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Inheritance of Ten Characters in Barley Crosses

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INHERITANCE OF TEN CHARACTERS IN BARLEY CROSSES

by

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Hasim Al-Jibouri

TABLE OF CONTENTS

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BARLEY CROSSES

Introduction

Inheritance of many characters in barley has been studied, and two or more genes have been located in each of the seven pairs of chromosomes. Studies of the mode of inheritance of these characters will aid plant breeders materially in working with plants of diverse genetic make-up. Hybridization followed by selection and testing can improve present varieties by replacing them with new ones having more desirable characters.

Barley (Hordeum sp.) is one of the few species of plants widely distributed which is well adapted to genetical analysis. This plant has a lower number of chromosomes, complete self fertility, and a wealth of easily classifiable, hereditary characters.

This study represents the data obtained in an investigation of ten characters in barley in the F_2 and F_3 generations. The nature of the inheritance, genes involved, and possible linkages have been determined.

REVIEW OF LITERATURE

Cytological and genetical investigations have been done extensively in the last fifty years on barley with numerous investigators making contributions. A fairly extensive review of the literature on inheritance and linkage relations of barley was recently given by Smith (31).

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

Characters Investigated

Fertility of lateral florets

Harlan (12) classified cultivated barley into four species on the basis of fertility of the lateral florets, namely: six-rowed (H. vulgare), intermediate (H. intermedium), two-rowed (H. distichon), and (H. deficiens). Recently, Aberg and Wiebe (1, 2) reclassified barley into three species, H. vulgare (six-row and intermedium), H. distichum (includes two-row and deficiens), and H. irregulare. The latter is characterized by having the central florets fertile, but the lateral florets reduced to rachillae in some cases and these are distributed irregularly on the spike, with the remaining lateral florets either fertile, sterile, or sexless.

Biffen (3) found a single factor pair difference for type of spike in crosses between vulgare x distichon, vulgare x deficiens, and deficiens x distichon. Robertson (22), Daane (5), and Buckley (4) reported a 3:1 ratio in crosses between non-vulgare x vulgare, for type of spike.

Harlan and Hayes (13) obtained seven classes from crosses of six-row x two-row. A homozygous intermedium was obtained from this cross. The result was explained on the basis of a difference of two factor pairs.

Englesow (7, 8) and Hor (15) concluded that an allelomorphic series of factors differentiated the type of lateral florets.

Leonard (19) and Woodward (36) reported that the partly fertile, infertile, and nonintermedium types were differentiated by genes belonging to a multiple-allelic series designated as I^hI^h, II, and ii respectively, with i dominant to I and I^h, and I dominant I^h.

Woodward (36), as a result of a series of crosses suggested an allelic series consisting of v, V^d, V, V^t, genes for six-row, two-row and _deficiens_. The two-rowed gene V^d, which exhibited a major factor difference in crosses with two-row V gene, has been added to the series.

Pigmentation in Barley

Color in the caryopsis and lemma of barley results from the presence of two types of pigments:

A. Anthocyanin pigment which gives the red, blue, and purple colors.

B. Melanin-like pigment which gives the black and grey colors.

A blue aleurone and a red pericarp produce a purple colored caryopsis. Black is often found in the pericarp, lemma, palea, awns, and culms.

Purple versus non-purple lemma and pericarp (P, p)

A single factor difference was found between purple versus non-purple lemma and pericarp by Biffen (3), Buckley (4), and Daane (5). Miyake and Imai (c. f. Smith, 31) thought the purple color was caused by two incompletely dominant genes with additive effect. Waddoups (33) observed a 3:1 ratio in the F_2 of a cross between purple x white, but one cross between non-purple parents gave a 9:7 ratio of purple to non-purple in F_2. Woodward (37, 38) in a series of crosses observed that not all crosses involving anthocyanin pigment segregation fit the expected 3:1 ratio, but rather many showed a 9:7 ratio when both parents were non-purple, and one family showed a 7:9 ratio. He concluded that two complementary factor pairs designated as (P, C) are responsible for the expression of the purple color. Gill (11) and Thieret (32) obtained similar results. Woodward (39) recently obtained a segregation of 9:7 from 18 crosses between purple x non-purple, suggesting that PPCC x ppcc genotypes are involved. Previously, a ppcc genotype had not been discovered.

Purple versus white straw (Pr, pr)

Robertson (24) and Woodward (38) concluded that purple versus white straw differs by a simple factor pair. Gill (11) observed in one cross a 9:7 ratio of purple to white straw in the F_2 generation.

