooled data for each cross. An interaction chi-square was calculated to check the consistency or inconsistency from family to family (Snedecor, 1950).

# EXPERIMENTAL RESULTS

When classifying the $F_2$ plants, more classes were used to describe the outer chaff color than are used in the presentation of the data. For example, three variations of brown were used: (1) light brown, (2) medium brown, and (3) dark brown. The black outer chaff was classed as: (1) black or (2) light speckled black. Two separations of outer chaff color were made for the bronze color: (1) medium bronze and (2) dark bronze. Only one outer chaff color classification each was made for the light bronze and the white classes.

A certain range of color variation was nearly always present among the individual heads of a single plant; consequently, plants were classified into their respective groups on the basis of the color exhibited by the majority of the heads. For purposes of analysis, all of the various outer chaff color classifications were grouped into five major color categories: black, brown, bronze, light bronze, and white. Thus "black" includes the black and speckled black classes; "brown" includes the light, medium, and dark brown classes; and "bronze" includes dark and medium bronze.

The central florets were either bronze or white, so only the two categories were necessary for inner chaff color.

Whenever segregation for both outer and inner chaff color was taking place, a simultaneous classification was made. Segregation for inner chaff color was observed within all classes of outer chaff color except bronze and white. No white central florets were observed in plants with bronze outer chaff, nor were bronze central florets observed in plants with white outer chaff; consequently, the double classification was not possible on white or bronze plants.

## Awns Versus Awnlessness

Awn inheritance is only incidental to this study; however, since segregation for this character was taking place in several crosses, opportunity was taken to add to the information presently available on awn inheritance. In crosses involving the awnless parent, Brevor, the $F_1$ plants were awnless, indicating the dominance of awnlessness over the awned condition. Short beaks and awn-tipped plants are here considered awnless. Table 3 summarizes the $F_2$ data for awn inheritance in crosses between Brevor and five awned parents.

Segregation for awn type can be explained on a monogenic basis. Individual family chi-squares, as well as the pooled chi-square data, fit the expected 3:1 ratio well. A small interaction chi-square value indicates homogeneity from cross to cross.

## Inheritance of Chaff Color

Chaff color data will be presented in three major groups. The crosses are grouped according to similarities in segregation patterns.

### 9:3:3:1 chaff color segregation

Crosses 558, 561, and 569 were segregating for both outer and inner chaff color. Data on inheritance patterns are presented by cross.

Cross 558 (F x D). Cross 558 involves black-bronze and brown-white parents. The $F_1$ plants exhibited medium brown outer chaff color and bronze inner chaff color. This indicates brown outer chaff is

Table 3. $F_2$ inheritance of awn type

| Cross | Family | Awnless Obs. | Awnless Exp.* | Awned Obs. | Awned Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|
| 562 | 1 | 102 | 95.25 | 25 | 31.75 | 127 | 1 | 1.9133 | .10 -.20 |
| | 2 | 77 | 78.75 | 28 | 26.25 | 105 | 1 | .1556 | .50 -.70 |
| | 3 | 74 | 78.75 | 31 | 26.25 | 105 | 1 | 1.1461 | .20 -.30 |
| | 4 | 60 | 61.50 | 22 | 20.50 | 82 | 1 | .1477 | .70 -.80 |
| | 5 | 70 | 69.75 | 23 | 23.25 | 93 | 1 | .0036 | .95 -.98 |
| 563 | 1 | 73 | 75.00 | 27 | 25.00 | 100 | 1 | .2133 | .50 -.70 |
| | 2 | 80 | 74.25 | 19 | 24.75 | 99 | 1 | 1.7810 | .10 -.20 |
| | 3 | 69 | 72.00 | 27 | 24.00 | 96 | 1 | .5000 | .30 -.50 |
| | 4 | 57 | 60.75 | 24 | 20.25 | 81 | 1 | .9257 | .30 -.50 |
| | 5 | 59 | 59.25 | 20 | 19.75 | 79 | 1 | .0043 | .90 -.95 |
| 564 | 1 | 100 | 106.50 | 42 | 35.50 | 142 | 1 | 1.5868 | .20 -.30 |
| | 2 | 91 | 92.25 | 36 | 31.75 | 127 | 1 | .0661 | .70 -.80 |
| | 3 | 81 | 81.00 | 27 | 27.00 | 108 | 1 | .0000 | .99-1.00 |
| | 4 | 61 | 61.50 | 21 | 20.50 | 82 | 1 | .0163 | .80 -.90 |
| | 5 | 102 | 93.75 | 23 | 31.25 | 125 | 1 | 2.9040 | .05 -.10 |
| 574 | 1 | 46 | 48.75 | 19 | 16.25 | 65 | 1 | .6250 | .30 -.50 |
| | 2 | 44 | 44.25 | 15 | 14.75 | 59 | 1 | .0057 | .80 -.90 |
| | 3 | 18 | 16.50 | 4 | 5.50 | 22 | 1 | .5455 | .30 -.50 |
| | 4 | 12 | 12.75 | 5 | 4.25 | 17 | 1 | .1767 | .50 -.70 |
| 575 | Composite | 10 | 9.75 | 3 | 3.25 | 13 | 1 | .2309 | .50 -.70 |
| Total $X^2$ | | | | | | | 20 | 12.9431 | .80 -.90 |
| Pooled $X^2$ | | 1287 | 1295.25 | 440 | 431.75 | 1727 | 1 | .2102 | .50 -.70 |
| Interaction $X^2$ | | | | | | | 19 | 12.7329 | .80 -.90 |

* Expected on the hypothesis of a 3:1 ratio.

dominant to black outer chaff color, and bronze inner chaff color is dominant to white inner chaff color.

Brown versus black outer chaff color (table 4) fits a 3:1 ratio in $F_2$. Bronze inner chaff versus white inner chaff (table 5) also fits a 3:1 ratio. To test inheritance patterns of outer and inner chaff color in combination, a 9:3:3:1 ratio was hypothesized (table 6). The close correspondence of observed and expected values, as evidenced by the high probability values, supports the suggested ratio and indicates the independent inheritance of outer and inner chaff color.

Cross 561 (D x E). Cross 561 is a cross between brown-bronze and black-white parents. The $F_1$ plants showed medium brown outer chaff and bronze inner chaff color, again indicating that brown outer chaff is dominant to black outer chaff color, and that bronze inner chaff is dominant to white inner chaff color.

In $F_2$ brown outer chaff dominated black outer chaff color (table 7), and bronze inner chaff dominated white inner chaff color in a 3:1 ratio (table 8).

A 9:3:3:1 hypothesized ratio was calculated to test inheritance of outer and inner chaff color in combination (table 9). The low chi-square values again indicate independent inheritance of the outer and inner chaff colors.

Cross 569 (B x F). Cross 569 involves light bronze-white and black-bronze parents. The $F_1$ plants possessed light speckled black outer chaff with the inner chaff color being bronze, which indicates that black is dominant to light bronze outer chaff, and again that bronze is dominant over white inner chaff color.

Tables 10 and 11 show a 3:1 segregation of black outer chaff over light bronze outer chaff color and a 3:1 segregation of bronze inner

Table 4. $F_2$ inheritance of black x brown outer chaff color (Cross 558)

| Family | Brown outer chaff | | Black outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 1 | 69 | 70.50 | 25 | 23.50 | 94 | 1 | .0992 | .70 -.80 |
| 2 | 60 | 63.75 | 25 | 21.25 | 85 | 1 | .8821 | .30 -.50 |
| 3 | 47 | 48.00 | 17 | 16.00 | 64 | 1 | .0833 | .70 -.80 |
| 4 | 69 | 69.00 | 23 | 23.00 | 92 | 1 | .0000 | .99-1.00 |
| 5 | 61 | 64.50 | 25 | 21.50 | 86 | 1 | .7597 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 1.8243 | .80 -.90 |
| Pooled $X^2$ | 306 | 315.75 | 115 | 105.25 | 421 | 1 | 1.2043 | .20 -.30 |
| Interaction $X^2$ | | | | | 421 | 4 | .6200 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

