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A Genetic Study of Linkage and Inheritance in Barley

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A GENETIC STUDY OF LINKAGE AND INHERITANCE IN BARLEY

by

Jerald Dean Oldham

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

of

MASTER OF SCIENCE

in

Crop Breeding

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Jerald Dean Oldham

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INTRODUCTION

With the exception of corn, barley has probably been used more than any other cultivated plant in genetic studies. It was one of several plants with which Erich von Tschermak-Seysenegg was working when he discovered Mendel's paper.

Barley is excellent material for use in genetic studies. It is adapted to many environments and has a large number of contrasting characters. Large populations can be grown on a small area of land in one season. It is a diploid with seven chromosome pairs. Each of these seven chromosome pairs can be identified cytologically.

There are seven linkage groups corresponding to the seven chromosome pairs. Previously a Roman numeral was assigned for each linkage group. However, in 1954, Kramer, Veyl, and Hanson (25) conducted an experiment involving translocation stocks which suggested linkage groups III and VII were actually located on the same chromosome. Since that time a new system using Arabic numerals to designate linkage was adopted by the Fourth Annual Barley Research Worker's Conference. This latter system will be followed throughout this study.

Many barley genes have been mapped and assigned to their appropriate chromosomes. Some of the genes involved in this study have not yet been assigned to a particular chromosome. Information regarding the inheritance and linkage relationships of the genes examined in this study should add useful information to our knowledge of barley genetics. It is also possible that some of these genes may be linked with economically valuable factors and might serve as marker genes.

REVIEW OF LITERATURE

The literature available in barley genetics is very extensive. A number of reviews have been published, Smith's (40) being the most extensive. The author will in no way attempt to review all of the literature in the field but will only refer to those articles which directly pertain to the material involved in this study.

Genes Investigated within Their Respective Linkage Groups

Linkage group 1

Normal (Br) versus brachytic (br) plants. The brachytic characteristic was first observed as a mutation in the variety Himalaya (31). It is characterized by short, broad leaves; short awns; and short distances between the internodes. It is recessive to normal plants.

A simple monofactorial inheritance has been postulated by Swenson (42), Gill (15), Rasmusson (31), Doney (8), and Heiner (17). However, in one cross Heiner (17) suggested that two or more genes appeared to be responsible or that modifying factors were present. Albrechtsen (1) obtained a linkage between normal versus brachytic growth type and hooded versus awned spikes, which is located in linkage group 4. This also suggests two genes may be involved.

Covered (N) versus naked (n) caryopses. Studies have been conducted on this gene pair by Biffen (4), Gaines (14), Kezer and Boyack (24), Tedin and Tedin (44), Neatby (30), Robertson (32, 33), and Buckley (5). These authors all agree that covered is dominant over naked caryopses and that the hereditary mechanism follows a 3:1 ratio.

Heavy pubescent (Pbg) versus sparse pubescent (pbg_1) versus nonpubescent (pbg) glumes. In the literature, this gene pair usually has the symbols (Gh, gh). But at the station from which these data were collected, the symbols (GH, gh) have been used to designate a variation of the length of normal glume awns (E). This author also used the symbols (Gh, gh) to designate glume-awn length. Therefore (Pbg, pbg), symbols which have also been used to designate degrees of pubescence previously in the literature, were chosen to represent this gene pair in this study.

Hor (18) reported that one factor pair was responsible for restricting pubescence on the glume. He also reported a linkage between pubescent versus nonpubescent glumes and covered versus naked caryopses. Smith (40) reported in his review that Dasananda concluded that there were three factor pairs acting to produce pubescence.

Linkage group 2

Normal (Tr) versus triple-awned (tr) lemmae. A simple Mendelian inheritance with normal being dominant over triple-awned lemmae has been reported by Immer and Henderson (21), Anderson (3), Heiner (17), Lebaron (26), Imam (19), and Doney (8). Doney (8) also reported that Kasha and Walker found a linkage of triple-awned lemmae with linkage group 3.

Normal (Li) versus liguleless (li) plants. Smith (40) reported that Lutkov obtained a liguleless mutant by x-ray treatments. It was recessive to the normal plant and a simple monofactorial ratio was obtained. Other workers--Heiner (17), Imam (19), and Doney (8) confirmed these findings by obtaining a ratio of three normal to one liguleless.

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike. Woodward (49), as a result of making intercrosses, proposed an allelic series consisting of the genes (v) six-rowed, (V^d) strong two-rowed, (V) weak two-rowed, and (V^t) deficiens spike. (V^t) seemed to be partially dominant followed by (V), (V^d), and (v) in descending order. An allelic series for fertility in the lateral florets consisting of (I^h), (I), and (i) was established with (I^h) being most dominant and (i) being the least dominant. This series is located in linkage group 4 and tends to modify the effect of the alleles involved in the number of rows of kernels in linkage group 2.

Several researchers have obtained results that support a simple Mendelian mode of inheritance of 3:1 or 1:2:1 ratios for the factors involved in this series of alleles. Some of the researchers who have obtained results which support this are Engledow (9); Fraser (12); Griffe (16); Tedin and Tedin (44); Swenson and Wells (43); Robertson, Wiebe, and Shands (37); Al-jibouri (2); Rasmusson (31); Woodward (50); Heiner (17); Imam (19); and Doney (8).

Long-awned (Lk_1) versus short-awned(Lk_2) versus awnletted (lk_3) spikes. The awn length factor seems to be highly affected by environmental conditions. Engledow (10) tried to put awn fluctuations into four classes--3/4 awn, 1/2 awn, 1/4 awn, and no awn. Difficulty was encountered in classification, and repetition of the sorting failed to give consistent results. He reported a linkage with the (V) series but he was unable to tell if the linkage was total or merely very high. Complete linkage was shown for the (V) series in relation to the (Lk) factors by Robertson, Wiebe, and Shands (37); and Robertson, Immer, Wiebe, and Stevens (36). Myler (28) reported four homozygous types of awned versus awnless plants in the F_4 generation--long awned, short-awned, awnletted, and awnless.

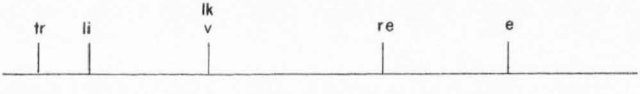
Litzenberger and Green (27), having crossed short-awned parents, obtained all long-awned spikes in the F_1 generation and a segregation into a ratio of 9 long-awned, 6 short-awned, and 1 awnletted spike in the F_2 generation. They also obtained a single factor difference between long and short awns with long awns apparently completely dominant over short awns. Long versus short-awned spikes showed a linkage with hooded versus awned spikes in linkage group 4 with a recombination value of 6.91 ± 3.48.

Normal (E) versus long-awned (e) glumes. A monofactorial mode of inheritance with normal being dominant over long-awned glumes has been reported by Robertson, Wiebe, Immer, and Stevens (36), Swenson and Wells (43), Gill (15), Anderson (3), Heiner (17), Lebaron (26), Imam (19), and Doney (8).

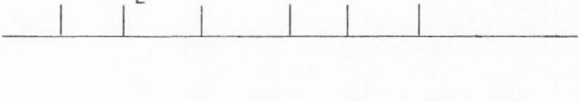
Lax (L) versus dense (l) spikes. Biffen (4) reported that lax spikes were dominant over dense spikes. He obtained a ratio of 3 lax to 1 dense spike in the F_2 generation. Other workers who obtained similar results were Fraser (12), Wheatley (47), Heiner (17), Imam (19), and Doney (8). Lebaron (26) obtained a monohybrid ratio but felt that other factors were involved in his study. Neatby (30) suggested that the density of the spike was governed by one main factor with modifying factors operating. Rasmusson (31) felt two or more genes were involved while Wexelsen (45, 46) suggested that as many as six factor pairs may have been involved. Smith (40) reported in his extensive review that factors influencing lax versus dense spikes have been placed in linkage groups 1, 2, and 4.