Black versus white glumes and pericarp (B, b)

Biffen (3), Leith (18), Hor (15), Sigfusson (29), Robertson (22), Buckley (4), and Woodward (37, 38) reported a single factor pair difference between black versus white glume and pericarp.

Woodward (34), in studies of crosses between colored parents that differ in the intensity of black pigment in the lemma and pericarp, found evidence of an allelomorphic series of at least three genes for degree of black pigmentation of lemma and pericarp: black BB, grey B^gB^g, and white bb. In each combination, the darker color was dominant over the lighter and seggregated monofactorially.

Hulled versus naked caryopsis (N, n)

Biffen (3), Gains (10), Hor (15), Robertson (22), Buckley (4), Sigfusson (28), and Daane (5) all reported that the F_2 of a cross, hulled x hull-less segregates in a ratio of three hulled to one hull-less caryopsis.

Hoods versus awns (K, k)

A 3:1 ratio of hoods to awns was obtained by the following investigators: Biffen (3), Hor (15), Hayes and Garber (14), Robertson (22), Buckley (4), and Daane (5).

Blue versus white aleurone (Bl, bl)

A single dominant gene is responsible for blue aleurone, with F1 progeny plants segregating in the ratio of three blue to one white. This was observed by Buckley (4), Robertson et al. (26), Myler (20), Woodward (37), Gill (11), and Smith (30). Myler and Stanford (21), and Robertson (unpublished) obtained a 9:7 ratio in the F2 of a cross between two white kerneled varieties, indicating the presence of two complementary factors.

Non-glossy versus glossy leaves (Gl, gl)

Woodward (37) found a single factor difference between non-glossy versus glossy leaf segragating in F_2 for three non-glossy to one glossy leaf. Smith (30) obtained similar results.

Immer and Henderson (16) observed a 3:1 ratio for non-glossy versus glossy seedling. Robertson and Coleman (27) found a simple Mendelian factor pair designated as Gl_2 gl_2 for non-glossy versus glossy plants.

Rough versus smooth awns (R, r)

Deane (5), Woodward (37), and Gill (11) reported a single factor pair difference between rough and smooth awns, with F_1 being rough and the F_2 segregating in a ratio of three rough to one smooth. Sigfusson (29) found evidence that rough awns were dependent on two factor pairs giving a 9:3:3:1 ratio in the F_2.

Friesen (9) studied the inheritance of awn barbing in crosses of barbing varieties having intermediate smooth and very smooth awned types and indicated that it is determined by two factor pairs. The factor S produces intermediate awn-barbing and it is partially dominant to its alleles. The other factor, termed S_1, is hypostatic to S, while its allele s_1, when homozygous (s_1 s_1), produces the very smooth awned condition.

Hehn (c. f. Smith, 31) reported rough awns to be determined by one factor pair in some crosses; by two in others.

Long versus short glume hairs (#3, #2)

Aberg and Wiebe (2) pointed out a difference in length of glume awns in barley and its importance in taxonomy. Woodward (37) and Gill (11) found a single factor difference between long versus short glume hairs.

Linkage Groups

Linkage group I

Non-six-row (VV) versus six-row (vv) in relation to purple (PP) versus non-purple lemma and pericarp (pp)

Daane (5) placed P, p in the first linkage group. Buckley (4) found a crossover value of 20 percent between non-six-rowed versus six-rowed (V, v) factors in relation to purple versus non-purple (P, p). Myler and Stanford (21) obtained 13.19 $\pm$ 2.17 percent crossing over. Woodward (37) reported that the combined data, F_2 and F_3, from four crosses showed a recombination value of 14.1 $\pm$ 0.36 percent for the gene (V^t, v^t) in relation to (P, p). The F_3 data, which is the more accurate when taken alone, gave a crossover value of 10.1 $\pm$ 1.0 percent. Thieret (32) and Gill (11) found the genes V, v linked with P, p giving 14.2 $\pm$ 0.7 percent, and 13.0 $\pm$ 1.2 percent recombination respectively.

Non-six-row (VV) versus six-row (vv) in relation to purple (Pr Pr) versus non-purple straw (pr pr)

Robertson (24), Woodward (37), and Gill (11) reported recombination values of 9.0 $\pm$ 0.68 percent, 11.5 percent, and 12.5 $\pm$ 3.3 percent, respectively, for these factor pairs.

