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Inheritance of 16 Barley Characters and Their Linkage Relationships

Tejpal Singh Gill

INHERITANCE OF 16 BARLEY CHARACTERS

AND THEIR LINKAGE RELATIONSHIPS

by

Tejpal Singh Gill

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INTRODUCTION

The assignment of genetic factors to definite loci in the hereditary mechanism has been a great step in the progress of biology. Of the cereal crops, barley (*Hordeum* sp.), a crop of economic importance, offers a superior opportunity for genetic studies. Its adaptation to wide varieties of conditions, with a wealth of easily differentiated characters and only seven pairs of chromosomes, the barley plant provides excellent material for linkage studies.

Although there is a vast amount of literature dealing with inheritance in barley, yet knowledge of the subject is still very limited. The mode of inheritance of about one hundred characters has been studied and linkage relations of nearly thirty-five characters have been made. The location of a relatively large number of them is still unknown. All the seven linkage groups are established and distinct viable characters are available in six of them, although but few in some cases. The desirability of making further studies in this crop is quite apparent.

This manuscript contains the results of observations and experiments with sixteen characters which include three new characters not reported in the literature. All character pairs in each cross studied were checked for possible linkages or independence. The importance of such a study in the future improvement of the barley crop needs no emphasis.

REVIEW OF LITERATURE

The genetic work on barley got its impetus at the beginning of the twentieth century and the last fifty years have added much to the knowledge. Barley is one of the few crops on which major genetic emphasis has been given.

A fairly extensive review of literature on inheritance and linkage relations is now available, including some 800 references. In this paper, the review of literature on the genetics of barley is confined to only those characters that have been used by the writer in his studies.

Individual Characters

Fertility of Lateral Florets

The genetic difference causing variations in degree of fertility of the lateral florets has been investigated perhaps more than any other set of characters in barley.

Biffen (1, 2) made reciprocal crosses between deficiens x distichon, vulgare x deficiens, and distichon x vulgare, and in each case obtained segregation in the F_2 which suggested a single factor difference.

Engledow (7, 8) comes to the conclusion based on his own observation and those of Biffen, that deficiens, distichon, and vulgare form an allelomorphic series with respect to fertility of the lateral florets of the spike. Dominance is in the order: deficiens, distichon, and vulgare.

Hor (16) confirms Engledow's conclusions. Neatby (27), Tedin and Tedin (41), and Robertson (29) obtained monohybrid segregation in F_2 of vulgare and distichon. Buckley (4), Daane (5), and Griffee (12) reported a simple 3 : 1 ratio in crosses between vulgare and non-vulgare.

Ubisch (44) explains the difference between common two-rowed barleys, (distichon), and six-rowed barley, (vulgare), on a two factor basis, the factor pairs being Zz Ww. Factor Z must be present in either homozygous or heterozygous condition if the plant is to be two-rowed. Factor W produces the transitional form between two-rowed and six-rowed types, which is intermedium. Common two-rowed has the constitution ZZ WW, six-rowed is zz ww, while intermedium is zz WW.

Gillis (11) supports Ubisch's view that two factors are involved between distichon and vulgare. However, he concludes that there is a third factor, D, for the fertility of the lateral florets. The deficiens form carries the recessive d as do the six-rowed forms. The expression of d for absence of the lateral florets can not occur without the Z factor.

Harlan and Hayes (14) gave the first complete genetic analysis of the results from such crosses, explaining the results on the basis of two factor pairs. They obtained true intermedium types in F_3. Robertson (29) obtained similar results. Leonard (23) found that the fertile, infertile, and nonintermedium types were differentiated by genes belonging to a multiple-allelic series, designated as $l^h l^h$, l l, and i i, respectively.

Woodward (48), as a result of series of crosses, suggested an allelic series consisting of v, V^d, V, V^t, genes for six-rowed, two-rowed, and deficiens. The two-rowed gene V^d, which exhibited a major factor difference in crosses with two-rowed V gene, has been added to the series. He also verified a second allele for fertility in the lateral florets consisting of l^h, l and i (two types of intermedium and infertility, respectively).