Table 5. $F_2$ inheritance of bronze x white inner chaff color (Cross 558)

| Family | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 1 | 68 | 70.50 | 26 | 23.50 | 94 | 1 | .3547 | .50 -.70 |
| 2 | 62 | 63.75 | 23 | 21.25 | 85 | 1 | .1921 | .50 -.70 |
| 3 | 48 | 48.00 | 16 | 16.00 | 64 | 1 | .0000 | .99-1.00 |
| 4 | 70 | 69.00 | 22 | 23.00 | 92 | 1 | .0580 | .80 -.90 |
| 5 | 64 | 64.50 | 22 | 21.50 | 86 | 1 | .0155 | .90 -.95 |
| Total $X^2$ | | | | | | 5 | .6203 | .98 -.99 |
| Pooled $X^2$ | 312 | 315.75 | 109 | 105.25 | 421 | 1 | .1781 | .50 -.70 |
| Interaction $X^2$ | | | | | 421 | 4 | .4422 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

Table 6. Combination of outer and inner chaff color inheritance in Cross 558 (black-bronze x brown-white, F x D)

| Family | Brown outer chaff | | | | Black outer chaff | | | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | Bronze inner | | White inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 50 | 52.875 | 19 | 17.625 | 18 | 17.625 | 7 | 5.875 | 94 | 3 | .4870 | .90 -.95 |
| 2 | 44 | 47.817 | 16 | 15.939 | 18 | 15.939 | 7 | 5.313 | 85 | 3 | 1.1075 | .70 -.80 |
| 3 | 35 | 36.000 | 12 | 12.000 | 13 | 12.000 | 4 | 4.000 | 64 | 3 | .1111 | .99-1.00 |
| 4 | 52 | 51.750 | 17 | 17.250 | 18 | 17.250 | 5 | 5.750 | 92 | 3 | .1352 | .98 -.99 |
| 5 | 45 | 48.375 | 16 | 16.125 | 19 | 16.125 | 6 | 5.375 | 86 | 3 | .8217 | .80 -.90 |
| Total $X^2$ | | | | | | | | | | 15 | 2.6625 | .99-1.00 |
| Pooled $X^2$ | 226 | 236.813 | 80 | 78.939 | 86 | 78.939 | 29 | 26.313 | 421 | 3 | 1.4217 | .70 -.80 |
| Interaction $X^2$ | | | | | | | | | 421 | 12 | 1.2408 | .99-1.00 |

* Expected on the hypothesis of a 9:3:3:1 ratio.

Table 7. $F_2$ inheritance of brown x black outer chaff color (Cross 561)

| Family | Brown outer chaff Obs. | Brown outer chaff Exp.* | Black outer chaff Obs. | Black outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 70 | 72.00 | 26 | 24.00 | 96 | 1 | .2223 | .50 -.70 |
| 2 | 94 | 92.25 | 29 | 30.75 | 123 | 1 | .1328 | .70 -.80 |
| 3 | 71 | 72.00 | 25 | 24.00 | 96 | 1 | .0556 | .80 -.90 |
| 4 | 64 | 60.75 | 17 | 20.25 | 81 | 1 | .6955 | .30 -.50 |
| 5 | 77 | 74.25 | 22 | 24.75 | 99 | 1 | .4075 | .50 -.70 |
| Total $X^2$ | | | | | | 5 | 1.5137 | .90 -.95 |
| Pooled $X^2$ | 376 | 371.25 | 119 | 123.75 | 495 | 1 | .2431 | .50 -.70 |
| Interaction $X^2$ | | | | | 495 | 4 | 1.2706 | .80 -.90 |

* Expected on the hypothesis of a 3:1 ratio.

Table 8. $F_2$ inheritance of bronze x white inner chaff color (Cross 561)

| Family | Bronze inner chaff Obs. | Bronze inner chaff Exp.* | White inner chaff Obs. | White inner chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 71 | 72.00 | 25 | 24.00 | 96 | 1 | .0556 | .80 -.90 |
| 2 | 91 | 92.25 | 32 | 30.75 | 123 | 1 | .0677 | .70 -.80 |
| 3 | 71 | 72.00 | 25 | 24.00 | 96 | 1 | .0556 | .80 -.90 |
| 4 | 61 | 60.75 | 20 | 20.25 | 81 | 1 | .0041 | .90 -.95 |
| 5 | 76 | 74.25 | 23 | 24.75 | 99 | 1 | .1649 | .50 -.70 |
| Total $X^2$ | | | | | | 5 | .3479 | .99-1.00 |
| Pooled $X^2$ | 370 | 371.25 | 125 | 123.75 | 495 | 1 | .0168 | .80 -.90 |
| Interaction $X^2$ | | | | | 495 | 4 | .3311 | .98 -.99 |

* Expected on the hypothesis of a 3:1 ratio.

Table 9. Combination of outer and inner chaff color inheritance in Cross 561 (brown-bronze x black-white, D x E)

| Family | Brown outer chaff | | | | Black outer chaff | | | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | Bronze inner | | White inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 52 | 54.000 | 18 | 18.000 | 19 | 18.000 | 7 | 6.000 | 96 | 3 | .2934 | .95 -.98 |
| 2 | 69 | 69.186 | 25 | 23.063 | 22 | 23.063 | 7 | 7.688 | 123 | 3 | .2726 | .95 -.98 |
| 3 | 50 | 54.000 | 21 | 18.000 | 21 | 18.000 | 4 | 6.000 | 96 | 3 | 1.9866 | .50 -.70 |
| 4 | 49 | 45.563 | 15 | 15.188 | 12 | 15.188 | 5 | 5.063 | 81 | 3 | .9314 | .80 -.90 |
| 5 | 59 | 55.688 | 18 | 18.563 | 17 | 18.563 | 5 | 6.188 | 99 | 3 | .5734 | .90 -.95 |
| Total $X^2$ | | | | | | | | | | 15 | 4.0574 | .99-1.00 |
| Pooled $X^2$ | 279 | 278.437 | 97 | 92.814 | 91 | 92.814 | 28 | 30.939 | 495 | 3 | .4849 | .90 -.95 |
| Interaction $X^2$ | | | | | | | | | 495 | 12 | 3.5725 | .98 -.99 |

* Expected on the hypothesis of a 9:3:3:1 ratio.

Table 10. $F_2$ inheritance of light bronze x black outer chaff color (Cross 569)

| Family | Black outer chaff Obs. | Black outer chaff Exp.* | L.brz.outer chaff Obs. | L.brz.outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 142 | 135.50 | 36 | 44.50 | 178 | 1 | 1.5758 | .20 -.30 |
| 2 | 107 | 111.00 | 41 | 37.00 | 148 | 1 | .5765 | .30 -.50 |
| 3 | 101 | 95.25 | 26 | 31.75 | 127 | 1 | 1.3884 | .20 -.30 |
| 4 | 107 | 109.50 | 39 | 36.50 | 146 | 1 | .2283 | .50 -.70 |
| 5 | 90 | 91.50 | 32 | 30.50 | 122 | 1 | .0984 | .70 -.80 |
| Total $X^2$ | | | | | | 5 | 3.8674 | .50 -.70 |
| Pooled $X^2$ | 547 | 540.75 | 174 | 180.25 | 721 | 1 | .2901 | .50 -.70 |
| Interaction $X^2$ | | | | | 721 | 4 | 3.5773 | .30 -.50 |

* Expected on the hypothesis of a 3:1 ratio.

Table 11. $F_2$ inheritance of bronze x white inner chaff color (Cross 569)

| Family | Bronze inner chaff Obs. | Bronze inner chaff Exp.* | White inner chaff Obs. | White inner chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 136 | 135.50 | 42 | 44.50 | 178 | 1 | .1865 | .50 -.70 |
| 2 | 111 | 111.00 | 37 | 37.00 | 148 | 1 | .0000 | .99-1.00 |
| 3 | 97 | 95.25 | 30 | 31.75 | 127 | 1 | .1287 | .70 -.80 |
| 4 | 110 | 109.50 | 36 | 36.50 | 146 | 1 | .0095 | .90 -.95 |
| 5 | 90 | 91.50 | 32 | 30.50 | 122 | 1 | .0984 | .70 -.80 |
| Total $X^2$ | | | | | | 5 | .4231 | .99-1.00 |
| Pooled $X^2$ | 544 | 540.75 | 177 | 180.25 | 721 | 1 | .0781 | .70 -.80 |
| Interaction $X^2$ | | | | | 721 | 4 | .3450 | .98 -.99 |

* Expected on the hypothesis of a 3:1 ratio.

chaff over white inner chaff color.

