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AN INHERITANCE AND LINKAGE STUDY

OF 19 FACTOR PAIRS IN BARLEY

by

Francis Cheney LeBaron

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

of

MASTER OF SCIENCE

in

Agronomy

UTAH STATE UNIVERSITY
Logan, Utah

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Francis Cheney LeBaron

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INTRODUCTION

Barley, during the past three decades, has been used considerably for the study of linkage groups and character inheritance. The commercial varieties are diploids, having seven pairs of chromosomes. Six linkage groups have been established. According to studies on interchange by Kramer et al. (1954), two linkage groups, formerly designated as III and VII, may be separate arms of the same chromosome. They are now generally considered as one linkage group.

Though more than two hundred characters have been investigated, less than sixty have been assigned relative positions on genetic maps. In many cases, selection for good characters is difficult and time consuming; however, a knowledge of linkages between desirable characters can greatly facilitate the work of the plant breeder.

The objectives of this study have been to determine new linkages, investigate several reported ones, and to further an understanding of the inheritance of unit characters in barley. Of the 19 factor pairs selected for this study, four have not been previously assigned to linkage groups.

REVIEW OF LITERATURE

A number of reviews of genetic research in barley have been published: Griffee (1925), Hayes and Garber (1927), Buckley (1930), Daane (1931), Robertson (1933, 1937), and Smith (1951).

Reviews of linkage studies have been presented by Robertson, Wiebe, and Immer (1941), Immer and Henderson (1943), Smith (1951), Robertson, Wiebe and Shands (1947, 1955), and Robertson (1957). Smith's (1951) review of the genetics and cytology of barley is the most comprehensive in the field. He perused about 1400 articles, of which over 900 are listed in his bibliography.

This review will present work on only those 19 factor pairs which are pertinent to this study.

Inheritance of Factor Pairs

Linkage group I

Normal vs triple-awned lemma (Tr tr). Reports by Immer and Henderson (1943), Heiner (1958) and Imam (1959) indicate that triple-awned lemma is recessive, segregating in a 3:1 ratio.

Deficiens (V^t) vs two-rowed (V) vs six-rowed (v). The complicated problem of fertility of the lateral florets and of the number of kernel rows in barley received a plausible explanation by Woodward (1947). Whereas Hor (1924) and Huber (Smith 1951), among others, had earlier concluded that the number of rows of florets was determined by an allelic series of three genes, Woodward (1947) demonstrated that an allelic series of four genes (V^t, V^d, V and v) were located in Linkage Group I. The deficiens character for rudimentary floral structures in the lateral florets behaves as an allele of the V, v factor for the two-rowed vs six-rowed condition and is at least partially dominant to them.

The studies of Buckley (1930), Daane (1931), Neatby (1926), and Heiner (1958) indicated that a single pair of genes was involved. Robertson (1929) suggested a two factor-pair inheritance. A ratio of one deficiens to two intermedium to one six-rowed was obtained by Byington (1940) and Waddoups (1949).

<u>Purple vs white lemma and pericarp (Re_2 re_2).</u> In most ratios involving purple and white lemmas, purple is a simple dominant over non-purple (Woodward 1949). Biffen (1907) found that purple lemma, while inherited in some crosses as a simple dominant, could in other crosses be inhibited by two dominant complementary genes. Waddoups (1949) observed a 3:1 ratio in the F_2 of a cross between purple- and white-chaffed parents, but one cross between two white-chaffed parents gave a 9:7 ratio of purple to white in F_2. So <u>et al</u>. (Smith 1951) reported 9:7, 15:1, and 1:2:1 ratios for deep purple, light purple and colorless in different crosses.

Woodward and Thieret (1953) and Heiner (1958) found both 3:1 and 9:7 ratios in the F_2, suggesting that two complementary factors were involved. Woodward (1949) obtained one 9:6:1 for dense, dilute purple and white, and another ratio of 12 purple, 3 blue to 1 white for pericarp and blue aleurone in F_2 segregation. Environmental factors, including sunlight, according to Woodward (personal communication), can cause considerable variation in color expressions involving purple and red.

Lax vs dense spike (L l). At the present time there is no all-inclusive explanation as to what factors determine the length and density of the barley spike. Smith's (1951) review of the subject indicated that one, two, three, four and six gene pairs have been reported.

The laxness or denseness of a spike, according to Rasmusson (1956), is determined by measuring the length of the ten internodes just above the second node. However, Aberg and Wiebe (Rasmusson 1956) stated that internode length varies greatly within a variety. Variations from year to year, place to place, and from spike to spike, they concluded, limited its usefulness as a very stable character. Earlier, Harlan and Hayes (1920) had reported that internode length in barley was a very stable character.

Normal vs long-awned glume (E e). There is general agreement that the non-awned glume is dominant and follows a simple Mendelian ratio. Workers reporting the involvement of a single gene pair were: Hor (1924), Neatby (1926), Immer and Henderson (1943), Robertson, Immer, Wiebe and Stevens (1944), Gill (1951), Woodward (1957), Andersen (1958), Heiner (1958), and Imam (1959).

Normal vs reduced laterals (Lr lr). Varied opinions were expressed in the literature as to the number of gene pairs which affected the presence or absence of lateral awning. Leonard (1942), after reviewing some of the earlier studies, decided that appendages (awns or hoods) on lateral florets were determined by one gene pair. He noted that normal was dominant over reduced appendages but that they were present only in six-rowed types. Smith (1951) quoted Dasananda and Fung as believing that "... one factor was mainly responsible for the development of the lateral lemma appendages." Smith continued:

> But Chia interpreted his data on awn inheritance in crosses among varieties differing in awn length on both central and lateral florets as the result of five gene pairs; one affected awn length on central florets, and four determined awnedness of lateral florets.

Linkage group II

Black vs white lemma and pericarp (B b). Smith (1951) listed 30 articles reporting that black glume is dominant to non-black glume and segregates in a 3:1 ratio in many crosses. Studies by Woodward (1941, 1942) revealed evidence of an allelomorphic series of three genes for degree of black pigmentation of lemma and pericarp: black, gray and white. The darker color, in each combination, was dominant over the lighter and segregated monofactorially.

Linkage Group III

Hulled vs hull-less caryopsis (N n). A single gene difference was recorded by Robertson (1929), Buckley (1930), Daane (1931), Byington (1940), Waddoups (1949), Woodward (1955), Heiner (1958, Al-Jibouri (1953), and Imam (1959). All reported that the F_2 generations segregated in a three hulled to one hull-less ratio.

Linkage Group IV

Hoods vs awns (K k). Several researchers, among them Buckley (1930), Daane (1931), Woodward (1949), Al-Jibouri (1953), and Heiner (1958), have observed that in most crosses hoods are dominant over awns in a 3:1 ratio. Wheatley (1955), however, reported both 3:1 and 9:7 ratios in F_2. In another F_2 study, Rasmusson (1956) obtained 9 hoods to 3 long awns to 4 short awns.

After studying data from the F_2 generation and a small F_3 population of crosses involving hooded and short-awned, hooded and long-awned, and long and short-awned plants, Albrechtsen (1957) concluded:

> The inheritance of hoods (K) and awns (k) in these crosses was determined by two factor pairs (KK and K_2K_2). One or more dominant genes from each of the two pairs is necessary for the development of hoods. Therefore there are four possible genotypes for the hooded plants (KK K_2K_2, Kk K_2K_2, KK K_2k_2, and Kk K_2k_2). Short awns develop when the recessive (kk) factor is present with the second factor in either a homozygous dominant (K_2K_2), heterozygous (K_2k_2), or homozygous recessive (k_2k_2) condition. Long (K_1) awns are developed when the recessive (k_2k_2) factor is present in combination with the first factor in the homozygous dominant (KK) or heterozygous (Kk) condition.

