Inheritance of Glume and Kernel Color, of Awnedness, and of Spike Density in a Cross Between Ridit and Sevier Wheat

Leslie W. Nelson

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INHERITANCE OF GLUME AND KERNEL COLOR, OF AWNEDNESS,
AND OF SPIKE DENSITY IN A CROSS BETWEEN RIDIT AND SEVIER WHEAT

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Submitted to the Department of Agronomy
Utah State Agricultural College

In Partial Fulfillment
of the
Requirements for the degree of
Master of Science

BY
Leslie W. Nelson
1931
ACKNOWLEDGEMENT

The writer takes this opportunity to express sincere appreciation for the help given by Dr. George Stewart, under whose direction this investigation was made.
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INHERITANCE OF GLUME AND KERNEL COLOR, OF AWNEDNESS, AND OF SPIKE DENSITY IN A CROSS BETWEEN RIDIT AND SEVIER WHEAT

**********

INTRODUCTION

This paper is devoted principally to the presentation and discussion of the results obtained when certain contrasting characters were brought together in a wheat cross between Ridit and Sevier 59. This is one of the crosses made in an attempt to develop a wheat adapted to this region with the following desirable qualities: Bunt resistance, strong straw, hard kernels, and heavy yield. How near this ideal is approached in succeeding generations can be told only by extensive tests. The genetic study herein presented was made to hasten the time when some of the progeny of this cross may become of economic value.

LITERATURE (GENERAL)

W. J. Spillman (2) working at the Washington Experiment Station was one of the first workers to try improvements in wheat by the hybridization method. The results of some of his crosses were of great economic importance in the Pacific Northwest.

Biffen (1), working at about the same time as Spillman, was the first to work on the individual character of awns in wheat. His work also showed how Mendelism could be applied in wheat breeding. Love and Craig (16), working at Cornell, reported one, two, and three factor differences in various crosses.

Florell (25) discusses a method of handling hybrids whereby populations are created by hybridization and grown in bulk for six or eight generations and then head selections made for testing in the usual way. He states that selections are made when the plants become homozygous. This ordinarily takes six or eight generations.
Of especial interest to breeders of cereals is the case reported by Stewart (21) in which rust resistance was obtained in a hybrid from two susceptible parents. Transgressive segregation for the character of rust resistance is given as the explanation.

**EXPERIMENTAL PROCEDURE**

The cross between a pure line of Sevier, known as Sevier 59, and Ridit was made at the Utah Station in 1927. The F₁ plants were grown in 1928 and the F₂ families in 1929. One of the most vigorous of these families was chosen to continue the experiment. The genetic study herein reported was made on 299 progenies from this family. The kernels from each of the 299 F₂ plants were used to seed an F₃ row. This made it possible to use the breeding behavior of the F₃ progenies as a basis for the genetic classification of the F₂ plants. This method has proved to be definitely superior to the method of classifying the F₂ material directly because so many characters exhibit such an intermediate appearance in the F₂ that it is impossible to classify all of them correctly.

The progeny rows were numbered to correspond with the F₂ plants and seeded in numerical order regardless of the appearance of the plant. The F₃ progeny rows were spaced one foot apart with a space between kernels of two to three inches. After each tenth row the two parental varieties, Sevier 59 and Ridit, were sown side by side. There were, equally spaced throughout the breeding plat, 29 rows of each parental variety. Data were taken on these parent rows in the same manner and at the same time as on the progeny rows. In all cases these data were compared to that obtained from the progeny rows.

In July 1930, the 299 ripened progeny rows, together with the 58 parental rows, were carefully pulled. Each row was tied in a separate bundle and given the same number as the F₂ plant from which it was produced. The bundles were then taken to the field house. Here each plant was examined and the data recor-
ded. The inheritance of awnedness, glume color, and kernel color was determined by observation. A leading spike from each plant was measured to determine the length of ten rachis internodes. This length was used as a basis for the study of spike density inheritance. A few rows contained less than 40 plants; most of them contained more in which case only 40 were recorded, the rest being examined for kernel color and other characters in order to be sure of obtaining representative ratios.

These data were all taken as soon as possible after harvest in order that the promising strains could be planted that fall for multiplication. During October, November, and December, 1930 and January, 1931, the data used in this paper were computed, tabulated, and summarized. No theory of inheritance was considered until all data were recorded and tabulated. Although the data taken on the F2 plants were not used in genetic classification, they proved valuable in two respects: in the first place the process of checking the F3 rows in the field was speeded up about 100 per cent by using these data, and secondly, comparison of the F2 plant with the F3 row minimized the possibility of error.

**DISCUSSION OF PARENTS**

**SEVIER 59**

Sevier 59 is a selection from the variety Sevier which was discovered and named by Stewart in Sevier County, Utah in 1918. The U. S. Department of Agriculture, Office of Cereal Investigations, later classified the wheat as a vulgare type and accepted the name.