To test for independent inheritance of outer and inner chaff color, the goodness of fit to a 9:3:3:1 ratio was again calculated. As shown in table 12, the suggested independence ratio fits the observed data.

In all three crosses both outer and inner chaff color appeared controlled by single but separate factor pairs. The observed numbers fit the expected values quite well. Small interaction chi-square values show the material is consistent from family to family, and validates the combination of data to obtain pooled chi-squares.

<u>3:1 chaff color segregation</u>

Crosses 559, 563, 564, 565, 571, and 574 were segregating only for outer chaff color since the parents involved possess the same inner chaff color (both white or both bronze).

<u>Cross 559 (B x D)</u>. Cross 559 is a cross between light bronze-white and brown-white parents. The $F_1$ plants exhibited medium brown outer chaff color and white inner chaff color, pointing to the dominance of brown over light bronze in the outer chaff color. $F_2$ segregation is presented in table 13, and the observed values fit a 3:1 ratio.

<u>Cross 563 (D x A)</u>. Cross 563 is a cross between brown-white and white parents. The $F_1$ plants possessed light brown color in the outer chaff and white inner chaff color. This indicates brown outer chaff color is dominant to white outer chaff color.

A comparison of the observed and expected values is presented in table 14. The low chi-square values obtained support the suggested 3:1 ratio.

Table 12. Combination of outer and inner chaff color inheritance in Cross 569 (black-bronze x light bronze-white, B x F)

| Family | Black outer chaff | | | | Light bronze outer chaff | | | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | Bronze inner | | White inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 109 | 100.125 | 33 | 33.375 | 27 | 33.375 | 9 | 11.125 | 178 | 3 | 1.3186 | .70 -.80 |
| 2 | 79 | 83.250 | 28 | 27.750 | 32 | 27.750 | 9 | 9.250 | 148 | 3 | .8268 | .80 -.90 |
| 3 | 76 | 71.442 | 25 | 23.814 | 21 | 23.814 | 5 | 7.938 | 127 | 3 | 1.5081 | .50 -.70 |
| 4 | 80 | 82.125 | 27 | 27.375 | 30 | 27.375 | 9 | 9.125 | 146 | 3 | .3135 | .95 -.98 |
| 5 | 67 | 68.625 | 23 | 22.875 | 23 | 22.875 | 9 | 7.625 | 122 | 3 | .2903 | .95 -.98 |
| Total $X^2$ | | | | | | | | | | 15 | 4.2573 | .99-1.00 |
| Pooled $X^2$ | 411 | 405.567 | 136 | 135.189 | 133 | 135.189 | 41 | 45.063 | 721 | 3 | .4794 | .90 -.95 |
| Interaction $X^2$ | | | | | | | | | 721 | 12 | 3.7779 | .98 -.99 |

* Expected on the hypothesis of a 9:3:3:1 ratio.

Table 13. $F_2$ inheritance of light bronze x brown outer chaff color (Cross 559)

| Family | Brown outer chaff Obs. | Exp.* | L.brz.outer chaff Obs. | Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 92 | 91.50 | 30 | 30.50 | 122 | 1 | .0109 | .80 -.90 |
| 2 | 79 | 86.25 | 36 | 28.75 | 115 | 1 | 2.4334 | .10 -.20 |
| 3 | 74 | 82.50 | 36 | 27.50 | 110 | 1 | 3.5031 | .05 -.10 |
| 4 | 76 | 75.00 | 24 | 25.00 | 100 | 1 | .5333 | .30 -.50 |
| 5 | 65 | 68.25 | 26 | 22.75 | 91 | 1 | .6191 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 7.0998 | .20 -.30 |
| Pooled $X^2$ | 386 | 403.50 | 152 | 134.50 | 538 | 1 | 3.0360 | .05 -.10 |
| Interaction $X^2$ | | | | | 538 | 4 | 4.0638 | .30 -.50 |

* Expected on the hypothesis of a 3:1 ratio.

Table 14. $F_2$ inheritance of brown x white outer chaff color (Cross 563)

| Family | Brown outer chaff Obs. | Exp.* | White outer chaff Obs. | Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 75 | 75.00 | 25 | 25.00 | 100 | 1 | .0000 | .99-1.00 |
| 2 | 73 | 74.25 | 26 | 24.75 | 99 | 1 | .0837 | .70 -.80 |
| 3 | 70 | 72.00 | 26 | 24.00 | 96 | 1 | .2223 | .50 -.70 |
| 4 | 56 | 60.75 | 25 | 20.25 | 81 | 1 | 1.4856 | .20 -.30 |
| 5 | 59 | 59.25 | 20 | 19.75 | 79 | 1 | .0042 | .90 -.95 |
| Total $X^2$ | | | | | | 5 | 1.7958 | .70 -.80 |
| Pooled $X^2$ | 333 | 341.25 | 122 | 113.75 | 455 | 1 | .8027 | .30 -.50 |
| Interaction $X^2$ | | | | | 455 | 4 | .9931 | .90 -.95 |

* Expected on the hypothesis of a 3:1 ratio.

Cross 564 (A x B). Cross 564 involves white and light bronze-white parents. The $F_1$ plants had light bronze color in the outer chaff and white in the inner chaff, indicating the dominance of light bronze over white outer chaff color. The segregation pattern for the $F_2$ is presented in table 15. If observed and expected values are compared, they support a 3:1 ratio.

Cross 565 (B x E). Cross 565 a cross involving light bronze-white and black-white parents gave $F_1$ plants with light speckled black outer chaff color and white inner chaff color. The coloring in the $F_1$ indicates that black is dominant over light bronze outer chaff color. $F_2$ segregation is presented in table 16. Observed numbers fit the expected 3:1 ratio.

Cross 571 (C x F). Cross 571 is a cross between bronze and black-bronze parents. The $F_1$ plants exhibited light speckled black outer chaff color and bronze inner chaff color. This points out that black is dominant to bronze outer chaff color.

A comparison of the observed and expected values is presented in table 17. The segregation fits a 3:1 ratio closely.

Cross 574 (A x E). Cross 574 involves parents with white and black-white chaff colors. The $F_1$ plants possessed light speckled black outer chaff color and white inner chaff color, indicating black is dominant to white outer chaff color. The $F_2$ segregation pattern presented in table 18 fits the 3:1 suggested ratio.

The outer chaff colors represented in this group are apparently controlled by allelic genes at a single locus. In all six crosses, the observed segregation fits the expected 3:1 ratio quite well. Small interaction chi-square values show consistency from family to family and validates the combination of data to obtain a pooled

Table 15. $F_2$ inheritance of white x light bronze outer chaff color (Cross 564)

| Family | L. brz. outer chaff Obs. | L. brz. outer chaff Exp.* | White outer chaff Obs. | White outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 104 | 105.50 | 38 | 35.50 | 142 | 1 | .2348 | .50 -.70 |
| 2 | 97 | 95.25 | 30 | 31.75 | 127 | 1 | .1286 | .70 -.80 |
| 3 | 79 | 81.00 | 29 | 27.00 | 108 | 1 | .1975 | .50 -.70 |
| 4 | 61 | 61.50 | 21 | 20.50 | 82 | 1 | .0163 | .80 -.90 |
| 5 | 99 | 93.75 | 26 | 31.25 | 125 | 1 | 1.1760 | .20 -.30 |
| Total $X^2$ | | | | | | 5 | 1.7532 | .80 -.90 |
| Pooled $X^2$ | 440 | 438.00 | 144 | 146.00 | 584 | 1 | .0365 | .80 -.90 |
| Interaction $X^2$ | | | | | 584 | 4 | 1.7167 | .70 -.80 |

* Expected on the hypothesis of a 3:1 ratio.

Table 16. $F_2$ inheritance of light bronze x black outer chaff color (Cross 565)

| Family | Black outer chaff Obs. | Black outer chaff Exp.* | L. brz. outer chaff Obs. | L. brz. outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 96 | 96.00 | 32 | 32.00 | 128 | 1 | .0000 | .99-1.00 |
| 2 | 117 | 120.75 | 44 | 40.25 | 161 | 1 | .4658 | .30 -.50 |
| 3 | 82 | 77.25 | 21 | 25.75 | 103 | 1 | 1.1682 | .20 -.30 |
| 4 | 81 | 83.25 | 30 | 27.75 | 111 | 1 | .2429 | .50 -.70 |
| 5 | 79 | 81.75 | 30 | 27.25 | 109 | 1 | .3700 | .50 -.70 |
| Total $X^2$ | | | | | | 5 | 2.2468 | .80 -.90 |
| Pooled $X^2$ | 455 | 459.00 | 157 | 153.00 | 612 | 1 | .1394 | .70 -.80 |
| Interaction $X^2$ | | | | | 612 | 4 | 2.1074 | .70 -.80 |

* Expected on the hypothesis of a 3:1 ratio.