Linkage group IV

Hoods (KK) versus awns (kk) in relation to blue (Bl Bl) versus white aleurone (bl bl)

Several investigators have reported linkage relationship between the factor pairs hoods versus awns (K, k) in relation to blue versus white aleuzone. Crossover values for these gene pairs are given below:

Investigator	Reference Number	Recomb. Percentage
Buckley	(4)	41.0
Immer and Henderson	(16)	44.0 ± 6.3
Myler and Stanford	(21)	24.7 ± 1.7
Woodward	(37)	27.5 ± 1.2
Jenkins	(17)	31.0 ± 2.3
Gill	(11)	30.4 ± 4.0
Smith	(30)	26.0 ± 2.1

Myler and Stanford (21) reported a second factor for blue, designated Bl_1 bl_1 which is found to be linked with hulled versus hull-less (N, n), placing it in linkage group III. The percentage crossover for this linkage was found to be 9.88 ± 0.4 percent.

<u>K versus k in relation to Gl versus gl</u>

Immer and Henderson (16) 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 (37), Jenkins (17), and Smith (30) obtained a recombination percentage of 23.5 ± 1.2, 24.12 ± 2.4, and 17.5 ± 2.8, respectively.

Robertson and Coleman (27), found linkage between the factor pairs for non-glossy versus glossy seedlings (Gl_2 gl_2) and hoods versus awns (K, k) with a recombination of 25.0 percent.

<u>Blue (Bl Bl) versus white aleurone (bl bl) in relation to non-glossy (Gl Gl) versus glossy (gl gl) leaves</u>

Immer and Henderson (16), Woodward (38), Jenkins (17), and Smith (30) reported that the gene pairs (Bl, bl) and (Gl gl) were linked with a 36.0 ± 3.3, 32.5, 35.12 ± 7.7, and 36.0 ± 4.5 percent recombination, respectively.