This variety is naturally a spring wheat with a faint winter habit and hardness. The head is short, fully awned, and compact but not clubbed. The glumes are glabrous, bronze in color, and rather stiff. The kernels are hard and translucent. The straw is short to mid-tall and weak, making it easy to lodge. The grain is held firmly in the chaff and no amount of weathering seems
to cause shattering. It is somewhat drought resistant and is thought by some to be slightly resistant to soil alkali. A condition which corresponds to "yellow berry" in red wheats is exhibited when it is grown under irrigation.

The variety is commercially important in Sevier Valley, Utah where it gives good yields and exhibits some resistance to the physiological forms of black stem rust.

RIDIT:

Ridit was developed at the Washington Agricultural Experiment Station from a cross between Turkey and Florence. The cross was made in 1915, and a selection made in 1919 resulted in the Ridit variety.

Ridit is adapted to mild winters and is ordinarily a fall wheat, but should not be grown where winter killing is dangerous. The head is lax with white, glabrous chaff, short apical awns, and does not shatter very easily. The straw is stiff and the kernels are red, hard, and vitreous with good milling quality. The outstanding characteristic of this wheat is its resistance to both types and several physiological races of bunt smut.

Ridit was first distributed for commercial growing in Washington in 1923 and since that time has rapidly increased in distribution. It is adapted to the panhandle of Idaho, to eastern Washington, and to other winter wheat sections where the winters are rather mild.

A summary of the contrasting parental characters is presented in Table 1.

Typical parent spikes and a head taken from the $F_1$ generation are shown in Figure 1.
Figure 1 -- Typical parent spikes and a head taken from the F1 plant.
Table 1 — Summary of the contrasting parent characters.

<table>
<thead>
<tr>
<th>Character</th>
<th>Ridit</th>
<th>Sevler 59</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glume color</td>
<td>White</td>
<td>Bronze</td>
</tr>
<tr>
<td>Kernel color</td>
<td>Red</td>
<td>White</td>
</tr>
<tr>
<td>Awnedness</td>
<td>Short apical awns</td>
<td>Fully awned</td>
</tr>
<tr>
<td>Spike density</td>
<td>Lax (10 intern. about 45 mm.)</td>
<td>Mid-dense (10 intern. about 34 mm.)</td>
</tr>
<tr>
<td>Smut resistance</td>
<td>Highly resistant</td>
<td>Susceptible</td>
</tr>
<tr>
<td>Stiffness of straw</td>
<td>Quite stiff</td>
<td>Extremely weak</td>
</tr>
</tbody>
</table>

**EXPERIMENTAL RESULTS AND THEIR INTERPRETATION**

The breeding behavior of every F₃ row was summarized and placed in a table for use in this study.

The character of spike density involved measurements for about 40 plants in each F₃ progeny row. From these measurements, means, standard deviations, and coefficients of variability were obtained. Comparisons of these biometrical constants made it possible to segregate the progenies into two homozygous and one heterozygous group for spike density. In the biometrical studies the mean value of the plants in each F₃ row was used, this being considered more accurate than a single figure from an F₂ plant.

Data on such characters as kernel color, glume color, and awn classes were grouped into homozygous and heterozygous progenies by observation. After all the data were secured and recorded, studies were made of those which concerned each individual character.
INHERITANCE OF INDIVIDUAL CHARACTERS

Inheritance studies were made of the following individual characters:
Glume color, kernel color, awniness, and spike density.

GLUME COLOR

<table>
<thead>
<tr>
<th>Literature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Love and Craig (8) crossed durum on common wheat and reported a 15:1 ratio for red and white chaff. This cross produced two plants with characteristics of the wild type, one of which produced progeny which segregated in a 3:1 ratio for red and white chaff.</td>
</tr>
<tr>
<td>In crosses between Koda and Hard Federation by Clark (16), the F₂ generation was studied for chaff color. This study seemed to indicate a variance from a monohybrid ratio. However, F₃ progenies were grown and the F₂ data, when corrected on this basis, proved that only a one factor difference was involved.</td>
</tr>
<tr>
<td>Clark and Hooker (17) in crosses of Marquis x Hard Federation report brown glume dominance and segregation in the F₂ approaching a simple 3:1 ratio. In the F₃ the white-glumed plants bred true, one-third of the brown-glumed plants bred true, and the other two-thirds of the brown-glumed plants segregated brown and white.</td>
</tr>
<tr>
<td>Hayes and Gerber (20) conclude that &quot;there are different factors in different varieties for the brownish-red color of glumes&quot;.</td>
</tr>
<tr>
<td>In a cross of Kanred x Sever, Stewart (23) studied the breeding behavior with reference to glume color and found that a one factor difference existed for this character.</td>
</tr>
<tr>
<td>Stewart and Tingey (24), in a cross of Federation x Marquis, report a dominance of bronze glumes. The F₂ approached a 3:1 ratio very closely and so a one major dominant factor difference was suggested for inheritance of chaff color.</td>
</tr>
</tbody>
</table>
The above writers have classed glumes variously as white, brown, bronze, and red. In the present study they are classed merely as bronze and white. Those classed as white vary from nearly white to yellowish, with sometimes a very slight tinge of bronze. Those classed as bronze vary from a dark to a light shade of bronze.