Purple (Re_2) versus white (re_2) lemmae and pericarp. Several workers have reported purple being dominant over white lemmae and pericarp. Biffen (4), Fraser (12), Buckley (5), Daane (7), and Doney (8) obtained ratios of 3 purple to 1 white when a purple parent was crossed with a white parent. Other workers--Woodward and Thieret (51), Anderson (3), and Imam (19)--obtained the same results as the above workers when crossing a purple parent with a white parent. However, in some cases when they crossed two white parents they obtained all purple F_1 plants and 9 purple to 7 white plants in the F_2 generation. This indicated two factors were involved in the Re_2 character. Woodward and Thieret (51) found that one gene for purple was in linkage group 2 and had a 12.8 percent recombination value in a linkage with the (V) series of alleles. The other gene was linked with the (B) factors in linkage group 5.

Maps of linkage group 2. Below is a map of linkage group 2 proposed by Robertson, Wiebe, and Shands (38) showing only those genes used in this thesis.



Below is a map of the genes used in this thesis in linkage group 2 as proposed by Woodward (50).



Linkage group 4

Hooded (K) versus awned (k) spikes. The origin of hooded barley traces back to a barley which was found in Nepal between 1830 and 1837. The lemmae of hooded barley terminate into trifurcated structures called hoods.

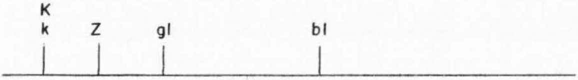
The hooded condition is dominant over the awned condition. Biffen (4), Gaines (14), Kezer and Boyack (24), Fraser (12), Robertson (32, 33), Buckley (5), Jenkins (23), Gill (15), Al-jibouri (2), Anderson (3), Heiner (17), and Lebaron (26) all reported a single factor inheritance. Wheatley reported that in some crosses he obtained a one factor difference while in others he obtained a two factor difference which segregated at a ratio of 9 hooded to 7 awned spikes. Woodward and Rasmussen (52) reported that two factor pairs were responsible for hooded versus awned spikes, and they obtained a ratio of 9 hooded, 3 long-awned, and 4 short-awned plants.

Non-glossy (Gl) versus glossy (gl) leaves. Immer and Henderson (21), Jenkins (23), Al-jibouri (2), Wheatley (47), Heiner (17), Imam (19), and Doney (8) reported that non-glossy leaves were dominant over glossy leaves. They also reported that this character was controlled by a single Mendelian factor pair. Heiner (17), Imam (19), and Doney (8) all had very low probability values which they attributed to seedling mortality or poor germination of glossy leaved plants. Lemmae on glossy leaved plants show a scalding appearance where chlorophyll has been destroyed.

Non-zoned (Z) versus zoned (z) leaves. Immer and Henderson (21), Jenkins (23), Gill (15), Wheatley (47), Anderson (3), Heiner (17), Lebaron (26), and Doney (8) reported that non-zoned leaves were dominant over zoned leaves and the plants segregated in a simple monofactorial manner. A low probability value was obtained by Wheatley (47), Anderson (3), Heiner (17), Lebaron (26), and Doney (8). They attributed the low probability values they obtained to high seedling mortality and reduction in vigor of the zoned plants.

Blue (Bl) versus white (bl) aleurone. Most researchers indicated that blue versus white aleurone was controlled by a single factor pair. Robertson, Demming and Koonce (34), Jenkins (22), Buckley (5), Wheatley (47), Heiner (17), and Lebaron (26) are some of the researchers that have reported ratios of this nature. Myler and Stanford (29) obtained a ratio of 3 blue to 1 white aleurone in most of their crosses. However, in one cross involving two white varieties they obtained a ratio of 9 blue to 7 white aleurone in the F_2 generation.

Map of linkage group 4. Below is a map of the genes used in this study in linkage group 4. This map was proposed by Robertson, Wiebe, and Shands (38).



Linkage group 5

Black (B) versus white (b) lemmae and pericarp. A monohybrid mode of inheritance for this character has been reported by Biffen (5), Griffe (16), Sigfusson (39), Robertson (32), Buckley (5), and Woodward and Thieret (51). Woodward and Thieret (51) reported that the black lemmae and pericarp factor was linked with one of the Re_2 factors. Woodward (48) postulated a series of alleles which consisted of black (BB), grey

(B^gB^g) and white (bb). He also noted other degrees of pigmentation but indicated it was difficult to determine segregating ratios.

Linkage group 6

White (O) versus orange (o) lemmae and pericarp. White appears to be dominant over orange lemmae and pericarp. A single monofactorial mode of inheritance has been reported by Buckley (5), Myler and Stanford (29), and Heiner (17).

Linkage group 7

Rough (R) versus smooth (r) awns. Several researchers--Daane (7), Byington (6), Jenkins (23), Gill (15), Anderson (3), and Doney (8)--have reported a monofactorial mode of inheritance for rough versus smooth awns with rough awns being dominant over smooth. Imam (19), Al-jibouri (2), and Heiner (17) reported single factor ratios in some crosses and two or more factors in other crosses. Griffe (16) also indicated that two factors were involved. He felt that rough versus smooth awns was controlled by a single factor as was intermediate smooth versus smooth awns. Robertson, Demming and Koonce (34) obtained results that were best explained by a two factor pair. Frey (13) reported a linkage between the rough awn versus smooth awn factor and the major factors determining heading.

Unassigned genes

Non-glossy (Gs) versus glossy (gs) stems and spikes. Immer and Henderson (21), Gill (15), Wheatley (47), Anderson (3), Heiner (17), Lebaron (26), Imam (19), and Doney reported that non-glossy stems and spikes were dominant over glossy stems and spikes. They also reported that this character was controlled by a single factor pair.

Normal (Gp) versus grandpa (gp). Immer and Henderson (21), Anderson (3), Heiner (17), Imam (19), and Doney (8) all reported that normal plants were dominant over grandpa plants and that this character was monofactorial. Heiner (17), Imam (19), and Doney (8) indicated that high seedling mortality, late maturity, and poor seed set may have been responsible for the low probability values obtained.

Long (Gh) versus short (gh) outer-glume hairs. Long outer-glume hairs are dominant over short outer-glume hairs. Several researchers--Gill (15), Anderson (3), Heiner (17), Al-jibouri (2), and Imam (19) have reported a single factor difference. Doney (8) obtained a single factor difference in one cross but indicated a two factor difference in another cross. Rasmusson (31) indicated that two or more genes were involved. Several of these researchers commented that considerable difficulty was encountered in their classification.

Normal (Rb) versus ribbon grass (rb) leaves. Gill (15), Wheatley (47), Anderson (3), Heiner (17), and Doney (8) reported that normal was dominant over ribbon grass leaves and the character had a single factor mode of inheritance. Wheatley (47) suggested that seedling mortality of the ribbon grass plants was responsible for the poor P values obtained. Many degrees of ribbon grass have been found. Also, it is susceptible to environmental effects.

Proposed Linkages

Linkage group 2

(V v) in relation to (Tr tr).

Recombination Value	Phase	Authority
38.19 ± 2.86	coupling	Imam (19)
39.0 ± 3.0	repulsion	Immer and Henderson (21)
30.5 ± 2.9	coupling	Woodward (50)
41.0 ± 3.4	coupling	Woodward (50)

(V v) in relation to (li li).

Recombination Value	Phase	Authority
36.0 ± 2.32	repulsion	Doney (8)
44.19 ± 4.05	coupling	Imam (19)
43.13 ± 2.73	repulsion	Imam (19)
33.3 ± 2.9	coupling	Woodward (50)
39.5 ± 5.4	repulsion	Woodward (50)

(V v) in relation to (E e).

Recombination value	Phase	Authority
23.5 ± 3.92	repulsion	Doney (8)
25.79 ± 3.0	coupling	Imam (19)
30.0 ± 4.7	repulsion	Heiner (17)
31.0 ± 2.4	coupling	Heiner (17)
39.5 ± 5.29		Gill (15)
28.0 ± 1.2	coupling	Immer and Henderson (21)
36.0 ±10.6	repulsion	Immer and Henderson (21)
48.0 ± 4.7	repulsion	Anderson (3)
21.5 ± 1.7	coupling	Anderson (3)
26.5 ± 2.0	coupling	Woodward (50)
27.0 ± 5.7	repulsion	Woodward (50)

(V v) in relation to (L l).