Long vs short awns (k_1 k_2). Bussell (1936) and Myler (1942) concluded that two gene pairs were responsible for the difference between certain long- and short-awned (or awnless) varieties. Miyake and Imai (Smith 1951) believed that there was only a single factor difference for length of awns in some crosses but that three genes determined the presence and length of awns in crosses between certain awned and awnless varieties.

Elevated hoods vs awns (K^e k). It was shown by Takahashi *et al.* (1953) that the normal (subjacent) hood, the elevated hood and the long-awn were governed by a multiple allelic series K, K^e and k. The gene K for normal hood was almost completely dominant over K^e for elevated hood and k for long-awn, while K^e was only slightly dominant over k. The multiple allelic hypothesis seemed to be supported by the fact that K and K^e are both linked with almost equal intensity with Bl for blue aleurone in linkage group IV.

Non-zoned vs zoned leaf (Z z). A simple Mendelian ratio of 3 non-zoned to 1 zoned leaf have been recorded by Immer and Henderson (1943), Wheatley (1955), and Heiner (1958). Woodward (1957), however, reported another factor pair for zoned leaf which has shown no linkage with any other gene pair.

Blue vs white aleurone (Bl bl). Buckley (1930), Daane (1931), Woodward (1949), Al-Jibouri (1953), Wheatley (1955), and Heiner (1958) have reported a 3 blue to 1 white ratio. Smith (1951) observed that not only is the expression of the character frequently influenced by environment but because the blue color is in the aleurone, xenia may be observed when the cross is made on the white seeded parent.

Factor pairs not classified

Long vs short glume hairs (Gh gh). From F_2 data on the inheritance of glume hair length, Woodward (1950), Isom (1951), Al-Jibouri (1953), and Heiner (1958) received 3:1 ratios. Gill (1951) took hard-to-classify-material into the F_3 from which he received a 1:2:1 ratio with a good chi-square fit. When Waddoups (1949) received 3:1, 1:2:1 and 1:1 F_2 ratios, he concluded that as many as three factor pairs were involved.

Non-glossy vs glossy sheath and spike (Gs gs). Simple inheritance in a 3:1 ratio, non-glossy being dominant, has been recorded by Immer and Henderson (1943), Waddoups (1949), Gill (1951) Wheatley (1955), Andersen (1958), and Heiner (1958).

Purple vs white auricle (Pr_a pr_a). Since the three references to auricle color were printed in German, Smith's (1951) review will be quoted in full:

Presence and absence of red pigment in the auricle was found to segregate in 3:1 and 10:6 ratios in different crosses (Huber 1920) [dating is mine]. It was assumed that one gene was mainly responsible for formation of anthocyanin in the auricle, but this gene did not express itself except in the heterozygous condition, unless the other, intensifier gene, was also present in the dominant condition. Ubisch (1919) observed that red color in the auricle, nodes and other places was dominant. Gassner and Straib (1937) observed that a deficiency of N or a higher concentration of CO_2 increased anthocyanin development, but that K or P by themselves were relatively ineffective in changing the concentration of the pigment.

Normal vs many-noded dwarf (Mnd mnd). In the summer of 1918, according to Harlan and Pope (1922), a two-rowed barley plant having a large number of extremely short internodes and an abundance of fine leaves was found in the World Collection at Aberdeen, Idaho. A few months earlier, Hor (1922) had described a variation of the same type, in a six-rowed barley which had been found in California. Harlan and Pope suggested:

> The double appearance of the variation seems to have one plausible explanation, namely, that it is a mutation where all the modifications which occur in the plant are caused by the same factor.

Out of four separate variety crosses made by Harlan and Pope, involving 233 F_2 plants, 181 normal and 52 "dwarfs" were observed. This is a 3.48:1 ratio.

Previously Reported Linkages

A summary of linkages pertinent to this study, as reported by various research workers, is presented below. The majority were taken directly from published reports of the workers themselves. A few linkages were found in unpublished Masters' theses at Utah State University. Where original reports were not available for personal study, the reference sources have been indicated.

Linkage group I

Purple vs white lemma and pericarp (Re_2 re_2) in relation to two-rowed vs six-rowed (V v).

Percent Recombination			Phase	Authority
13.9	±	2.17		Myler and Stanford (1924)
13.0	±	1.2	Coupling	Gill (1951)
4 to 8				Woodward and Thieret (1953)
13.2	±	0.9	Coupling	Woodward and Thieret (1953)
12.0	±	3.0 (F_3)	Coupling	Al-Jibouri (1953)
12.5	±	2.4 (F_3)	Coupling	Al-Jibouri (1953)
17.1	±	0.7	Coupling	Woodward (1957)
14.0	±	1.3	Coupling	Woodward (1957)
10.0	±	4.8	Repulsion	Woodward (1957)
22.1	±	16.3	Repulsion	Woodward (1957)
26.5	±	1.89	Coupling	Albrechtsen (1957)
12.0	±	1.3		Andersen (1958)
33.0	±	4.0		Andersen (1958)
15.0	±	2.2	Coupling	Heiner (1958)
14.5	±	6.5	Repulsion	Heiner (1958)
15.6	±	1.5	Coupling	Imam (1959)

Purple vs white lemma and pericarp (Re_2 re_2) in relation to deficiens vs six-rowed.

Percent Recombination	Phase	Authority
18.0 ± 3.2	Coupling	Waddoups (1949)
12.0 ± 2.6	Coupling	Waddoups (1949)
32.36 ± 1.59	Coupling	Imam (1959)

Purple vs white lemma and pericarp (Re_2 re_2) in relation to normal vs long-awned glume (E e).

Percent Recombination	Phase	Authority
26.5 ± 2.0	Coupling	Woodward (1957)
27.0 ± 5.7	Repulsion	Woodward (1957)
None	Repulsion	Woodward (1957)
28.5 ± 5.2	Coupling	Heiner (1958)
47.0 ± 5.3	Repulsion	Heiner (1958)
44.71 ± 6.06	Coupling	Imam (1959)

Purple vs white lemma and pericarp (Re_2 re_2) in relation to lax vs dense spike (L l).

Percent Recombination	Phase	Authority
41.3 ± 2.6	Coupling	Woodward (1957)
35.0 ± 5.8	Coupling	Heiner (1958)
36.0 ± 5.9	Repulsion	Heiner (1958)
46.05 ± 7.16	Coupling	Imam (1959)

Normal vs long-awned glume (E e) in relation to lax vs dense spike (L l).

Percent Recombination	Phase	Authority
11.8 ± 5.9	Repulsion	Waddoups (1949)
21.2 ± 1.5	Coupling	Woodward (1957)
31.5 ± 4.0	Repulsion	Woodward (1957)
18.13 ± 2.5	Coupling	Imam (1959)

Linkage group IV

Hoods vs awns (K k) in relation to blue vs white aleurone (Bl bl).