Each F3 plant was classified for glume color on this basis and the breeding behavior of the rows was thus determined. Of the 299 progeny rows, 77 bred true for bronze chaff; 75 bred true for white chaff; and 147 segregated. These numbers suggest a 1:2:1 ratio or a one factor difference for color of glumes. A comparison of this hypothesis with the actual counts is made in Table 2.

Table 2 -- Goodness of fit of three groups of F3 progenies for glume color compared to a 1:2:1 ratio.

<table>
<thead>
<tr>
<th>Progeny group</th>
<th>Observed (O)</th>
<th>Calculated (C)</th>
<th>O-C</th>
<th>(O-C)^2</th>
<th>(O-C)^2 \times \frac{1}{2}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homozygous Bronze</td>
<td>77</td>
<td>74.75</td>
<td>-2.25</td>
<td>5.06</td>
<td>0.667</td>
</tr>
<tr>
<td>Heterozygous</td>
<td>147</td>
<td>149.50</td>
<td>+2.50</td>
<td>6.25</td>
<td>0.041</td>
</tr>
<tr>
<td>Homozygous White</td>
<td>75</td>
<td>74.75</td>
<td>-0.25</td>
<td>0.06</td>
<td>0.003</td>
</tr>
</tbody>
</table>

\[ X^2 = 0.111 \quad P = 0.9256 \]

This value of \( P \) indicates that a worse fit might be expected in 92 cases out of 100 due to chance alone. There seems little doubt regarding there being a one factor difference for glume color.

The F1 plants had lighter colored glumes than Sevier and were darker than Ridit; also, in the F2 and F3 generations there were degrees of bronzeness which varied from the dark bronze color of Sevier to shades so light as to be almost indistinguishable from plants classed as white. These two facts suggest an incomplete dominance of the factors for bronzeness, although the ratios prove the dominance of the bronze color.
KERNEL COLOR

Literature:

Clark (16), in crosses of Kota x Hard Federation, found two factor differences to exist for kernel color. In the F3 he obtained true breeding red and true breeding white progenies, and two other groups, one of which segregated in a 15 red : 1 white ratio, and the other in the ratio of 3 red : 1 white. In making reciprocal crosses he found evidence of slight maternal influence on this character. He also found, as have other workers, that the white-kernelled strains bred true for that color.

A three factor difference for kernel color was found to exist in a Kanred x Sevier cross by Stewart (23). The F3 yielded 5 groups which occurred in proportions which approached the following ratio:

8 segregating 63 red : 1 white
12 segregating 15 red : 1 white
6 segregating 3 red : 1 white
1 true breeding white grain.

Because of the scarcity of white kernels in the segregating class of 63 red : 1 white, it was necessary to grow an F4 to make some F3 corrections. Cases of doubt in other classes were also eliminated by growing the F4.

When Marquis (red grain) was crossed with Federation (white grain), Stewart and Tingey (24) found that the segregation in the F2 was near a 15:1 ratio with red grain dominant. The F3 segregated into 4 groups in the following proportions:

1 breeding true for white grain
4 segregating 3 red : 1 white
4 segregating 15 red : 1 white
7 breeding true for red grain.

This was due to a two factor difference for grain color.

Nilsson-Ehle (16) reported 15:1 and 63:1 segregations, proving the presence of two and three factor differences.

Howard and Howard (3), Gaines (5), and Clark and Hooker (17) report similar segregations in various wheat crosses.
In the cross here reported, red proved dominant, as usual, in the F₁. Twenty-one of the 299 progenies studied in this cross produced white kernels in the F₂. This is 7 per cent of the total. The remaining 278 plants, or 93 per cent of the total, produced red kernels. Minute examination of red kernels from a large number of plants disclosed no significant difference in the degree of redness, although Hayes and Garber (20) maintain that the factors for kernel color are cumulative and that two factors will give a darker color than will one of the factors alone.

The percentages of red and white kernels, 93 and 7 respectively, suggested a two factor difference for this character. The breeding behavior in the F₃ established this hypothesis still more definitely. All of the white-kernelled plants bred true in the F₃, while the remaining 278 showed the following breeding behavior:

141 plants bred true for red kernels
67 segregated in the ratio of 3 red : 1 white
70 segregated in the ratio of 15 red : 1 white.

