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Genetic Study of Certain Spike and Floral Characters in Barley

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GENETIC STUDY OF CERTAIN SPIKE

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TABLE OF CONTANTS

GENETIC STUDY OF CERTAIN SPIKE AND FLORAL CHARACTERS IN BARLEY

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INTRODUCTION

Due to the commercial importance of barley many hybridization studies have been prosecuted in an effort to produce superior economic strains. While the economic breeding is still important, at present there is considerable scientific interest in the inheritance of the characters and in the location of the genes in the different linkage groups.

Barley is rather favorable genetic material for such study. There is a great number of cultivated varieties and strains which differ widely in heritable characters. Barley can be grown under a wide range of climatic conditions and will produce rather large F_2 families. The fact that it has only seven chromosomes makes linkage studies more feasible than in wheat or oats with their greater chromosome complements.

The characters studied in this paper are: black versus white glume color, long haired versus short haired rachilla, rough versus smooth awns, and branched versus unbranched style.

REVIEW OF LITERATURE

Since rather extensive reviews of the literature dealing with the genetics of barley has been made by Griffee (2), by Hayes and Garber (3), and by Robertson (7), only the papers specifically dealing with the characters studied are here noted.

Black versus white glume color-- Hayes et al (3), Griffee (2), Robertson (7), and Sigfusson (9) have reported a single factor difference between black and white glume color with black dominant.

Long versus short haired rachilla-- In some varieties the rachilla has long bristly hairs and in other varieties the rachilla has short, rather woolly hairs. Hor (5), Robertson (7), Sigfusson (9), and Buckley (1) have all reported a single factor difference between these characters with the long haired character dominant.

Rough versus smooth awns-- Barley varieties are classified as rough and smooth according to the amount of serrations on the awns. The degree of smoothness differs in varieties. The smooth awn varieties have serrations on the tip and at the base of the awn. Hayes et al (3) report that the F_1 plants in crosses between rough and smooth awned varieties have rough awns, while the F_2 generation segregated into rough and smooth awned plants in an approximate 3:1 ratio. However, considerable variation in degree of roughness was found in the smooth awn class.

Griffee (2) reports a two factor difference for roughness of awn. He divides the F_2 plants into three phenotypes based on an arbitrary awn index division. The types rough, intermediate-smooth, and smooth were obtained in a 12:3:1 ratio. The factor R produces rough awn, while the factor S is hypostatic to R and in the absence of R produces intermediate-smooth awns. The double recessive rrss produces smooth awn.

Sigfusson (9) classified the F_2 plants into four groups according to the degree of roughness. He states: "The rough and intermediate-rough classes have barbs the entire length of the awn, but the awns of the latter class are not nearly as scabrous. When heads of these phenotypes were examined in sunlight, and when held at the correct distance from the eye to be properly focussed, the difference could be easily discerned." According to Sigfusson (9) the intermediate-smooth and smooth classes were similar in degree of smoothness at the base of the awns, but the intermediate-smooth class had barbs on the upper half of the awn, while the smooth class had barbs which seldom extended over 3/4 inch from the tip. However, the barbing varied in each of the phenotypes. The distribution of F_2 plants indicated a two factor difference for roughness of awn and showed the factors to be cumulative in effect as the segregation was very close to a 9:3:3:1 ratio. The factor R, either single or in duplicate, and in the absence of S produced the intermediate-rough condition and likewise the factor S, in the absence of R, produced the intermediate-smooth condition. Both factors are necessary to produce the fully barbed condition. The double recessive, rrss, produced the smooth class.

Griffee and Sigfusson differ in their results in the number of phenotypes found and in the behavior of the factors R and S.

Style branching-- Robertson and Deming (8) report a three factor difference between the unbranched type of style of Lion and the branched style of Coast. The F_1 plants have fully branched styles and in the F_2 a graded series is found, running all the way from the unbranched to fully branched styles. The numbers obtained indicated the segregation observed could be accounted for by the existence of three pairs of cumulative factors which determine the degree of branching of the style.

Linkage relation of factors studied-- Hor (5) reports linkage between black versus white glume color, rough versus smooth awn, and long versus short haired rachilla.

Robertson (7), Sigfusson (9), and Buckley (1) found the factor pairs for black glume color and length of rachilla hairs to be inherited independently.

Hayes et al (4), Griffee (2), and Sigfusson (9) found the factors for black glume color and roughness of awn to be inherited independently.

