5-1953

A Linkage Study of Chromosome IV in Barley

Earl William Smith

A LINKAGE STUDY OF CHROMOSOME IV IN BARLEY

by

Earl William Smith

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Agronomy

UTAH STATE AGRICULTURAL COLLEGE
Logan, Utah

1953

ACKNOWLEDGMENT

My sincere thanks are due to Dr. Woodward for furnishing the material and aid which made this thesis possible. I am also grateful for the valuable suggestions of Professor D. C. Tingey.

Earl William Smith

TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Barley (Hordeum sp.) is a principal cereal crop throughout much of the world and is of great economic importance in the United States. Spring barley is a leading cereal crop in Utah.

Barley has many desirable characteristics which make it an excellent plant for genetic studies. Some of these characteristics are low chromosome number, almost complete self-fertilization, relative ease of hybridization, and easily classified hereditary characters.

The establishment of genes or factors at definite loci in linkage groups is a valuable aid in furthering breeding programs and the ultimate improvement of barley. All seven linkage groups have been established although the location of only a small number of genes is known in some of them and most of these genes were mapped from information obtained from crosses involving only two or three factor pairs.

This thesis deals with determining the location of five genes believed to be in linkage group IV and to establish new linkages if possible. Specifically planned crosses involving from two to five of these genes were used in this study.

REVIEW OF LITERATURE

Barley is one of the few crops on which major genetic emphasis has been given, thus making a large amount of literature available to the investigator.

Review of literature on the genetics of barley is limited here to those characters used in this study.

Individual Characters

Blue aleurone (Bl) vs. white aleurone (bl)

Most of the literature indicates that a single dominant gene is responsible for blue aleurone with the F_2 plants segregating in the simple Mendelian ratio of 3 blue to 1 white aleurone. This is substantiated by the investigations of Buckley (1), Robertson, et al. (11), Gill (5) and Woodward (14). Myler and Stanford (8), however, obtained a 9:7 ratio in the F_2 of a cross between two white varieties indicating the presence of two complementary factors.

Hoods (K) vs. awns (k)

Numerous workers, among those Buckley (1), Deane (2), Fraser (4), Gill (5) and Woodward (14), have reported that in crosses between hooded and awned forms the F_2 segregates three-fourths hooded to one-fourth awned plants concluding that a single dominant gene is responsible for hoods.

So, et al, according to Smith (12), obtained 3:1 ratios in some crosses and 9:7 ratios in others, indicating the possibility of a second factor. Gill (5) states that Ubish

explains the segregation of his crosses on a two factor basis, with a dominant KK factor for hoods, and an AA factor for long awns. Thus KKAA and KKaa plants are hooded while kkAA are long awned, and kkaa are short awned individuals.

Non-zoned (Z_0) vs. Colorado zoned leaf (z_0)

Colorado zoned leaves are marked by transverse yellowish stripes. Zoned leafed plants are frequently yellowish in color until almost fully developed. These plants are characterized by a reduced size and lateness of maturity.

Investigations by Gill (5) and Woodward (14) show non-zoned leaves to be dominant in the F_1 generation with the F_2 plants segregating in the simple Mendelian ratio of 3 non-zoned to 1 Colorado zoned leaf.

Non-glossy (Gl) vs. glossy leaf (gl)

The glossy leafed plants in this study are characterized by waxy bloomless leaves. Such plants may be further identified by a scalded appearance of the heads.

Woodward (14) found non-glossy leaves to be dominant with the F_2 segregating into 3 non-glossy to 1 glossy leafed plant.

Robertson and Coleman (10) described an additional factor pair for non-glossy versus glossy plants (Gl_2, gl_2). Their report is not clear as to whether the entire plant was glossy or the foliage only. Such plants were somewhat weaker than normal ones. Crosses between non-glossy x glossy plants segregated 3 non-glossy to 1 glossy in the F_2 generation. Immer and Henderson (6) used Gl, gl for non-glossy versus glossy seedlings and obtained a 3:1 ratio in the

first segregating generation, again indicating that a single factor pair governs the inheritance of this character.

Non-intermedium (i) vs. partly fertile intermedium (I or I^h)

Factors I, I^h and i effect the degree of development of the lateral florets in barley. This allelic series was established by the work of Leonard (7) and more recently verified by Woodward (15). Factors II and I^hI^h give two types of partly fertile intermediums, while ii is the typical two row plant showing no kernel development in the lateral florets. The i is dominant to I and I^h while I is dominant to I^h, although dominance is not complete.