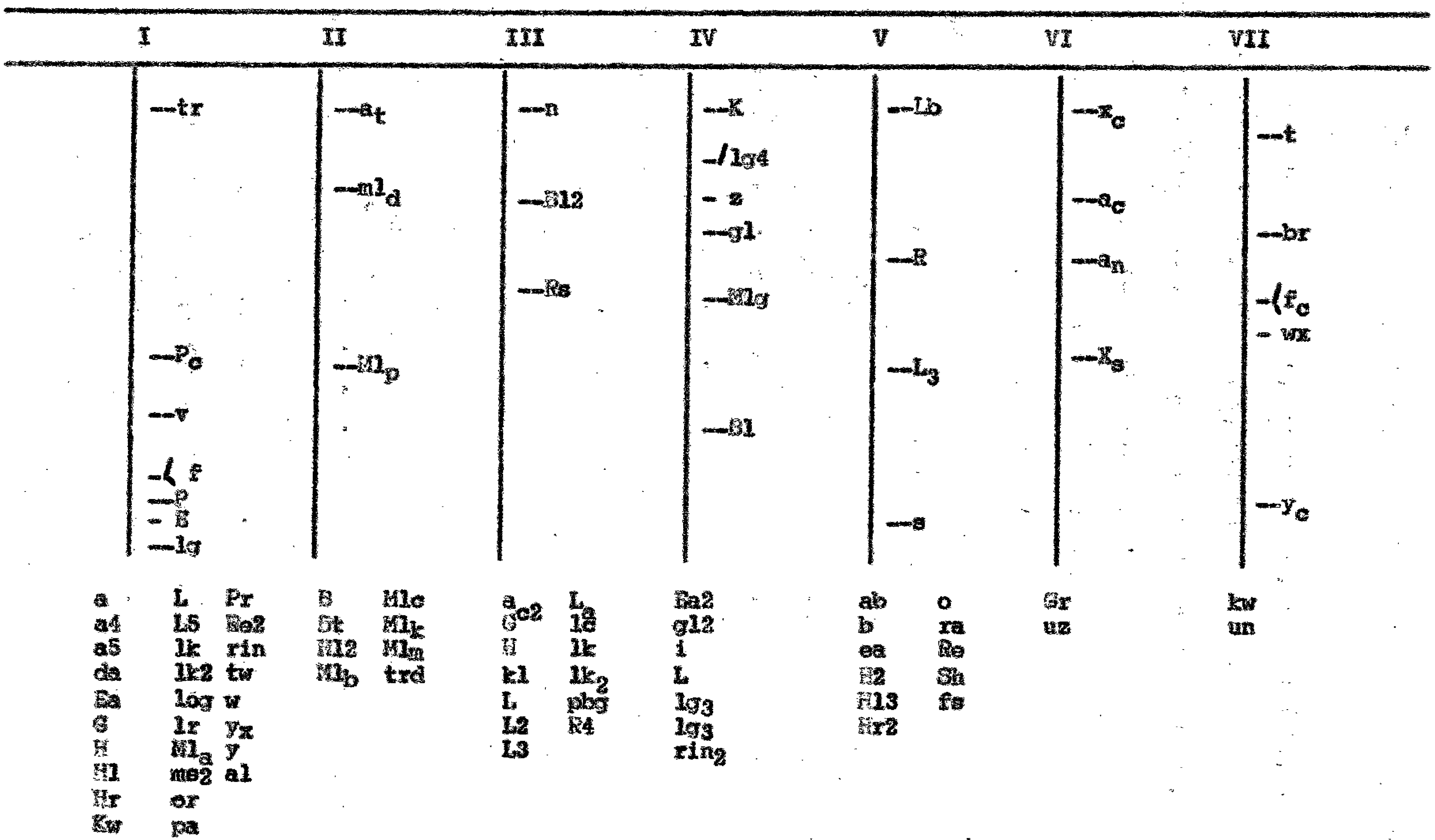

Figure 1. Linkage Groups in barley. The orders and percentages of recombination of genes have been fairly definitely established. Other genes that have been found to be associated with the various groups are listed below their respective group. (Adapted from Smith, 31)

METHODS AND MATERIALS

Crosses used in this study were a part of a larger number, many of which were studied as F_2's in 1951 and seemed to deviate from expected ratios based on previous data. Most crosses studied were grown in F_3 during 1952 and a few additional F_2 crosses were used to supplement the F_3 data. These crosses were made by Dr. R. W. Woodward in 1949 and 1950. Each cross consisted of 2 to 5 families of some 75 to 150 plants each. F_2 plants were spaced two inches apart in rows 30 feet long and one foot apart, while F_3's were seeded in 5 foot rows with a Columbia seeder. After the plants were well emerged, they were sprayed with one pound of 2-4-D and irrigated once or twice during the season.

Plants in F_2 were tied for those characters not classifiable at maturity, such as the glossy leaf and stem. Each family of plants was pulled, labeled, and tied for later study in the laboratory. During the fall and winter, F_2 plants were examined and these characters under investigation were recorded by symbols permitting linkage analysis. A few heads from each plant were placed in envelopes for seeding to obtain F_3 plants for further study.

After collecting the data, it was first analyzed for individual contrasting character segregation; then two pairs were compared at a time for independence or association. Chi-squares were calculated and probability (P) values determined and used as a measure of goodness of fit. When the probability value was less than one percent, the data were subjected to the product method for percentage recombination.

Special genetic combinations found in some of the segregating families were saved for use as future testers to be used in crosses.

<u>Characters used in the inheritance studies</u>

The following table shows the contrasted characters involved and symbols used in the present study:

Number	Contrasted Character	Symbol
1.	Non-six-row versus six-row	V v
2.	Deficiens versus two-row	V^t V
3.	Purple versus non-purple lemma and pericarp	P p
4.	Purple versus white straw	Pr Pr
5.	Black versus white glumes and pericarp	B b
6.	Hulled versus hull-less caryopsis	N n
7.	Hoods versus awns	K k
8.	Blue versus white aleurone	Bl bl
9.	Non-glossy versus glossy leaves	Gl gl
10.	Rough versus smooth awns	R r
11.	Long versus short glume hairs	#3 #2

List of crosses showing Utah numbers and parents involved in the present study:

B 621	C 1456 x C. I. 1083
B 666	Colsess I x gl VI Kerio
B 669	Row 40 x row 39 Pr x Pr
B 681	Row 6 x Row 47
B 684	Row 12 x row 39
B 652	Ums B6-2 x 2 row K
B 850	White Def. x Lion C. I. 923
B 881	881-1483 n n x Gem.
B 882	C. I. 2222 n n x C. I. 7008
B 888	C. I. 3024 - 1 n n 36 x Gem.
B 890	C. I. 3024 - 1 n n x Lincoln C. I. 1089
B 910	Zoned leaf Wisc. Rust Res. 294 x Colsess I
B 911	Unknown
B 944	vvii-70 x row 134 B 306-10-1

EXPERIMENTAL RESULTS

Experimental results will be presented in the following sequence: the inheritance of the individual characters; the independently inherited character pairs; and the linkage relationships.