Recombination value	Phase	Authority
25.24 ± 2.97	coupling	Imam (19)
37.65 ± 3.00	coupling	Imam (19)
35.0 ± 6.50		Albrechtsen (1)
33.5 ± 3.5	coupling	Heiner (17)
41.3 ± 2.6	coupling	Woodward (50)

(V v) in relation to (Re_2 re_2).

Recombination Value	Phase	Authority
12.5 ± 2.4		Al-jibouri (2)
12.0 ± 3.0		Al-jibouri (2)
12.5 ± 3.3		Gill (15)
12.0 ± 1.3		Anderson (3)
*33.0 ± 4.3		Anderson (3)
17.1 ± .7	coupling	Woodward (50)
*14.0 ± 1.3	coupling	Woodward (50)
10.0 ± 4.8	repulsion	Woodward (50)
*22.1 ±16.3	repulsion	Woodward (50)

*Two genes for (Re_2 re_2)

(Tr tr) in relation to (Li li).

Recombination Value	Phase	Authority
46.01 ± 2.65	repulsion	Imam (19)

(Tr tr) in relation to (E e).

Recombination Value	Phase	Authority
40.88 ± 3.72	coupling	Imam (19)
42.0 ± 3.7	repulsion	Immer and Henderson (21)
41.0 ± 5.2	repulsion	Woodward (50)

(Re_2 re_2) in relation to (Li li).

Recombination Value	Phase	Authority
40.0 ± 4.8	coupling	Woodward (50)

(Re_2 re_2) in relation to (E e).

Recombination Value	Phase	Authority
25.0 ± 13.7		Gill (15)
39.5 ± 2.7	coupling	Woodward (50)
41.5 ± 6.2	repulsion	Woodward (50)

(L l) in relation to (Li li).

Recombination Value	Phase	Authority
26.6 ± 6.0	repulsion	Woodward (50)
27.5 ± 3.0	coupling	Woodward (50)

(E e) in relation to (L l).

Recombination Value	Phase	Authority
18.13 ± 2.5	coupling	Imam (19)
42.0 ± 5.9	coupling	Lebaron (26)
23.0 ± 2.0	coupling	Heiner (17)
21.2 ± 1.5	coupling	Woodward (50)
31.5 ± 4.0	repulsion	Woodward (50)

Linkage group 4

(K k) in relation to (Z z).

Recombination Value	Phase	Authority
27.0 ± 4.6		Wheatley (47)
35.5 ± 3.8		Wheatley (47)
5.0 ± .8	coupling	Immer and Henderson (21)
18.2 ± 2.54		Albrechtsen (1)
4.5 ± 2.4	coupling	Heiner (17)
17.5 ± 7.4	repulsion	Heiner (17)
38.0 ± 9.7		Gill (15)
14.0 ± 1.8	repulsion	Woodward (50)
12.8 ± 1.8	coupling	Woodward (50)

(K k) in relation to (Bl bl).

Recombination Value	Phase	Authority
43.4 - 3.35	repulsion	Imam (19)
26.3 ± 2.3		Isom (22)
23.3 ± 2.1		Isom (22)
24.72 ± 1.73		Myler and Stanford (29)
37.0 ± 3.58		Albrechtsen (1)
30.4 ± 4.07		Gill (15)
28.5 ± 0.9	coupling	Woodward (50)
31.5 ± 7.1	repulsion	Woodward (50)

(K k) in relation to (Gl gl).

Recombination Value	Phase	Authority
25.5 ± 1.9		Wheatley (47)
19.3 ± 1.4		Isom (22)
3.0 ± 1.3	coupling	Immer and Henderson (21)
30.5 ± 3.0		Al-jibouri (2)
26.3 ± 2.32		Albrechtsen (1)
18.5 ± 3.42		Albrechtsen (1)
16.0 ± 3.5	coupling	Heiner (17)
28.0 ± 8.6	repulsion	Heiner (17)
22.2 ± 0.8	coupling	Woodward (50)
22.5 ± 1.9	coupling	Woodward (50)
16.5 ± 2.1	repulsion	Woodward (50)

(Z z) in relation to (Bl bl).

Recombination Value	Phase	Authority
38.0 ± 1.4	coupling	Woodward (50)
38.5 ± 2.5	repulsion	Woodward (50)

(Z z) in relation to (Gl gl).

Recombination Value	Phase	Authority
8.5 ± 1.16	coupling	Doney (8)
12.5 ± 1.55	coupling	Doney (8)
7.0 ± 3.3	coupling	Immer and Henderson (21)
3.0 ± 1.3	repulsion	Immer and Henderson (21)
30.0 ± 3.98		Albrechtsen (1)
8.5 ± 1.05		Albrechtsen (1)
9.3 ± 0.5	coupling	Woodward (50)
14.0 ± 5.3	repulsion	Woodward (50)

(Bl bl) in relation to (Gl gl).

Recombination Value	Phase	Authority
25.0 ± 4.64	repulsion	Imam (19)
32.5 ± 2.4		Isom (22)
30.0 ± 2.7	coupling	Woodward (50)
25.0 ± 3.8	repulsion	Woodward (50)

MATERIALS AND METHODS

The crosses used in this study were selected from a number of crosses furnished by Dr. Rollo Woodward. Two crosses were made in 1958, three in 1959, and four were made in 1960. F_o seed from the crosses made in 1958 and 1959 was space planted by hand in rows that were two feet apart. The kernels were spaced about 12 inches apart within the rows to obtain large F_1 plants. F_o seed from the crosses made in 1960 was sent to Arizona and the plants were grown there during the winter of 1960-1961. The F_1 plants were sent back to Logan in the spring of 1961. Seed from all F_1 plants was space planted in 30 foot rows one foot apart. The seed of F_2 plants from crosses made in 1958 was planted in F_3 rows five feet long and one foot apart. Plants from two crosses that were made in 1960 were also planted in F_3 rows to facilitate re-classification of certain characters.

Plants studied in the F_2 generation which had characters that were difficult or impossible to identify at maturity were tied with assigned colored strings at the time the characters were readily distinguishable. These characters included glossy stems and spikes, glossy leaves, ribbon grass, grandpa, zoned leaves, and purple lemmae and pericarp. At maturity each family of plants was pulled and tied for later studies. When the characters were studied in the F_3 generation they were classified according to the segregation of the genes with which they were associated within the rows.

After the data were collected, individual contrasting characters were analyzed within each family. Families were then grouped together and characters were analyzed as a complete cross. The data from all crosses were then pooled and analyzed as a group. When combining two factors in a test for independence, the data were analyzed on the cross level. The product method, as proposed by Fischer and Balmukend (11) and described by Immer (20), was used in testing for linkages or independence. The probability values for chi-squares were taken from Snedecor (41).

Characters Used in this Study and their Gene Symbols

Symbols, except for (Gh, gh) and (Pbg, pbg_1, pbg), are in accordance with those proposed by Robertson, Wiebe, and Shands (37, 38).