Robertson (9) and Leonard (7) found that the development of lateral florets is simple in inheritance. The F_2 of a non-intermedium (two row) crossed with a partly fertile intermedium segregated 3 non-intermedium to 1 partly fertile intermedium.

Non-glossy (Gs) vs. glossy culms and spikes (gs)

Culms and spikes of plants recessive for the gene gs are waxy and without bloom.

Woodward (14) and Gill (5) found that the F_2 of crosses involving non-glossy versus glossy culms and spikes (Gs, gs) segregate in a simple monofactorial ratio of 3 non-glossy to 1 glossy.

Previous Linkage Studies

Zo vs. z_o in relation to K vs. k

Immer and Henderson (6) in their linkage studies in barley found the non-zoned versus zoned leaf (Z_o, z_o) factor pair to be linked with the hooded versus awned factor pair

(K, k) showing a 6.0 ± 0.8 percent recombination. In similar studies Woodward (14) obtained a 13.0 ± 3.1 percent recombination, while Gill (5) reported a 38.0 ± 9.7 percent value with a small amount of data.

K vs. k in relation to I vs. I or I^h

Robertson (9) found the factor pairs for partly fertile intermedium versus non-intermedium (I, i) and hoods versus awns (K, k) to be linked with a 15.12 ± 0.65 percent recombination. Leonard (7) obtained a 14.32 ± 0.61 percent recombination between the non-intermedium versus partly fertile intermedium (i, I^h) and hoods versus awns (K, k) gene pairs.

K vs. k in relation to Bl vs. bl

Linkage relations between hoods versus awns (K, k) and blue versus white aleurone (Bl, bl) have been studied by various investigators.

Buckley (1) in a cross involving the repulsion phase obtained a recombination value of 40.5 percent while Robertson, et al. (11) with more extensive data obtained a recombination value of 22.58 ± 0.8 percent.

Myler and Stanford (8) reported two complementary factors for blue aleurone. One of these factor pairs (Bl, bl) was linked with the factor pair for hoods versus awns (K, k), placing it in linkage group IV with a recombination value of 24.72 ± 1.73 percent. The second factor pair was designated as Bl_1, bl_1 and was found to be linked with the factor pair for hulled versus naked kernel (N, n) which placed it in linkage group III.

Immer and Henderson (6) obtained a recombination value

value of 44.0 ± 6.3 percent for the factor pairs for blue versus white aleurone (Bl, bl) and hooded versus awned spikes (K, k). Gill (5) in a similar study found these gene pairs to be linked in three crosses involving only a small number of plants with the following recombination percentages: 24.0 ± 6.1, 33.0 ± 6.0 and 36.0 ± 7.7. Woodward (14) obtained an average recombination percentage of 27.5 ± 1.2 from fourteen crosses.

K vs. k in relation to Gl vs. gl

Immer and Henderson (6) found the factor pair for hooded versus awned spikes (K, k) to be linked with the non-glossy versus glossy leaf (Gl, gl) factor pair, showing a recombination percentage of 10.0 ± 0.8. Woodward (14) obtained an average recombination percentage of 23.5 ± 1.2 from seven crosses involving these same pairs.

Robertson and Coleman (10) found linkage between the factor pairs for non-glossy versus glossy leaf (Gl_2, gl_2) and hoods versus awns (K, k) with a 25.0 percent recombination.

Bl vs. bl in relation to Gl vs. gl

Immer and Henderson (6) reported that the gene pairs (Bl, bl) for blue versus white aleurone and (Gl, gl) for non-glossy versus glossy leaf were linked with a 36.0 ± 3.3 percent recombination. Woodward (14) obtained an average recombination percentage of 41.5 ± 2.6 from four crosses involving the genes Bl, bl and Gl, gl.

Bl vs. bl in relation to Za vs. za

Woodward (14) obtained a linkage of the factor pair (Bl, bl) for blue versus white aleurone and the factor pair

(Z_c, z_c) for non-zoned versus zoned plants with a recombination value of 26.9 ± 4.5 percent.