Table 17. $F_2$ inheritance of bronze x black outer chaff color (Cross 571)

| Family | Black outer chaff Obs. | Black outer chaff Exp.* | Bronze outer chaff Obs. | Bronze outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 114 | 115.50 | 40 | 38.50 | 154 | 1 | .0779 | .70 -.80 |
| 2 | 110 | 108.00 | 34 | 36.00 | 144 | 1 | .1481 | .50 -.70 |
| 3 | 83 | 81.75 | 26 | 27.25 | 109 | 1 | .0765 | .70 -.80 |
| 4 | 97 | 98.00 | 31 | 32.00 | 128 | 1 | .0415 | .80 -.90 |
| 5 | 85 | 84.75 | 28 | 28.25 | 113 | 1 | .0029 | .95 -.98 |
| Total $X^2$ | | | | | | 5 | .3469 | .99-1.00 |
| Pooled $X^2$ | 489 | 486.00 | 159 | 162.00 | 648 | 1 | .0741 | .70 -.80 |
| Interaction $X^2$ | | | | | 648 | 4 | .2728 | .99-1.00 |

* Expected on the hypothesis of a 3:1 ratio.

Table 18. $F_2$ inheritance of white x black outer chaff color (Cross 574)

| Family | Black outer chaff Obs. | Black outer chaff Exp.* | White outer chaff Obs. | White outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 47 | 48.75 | 18 | 16.25 | 65 | 1 | .2513 | .50 -.70 |
| 2 | 44 | 44.25 | 15 | 14.75 | 59 | 1 | .0057 | .90 -.95 |
| 3 | 17 | 16.50 | 5 | 5.50 | 22 | 1 | .0608 | .80 -.90 |
| 4 | 13 | 12.75 | 4 | 4.25 | 17 | 1 | .0196 | .80 -.90 |
| Total $X^2$ | | | | | | 4 | .3374 | .98 -.99 |
| Pooled $X^2$ | 121 | 122.25 | 42 | 40.75 | 163 | 1 | .0511 | .80 -.90 |
| Interaction $X^2$ | | | | | 163 | 3 | .2863 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

chi-square. The only cases where significant deviations from the expected ratios were approached, were families two and three of Cross 559. It is probable that the difficulty in accurate classification of the light brown and the light bronze segregates is responsible for the larger than usual deviations.

Special segregation patterns

As pointed out under materials and methods, two exceptions to the apparently independent inheritance of outer and inner chaff color were noted. Plants classified as bronze (medium or dark bronze classes) never exhibited white center florets, nor did plants possessing white outer chaff ever exhibit bronze center florets. Crosses 562, 566, 570, 572, and 575 involve parents which possess white and bronze chaff in certain critical combinations.

Inner chaff segregation patterns in these crosses are modified by the apparent masking effect that bronze outer chaff has on the expression of white in the central florets, and by the apparent lack of pigment development in the central florets of white chaffed plants. If the assumptions are made that normal genetic segregation for inner chaff coloration takes place in these crosses, but, that bronze color in the outer chaff masks the expression of white in the center florets, and that white chaffed plants are incapable of developing or expressing bronze color in the center florets, logical ratios can be suggested for the observed segregation patterns.

Cross 562 (A x C). Cross 562 involves the bronze and white parents and shows no segregation for inner chaff color. The $F_1$ plants showed bronze outer and inner chaff, indicating bronze chaff color is dominant to white chaff color.

Bronze versus white outer chaff color is apparently controlled by a single factor pair, giving a 3:1 ratio in $F_2$ (table 19). The interaction chi-square value shows consistency from family to family, and justifies the combination of data to obtain a pooled chi-square.

Inner chaff color was identical with outer chaff color, as would be expected on the basis of the two assumptions made at the beginning of this section.

Cross 566 (C x E). Cross 566 is a cross between bronze and black-white parents. The $F_1$ plants possessed black outer and bronze inner chaff color, indicating that black outer chaff color is dominant over bronze outer chaff, and that bronze inner chaff color is again dominant over white inner chaff color.

Outer chaff color in the $F_2$ segregated three black to one bronze (table 20).

The observed segregation for bronze versus white inner chaff also fits the expected 13:3 ratio (table 21).

In testing for independent inheritance of outer and inner chaff color in Cross 566, the 9:3:3:1 ratio is not applicable, inasmuch as the "1" would represent a bronze-white plant, which phenotypically does not exist in this cross. In keeping with the assumption that white centers are masked by bronze outer chaff, the expected independence ratio would now be 9:3:4. The observed data are consistent with this hypothesis, as is evidenced by table 22.

The application of the 9:3:4 and 13:3 ratios to the data from Cross 566 can possibly be seen best in terms of suggested genotypes. Letting $Br_3$ represent black outer chaff, $Br_2$ represent bronze outer chaff, B represent bronze inner chaff, and b represent white inner chaff, the ratios can be demonstrated in table 23.

Table 19. $F_2$ inheritance of bronze x white outer chaff color (Cross 562)

| Family | Bronze outer chaff Obs. | Bronze outer chaff Exp.* | White outer chaff Obs. | White outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 90 | 95.25 | 37 | 31.75 | 127 | 1 | 1.1575 | .20 -.30 |
| 2 | 73 | 78.75 | 32 | 26.25 | 105 | 1 | 1.6794 | .10 -.20 |
| 3 | 78 | 78.75 | 27 | 26.25 | 105 | 1 | .0286 | .80 -.90 |
| 4 | 64 | 61.50 | 18 | 20.50 | 82 | 1 | .4064 | .50 -.70 |
| 5 | 73 | 69.75 | 20 | 23.25 | 93 | 1 | .6079 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 3.8798 | .50 -.70 |
| Pooled $X^2$ | 378 | 384.00 | 134 | 128.00 | 512 | 1 | .3750 | .50 -.70 |
| Interaction $X^2$ | | | | | 512 | 4 | 3.5048 | .30 -.50 |

* Expected on the hypothesis of a 3:1 ratio.

Table 20. $F_2$ inheritance of bronze x black outer chaff color (Cross 566)

| Family | Black outer chaff Obs. | Black outer chaff Exp.* | Bronze outer chaff Obs. | Bronze outer chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 102 | 104.25 | 37 | 34.75 | 139 | 1 | .1943 | .50 -.70 |
| 2 | 76 | 79.50 | 30 | 26.50 | 106 | 1 | .6164 | .30 -.50 |
| 3 | 65 | 65.25 | 22 | 21.75 | 87 | 1 | .0039 | .95 -.98 |
| 4 | 97 | 98.25 | 34 | 32.75 | 131 | 1 | .0636 | .80 -.90 |
| 5 | 84 | 88.25 | 34 | 29.50 | 118 | 1 | .9152 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 1.7934 | .80 -.90 |
| Pooled $X^2$ | 424 | 435.75 | 157 | 145.25 | 581 | 1 | 1.3534 | .20 -.30 |
| Interaction $X^2$ | | | | | 581 | 4 | .4400 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

Table 21. $F_2$ inheritance of bronze x white inner chaff color (Cross 566)

| Family | Bronze inner chaff Obs. | Bronze inner chaff Exp.* | White inner chaff Obs. | White inner chaff Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 113 | 112.938 | 26 | 26.063 | 139 | 1 | .0185 | .80 -.90 |
| 2 | 83 | 86.125 | 23 | 19.875 | 106 | 1 | .6047 | .30 -.50 |
| 3 | 67 | 70.688 | 20 | 16.313 | 87 | 1 | .8347 | .30 -.50 |
| 4 | 102 | 106.438 | 29 | 24.563 | 131 | 1 | .9911 | .30 -.50 |
| 5 | 98 | 95.875 | 20 | 22.125 | 118 | 1 | .2512 | .50 -.70 |
| Total $X^2$ | | | | | | 5 | 2.7002 | .70 -.80 |
| Pooled $X^2$ | 463 | 472.063 | 118 | 108.938 | 581 | 1 | .9279 | .30 -.50 |
| Interaction $X^2$ | | | | | 581 | 4 | 1.7723 | .70 -.80 |

* Expected on the hypothesis of a 13:3 ratio.