Linkage group 1

Normal versus brachytic plants	Br, br
Covered versus naked caryopses	N, n
Heavy pubescent versus sparse pubescent versus non-pubescent glumes	Pbg, pbg_1, pbg

Linkage group 2

Normal versus triple-awned lemmae	Tr, tr
Deficiens versus two-rowed versus six-rowed spikes	V^t, V, v
Long-awned versus short-awned versus awnletted spikes	Lk_1, Lk_2, Lk_3
Normal versus long-awned glumes	E, e
Lax versus dense spikes	L, l
Purple versus white lemmae and pericarp	Re_2, re_2
Normal versus liguleless plants	Li, li

Linkage group 4

Hooded versus awned spikes	K, k
Non-glossy versus glossy leaves	Gl, gl
Normal versus zoned leaves	Z, z
Blue versus non-blue aleurone	Bl, bl

Linkage group 5

Black versus white lemmae and pericarp	B, b

Linkage group 6

White versus orange lemmae and pericarp	O, o

Linkage group 7

Rough versus smooth awns	R, r

Unassigned characters

Non-glossy versus glossy stems and spikes	Gs, gs
Normal versus grandpa plants	Gp, gp
Long versus short outer-glume hairs	Gh, gh
Normal versus ribbon grass plants	Rb, rb

Crosses, Parents and Segregating Factors Involved in this Study

Cross	Parents	Factors involved in this study
Crosses made in 1958		
B 1791[1]	T918	tr N rb L Gs Gl Br bl e r_2 V Lk_1
	T136	Tr n Rb l gs gl br Bl E r_1 v Lk_3

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[1] In several instances data from cross B 1791 fit the hypothesized ratios rather poorly and showed linkages which are inconsistent with those in the literature. The author presents the material from this cross with some reservation.

B 1764	T778	Gs Gl N Br k E v l Gh R Tr lk
	B1286-1	Unknown

Crosses made in 1959

B 1836	T841	gs Gp k V^t b o
	T525	Gs gp K v B O
B 1852	T118	v gp n E B R Tr
	T918	V Gp N e b r tr
B 1857	T841	gs b k V^t o
	T538a	Gs B K v O

Crosses made in 1960

B 1865	T105	Gs Gl rb N v r
	T137	gs gl Rb n V R
B 1868	T945	Gs Tr e B k N Z
	T838	gs tr b K n z
B 1869	T945	l V^t e li B R Rb
	T225	L v E Li b r rb
B 1871	T945	Gs li e B l V^t R
	T340	gs Li E b L v r

EXPERIMENTAL RESULTS

Inheritance of Individual Genes

Linkage group 1

Normal (Br) versus brachytic (br) plants. This character was studied in the F_3 generation. There were not enough segregating rows to obtain the type of chi-square value that would be in keeping with a suggested monofactorial ratio. This is shown in Table 1. However, when the segregating rows were grouped with the homozygous normal rows of plants a reasonable chi-square was obtained for a 3:1 ratio. These results are shown in Table 2 and indicate that a simple monofactorial inheritance is operating.

Table 1. Segregation of normal (Br) versus brachytic (br) plants in the F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross	Br	S	br	Total	X^2	P
B 1791	147	193	106	446	15.94	<.01

Table 2. Segregation of normal (Br) versus brachytic (br) plants in the F_3 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	Br	br	Total	X^2	P
B 1791	340	106	446	.33	.50 - .75

Covered (N) versus naked (n) caryopses. Table 3 suggests that the hereditary mechanism for covered versus naked caryopses is controlled by a simple Mendelian pattern with covered being dominant over naked caryopses. However a low probability value was obtained for the cross B 1791.

Table 3. Segregation of covered (N) versus naked (n) caryopses in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	N	S	n	Total	X^2	P
B 1868 (F_2)	553		162	715	1.6	.10 - .25
B 1852 (F_2)	366		145	511	3.01	.05 - .10
B 1865 (F_2)	370		146	516	2.99	.05 - .10
B 1764 (F_3)	163	296	148	607	1.08	.50 - .75
B 1791 (F_3)	135	188	117	440	10.78	$<.01$
Sum of 5 chi-squares					19.46	$<.01$
Total	2071[a]		718	2789	.83	.25 - .50
Interaction					18.63	$<.01$

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Heavy pubescent (Pbg) versus sparse pubescent (pbg_1) versus non-pubescent (pbg) glumes. This character was present in two crosses involved in this study. In one cross the author was unable to make a proper classification. However, in cross B 1852 the author feels a fair classification was obtained. As indicated by the data in Table 4 two families had high chi-square values as did the total. This character was reclassified three times, and the author feels that three gene pairs were involved. Plants that expressed the (e) factor were always pulled out when working with the other factors because when (e) was present pubescence was always absent.

Table 4. Segregation of heavy pubescent (Pbg) versus sparse pubescent (pbg_1) glumes in the F_2 generation according to families within the cross. Chi-square and P values are based on a 54:10 ratio.

Family	Pbg	pbg_1	Total	X^2	P
B 1852-1	55	22	77	9.87	<.01
B 1852-2	81	29	110	10.02	<.01
B 1852-3	68	15	83	.37	.50 - .75
B 1852-4	56	11	67	.12	.50 - .75
B 1852-5	66	8	74	1.59	.10 - .25
Sum of 5 chi-squares				21.97	<.01
Total	326	85	411	8.17	<.01
Interaction				13.80	<.01

With three factor pairs a ratio of 27:9:9:9:3:3:3:1 should be obtained. In this classification the author grouped the 27:9:9:9 ratio into one group and the 3:3:3:1 ratio into the other group giving a ratio of 54:10. There were many visible variations of pubescence noted. Generally there were three major types: (a) hairs covering the glume, (b) hairs in three rows down the length of the glume, and (c) hairs in one row down the center of the glume. Varying degrees of density and length of hairs were noted in each of these groups. Plants that were classified as (pbg_1) all had very short hairs on the glumes. Most of these were type 3 with one row of hair down the center of the glume. The other types were present however.

Although this classification is not completely satisfactory, considerable information was obtained. Further studies should be conducted with this character. In a properly planned experiment, this author feels that a 27:9:9:9:3:3:3:1 ratio can be obtained if several crosses and intercrosses were properly planned and made.

Linkage group 2

Normal (Tr) versus triple-awned (tr) lemmae. The data for normal versus triple-awned lemmae are presented in Table 5. Very low probability values were obtained for a single gene pair inheritance. This author believes the reason that the low probability values were obtained is that some plants which were carrying the genes for triple-awned lemmae did not express the character. In some crosses only one or two triple-awned lemmae are expressed on a particular spike while other spikes on

Table 5. Segregation of normal (Tr) versus triple-awned (tr) lemmae in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Tr	S	tr	Total	X^2	P
B 1791 (F_3)	151	127	37	315	93.68	$<.01$
B 1852 (F_2)	404		110	514	3.47	.05 - .10
Sum of 2 chi-squares					97.15	$<.01$
Total	682[a]		147	829	23.18	$<.01$
Interaction					73.97	$<.01$

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

the same plant do not even express the character. It is known that there is variation in homozygous genotypes.

Normal (Li) versus liguleless (li) plants. A single gene difference for normal versus liguleless plants is suggested by the data found in Table 6. A few families--B 1764-4, B 1764-5a and B 1869-1--are causing high chi-square values.

Table 6. Segregation of normal (Li) versus liguleless (li) plants in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Li	S	li	Total	X^2	P
B 1764 (F_3)	171	282	164	617	4.72	.05 - .10
B 1871 (F_2)	481		192	673	4.59	.02 - .05
B 1868 (F_2)	550		186	736	.03	.75 - .90
B 1869 (F_2)	553		211	764	2.79	.05 - .10
Sum of 4 chi-squares					12.13	.02 - .05
Total	2037[a]		753	2790	5.94	.01 - .02
Interaction					6.19	.10 - .25

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Deficiens (V^t) versus two-rowed (v) spikes. Data in Table 7 indicate that deficiens is dominant over two-rowed spikes, and the character is controlled by a single factor pair.

Two-rowed (V) versus six-rowed (v) spikes. Data from Table 8 indicate that two-rowed is dominant over six-rowed spikes and the character is controlled by a single factor pair.