Percent Recombination	Phase	Authority
40.6 ± 2.26	Repulsion	Buckley (1930)
22.0		Robertson, Deming and Koonce (1932)
24.72 ± 1.73		Myler and Stanford (1942)
44.0 ± 6.3		Immer and Henderson (1943)
30.4 ± 4.07	Coupling	Gill (1951)
26.5 ± 1.5	Coupling	Isom (1951)
21.8		Takahashi (1953)
30.0 ± 2.0	Coupling	Al-Jibouri (1953)
35.5 ± 1.9	Coupling	Wheatley (1955)
28.5 ± 0.9	Coupling	Woodward (1957)
31.5 ± 7.1	Repulsion	Woodward (1957)
37.0 ± 3.3	3:1:3:1	Woodward (1957)
None		Woodward (1957)
37.0 ± 3.58	Coupling	Albrechtsen (1957)
43.4 ± 3.35	Repulsion	Imam (1959)

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

Percent Recombination	Phase	Authority
5.0 ± 0.8	Coupling	Immer and Henderson (1943)
38.0 ± 9.7	Repulsion	Gill (1951)
27.0 ± 4.6	Repulsion	Wheatley (1955)
38.0 ± 1.4	Coupling	Woodward (1957)
35.5 ± 2.5	Repulsion	Woodward (1957)
None	Coupling	Woodward (1957)
18.2 ± 2.54	Repulsion	Albrechtsen (1957)
4.5 ± 2.4	Coupling	Heiner (1958)
17.5 ± 7.4	Repulsion	Heiner (1958)

MATERIALS AND METHODS

The seven crosses used in this study were made during 1957 by Dr. Rollo W. Woodward at Utah State University. The F_1 plants were harvested and kept separate so that each plant constituted a family. There were two to eleven families in each cross.

In the Spring of 1958 the F_2 generation was thinly planted in 35-foot rows, one foot apart, by means of a four-row cone seeder.

Plants having characteristics subject to change before maturity were tied with colored strings. These particular characteristics were: glossy leaf, glossy sheath and head, purple auricle, and zoned leaf. At maturity all plants were pulled, bundled, tied into family groups, and properly labeled.

The material was classified according to phenotypic expressions. Two or three heads from particular character combinations were kept for future plantings. Two factor pairs were then studied in relation to each other for independent inheritance or linkage. Chi-square was calculated as a test for goodness of fit for each segregating factor pair and for every dihybrid combination of factor pairs. The probability values for chi-square were taken from Ostle (1956). Linkages were determined by the product method, as reported by Fisher and Balmukand (1928).

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Factor Pairs Used in This Study and Their Gene Symbols

Linkage group I

Normal vs triple-awned lemma	Tr tr
Deficiens vs two-rowed spike	V^t V
Two-rowed vs six-rowed spike	V v
Purple vs white lemma and pericarp	Re_2 re_2
Normal vs long-awned glume	E e
Lax vs dense spike	L l
Normal vs reduced lateral	Lr lr

Linkage group II

Black vs white lemma and pericarp	B b

Linkage group III

Hulled vs hull-less	N n

Linkage group IV

Hoods vs long awns	K k_1
Elevated hoods vs awns	K^e k
Elevated hoods vs long awns	K^e k_1
Long awns vs short awns	k_1 k_2
Non-zoned vs zoned leaf	Z z
Blue vs white aleurone	Bl bl

Non-classified factor pairs

Long vs short glume hairs	Gh gh
Non-glossy vs glossy sheath and spike	Gs gs
Purple vs white auricle	Pr_a pr_a
Normal vs many-noded dwarf	Mnd mnd

Crosses With Their Segregating Factor Pairs
as Used in This Study

B 1619	T 258	re_2	E	N					
	T 339	Re_2	e	n					
B 1620	T 258	re_2	v	N	Gh				
	T 365	Re_2	V	n	gh				
B 1629	T 258	E	L	k_1	Z				
	T 104	e	l	K	z				
B 1632	T 665	e	tr	k_1					
	T 352	E	Tr	K					
B 1642	T 336	re_2	k	bl	Gs				
	T 202	Re_2	K^e	Bl	gs				
B 1643	T 417	re_2	V	n	b	k_1	Pr_a	Gs	
	T 202	Re_2	V^t	N	B	K^e	pr_a	gs	
B 1640	T 609	Re_2	Lr*	Mnd	k_2				
	T 742	re_2	lr	mnd	k_1				

* Phase as suggested by the author

EXPERIMENTAL RESULTS

The data from this study will be presented in the following sequence:

1. The inheritance of individual characters.
2. Factor pairs suggesting independent inheritance.
3. Factor pairs suggesting linkage.

Inheritance of Individual Characters

Linkage group I

Normal vs triple-awned lemma (Tr tr). Table 1 indicates that simple Mendelian inheritance is present. The 3:1 ratio is in accord with earlier research data.

Two-rowed vs six-rowed spike (V v). Each of the 11 families in table 2 presents substantial evidence that a single factor differis operating in this cross.

Deficiens vs two-rowed spike (V^t V). Deficiens is dominant to two-rowed, segregating in a 3:1 ratio (table 3). Though the literature revealed inheritance data regarding only deficiens vs six-rowed spike, it follows reason that since the two-rowed factor is an allele of the one for six-rowed, either factor should segregate alike in the expected 3:1 ratio. Apparently, the hypothesis is confirmed.

Table 1. Segregation of normal vs triple-awned lemma (Tr tr) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1632

Family	Tr	tr	Total	X^2	P
1	63	22	85	.035	.8 - .9
2	25	15	40	2.133	.1 - .2
Sum of 2 chi-squares				2.168	.3 - .4
Total	88	37	125	1.536	.2 - .3
Interaction				.632	.4 - .5

Table 2. Segregation of two-rowed vs six-rowed spike (V v) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. B 1620

Family	V	v	Total	X^2	P
1	58	22	80	.267	.6 - .7
2	106	31	137	1.229	.2 - .3
3	79	20	99	1.338	.2 - .3
4	37	13	50	.027	.8 - .9
5	43	9	52	1.640	.2 - .3
6	92	35	127	1.129	.2 - .3
7	75	22	96	.209	.6 - .7
8	94	24	118	.915	.3 - .4
9	104	37	141	.091	.7 - .8
10	96	23	119	2.042	.1 - .2
11	34	12	46	.224	.6 - .7
Sum of 11 chi-squares				9.111	.6 - .7
Total	817	248	1065	1.624	.2 - .3
Interaction				7.487	.6 - .7

Table 3. Segregation of deficiens vs two-rowed spike (V^t V) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. 1643

Family	V^t	V	Total	X^2	P
1	43	13	56	.095	.7 - .8
2	34	13	47	.177	.6 - .7
3	73	27	100	.303	.5 - .6
4	85	22	107	1.125	.2 - .3
5	36	15	51	.529	.4 - .5
6	43	12	55	.257	.6 - .7
7	85	19	104	2.508	.1 - .2
Sum of 7 chi-squares				4.994	.6 - .7
Total	399	121	520	.831	.3 - .4
Interaction				4.163	.6 - .7

Table 4. Segregation of purple vs white lemma and pericarp (Re_2 re_2) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1619

Family	Re_2	re_2	Total	X^2	P
2	79	21	100	.853	.3 - .4
3	116	48	164	1.593	.2 - .3
4	91	41	132	2.585	.1 - .2
5	64	17	81	1.337	.2 - .3
8	46	45	91	28.161	$<$.01
Sum of 5 chi-squares				34.529	$<$.01
Total	350	127	477	8.451	$<$.01
Interaction				26.078	$<$.01

Purple vs white lemma and pericarp (Re_2 re_2). One cross (table 5) shows 3:1 segregation while four crosses (table 6) give 9:7 ratios. Evidently, there are one and two genes, respectively, operating within these crosses. Differences in the concentration of color were observed; unfortunately, these were not distinguished between during the classification period.

The low P value for Cross 1643 results from 3 families having low P values themselves. Deviations among the small number of plants in two of the families increased the chi-square values considerably.

The cross B 1640, as recorded in table 6, was affected by the factor pair for many-noded dwarf. The F_2 population of 483 plants was made up of 322 normal plants and 161 dwarfs. Because one third of the dwarfs failed to head and some of the remaining two-thirds were somewhat green, only the normal plants were analyzed for purple vs white chaff.