Zc vs. za in relation to Gl vs. gl

Immer and Henderson (6) found the genes for non-zoned versus zoned leaf (Z_c, z_c) to be linked with the gene pair (Gl, gl) for non-glossy versus glossy leaves with a 3.0 ± 0.5 recombination.

Gl2 vs. gl2 in relation to I vs. i

Robertson and Coleman (10) obtained a recombination value of 28.0 percent for the factor pairs (Gl_2, gl_2) non-glossy versus glossy leaf and (I, i) partly fertile versus non-fertile intermedium.

Gene Order on Chromosome IV as Previously Proposed

Immer and Henderson (6) gave the known gene order on chromosome IV as follows: i k z gl bl, with the gl and bl 36 units apart.

Smith (12) proposes the following gene order after reviewing the available literature: k z gl bl.

MATERIAL AND METHOD

The crosses used in this study were made in the spring of 1950, by Dr. R. W. Woodward at the experimental farm North Logan, Utah.

Approximately sixteen florets, usually the central ones on each of two or more plants were emasculated and pollinated for each cross. The F_1 plants resulting from these crosses were grown approximately twelve inches apart in rows two feet apart to aid in obtaining large plants with a maximum number of seeds.

Three of these F_1 plants having four contrasting factor pairs were used as pollen parents in an attempted back cross study. Two anthers were removed from many of the florets and used to pollinate a genetic tester recessive for bl, k, i, and z. It was believed that gl was also present. Some 400 florets were included in these pollinations.

Back cross progenies were seeded in the same manner as the F_1's described above while F_2 plants were grown in rows one foot apart with from one to three inches between plants. Each F_2 cross consisted of three to five rows, each row representing a family.

Plants with characters difficult to distinguish at time of harvest, namely, zoned leaf, glossy leaf, and glossy culm and spikes, were tied in the field with colored string at the time these characters could be most easily observed.

The F_2 plants when matured were harvested and the individual plants were examined for contrasting characters involved in each cross. Several heads from each plant were saved for re-examination or for F_3 seeding. Also certain selections from the F_2 will be used as parents for a future breeding program.

To calculate recombination values, the product method was used with the values being those calculated by Fisher and Balmukand (3). The chi-square test of goodness of fit was used to interpret the data. The P values for chi-square were taken from Snedecor (13).

Symbols of the six Mendelian characters used in this study are as follows:

Blue vs. white aleurone	Bl bl
Hoods vs. awns	K k
Normal vs. Colorado zoned leaf	Z_c z_c
Normal vs. glossy leaf	Gl gl
Two row vs. fertile intermedium	i I or I^h
Normal vs. glossy culm and spike	Gs gs

The following are the crosses which were used in this study with the numbers assigned them and the parents used:

B 864 2R Tester x B 430-158

B 853 B 318-1-1 x 2R Tester

B 846 B 309-9-2 x B 318-15-2

B 847 B 318-15-2 x B 476-3 gl

B 848 B 318-15-2 x B 306-9-1

B 849 Ums 7138 x Hooded zoned leaf

B 860 B 309-9-2 x B 318-15-5

B 858 B 476-3 x B 318-1-1

B 916 Wisc. zoned leaf x X_c x_c

B 867 C 1343 Ribbon Grass x B 318-15-3 zoned leaf

B 887 C. I. 3910-1n x C. I. 7008

B 905 2 R Tester x zoned leaf K V I

B 900 Ums 7137 x Hooded zoned leaf Ums

B 859 B 318-1-4 x B 476-3

B 904 2R Tester V V ii C. I. 7139 x Glossy Ums

B 958 B 318-15-2 x zoned leaf Wisc.

B 591 Colsess I x zoned leaf Wisc.

B 666 Colsess I x gl VI

B1060 Back cross F, #1 x T 43 k z c bl

EXPERIMENTAL RESULTS

The experimental results are presented in the following sequence: the mode of inheritance of the Mendelian characters; the independently inherited character pairs; the alleles which are linked; the linkage maps; and the results of the back cross study.

Inheritance of Mendelian Characters

Non-glossy vs. glossy leaves

The phenotypic ratio of the F_2 generation as given in table 1, shows that non-glossy versus glossy leaf is monofactorial.