Sigfusson (9) obtained a linkage between long versus short haired rachilla and the main factor for roughness of awn. The segregation of his intermediate-smooth plants in the F_3 generation gave results which showed the factors S and l to be inherited independently. He concluded that the linkage was between the main factor R for roughness of awn and the factor l for short haired rachilla. The percent crossing over was figured on the rough and intermediate-rough groups combined, and the intermediate-smooth and smooth groups combined. Emerson's formulae was used for calculating the linkage intensity. The crossover value found was 30.8 percent.

Hor (5) also obtained a linkage between the factor pairs for rachilla hairs and roughness of awns. A crossover percentage of 28.70 ± 3.43 was obtained in the repulsion phase, and 34.54 ± 2.89 in the coupling phase.

MATERIAL AND METHODS

The varieties used in this study, Coast C.I. No.2791 and Lion C.I.No. 923 belong to the species vulgare, and were found to be homozygous for the characters investigated.

Coast has white glumes, short haired rachillas, branched styles, and rough awns. The barbing extends the full length of the awn.

Lion has black glumes, long haired rachillas, unbranched styles, and smooth awns. However, there is barbing of the awns at the base which was disregarded in this study. Also, there is some barbing on the tip of the awns which varies as is shown by the awn indices.

The results given here are from a cross Coast X Lion made at the Colorado Experiment Station by D.W. Robertson. The F_2 generation was grown in the field at the Fort Collins Station and data taken on the style branching. The material was given to the writer in 1930. About 50 seeds from each F_2 plant were planted in 1930 at the Fort Lewis Substation for study of the F_3 population.

The probable errors of Mendelian ratios were obtained from the tables of probable errors from the Department of Plant Breeding, Cornell University.

EXPERIMENTAL RESULTS

The characters under investigation are first considered separately and later in their relation to each other.

Glume color-- If the plants are allowed to grow until mature there is little difficulty in separating the black and white glumed plants in the F_2 families. Table 1 gives the segregation of the F_2 plants. The results indicate that black versus white glume color is dependent upon a single factor pair (Bb).

Table 1. Segregation of black versus white glume color (Bb) in the F_2 generation of a cross, Coast X Lion.

Black	White	Total	
822	285	1107	observed
830.25	276.75	1107	calculated, 3:1 ratio
	8.25 deviation		D/PE 0.85

Rachilla hairs-- The segregation of the F_2 generation as given in table 2, shows that long versus short haired rachillas differ by a single factor pair (Ss).

Table 2. Segregation of long versus short haired rachillas (Ss) in the F_2 generation of a cross, Coast X Lion.

Long-haired	Short-haired	Total	
816	291	1107	observed
830.25	276.75	1107	calculated, 3:1 ratio
	14.25 deviation		D/PE 1.46

Roughness of awn-- The F_2 plants of the cross, Coast X Lion were classified into three groups, rough, intermediate-smooth, and smooth. The method used was the same as that used by Hayes et al (4) and by Griffee (2). An awn of average length was taken from the center of the main spike of each plant and examined under the microscope. Hayes et al (4) states, "The distance on the tip of the awn upon which teeth were regularly borne was measured. The total length of the awn was divided by the length of the tip upon which teeth were found. The result obtained was called the awn index; the larger the index the smoother the awn and vice versa."

Coast and the rough F_2 plants have an awn index of 1. The awn indices of one hundred plants of the Lion parent were determined. The awn indices of this group varied from 2.7 to 7.6 with an average of 4.3. A division of the partially smooth plants was made at the awn index of 2.7 which was the lower limit of the Lion plants. The plants with an awn index of 2.7 or more were classified as smooth, and the plants of an awn index of 1.1 to and including 2.6 were classified as intermediate-smooth.

As shown in table 3 the observed segregation approached a 12:3:1 ratio. When tested for goodness of fit, a X^2 value of 2.28 was obtained with a P value of 0.3273, which is a fair fit. a fit as bad or worse could be expected in 33 out of 100 trials due to chance alone. This segregation can best be explained on a two factor difference for roughness of awn. R and R' are used to designate the factors for roughness of awn, and r and r' denotes the absence of the rough condition. When the factor R is present the awn is rough. The factor R' is hypostatic to R and in the absence of R gives intermediate-smooth group. The double recessive, rr'rr', gives the smooth group similar to the Lion parent.

Table 3. Segregation in the F_2 generation for rough, intermediate-smooth and smooth awns (RrR'r') in a cross, Coast X Lion.