In addition to white, three aleurone colors were observed within this cross. In the order of most frequent occurrence or amount of dominance when two or all three colors appeared to be present, were the colors purple, red and blue.

Lax vs dense spike (L l). The data of table 7 suggests a 3:1 ratio for Cross B 1619. It may or may not be the true case since internode length appeared to be too flexible as a standard. In this cross there were not just long and short internodes but quite a gradation of them. This prompts the author to believe that there are more than one pair of contributing genes and/or that environment exerts some influence.

Table 5. Segregation of purple vs white lemma and pericarp (Re_2 re_2) in the F_2 generation. Chi-square and P values are based on a 9:7 ratio.

Cross No.	No. of Families	Re_2	re_2	Total	X^2	P
B 1620	11	388	284	672	.557	.4 - .5
B 1642	9	192	150	342	.200	.6 - .7
B 1643	7	190	121	311	17.632	.01
Sum of 3 chi-squares					18.389	<.01
Total	27	770	555	1325	.306	.5 - .6
Interaction					18.083	<.01

Table 6. Segregation of purple vs white lemma and pericarp (Re_2 re_2) in the F_2 generation. Chi-square and P values are based on a 9:7 ratio. Cross No. B 1640

Family	P	p	Total	X^2	P
3	41	21	62	2.458	.1 - .2
8	59	42	101	.192	.6 - .7
11	59	31	90	3.067	.05- .1
12	36	33	69	.466	.4 - .5
Sum of 4 chi-squares				6.183	.1 - .2
Total	195	127	322	2.975	.05 - .1
Interaction				3.208	.3 - .4

Table 7. Segregation of lax vs dense spike (L 1) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1619

Family	L	l	Total	X^2	P
2	56	44	100	19.253	<.01
3	107	57	164	8.325	<.01
4	101	31	132	.161	.6 - .7
5	59	22	81	.200	.6 - .7
Sum of 4 chi-squares				27.939	<.01
Total	323	154	477	13.501	<.01
Interaction				14.438	<.01

Normal vs long-awned glume (E e). Three ratios were observed for this character pair: 3:1 (table 8), 9:7 (table 9), and 15:1 (table 10). The 9:7 ratio loses some importance because all of the heterozygotes were included in with the homozygous recessives. Cross B 1619 which gave the 15:1 ratio, produced very few long awns or hoods on the glumes when the character was manifested. Not one plant of the 568 which were classified was completely glume-awned or -hooded as was expected for the homozygous recessive. B 1632, the cross having the 3:1 ratio, appeared to be the only cross where the spike was fully glume-awned or -hooded, depending, of course, upon whether the same spike was normally awned or hooded. Therefore, it appears that one to two factor pairs conditions this characteristic within these crosses.

Normal vs reduced lateral (Lr lr). The 1:2:1 ratio in table 11 suggests a monofactorial inheritance for this characteristic. This cross, B 1640, had the many-noded dwarf factor present; consequently, only the 322 normal plants were classified. Very few of the dwarfs appeared homozygous recessive for the reduced laterals.

Linkage group II

Black vs white lemma and pericarp (B b). A single factor difference is indicated in table 12 for the inheritance of black vs white lemma and pericarp.

Linkage group III

Hulled vs hull-less (N n). Table 13 suggests a monofactorial inheritance for this factor pair.

Table 8. Segregation of normal vs long-awned glume (E e) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1632

Family	E	e	Total	X^2	P
1	60	25	85	.883	.3 - .4
3	22	18	40	8.533	< .01
Sum of 2 chi-squares				9.416	< .01
Total	88	43	125	1.411	.2 - .3
Interaction				8.005	< .01

Table 9. Segregation of normal vs long-awned glume (E e) in the F_2 generation. Chi-square and P values are based on a 9:7 ratio. Cross No. B 1629

Family	E	e	Total	X^2	P
2	27	16	43	.746	.3 - .4
3	71	43	114	1.684	.1 - .2
5	54	60	114	.606	.4 - .5
Sum of 3 chi-squares				3.036	.3 - .4
Total	152	119	271	.002	.95 - .975
Interaction				3.034	.2 - .3

Table 10. Segregation of normal vs long-awned glume (E e) in the F_2 generation. Chi-square and P values are based on a 15:1 ratio. Cross No. B 1619

Family	E	e	Total	X^2	P
2	94	6	100	.016	.8 - .9
3	156	8	164	.463	.4 - .5
4	127	5	132	2.134	.1 - .2
5	73	8	81	1.922	.1 - .2
8	79	12	91	7.460	< .01
Sum of 5 chi-squares				11.995	.025 - .05
Total	529	39	568	.368	.5 - .6
Interaction				11.627	.01 - .025

Table 11. Segregation of normal vs reduced lateral (Lr lr) in the F_2 generation. Chi-square and P values are based on a 1:2:1 ratio. Cross No. B 1640

Family	Normal	Intermediates	Reduced	Total	X^2	P
3	23	23	16	62	5.710	.01 - .025
8	28	51	22	101	.723	.3 - .4
11	23	49	18	90	1.267	.2 - .3
12	25	35	9	69	7.435	< .01
Sum of 4 chi-squares					15.135	< .01
Total	99	158	65	322	7.244	< .01
Interaction					7.891	.025 - .05

Table 12. Segregation of black vs white lemma and pericarp (B b) in F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1643

Family	B	b	Total	X^2	P
1	36	20	56	3.428	.05 - .1
2	33	14	47	.575	.4 - .5
3	76	24	100	.053	.8 - .9
4	84	23	107	.695	.4 - .5
5	34	17	51	1.888	.1 - .2
6	48	7	55	4.417	.025 - .05
7	81	23	104	.461	.4 - .5
Sum of 7 chi-squares				11.517	.1 - .2
Total	392	128	520	.044	.8 - .9
Interaction				11.473	.05 - .1

Table 13. Segregation of hulled vs hull-less (N n) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	No. of Families	N	n	Total	X^2	P
B 1619	5	425	143	568	.009	.95 - .975
B 1620	11	780	285	1065	1.953	.1 - .2
B 1643	4	272	95	367	.153	.7 - .8
Sum of 3 chi-squares					2.115	.5 - .6
Total	20	1477	523	2000	1.369	.2 - .3
Interaction					.746	.6 - .7

Linkage group IV

Hoods vs awns (K k). The data in tables 14, 15, and 16 indicate that hoods and awns are inherited in a ratio of 3 hoods to 1 awn, regardless of the length of the appendage.

Long vs short awns ($k_1 k_2$). Long awns are dominant to short awns, according to table 17. Simple Mendelian inheritance is suggested.

This is another characteristic which was classified from the normal plants of B 1640. While this characteristic was evident among the dwarfed plants, it was felt that since one-third of the dwarfs had no spikes a more accurate ratio would be gained through classifying only the normal plants.

Non-zoned vs zoned leaf (Z z). Table 18 suggests that one factor pair is involved in this cross for this character. The low probability values are very probably influenced by the mortality of some immature chlorophyll-deficient plants.

Blue vs white aleurone (Bl bl). The data in table 19 substantiates the reports of previous workers. This character pair is manifested in the ratio of 3 blue to 1 white aleurone. Some difficulty was encountered in determining the homozygous recessive whites.

Factor pairs not classified

Long vs short glume hairs (Gh gh). Long glume hairs are dominant to short glume hairs and segregate in a 3:1 ratio (table 20).

Non-glossy vs glossy sheath and spike (Gs gs). This factor pair segregated in a 3:1 ratio, as is evidenced in table 21.

