5-1955

Linkage Relationships in Group IV in Barley

George W. Wheatley
Utah State University

LINKAGE RELATIONSHIPS IN GROUP IV IN BARLEY

by

George W. Wheatley

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

of

MASTER OF SCIENCE

in

PLANT BREEDING

UTAH STATE AGRICULTURAL COLLEGE
Logan, Utah

1955

ACKNOWLEDGEMENT

The author wishes to express his deepest appreciation to Dr. R. W. Woodward who furnished the material for this study and for his guidance in the preparation of this manuscript.

George W. Wheatley

TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

The development of new and better varieties of plants through plant breeding is essential to meet certain needs of a changing world. Genetics and a knowledge of its principles are the basis for such improvement.

Barley has been used rather extensively in linkage relations studies. Its desirable characteristics are: (1) interspecific fertility and relative ease of hybridization, (2) numerous characters that are easily differentiated, (3) its commercial importance as a crop and (4) there are seven chromosome pairs in each of the four cultivated species.

More than one hundred characters in barley have been investigated. Seven linkage groups in which two or more characters have been located are reported (Robertson 1939). The leading barley breeders now are suggesting that only six chromosomes are involved.

When a large number of genes are properly located in their respective linkage groups, barley improvement will undoubtedly be accelerated.

This study is an effort to determine the location of genes already reported in linkage group IV and to establish new linkages if possible. A study of the inheritance of some genes, as yet not placed in any of the seven linkage groups has also been made.

REVIEW OF LITERATURE

The research in barley genetics previously done has been reviewed rather extensively by many investigators: Hayes and Garber (1927), Buckley (1930), Daane (1931), Robertson (1933), (1937), and Smith (1951).

Linkage studies in barley have been thoroughly reviewed by Robertson, Wiebe and Immer (1941), Immer and Henderson (1943), Robertson, Wiebe and Shands (1947) and Smith (1951). Therefore, the work reviewed here will be that which pertains particularly to the genetic factors in linkage group IV and other factors involved in the material studied, which as yet are not definitely located.

Individual Characters in Linkage Group IV

Hoods (K) versus awns (k)

Buckley (1930), Daane (1931), Woodward (1950) and Al-Jibouri (1953) have reported simple Mendelian inheritance when hooded and awned forms of barley were crossed. The F_2 plants segregated 3 hooded to one awned indicating a single dominant gene responsible for hoods.

Gill (1951) indicates that Ubisch explains segregation of hoods and awns in his crosses on a two factor basis.

Non-zoned (Z) versus zoned (z) leaf

Transverse yellowish stripes in the leaves of viable barley plants indicate the expression of a genetic factor known as zoned leaf (z). Immer and Henderson (1942), Gill (1951) and Woodward (1953) report 3 non-zoned leaf plants to one zoned leaf plant in the F_2 generation.

Blue aleurone (Bl) versus white aleurone (bl)

The investigations of Buckley (1930), Robertson, Wiebe and Immer

(1941) and Woodward (1950) show a simple Mendelian ratio of 3 blue to 1 white aleurone.

In a number of crosses involving color differences in aleurone Myler and Stanford (1942) reported a segregation of 9 blue to 7 white aleurone indicating a two factor pair difference. Their data indicate one factor pair is linked with group IV and the other is in linkage group III.

Non-glossy (Gl) versus glossy (gl) leaf

Glossy leaf plants are characterized by a scalded appearance of the heads and waxy bloomless leaves. Al-Jibouri (1953) showed simple Mendelian inheritance with non-glossy leaves being dominant to glossy leaves.

Another factor pair for non-glossy versus glossy plants (Gl_2, gl_2) was described by Robertson, Wiebe and Immer (1941) and by Robertson, and Coleman (1942). Immer and Henderson (1943) obtained 3 non-glossy to 1 glossy in the F_2 segregates, indicating the inheritance of this character is governed by a single factor pair.

Other Individual Characters

Green (normal) leaf (Rb) versus ribbon grass (longitudinal white streaked) leaf (rb)

Plants that express the ribbon grass character have white streaks running parallel to the veins.

Robertson, Wiebe and Shands (1947) indicate normal green versus white streaked leaves is a character difference controlled by a single factor pair. Their information is taken from literature that was written between 1940 and 1946.

Lax (L) versus dense (l) spike

Neatby (1929) obtained information indicating a single factor pair

difference between lax (L) versus dense (l) spike. However, he suggests subsidiary factors probably operate also. This agrees with Hayes and Harlan (1920). In some cases a single factor difference was indicated, while other results suggested multiple factors.

Smith (1951) refers to the factor for lax spike (L) as being placed in linkage groups I, III and IV. Woodward (1951) found linkage between lax (L) versus dense (l) spike and normal (awned) outer glume (E) versus elongated (awned) outer glume (e) with recombination percentages ranging from 10.0 to 31.5. This would place at least one factor pair in linkage group I.