The $V^d v$, and V v combinations in the presence of i i showed infertile lateral florets, ie., dominance of V^d and V. With l^h l^h, both $V^d v$ and V v showed complete fertility similar to six-rowed (distinguished from six-rowed by short or missing lateral awns), ie., dominance of v factor.

In order of decreasing fertility of laterals, combinations of $l^h l$, $l^h i$, and I i with $V^d v$ and V v gave types intermediate between the fully fertile and infertile.

Lesser fertility genes in the l series showed almost complete dominance over fertility when associated with two-rowed $V^d v^d$ or V v genotypes. Thus, i was dominant to l and l^h, and l dominant to l^h. The presence of modifying or minor factors was suggested to account for the considerable genetic variability found in lateral florets.

Pigmentations in Barley

Pigmentation in the caryopsis of barley is the result of either of two pigments, anthocyanin, which gives the red, blue, and purple colors, and a melalin-like pigment, which is responsible for black. If pigment is absent in either the aleurone layer or pericarp, the caryopsis is white. If the aleurone is blue and the pericarp colorless, the caryopsis is blue. A red pericarp and blue aleurone produce a purple colored caryopsis. Black is found only in the pericarp.

The lemma may be colored black, purple, or orange. Anthocyanin may be confined to the veins, in which case the veins of the glumes are purple.

Purple vs. White Pericarp (Pr pr)

The F_2 of a cross, purple x white lemma, was noted by Biffen (2) to segregate three purple to one white.

Miyake and Imai (25) explains their result on a two-gene basis, P_1 and P_2. P_1P_2 is dark purple, P_1p_2 is light purple, while p_1p_2 is white. The F_2 of the cross, dark purple x white, segregated nine dark purple, six light purple, to one white.

Buckley (4) reported that purple behaved as a simple dominant. The

F_1 was purple. The F_2 segregated in the normal ratio of three purple, to one white. Daane (5) also concluded that purple vs. white pericarp as due to a single factor.

From his four crosses between purple and white parents, Myler (26) found a segregation of twelve purple, to three blue, to one white. It shows a two-factor difference in color segregation. This also indicates that the factors for purple pericarp and blue aleurone are independent.

Purple vs. White Straw (P p)

Robertson (30) studied the inheritance of straw color in a cross between Nilsson Ehle No. 2 and Trebi. These data indicated that purple versus white straw color differs by a simple Mendelian factor pair.

Normal vs. Long Awned Outer Glume (E e)

The inheritance of the character, long awn development, has been found by many workers to depend on a single factor. Long awned outer glumes were found to be a simple recessive character by Biffen (2), but Hor (16) has recorded the appearance of the long awned outer glumed type in the F_3 generation of crosses of the normal glumed forms.

Bose et al. (3) and Swenson (40) also found a single factor responsible for normal and long awned outer glumes.

Early vs. Late Heading (Ea ea)

Griffee (12) made a study of the date of heading in 135 F_3 families of the cross, Svanhals x Lion. The F_3 lines proved to be of three kinds. One like Svanhals, one like Lion, while a third produced both early and late plants with a preponderance of plants heading early. These three types appeared in approximately a 1 : 2 : 1 ratio. The results show a one-factor difference between Lion and Svanhals, early heading being dominant.

Neatby (27) concluded that three factors are concerned in the inheritance of earliness. When all three factors are in homozygous recessive condition, the plants develop the winter habit of growth.

Black vs. White Glumes

Tschermak (43) found that the F_2 of black x non-black segregates in a simple Mendelian ratio of three black to one white. This has been corroborated by many later investigators, including, Biffen (2), Keser and Boyack (21), Hor (16), Robertson (29), Sigfusson (37), McGregor (24), and Buckley (4). All reported mono-genetic ratios of black vs. white caryopsis or glumes.

Woodward (46), in his studies of crosses between colored parents that differed in the intensity of black pigment in the lemma and caryopsis, suggested an allelomorphic series of factors causing various color-intensity expression. The factors definitely established were, black (BB), gray (B^gB^g), and white (bb). The denser color was always dominant over the lighter one.

Woodward (46) further pointed out that pigment formation in both the pericarp and the flowering glume appeared to be controlled by a single series of allelomorphic genes.