Table 22. Combination of outer and inner chaff color inheritance in Cross 566 (bronze x black-white, C x E)

| Family | Black outer chaff | | | | Bronze outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | Bronze inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 76 | 78.188 | 26 | 26.063 | 37 | 34.75 | 139 | 2 | .2219 | .80 -.90 |
| 2 | 53 | 59.625 | 23 | 19.875 | 30 | 26.50 | 106 | 2 | 1.6897 | .30 -.50 |
| 3 | 45 | 48.938 | 20 | 16.313 | 22 | 21.75 | 87 | 2 | 1.1533 | .50 -.70 |
| 4 | 68 | 73.688 | 29 | 24.563 | 34 | 32.75 | 131 | 2 | 1.2884 | .50 -.70 |
| 5 | 64 | 66.375 | 20 | 22.125 | 34 | 29.50 | 118 | 2 | .9755 | .50 -.70 |
| Total $X^2$ | | | | | | | | 10 | 5.3288 | .80 -.90 |
| Pooled $X^2$ | 306 | 326.813 | 118 | 108.939 | 157 | 145.25 | 581 | 2 | 3.0298 | .20 -.30 |
| Interaction $X^2$ | | | | | | | 581 | 8 | 2.2990 | .95 -.98 |

* Expected on the hypothesis of a 9:3:4 ratio.

Table 23. Suggested genotype, phenotype, and segregation patterns in the $F_2$ of Cross 566

| Genotype[a] | Relative number | Color outer-inner | Combination of outer-inner ratio | Inner chaff color ratio |
|---|---|---|---|---|
| $Br_3Br_3BB$ | 1 | Black-bronze | 9 black-bronze | |
| $Br_3Br_3Bb$ | 2 | Black-bronze | | 13 bronze |
| $Br_3Br_3bb$ | 1 | Black-white | | |
| $Br_3Br_2BB$ | 2 | Black-bronze | 3 black-white | |
| $Br_3Br_2Bb$ | 4 | Black-bronze | | |
| $Br_3Br_2bb$ | 2 | Black-white | | 3 white |
| $Br_2Br_2BB$ | 1 | Bronze | 4 bronze | |
| $Br_2Br_2Bb$ | 2 | Bronze | | |
| $Br_2Br_2bb$ | 1 | Bronze[b] | | |

a $Br_3$ = black outer chaff color, $Br_2$ = bronze outer chaff color, B = bronze inner chaff color, and b = white inner chaff color.

b Genotypically bronze-white, but since bronze outer chaff masks white inner chaff, this plant is phenotypically bronze.

Cross 570 (C x D). Cross 570 is a cross involving bronze and brown-white parents. The $F_1$ plants had medium brown outer chaff and bronze inner chaff, indicating that brown outer chaff color is dominant to bronze outer chaff color. Again bronze inner chaff was dominant over white inner chaff.

The comparison of brown versus bronze outer chaff fits a 3:1 ratio, and bronze inner chaff color versus white inner chaff color conforms to an expected 13:3 ratio (tables 24 and 25).

The $F_2$ segregation patterns in Cross 570 were similar to those just discussed for Cross 566. The suggested 9:3:4 ratio fits the observed data rather closely (table 26), and it indicates independence in the inheritance of the two color systems.

Table 27 shows the suggested genotypes and the application of the 9:3:4 and 13:3 ratios.

Cross 572 (C x B). Cross 572 has the bronze and light bronze-white selections as parents. $F_1$ plants showed bronze outer chaff and bronze inner chaff color. This indicates that bronze outer chaff is dominant to light bronze outer chaff color. It also indicates that bronze inner chaff color is dominant to white inner chaff color.

In $F_2$ the segregation for bronze versus light bronze outer chaff fits the expected 3:1 ratio (table 28). The observed segregation for bronze versus white inner chaff also fits the expected 15:1 ratio (table 29).

The combination ratio of outer and inner chaff colors differ from any of the previous crosses discussed, however. They also fall into consistent, predictable ratios (table 30) if the previously stated assumption is made, that bronze outer chaff masks the expression of white in the central florets. Using $Br_2$ to represent bronze and

Table 24. $F_2$ inheritance of bronze x brown outer chaff color (Cross 570)

| Family | Brown outer chaff Obs. | Exp.* | Bronze outer chaff Obs. | Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 56 | 57.00 | 20 | 19.00 | 76 | 1 | .0702 | .70 -.80 |
| 2 | 58 | 60.75 | 23 | 20.25 | 81 | 1 | .4980 | .30 -.50 |
| 3 | 40 | 38.25 | 11 | 12.75 | 51 | 1 | ..3221 | .50 -.70 |
| 4 | 59 | 60.00 | 21 | 20.00 | 80 | 1 | .0667 | .70 -.80 |
| 5 | 71 | 67.50 | 19 | 22.50 | 90 | 1 | .7259 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 1.6829 | .80 -.90 |
| Pooled $X^2$ | 284 | 283.50 | 94 | 94.50 | 378 | 1 | .0035 | .95 -.98 |
| Interaction $X^2$ | | | | | 378 | 4 | 1.6794 | .70 -.80 |

* Expected on the hypothesis of a 3:1 ratio.

Table 25. $F_2$ inheritance of bronze x white inner chaff color (Cross 570)

| Family | Bronze inner chaff Obs. | Exp.* | White inner chaff Obs. | Exp. | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| 1 | 61 | 61.750 | 15 | 14.250 | 76 | 1 | .0486 | .80 -.90 |
| 2 | 66 | 65.813 | 15 | 15.188 | 81 | 1 | .0028 | .95 -.98 |
| 3 | 42 | 41.438 | 9 | 9.563 | 51 | 1 | .0407 | .80 -.90 |
| 4 | 66 | 65.000 | 14 | 15.000 | 80 | 1 | .0820 | .70 -.80 |
| 5 | 74 | 73.125 | 16 | 16.875 | 90 | 1 | .0558 | .80 -.90 |
| Total $X^2$ | | | | | | 5 | .2299 | .99-1.00 |
| Pooled $X^2$ | 309 | 307.125 | 69 | 70.875 | 378 | 1 | .0611 | .80 -.90 |
| Interaction $X^2$ | | | | | 378 | 4 | .1688 | .99-1.00 |

* Expected on the hypothesis of a 13:3 ratio.

Table 26. Combination of outer and inner chaff color inheritance in Cross 570 (bronze x brown-white, C x D)

| Family | Brown outer chaff | | | | Bronze outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | Bronze inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 41 | 42.75 | 15 | 14.25 | 20 | 19.00 | 76 | 2 | .1637 | .90 -.95 |
| 2 | 43 | 45.54 | 15 | 15.18 | 23 | 20.24 | 81 | 2 | .5302 | .70 -.80 |
| 3 | 31 | 28.71 | 9 | 9.57 | 11 | 12.76 | 51 | 2 | .4594 | .70 -.80 |
| 4 | 45 | 45.00 | 14 | 15.00 | 21 | 20.00 | 80 | 2 | .1167 | .90 -.95 |
| 5 | 55 | 50.60 | 16 | 16.88 | 19 | 22.50 | 90 | 2 | .9729 | .50 -.70 |
| Total $X^2$ | | | | | | | | 10 | 2.2424 | .99-1.00 |
| Pooled $X^2$ | 215 | 212.62 | 69 | 70.88 | 94 | 94.50 | 378 | 2 | .0788 | .70 -.80 |
| Interaction $X^2$ | | | | | | | 378 | 8 | 2.1641 | .98 -.99 |

* Expected on the hypothesis of a 9:3:4 ratio.