Non-glaucous (Gs) versus glaucous (gs) sheath and spike

The plants that express the character for glaucous sheath (gs) are waxy and without bloom on the culm and spike. This character can be differentiated in plants partly to fully developed.

The results of Immer and Henderson (1943) show the F_2 plants segregating into 3 non-glaucous (Gs) to 1 glaucous (gs) sheath and spike indicating a single factor pair for this character.

Woodward (1950) found plants segregating 3 non-glaucous (Gs) to 1 glaucous (gs) sheath and spike in the F_2 generation in crosses involving this character.

Previously Reported Linkages

Blue (Bl) versus white (bl) aleurone in relation to hoods (K) versus awns (k)

This linkage has probably been studied by more barley workers than any other known linkage in group IV.

Buckley (1930) obtained a recombination value of 40.5 percent and Robertson, Wiebe and Immer (1941) showed 22.58 ± 0.8 percent recombination.

One of the two complimentary factor pairs (Bl bl) for blue aleurone mentioned in Myler and Stanford's work (1942) was linked with the factor pair for hoods (K) versus awns (k) showing a recombination value of 24.73 ± 1.73 percent. The other factor pair (Bl_1 bl_1) was found to be linked with factors in linkage group III.

Blue versus white aleurone (Bl, bl) and hooded versus awned spikes (K, k) were linked in the work done by Immer and Henderson (1943) having a recombination value of 44.0 ± 6.3 percent.

From fourteen crosses involving blue versus white aleurone and hoods versus awns Woodward (1950) obtained an average recombination percentage of 27.5 ± 1.2. Smith (1953) reported a recombination value of 26.0 ± 2.1 percent from six crosses involving blue versus white aleurone and hoods versus awns.

Blue (Bl) versus white (bl) aleurone in relation to non-zoned (Z) versus zoned (z) leaf

A recombination value of 26.9 ± 4.5 percent was found by Woodward (1950) between the factor pair (Bl, bl) for blue versus white aleurone and the factor pair (Z, z) for non-zoned versus zoned plants. Smith (1953) reported a linkage between blue aleurone versus white aleurone (Bl, bl) and non-zoned versus zoned (Z, z) plants with a recombination value of 34.5 ± 4.3 percent.

Blue (Bl) versus white (bl) aleurone in relation to non-glossy (Gl) versus glossy (gl) leaf

Immer and Henderson (1943) obtained a recombination value of 36.0 ± 3.3 percent in crosses involving blue aleurone (Bl) versus white aleurone (bl) in relation to non-glossy (Gl) versus glossy (gl) leaves. Woodward (1950) reported 41.5 ± 2.6 percent recombination as an average of four crosses involving the genes Bl, bl and Gl, gl.

Smith (1953) with five crosses in the repulsion phase obtained a recombination value of 36.0 ± 4.5 percent.

Hoods (K) versus awns (k) in relation to non-zoned (Z) versus zoned (z) leaf

Immer and Henderson (1943) found the non-zoned (Z) versus zoned (z) leaf factor pair was linked with the factor pair for hoods (K) versus awns (k) having a recombination value of 6.0 ± 0.8 percent. Woodward (1950) had material which showed 13.0 ± 3.1 percent recombination for these same factor pairs. Smith (1953) obtained a recombination value of 19.5 ± 4.4 percent with hoods (K) versus awns (k) in relation to non-zoned (Z) versus zoned (z) factor pairs.

Hoods (K) versus awns (k) in relation to non-glossy (Gl) versus glossy (gl) leaf

Recombination values range from 10.0 ± 0.8 percent as reported by Immer and Henderson (1943) to 23.5 ± 1.2 percent obtained by Woodward (1950) for hoods (K) versus awns (k) in relation to non-glossy (Gl) versus glossy (gl) leaves.

Another factor pair (Gl_2, gl_2) for non-glossy versus glossy leaves in relation to the factor pair (K, k) for hoods versus awns was reported by Robertson and Coleman (1942) having a recombination value of 25 percent.

Non-glossy (Gl) versus glossy (gl) leaf in relation to non-zoned (Z) versus zoned (z) leaf

Immer and Henderson (1943) obtained an average recombination value of 3.0 ± 0.5 percent from several crosses involving the gene pairs Gl, gl and Z, z. Smith (1953) from three crosses in the repulsion phase obtained linkage between the factor pair non-glossy versus glossy leaves and normal versus zoned leaves with 14.0 ± 5.3 percent recombination.

Possible linkages between normal (Rb) versus ribbon grass (rb) leaf in relation to non-glaucous (Gs) versus glaucous (gs) sheath and spike previously reported.