Table 7. Segregation of deficiens (V^t) versus six-rowed (v) spikes in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	V^t	v	Total	X^2	P
B 1871	525	147	672	3.49	.05 - .10
B 1836	279	107	386	1.61	.10 - .25
B 1869	586	177	763	1.37	.10 - .25
B 1857	288	89	377	.35	.50 - .75
Sum of 4 chi-squares				6.82	.10 - .25
Total	1678	520	2198	2.08	.10 - .25
Interaction				4.74	.10 - .25

Table 8. Segregation of two-rowed (V) versus six-rowed (v) spikes in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	V	S	v	Total	X^2	P
B 1764 (F_3)	153	312	145	610	.49	.75 - .90
B 1791 (F_3)	111	211	120	442	1.37	.50 - .75
B 1852 (F_2)	389		125	514	.12	.50 - .75
B 1865 (F_2)	415		107	522	5.56	.01 - .02
Sum of 4 chi-squares					7.54	.25 - .50
Total	1591[a]		497	2088	1.58	.10 - .25
Interaction					5.96	.25 - .50

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Long-awned (Lk_1) versus short-awned (Lk_2) versus awnletted (Lk_3) spikes. Four homozygous types of awned condition were observed in F_3 studies--long-awned (Lk_1), short-awned (Lk_2), awnletted (Lk_3), and awnless (Lk_4) in descending order with long-awned being dominant. It has been suggested by several workers that this factor is highly affected by environmental conditions.

Only four rows of completely awnless spiked plants were observed so these rows were grouped in with the awnletted spike group in calculating a goodness of fit. Table 9 suggests that two factor pairs are involved.

Table 9. Segregation of long-awned (Lk_1) versus short-awned (Lk_2) versus awnletted (Lk_3) spikes in the F_3 generation. Chi-square and P values are based on a 1:2:1:12 ratio.

Cross	Lk_1	Lk_2	Lk_3	S	Total	X^2	P
B 1791	39	43	26	335	443	7.11	.05 - .10

Long-awned (Lk_1) versus short-awned (Lk_2) spikes. Although the attempted classification in F_2 fails to provide supporting evidence, this character is probably controlled by a single gene pair. In this classification the assigning of awn lengths was merely relative, and it would be impossible to be sure of any classification unless plants were studied in the F_3 generation. Data are presented in Table 10.

Normal (E) versus long-awned (e) glumes. Table 11 suggests that a simple Mendelian mode of inheritance is present with normal being dominant over long-awned glumes. The families in cross B 1791 had high chi-square values which do not support the expected 1:2:1 ratio. Although the author cannot explain these results he does not feel that more than one factor pair is involved.

Table 10. Segregation of long-awned (Lk_1) versus short-awned (Lk_2) spikes in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	Lk_1	Lk_2	Total	X^2	P
B 1865	418	102	520	8.04	$< .01$

Table 11. Segregation of normal (E) versus long-awned (e) glumes in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	E	S	e	Total	X^2	P
B 1791 (F_3)	163	186	95	444	32.62	$< .01$
B 1871 (F_2)	516		156	672	1.15	.25 - .50
B 1868 (F_2)	528		206	734	3.77	.05 - .10
B 1852 (F_2)	411		103	514	6.61	.01 - .02
B 1869 (F_2)	586		177	763	1.36	.10 - .25
B 1865 (F_2)	409		113	522	3.05	.05 - .10
Sum of 6 chi-squares					48.56	$< .01$
Total	2799[a]		850	3649	5.62	.01 - .02
Interaction					42.94	$< .01$

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Lax (L) versus dense (l) spikes. Lax seems to be dominant over dense spikes and the character is controlled by a single factor pair in crosses involved in this study. Data are presented in Table 12.

Purple (Re_2) versus white (re_2) lemmae and pericarp. Table 13 indicates that two factor pairs were involved in the inheritance of

Table 12. Segregation of lax (L) versus dense (l) spikes in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	L	S	l	Total	X^2	P
B 1764 (F_3)	162	294	151	607	.92	.50 - .75
B 1791 (F_3)	87	217	80	384	6.77	.02 - .05
B 1871 (F_2)	508		164	672	.12	.50 - .75
B 1869 (F_2)	560		202	762	.97	.25 - .50
Sum of 4 chi-squares					8.78	.10 - .25
Total	1828[a]		597	2425	.18	.50 - .75
Interaction					8.60	.10 - .25

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Table 13. Segregation of purple (Re_2) versus white (re_2) lemmae and pericarp in the F_2 generation. Chi-square and P values are based on a 9:7 ratio.

Cross	Re_2	re_2	Total	X^2	P
B 1871	360	308	668	1.55	.10 - .25
B 1836	192	190	382	5.30	.01 - .02
Sum of 2 chi-squares				6.85	.02 - .05
Total	552	498	1050	5.88	.01 - .02
Interaction				.97	.25 - .50

purple versus white lemmae and pericarp. A 9:7 ratio was obtained with purple being dominant over white. A good classification was not obtained in the field so the kernels were reclassified in the laboratory after being treated with HCl to bring out the anthocyanin pigment.

Hooded (K) versus awned (k) spikes. The data presented in Table 14 indicate that hooded is dominant over awned spikes. A single monofactorial mode of inheritance seems to be involved in this character. Families in cross B 1868 and families 3, 4, and 6 in cross B 1764 have high chi-square values. In these particular families the zoned leaf gene is also present. The zoned leaf gene is highly lethal and is linked with hooded versus awned spikes. It is quite evident that this linked lethal gene is the cause of the high chi-square value.

Table 14. Segregation of hooded (K) versus awned (k) spikes in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	K	S	k	Total	X^2	P
B 1764 (F_3)	67	216	117	400	15.06	< .01
B 1868 (F_2)	511		223	734	11.51	< .01
B 1836 (F_2)	271		115	386	4.88	.02 - .05
B 1857 (F_2)	279		98	377	.23	.50 - .75
Sum of 4 chi-squares					31.68	< .01
Total	1344[a]		553	1897	17.56	< .01
Interaction					14.12	< .01

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Non-glossy (Gl) versus glossy (gl) leaves. Table 15 indicates a very low P value based on a 3:1 ratio for this character. When the glossy leaved plants were growing in the field they seemed to be quite vigorous. When the author started this investigation he thought that two genes were involved in the inheritance of this character.

Table 15. Segregation of non-glossy (Gl) versus glossy (gl) leaves in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Gl	S	gl	Total	X^2	P
B 1764 (F_3)	119	107	15	241	93.18	< .01
B 1791 (F_3)	109	248	89	446	7.20	.02 - .05
B 1868 (F_2)	663		75	738	86.45	< .01
B 1868 (F_3)	420	112	51	583	686.46	< .01
B 1869 (F_2)	667		97	764	61.68	< .01
B 1869 (F_3)	403	140	53	596	578.61	< .01
B 1865 (F_2)	417		112	529	4.04	.02 - .05
Sum of 7 chi-squares					1517.62	< .01
Total	3505[a]		392	3897	463.64	< .01
Interaction					1118.41	< .01

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Data indicate a trend for a lethal characteristic. Two crosses, B 1868 and B 1869, had low P values in the F_2 generation and were planted in the F_3 generation to determine the reason for this low value. All of the plants were not planted because of lack of space. Plants were selected at random from all F_2 plants that had produced five or more kernels. In the F_2 generation 10.16 percent of the plants were homozygous glossy leaved. In the F_3 generation 8.75 percent of the rows were homozygous glossy leaved. These percentages indicate that some glossy leaved plants were being lost. Further studies should be centered around germination percentages, survival after emergence, and seed set to see where the glossy leaved plants are being lost.

Non-zoned (Z) versus zoned (z) leaves. It is reported in the literature that non-zoned leaves are dominant over zoned leaves, and this factor pair segregates in a simple Mendelian manner. A very high chi-square value for a single gene factor pair was obtained as is indicated by Table 16. The high chi-squares are probably due to high seedling mortality and reduction in vigor of the zoned leafed plants because of the lack of chlorophyll.

Table 16. Segregation of non-zoned (Z) versus zoned (z) leaves in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Z	S	z	Total	X^2	P
B 1764 (F_3)	102	131	1	234	91.08	$< .01$
B 1868 (F_2)	700		38	738	154.65	$< .01$
B 1868 (F_3)	390	169	24	583	560.88	$< .01$
Sum of 3 chi-squares					806.61	$< .01$
Total	1492[a]		63	1555	364.35	$< .01$
Interaction					442.26	$< .01$

[a] F_3 segregating rows were combined with homozygous dominant rows in the total.