Rough 1	Int-smooth 1.1 to 2.6	Smooth 2.7 or more	Total	
852	191	64	1107	observed
830.25	207.5625	69.1875	1107	calculated, 12:3:1 ratio

$X^2 = 2.28$ $P = 0.3273$

Style branching-- The style branching of the F_2 plants of the Coast X Lion cross varied from profusely branched styles to unbranched styles. Table 4 shows the segregation of the F_2 plants for style branching as determined by the behavior of the F_3 population. The segregation suggested a 63:1 ratio and the numbers calculated on this basis agreed very closely with the observed numbers. This segregation of the F_2 plants can best be explained on the basis of a three factor difference, with the factors cumulative in their effect and only the triple recessive producing the unbranched style of the Lion type.

Table 4. Segregation of branched versus unbranched styles (GgG'g'G"g") in the F_2 generation of a cross, Coast X Lion.

Branched style	Unbranched style	Total	
1088	19	1107	observed
1089.7	17.3	1107	calculated, 63:1 ratio

1.7 deviation D/PE = 0.607

The behavior of about 50 F_3 plants from each F_2 family was studied. On the hypothesis that there are three cumulative factors involved, the F_3 families should show the following behavior with independent segregation: The ratio should be 37 branched, to 12 which segregate 15 branched :1 unbranched, to 8 which segregate 63 branched:1 unbranched, to 6 which segregate 3 branched:1 unbranched to 1 unbranched (triple recessive). The F_3 data obtained did not show this segregation as a whole. However, the F_3 families were small; larger families were needed to show segregations of 63:1 and 15:1.

The following data were obtained from the F_3 families: 45 F_3 families segregated 15:1. The observed segregation was 2005 branched to 147 unbranched. D/PE was 1.64. 35 F_3 families segregated 3:1. The observed segregation was 1227 branched to 434 unbranched. D/PE was 2.83. 17 F_3 families segregated 63:1. The observed segregation was 766 branched to 17 unbranched. D/PE was 2.04.

While the number of segregating F_3 families was low according to the calculated ratio of 37:12:8:6:1, the calculated numbers on these ratios fit the observed segregations very well. In no case was the deviation three times the probable error. Much larger F_3 families are necessary to obtain accurate data on the various segregations. However, the check on the unbranched plants was accurate. From the small deviation of the F_2 segregation from the calculated 63:1 ratio, and from the various segregations of the F_3 families it may be concluded that these results are best explained on a three factor hypothesis. These factors are cumulative in their effect and it is necessary for all the factors to be recessive to produce the unbranched style of the Lion type.

INDEPENDENT SEGREGATION FOR DIFFERENT BOTANICAL CHARACTERS

Black versus white glume color (Bb) and long versus short haired rachillas (Ss)-- The F_2 data are given in table 5. These results indicate that the factor pairs Bb and Ss are inherited independently.

Table 5. Segregation in F_2 for glume color (Bb) and rachilla hairs (Ss) in a cross, Coast X Lion.

Black glumes		White glumes			
Long	Short	Long	Short		
615	206	200	86	1107	observed
622.7	207.6	207.6	69.2	1107	calculated, 9:3:3:1 ratio

$X^2 = 4.47$ P = 0.2195

Black versus white glume color (Bb) and rough versus smooth awn (RrR'r')-- From the segregation of the F_2 plants, table 6, for black glume color and roughness of awn, it can be concluded that these characters are inherited independently.

Table 6. Segregation in F_2 for glume color (Bb) and roughness of awn (RrR'r') in a cross, Coast X Lion.

Black glumes			White glumes				
Rough	Int-smooth	Smooth	Rough	Int-smooth	Smooth		
635	138	49	217	53	15	1107	observed
616.5	154.125	54.375	213.75	53.4375	17.8175	1107	calculated on basis of two 12:3:1 ratios
Total 822			Total 285				

$X^2 = 2.85$ P = 0.5845

Black versus white glumes (Bb) and branched versus unbranched styles (GgG'g'G"g")-- The data for this segregation are given in table 7. The X^2 figured on the basis of two 3:1 ratios is 1.35 with a P value of 0.5230. A worse fit than this could be expected due to chance alone in one out of two trials. Therefore, it can be concluded that glume color and style branching are inherited independently.

Table 7. Segregation in F_2 for glume color (Bb) and style branching (GgG'g'G"g") in a cross, Coast X Lion.

Branched style Black	Branched style White	Unbranched style Black	Unbranched style White		
806	282	16	3	1107	observed
816	272	14.25	4.75	1107	calculated on basis of two 3:1 ratios
Total 1088		Total 19			
$X^2 = 1.35$		P = 0.5230			

Long versus short haired rachillas (Ss) and branched versus unbranched styles (GgG'g'G"g")-- The data presented in table 8 indicate that the factors for rachilla hairs and style branching are inherited independently.