Purple vs white auricle (Pr_a pr_a). Purple auricles are dominant to white auricles. Data in table 22 suggest a single factor difference.

Table 14. Segregation of hoods vs long awns ($K\ k_1$) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	No. of Families	K	k_1	Total	X^2	P
B 1629	2	192	79	271	2.363	.1 - .2
B 1632	2	97	28	125	.385	.5 - .6
Sum of 2 chi-squares					2.748	.2 - .3
Total	4	289	107	396	.961	.3 - .4
Interaction					1.787	.1 - .2

Table 15. Segregation of elevated hoods vs awns ($K^e\ k$) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1642

Family	K^e	k	Total	X^2	P
1	83	29	112	.048	.8 - .9
2	51	19	70	.172	.6 - .7
3	28	7	35	.467	.4 - .5
4	47	20	67	.841	.3 - .4
5	91	30	121	.003	.95 - .975
6	7	1	8	.667	.4 - .5
7	66	28	94	1.149	.2 - .3
8	98	29	127	.317	.5 - .6
9	71	26	97	.168	.6 - .7
Sum of 9 chi-squares				3.832	.9 - .95
Total	542	189	731	.263	.6 - .7
Interaction				3.569	.8 - .9

Table 16. Segregation of elevated hoods vs long awns (K^e k_1) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1643

Family	K^e	k_1	Total	X^2	P
1	34	22	56	6.095	.01 - .025
2	36	11	47	.054	.8 - .9
3	76	24	100	.053	.8 - .9
4	80	27	107	.003	.95 - .975
5	32	19	51	4.085	.025 - .05
6	34	21	55	5.097	.01 - .025
7	74	30	104	.820	.3 - .4
Sum of 7 chi-squares				16.207	< .01
Total	366	154	520	5.907	.01 - .025
Interaction				11.300	< .01

Table 17. Segregation of long vs short awns (k_1 k_2) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1640

Family	k_1	k_2	Total	X^2	P
3	42	20	62	1.771	.1 - .2
8	63	38	101	8.584	< .01
11	58	32	90	5.348	.01 - .025
12	46	23	69	2.556	.1 - .2
Sum of 4 chi-squares				18.259	< .01
Total	209	113	322	17.494	< .01
Interaction				.765	.8 - .9

Table 18. Segregation of non-zoned vs zoned leaf (Z z) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. 1629

Family	Z	z	Total	X^2	P
2	100	14	114	9.836	< .01
3	39	4	43	5.652	.01 - .025
5	92	22	114	1.976	.1 - .2
Sum of 3 chi-squares				17.464	< .01
Total	231	40	271	15.155	< .01
Interaction				2.309	.3 - .4

Table 19. Segregation of blue vs white aleurone (Bl bl) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. 1642

Family	Bl	bl	Total	X^2	P
1	75	37	112	3.857	.025 - .05
2	50	20	70	.476	.4 - .5
3	26	9	35	.007	.9 - .95
4	43	24	67	4.184	.025 - .05
5	87	34	121	.620	.4 - .5
6	6	2	8	.000	1.0
7	67	27	94	.696	.4 - .5
8	98	29	127	.317	.5 - .6
9	75	22	97	.268	.6 - .7
Sum of 9 chi-squares				10.425	.3 - .4
Total	527	204	731	3.295	.05 - .1
Interaction				7.130	.5 - .6

Table 20. Segregation of long vs short glume hairs (Gh gh) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1620

Family	Gh	gh	Total	X^2	P
1	62	18	80	.866	.3 - .4
2	111	26	137	2.503	.1 - .2
3	83	16	99	5.320	.025 - .01
4	37	13	50	.027	.8 - .9
5	46	6	52	5.025	.025 - .01
6	95	32	127	.003	.95 - .975
8	75	21	96	.500	.4 - .5
9	87	31	118	.045	.8 - .9
10	107	34	141	.038	.8 - .9
11	93	26	119	.712	.3 - .4
12	42	4	46	5.854	.010 - .025
Sum of 11 chi-squares				20.893	.025 - .05
Total	838	227	1065	7.610	<.01
Interaction				13.283	.2 - .3

Table 21. Segregation of non-glossy vs glossy sheath and spike (Gs gs) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1643

Family	Gs	gs	Total	X^2	P
1	41	15	56	.095	.7 - .8
2	32	15	47	1.226	.2 - .3
3	76	24	100	.053	.8 - .9
4	78	29	107	.819	.3 - .4
5	35	16	51	1.098	.2 - .3
6	45	10	55	1.363	.2 - .3
7	77	27	104	.532	.4 - .5
Sum of 7 chi-squares				5.186	.6 - .7
Total	384	136	520	.369	.5 - .6
Interaction				4.817	.5 - .6

Table 22. Segregation of purple vs white auricle (Pr_a pr_a) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. B 1643

Family	Pr_a	pr_a	Total	X^2	P
1	38	18	56	1.524	.2 - .3
2	30	17	47	.588	.4 - .5
3	80	20	100	1.333	.2 - .3
4	80	27	107	.003	.95 - .975
5	43	8	51	2.359	.1 - .2
6	37	18	55	1.751	.1 - .2
7	68	36	104	.517	.4 - .5
Sum of 7 chi-squares				8.075	.3 - .4
Total	376	144	520	2.010	.1 - .2
Interaction				6.065	.4 - .5

Normal vs many-noded dwarf (Mnd mnd). This character warrants a lengthier report than do the other factor pairs because it has been studied less.

Many of the same typical characters possessed by the Aberdeen, Idaho mutant appeared in the F_2 generation of this study. One exception was that the plants of this study were all six-rowed whereas the original had a two-rowed spike.

The non-normal plants, contrary to their name, were more like brachytics than true dwarfs. From crown to tip of awns the plants measured about 18 inches. Whereas the number of nodes in ordinary varieties of barley varies from three to seven, with the uppermost node being always the longest - this freak had from 10 to 26 nodes on each tiller without an elongation of the uppermost internode. Branching from the approximately 17 culms per plant was profuse, with 49 branches being the maximum number observed.

The factor governing the "dwarf" habit appears (from data in table 23) to be a simple one for it follows a 3:1 ratio. Usually, one expects the number of dwarf plants to be less than the expected ratio for recessives. Contrariwise, in each of the four families which were classified the total of many-noded dwarfs exceeded the expected number, insomuch that they almost fit a 2:1 ratio. However, a 2:1 ratio was not probable because of the great number of recessive plants; this also indicated that there were no lethal factors present.

Three colors besides white were observed in the caryopses: purple, red, and blue. These were readily examined because the cross was all hull-less. If chemical tests had been run on the pericarp and aleurone colors, a greater amount of information could have been gathered on the inheritance of these factors.

Out of the 162 dwarfed plants, 56 failed to produce spikes in any degree of development. Some developed spikes were yet green; this prevented a total classification of chaff and caryopsis colors. It was because of this that the classifications for purple vs white chaff, long vs short awns, and normal vs reduced lateral were presented from data on the normal plants only.

Table 23. Segregation of normal vs many-noded dwarf (Mnd mnd) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio. Cross No. 1640

Family	Mnd	mnd	Total	X^2	P
3	62	26	88	1.387	.2 - .3
8	110	58	168	8.127	< .01
11	101	46	147	3.104	.05 - .01
12	80	32	112	.761	.3 - .4
Sum of 4 chi-squares				13.379	< .01
Total	353	162	515	11.449	< .01
Interaction				1.930	.5 - .6

Factor Pairs Suggesting Independent Inheritance

Linkage group I

Normal vs triple-awned lemma (Tr tr) in relation to normal vs long outer glume (Ee). Data in table 24 indicate independent inheritance between these factor pairs. This is contrary to the reports of other workers. The recombination percentage is 56.7

Two-rowed vs six-rowed spike (V v) in relation to other factor pairs. Independent inheritance is suggested in table 25 between V:v and N:n as well as between V:v and Gh:gh.