On the basis of a two factor difference for kernel color it was calculated that each 16 plants should breed as follows:

7 breeding true for red grain
4 segregating 15 red : 1 white
4 segregating 3 red : 1 white
1 breeding true for white grain
16 Total.

When this theoretical expectation was compared to the actual data, a fairly close fit was observed. The group breeding true for red grain numbered about 7 per cent more than was calculated, while the two segregating groups were each a little smaller than was expected. The true-breeding white-kernelled plants approached very close to expectations. Seven of the segregating groups were right on the border between 3:1 ratios and 15:1 ratios, so in the final grouping of data (given above) it was decided to put 3 of these groups in the 3:1 class and the other 4 in the 15:1 class. If any of the ratios were seriously affected by these 7 doubtful progenies, an F₄ could be grown and its breeding
behavior would eliminate the doubt in this classification. Outside of these 7 groups, no difficulty was experienced in classification of kernel color as all of the other 299 progenies presented clear cut breeding behavior. The two factor hypothesis suggested to explain this breeding behavior was made the basis of the closeness of fit comparison in Table 3.

Table 3 -- Closeness of fit of four groups of F3 progenies on a two factor difference in the parents for kernel color, compared with a 7:4:4:1 ratio.

<table>
<thead>
<tr>
<th>Progeny group</th>
<th>Observed</th>
<th>Calculated</th>
<th>(O-C)</th>
<th>(O-C)^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homozygous red grain</td>
<td>141</td>
<td>131</td>
<td>10</td>
<td>100</td>
</tr>
<tr>
<td>Segregating 3 red : 1 white</td>
<td>67</td>
<td>74.7</td>
<td>-7.7</td>
<td>53.4</td>
</tr>
<tr>
<td>Segregating 15 red : 1 white</td>
<td>70</td>
<td>74.7</td>
<td>-4.7</td>
<td>22.09</td>
</tr>
<tr>
<td>Homozygous white grain</td>
<td>21</td>
<td>18.6</td>
<td>2.4</td>
<td>5.76</td>
</tr>
</tbody>
</table>

\[ X = 2.13 \quad \quad P = .5637 \]

The value of \( P \) (taken from Pearsons tables) indicates a fit so good that a worse one would be expected in 57 out of each 100 cases due to chance alone.

AWNEDNESS

Literature:

Clark and Hooker (17) studied the inheritance of awns in a cross between Hard Federation, classed as awnless, and Marquis, which has short tip awns. Putting the awned progeny into two awn classes, he found a ratio of 1:12:3 in one case and a ratio of 1:11:4 in another. If the awned progeny were all put in one class a 15:1 ratio was obtained. This led to the suggestion of a two
factor difference to explain the resulting awn segregation. In the F2 generation, true-breeding classes were found for both parental types and also for one intermediate type.

Gaines and Singleton (16) report a cross between Marquis and Turkey in which the segregation of awns approached a 2:5:1 ratio in the F2, but the breeding behavior in the F3 generation showed 34 awnless, 90 heterozygous, and 32 awned. This approaches a 1:2:1 ratio and the conclusion was that there was a single factor difference in these two wheats.

Biffen (1) stated that the awnless condition is a dominant, the awned a recessive character.

The Howards (3) obtained single factor differences for awns in some crosses but in others, between fully awned and absolutely awnless parents, they were able to separate the F2 progeny into five or six classes. When all the awned and tip-awned classes were grouped together, a 15:1 ratio was obtained, indicating a two factor difference. These researches and other later studies have brought about the conclusion by most breeders that awnlessness cannot be classed as a completely dominant character.

In crosses between Kota and Hard Federation, Clark (16) obtained five distinct awn classes. He partially explained the inheritance on a dihybrid mendelian ratio in which the awned and short-awned classes were shown to be recessive to the awnless and apically-awnletted classes. As neither the awned nor awnless classes bred true in the F3, a multiple factor hypothesis was advanced to explain homozygosity in these classes. Studies of certain parts of his results led Clark to advance the theory that the maternal parent has more influence on the inheritance of awns than the paternal parent.

Working at the Utah Station, Stewart (19) crossed Sevier and Federation and obtained a peculiar awn inheritance. The parental types were recovered in the F3 in a homozygous condition. Besides four true-breeding classes, there
were five other classes which segregated in various ways. The fact that the two parental classes were much more numerous led to the suggestion of linkage. The results were finally explained on the hypothesis that there are two factors for awns located in the same chromosome and that there is 35 per cent crossing over.

Clark, Florell, and Hooker (22) studied the inheritance of awns in Bob Propo and Hard Federation crosses at the California Station. They concluded that there is imperfect dominance of awnlessness and that there may be as "many as four genetic factors involved in inheritance of awnedness in wheat". The Hard Federation x Propo crosses were the most complicated and in this case they concluded that the inheritance of awns was due to two major and one minor factors.