Hulled vs. Naked Caryopsis

Biffen (2) found that the F_2 of a cross, hulled x hulless segregated in the simple Mendelian ratio: three hulled : one hulless or naked. Other investigators, Thatcher (42), Gaine (10), Hor (16), Neatby (27), Tedin and Tedin (41), Robertson (29), Buckley (4), Daane (5), and Sigfusson (37), have confirmed Biffen's observation.

Green vs. Zoned Leaf (Z z)

Zoned leaves of seedlings are marked by transverse yellowish stripes. Plants frequently are yellowish in color until almost fully developed. Such plants are viable.

Immer and Henderson (18) studied the inheritance of transverse yellowish stripes. Green leaves were dominant in the F_1 generation. In the F_2, the plants segregated in the simple Mendelian ratio of three green to one zoned leaf.

Blue vs. White Aleurone (Bl bl)

Hayes and Garber (13), Buckley (4), and Robertson et al. (33), found that the F_2 of a cross between blue and white aleurone segregated into three blue to one white, indicating the characters differ by a single Mendelian factor pair.

Myler (26) also found a single factor difference for blue and white aleurone which is in agreement with Buckley and Robertson et al.

Hooded vs. Awned (K k)

The investigations of Biffen (2), Kezer and Boyak (21), Hayes and Garber (13), Hor (16), Robertson (29), McGregor (24), and Buckley (4) show there is but a simple factor difference in crosses involving hoods versus awns and that the hooded condition is dominant.

Ubisch (44) explains the segregation of his crosses on a two factor basis. Factor K is dominant for hooded, A for long awns, KK AA and KK aa individuals are hooded, kk AA are long awned, and kk aa are short awned.

Rough vs. Smooth Awn (R r)

The literature on awn-barbing in barley is fairly extensive and shows the existence of two genes governing that character.

Deans (5), Hayes et al. (15) have reported a single factor difference between rough and smooth awns with the F_1 being rough and the F_2 segregating in a ratio of three rough and one smooth.

Griffee (12) using the cross, Lion x Svanhals reported two dominant genes, R for rough awns and S for intermediate smooth awns with R being epistatic to S and the F_2 phenotypic ratio of 12 : 3 : 1 of rough, intermediate, and smooth.

A similar explanation was given by Robertson et al. (32) for their results obtained from the cross, Coast x Lion and by Johnston and Aamodt (20) for their results with Velvet x Trebi, and Glabron x Trebi.

Sigfusson (37) found rough awns due to two complementary factors, the factor R producing a greater effect than the factor S. The factor R in the absence of S produces the intermediate-rough awn. Both factors are necessary to produce a fully rough awn, and a smooth awn is the results when both are absent. A 9 : 3 : 3 : 1 ratio was obtained in the F_2. He, therefore, concludes that another phenotype (intermediate-rough) not previously reported, and which consists of two genotypes, is involved.

Friesen (9) studied the inheritance of awn barbing in crosses of barley varieties having intermediate smooth and very smooth awns and lacking the gene R for rough awns. Two genes were found to govern awn smoothness in these varieties, one being S hypostatic to R as previously reported and the other, termed S_1 hypostatic to S. The genotype rr SS S_1S_1 has intermediate smooth awns, rr ss S_1S_1, has smooth awns, and rr ss s_1s_1 very smooth awns. Slight variation in smooth and very smooth types was indicated to the possible presence of one or more modifying factors.

Long vs. Short Haired Rachilla (S s)

The rachilla at the base of the barley is covered either with long, unbranched hairs or short, unbranched hairs.

Biffen (2), Buckley (4), Engledow (6), Hor (16), Robertson (29), and Sigfusson (37) have all reported simple Mendelian inheritance for the length of rachilla hairs in barley. A single factor difference, with F_1 being long-haired and a segregation in F_2 of three long and one short is suggested by these workers.

Normal vs. Brachytic Plant (Br br)

A brachytic plant is somewhat stunted with all the essential parts, internodes, rachis nodes, awns, etc., shortened as compared to the normal plant.

Powers (28) and Swenson (39) studied the inheritance of brachytic habit of the plant and found that the character is simply inherited, the F_1 being normal and the F_2 generation segregating into three normal to one brachytic.

Linkage Groups

In the following review of linkage groups only those characters have been reviewed which are included in the present study. Crossover values calculated by the various workers, with the chromosome map, wherever possible, are given below.