Gill (1951) with a relatively small number of plants obtained a recombination value of 36.0 ± 6.6 percent for normal leaves (Rb) versus streaked (rb) leaves in relation to non-glaucous sheath (Gs) versus glaucous (gs) sheath and spike.

Gene Arrangements on Chromosome IV as Previously Proposed

Immer and Henderson (1943) suggested the following gene arrangement on chromosome IV.

K	Z	Gl		Bl
k	z	gl		bl
6.0	3.0		36.0	

After a thorough review of the available literature up to 1950 Smith (1951) gave the same order for the genes on chromosome IV.

Smith (1953) proposed the following gene order for linkage group IV.

Z		Gl		K		Bl
z	14.0 ± 5.3	gl	17.5 ± 2.8	k	26.0 ± 2.1	bl

36 ± 4.4

19.5 ± 4.4

32.5 ± 4.4

METHOD AND MATERIAL

The crosses for this study were made in 1951 or earlier by Dr. R. W. Woodward from selected genetic material. Progeny from these crosses were grown twelve inches apart in rows two feet apart on the Evans Experimental Farm south of Logan.

The heads from each plant were gathered in August 1952 and kept separately so that each plant constituted a family. Crosses contained three to seven families each.

Each family in the F_2 generation was planted in a separate row 36 feet long. Plants were spaced from one to two inches apart in rows one foot apart so that individual plants could be easily separated for classification.

Plants with characters difficult to distinguish at time of harvest, such as glaucous sheath and spike, zoned leaf, ribbon grass and glossy leaf were tied in the field with colored string at the time each character could be most easily observed. Each family was pulled when mature, labeled and tied for further study in the laboratory.

Plants were classified individually and the characters under investigation were recorded for analysis. Several heads from each plant were saved for F_3 seeding if necessary. Some of the selections from this study were added to Dr. Woodward's collection of genetic testers for future breeding work.

The data were first analyzed for individual contrasting character pairs; then two pairs were studied in relation to each other for independence or association. A chi-square was calculated, as a test for

goodness of fit, for each segregating character pair and for every dihybrid combination of factor pairs. The P values for chi-square were taken from Snedecor (1950). Linkages were determined by the product method, reported by Immer (1930). Characters used in this study and their symbols are as follows:

Blue versus white aleurone	Bl bl
Non-glossy versus glossy leaf	Gl gl
Non-zoned versus zoned leaf (Colorado)	Z z
Hoods versus awns	K k
Normal versus ribbon grass (longitudinal white streaked) leaf	Rb rb
Lax versus dense spike	L l
Non-glaucous versus glaucous sheath	Gs gs

A list of the barley crosses used in this study with their assigned numbers and parentages follows:

B 310	Colsess I x zoned leaf Colorado
B 430	Glossy Ingersol x Colsess I
B 463	Tester 2 Rn B 122-9 x Colsess I BlGl
B 612	Coast 1 x glossy leaf ums
B 846	B 309-9-2 x B 318-15-2
B 847	B 318-15-2 x 476-3 gl
B 849	Ums C.I. 7138 x hooded zoned leaf
B 887	zw x Row 55
B 969	Trebi Bl x C.I. 1326
B 998	T-424 x Li
B 1010	T-268 x T-160
B 1016	Orange lemma x Gp
B 1019	Orange lemma x T-380
B 1020	T-405 x T-380

B 1037 T-8 x T-7

B 1038 T-8 x Abd 1415

B 1039 Abd x T-54

B 1118 Ribbon grass x C.I. 6315

B 1119 Rg x T-267

B 1142 M-8 x T-185

Each cross will be referred to by its number throughout this study.

EXPERIMENTAL RESULTS

The data from the experiment will be presented in the following sequence: the mode of inheritance of the simple Mendelian characters; the character pairs inherited independently; the factor pairs which are linked and the suggested linkage maps.

Inheritance of Simple Mendelian Characters

Blue aleurone versus white aleurone

The segregation in the F_2 generation for blue versus white aleurone is given in table 1. Individual crosses support the opinion that blue versus white aleurone differ by a single factor pair (Bl, bl). Totals for all crosses show blue versus white aleurone may differ by two factor pairs (Bl bl and Bl_2 bl_2). The small interaction shows individual cross trends to be similar.

Hoods versus awns

Table 2, with data on the F2 segregation of hoods versus awns indicates a one factor difference.

Cross B 1038 (Table 3) with a relatively large number of plants shows a near perfect 9:7 ratio. This suggests a two factor pair difference for hoods versus awns.

Non-zoned versus zoned leaves

The data on F_2 segregation of non-zoned versus zoned leaf plants are given in table 4. Evidence indicates a single factor difference between non-zoned versus zoned leaf. Low P values in this character pair test are often the result of high seedling mortality for zoned leaf plants.