In a cross between Federation (awnless) and a hybrid of Sevier and Dicklow (awned), made by Stewart and Heywood (23) at the Utah Station, four true-breeding awn classes and five segregating classes were reported in the F3. The F3 rows were put in 9 awn groups and the counts showed a rather close fit to a 1:2:2:4:1:2:1:2:1 ratio. This ratio, they concluded, was due to a two factor difference with independent segregation. It was also concluded that different segregates in which Sevier wheat is one of the parents may behave differently in regards to awn inheritance.

A peculiar case of transgressive segregation for awns in a Marquis x Federation cross is reported by Stewart and Tingey (24). Marquis has short apical awns and Federation is considered awnless. When the two were crossed a true-breeding class was found in the F3 in which the awn length exceeded the parent type. In the F3 the homozygous beaked progenies, the heterozygous progenies, and the homozygous awned progenies occurred in the proportions of 98:167:96, or a 1:2:1 ratio. This indicates a single factor difference.
In the present study the awns were divided according to appearance into three groups which were known merely as awns 2, 3, or 4. Those plants in the awn 2 class bore short beaks along the side of the spike with partial awn development at its apical part. These plants resembled the Ridel parent. Those in awn class 4 were fully awned and bore awns corresponding to those on the Sevier parent. In this class the awns were long and covered the entire spike. The plants in awn class 3 were intermediate in their awn development, were considerably longer than those of class 2, and short awns were found as far as halfway down the spike. The awn development in this class varied considerably more than either of the other two groups. In this case the apical awns were considerably longer than those of awn class 2 and generally quite long awns could be found over all of the apical half of the spike.

The awn types of the parents and also of the F1 are shown in Figure 1. Figure 2 shows several plants of each of the three awn classes recovered in the F3 generation. The F1 generation appeared to be intermediate to the two parents in the production of awns, although it resembled the Ridel parent much more in this respect than it did the Sevier.

All of the F2 plants which were classed as having awns 4 bred true in F3, but it was impossible in the F2 to distinguish between the plants which had strong awns 3 and those which had awns 3. Several experiments have shown that plants with awn class 2 or 4 will breed true while those with awns 3 will segregate. The F3 thus clearly separated these two groups. In taking the data on the F3 progenies, clear-cut cases of segregation could be seen and these groups were easily classified. For this reason measurements of the awns were not made.

Awn classes are many and varied, consequently different workers do not always agree in their classifications. Awn class 3 is the most varied, some-
Figure 2 — Typical spikes of each of the three awn classes found in the $F_3$ generation. Classes 2 and 4 breed true and class 3 was found only in segregating groups.
times being as described in this paper and sometimes as described by the Howards (3); that is, as being rather short but covering the larger portion of the spike. When the 293 F₃ progenies were studied as a basis for the genotypic classification of the F₂ plants, it was found that 68 rows were breeding true for awn class 4; 150 rows were segregating for all three awn classes, with the most common segregation being in a 1:2:1 ratio. There was a huge variation in the awn types of these segregating rows. The remaining 81 rows bred true for awns class 2. This classification approaches a 1:2:1 ratio and suggests a one factor difference.

Because of the fact that awnlessness is not always dominant, Stewart (26) departs from Biffin (1) and uses the dominant factor to represent the positive character. This method is used in the following genotypic designation of the difference in awn classes of Ridit and Sevier 59:

Ridit (awn class 2) ———— Genotype  aa
Sevier (awn class 4) ———— "  AA
F₁ (awn class 3) ———— "  Aa.

On the assumption that there is a one factor difference for awns, the genotypes of the F₂ plants would be as shown in table 4. This table also shows the expected proportions in F₂ and the expected breeding behavior in the F₃.

Table 4 — Probable awn class genotypes of the F₂ of a cross between Ridit and Sevier 59, based on a one factor difference. Also expected segregation proportions and expected breeding behavior.

<table>
<thead>
<tr>
<th>Awn Class</th>
<th>Expected Proportions</th>
<th>Genotype</th>
<th>Expected breeding behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>1</td>
<td>AA</td>
<td>Breed true for awn class 4</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>Aa</td>
<td>Segregates for awns 2, 3, and 4</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>aa</td>
<td>Breed true for awn class 2</td>
</tr>
</tbody>
</table>
The goodness of fit between the observed data and the calculated frequencies is presented in Table 5.

Table 5 -- Goodness of fit of 3 awn genotype classes of the F₃ progenies when compared with 1:2:1 ratio which would theoretically be obtained in the segregation of a one factor difference.