First Linkage Group

Vv vs. Ee

The linkage relations of non-six-rowed vs. six-rowed spikes (Vv) and awnless vs. long awned outer glume (Ee) have been studied by the various investigators. Their results are summed up as follows:

Investigators	Crossover Value
Bose *et al.* (3)	24.7 %
Robertson *et al.* (34)	26.6 ± 0.6 %
Immer and Henderson (18)	28.0 ± 1.2 %
Swenson and Wells (40)	26.7 ± 1.7 %

V v vs. Pr pr

Buckley (4), and Myler (26), during their work on inheritance and linkage studies in barley found crossover values of 20 per cent and 13.19 ± 2.17 per cent, respectively, between non-six-rowed vs. six-rowed (V v) and purple vs. white pericarp. Daane (5) also placed (Pr pr) character pairs in the first linkage group.

Woodward (47) reported that the combined data, F_2 and F_3, from all crosses showed a recombination value of 14.1 ± 0.36 per cent for genes $V^t v^d$ and Pr pr. For the more accurate F_3 data, when taken alone, this value was 10.1 ± 1.033 per cent.

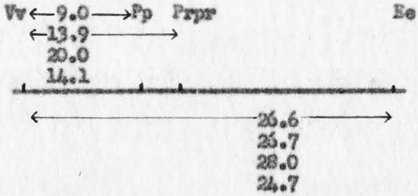
V v vs. P p

Robertson (30) indicated that the factor pair (V v) for non-six-row versus six-row is linked with factor pair (P p) for purple versus colorless straw with about 9.0 ± .68 per cent crossing over.

V v vs. Ea ea

Griffee (12) reported that linkage is exhibited between non-six-rowed versus six-rowed (V v) and early versus late heading (Ea ea). The linkage intensity was very low, the crossover value being 42.0 per cent. Neatby (27) and Wexelson (45) also correlated the early and late heading character with the head type, but they concluded that there are several factors causing the plant to be early or late in heading.

Map of Linkage Group I



Second Linkage Group

Because only one character pair, ie., (B b) Black vs. White flowering glumes is being studied from this group, it is quite independent of the other character pairs included in this study.

Third Linkage Group

Hulled vs. naked caryopsis (N n) is again the only character taken for studies from this group and it is independent of all the known character pairs included in this work. It is reported by Robertson et al. (32) and Buckley (4) that one of the factors for blue aleurone Bl_1Bl_1 was linked with N n, with a recombination value of 9.9 ± .44 per cent.

Fourth Linkage Group

Zd zd vs. K k

Immer and Henderson (18), in their linkage studies in barley, found the normal leaf versus zoned leaf (Zd zd) to be linked with the hooded versus awned character pair showing a 6.0 ± .8 per cent crossing over.

K k vs. Bl bl

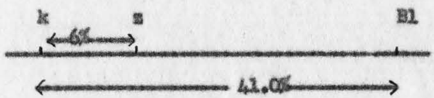
Buckley (4) reported a linkage of the factor pairs Bl bl for blue versus white aleurone and Kk for hoods versus awns. A minimum X^2 value of 2.23 was obtained at a crossover value of 41.0 per cent.

Robertson et al. (32), with considerably more data, placed the factor pair Bl bl for blue versus white aleurone in the fourth group with a crossover value of 22.58 ± 0.82 per cent with the factor for hooded versus awned spikes (K k).

Myler (26) reported two complementary factors for blue aleurone. One of these factors previously reported by Robertson et al. and Buckley and designated as Bl bl, was linked with the hooded versus awned character with a crossover value of 24.72 ± 1.73 per cent. The second factor was designated as Bl_1 bl_1 and was found to be linked with hulled versus naked character (N n) which placed it in linkage group III.

Immer and Henderson (18) found the two factor pairs Bl bl for blue versus white aleurone and K k for hooded versus awned to be linked with a crossover value of 44.0 ± 6.3 per cent.