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

Cross No.	Bl	bl	Total	X^2	P
	(number of plants)				
B 310	99	39	138	.69	.3-.5
B 430	46	17	63	.13	.7-.8
B 463	44	16	60	.09	.7-.8
B 887	54	28	82	3.56	.05-.1
B 1039	307	121	428	2.44	.1-.2
B 1142	195	77	272	1.58	.2-.3
Sum of 6 chi-squares				8.49	.2-.3
Total	745	398	1043	7.09	less than .01
Interaction				1.40	.9-.95

Table 2. Segregation of hoods versus awns, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	K	k	Total	X^2	P
	(number of plants)				
B 430	193	78	271	2.06	.1-.2
B 846	68	36	104	5.12	.05-.1
B 849	215	86	301	2.04	.1-.2
B 887	54	28	82	3.56	.05.1
B 969	297	82	379	2.28	.1-.2
B 1016	417	148	565	.42	.5-.7
B 1039	325	103	428	.19	.5-.7
Sum of 7 chi-squares				15.67	.02-.05
Total	1569	561	2130	2.03	.1-.2
Interaction				13.64	.02-.05

Table 3. Segregation of hoods versus awns, chi-square and P values based on a 9:7 ratio in the F_2 generation of barley.

Cross No.	K	k	Total	X^2	P
	(number of plants)				
B 1038	354	273	627	.006	.9-.95

Table 4. Segregation of non-zoned versus zoned leaves, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	Z	z	Total	X^2	P
	(number of plants)				
B 310	107	31	138	.47	.3-.5
B 847	97	30	127	.12	.7-.8
B 887	61	21	82	.01	.9-.95
B 1037	126	36	162	.67	.3-.5
B 1119	245	90	335	.62	.3-.5
B 1142	221	51	272	5.66	.01-.02
Sum of 6 chi-squares				7.55	.2-.3
Total	857	259	1116	1.91	.1-.2
Interaction				5.64	.3-.5

Table 5. Segregation of non-glossy versus glossy leaves, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	Gl	gl	Total	X^2	P
	(number of plants)				
B 430	208	63	271	.44	.5-.7
B 1039	328	100	428	.60	.3-.5
Sum of 2 chi-squares				1.04	.5-.7
Total	536	163	699	1.05	.5-.7
Interaction				-.01	.9-.95

Non-glossy versus glossy leaves

Data in table 5 show a monofactorial difference between non-glossy versus glossy leaves in the F_2 generation, non-glossy leaves being dominant.

Non-glaucous versus glaucous sheath and spike

The segregation in F_2, table 6, indicate a single factor pair difference between non-glaucous and glaucous sheath and spike.

Lax versus club head

Table 7 gives the data on the F_2 segregation for lax versus club head. The results indicate this character differs by a single factor pair, lax head being dominant.

Normal versus ribbon grass (longitudinal white streaked) leaves

Crosses segregating three normal green to one ribbon grass (longitudinal white streaked) leaf plant indicate a monofactorial character difference as shown in table 8. Some seedling mortality in ribbon grass plants may be responsible for relatively low P values.

Character Pairs Inherited Independently

Character pair studies between normal green (Rb) versus ribbon grass (longitudinal white streaked) leaf (rb) plants in relation to four other character pairs were made to determine whether Rb, rb is inherited independent of or linked with them.

The chi-square test has been used to test the frequency of the four classes identified by the symbols XY, Xy, xY and xy. Table 9 shows the data for the F_2 segregation between Rb versus rb in relation to four other characters.

The P value for goodness of fit in cross B 1142 for Rb versus rb in relation to Bl versus bl shows independence between these two factor pairs.

Table 6. Segregation of non-glaucous versus glaucous sheath and spike, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	Gs	gs	Total	X^2	P
	(number of plants)				
B 1010	507	158	665	.54	.3-.5
B 1019	124	44	168	.09	.7-.8
B 1020	420	154	574	1.02	.3-.5
Sum of 3 chi-squares				1.65	.1-.2
Total	1051	356	1407	.06	.8-.9
Interaction				1.59	.3-.5

Table 7. Segregation of lax versus dense spike, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	L	l	Total	X^2	P
	(number of plants)				
B 998	242	98	340	2.66	.1-.2
B 1037	120	42	162	.07	.7-.8
B 1119	263	72	335	2.19	.1-.2
Sum of 3 chi-squares				4.92	.1-.2
Total	625	212	837	.04	.8-.9
Interaction				4.88	.05-.1

Table 8. Segregation of normal green versus ribbon grass (longitudinal white streaked) leaf plants, chi-square and P values based on a 3:1 ratio in the F_2 generation of barley.