Table 1. Segregation of non-glossy vs. glossy leaves in the F_2 generation with the chi-square values based on a 3:1 ratio

Cross No.	Gl	gl	Total	X^2	P
B 846	74	17	91	1.937	.15
B 847	80	22	102	.640	.45
B 860	106	36	142	.009	.95
B 858	49	15	64	.076	.80
B 859	50	12	62	1.054	.30
B 864	13	4	17	.020	.90
B 666	50	18	68	.078	.80
Sum of 7 chi-squares				3.814	.80
Total	422	124	546	1.526	.20
Interaction				2.288	.90

Blue vs. white aleurone

Table 2 gives the F_2 segregation for blue versus white aleurone. The results signify that blue versus white aleurone differ by a single factor pair (Bl, bl) in all crosses except B 848. Cross B 848 fits the 9:7 ratio for blue versus white aleurone suggesting a difference of two factor pairs responsible for the expression of blue aleurone.

Table 2. Segregation of blue vs. white aleurone (Bl, bl) in the F_2 generation and chi-square values based on a 3:1 ratio

Cross No.	Bl	bl	Total	X^2	P
B 864	11	6	17	.960	.35
B 846	73	18	91	1.332	.25
B 849	152	47	199	.203	.65
B 860	102	40	142	.761	.40
B 916	110	34	144	.148	.70
B 887	73	28	101	.399	.55
B 905	28	9	37	.009	.95
B 859	49	13	62	.538	.45
B 904	111	50	161	3.148	.10
B 958	46	19	65	.620	.45
B 571	77	18	95	1.854	.20
B 666	53	15	68	.313	.60
B 905	38	15	53	.298	.60
Sum of 13 chi-squares				10.538	.70
Total	923	312	1235	.045	.85
Interaction				10.493	.60
B 848*	10	7	17	.046	.85

*Based on a 9:7 ratio

Hoods vs. awns

Crosses segregated three hooded (K) to one awned (k) plant in the F_2 generation indicating a one factor difference as shown in table 3.

Table 3. Segregation of hoods vs. awns (K, k) in the F_2 generation and chi-square values based on a 3:1 ratio

Cross No.	K	k	Total	χ^2	P
B 853	93	37	130	.830	.40
B 846	17	7	24	.222	.65
B 847	65	27	92	.839	.40
B 848	40	19	59	1.632	.20
B 849	152	47	199	.202	.65
B 858	91	24	115	1.047	.30
B 916	335	117	452	.189	.65
B 867	148	47	195	.084	.80
B 887	74	27	101	.161	.70
B 905	26	11	37	.441	.50
B 859	48	14	62	.193	.65
B 571	70	25	95	.087	.75
B 864	9	8	17	4.408	.05
B 900	33	20	53	4.585	.05
B 958	42	23	65	3.738	.05
Sum of 15 chi-squares				18.658	.25
Total	1243	453	1696	2.645	.10
Interaction				16.013	.30

Non-glossy vs. glossy culms and spikes

Table 4 gives the segregation of F_2 plants for non-glossy

versus glossy culms and spikes. The results indicate that this character differs by a single factor pair (Gs, gs).

Table 4. Segregation of non-glossy vs. glossy culms and spikes (Gs, gs) in the F_2 generation and chi-square values based on a 3:1 ratio

Cross No.	Gs	gs	Total	X^2	P
B 847	70	22	92	.058	.80
B 858	88	27	115	.139	.70
B 859	51	11	62	1.742	.20
Sum of 3 chi-squares				1.939	.60
Total	209	60	269	1.041	.30
Interaction				.898	.60

Two-row vs. partly fertile intermedium

The segregation in F_2, table 5, shows that two-row versus partly fertile intermedium plants differ by a single Mendelian factor pair (i, I or I^h) for this fertility character.

Table 5. Two-row vs. partly fertile intermedium segregation in the F_2 generation and the chi-square values based on a 3:1 ratio

Cross No.	i	I or I^h	Total	X^2	P
B 846	20	4	24	.889	.35
B 847	47	20	67	.841	.40
B 905	59	19	78	.017	.90
B 904	122	39	161	.052	.80
Sum of 4 chi-squares				1.799	.70
Total	248	82	330	.004	.95
Interaction				1.795	.70
B 853*	55	53	108	.037	.85

*Based on a 1:1 ratio

Cross B 853 gives a good fit to a 1:1 ratio. F_3 plants will be grown to see if a solution is possible for this unexplained behavior.