<table>
<thead>
<tr>
<th>Progeny group</th>
<th>Observed value (O)</th>
<th>Calculated value (C)</th>
<th>(O-C)</th>
<th>(O-C)²</th>
<th>(\frac{(O-C)^2}{2})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homozygous awns 1</td>
<td>68</td>
<td>74.75</td>
<td>-6.75</td>
<td>45.56</td>
<td>.6100</td>
</tr>
<tr>
<td>Heterozygous</td>
<td>150</td>
<td>149.50</td>
<td>.50</td>
<td>.25</td>
<td>.0016</td>
</tr>
<tr>
<td>Homozygous awns 2</td>
<td>81</td>
<td>74.75</td>
<td>6.25</td>
<td>39.06</td>
<td>.5225</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 1.134 \quad P = .5755 \]

On the basis of 3 awn classes, \(\chi^2 = 1.134\) and \(P = .5755\); a rather close fit, in fact a worse fit would be obtained in 58 out of 100 cases due to chance alone.

SPIKE DENSITY

**Literature:**

Parker (4) emphasized the importance of determining density by measuring internode length instead of classifying by simply judging the length of the spike.

Hayes and Harlan (10), in some crosses with barley, found a one factor difference for head density; in others a 2 or 3 factor difference; and in still others certain modifying influences.

Boshnakian (11) states that density is dominant over laxness in the ratio of 3:1. He found heterozygous forms to be a little more lax than dense forms, but by no means intermediate between the dense and lax parents. He suggests that different density factors form allelomorphic series or that they belong to
a multiple series. He also concluded that compactness of spikes was in some way correlated with a tendency to shorten culms.

Stewart (19) found the same type of spike density segregation to occur in a cross between Federation and Sevier as between Kanred and Sevier (19), and he concluded that there was one major factor and a series of minor factors involved in this inheritance.

Stewart (23) crossed Kanred and Sevier at the Utah Station and found the F1 plants to be intermediate for spike density. The numbers of homozygous dense, heterozygous, and homozygous lax obtained in the F3 came very close to a 1:2:1 ratio. In each of these groups, however, there was a series of differences between various progeny. There were some true-breeding dense progenies with a very much greater degree of density than others and the same was true of the heterozygous and true-breeding lax progenies. Only one of the 263 progenies even came near the Sevier parent in head density. Stewart was led by these facts to state, "there is good evidence of the presence of minor factors in spike density inheritance".

Nilsson-Ehle (19) explained results he obtained in spike density inheritance by designating the compact parent as C0L1 L1 L2 and the mid-dense parent as cc ll 11 12 12. C produced short internodes and also inhibited the lengthening influence of the L1 and L2 factors.

Stewart and Heywood (28) found the same three groups occurring in the F3 progeny of a cross between Federation and 111 C-18 (a hybrid strain from a Sevier x Dicklow cross). In this case, also, the homozygous dense progenies transgressed the range of the dense parent in mean spike density, all being more dense than the parent. The range of mean spike densities for the heterozygous progenies covers those of the denser parent entirely but do not overlap into the density range of the homozygous dense progeny.
In the present study the F₁ did not resemble either parent for spike density, but was intermediate. In the F₂ segregation all degrees of spike density were observed, some plants having more lax heads than Ridit and others having much denser heads than Sevier 59. The F₃ breeding behavior was used as the basis for determining the inheritance of this character and was studied by measuring ten rachis internodes on a leading spike of each plant. In making these measurements the extreme tip and base of the spike were avoided because of the variability at these points. All plants in an F₃ progeny, or the first forty, were taken at random and used to represent the genotype of the F₂ plant which was their parent. The coefficients of variability (C.V.) were also calculated and used as the basis for separating homozygous progenies from heterozygous.

The parental rows of Ridit had an average spike density of 44.58 mm. and showed coefficients of variability ranging from 3.8 per cent to 6 per cent, with a mean of 4.73 per cent. The parental rows of Sevier 59 had an average spike density of 33.9 mm. and the coefficients of variability ranged from 4.4 per cent to 8.7 per cent, with a mean C.V. of 5.78 per cent.

The average length of 10 internodes of all the homozygous dense rows was 23.6 mm. and the coefficients of variability in this group ranged from 5.4 per cent to 16.2 per cent, the mean C.V. being 10.5 per cent. The homozygous lax progeny averaged 52.63 mm. for length of 10 internodes and showed a mean C.V. of 6.67 per cent. The heterozygous rows showed coefficients of variability ranging from 22 per cent to 40.8 per cent with a mean of 30.7 per cent. Only one of the heterozygous progeny went down to a C.V. of 22 per cent and few were below 27 per cent.

This method of spike density classification showed the three segregating groups in a clear cut manner. The mean spike density classes and the coefficient of variability (C.V.) classes of the parent rows and of the three segregating groups are shown in Table 6.
Table 6 -- Mean spike density and coefficient of variability (C.V.) classes of ridit and sever 59 wheats, and of the three groups of 
F_3 progenies of their cross - homozygous dense, heterozygous, and 
homozygous lax.