Cross No.	Rb	rb	Total	X^2	P
	(number of plants)				
B 1020	422	152	574	.67	.3-.5
B 1118	111	39	150	.20	.5-.7
B 1119	232	103	335	5.89	.01-.02
B 1142	215	57	272	2.73	.05-.1
Sum of 4 chi-squares				9.49	.02-.05
Total	980	351	1331	1.33	.2-.3
Interaction				8.16	.02-.05

Table 9. Normal Green (Rb) versus ribbon grass (longitudinal white streaked) leaf (rb) in relation to other character pairs, chi-square and P values based on a 9:3:3:1 ratio in the F_2 generation of barley. Recombination percentages were determined for crosses having P values less than .01. The four classes are designated by the symbols XY, Xy, xY, xy.

Cross No.	XY	Xy	xY	xy	Total	X^2	P	Recomb.%	S.E.
	(number of plants)								
	(Rb versus rb in relation to Bl versus bl)								
B 1142	70	26	21	9	126	.68	.8-.9		
	(Rb versus rb in relation to Z versus z)								
B 1119	174	58	71	32	335	13.09	less .01	45.5	3.9
B 1142	79	17	26	4	126	5.04	.1-.2		
Total	253	75	97	36	461	4.63	.2-.3		
	(Rb versus rb in relation to Gs versus gs)								
B 1020	319	101	103	51	574	7.02	.05-.1		
	(Rb versus rb in relation to L versus l)								
B 1119	178	85	54	18	335	13.87	less .01	44.5	4.3

Table 10. Non-zoned (Z) versus zoned (z) leaf in relation to lax (L) versus dense (l) spike, chi-square and P values based on a 9:3:3:1 ratio in the F_2 generation of barley.

Cross No.	ZL	Zl	zL	zl	Total	X^2	P
	(number of plants)						
B 1037	95	31	25	11	162	1.20	.7-.8
B 1119	187	58	76	14	335	5.52	.1-.2
Total	282	89	101	25	497	2.05	.5-.7

Cross B 1119 shows a recombination percent near fifty, including one standard deviation, for Rb versus rb in relation to Z versus z. This shows the factor pairs to be near fifty genetic units apart. The total for crosses involving normal green versus ribbon grass leaf in relation to normal versus zoned leaf shows the character pairs are inherited independently of each other.

The data in table 9 show normal green versus ribbon grass leaf is inherited independently of non-glaucous versus glaucous sheath and spike.

In the F_2 segregation from cross B 1119 we get a recombination value which may indicate linkage between normal green versus ribbon grass leaf and lax versus club head type. When one standard error is added to the recombination value the information then shows the two character pairs to be near fifty genetic units apart.

Table 9 does not contain sufficient information to show a linkage between normal green versus ribbon grass (longitudinal white streaked) leaf and any of the four character pairs studied.

Non-zoned (Z) versus zoned (z) leaf in relation to lax (L) versus dense (l) spike

Table 10 gives the data on the F_2 segregation of normal versus zoned leaf in relation to lax versus club head. The P value for goodness of fit shows normal versus zoned leaf to be inherited independent of lax versus dense spike.

Inheritance of Linked Character Pairs and the Observed Linkage Values

Some factor pairs show deviation from theoretical independent segregation (9:3:3:1) in the F_2 generation.

Tables 11 through 15 show the deviations in the chi-square and P values. Recombination percentages have been calculated and recorded.

Crosses in the repulsion phase are indicated with an asterisk.

Blue (Bl) versus white (bl) aleurone in relation to hoods (K) versus awns (k)

Linkages of Bl, bl in relation to K, k are shown in table 11. The data from all crosses indicate that the factor pair (Bl, bl) for blue versus white aleurone is linked with the factor pair (K, k) for hoods versus awns having a recombination value of 35.5 ± 1.9 percent.

Crosses B 430, B 463* and B 887* have relatively small numbers of plants, and their individual P values may suggest independent segregation.

Blue (Bl) versus white (bl) aleurone in relation to non-zoned (Z) versus zoned (z) leaf.

The data in table 12 show the linkage relation of factor pairs (Bl, bl) for blue versus white aleurone and (Z, z) for non-zoned versus zoned leaf with a recombination value of 28.0 ± 2.5 percent. The P value for cross B 1142 may suggest independent inheritance for these two factor pairs, but the pooled or total P value for all crosses involving Bl versus bl and Z versus z show linkage.

Blue (Bl) versus white (bl) aleurone in relation to non-glossy (Gl) versus glossy (gl) leaf

Table 13 shows the linkage for the gene pairs (Bl, bl) for blue versus white aleurone in relation to (Gl, gl) for non-glossy versus glossy leaf plants. The P value for cross B 430 may suggest independent inheritance of these factor pairs. All other P values indicate linkages. A recombination value of 33.0 ± 2.2 percent was calculated for the total of three crosses.