Non-zoned vs. zoned leaves

Table 6 which gives data on F_2 segregation, shows evidence that the character non-zoned versus zoned leaf results from a single factor pair difference (Z_o, z_c). The large value of chi-square for the totals of the same crosses indicated that the data does not give a good fit to the theoretical ratio. High seedling mortality of zoned leaf plants accounts at least partially for the low P value.

Table 6. Crosses between non-zoned vs. zoned leaf (Z_o, z_c) plants showing the F_2 segregation and the chi-square values based on a 3:1 ratio

Cross No.	Z_o	z_c	Total	X^2	P
B 847	69	23	92	.000	.99
B 848	47	12	59	.683	.45
B 849	88	25	113	.498	.50
B 860	113	29	142	1.587	.20
B 867	160	35	195	5.170	.02
B 905	32	5	37	2.603	.10
Sum of 6 chi-squares				10.541	.10
Total	509	129	638	7.776	less.01
Interaction				2.765	.75

An Independently Inherited Character Pair

A study was made between the character pair (Gs, gs) for non-glossy versus glossy culms and spikes and three other character pairs to determine whether Gs, gs is inherited independent of, or linked with them.

To determine whether the character pairs are independent the chi-square test is used to test the frequencies of the four classes designated by the symbols XY, Xy, xY and xy.

Table 7. Inheritance of characters in relation to non-glossy vs. glossy culms and spikes from F_2 data based on a 9:3:3:1 ratio

Cross No.	XY	Xy	xY	xy	Total	X^2	P
	(Gs vs. gs in relation to K vs. k)						
B 847	54	16	11	11	92	7.701	.05
B 858	72	16	19	8	115	2.657	.50
B 859	40	11	8	3	62	2.227	.50
Total	166	43	38	22	269	12.585	.20
	(Gs vs. gs in relation to Gl vs. gl)						
B 847	57	13	13	9	92	4.462	.20
B 858	76	12	21	6	115	6.371	.10
B 859	39	12	11	0	62	4.586	.20
Total	172	37	45	15	269	15.419	.10
	(Gs vs. gs in relation to Bl vs. bl)						
B 859	39	12	10	1	62	3.045	.40

The P values for goodness of fit in the above table show Gs versus gs to be inherited independent of, or fifty or more genetic units from the factor pairs (K, k), for hoods and awns, (Gl, gl) for non-glossy versus glossy leaf, and (Bl, bl) for blue versus white aleurone.

Segregation of Character Pairs that are Known to be in Linkage Group IV and the Observed Linkage Values

Tables 8 to 14 inclusive show the deviation from theoretical independent segregation (9:3:3:1) and also the calculated recombination percentages. All crosses were in the coupling

phase unless otherwise indicated.

K vs. k in relation to Bl vs. bl

Linkages of the factor pairs for hoods versus awns (K, k) in relation to blue versus white aleurone (Bl, bl) is shown in table 8. In six crosses in the coupling phase, the data indicates that the factor pair (K, k) for hoods and awns is linked with the factor pair (Bl, bl) for blue and white aleurone giving a recombination value of 26.0 ± 2.1 percent

Crosses B 905, B 859 and B 571 have P values which do not indicate linkages for the factor pairs K versus k in relation to Bl versus bl.

Table 8. K vs. k in relation to Bl vs. bl, chi-square values and cross over percentages based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 864	9	0	2	6	17	28.804	less .01	14.5	9.3
B 849	131	21	24	23	199	25.137	less .01	27.0	3.7
B 916	90	20	10	24	144	38.517	less .01	21.5	3.9
B 887	61	13	12	15	101	16.889	less .01	27.5	5.4
B 958	37	5	9	14	65	29.883	less .01	21.0	5.8
B 900	25	8	13	7	53	6.228	.10	43.0	9.4
Sum of chi-squares						147.583	less .01		
Total	353	67	70	89	579	106.215	less .01	26.0	2.1
Interaction						41.368	less .01		
B 905	21	5	7	4	37	1.704	.60	38.0	10.6
B 859*	35	13	14	0	62	4.452	.20	20.5	12.1
B 571*	55	15	22	3	95	2.889	.40	40.5	8.4

*Repulsion

Bl vs. bl in relation to Gl vs. gl

Linkages of Bl, bl in relation to Gl, gl are shown in table 9. Blue versus white aleurone (Bl, bl), when tested for independence in relation to non-glossy versus glossy leaf (Gl, gl) gave P values of .55, .70, .15, .25, and .25 for the five respective crosses. These P values normally would indicate independence for these two factor pair but on the basis of other information which shows them to be linked it seems safe to assume that the recombination percentage is approaching 50. A linkage value of 36.0 ± 4.5 was calculated for the total of the five crosses.