<table>
<thead>
<tr>
<th>Parent of Progeny</th>
<th>Spike Density Classes</th>
<th>Total</th>
<th>C.V. Classes</th>
</tr>
</thead>
<tbody>
<tr>
<td>RIDIT PARENT</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean C.V.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average spike density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SEVER 59 PARENT:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean C.V.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average spike density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HOMOZYGOUS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dense Progeny</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean C.V.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average spike density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HETEROZYGUS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lax Progeny</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean C.V.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average spike density</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The vertical columns represent spike density classes of the means of the 
parental rows and F_3 progenies, grouped horizontally into three major 
progeny groups and the two parental groups. The horizontal lines with-
in each group represent the coefficient of variability classes.
In figure 3 the spike density curves of the Ridit and Sevier parents, together with the curves for the three groups of F₃ progenies, are shown graphically.

Figure 4 shows the racches and spikes from parents and progeny of the Ridit x Sevier 59 cross.

The mean coefficients of variability were greater for both true breeding F₃ progeny than for either of the two parent rows. In comparing the variability of the homozygous dense with the homozygous lax it was found that the homozygous lax group showed much less variability than the homozygous dense rows; also, Ridit was less variable than Sevier 59. The coefficient of variability of the least variable heterozygous progeny exceeds that of the most variable homozygous progeny in every case.

When counts were made of the F₃ progenies in each of the three groups, it was found that there were 66 homozygous for lax spikes, 164 heterozygous, and 69 homozygous for dense spikes. Table 7 gives the calculation for closeness of fit on a one factor difference for spike density.

Table 7 -- Closeness of fit of three groups of F₃ families compared to a 1;2;1 ratio.

<table>
<thead>
<tr>
<th>Spike density group</th>
<th>Observed value (O)</th>
<th>Calculated value (C)</th>
<th>O-C</th>
<th>(O-C)^2</th>
<th>(\frac{(O-C)^2}{2})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homozygous dense</td>
<td>69</td>
<td>74.75</td>
<td>5.75</td>
<td>33.06</td>
<td>.442</td>
</tr>
<tr>
<td>Heterozygous</td>
<td>164</td>
<td>149.50</td>
<td>14.5</td>
<td>210.25</td>
<td>1.407</td>
</tr>
<tr>
<td>Homozygous lax</td>
<td>66</td>
<td>74.75</td>
<td>8.75</td>
<td>76.56</td>
<td>1.024</td>
</tr>
</tbody>
</table>

\[ x^2 = 2.873 \] \[ p = .242 \]

This value of \( p \) indicates that the probability is very great that the proposed one factor hypothesis is essentially correct.
Figure 3 -- Spike density curves of Ridit and Sevier 59 parents, and of three F2 progeny groups. Percentage of total progenies in each group are represented by figures on vertical axis and spike density (mm. length of 10 rachis internodes) classes on horizontal axis.
Figure 4 -- Spikes and rachis from parents and progeny of a Ridit x Sevier 59 cross.

Top - Ridit and Sevier 59 parents
A - Representative spike and rachis of homozygous lax progeny
B - Representative spikes and rachis from the heterozygous progeny group.
C - A spike and rachis of a typical homozygous dense progeny.
There are several considerations, however, which lend to the belief that there are also minor factors involved in the expression of spike density in this cross. In the first place, the homozygous dense progeny were without exception more dense than the dense parent. That this was a real difference and not due to fluctuating variation is shown by the fact that the difference in the length of 10 internodes was 9.2 times the probable error. This is shown as follows:

<table>
<thead>
<tr>
<th></th>
<th>Mean length of 10 internodes</th>
<th>Probable error (P.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Savier 39</td>
<td>33.9 mm.</td>
<td>.73</td>
</tr>
<tr>
<td>Homozygous dense progeny</td>
<td>22.6</td>
<td>.85</td>
</tr>
<tr>
<td>Difference</td>
<td>10.3</td>
<td>1.12</td>
</tr>
</tbody>
</table>

\[ \frac{D}{\text{P.E.}} = 9.2 \text{ or odds of over } 1 \text{ billion to } 1 \] that there is a significant difference.

Secondly, the lax group showed a far greater degree of laxness than the lax parent (Ridit), as is shown by a comparison drawn in the same manner:

<table>
<thead>
<tr>
<th></th>
<th>Mean length of 10 internodes</th>
<th>Probable error (P.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ridit</td>
<td>44.58</td>
<td>.602</td>
</tr>
<tr>
<td>Homozygous lax progeny</td>
<td>52.83</td>
<td>.554</td>
</tr>
<tr>
<td>Difference</td>
<td>8.25</td>
<td>1.07</td>
</tr>
</tbody>
</table>

\[ \frac{D}{\text{P.E.}} = 7.71 \text{ or odds of } 500,000 \text{ to } 1 \] that there is a real difference.