Table 27. Suggested genotype, phenotype, and segregation patterns in the $F_2$ of Cross 570

| Genotype[a] | Relative number | Color outer-inner | Combination of outer-inner ratio | Inner chaff color ratio |
|---|---|---|---|---|
| $Br_4Br_4BB$ | 1 | Brown-bronze | 9 brown-bronze | |
| $Br_4Br_4Bb$ | 2 | Brown-bronze | | |
| $Br_4Br_4bb$ | 1 | Brown-white | | 13 bronze |
| $Br_4Br_2BB$ | 2 | Brown-bronze | | |
| $Br_4Br_2Bb$ | 4 | Brown-bronze | 3 brown-white | |
| $Br_4Br_2bb$ | 2 | Brown-white | | 3 white |
| $Br_2Br_2BB$ | 1 | Bronze | | |
| $Br_2Br_2Bb$ | 2 | Bronze | 4 bronze | |
| $Br_2Br_2bb$ | 1 | Bronze[b] | | |

a $Br_4$ = brown outer chaff color, $Br_2$ = bronze outer chaff color, B = bronze inner chaff color, and b = white inner chaff color.

b Genotypically bronze-white, but since bronze outer chaff color masks white inner chaff, this plant is phenotypically bronze.

Table 28. $F_2$ inheritance of bronze x light bronze outer chaff color (Cross 572)

| Family | Bronze outer chaff | | L. brz. outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 1 | 59 | 59.25 | 20 | 19.75 | 79 | 1 | .0042 | .90 -.95 |
| 2 | 71 | 69.75 | 22 | 23.25 | 93 | 1 | .0896 | .80 -.90 |
| 3 | 45 | 42.75 | 12 | 14.25 | 57 | 1 | .4737 | .30 -.50 |
| 4 | 50 | 52.50 | 20 | 17.50 | 70 | 1 | .4761 | .30 -.50 |
| 5 | 56 | 59.25 | 23 | 19.75 | 79 | 1 | .7131 | .30 -.50 |
| Total $X^2$ | | | | | | 5 | 1.7567 | .80 -.90 |
| Pooled $X^2$ | 281 | 283.50 | 97 | 94.50 | 378 | 1 | .1728 | .50 -.70 |
| Interaction $X^2$ | | | | | 378 | 4 | 1.5839 | .80 -.90 |

* Expected on the hypothesis of a 3:1 ratio.

Table 29. $F_2$ inheritance of bronze x white inner chaff color (Cross 572)

| Family | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 1 | 74 | 74.07 | 5 | 4.94 | 79 | 1 | .0011 | .95 -.98 |
| 2 | 88 | 87.20 | 5 | 5.81 | 93 | 1 | .1189 | .70 -.80 |
| 3 | 55 | 53.45 | 2 | 3.56 | 57 | 1 | .1133 | .70 -.80 |
| 4 | 65 | 65.63 | 5 | 4.38 | 70 | 1 | .0952 | .70 -.80 |
| 5 | 73 | 73.07 | 6 | 4.94 | 79 | 1 | .2473 | .50 -.70 |
| Total $X^2$ | | | | | | 5 | .5758 | .98 -.99 |
| Pooled $X^2$ | 355 | 354.44 | 23 | 23.63 | 378 | 1 | .1768 | .50 -.70 |
| Interaction $X^2$ | | | | | 378 | 4 | .3990 | .98 -.99 |

* Expected on the hypothesis of a 15:1 ratio.

Table 30. Combination of outer and inner chaff color inheritance in Cross 572 (bronze x light bronze-white, C x B)

| Family | Bronze outer chaff | | Light bronze outer chaff | | | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | Bronze inner | | White inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | | | | |
| 1 | 59 | 59.244 | 15 | 14.811 | 5 | 4.938 | 79 | 2 | .0042 | .95 -.98 |
| 2 | 71 | 69.756 | 17 | 17.439 | 5 | 5.813 | 93 | 2 | .1489 | .90 -.95 |
| 3 | 45 | 42.756 | 10 | 10.689 | 2 | 3.563 | 57 | 2 | .6006 | .70 -.80 |
| 4 | 50 | 52.500 | 15 | 13.125 | 5 | 4.375 | 70 | 2 | .4000 | .80 -.90 |
| 5 | 56 | 59.244 | 17 | 14.814 | 6 | 4.938 | 79 | 2 | .7299 | .50 -.70 |
| Total $X^2$ | | | | | | | | 10 | 1.8836 | .99-1.00 |
| Pooled $X^2$ | 281 | 283.500 | 74 | 70.875 | 23 | 23.625 | 378 | 2 | .1764 | .90 -.95 |
| Interaction $X^2$ | | | | | | | 378 | 8 | 1.7072 | .98 -.99 |

* Expected on the hypothesis of a 12:3:1 ratio.

$Br_1$ to represent light bronze outer chaff color, and B and b to represent bronze and white inner chaff color, respectively, the suggested genotypes and expected phenotypic ratios based on this assumption are shown in table 31.

Cross 575 (F x A). Cross 575 is a cross between black-bronze and white parents. The $F_1$ plants possessed light speckled black outer chaff color and bronze inner chaff color. This indicates black outer chaff is dominant to white outer chaff, and bronze inner chaff is dominant to white.

A severe dwarfing characteristic showed up in the $F_1$ and $F_2$ of Cross 575. The $F_1$'s were dwarfed and produced only a small amount of shrivelled seed. Most of the resulting $F_2$'s were severely dwarfed and most failed to head. Only 13 plants headed and matured to a point where a color classification could be made.

Segregation occurred for both outer and inner chaff colors, and although no valid conclusions can be drawn from a population this small, the observed segregation was consistent with the patterns and assumptions thus far discussed.

The outer chaff color segregation fits the hypothesized ratio of three black to one white (table 32a). The inner chaff color ratio fits an expected 9:7 (table 32b). This was the only 9:7 ratio observed in this study, but was the ratio to be expected, if the assumption is true that plants with white outer chaff lack the ability to develop or express bronze color in the central florets. The combined outer and inner chaff color ratio conforms to an expected 9:3:4 (table 32c). Table 33 illustrates the derivation of the expected 9:3:4 and 9:7 ratios in Cross 575.

Table 31. Suggested genotype, phenotype, and segregation patterns in the $F_2$ of Cross 572

| Genotype[a] | Relative number | Color outer-inner | Combination of outer-inner ratio | Inner chaff color ratio |
|---|---|---|---|---|
| $Br_2Br_2BB$ | 1 | Bronze | | |
| $Br_2Br_2Bb$ | 2 | Bronze | 12 bronze | |
| $Br_2Br_2bb$ | 1 | Bronze[b] | | |
| $Br_2Br_1BB$ | 2 | Bronze | | 15 bronze |
| $Br_2Br_1Bb$ | 4 | Bronze | | |
| $Br_2Br_1bb$ | 2 | Bronze[b] | | |
| $Br_1Br_1BB$ | 1 | L. bronze-bronze | 3 L. bronze-bronze | |
| $Br_1Br_1Bb$ | 2 | L. bronze-bronze | | |
| $Br_1Br_1bb$ | 1 | L. bronze-white | 1 L. bronze-white | 1 white |

a $Br_2$ = bronze outer chaff color, $Br_1$ = light bronze outer chaff color, B and b = bronze and white inner chaff, respectively.

b Genotypically bronze-white, but phenotypically bronze.

Table 32a. $F_2$ inheritance of black x white outer chaff color (Cross 575)

| Family | Black outer chaff | | White outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| Composite | 11 | 9.75 | 2 | 3.25 | 13 | 1 | .6410 | .30 -.50 |

* Expected on the hypothesis of a 3:1 ratio.

Table 32b. $F_2$ inheritance of bronze x white inner chaff color (Cross 575)

| Family | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| Composite | 8 | 7.313 | 5 | 5.688 | 13 | 1 | .1511 | .50 -.70 |

* Expected on the hypothesis of a 9:7 ratio.

Table 32c. Combination of outer and inner chaff color inheritance in Cross 575 (black-bronze x white, F x A)

| Family | Black outer chaff | | | | White outer chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | Bronze inner | | White inner | | White inner | | | | | |
| | Obs. | Exp.* | Obs. | Exp. | Obs. | Exp. | | | | |
| Composite | 8 | 7.313 | 3 | 2.438 | 2 | 3.250 | 13 | 1 | .6742 | .70 -.80 |

* Expected on the hypothesis of a 9:3:4 ratio.