Inheritance of individual characters

Non-six-row (VV) versus six-row (vv)

Table 1 gives the F_2 and F_3 data for non-six-row versus six-row (Vv). Results indicate a single factor pair difference. Combined data for F_2 and F_3 are shown in Table 2.

Table 1. Data for non-six-row versus six-row in the F_2 and F_3 generation and chi-square and P values based on a 3:1 ratio

	Cross No.	V	v	Total	X^2	P
F_2	B 850	106	48	154	3.493	.07
	B 881	139	38	177	1.088	.2-.3
	B 882	65	15	80	1.666	.1-.2
	B 944	233	85	318	.506	.4-.5
F_3	B 621	181	52	233	.828	.3-.4
	B 652	124	44	168	.126	.7-.8
	B 666	70	17	87	1.520	.2-.3
	B 669	72	21	93	.227	.6-.7
	B 681	97	37	134	.361	.5-.6
	B 684	75	19	94	1.335	.2-.3
Total F_2		543	186	729	.116	.7-.8
Total F_3		619	190	809	.949	.3-.4

Table 2. Combined data for the F_2 and F_3 generations and chi-square and P values

Cross No.	V	v	Total	X^2	P
Total				11.130	.3-.5
Pooled	1162	376	1538	.044	.8-.9
Interaction				11.086	.2-.3

Deficiens versus two-row

Data in Table 3 show a monofactorial difference between deficiens and two-row (Vt V) in the F_3 generation, deficiens being dominant.

Table 3. Data for deficiens versus two-row in the F_2 generation and chi-square and P values based on a 3:1 ratio

Cross No.	Vt	V	Total	X^2	P
B 850	82	36	118	1.094	.2-.3

Purple (PP) versus non-purple lemma and pericarp (pp)

Segregation of purple x non-purple lemma and pericarp in the F_2 and F_3 generation, as given in Table 4, shows a monofactorial difference between purple and non-purple, purple being dominant. In crosses where both parents were non-purple, the F_2 and F_3 segregated 9 purple to 7 white (Table 5). This indicates the possibility of a difference of two complementary factors responsible for the expression of purple lemma and pericarp.

Table 4. Data for purple versus non-purple lemma and pericarp in the F_2 and F_3 generation and chi-square and P values based on a 3:1 ratio

Cross No.	Parent Color	P	p	Total	X^2	P
F_2 B 621	purple x white	95	35	130	.161	.6-.7
F_3 B 621	purple x white	145	45	190	.112	.7-.8

Table 5. Data for purple versus non-purple lemma and pericarp in F_2 and F_3 generation and chi-square and P values based on a 9:7 ratio

Cross No.	Parent Color	P	p	Total	X^2	P
B 681	White x white	47	29	76	.856	.3-.4
F_2 B 684	White x white	241	217	458	2.565	.1-.2
B 911	Unknown	114	65	179	3.839	.05
B 681	White x white	61	38	99	1.027	.3-.5
F_3 B 684	White x white	56	45	101	.039	.8-.9
B 669	White x white	56	37	93	.697	.4-.5
Total F_2		402	311	713	.005	.90-.95
Total F_3		173	120	293	.388	.3-.5

<u>Purple (Pr Pr) versus white straw (pr pr)</u>

Table 6 gives F_3 data for a segregation of 9 purple to 7 white, indicating that there was a two factor pair difference.

Table 6. Data for purple versus white straw in the F_3 generation and the chi-square and P values based on a 9:7 ratio

Cross No.	Parent Color	Pr	pr	Total	X^2	P
B 666	White x white	170	139	309	.209	.6-.7

<u>Black (BB) versus white glume and pericarp (bb)</u>

Segregation of the F_2 generation as shown in Table 7 indicates that black versus white glumes and pericarp differ by a single factor pair (B, b).

Table 7. Data for black versus white glumes and pericarp in the F_2 generation and chi-square and P values based on a 3:1 ratio

Cross No.	B	b	Total	X^2	P
B 850	108	46	154	1.948	.1-.2
B 881	130	47	177	.271	.6-.7
B 882	62	18	80	.166	.6-.7
B 888	32	12	44	.113	.7-.8
B 890	261	75	336	1.285	.2-.3
Total	593	198	791	.006	.90-.95

Hulled (NN) versus hull-less caryopsis (nn)

Table 8 shows data indicating a monofactorial difference between hulled versus hull-less (N, n) with the hulled factor being dominant.