The spike density of Savier was not recovered at all in the F3 and that of Ridit only in one case. Since there were 299 F3 families, the number of segregates breeding true to either one of the parents is so small that it is clear that some minor factors are involved. This is further borne out by a comparison of the spike density ranges of the parents and F3 progeny. A summary of the range of densities is given in Table 8.
Table 8 -- The range of mean spike densities and the mean of mean spike densities of Ridit and Sevier 59 and of three groups of F3 families. Also coefficients of variability (C.V.) of mean spike densities for all groups.

<table>
<thead>
<tr>
<th>Parent or segregates</th>
<th>Range of Spike Densities</th>
<th>Mean Spike Density</th>
<th>C. V. of mean Spike Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ridit</td>
<td>42.2 - 46</td>
<td>44.58 mm.</td>
<td>4.73</td>
</tr>
<tr>
<td>Sevier 59</td>
<td>31.7 - 34.3</td>
<td>33.9 mm.</td>
<td>4.78</td>
</tr>
<tr>
<td>Homozygous dense</td>
<td>19.2 - 28.3</td>
<td>26.6 mm.</td>
<td>10.5</td>
</tr>
<tr>
<td>Heterozygous</td>
<td>26.7 - 48.7</td>
<td>34.75 mm.</td>
<td>30.7</td>
</tr>
<tr>
<td>Homozygous lax</td>
<td>46.3 - 58.6</td>
<td>52.83 mm.</td>
<td>6.67</td>
</tr>
</tbody>
</table>

On an average the variability of the means of homozygous F3 families is about twice as great as that of the 29 parent rows. This added to the fact that there is a series of steps throughout the range of variation points to one or more minor factors which modify the expression of the one major factor for spike density.

As yet no genetic hypothesis has been advanced that will explain the fact of wide transgressive segregation in both directions and still account for the very infrequent recovery of the spike density of the parents.

**SUMMARY**

A selection of Sevier was crossed with Ridit. The F1 generation was intermediate for spike density and awnedness; the kernels were red and the glumes were bronze. Grain from each F2 plant was used to seed one F3 progeny row. Each row was about 12 feet long and contained about 40 plants. The rows were spaced about 12 inches apart. Paired plantings of the two parents were made in the same manner and at the same time after each 10 progeny rows. Each F3 progeny row was considered to represent the genetic constitution of its F3 parent plant. Data were collected for the various plant characters by measure-
ment and observation.

The characters studied in this cross were: glume color, kernel color, awnedness, and head density.

A one factor difference, suggested as the basis for glume color inheritance, gave, when compared to a 1:2:1 ratio, a $p$ of .9256.

Kernel color was inherited on the basis of a two-factor difference with independent segregation. As red was dominant, the $F_2$ segregation approached a 15:1 ratio. When the breeding behavior in $F_3$ was compared to that expected from a two factor difference, a fairly close fit (of $p = .5687$) was obtained. Close scrutiny of the red kernels failed to reveal any cumulative effect of the factors for red grain.

Awnedness was found to be inherited on the basis of a single factor difference. Homozygous progenies were found in the $F_3$ that were breeding true for each of the parental awn types. The numbers expected on the basis of a 1:2:1 ratio fit the observed numbers very closely as indicated by $p = .5755$.

Spike density exhibited peculiar inheritance. Three groups were found in the $F_3$ progenies in numbers which suggested a 1:2:1 ratio; with a goodness of fit as indicated by $p = .242$. The homozygous dense progenies transgress the range of the dense parent in mean spike density and the homozygous lax progenies transgress the range of the lax parent. The dense parent is not recovered in a single progeny and the lax parent in very few. The range of densities of the heterozygous progenies covers completely the range of the denser parent. Evidently there is one or more minor factors present in the inheritance of spike density.
SOIL HETEROGENEITY

A study was made of the soil heterogeneity of the experimental plot. The Harris (20) method was used in this study and as the 29 pairs of parent rows were grown side by side at regular intervals throughout the plot, they were used as the basis.

The contiguous rows received identical treatment and the extent of fluctuation due to environment was determined by a correlation study between the spike density measurements of the Ridit and Sevier 59 parents. According to Harris (20), this correlation coefficient measures the degree to which nearby plots or rows are different and allows a comparison of soil heterogeneity. The coefficient will be in proportion to the soil heterogeneity; that is, the larger the positive value of \( r \), the greater the degree of soil heterogeneity.

In this case the coefficient of correlation was \( +.29 \) with a probable error of \( \pm .11 \). When the value of \( r \) is changed to per cent by the formula \( V = 100 \left( 1 - \sqrt{1-r^2} \right) \), \( V \) = variation in per cent), we find that there is 5 per cent variability. This indicates that a small amount of the variation in this experiment was due to soil heterogeneity.
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