Table 33. Suggested genotype, phenotype, and segregation patterns in the $F_2$ of Cross 575

| Genotype[a] | Relative number | Color outer-inner | Combination of outer-inner ratio | Inner chaff color ratio |
|---|---|---|---|---|
| $Br_3Br_3BB$ | 1 | Black-bronze | 9 black-bronze | |
| $Br_3Br_3Bb$ | 2 | Black-bronze | | |
| $Br_3Br_3bb$ | 1 | Black-white | | 9 bronze |
| $Br_3Br_0BB$ | 2 | Black-bronze | 3 black-white | |
| $Br_3Br_0Bb$ | 4 | Black-bronze | | |
| $Br_3Br_0bb$ | 2 | Black-white | | 7 white |
| $Br_0Br_0BB$ | 1 | White[b] | | |
| $Br_0Br_0Bb$ | 2 | White[b] | 4 white | |
| $Br_0Br_0bb$ | 1 | White | | |

a $Br_3$ = black outer chaff color, $Br_0$ = white outer chaff color, B = bronze inner chaff color, and b = white inner chaff color.

b Genotypically white-bronze, but phenotypically white.

Cross 567 (E x F). Cross 567 involves black-bronze and black-white parents, and shows no segregation for outer chaff color, since both parents possess black outer chaff. However, the inner chaff color segregated bronze and white.

The $F_1$ plants exhibited bronze inner chaff color, indicating that bronze inner chaff is dominant to white. The segregation for bronze versus white inner chaff color is shown in table 34. The observed values closely fit the expected 3:1 ratio.

Table 34. $F_2$ inheritance of bronze x white inner chaff color (Cross 567)

| Family | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 1 | 113 | 112.50 | 37 | 37.50 | 150 | 1 | .0088 | .90 -.95 |
| 2 | 104 | 106.50 | 38 | 35.50 | 142 | 1 | .0763 | .70 -.80 |
| 3 | 78 | 80.25 | 27 | 26.75 | 107 | 1 | .2524 | .50 -.70 |
| 4 | 68 | 70.50 | 26 | 23.50 | 94 | 1 | .3547 | .50 -.70 |
| 5 | 73 | 73.50 | 25 | 24.50 | 98 | 1 | .0136 | .90 -.95 |
| Total $X^2$ | | | | | | 5 | .7058 | .98 -.99 |
| Pooled $X^2$ | 436 | 443.25 | 155 | 147.75 | 591 | 1 | .4744 | .30 -.50 |
| Interaction $X^2$ | | | | | 591 | 4 | .2314 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

# DISCUSSION AND SUMMARY

Tables 35, 36, and 37 summarize inheritance patterns comparing the crosses, rather than families within a cross as was done previously. Table 35 shows the inheritance of bronze versus white inner chaff color in all crosses showing a simple 3:1 ratio. The observed numbers fit the expected ratios very well. It appears that the expression of bronze and white inner chaff color is controlled by a single factor pair.

Table 36 summarizes the inheritance of bronze x white inner chaff color on a 13:3 basis when the bronze parent was involved with a parent possessing white inner chaff. Again a single gene pair appears to condition color expression in the central florets, the departure from the 3:1 ratio being explained by the suggested masking effect of bronze outer chaff color over white inner chaff.

The data on outer chaff color inheritance for all of the crosses used in this study are summarized in table 37. The five chaff colors crossed in all combinations fit a 3:1 ratio in all instances, indicating the existence of a multiple allelic series governing outer chaff color. Cross 559 comes the nearest to departing from the 3:1 ratio. This can probably be explained by the difficulty in separating light brown and light bronze plants.

Based on the results of this study, the following genotypes are suggested as a possible explanation of the observed segregation patterns for outer and inner chaff color in the six wheat selections tested.

Table 35. Summary of $F_2$ inheritance of bronze x white inner chaff color of all crosses showing 3:1 segregation patterns

| Cross | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 558 | 312 | 315.75 | 109 | 105.25 | 421 | 1 | .1781 | .50 -.70 |
| 561 | 370 | 371.25 | 125 | 123.75 | 495 | 1 | .0168 | .80 -.90 |
| 562 | 378 | 384.00 | 134 | 128.00 | 512 | 1 | .3750 | .50 -.70 |
| 567 | 436 | 443.25 | 155 | 147.75 | 591 | 1 | .4744 | .30 -.50 |
| 569 | 544 | 540.75 | 177 | 180.25 | 721 | 1 | .0781 | .70 -.80 |
| Total $X^2$ | | | | | | 5 | 1.1224 | .95 -.98 |
| Pooled $X^2$ | 2040 | 2055.00 | 700 | 685.00 | 2740 | 1 | .4379 | .50 -.70 |
| Interaction $X^2$ | | | | | 2740 | 4 | .6845 | .95 -.98 |

* Expected on the hypothesis of a 3:1 ratio.

Table 36. Summary of $F_2$ inheritance of bronze x white inner chaff color of all crosses showing 13:3 segregation patterns

| Cross | Bronze inner chaff | | White inner chaff | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Obs. | Exp. | | | | |
| 566 | 463 | 472.063 | 118 | 108.937 | 581 | 1 | .9279 | .30 -.50 |
| 570 | 309 | 307.125 | 69 | 70.875 | 378 | 1 | .6011 | .80 -.90 |
| Total $X^2$ | | | | | | 2 | .9890 | .50 -.70 |
| Pooled $X^2$ | 772 | 779.188 | 187 | 179.812 | 959 | 1 | .3536 | .50 -.70 |
| Interaction $X^2$ | | | | | 959 | 1 | .6354 | .30 -.50 |

* Expected on the hypothesis of a 13:3 ratio.

Table 37. Summary of $F_2$ inheritance of outer chaff colors of all crosses showing 3:1 segregation patterns

| Cross | Dominant outer chaff color | | | Recessive outer chaff color | | | Total plants | d.f. | $X^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | Obs. | Exp.* | Color | Obs. | Exp. | Color | | | | |
| 558 | 306 | 315.75 | Brown | 115 | 105.25 | Black | 421 | 1 | 1.2043 | .20 -.30 |
| 559 | 386 | 403.50 | Brown | 152 | 134.50 | Light bronze | 538 | 1 | 3.0360 | .05 -.10 |
| 561 | 376 | 371.25 | Brown | 119 | 123.75 | Black | 495 | 1 | .2431 | .50 -.70 |
| 562 | 378 | 384.00 | Bronze | 134 | 128.00 | White | 512 | 1 | .3750 | .50 -.70 |
| 563 | 333 | 341.25 | Brown | 122 | 113.75 | White | 455 | 1 | .8027 | .30 -.50 |
| 564 | 440 | 438.00 | Light bronze | 144 | 146.00 | White | 584 | 1 | .0365 | .80 -.90 |
| 565 | 455 | 459.00 | Black | 157 | 153.00 | Light bronze | 612 | 1 | .1394 | .70 -.80 |
| 566 | 424 | 435.75 | Black | 157 | 145.25 | Bronze | 581 | 1 | 1.3534 | .20 -.30 |
| 569 | 547 | 540.75 | Black | 174 | 180.25 | Light bronze | 721 | 1 | .2901 | .50 -.70 |
| 570 | 284 | 283.50 | Brown | 94 | 94.50 | Bronze | 378 | 1 | .0035 | .95 -.98 |
| 571 | 489 | 486.00 | Black | 159 | 162.00 | Bronze | 648 | 1 | .0741 | .70 -.80 |
| 572 | 281 | 283.50 | Bronze | 97 | 94.50 | Light bronze | 378 | 1 | .1728 | .50 -.70 |
| 574 | 121 | 122.25 | Black | 42 | 40.75 | White | 163 | 1 | .0511 | .80 -.90 |
| 575 | 11 | 9.75 | Black | 2 | 3.25 | White | 13 | 1 | .6410 | .30 -.50 |
| Total $X^2$ | | | | | | | | 14 | 8.4230 | .80 -.90 |
| Pooled $X^2$ | 4831 | 4874.25 | | 1668 | 1624.75 | | 6499 | 1 | 1.5350 | .20 -.30 |
| Interaction $X^2$ | | | | | | | 6499 | 13 | 6.8880 | .90 -.95 |

* Expected on the hypothesis of a 3:1 ratio.

The alleles governing outer chaff color are designated in all cases by the genetic symbol Br. To denote dominance of color, the symbols 4, 3, 2, 1, and 0 are used as subscripts to Br, 4 being most dominant, followed by 3, 2, 1, and 0 in descending order.