Blue (Bl) versus non-blue (bl) aleurone. Table 17 indicates that the inheritance of this character is controlled by two gene pairs. This character was studied in the F_3 generation, and a ratio of 1 blue, 8 segregating, and 7 white was obtained. This ratio indicates that, although blue aleurone is dominant over white, dominant genes must be present at both loci to produce the blue aleurone character. These results are in accordance with those obtained by Myler and Stanford (29).

Table 17. Segregation of blue (Bl) versus non-blue (bl) aleurone in the F_3 generation. Chi-square and P values are based on a 1:8:7 ratio.

Cross	Bl	S	bl	Total	X^2	P
Total	8	112	84	204	3.18	.10 - .25

One unexplainable fact is that one parent in this cross expressed the blue aleurone characteristic while the other expressed the white. To obtain the 1:8:7 ratio obtained in this cross, both parents should express the white aleurone characteristic. Perhaps the blue aleurone parent was segregating for white aleurone.

Black (B) versus white (b) lemmae and pericarp. Table 18 suggests that black is dominant over white lemmae and pericarp and that a monohybrid mode of inheritance is present.

Linkage group 6

White (O) versus orange (o) lemmae and pericarp. Data presented in Table 19 indicates that white is dominant over orange lemmae and pericarp. This factor pair is controlled by a simple monofactorial mode of inheritance.

Table 18. Segregation of black (B) versus white (b) lemmae and pericarp in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	B	b	Total	X^2	P
B 1871	481	191	672	4.20	.02 - .05
B 1868	528	199	727	2.12	.10 - .25
B 1836	288	98	386	.04	.75 - .90
B 1852	382	132	514	.16	.50 - .75
B 1869	571	191	762	.01	$>$ .90
B 1857	268	109	377	3.19	.05 - .10
Sum of 6 chi-squares				9.72	.10 - .25
Total	2518	920	3438	5.73	.01 - .02
Interaction				3.99	.50 - .75

Table 19. Segregation of white (O) versus orange (o) lemmae and pericarp in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	O	o	Total	X^2	P
B 1836	307	78	385	4.49	.02 - .05
B 1857	287	90	377	.23	.50 - .75
Sum of 2 chi-squares				4.72	.05 - .10
Total	594	168	762	3.32	.05 - .10
Interaction				1.40	.10 - .25

Linkage group 7

Rough (R) versus smooth (r) awns. Data for this character are presented in Tables 20 and 21. A simple Mendelian ratio with rough being dominant over smooth awns was observed in five crosses while a two factor pair segregation was observed in one cross.

Table 20. Segregation of rough (R) versus smooth (r) awns with two factors involved in the F_3 generation. Chi-square and P values are based on a 4:10:2 ratio.

Cross	R	S	r	Total	X^2	P
B 1791	56	138	24	218	.43	.75 - .90

Table 21. Segregation of rough (R) versus smooth (r) awns with one factor involved in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	R	r	Total	X^2	P
B 1871	518	154	672	1.56	.10 - .25
B 1852	385	129	514	.01	$>$.90
B 1869	566	196	762	.23	.50 - .75
B 1857	76	21	97	.50	.25 - .50
B 1865	396	126	522	.21	.50 - .75
Sum of 5 chi-squares				2.51	.75 - .90
Total	1941	626	2567	.53	.25 - .50
Interaction				1.98	.50 - .75

Unassigned genes

Non-glossy (Gs) versus glossy (gs) stems and spikes. Non-glossy is dominant over glossy stems and spikes. This character is controlled by a single factor pair. These data are presented in Table 22.

Table 22. Segregation of non-glossy (Gs) versus glossy (gs) stems and spikes in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Gs	S	gs	Total	X^2	P
B 1764 (F_3)	155	296	157	608	.44	.75 - .90
B 1791 (F_3)	123	198	123	444	5.18	.05 - .10
B 1871 (F_2)	525		150	675	2.85	.05 - .10
B 1868 (F_2)	523		215	738	6.85	$<$.01
B 1836 (F_2)	306		80	386	3.67	.05 - .10
B 1857 (F_2)	280		97	377	.14	.50 - .75
B 1865 (F_2)	396		133	529	.01	$>$.90
Sum of 7 chi-squares					19.14	.06 - .02
Total	2802[a]		955	3757	.28	.50 - .75
Interaction					18.86	.01 - .02

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Normal (Gp) versus grandpa (gp). Table 23 indicates a poor fit for a single factor pair inheritance. High seedling mortality, late maturity, and poor seed set, which are probably due to the small amount of chlorophyll that the plant contains, may be responsible for the failure to conform to a 3:1 ratio.

Table 23. Segregation of normal (Gp) versus grandpa (gp) plants in the F_2 generation. Chi-square and P value are based on a 3:1 ratio.

Cross	Gp	gp	Total	X^2	P
B 1836	357	29	386	62.76	$<$ .01
B 1852	474	40	514	81.07	$<$ .01
Sum of 2 chi-squares				143.83	$<$ .01
Total	831	69	900	144.21	.01
Interaction				.38	.50 - .75

Long (Gh) versus short (gh) outer-glume hairs. Table 24 indicates that a single factor pair is involved in the inheritance of long versus short outer-glume hairs. A high interaction value was obtained between families of both crosses. This indicates that there was some inconsistency in classification. Several researchers who have worked with this character expressed difficulty in classifying it.

Table 24. Segregation of long (Gh) versus short (gh) outer-glume hairs in the F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross	Gh	S	gh	Total	X^2	P
B 1764	103	235	114	452	1.25	.25 - .50
B 1791	67	128	72	267	.56	.75 - .90
Sum of 2 chi-squares					1.81	.75 - .90
Total	170	363	186	719	.80	.50 - .75
Interaction					1.01	.50 - .75

Normal (Rb) versus ribbon grass (rb) leaves. Table 25 indicates that a single factor pair is involved in the inheritance of normal versus ribbon grass leaves with normal being dominant. Cross B 1865 has a high chi-square and a low P value based on a 3:1 ratio. This author believes that some plants that carry the genes for ribbon grass leaves do not express the character. Cross B 1869 was grown in the spring of 1962 in the F_3 generation. When the author first classified these plants not enough plants with the ribbon grass character were observed to obtain a reasonable chi-square value for a 1:2:1 ratio. After this classification was made the weather turned stormy and cold. This brought out the character and several plants that had not shown the character before expressed it after the stormy weather. A reclassification was made.

Table 25. Segregation of normal (Rb) versus ribbon grass (rb) leaves in the F_2 and F_3 generations. Chi-square and P values are based on 3:1 and 1:2:1 ratios.

Cross	Rb	S	rb	Total	X^2	P
B 1791 (F_3)	123	204	111	438	2.86	.10 - .25
B 1869 (F_3)	148	292	155	595	.83	.97 - .99
B 1865 (F_2)	419		72	491	28.22	$<$ .01
Sum of 3 chi-squares					31.41	$<$ .01
Total	1186[a]	338	338	1524	6.47	.02 - .05
Interaction					24.94	$<$ .01

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows in the total.

Factors Showing Linkage

Linkages found in linkage group 1

Normal (Br) versus brachytic (br) plants in relation to other factor pairs. The linkage of normal (Br) versus brachytic (br) plants in relation to other factor pairs is presented in Table 26.

Table 26. Linkages obtained in linkage group 1

Cross	Phase	XY	XY	xY	xy	Total	Crossover value
	(Br, br) in relation to (N, n)						
B 1791 F_3	Coupling	265	81	68	36	450	42 ± 3.21
	(Br, br) in relation to (Tr, tr)						
B 1791 F_3	Coupling	232	14	45	23	314	24 ± 2.84
	(Pbg, pbg_1) in relation to (N, n)						
B 1852 F_2	Coupling	250	75	37	48	410	19[a]
	(Pbg, pbg_1) in relation to (R, r)						
B 1852 F_2	Coupling	273	53	30	55	411	17[a]
	(Pbg, pbg_1) in relation to (B, b)						
B 1852 F_2	Coupling	259	67	46	39	411	27[a]
	(Pbg, pbg) in relation to (E, e)						
B 1852 F_2	Coupling	411	0	0	103	514	0
	(N, n) in relation to (L, 1)						
B 1764 F_3	Repulsion	322	136	132	15	605	32 ± 3.6

[a] Crossover values are only approximations.