Table 9. Linkages of Bl, bl in relation to Gl, gl, chi-squares and recombination values based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 666*	37	16	13	2	60	2.064	.55	35.5	10.4
B 864*	8	5	3	1	17	1.286	.70	41.0	19.9
B 846*	40	16	16	8	72	5.432	.15	19.0	11.3
B 860*	75	27	32	8	142	4.103	.25	44.5	6.7
B 859*	37	13	12	0	62	4.197	.25	22.5	11.9
Sum of chi-squares						17.082	.30		
Total	197	77	76	11	361	8.391	.05	36.0	4.5
Interaction						8.691	.70		

*Repulsion

Bl vs. bl in relation to Z_o vs. z_o

Table 10 shows the linkage for the gene pairs of blue versus white aleurone (Bl, bl) in relation to non-zoned versus zoned plants (Z_o, z_o). Totals from four crosses in the repulsion phase gave a recombination percentage of 32.5 ± 4.4.

No doubt the P values of .40, .10 and .20 for crosses B 848, B 860 and B 905 are not low enough to suggest linkage. On examining the data in table 10, P values are low for both the sum of chi-squares and the chi-square on the pooled or total values which indicate linkage. Low chi-square values for interaction supplies evidence that the progeny ratios are consistent.

Table 10. Bl vs. bl in relation to Z_s vs. z_c, chi-square and linkage values based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 849*125	30	41	3	199	10.452	less .01	28.5	6.4
B 848* 7	3	6	1	17	3.141	.40	37.0	20.6
B 860* 77	25	36	4	142	6.331	.10	37.5	7.1
B 905* 24	4	9	0	37	4.750	.20	34.5	14.2
Sum of chi-squares					24.674	.02		
Total 233	62	92	8	395	18.148	less .01	34.5	4.3
Interaction					6.526	.70		
*Repulsion								

K vs. k in relation to Gl vs. gl

Table 11 shows the linkage relation of factor pairs (K, k) for hoods versus awns and (Gl, gl) for non-glossy versus glossy leaf. Totals for three crosses, B 847, B 858, and B 859, gave a recombination percentage of 17.5 ± 2.8. These crosses were all in the coupling phase and gave a P value of less than .01 for independent segregation.

The P value for interaction means the classes vary consistently from the expected 9:3:3:1 ratio in each cross.

Table 11. K vs. k in relation to Cl vs. gl, values for chi-square and recombination percentages based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 847	60	5	10	17	92	33.481	less .01	16.5	4.3
B 858	43	4	6	11	64	21.943	less .01	17.0	5.2
B 859	44	4	6	8	62	14.320	less .01	19.0	5.6
Sum of chi-squares						69.744	less .01		
Total	147	13	22	36	218	69.256	less .01	17.5	2.8
Interaction						.488	.99		

Cl vs. gl in relation to Z_c vs. z_c

Linkage of factor pairs (Z_c, z_c) for non-zoned versus zoned leaf and (Cl, gl) for non-glossy versus glossy leaf is shown in table 12. The low P values obtained do not suggest independence. These factor pairs were found to be linked with a recombination value of 14.0 ± 5.3 percent for the totals. All crosses were in the repulsion phase.

Table 12. Cl vs. gl in relation to Z_c vs. z_c, chi-squares and recombination values based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 846*	62	12	17	0	91	9.471	.02	25.5	9.7
B 847*	57	23	22	0	102	7.921	.05	16.0	9.6
B 860*	78	28	35	1	142	9.764	.02	19.0	8.0
Sum of chi-squares						27.156	less .01		
Total	197	63	74	1	335	24.766	less .01	14.0	5.3
Interaction						2.390	.50		

*Repulsion

K vs. k in relation to Z_c vs. z_c

The association of factor pairs (K, k) for hoods versus

awns and (Z_c, z_c) for non-zoned versus zoned leaf is shown in table 13. The recombination value for the factor pairs was checked in four crosses, B 847, B 848, B 849, and B 867. All of these crosses were in the repulsion phase. The values were 25.5 ± 9.6, 17.0 ± 12.6, 24.0 ± 8.1 and 13.0 ± 7.0 percent respectively. The total of these crosses gave a recombination value of 19.5 ± 4.4 percent. Probability is less than one percent that these characters are inherited independently. A high P value for interaction suggests consistency of the progeny ratios.