Table 8. Data for hulled versus hull-less caryopsis in the F_2 and F_3 generations and chi-square and P values based on 3:1 ratio

Cross No.	N	n	Total	X^2	P
F_2 (B 881	135	42	177	.120	.7-.8
F_2 (B 882	44	24	68	3.842	.05
F_2 (B 890	267	69	336	3.570	.06
F_2 (B 911	137	42	179	.266	.6-.7
F_2 (B 944	233	85	318	.506	.4-.5
F_3 (B 621	87	36	123	1.077	.3-.5
F_3 (B 681	75	24	99	.063	.8-.9
Total F_2	816	262	1078	.315	.5-.7
Total F_3	162	60	222	.535	.3-.5

Hoods (KK) versus awns (kk)

Table 9 gives the F_2 and F_3 data on segregation for hoods and awns. Results indicate that hooded versus awned is dependent upon a single factor pair (K, k).

Table 9. Data on segregation of hoods versus awns in the F_2 and F_3 generations and chi-square and P values based on a 3:1 ratio

Cross No.	K	k	Total	X^2	P
F_2(B 910	187	78	265	2.904	.09
F_3(B 652	349	112	461	.106	.7-.8
F_3(B 666	250	59	309	5.433	.02
Combined data for F_2 and F_3 generations					
Total				8.443	.04
Pooled	786	249	1035	.513	.3-.5
Interaction				7.930	.02

Blue (Bl Bl) versus white aleurone (bl bl)

Table 10 shows data indicating a monofactorial difference between blue versus white aleurone (Bl, bl) in the F_2 and F_3 generation.

Table 10. Data for blue versus white aleurone in the F_2 and F_3 generations and chi-square and P values based on a 3:1 ratio

Cross No.	Bl	bl	Total	X^2	P
F_2(B 910	192	73	265	.988	.3-.5
F_3(B 652	340	121	461	.417	.5-.7
F_3(B 666	53	15	68	.313	.5-.7
Combined data for F_2 and F_3 generations					
Total				1.718	.5-.7
Pooled	585	209	794	.672	.3-.7
Interaction				1.046	.5-.7

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

Segregation of non-glossy versus glossy leaves in the F_3 generation, as shown in Table 11, indicates a single factor pair difference, with non-glossy being dominant.

Table 11. Data on segregation of non-glossy versus glossy leaves in F_3 generation and chi-square and P values based on 3:1 ratios

Cross No.	Gl	gl	Total	X^2	P
B 666	50	18	68	.078	.7-.8
B 669	75	18	93	1.444	.2-.3
B 684	75	19	94	1.335	.2-.3
Total				2.857	.3-.5
Pooled	200	55	255	1.690	.1-.2
Interaction				1.167	.5-.7

Rough (RR) versus smooth awns (rr)

The F_2 plants were classed into two groups, rough and awned plants. Very smooth and semi-smooth were grouped as smooth awned. The F_2 and F_3 data indicate that the character pair, rough versus smooth awn, depends on a single Mendelian factor (R, r) (Table 12). One family, however, showed a segregation in the F_3 generation of 15 rough to 1 smooth, suggesting a two factor pair difference. These data are shown in Table 13.

Table 12. Data for rough versus smooth awns in the F_2 and F_3 generations and chi-square and P values based on a 3:1 ratio

Cross No.	R	r	Total	X^2	P
F_2 (B 881	142	35	177	2.449	.1-.2
F_2 (B 888	31	13	44	.484	.4-.5
F_2 (B 911	130	49	179	.474	.4-.5
F_3 (B 621	100	23	123	2.764	.1-.2
Combined data for F_2 and F_3 generations					
Total				6.171	.1-.2
Pooled	403	120	523	1.231	.1-.3
Interaction				4.940	.1-.2

Table 13. Data on segregation of rough versus smooth awns in the F_3 generation and chi-square and P values based on a 15:1 ratio

Cross No.	R	r	Total	X^2	P
B 621	104	6	110	.151	.6-.7

<u>Long (#3 #3) versus short glume hairs (#2 #2)</u>

Table 14 shows data suggesting a monofactorial difference between long versus short glume hairs (#3, #2). The F_3 rows were classified into three groups, one homozygous for long glume hairs, one with short glume hairs, while the third segregated for long and short glume hairs. These three types appeared in approximately a 1:2:1 ratio.

Table 14. Data for long versus short glume hairs in F_3 generation and their chi-square and P values based on a 3:1 ratio

Cross No.	#3	#2	Total	X^2	P
B 681	77	22	99	.481	.3-.5

Character pairs independently inherited

Following the study of single contrasting characters, a study for independence between pairs was made.