Table 11. Blue (Bl) versus white (bl) aleurone in relation to hoods (K) versus awns (k), chi-square values and percent recombination based on a 9:3:3:1 ratio in F_2 generation of barley.

Cross No.	BlK	Blk	blK	blk	Total	X^2	P	Recomb.%	S.E.
	(number of plants)								
B 430	40	6	9	8	63	6.19	.1-.2	27.5	6.8
B 463*	27	17	13	3	60	4.68	.1-.2	36.0	11.1
B 846	29	15	39	21	104	67.74	less .01	46.5	6.9
B 849	160	41	55	45	301	41.23	less. 01	34.5	3.5
B 887*	40	14	22	6	82	9.68	.02-.05	46.0	8.6
B 1039	263	44	62	59	428	61.48	less .01	28.0	2.6
Sum of 6 chi-squares						161.00	less .01		
Total	559	137	200	142	1038	109.37	less .01	35.5	1.9
Interaction *Repulsion						51.63	less .01		

Table 12. Blue (Bl) versus white (bl) aleurone in relation to non-zoned (Z) versus zoned (z) leaf, chi-square values and percent recombination based on a 9:3:3:1 ratio in F_2 generation of barley.

Cross No.	BlZ	Blz	blZ	blz	Total	X^2	P	Recomb.%	S.E.
	(number of plants)								
B 310	86	13	21	18	138	18.41	less .01	28.0	4.6
B 849	184	17	72	28	301	37.61	less .01	31.0	3.3
B 887*	36	18	25	3	82	9.37	.02-.05	30.5	9.8
B 1142	77	14	28	7	126	6.13	.1-.2	45.5	6.3
Sum of 4 chi-squares						71.52	less .01		
Total	383	62	146	56	647	40.95	less .01	38.0	2.5
Interaction *Repulsion						30.57	less .01		

Table 13. Blue (Bl) versus white (bl) aleurone in relation to non-glossy (Gl) versus glossy (gl) leaf, chi-square values and percent recombination based on a 9:3:3:1 ratio in F_2 generation of barley.

Cross No.	BlGl	Blgl	blGl	blgl	Total	X^2	P	Recomb.%	S.E.
	(number of plants)								
B 430	39	7	11	6	63	3.41	.1-.2	35.0	7.7
B 612*	105	23	52	3	183	19.10	less .01	32.0	6.5
B 1039	271	36	59	62	428	80.25	less .01	23.5	2.4
Sum of 3 chi-squares						102.76	less .01		
Total	415	66	122	71	674	50.42	less .01		
*Repulsion									

Table 14. Hoods (K) versus awns (k) in relation to non-zoned (Z) versus zoned (z) leaf, chi-square values and percent recombination based on a 9:3:3:1 ratio in F_2 generation of barley.

Cross No.	KZ	Kz	kZ	kz	Total	X^2	P	Recomb.%	S.E.
	(number of plants)								
B 849*	173	42	83	3	301	29.57	less .01	25.0	5.3
B 887*	43	19	18	2	82	3.41	13-.5	31.0	9.9
Sum of 2 chi-squares						32.98	less .01		
Total of 2 crosses	216	61	101	5	383	28.40	less .01	27.0	4.6
Interaction						4.58	.2-.3		
Cross No.									
B 847*	76	24	21	6	127	1.09	.7-.8		
Sum of 3 chi-squares						34.08	less .01		
Total of 3 crosses	292	85	122	11	510	22.13	less .01	35.5	3.8
Interaction						11.95	.05-.1		
*Repulsion									

Hoods (K) versus awns (k) in relation to non-zoned (Z) versus zoned (z) leaf

Linkages of K, k in relation to Z, z are shown in table 14. The total from three crosses in the repulsion phase show a recombination value of 35.5 ± 3.8 percent for hoods versus awns in relation to non-zoned versus zoned leaf plants. Cross B 847 has a high P value which suggests there is no linkage between these two factor pairs. When crosses B 849 and B 887 are combined a recombination value of 27.0 ± 4.6 percent is obtained for hoods versus awns in relation to non-zoned versus zoned leaf characters.

Hoods (K) versus awns (k) in relation to non-glossy (Gl) versus glossy (gl) leaf

Table 15 shows the linkage for hoods versus awns (K, k) in relation to normal versus glossy (Gl, gl) leaves. Both crosses in the coupling phase, show definite deviation from a 9:3:3:1 ratio for independent inheritance. Totals from the two crosses gave a recombination percentage of 25.5 ± 1.9.

The relatively small chi-square for interaction shows both crosses are consistent in their progeny ratios.