The alleles representing bronze and white inner chaff color are represented by BB and bb, respectively. The six parents than have the following suggested genotypes: $Br_4Br_4bb$ is the brown-white parent, $Br_3Br_3bb$ is the black-white parent, $Br_3Br_3BB$ denotes the black-bronze parent, $Br_2Br_2BB$ denotes the bronze parent, $Br_1Br_1bb$ is the light bronze-white parent, and $Br_0Br_0bb$ denotes the white parent.

Table 38 illustrates the phenotype and suggested genotypes of the parents involved in each of the 15 crosses used in this study. Table 39 shows the phenotype and suggested genotypes of the 15 $F_1$ populations used in this study.

Table 38. Suggested genotype and phenotype of the parental selections used in each cross

| Cross | Suggested genotype of parents | Phenotype of parents[a] |
|---|---|---|
| 558 | $Br_3Br_3BB$ x $Br_4Br_4bb$ | Black-bronze x brown-white |
| 559 | $Br_1Br_1bb$ x $Br_4Br_4bb$ | Light bronze-white x brown-white |
| 561 | $Br_4Br_4BB$* x $Br_3Br_3bb$ | Brown-bronze x black-white |
| 562 | $Br_0Br_0bb$ x $Br_2Br_2BB$ | White x bronze |
| 563 | $Br_4Br_4bb$ x $Br_0Br_0bb$ | Brown-white x white |
| 564 | $Br_0Br_0bb$ x $Br_1Br_1bb$ | White x light bronze-white |
| 565 | $Br_1Br_1bb$ x $Br_3Br_3bb$ | Light bronze-white x black-white |
| 566 | $Br_2Br_2BB$ x $Br_3Br_3bb$ | Bronze x black-white |
| 567 | $Br_3Br_3bb$ x $Br_3Br_3BB$ | Black-white x black-bronze |
| 569 | $Br_1Br_1bb$ x $Br_3Br_3BB$ | Light bronze-white x black-bronze |
| 570 | $Br_2Br_2BB$ x $Br_4Br_4bb$ | Bronze x brown-white |
| 571 | $Br_2Br_2BB$ x $Br_3Br_3BB$ | Bronze x black-bronze |
| 572 | $Br_2Br_2BB$ x $Br_1Br_1bb$ | Bronze x light bronze-white |
| 574 | $Br_0Br_0bb$ x $Br_3Br_3bb$ | White x black-white |
| 575 | $Br_3Br_3BB$ x $Br_0Br_0bb$ | Black-bronze x white |

a The first term of a hyphenated color classification refers to outer chaff and the second term to inner chaff.

* In this cross the brown parent apparently possessed bronze inner chaff, instead of the usual white.

Table 39. Suggested genotype and phenotype of $F_1$ plants

| Cross | Suggested genotype of $F_1$'s | Phenotype of $F_1$'s* |
|---|---|---|
| 558 | $Br_3Br_4Bb$ | Medium brown-bronze |
| 559 | $Br_1Br_4bb$ | Medium brown-white |
| 561 | $Br_4Br_3Bb$ | Brown-bronze |
| 562 | $Br_0Br_2Bb$ | Light brown-bronze |
| 563 | $Br_4Br_0bb$ | Light brown-white |
| 564 | $Br_0Br_1bb$ | Light bronze-white |
| 565 | $Br_1Br_3bb$ | Light speckled black-white |
| 566 | $Br_2Br_3Bb$ | Light speckled black-bronze |
| 567 | $Br_3Br_3Bb$ | Light speckled black-bronze |
| 569 | $Br_1Br_3Bb$ | Light speckled black-bronze |
| 570 | $Br_2Br_4Bb$ | Medium brown-bronze |
| 571 | $Br_2Br_4BB$ | Light speckled black-bronze |
| 572 | $Br_2Br_1Bb$ | Medium bronze-bronze |
| 574 | $Br_0Br_3bb$ | Light speckled black-white |
| 575 | $Br_3Br_0Bb$ | Light speckled black-bronze |

* The first term of hyphenated color classification refers to outer chaff and the second term to inner chaff color.

# CONCLUSIONS

Six wheat selections representing different chaff color variations were crossed in all combinations and a genetic analysis made of the $F_1$ and $F_2$ generations.

Based on the results of this study, the following observations and conclusions are drawn.

1. The outer chaff colors of brown, black, bronze, light bronze, and white are conditioned by a series of multiple alleles, with brown being most dominant, followed, in order, by black, bronze, light bronze, and white. Segregation for any two colors taken together can be explained on a single gene basis.

2. The $F_1$ plants in all crosses appeared to be lighter in color than the dominant parent, indicating dominance is not absolute.

3. Bronze and white inner chaff colors are allelic to each other, but are not allelic to the outer chaff colors.

4. Segregation for inner chaff color is also monogenic. The factors for outer and inner chaff colors are located at different loci and are inherited independently of each other.

5. Bronze pigmentation in the outer chaff apparently masks or suppresses the expression of white in the center florets.

6. Plants possessing white outer chaff apparently are unable to develop or express bronze pigmentation in the center florets.

7. All of the deviations from a 3:1 ratio for inner chaff color, or from a 9:3:3:1 ratio, when outer and inner chaff color are

considered together, can be explained on the basis of these two assumptions (items 5 and 6).

8. Awnlessness appears to be dominant over awned in a simple 3:1 ratio, when the short awns and beaked tips are classed with the awnless class.

LITERATURE CITED

Beach, F. M. 1923. Hybridization of wheat. (M. S. Thesis. Dept. of Agronomy) Utah State University, Logan, Utah.

Biffen, R. H. 1905. Mendel's law of inheritance and wheat breeding. Jour. Agr. Sci. 1: 4-48.

_______. 1916. The suppression of characters on crossing. Jour. Genetics 5: 225-228.

Clark, J. A. 1924. Segregation and correlated inheritance in crosses between Kota and Hard Federation wheats for rust and drought resistance. Jour. Agr. Res. 29: 201-202.

_______, and J. N. Hooker. 1926. Segregation of correlated inheritance in Marquis and Hard Federation crosses with factors for yield and quality of spring wheat in Montana. U. S. Dept. Agr. Bul. 1430.

_______, H. J. Martin, and R. C. Ball. 1922. Classification of American wheat varieties. U. S. Dept. Agr. Bul. 1074.

Dewey, W. G. 1956. Genetic and pathological studies with dwarf bunt of winter wheat. (Ph. D. Dissertation. Dept. of Plant Breeding) Cornell University, New York.

Dhesi, N. S. 1950. Inheritance of resistance to races of covered smut, awns, and chaff color in a wheat cross. (M. S. Thesis. Dept. of Agronomy) Utah State University, Logan, Utah

Harrington, J. B. 1922. The mode of inheritance of certain characters in wheat. Sci. Agr. 2: 319-324.

Hays, H. R. 1918. Natural cross pollination in wheat. Jour. Amer. Soc. Agron. 10: 120-122.

Johnson, L. P. V. 1948. Dr. W. J. Spillman's discoveries in genetics. Jour. Genetics 39: 51-55.

Kezer, A., and B. Boyack. 1918. Mendelian inheritance in wheat and barley crosses. Colo. Agr. Exp. Sta. Bul. 249: 1-139.

Love, H. H., and W. T. Craig. 1919. The synthetic production of wild wheat forms. Jour. Heredity 10: 51-64.

Matsuura, H. 1929. A bibliographical monograph on plant genetics (gene analysis). Tokyo Imperial University, Tokyo. Pp. 260.

Mortenson, J. L. 1922. Mendelian inheritance in wheat hybrids. (M. S. Thesis. Dept. of Agronomy) Utah State University, Logan, Utah.

Snedecor, G. W. 1950. Statistical methods. Ames, Iowa: The Iowa State College Press.

Spillman, W. J. 1902. Exceptions to Mendel's laws. Science 16: 794-796.

Stewart, G., and D. C. Tingey. 1928. Transmission and normal segregation in a cross of Marquis x Federation wheats. Jour. Amer. Soc. Agron. 20: 620-634.

Tingey, D. C. 1924. The inheritance of chaff color, head shape, and grain texture in wheat. (M. S. Thesis. Dept. of Agronomy) Utah State University, Logan, Utah.

________, R. W. Woodward, and G. Stewart. 1934. Miscellaneous genetic data from wheat crosses. Jour. Amer. Soc. Agron. 26: 249-250.

Worzella, W. W. 1942. Inheritance and interrelationships of components of quality, cold resistance, and morphological characters in wheat hybrids. Jour. of Agr. Res. 65.