Table 15 gives data indicating the independence of long versus short glume hairs (#3, #2) in relation to the various other characters found in the same cross.

Table 15. Data for long versus short glume hairs in relation to other characters

#3, #2 versus N n					9:3:3:1 ratio	
Cross No.	#3N	#3n	#2N	#2n	X^2	P
B 681	60	17	15	7	1.18	.2-.3
#3, #2 versus V v					9:3:3:1 ratio	
Cross No.	#3V	#3v	#2V	#2v	X^2	P
B 681	52	22	18	4	1.05	.3-.5
#3, #2 versus B b					9:3:3:1 ratio	
Cross No.	#3B	#3b	#2B	#2b	X^2	P
B 681	54	23	13	9	3.84	.05
#3, #2 versus P p					27:21:9:7 ratio	
Cross No.	#3P	#3p	#2P	#2p	X^2	P
B 681	44	33	17	5	4.10	.02

Independent inheritance was found between the following factor pairs:

V v and B b, N n, Bl bl, Gl gl, and R r

P p and N n, K k, Gl gl, Bl bl, and R r

B b and N n, R r

N n and R r

Linkage Relationship

Some factor pairs showed considerable deviation from theoretical independence and suggested linkage.

P versus p in relation to V versus v

Data in Table 16 show that the factor pair (P, p) for purple versus non-purple lemma and pericarp is linked with the factor pair (V, v) for non-six-row versus six-row with a recombination value of 23.0 ± 2.7 in F_2, and 12.5 ± 2.4 in the F_3 generation. This behavior was obtained from data in two crosses.

Crosses in which a ratio of 9 purple to 7 non-purple was observed in the F_2 and F_3 generation had a recombination value of 19.5 ± 3.0 in F_2, and of 12.0 ± 3.0 in the F_3 generation. These results are given in Table 17.

Table 16. Data on segregation of 3:1 for purple versus non-purple lemma and pericarp in relation to non-six-row versus six-row segregating 3:1

Cross No.	PV	Pv	pV	pv	P	% C.O.
F_2 B 949	193	29	40	56	Less than .01	23.0 ± 2.7
F_3 B 621	144	3	39	32	Less than .01	12.5 ± 2.4

Table 17. Data on segregation of purple versus non-purple in relation to six-row versus non-six-row when 9:7 and 3:1 ratios were respectively obtained

Cross No.	27 PV	9 Pv	21 pV	7 pv	P	% C.O.
F_2 B 669	40	2	33	18	Less than .01	20.5 ± 6.8
F_2 B 681	93	7	42	36	Less than .01	12.0 ± 3.8
F_2 B 911	87	27	27	38	Less than .01	22.0 ± 5.0
F_3 B 669	54	2	18	19	Less than .01	6.0 ± 3.9
F_3 B 681	54	7	19	19	Less than .01	15.0 ± 5.7
F_3 B 684	53	3	22	16	Less than .01	11.0 ± 5.1
F_2 totals	220	36	102	92	Less than .01	19.5 ± 3.0
F_3 totals	161	12	59	54	Less than .01	12.0 ± 3.0

Pr versus pr in relation to V versus v

The factor pair (Pr, pr) for purple versus white straw was found to be linked with the factor pair (V, v) for non-six-row versus six-row, with a recombination value of 28.0 ± 4.4 percent in the F_3 generation.

Table 18. Data on segregation of 9:7 for purple versus white straw in relation to non-six-row versus six-row segregating 3:1

	Ratio					
	27	9	21	7		
Cross No.	PrV	Prv	prV	prv	P	% C.O.
B 666	154	16	108	33	Less than .01	28.0 ± 4.4

K versus k in relation to Bl versus bl

A total of all crosses shows the recombination value in the F_3 generation of K k, for hooded versus awned in relation to Bl, bl for blue versus white aleurone was 30.0 ± 2.0 percent.

Table 19. Data on segregation for hoods versus awns (3:1) in relation to blue versus white aleurone (3:1)

Cross No.		K Bl	K bl	k Bl	k bl	P	% C.O.
F_2	B 910	161	26	31	47	Less than .01	23.0 ± 3.0
F_3	B 652	285	54	45	67	Less than .01	24.5 ± 2.3
	B 666	221	29	52	7	Less than .01	49.5 ± 4.2
F_3 Total		516	83	97	74	Less than .01	30.0 ± 2.0

K versus k in relation to Gl versus gl

On one F_2 and F_3, cross, B 666, a recombination value of 33.5 ± 1.3 percent, and 39.5 ± 3.0 percent, respectively, was obtained between hoods versus awns and non-glossy versus glossy leaves. These data are shown in Table 20 and are somewhat higher than reported previously.