Table 15. Hoods (K) versus awns (k) in relation to non-glossy (Gl) versus glossy (gl) leaf, chi-square values and percent recombination based on a 9:3:3:1 ratio in F_2 generation of barley.

Cross No.	KGl	Kgl	kGl	kgl	Total	X^2	P	Recomb.%	S.E.
B 430	171	22	37	41	271	58.71	less .01	23.5	3.0
B 1039	279	46	49	54	428	60.62	less .01	26.0	2.5
Sum of 2 chi-squares						119.33	less .01		
Total	450	68	86	95	699	114.81	less .01	25.5	1.9
Interaction						4.52	2.-.3		

Suggested Linkage Maps

Five linkage maps have been constructed on the basis of data presented in this study. The first four are constructed from information obtained in crosses B 430, B 849, B 887 and B 1039 respectively. Recombination percentages calculated from total values as shown in tables 11 through 15 are the basis for the final linkage map.

Cross B 430 shows the gene order to be G1 K B1, while the cross B 1039 indicates K and G1 have changed positions to B1 G1 K. The linkage maps obtained from crosses B 849 to B 1039 shows the gene order to be K Z B1.

The linkage maps plotted from recombination values based on total values give the following gene order: Z K G1 B1. The calculated values from B1 to the other three gene loci are given with the linkage map for totals.

B 430

G1 ——— K ——— B1

27.5

23.5

35.0

B 849

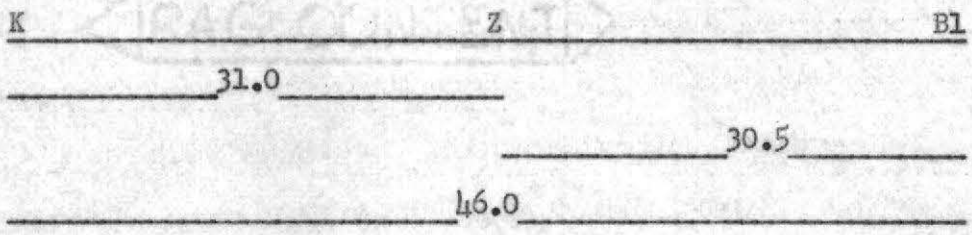
K ——— Z ——— B1

31.0

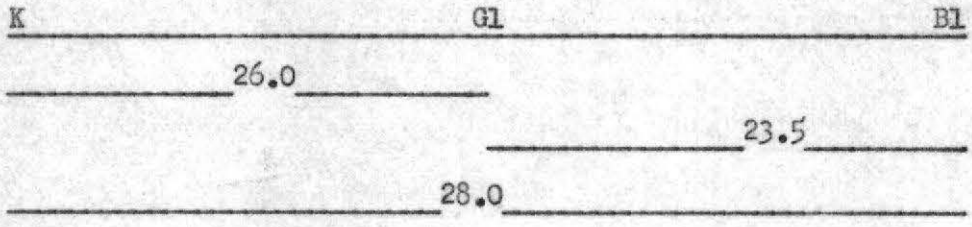
34.5

25.0

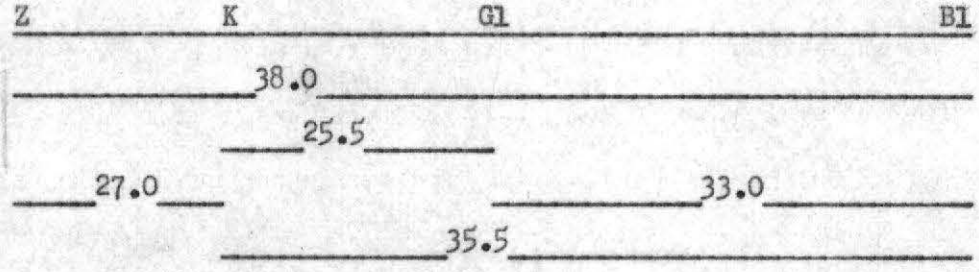
B 887



B 1039



All Crosses



DISCUSSION

Although barley has been used quite extensively in genetic studies many factors tend to prevent it from being the ideal plant for such experimentation. High seedling mortality due to several recessive factors in one individual prevents the analysis of all F_2 individuals, thus altering true segregation counts. A zoned and glossy leaf plant that survives the seedling stage seldom produces more than one small spike. Plants with ribbon grass (longitudinal white streaked) and zoned leaves are usually so chlorophyll deficient they hardly set seed. This could partially account for the wide differences that exist in the recombination values of these genes in linkage group IV.