Deficiens vs two-rowed spike (V^t V) in relation to other factor pairs. Table 26 lists four factor pairs which are inherited independent of deficiens vs two-rowed. They are: B:b, N:n, $K^e:k_1$, and Gs:gs. None showed recombination percentages of any significance.

Purple vs white lemma and pericarp (Re_2 re_2) in relation to other factor pairs. Those factor pairs which were found to segregate independently in relation to purple vs white lemma and pericarp were: N:n, B:b, $K^e:k_1$, K^ek, Bl:bl, Gs:gs, and Gh:gh. Three characters from Cross No. B 1643 show unusually high chi-square values yet their percentages of recombination were never lower than 45.1. These characters, as shown in table 27, are: B:b, $K^e:k_1$, and Gs:gs.

Normal vs long-awned glume (Ee) in relation to other factor pairs. Linkages were not found in either of the two crosses, according to table 28, between normal vs long-awned glume and Tr:tr, $K:k_1$, L:l, and N:n. Cross B 1632 has such few numbers that the low P value can be regarded as insignificant, especially when the percent of recombination for both Tr:tr and $K:k_1$ is above 56.7.

Table 24. Normal vs triple-awned lemma (Tr tr) in relation to normal vs long-awned glume (E e). Chi-square and P values are based on a 9:3:3:1 ratio.

Tr:tr in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
E:e	B 1632	C	55	27	33	10	125	8.388	.025 - .05

Table 25. Two-rowed vs six-rowed spike (V v) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

V:v in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
N:n	B 1620	R	604	213	176	72	1065	4.813	.2 - .3
Gh:gh	B 1620	R	637	180	201	47	1065	9.980	.01 - .025

Table 26. Deficiens vs two-rowed spike (V^t V) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

V^t:V in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
B:b	B 1643	C	301	98	91	30	520	.875	.8 - .9
N:n	B 1643	C	211	75	61	20	367	2.826	.4 - .5
K^e:k_1	B 1643	C	289	110	77	44	520	5.995	.1 - .2
Gs:gs	B 1643	R	298	101	86	35	520	1.777	.6 - .7

Table 27. Purple vs white lemma and pericarp (Re_2 re_2) in relation to other factor pairs.

Re_2:re_2 in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square is based on a 9:3:3:1 ratio						
N:n	B 1619	R	272	102	76	27	477	4.000	.2 - .3
			Chi-square is based on a 27:21:9:7 ratio						
B:b	B 1643	R	254	86	138	42	520	28.846	< .01
N:n	B 1620	R	456	155	324	130	1065	6.131	.1 - .2
N:n	B 1643	C	174	62	98	33	367	10.342	.01 - .025
K^e:k	B 1642	C	307	235	98	91	731	1.764	.6 - .7
K^e:k_1	B 1643	C	248	92	118	62	520	25.296	< .01
Bl:bl	B 1642	R	306	99	221	105	731	9.489	.01 - .025
Gs:gs	B 1642	R	298	107	243	83	731	1.727	.6 - .7
Gs:gs	B 1643	R	251	89	133	47	520	18.015	< .01
Gh:gh	B 1620	R	471	140	367	87	1065	10.028	.01 - .025

Table 28. Normal vs long-awned glume (E e) in relation to other factor pairs.

E:e in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
		Chi-square based on a 9:3:3:1 ratio							
Tr:tr	B 1632	C	55	27	33	27	125	8.388	.025 - .05
$K:k_1$	B 1632	C	59	23	38	5	125	11.879	< .01
		Chi-square based on a 45:15:3:1 ratio							
L:l	B 1619	R	277	130	44	26	477	80.258	< .01
N:n	B 1619	C	325	49	82	21	477	64.648	< .01

A linkage between E:e and L:l in Cross No. B 1619 is doubtful because the two factor pairs have a recombination of 54.0 ± 7.4 percent. Classification of head density was not as accurate as the author wishes it could have been. That, undoubtedly, has influenced the data of table 28. Recombination of E:e in relation to N:n is 41.0 ± 8.0 percent.

Lax vs dense spike (L l) in relation to other factor pairs. Table 29 shows lax vs dense heads in relation to hoods vs awns, and hulled vs hull-less. The high chi-square value is definitely influenced by the method of classification. The author places little faith in the accuracy of the data in this table.

Linkage group II

Black vs white lemma and pericarp (B b) in relation to other factor pairs. The data reported in table 30 indicate an independent inheritance of B:b in relation to: V^t:V, N:n, K^e:k_1, Gs:gs, Pr_a:pr_a, and Re_2:re_2. The data for B:b in relation to Re_2:re_2 show a low probability value but the percentage for recombination does not indicate linkage.

Linkage group III

Hulled vs hull-less (N n) in relation to other factor pairs. The two crosses, B 1620 and B 1643, in which hulled vs hull-less were present, have reliable probability values which suggest that this factor pair is inherited independent of: V:v, V^t:V, B:b, K^e:k_1, Gs:gs, and Re_2:re_2 (table 31).

Table 29. Lax vs dense spike (L l) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

L:l in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
$K:k_1$	B 1629	R	66	126	36	43	271	374.371	<.01
N:n	B 1619	R	250	124	73	30	477	17.617	<.01

Table 30. Black vs white lemma and pericarp (B b) in relation to other factor pairs.

B:b in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
		Chi-square based on a 9:3:3:1 ratio							
$V^t:V$	B 1643	C	301	91	98	30	520	.875	.8 - .9
N:n	B 1643	C	204	73	68	22	367	.324	.95 - .975
$K^e:k_1$	B 1643	C	276	116	90	38	520	5.949	.1 - .2
Gs:gs	B 1643	R	287	105	97	31	520	.752	.8 - .9
$Pr_a:pr_a$	B 1643	R	277	115	99	29	520	1.535	.5 - .6
		Chi-square based on a 27:21:9:7 ratio							
$Re_2:re_2$	B 1643	C	254	138	86	42	520	28.846	<.01

Table 31. Hulled vs hull-less (N n) in relation to other factor pairs.

N:n in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square based on a 9:3:3:1 ratio						
V:v	B 1620	R	604	176	213	72	1065	4.183	.2 - .3
V^t:V	B 1643	C	211	61	75	20	367	2.826	.4 - .6
B:b	B 1643	R	204	68	73	22	367	.324	.95 - .975
K^e:k_1	B 1643	R	190	82	74	21	367	4.100	.2 - .3
Gs:gs	B 1643	R	199	73	73	22	367	.817	.8 - .9
			Chi-square is based on a 27:21:9:7 ratio						
Re_2:re_2	B 1620	R	456	324	155	130	1065	6.131	.1 - .2
Re_2:re_2	B 1643	C	174	98	62	33	367	10.342	.01 - .025

Linkage group IV

Hoods vs long awns ($K\ k_1$) in relation to normal vs long-awned glume. There is no linkage between $K:k_1$ and E:e although table 32 data suggest the possibility of it. The calculated recombination is greater than sixty percent.

Elevated hoods vs awns ($K^e\ k$) in relation to other factor pairs. The relationship of $K^e:k$ to other characters is considered in table 33. Spike appendages in the form of awns or hoods were found to be independent of Gs:gs and $Re_2:re_2$.