Table 20. Data on segregation for hoods versus awns (3:1) in relation to non-glossy versus glossy leaves (3:1)

Cross No.	K Gl	K gl	k Gl	k gl	P	% C.O.
F_2 B 666	312	41	63	29	Less than .01	33.5 ± 1.3
F_3 B 666	156	24	23	17	Less than .01	30.5 ± 3.0

Bl versus bl in relation to Gl versus gl

Data from one cross, B 666, indicates that the factor pair (Bl, bl) for blue versus white aleurone is linked with the factor pair (Gl, gl) for non-glossy versus glossy leaves with a recombination value of 40.0 ± 4.4 percent in the F_3 generation.

Table 21. Data on segregation for blue versus white aleurone in relation to non-glossy versus glossy leaves where both pairs were monofactorial

Cross No.	Bl Gl	Bl gl	bl Gl	bl gl	P	% C.O.
F_3 B 666	159	32	22	9	Less than .01	40.0 ± 4.4

DISCUSSION AND CONCLUSIONS

This study consisted of a number of crosses designed to support a project previously investigated, but not adequately solved. A rather wide coverage of factor pair inheritances ultimately results from the study of these unrelated crosses.

A few summary statements may help to reduce these data to significant contributions. By combining all crosses having similar contrasting character pairs, the mode of inheritance has been verified in many cases. The inheritance of purple lemma and pericarp, for example, is either monofactorial or dihybrid depending on the parents involved.

A second significant contribution of this study reveals the independent relationship between factor pairs, some of which have not yet been located in linkage groups. This information indicates that the gene pairs concerned are either on different chromosomes or at least 50 genetic units apart if on the same chromosome.

More important to the barley geneticist is the linkage relationship found between gene pairs studied in the same crosses. It takes a number of crosses to establish a linkage accurately enough for chromosome mapping. Several linkages have been found in these studies and each is treated separately as it fits into the picture.

One new linkage between purple straw (Pr, pr) and row type (V, v) appears to be independent of purple color in the lemma and pericarp which also shows linkage with V, v. A follow-up study of the new linkage should be made.

Several linkages in group IV are presented in one to three crosses giving recombination values consistent with previously recorded linkages. These crossing-over percentages for the Bl, Gl, and K genes will assist in more accurately locating the map distance for these factor pairs. Two or more factors are often found to be responsible for some characters, for example, the purple color, blue aleurone, and smooth awns. In some cases, these factors are complementary; while in other instances, they are duplicate or entirely different genes on different chromosomes conditioning the same character.

SUMMARY

Eight crosses in F_2 and six crosses in the F_3 generation were studied for their allelic ratios and for associations between different factor pairs.

Nine factor pairs, (V, v), (Vt, v), (P, p), (B, b), (N, n), (K, k), (Bl, bl), (Gl, gl), and (#3, #2) showed simple Mendelian inheritance in one or more crosses, while three characters showed a two factor pair difference responsible for their inheritance. These three characters were purple lemma (P C), purple straw (Pr C), and smooth awns (r r r_1 r_1).

Independent inheritance was observed between the following pairs of factors:

#3, #2 and P p, V v, B b, and N n.

Vv and B b, N n, K k, Gl gl, Bl bl, and R r.

P p and N n, K k, Gl gl, Bl bl, and R r.

B b and N n, R r.

N n and R r.

Linkages were observed between the following pairs of factors:

(P, p) in relation to (V, v) segregating 3:1 and 3:1 respectively with crossover value 12.5 ± 2.4

(P, p) in relation to (V, v) segregating 9:7 and 3:1 respectively with crossover value 12.0 ± 3.0

(Pr, pr) in relation to (V, v) segregating 9:7 and 3:1 respectively with crossover value 28.0 ± 4.4

(K, k) in relation to (Bl, bl) segregating 3:1 and 3:1 respectively with crossover value 30.0 ± 2.0

(K, k) in relation to (Gl, gl) segregating 3:1 and 3:1 respectively with crossover value 30.5 ± 3.0

(Gl bl) in relation to (Gl, gl) segregating 3:1 and 3:1 respectively with crossover value 40.0 $\pm$ 4.4

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