An inadequate character description and a lack of proper symbols for the characters have caused some results to be interpreted differently. It is known that there are two zoned factors - one called Wisconsin zoned and the other is called Colorado zoned. The Wisconsin zoned is not linked with genes in linkage group IV, but the Colorado zoned is the one referred to in this linkage group. The literature which reports zoned leaf not linked with these factors probably refers to the Wisconsin zoned factor. Studies made in the future should be conducted with a knowledge of which zoned factor is being used.

Blue aleurone is often hard to differentiate from white aleurone in hulled barleys. The shades of blue aleurone vary considerably and often blend into white. Hulless barley for studying color of caryopsis experiments would greatly assist the plant breeder.

Blue versus white aleurone may be controlled by a two factor difference, as is indicated by the totals for all crosses involving this character in this study. This is not entirely in conflict with the results of previous workers, however, it would help to explain some of the wide differences resulting from segregation counts deviating from a 3:1 ratio for blue versus white aleurone, in the F_2 generation.

The two factor difference reported in this study for hoods versus awns should be further investigated.

Additional crosses of the parents producing the 9:7 ratio for hood versus awn should furnish valuable information concerning these factors. The two factor pair difference for hoods versus awns would explain some obvious deviation from a 3:1 ratio often reported or discarded because it failed to fit an expected 3:1.

It is recommended that future studies on linkage relations in chromosome IV in barley should be conducted with material possessing several linked factors in this group to determine their proper linkage relations.

Factor pair (Rb, rb) for normal green versus ribbon grass (longitudinal white streaked) leafed plants was found to be inherited independently of two genes in linkage group IV. Two other gene pairs studied in relation to Rb versus rb were also found to segregate independently.

The non-zoned versus zoned leaf factor pair segregated independently of the factor pair (L, l) for lax versus dense spike.

SUMMARY

Twenty crosses in the F_2 generation were studied for their allelic ratios and thirteen of these were studied for associations between different factor pairs.

Six factor pairs (Bl, bl), (Z, z), (Gl, gl), (Gs, gs), (L, l) and (Rb, rb) show simple Mendelian inheritance in two or more crosses.

In seven crosses the factor pair K, k showed a single factor difference, while one cross, with a relative large number of plants, showed a two factor difference.

Independent inheritance was found between the following factor pairs:

Rb rb and Bl bl, Z z, Gs gs and L l

Z z and L l

Factor pairs which showed linkage and their recombination percentages with standard errors are as follows:

Bl bl versus K k	35.5 ± 1.9
Bl bl versus Z z	38.0 ± 2.5
Bl bl versus Gl gl	33.0 ± 2.2
K k versus Gl gl	25.5 ± 1.9
K k versus Z z for 2 crosses	27.0 ± 4.6
K k versus Z z for 3 crosses	35.5 ± 3.8

The gene order Z K Gl Bl is suggested by this study for linkage group IV.

LITERATURE CITED

Al-Jibouri, H. A. 1953. Inheritance of ten characters in barley crosses. (M.S. Thesis. Dept. of Agron.) Utah State Agricultural College.

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

Doane, A. 1931. Linkage relations in barley. Minn. Agr. Exp. Sta. Bul. 78.

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

Hayes, H. K. and Garber, R. J. 1927. Breeding crop plants. 2nd Ed. 438 pp. p 190-197.

_____, and Harlan, H. V. 1920. The inheritance of the length of internode in the rachis of barley spike. U.S.D.A. Bul. 869.

Immer, F. K. 1930. Formulae and tables for calculating linkage intensities. Genetics 15:81-98.

_____, and Henderson, M. T. 1943. Linkage studies in barley. Genetics 28:419-440.

Myler, J. L. and Stanford, E. H. 1942. Color inheritance in barley. Jour. Am. Soc. of Agron. 34:427-436.

Neatby, K. W. 1929. An analysis of the inheritance of quantitative character and linkage in barley. Sci. Agr. 9:701-718.

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

_____, 1937. Inheritance in barley. II Genetics 22:443-451.

_____ and Coleman, O. H. 1942. Location of glossy and yellow seedling in two linkage groups. Jour. Am. Soc. Agron. 34:1028-1034.

_____, Wiebe, G. A. and Immer, F. R. 1941. A summary of linkage studies in barley. Am. Soc. Agron. Jour. 33:47-64.

_____, Wiebe, G. A. and Shands, R. G. 1947. A summary of linkage studies in barley. Supplement I 1940-1946. Jour. Am. Soc. Agron. 39:364-473.

Smith, E. W. 1953. A linkage study of chromosome IV in barley. (M.S. Thesis. Dept. of Agron.) Utah State Agricultural College.

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

Snedecor, G. W. 1950. Statistical methods, 4th Ed. Ames, Iowa: Iowa State College Press.

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

_____ 1951. U.S.D.A. annual report. Division of Cereal Crops.

_____ 1953. U.S.D.A. annual report. Division of Cereal Crops.