Arrangement of the genes on the chromosome



Fifth Linkage Group

Rr vs. Ss

Several investigators have worked out the linkage relationship of the factor pairs: Rough versus smooth awn and long versus short haired rachilla. Crossover values are given below:

Investigators	Crossover Value
Hor (16)	35.0 %
McGregor (24)	42.7 %
Sigfusson (37)	30.8 %

Investigators	Crossover Value
Robertson *et al.* (32)	34.6 %
Daane (5)	28.1 %
Wexelson (45)	30.0 %

Seventh Linkage Group

The only factor pair which is being observed in this study is Br br which stands for normal versus brachytic habit of growth.

Power (28) found it to be independent of the first and second linkage group. Swenson (39) placed it in the seventh linkage group as it was linked with the factor pair Fe fe for green versus chlorina (dull green yellow) seedling with a crossover value of 9.29 ± 0.90 per cent and was independent of the first six groups.

MATERIAL AND METHOD

Crosses

The crosses studied were made at the North Logan Farm, by Dr. R. W. Woodward in the spring of 1947.

Approximately sixteen florets, usually the central ones on each of two or more plants, were emasculated and pollinated for each cross. Seeds resulting from such crosses were then space planted nearly twelve inches apart in rows two feet apart, in order to get large plants with a maximum number of seeds.

The F_2 kernels from each F_1 plant were sown by hand in fifty foot rows, one foot apart, with plants three to four inches apart in the row. Several such families from different F_1 plants, making up fairly large populations of each cross, were studied separately where more than one factor pair or linkage was involved.

In a few crosses where classification of some character pair was hard to establish in F_2 generation, the F_3 kernels from each F_2 plant were grown in five rows, one foot apart, and sown by a hand planting machine which saved time. Parental lines were grown after every fifty rows for comparison, as a help in classifying the F_3 plants.

The hybrid progenies as well as parental strains were grown in the field. Spikes from each individual F_1 and F_2 plant were harvested and stored in an envelope bearing the pedigree number for laboratory study, while the examination of all the F_3 plants was made in the field.

Certain characters which were difficult to find at harvest were tied in the seedling or heading stage with colored strings.

The F_2 heads were thrashed in the laboratory with the help of a Waring Blender.

Statistics

Tests of significance were made through use of the X^2 test for goodness of fit and Immer and Burnham table of probability (17). Recombination percentages were determined by the product method.

Classification of Plants

No great difficulty was encountered in the classification of plants. In the case of the fertility of the lateral spikelets, all heads not exhibiting the six-rowed characters were classed as non-six-rowed; that is, the two-rowed and the intermediate were grouped into one class.

The only difficulty encountered in classification was with the factor pair, long versus short glume hairs. To get clear ideas and evidence, F_3 tests were made and the segregating ratio secured.

Mendelian Factors

The paper presents studies of inheritance of sixteen Mendelian factors and their possible linkage relations. The symbols used are those recommended in the summary by Robertson, Wiebe and Immer (31).

1. Normal vs. long awned outer glume	E e
2. Purple vs. white pericarp	P p
3. Purple vs. white straw	Pr pr
4. Non-six-row vs. six-row	V v
5. Early vs. late heading	Ea ea
6. Black vs. white glume color	B b
7. Hulled vs. naked caryopsis	N n
8. Green vs. Zoned leaf	Z z

9. Blue vs. white aleurone — Bl bl

10. Hoods vs. awns — K k

11. Rough vs. smooth awn — R r

12. Long vs. short haired rachilla — S s

13. Normal vs. brachytic plant — Br br

14. Normal vs. ribbon grass leaves (streaked) — Rb rb

15. Normal vs. glaucous sheaths — Gs gs
Classification for normal (non-glaucous) versus glaucous sheath can be made clearly in plants on which the sheath is exposed and until the plants are almost mature.

16. Long vs. short glume hairs — #3 #2

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

B 209	3951-2 x grandpa
B 211	Cold temp. Alb. x Brachytic
B 223	Cold temp. Alb. x awnless
B 224	Cold temp. Alb. x Hooded (Um.)
B 253	Normal 1483-2 x White deficiens
B 284	1462-2 x C. I. 3951
B 311	E e x Colsess I Bl Bl
B 314	lg_2lg_2 x Colsess I Bl Bl
B 316	E. 36 - 503 - 3 lg x Zoned leaf
B 318	Zoned leaf Colorado x C. I. 6780
B 326	C. I. 3951-2 x Brachytic
B 328	C. I. 3951-2 x 149-1-2
B 329	C. I. 3951-2 x Velvon
B 334	Cold Temp. Alb. x Velvon
B 357	9 A - 13 x Black deficiens

B 362 Zoned leaf Colorado x Zoned leaf Wisc.