Table 8. Segregation in F_2 for rachilla hairs (Ss) and style branching (GgG'g'G"g") in a cross, Coast X Lion.

Branched style Long	Branched style Short	Unbranched style Long	Unbranched style Short		
803	285	13	6	1107	observed
816	272	14.25	4.75	1107	calculated on basis of two 3:1 ratios
Total 1088		Total 19			
$X^2 = 1.27$		P = 0.5421			

LINKAGE RELATIONS

It has been shown that there is independent inheritance between the factor pairs: black glume color (Bb) and rachilla hairs (Ss), black glume color (Bb) and roughness of awn (RrR'r'), black glume color (Bb) and style branching (GgG'g'G"g"), and rachilla hairs (Ss) and style branching (GgG'g'G"g").

The following segregations deviate rather widely from the calculated for independent inheritance.

Long versus short haired rachilla (Ss) and rough versus smooth awn (RrR'r')-- An examination of table 9 shows that in the short haired rachilla group, the rough class has too many plants, while the intermediate-smooth and smooth classes do not have enough plants. The opposite is true of the long haired rachilla group. The test for goodness of fit for this segregation, based on two 12:3:1 ratios gave a X^2 value of 33.17. The value of P was very low, which indicates a poor fit for independent inheritance. This unbalanced segregation suggests that the factor pair for rachilla hairs (Ss) is perhaps linked with one of the factor pairs for roughness of awn (RrR'r').

Table 9. Segregation in F_2 for rachilla hairs (Ss) and roughness of awn (RrR'r') in a cross, Coast X Lion.

Long haired rachilla			Short haired rachilla			
Rough	Int-smooth	Smooth	Rough	Int-smooth	Smooth	
593	169	54	259	22	10	1107 observed
612	153	51	218.25	54.5625	18.1875	1107 calculated, basis of two 12:3:1 ratios
Total 816			Total 291			

$X^2 = 33.17$ P very low

The main factor for roughness of awn (Rr) is present in the dominant condition only in the rough phenotypes. The intermediate-smooth and smooth phenotypes contain this factor only in the recessive condition. If the linkage suggested is between the factor pairs Rr and Ss, a separation of phenotypes into rough and smooth awned classes should show indications of such linkage. Table 10 gives this segregation compared with the expected numbers on the basis of two 3:1 ratios.

Table 10. Segregation in F_2 for long versus short haired rachilla (Ss) and rough versus intermediate-smooth and smooth awns combined, in a cross, Coast X Lion.

Long haired rachilla		Short haired rachilla			
Rough	Int-smooth Smooth	Rough	Int-smooth Smooth		
593	223	259	32	1107	observed
612	204	218.25	72.75	1107	calculated, basis of two 3:1 ratios
Total 816		Total 291			

$X^2 = 32.79$ P very low

Sigfusson (9) in testing the behavior of F_3 families for the segregation of intermediate-smooth versus smooth awns and long versus short haired rachillas found these factor pairs inherited independently. If such is the case, the intermediate-smooth and smooth phenotypes can be combined in the study of linkage between the factor pairs Rr and Ss.

According to the symbols used in this paper the Lion parent has the genetic constitution, rrr'r'SS, and the Coast parent has the genetic constitution, RRR'R'ss, for the characters roughness of awn and rachilla hairs. The linkage exhibited is in the repulsion phase, since the factor pairs, RR and ss, and, rr and SS, enter the cross together. The dominant factor R concerned in this linkage is in the rough class only, while the recessive factor r is in the intermediate-smooth and smooth classes. The factor pair R'r' is common to both classes but should not interfere in the calculations as it is not concerned in this linkage. The linkage was calculated on the basis of two 12:4 ratios or rather two 3:1 ratios. The crossover percentage calculated from the segregation in table 10, by Immer's formulae, was 34.63 ± 1.76. The probable error was also determined from Immer's tables (6). The observed data are compared with the calculated on the basis of a crossover percentage of 34.63 in table 11.

Table 11. Comparison of the observed and the calculated on the basis of a crossover percentage of 34.63 for the characters, rachilla hairs (Ss) and roughness of awn (Rr).

Long haired rachilla		Short haired rachilla			
Rough	Int-smooth Smooth	Rough	Int-smooth Smooth		
593	223	259	32	1107	observed
612	204	218.25	72.75	1107	calculated, basis of two 3:1 ratios
576.6	239.4	256.1	34.9	1107	calculated with a crossover percentage of 34.63
Total 816		Total 291			

$X^2 = 1.86$ P = 0.4004

Emerson's mehtod was used to calculate the theoretical distribution. Two 3:1 ratios were used instead of the usual 9:3:3:1 ratio. The usual gametic ratio for independent inheritance is 1:1:1:1. With a crossover value of 34.63 percent, the gametic ratio is 1:1.888:1.888:1.