Table 13. K vs. k in relation to Z_c vs. z_c, chi-square values and recombination percentages based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
B 847*	44	21	25	2	92	7.092	.05	26.5	9.6
B 848*	28	12	19	0	59	10.319	.02	17.0	12.6
B 849*	82	24	26	1	133	7.213	.05	24.0	8.1
B 867*	113	35	47	0	195	15.921	less .01	13.0	7.0
Sum of chi-squares						40.545	less .01		
Total	267	92	117	3	479	32.513	less .01	19.5	4.4
Interaction *Repulsion						8.032	.50		

i vs. I and I^h in relation to other factor pairs in linkage group IV

In all the crosses involving i vs. I or I^h and other factor pairs, the high P values give evidence of independent inheritance as shown in table 14. Recombination percentages were calculated but furnished no information as to the location of the allelic series i, I and I^h.

Table 14. i vs. I or I^h in relation to other factor pairs in linkage group IV, chi-square and recombination values based on a 9:3:3:1 ratio

Cross	XY	Xy	xY	xy	Total	X^2	P	Recom %	SE
					(K vs. k in relation to i vs. I or I^h)				
B 847*	32	16	15	4	67	2.325	.50	41.0	10.0
B 905*	17	9	10	1	37	3.907	.30	28.0	14.9
B 846*	14	3	6	1	24	1.185	.75	46.5	15.8
Total	63	28	31	6	128	7.417	.60	38.5	7.4
					(Bl vs. bl in relation to i vs. I or I^h)				
B 846*	27	13	13	1	54	6.115	.10	26.0	12.5
B 905*	40	13	19	6	78	2.082	.50	49.0	8.6
Total	67	26	29	7	132	8.197	.25	42.0	7.1
					(Gl vs. gl in relation to i vs. I or I^h)				
B 846	15	7	5	3	30	1.265	.70	46.5	13.1
B 847*	35	17	12	3	67	2.150	.50	40.5	10.1
					(Z_c vs. s_c in relation to i vs. I or I^h)				
B 847	41	10	6	10	67	12.047	less .01	26.0	6.4
B 905*	23	9	4	1	37	3.137	.40	43.5	13.2

*Repulsion

Linkage Maps

The first three linkage maps were plotted from information obtained from cross B 847, B 864, and B 848. The final one was charted from recombination percentages calculated from the total values as shown in tables 8 to 13 inclusive.

The linkage map obtained from cross B 847 shows the gene order to be Z_c Gl K. B 864 places Gl and Bl on the opposite sides of K; the order being Gl K Bl, while cross B 848 shows the arrangement of genes in the order Z_c K Bl.

A linkage map plotted from recombination percentages

based on total values gives the following gene order: Z_c Gl K Bl. Calculated values from bl to gl and s_o are given but P values in tables 11 and 13 indicate that bl is 50 or more genetic units from the other two gene loci.

B 847 Z_o Gl K
16.5
26.5
16.0

B 864 Gl K Bl
14.5
41.0

B 848 Z_o K Bl
17.0
37.0

ALL Z_o Gl K Bl
26.0
17.5
19.5
14.0
36.0
34.5

Backcross Data

Data on the backcross plants is given in table 15.