B 363 9 A - 14 x White deficiens

B 380 E e x Childs (Um.)

B 443 C. I. 460-2 x Colsess I

B 465 Colsess I x Zoned leaf Wisc.

B 475 C. I. 3951-2 x 6 R. Volvon

B 476 Glossy Ingersol gl gl x C. I. 3951-2

B 478 C. I. 3951-2 x lg_2lg_2

B 479 C. I. 3951-2 x Brachytic

B 481 B 149-1-2 x C. I. 3951-2

B 485 Zoned leaf Colorado x C. I. 6780

B 493 Ribbon grass x C. I. 3951-2

B 494 E e x Colsess I Bl Bl

EXPERIMENTAL RESULTS

The experimental results have been grouped into three distinct parts. First, the inheritance of the Mendelian character is discussed, then the character pairs independently inherited and lastly, the association of characters.

Inheritance of Mendelian Characters

Normal vs. long awned outer glume

Table 1 gives the segregation of the F_2 plants. The results indicate that normal versus long awned outer glume differ by a single factor (E e).

Table 1. Segregation of Normal versus long awned outer glume (E e) in the F_2 generation.

Cross No.	E	e	Total	X^2	P
B 380	188	60	248	0.086	.80
B 494	34	14	48	0.444	.50
Total	222	74	296	0.000	.99

Purple vs. white glumes and pericarp

The observed segregation in all the crosses, except cross B 253, involving purple vs. white (Pr pr), shows a ratio of 3 : 1, indicating a one factor difference as shown in table 2. In the case of the cross B 253, the segregation in the F_2 generation is nine purple to seven white, which points to the possibility that there are two complementary factors responsible for the expression of purple.

Table 2. Segregation of purple versus white pericarp (Pr pr) in F_2.

Cross No.	Pr	pr	Total	X^2	P
B 209	176	60	236	0.022	.90
B 284	72	21	93	0.290	.70
B 326	34	12	46	0.029	.90
B 329	44	18	62	0.537	.50
B 475	178	62	240	0.088	.80
B 476	219	78	297	0.252	.65
B 478	112	34	146	0.228	.65
B 479	84	23	107	0.701	.45
B 481	122	37	159	0.254	.65
Total	1044	345	1389	0.019	.90
B 253	343	277	260	0.217	.65

<u>Purple versus white straw</u>

The segregation of the F_2 generation as given in table 3, shows that purple versus white straw differs by two factor pairs, the two factors being complementary to each other and thus giving an F_2 ratio of nine purple to seven white plants. There was no purple coloring in the spikes of this cross, although the awns showed purple.

Table 3. Purple versus white straw (PPcc ppCC), segregation in the F_2 generation.

Cross No.	Purple	White	Total	X^2	P
B 380	138	110	248	0.037	.85

Non-six-row versus six-row

Table 4 shows that segregation for the character pair, non-six-row versus six-row (V v) in the F_2 generation, is monofactorial. Seventeen crosses showed segregation for this condition and all gave reasonable fits.

Table 4. Segregation of Non-six-row versus six-row (V v).

Cross No.	Non-six-row	six-row	Total	X^2	P
B 209	185	55	240	0.556	.50
B 211	147	53	200	0.240	.65
B 223	91	34	125	0.322	.60
B 224	74	21	95	0.425	.50
B 253	467	153	620	0.034	.85
B 284	73	20	93	0.607	.48
B 314	97	37	134	0.488	.50
B 318	37	14	51	0.163	.70
B 326	34	12	46	0.029	.85
B 329	30	11	41	0.073	.80
B 357	59	22	81	0.202	.65
B 362	56	18	74	0.018	.90
B 380	188	60	248	0.086	.80
B 475	181	59	240	0.022	.90
B 479	78	29	107	0.252	.65
B 493	118	47	165	1.069	.30
B 485	103	39	142	0.460	.50
Total	2018	684	2702	0.143	.70