In comparing the observed data with the calculated on the basis of 34.63 percent crossover, a X^2 value of 1.86 was obtained with a P value of 0.4004. This is a good fit and indicates a high probability of linkage between the factor pairs Rr and Ss.

The crossover percent of 34.63 ± 1.73 found, agrees fairly well with that found by Sigfusson (9) which was 30.8 percent, and with that found by Hor (5) which was 28.70 ± 3.43 in the repulsion phase, and 34.54 ± 2.89 in the coupling phase.

Rough versus smooth awns (RrR'r') and branched versus unbranched styles (GgG'g'G"g")-- An examination of table 12 shows a wide variation from the calculated for independent inheritance. When tested for goodness of fit, a X^2 value of 156.54 was obtained, with a very low value for P.

Table 12. Segregation in F_2 for roughness of awns (RrR'r') and style branching (GgG'g'G"g") in a cross, Coast X Lion.

Branched style Rough	Int-smooth	Smooth	Unbranched style Rough	Int-smooth	Smooth		
850	188	50	2	3	14	1107	observed
816	204	68	14.25	3.5625	1.1875	1107	calculated, basis of two 12:3:1 ratios
Total 1088			Total 19				

$X^2 = 156.54$ P very low

The segregation in table 12 is between a two factor difference for roughness of awn and a three factor difference for style branching. The unbranched style group has only 19 plants. However, the unbranched style smooth awn class is high and the unbranched style rough awn class is low when compared with the calculated for independent inheritance. The reverse is true to a lesser extent in the branched style group. The probable cause of this unbalanced segregation is linkage. The dominant factors concerned in this segregation enter the cross together (from the Coast parent) and the recessive factors also enter together (from the Lion parent). Therefore, the linkage exhibited is in the coupling phase. as the numbers calculated for independent inheritance do not vary greatly from the observed numbers in the intermediate-smooth classes, it is probable that the linkage exhibited is between the factor pair Rr for roughness of awn and one of the factor pairs for style branching. The data are not sufficient to calculate the crossover percentage.

DISCUSSION

According to Sigfusson (9) and Hor (5) the factors for roughness of awn (Rr) and rachilla hairs (Ss) are located in the same linkage group. The evidence presented here gave the same result. However, the crossover percentage found was higher but conforms fairly well to that found by Sigfusson , when the probable error is taken into consideration.

Linkage was also indicated between the factors for roughness of awn and style branching. Therefore, the segregation between the factors for rachilla hairs and style branching should also have indicated linkage. However the observed segregation, table 8, indicated independent inheritance. It is possible to explain this condition by the location of the genes in the chromosomes. The factor for rachilla hairs could be located near one end of the chromosome and the factor for style branching, concerned in this linkage, could be located near the other end, with the factor for roughness of awn located between. The crossover percentage between the factors for rachilla hairs and style branching could approach fifty percent. In which case the behavior of the segregation would be the same as for independent inheritance.

SUMMARY

In a cross, Coast X Lion the following characters were studied: black versus white glume color (Bb), long versus short haired rachilla (Ss), rough versus smooth awn (RrR'r'), and branched versus unbranched style (GgG'g'G"g").

A single factor difference was found in the inheritance of glume color (Bb) and rachilla hairs (Ss).

A two factor difference was found for the inheritance of roughness of awn (RrR'r'). The segregation found approached a 12:3:1 ratio. The double recessive (rrr'r') produced the smooth awned class.

A three factor difference was found for the inheritance of style branching (GgG'g'G"g"), with the dominant factors cumulative in their effect. The triple recessive only produced the unbranched style of the Lion type.

The factors for glume color (Bb) were found to be inherited independently of the other factors studied.

The factors for rachilla hairs (Ss) were found to be linked with the main factor for roughness of awn (Rr) with a crossover value of 34.63 ± 1.76 percent.

A strong indication of linkage was also found between one of the factor pairs for roughness of awn (RrR'r') and one of the factor pairs for style branching (GgG'g'G"g").

The segregation between the factors for rachilla hairs (Ss) and style branching (GgG'g'G"g") indicated independent inheritance. This segregation would also be obtained with a crossover value approaching fifty percent. Therefore, it is probable that the factor pairs Ss and Rr and one of the factor pairs for style branching (GgG'g'G"g") are in the same linkage group.

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