Table 15. Backcross data, chi-square values for cross B 1060 based on a 1:1 ratio

Character	Total	X^2	P
K vs. k 12 24	36	4.000	.05
Z_o vs. s_o 31 5	36	18.776	less .01
I vs. I 16 20	36	.444	.50
Bl vs. bl 20 16	36	.444	.50

Thirty six backcross plants were examined to determine possible linkage values. The P values in table 15 show that only the factors Bl versus bl and i versus I give a good fit to the expected 1:1 ratio. A recombination percentage of 60 was calculated for these two factor pairs. Thus Bl versus bl was found to be inherited independent of, or 50 or more genetic units from the i alleles.

to be in linkage group IV. In this investigation however, this series was not found to be linked to any other factors studied. This may be due to the difficulty in classifying two-row (ii) and intermedium (II) plants, and the small plant populations available. The V^b and v genes for deficiens and six-row respectively are epistatic to the i, I, I^h allelic series. In future crosses to determine the linkage relationship of this series one should use the following genotypes as parent plants: VV ii and V V I^h I^h. By doing this, large populations of more easily classifiable plants should be available. The I^h I^h plant has a much higher percent of fertility of lateral florets than the I I plant and is thus easier to contrast with the two-row plant.

No previous attempts to study linkages on back cross data in barley have been reported in the literature. Percentage of seed set in the back cross material was low, making only a small number of plants available for study. The recessive genetic tester, bl, k, i and z was used as the pistilate parent in making these crosses. In future back crosses it is recommended that the genetic tester be used as the pollen parent because the plants with recessive genes for both zoned and glossy leaf are weakened and set very few seeds.

SUMMARY

The following allelic pairs exhibited a single factor difference for their inheritance:

Bl bl	Blue vs. white aleurone
K k	Hooded vs. awned
Z_c z_c	Normal vs. Colorado zoned
Gl gl	Normal vs. glossy leaf
i I I^h	Two-row vs. fertile intermedium
Gs gs	Normal vs. glossy culms and spikes

Independent inheritance was found between the following factor pairs:

Gs gs and K k

Gs gs and Gl gl

Gs gs and Bl bl

i vs. I (or I^h) and Bl bl

i vs. I (or I^h) and Gl gl

i vs. I (or I^h) and K k

i vs. I (or I^h) and Z_c z_c

Presented below are the factor pairs which showed linkage and their recombination percentages with standard errors.

K k vs. Bl bl	26.0 ± 2.1
K k vs. Gl gl	17.5 ± 2.8
K k vs. Z_c z_c	19.5 ± 4.4
Bl bl vs. Z_c z_c	32.5 ± 4.4
Gl gl vs. Z_c z_c	14.0 ± 5.3

Bl bl vs. Gl gl 36.0 ± 4.5

The following gene order for linkage group IV is proposed: Z_0 Gl K Bl.

LITERATURE CITED

(1) Buckley, G. F. H. Inheritance in barley with special reference to the color of caryopsis and lemma. Sci. Agr. 10:460-492. 1930.

(2) Deane, A. Linkage relations in barley. Minn. Agr. Exp. Sta. Tech. Bul. 78. 1931.

(3) Fisher, R. A., and Balmukand, B. The estimate of linkages from the offspring of selfed heterozygotes. Jour. Gen. 20:78-92. 1920.

(4) Fraser, J. C. C. The dominant Mendelian characters in barley breeding. Sci. Agr. 2:113-116. 1922.

(5) Gill, T. S. Inheritance of 16 barley characters and their linkage relationships. (M. S. Thesis. Dept. of Agron.) Utah State Agricultural College, 1951.

(6) Immer, F. R., and Henderson, M. T. Linkage studies in barley. Genetics 28:419-440. 1943.

(7) Leonard, W. H. Inheritance of fertility in the lateral spikelets of barley. Genetics 27:299-316. 1942.

(8) Nylor, J. L., and Stanford, E. H. Color inheritance in barley. Jour. Amer. Soc. Agron. 34:427-436. 1942.

(9) Robertson, D. W. Inheritance in barley. Genetics 18: 148-159. 1933.

(10) _____ and Coleman, O. H. Location of glossy and yellow seedlings in two linkage groups. Jour. Amer. Soc. Agron. 34:1028-1034. 1942.

(11) _____ Weibe, G. A., and Immer, F. R. A summary of linkage studies in barley. Jour. Amer. Soc. Agron. 33:47-64. 1941.

(12) Smith, L. Cytology and genetics of barley. Bot. Rev. 17:1-355. 1951.

(13) Snedecor, G. W. Statistical Methods. 4th ed. Ames, Iowa: Iowa State College Press, 1950.

(14) Woodward, R. W. U. S. D. A. annual report. Division of Cereal Crops. 1950.

(15) _____ The inheritance of fertility in the lateral florets of the four barley groups. Jour. Amer. Soc. Agron. 41:317-322. 1949.