Although (N, n) is in the same linkage group as (Br, br) these characters have not been reported as being linked. A possible explanation is that there is probably a slight linkage between the two characters, and through distance alone a smaller than normal crossover value was obtained.

Linkage was also noted between (Br, br) and (Tr, tr). When the parents were crossed they were in the repulsion phase. However, in classification of the progeny, the linkage was noted in the coupling phase. A very high chi-square value was obtained for (Tr, tr) in this cross. Not enough triple-awned (tr) recessive and segregating rows were obtained to fit a one factor hypothesis. Perhaps some of the normal (Br) plants were inhibited in expressing the recessive (tr) character while no inhibition was present in the brachytic (br) plants. The factor pair (Br, br) has been located in linkage group 1 while the factor pair (Tr, tr) is located in linkage group 2.

Although the above mentioned linkages may be possible, this author feels the results are questionable because they are inconsistent with results reported by other workers, and both linkages were obtained in cross B 1791.

Heavy pubescent (Pbg) versus sparse pubescent (pbg_1) versus non-pubescent (pbg) glumes in relation to other factor pairs. Data showing the linkage relationship between (Pbg, pbg_1, pbg) and other factors are presented in Table 26. This character deserves more consideration because of the small amount of information that is in the literature and because of the results that were discovered in this study. A linkage was obtained with (N, n) which was in agreement with the findings of Hor (18).

A very close linkage was found between heavy pubescent versus sparse pubescent glumes and the smooth awn factor pair. This information could be useful in breeding for non-pubescent glumes. In breeding programs it is quite time consuming to check each plant with a hand lens to see if hair is present on the glumes. If knowledge of this linkage is used, much time can be saved.

In every case in which long-awned (e) glumes were present the glumes were completely hairless. In some instances hair could be noted on the rachis, but none was noted on the glumes. In calculating all linkages other than those involving (Pbg, pbg) in relation to (E, e), the plants expressing (e) were pulled out so that proper linkages could be observed.

A linkage was also obtained between black versus white lemmae and pericarp (B, b) and glume pubescence. Glume hairs are the same color as the white lemmae and pericarp. Perhaps the glume hairs on the black lemmae and pericarp are more easily seen because of the contrasting background which may give the impression that more hair is present than on the white lemmae and pericarp.

The only linkage data this author found reported in the literature were presented by Hor (18) with the (N, n) factor pair in relation to (Pbg, pbg).

Covered (N) versus naked (n) caryopses in relation to other factor pairs. (N, n) showed linkage with lax versus dense spikes (L, l) in cross B 1764. Both of these factor pairs were in cross B 1791 but no linkage was obtained. This can be explained by the fact that the (L, l) factor pair has been reported in several linkage groups. This suggests that different factor pairs for lax versus dense spikes (L, l) were involved in the two crosses in this study. Data showing the linkage relationship between (N, n) and (L, l) are presented in Table 26.

Linkages found in linkage group 2

Normal (Tr) versus triple-awned (tr) lemmae in relation to other factor pairs. Data showing the linkage relationship between (Tr, tr) and other factors are presented in Table 27. Linkages were obtained with

Table 27. Linkages obtained in linkage group 2

Cross	Phase	XY	XY	xY	xy	Total	Crossover value
	(Tr, tr) in relation to (R, r)						
B 1791 F_3	Repulsion	168	18	19	0	205	24[a]
	(Tr, tr) in relation to (E, e)						
B 1791 F_3	Repulsion	206	71	31	6	314	42 ± 4.6
B 1852 F_2	Repulsion	301	95	110	8	514	30 ± 3.95
	(Tr, tr) in relation to (Gh, gh)						
B 1791 F_3	Coupling	136	39	7	7	189	33 ± 4.32
	(Li, li) in relation to (V^t, V, v)						
B 1869 F_2	Repulsion	411	142	174	35	762	42 ± 2.95
B 1871 F_2	Repulsion	362	118	162	28	670	41 ± 3.17
B 1764 F_3	Coupling	363	86	102	59	610	38 ± 2.61
	(Li, li) in relation to (Rb, rb)						
B 1869 F_2	Repulsion	299	142	141	13	595	28 ± 3.73
	(Li, li) in relation to (E, e)						
B 1871 F_2	Coupling	378	102	136	54	670	45 ± 2.73
	(Li, li) in relation to (Re_2, re_2)						
B 1871 F_2	Coupling	290	187	70	119	666	30 ± 3.11
	(Li, li) in relation to (L, l)						
B 1871 F_2	Repulsion	257	123	149	41	570	42 ± 3.41
	(Li, li) in relation to (Z, z)						
B 1868 F_2	Repulsion	519	31	181	5	736	39 ± 3.09
B 1868 F_3	Repulsion	410	21	149	3	583	37 ± 3.52
	(V^t, V, v) in relation to (E, e)						
B 1871 F_2	Repulsion	380	145	136	11	672	29 ± 3.49
B 1869 F_2	Repulsion	430	156	156	21	763	36 ± 3.11
B 1865 F_2	Repulsion	319	96	90	17	522	43 ± 3.52
B 1791 F_3	Repulsion	237	84	110	10	441	31 ± 4.24
B 1852 F_2	Repulsion	291	98	120	5	514	23 ± 4.13
	(V^t, V, v) in relation to (Re_2, re_2)						
B 1871 F_2	Repulsion	361	262	99	46	768	38 ± 5.31
B 1836 F_2	Coupling	163	113	29	77	382	24 ± 3.65
	(V^t, V, v) in relation to (R, r)						
B 1857 F_2	Coupling	59	12	17	9	97	37 ± 6.48
B 1791 F_3	Coupling	190	20	4	4	218	15[a]

Table 27. (Cont.)

Cross	Phase	XY	Xy	xY	xy	Total	Crossover value
	(V^t, V, v) in relation to (Lk_1, Lk_3)						
B 1791 F_3	Coupling	320	3	95	23	441	6 ± 3.18
	(V^t, V, v) in relation to (Lk_1, Lk_2)						
B 1865 F_2	Coupling	315	98	103	4	520	23 ± 4.11
	(V^t, V, v) in relation to (Gh, gh)						
B 1791 F_3	Coupling	142	39	53	33	267	39 ± 4.01
B 1764 F_3	Repulsion	245	110	93	4	452	21 ± 4.41
	(Lk_1, Lk_3) in relation to (E, e)						
B 1791 F_3	Repulsion	325	91	22	4	442	43 ± 8.38
	(Lk_1, Lk_2) in relation to (E, e)						
B 1865 F_2	Coupling	337	82	70	31	520	42 ± 2.99
	(E, e) in relation to (Re_2, re_2)						
B 1871 F_2	Coupling	301	213	61	95	670	33 ± 3.27
	(E, e) in relation to (R, r)						
B 1791 F_3	Coupling	141	12	53	11	217	34[a]
	(L, l) in relation to (Re_2, re_2)						
B 1871 F_2	Coupling	307	198	53	110	668	27 ± 2.93

[a] Crossover values are only approximations.

(Tr, tr) in relation to (E, e), (Gh, gh) and (R, r). Although the factors (Tr, tr) and (V, v) are reportedly located on the same chromosome no linkage was obtained in this study.

A very poor chi-square was obtained for (Tr, tr) which may suggest misclassification. This might explain why there was no linkage with the (V) series of alleles. In one cross involving the (R, r) factor no linkage was obtained.

Normal (Li) versus liguleless (li) plants in relation to other factor pairs. This factor pair was studied in four crosses for linkages, and these data are presented in Table 27. In three crosses the (V^t, V, v) series of alleles were involved, and in all crosses a slight linkage was noted.

(E, e), which is in the same linkage group, was also studied in three crosses. Only one cross showed a slight linkage. The other two crosses showed no linkage. This indicates that the (Li, li) and (E, e) factors must be located quite some distance from each other on the chromosome.