Elevated hoods vs long awns ($K^e\ k_1$) in relation to other factor pairs. As is shown in table 34, $K^e\ k_1$ is inherited independently of: $V^t:V$, B:b, N:n, Gs:gs, $Pr_a:pr_a$, and $Re_2:re_2$. However, there is a suggestion of linkage between $K^e:k_1$ and $Pr_a:pr_a$, and $K^e:k_1$ and $Re_2:re_2$. Not only do these two factor pairs, $Pr_a:pr_a$ and $Re_2:re_2$, have low probability values but they recombine with 41.2 and 45.1 percentage, respectively. However, they are very closely linked in group I; therefore, it is suggested that there is no association with group IV.

Non-zoned vs zoned (Z z) leaf in relation to other factor pairs.

Table 35 considers the relationship of Z:z with E:e and L:l, respectively. The nature of the data may suggest linkage especially when Z:z recombines with E:e (33.77 ± 10.1), and with L:l (30.58 ± 5.4). Nonetheless, according to table 18, some mortality of the immature chlorophyll-deficient plants may have occurred. Improper classification for L:l and E:e would cause bias. In interpreting the data, these extraneous factors must be considered.

Table 32. Hoods vs long awns ($K\ k_1$) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

$K:k_1$ in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
E:e	B 1632	C	59	38	23	5	125	11.874	<.01

Table 33. Elevated hoods vs awns ($K^e\ k$) in relation to other factor pairs.

$K^e:k$ in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
		Chi-square based on a 9:3:3:1 ratio							
Gs:gs	B 1642	R	409	133	132	57	731	4.871	.1 - .2
		Chi-square based on a 27:21:9:7 ratio							
$Re_2:re_2$	B 1642	C	307	235	98	91	731	1.764	.6 - .7

Table 34. Elevated hoods vs long awns (K^e k_1) in relation to other factor pairs.

K^e:k_1 in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square based on a 9:3:3:1 ratio						
V^t:V	B 1643	C	289	77	110	44	520	5.995	.1 - .2
B:b	B 1643	C	276	90	116	38	520	5.949	.1 - .2
N:n	B 1643	R	190	74	82	21	367	4.390	.2 - .3
Gs:gs	B 1643	R	272	94	112	42	520	6.496	.05 - .1
Pr_a:pr_a	B 1643	R	252	114	124	30	520	15.794	< .01
			Chi-square based on a 27:21:9:7 ratio						
Re_2:re_2	B 1643	C	248	118	92	62	520	25.296	< .01

Table 35. Non-zoned vs zoned leaf (Z z) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

Z:z in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
E:e	B 1629	C	136	95	16	24	271	18.430	<.01
L:l	B 1629	C	103	9	138	31	281	217.629	<.01

Blue vs white aleurone (Bl bl) in relation to other factor pairs. Table 36 presents data showing that Bl:bl is independent of Gs:gs and $Re_2:re_2$.

Factor pairs not classified

Long vs short glume hairs (Gh gh) in relation to other factor pairs. Two factor pairs, V:v and $Re_2:re_2$, were found to be inherited independent of Gh:gh, according to table 37.

Non-glossy vs glossy sheath and spike (Gs gs) in relation to other factor pairs. Seven of nine factor pairs in table 38 may be seen to segregate readily in relation to Gs:gs. These are: V^t:V, B:b, N:n, K^e:k, $K^e:k_1$, $Pr_a:pr_a$, and $Re_2:re_2$ of Cross B 1642. The other two pairs of factors, Bl:bl and $Re_2:re_2$ of Cross B 1643, show low probability values. However, both characters are in the less reliable phase, that of repulsion. In addition, their percent of recombination is not significant enough to suggest linkage.

Purple vs white auricle (Pr_a pr_a) in relation to other factor pairs. Three factor pairs were found to have no linkage with the color of auricles. Table 39 lists them as: B:b, $K^e:k_1$, and Gs:gs. Since auricle color was found to be closely linked with $Re_2:re_2$, it is doubtful that the low probability value found for $K^e:k_1$ carries much weight, especially when it is in the repulsion phase.

Table 36. Blue vs white aleurone (Bl bl) in relation to other factor pairs.

Bl:bl in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square based on a 9:3:3:1 ratio						
Gs:gs	B 1642	R	385	142	152	52	731	4.345	.2 - .3
			Chi-square based on a 27:21:9:7 ratio						
Re_2:re_2	B 1642	R	306	221	99	105	731	9.345	.025 - .05

Table 37. Long vs short glume hairs (Gh gh) in relation to other factor pairs.

Gh:gh in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square based on a 9:3:3:1 ratio						
V:v	B 1620	R	637	201	180	47	1065	9.980	.01 - .025
			Chi-square based on a 27:21:9:7 ratio						
Re_2:re_2	B 1620	R	471	367	140	87	1065	10.028	.01 - .025

Table 38. Non-glossy vs glossy sheath and spike (Gs gs) in relation to other factor pairs.

Gs:gs in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
			Chi-square based on a 9:3:3:1 ratio						
V^t:V	B 1643	R	298	86	101	35	520	1.777	.6 - .7
B:b	B 1643	R	287	97	105	31	520	.752	.8 - .9
N:n	B 1643	R	198	74	74	21	367	.817	.8 - .9
K^e:k	B 1642	R	409	132	133	57	731	4.871	.1 - .2
$K^e:k_1$	B 1643	R	272	112	94	42	520	6.496	.05 - .1
Bl:bl	B 1642	R	385	152	142	52	731	12.184	< .01
$Pr_a:pr_a$	B 1643	C	281	103	95	41	520	3.049	.3 - .4
			Chi-square based on a 27:21:9:7 ratio						
$Re_2:re_2$	B 1642	R	298	243	107	83	731	1.727	.6 - .7
$Re_2:re_2$	B 1643	R	251	133	89	47	520	18.015	< .01

Table 39. Purple vs white auricle (Pr_a pr_a) in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

$Pr_a:pr_a$ in relation to:	Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P
B:b	B 1643	R	277	94	115	29	520	1.535	.6 - .7
$K^e:k_1$	B 1643	R	252	124	114	30	520	15.794	< .01
Gs:gs	B 1643	C	281	95	103	41	520	3.049	.3 - .4

Factor Pairs Suggesting Linkage

Linkage group I

Purple vs white lemma and pericarp (Re_2 re_2) in relation to other factor pairs. Table 40 summarizes five suggested linkages for this factor pair. The associations of Re_2:re_2 of this study with L:l, V:v, V^t:V, and E:e are in accord with previous reports. One new linkage was found to exist between Re_2:re_2 and Lr:lr. Their recombination value is 31.3 $\pm$ 8.5 percent. A note of caution, however, is in order. When the many-noded dwarf cross, B 1640, was being classified, the author observed that the prominent reduced lateral characteristic had not been listed for the parents. It was known from Leonard's (1942) studies that Lr:lr was associated with linkage group I. If the normal vs reduced lateral was appearing in the repulsion phase, the recombination value would be greater than 60 percent. If, on the other hand, the characters appeared in the coupling phase then linkage may be presumably established.

Normal vs long-awned glume (E e) in relation to lax vs dense spike (L l). The observed percent recombination in table 40 is overly high, compared with results from other workers. The spikes of Cross B 1629 were difficult to classify for outer glume appendages (awns or hoods) and for spike density. Consequently, the values for each demonstrated character recessive may be considered unreliable, and will not be listed in the summary.

Linkage group IV

Hoods vs long awns (K k_1) in relation to other factor pairs. According to table 40, a recombination of 18.8 $\pm$ 4.1 percent was

Table 40. Factor pairs suggesting linkage. Chi-square, P values, and recombination percentages are calculated for the indicated ratios.

Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P	Percent Recomb.
$(Re_2:re_2)$ in relation to (L:l) - (9:3:3:1 ratio):									
B 1619	C	244	106	74	50	477	9.299	.025 - .05	43.1 ± 3.7
$(Re_2:re_2)$ in relation to $(V^t:V)$ - (27:21:9:7 ratio):									
B 1643	C	306	34	93	87	520	164.958	<.01	14.6 ± 2.5
$(Re_2:re_2)$ in relation to (V:v) - (27:21:9:7 ratio):									
B 1620	C	572	39	245	209	1065	443.746	<.01	11.0 ± 1.5
$(Re_2:re_2)$ in relation to (E:e) - (45:15:3:1 ratio):									
B 1619	R	421	84	179	6	690	94.969	<.01	31.3 ± 8.5
$(Re_2:re_2)$ in relation to (Lr:lr) - (27:21:9:7 ratio):									
B 1640	C	173	22	84	43	322	28.020	<.01	23.6 ± 3.9
(E:e) in relation to (L:l) - (27:21:9:7 ratio):									
B 1629	C	90	12	141	28	271	53.510	<.01	42.0 ± 5.9
$(K:k_1)$ in relation to (E:e) - (27:21:9:7 ratio):									
B 1629	R	82	110	70	8	271	56.623	<.01	<1.00
$(K:k_1)$ in relation to (Tr:tr) - (9:3:3:1 ratio):									
B 1632	C	76	21	12	16	125	19.943	<.01	29.7 ± 5.0
$(K:k_1)$ in relation to (Z:z) - (9:3:3:1 ratio):									
B 1629	R	307	77	155	3	542	62.257	<.01	18.8 ± 4.1
$(K^e:k)$ in relation to (Bl:bl) - (9:3:3:1 ratio):									
B 1642	C	452	90	75	114	731	186.890	<.01	24.9 ± 1.9

observed for $K:k_1$ in relation to Z:z. This is within the range of previously reported values.

Associations of $K:k_1$ in relation to Tr:tr and E:e were observed. in Cross B 1629. The literature revealed no close relationships, as are indicated in table 40. The values recorded for Tr:tr are believed to be accurate. On the other hand, those for E:e are not reliable because all heterozygotes, recognized when only a portion of the spike is glume-awned or -hooded, were included with the homozygous recessive totals. This latter recombination percentage will not be included in the summary.

Elevated hoods vs awns (K^e k) in relation to blue vs white aleurone (Bl bl). The recombination percent of 24.9 ± 1.9 between these two factor pairs is in general agreement with the results of other workers.

Factor pairs not classified

Long vs short glume hairs (Gh gh) in relation to hulled vs hull-less (N n). Table 41 data indicate that these two factor pairs may be in the same linkage group. A recombination of 37.9 ± 2.0 was observed.

Purple vs white auricle (Pr_a pr_a) in relation to other factor pairs. Auricle color, according to table 41, may have an association with two linkage groups. It is found to be rather tightly linked with $Re_2:re_2$, loosely with $V^t:V$, and there is a suggestion of linkage with N:n. An examination of the data, however, indicates that the high chi-square value for $Pr_a:pr_a$ in relation to N:n is actually due to chance alone, and not because the two factor pairs are linked.

Normal vs many-noded dwarf (Mnd mnd) in relation to purple vs white lemma and pericarp (Re_2 re_2). Data in table 41 indicate that the factor for many-noded dwarf is located in linkage group I. A recombination value of 12.0 ± 2.9 exists between the two factor pairs.

In classifying the dwarfed plants for lemma color, the author found that he could use only 100 out of 162 dwarfs because 56 plants had failed to develop spikes in any noticeable degree of development and six plants had spikes too green to classify.

Table 41. Factor pairs suggesting linkage. Chi-square, P values, and recombination percentages are calculated for the indicated ratios.

Cross No.	Phase	XY	Xy	xY	xy	Total	X^2	P	Percent Recomb.
(Gh:gh) in relation to (N:n) - (9:3:3:1 ratio):									
B 1620	C	647	190	133	95	1065	38.730	<.01	37.9 ± 2.0
(Pr_a:pr_a) in relation to V^t:V) - (9:3:3:1 ratio):									
B 1643	R	278	98	121	23	520	9.162	.025 - .05	41.3 ± 3.7
(Pr_a:pr_a) in relation to (Re_2:re_2) - (27:21:9:7 ratio):									
B 1643	R	223	153	117	27	520	52.943	<.01	4.2 ± 0.5
(Pr_a:pr_a) in relation to (N:n) - (9:3:3:1 ratio):									
B 1643	R	183	83	89	12	367	16.728	<.01	32.1 ± 3.9
(Mnd:mnd) in relation to (Re_2:re_2) - (27:21:9:7 ratio):									
B 1640	C	147	175	7	93	422	112.111	<.01	12.0 ± 2.9

SUMMARY

Seven crosses, involving from two to eleven families each, were studied in the F_2 generation for independent inheritance and linkage of factor pairs.

Simple Mendelian inheritance was observed for: Tr:tr, V^t:V, V:v, L:l, Lr:lr, B:b, N:n, K:k_1, K^e:k, K^e:k_1, k_1:k_2, Z:z, Bl:bl, Gh:gh, Gs:gs, Pr_a:pr_a, and Mnd:mnd.

A mono- and dihybrid inheritance is suggested for the following factor pairs:

Re_2:re_2 (One 3:1 and four 9:7 out of five crosses)

E:e (One 3:1 and one 15:1 out of two crosses)

Factor pairs showing independent inheritance were:

Tr:tr in relation to E:e.

Re_2:re_2 in relation to B:b, K^e:k, and Bl:bl.

E:e in relation to L:l and N:n.

B:b in relation to V^t:V, Re_2:re_2, and N:n.

N:n in relation to V^t:V, V:v, Re_2:re_2, L:l, B:b, and K^e:k_1.

K:k_1 in relation to E:e and L:l.

K^e:k_1 in relation to V^t:V, Re_2:re_2, E:e, and B:b.

Z:z in relation to E:e and L:l.

Gh:gh in relation to V:v and Re_2:re_2.

Gs:gs in relation to V^t:V, Re_2:re_2, B:b, N:n, K^e:k, K^e:k_1, and Bl:bl.

Pr_a:pr_a in relation to B:b, N:n, K^e:k_1, and Gs:gs.

Factor pairs which suggested linkage, together with their phases and recombination percentages, were as follows:

Linkage group I

Re_2:re_2 in relation to L:l	Coupling	43.1 ± 3.6
Re_2:re_2 in relation to V^t:V	Coupling	14.6 ± 2.5
Re_2:re_2 in relation to V:v	Coupling	11.0 ± 1.5
Re_2:re_2 in relation to E:e	Repulsion	31.3 ± 8.5
Re_2:re_2 in relation to Lr:lr	Coupling	23.6 ± 3.9
E:e in relation to L:l	Coupling	42.0 ± 5.9

Linkage group IV

K:k_1 in relation to Tr:tr	Coupling	29.7 ± 5.0
K:k_1 in relation to Z:z	Repulsion	18.8 ± 4.1
K^e:k in relation to Bl:bl	Coupling	24.9 ± 1.9

Factor pairs not classified

Gh:gh in relation to N:n	Coupling	37.9 ± 2.0
Pr_a:pr_a in relation to V^t:V	Repulsion	41.3 ± 3.6
Pr_a:pr_a in relation to Re_2:re_2	Repulsion	4.2 ± 0.5
Mnd:mnd in relation to Re_2:re_2	Coupling	12.0 ± 2.9

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