Linkage was noted between (Li, li) and (Rb, rb). The ribbon grass factor has not yet been assigned to a linkage group. Only one cross was involved and further studies should be made to see if this linkage is consistent or if this was just a chance occurrence.

Linkage was also observed between (Li, li) in relation to the (L, l) factors. In one cross (L, l) showed independence. This can be explained by the fact that (L, l) has been reported in several linkage groups.

In cross B 1868 a slight linkage was noted with normal versus zoned leaved plants and Li vs. li in both the F_2 and F_3 generations. This is not in accordance with the findings of other workers and may have been caused by the loss of a large number of zoned leaved plants.

A linkage was also observed between (Li, li) and (Re_2, re_2).

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spikes in relation to other factor pairs. Linkages were obtained between (V^t, V, v) in relation to (E, e), (Re_2, re_2), (Lk_1, Lk_3), (Lk_1, Lk_2), (Gh, gh) and (R, r). Data are presented in Table 27. In previous studies it has been found that (Lk) spikes were completely linked with the (V) series of alleles. This was studied in cross B 1791, and as was stated previously the few awnless spikes that were present were grouped with the awnletted (Lk_3) group.

Long-awned (Lk_1) versus short-awned (Lk_2) versus awnletted (Lk_3) spikes in relation to other factor pairs. As indicated in Table 27 linkages were obtained between (Lk_1, Lk_3) and (E, e), and (Lk_1, lk_2) and (E, e).

Normal (E) versus long-awned (e) glumes in relation to other factor pairs. Linkages were obtained between (E, e) and (Re_2, re_2), (R, r), and (Gh, gh). Data are presented in Table 27.

Lax (L) versus dense (l) spikes in relation to purple (Re_2) versus white (re_2) lemmae and pericarp. As indicated in Table 27 the gene responsible for lax versus dense spikes is linked with purple versus white lemmae and pericarp and is located in linkage group 2. In the literature the lax versus dense spikes factor has been located in several linkage groups.

Linkages found in linkage group 4

Hooded (K) versus awned (k) spikes in relation to other factor pairs. Linkages were obtained with (K, k) in relation to (Gl, gl) and in relation to (Z, z). Data are presented in Table 28.

Table 28. Linkages obtained in linkage group 4

Cross	Phase	XY	Xy	xY	xy	Total	Crossover value
	(K, k) in relation to (Gl, gl)						
B 1868 F_2	Repulsion	443	68	216	7	734	29 ± 3.34
B 1868 F_3	Repulsion	340	48	192	3	583	22 ± 3.91
B 1764 F_3	Repulsion	141	12	81	1	235	25 ± 6.06
	(K, k) in relation to (Z, z)						
B 1868 F_2	Repulsion	485	26	215	8	734	45 ± 2.92
B 1868 F_3	Repulsion	365	23	194	1	583	19 ± 3.95
	(Gl, gl) in relation to (Bl, bl)						
B 1791 F_3	Repulsion	89	78	31	6	204	1 ± 361.11
B 1764 F_3	Coupling	171	51	7	6	234	36 ± 4.09
	(Gl, gl) in relation to (Z, z)						
B 1868 F_2	Repulsion	626	37	74	1	788	30 ± 3.3
B 1868 F_3	Repulsion	510	22	51	0	583	30 ± 3.72

Non-glossy (Gl) versus glossy (gl) leaves in relation to other factor pairs. Linkages were obtained with (Gl, gl) in relation to (Gs, gs), (Bl, bl), and (Z, z), and these data are presented in Table 28. The linkage involving (Gs, gs) was slight and could be caused by a high loss of (gl) plants. Three other crosses showed that (Gl, gl) and (Gs, gs) were independent of each other.

In the linkage with (Z, z) few recessive plants were noted which may be caused by both characters (gl) and (z) being lethal. Perhaps when (z) and (gl) come to expression on the same plants a high mortality rate may result.

Linkages found in linkage group 5

Black (B) versus white (b) lemmae and pericarp in relation to other factor pairs. A linkage between (B, b) and (Re_2, re_2) was obtained in one cross, but no linkage was obtained in the other cross in which both characters were present. Both crosses had two factor pairs for (Re_2, re_2) involved. The author has no explanation why linkage was not obtained in cross B 1871.

In cross B 1857 a linkage was obtained between (B, b) in relation to rough (R) versus smooth (r) awns, but there were only a few plants involved. A high interaction was obtained between families. This author feels that this was just a chance occurrence. Data are presented in Table 29.

Table 29. Linkages obtained in linkage group 5

Cross	Phase	XY	Xy	xY	xy	Total	Crossover value
	(B, b) in relation to (Re_2, re_2)						
B 1836 F_2	Repulsion	129	158	63	32	382	21 ± 13.01
	(B, b) in relation to (R, r)						
B 1857 F_2	Repulsion	55	19	21	2	97	32 ± 9.03

Linkages found in linkage group 7

Rough (R) versus smooth (r) awns in relation to other factor pairs. A linkage was obtained with (R, r) in relation to (Gh, gh). Data are presented in Table 30. (R, r) seems to be linked in group 2 in this cross as does (Gh, gh).

Table 30. Linkages obtained in linkage group 7

Cross	Phase	XY	Xy	xY	xy	Total	Crossover value
	(R, r) in relation to (Gh, gh)						
B 1791 F_3	Repulsion	104	26	11	1	142	34[a]

[a] Crossover value is only an approximation.

Factors Showing Independence

Independence was noted in the following factor pairs:

Br in relation to V^t, Lk, E, L, Gl, Bl, R, Gs, Gh, and Rb.

N in relation to Tr, V^t, Lk, E, Gl, R, Gs, Bl, Gh, Rb, Li, K, Z, B, Gp, and L.

Pbg in relation to Tr, V, and Gp.

Tr in relation to V^t, L, Gl, Bl, Gs, Rb, B, Gp, Lk, and R.

V^t in relation to L, Gl, Bl, Rb, B, Gp, K, O, R, and Gs.

Lk in relation to L, Gl, Bl, R, Gs, Gh, and Rb.

E in relation to Gl, Bl, Gs, Rb, Li, K, Z, B, Gp, L, and R.

L in relation to Gl, Bl, R, Gs, Gh, Rb, K, B, and Li.

Gl in relation to R, Gh, Rb, B, Li, and Gs.

Bl in relation to R, Gs, Gh, and Rb.

R in relation to Gs, Rb, B, Gp, Li, Re_2, O, and K.

Gh in relation to Rb, K, Gs, and Li.

Gs in relation to Z, K, Li, Rb, B, Re_2, O, and Gp.

Rb in relation to B and Li.

Li in relation to K, Z, and B.

K in relation to B, Re_2, O, and Gp.

Z in relation to B.

B in relation to Gp, Re_2, and O.

Gp in relation to O and Re_2.

O in relation to Re_2.

SUMMARY AND CONCLUSIONS

Nine crosses were used in studies involving inheritance, linkages, and independence of a number of genetic factors in barley.

A one factor pair inheritance was obtained with the following genes: Tr, Li, V^t, E, L, K, Gl, Z, B, O, Gs, N, Br, Gp, Gh, and Rb.

A one factor pair inheritance was obtained in some instances and a two factor pair inheritance was obtained in others with the following genes: Lk_1 and R.

A two factor pair inheritance was obtained with the following genes: Re_2 and Bl.

A three factor pair inheritance was obtained with Pbg.

Independence was tested in various combinations for 21 genes.

Genes contributing to the pubescent glume character (Pbg) were found to be located in several linkage groups: linkage group 1 in relation to (N, n), linkage group 5 in relation to (B, b), and linkage group 7 in relation to (R, r). It was also found that when (e) was present, pubescence on the glume was absent.

Further studies should be conducted on the pubescent glume factor in relation to (B, b) to see if this linkage was due to the contrasting background of the black lemmae and pericarp beneath the white glume hairs when B is present. Further studies should be carried out to clarify the inheritance of pubescent glumes.

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