Early versus late heading

A study was made of the date of heading in three crosses. The F_3 lines proved to be of three kinds. One like the early parents, one like the late parents, and the third giving both early and late plants. In the first cross, these three types appeared in approximately 1 : 2 : 1 ratio, while in the other two crosses it appeared to be 9 : 6 : 1 ratio. The early and segregating types were grouped together, thus giving a ratio of 3:1 and 15:1 in the two cases, respectively. In the first cross, early versus late heading differs by a single factor, while in the other two crosses, two factors seem to be responsible for the difference. Table 5 gives the F_2 results of the three crosses.

Table 5. F_2 segregation of early versus late heading.

Cross No.	Early	Late	Total	X^2	P
B 380	185	63	248	0.022	.90
B 475	225	15	240	0.000	.99
B 493	153	12	165	0.295	.65

Black versus white pericarp

The segregation of the F_2 generation as shown in table 6, indicates that black versus white pericarp differ by a single factor pair (B b).

Table 6. Segregation of black versus white pericarp (B b) in the F_2 generation.

Cross No.	B	b	Total	X^2	P
B 223	96	31	127	0.024	.90
B 314	48	18	66	0.182	.70
B 316	30	11	41	0.073	.80
B 357	61	20	81	0.004	.95
Total	235	80	315	0.026	.90

Hulled versus naked caryopsis

Table 7, which gives F_2 segregation, shows that the character pair, hulled versus naked caryopsis, differ by a single Mendelian factor pair (N n).

Table 7. Crosses showing F_2 segregation for hulled versus naked caryopsis (N n).

Cross No.	N	n	Total	X^2	P
B 211	148	52	200	0.107	.70
B 314	103	31	134	0.249	.65
B 316	32	9	41	0.203	.65
B 318	40	11	51	0.320	.60
B 357	58	23	81	0.498	.50
Total	381	126	507	0.006	.95

Green versus zoned leaf

In the cross B 362, the character pair, green versus zoned leaf, segregated in a ratio of three green to one zoned plant in the F_2 generation.

The result shows that green versus zoned leaf differ by a single factor.

Table 8. F_2 segregation of green versus zoned leaf (Z z).

Cross No.	Z	z	Total	X^2	P
B 362	56	18	74	0.018	.90

Hooded versus awned

Table 9 gives the F_2 segregation for hoods and awns. The results indicate that hooded versus awned is dependent upon a single factor pair (K k).

Table 9. Segregation of hooded versus awned in the F_2 generation.

Cross No.	K	k	Total	X^2	P
B 311	214	72	286	0.005	.95
B 314	102	32	134	0.089	.80
B 316	33	8	41	0.658	.50
B 443	113	44	157	0.766	.40
B 465	114	42	156	0.308	.60
Total	576	198	774	0.139	.70

Rough versus smooth awn

The F_2 plants were classed into only two groups, ie., rough and smooth awned plants. Very smooth and semi-smooth were grouped as smooth awned. The F_2 segregation indicates that the character pair rough versus smooth awn depends on a single Mendelian factor (R r) in these crosses.

Table 10. Segregation of rough versus smooth awn (R r) in the F_2 generation.

Cross No.	R	r	Total	X^2	P
B 326	35	11	46	0.029	.90
B 329	49	15	64	0.083	.80
B 357	61	20	81	0.004	.95
B 443	68	29	97	1.241	.30
B 465	33	9	42	0.286	.70
B 475	181	59	240	0.022	.90
B 478	113	33	146	0.447	.50
B 479	81	26	107	0.028	.90
B 493	127	40	167	0.098	.70
Total	748	242	990	0.163	.70

Long versus short haired rachilla

The segregation in F_2, table 11, shows that long versus short haired rachilla differ by a single Mendelian factor pair (S s).

Table 11. Segregation of long versus short haired rachilla (S s) in the F_2 generation.

Cross No.	S	s	Total	X^2	P
B 314	103	31	134	0.249	.65
B 329	44	17	61	0.268	.65
B 465	119	37	156	0.137	.70
B 475	47	18	65	0.251	.65
B 476	150	56	206	0.526	.50

Table 11 - (Continued)

Cross No.	S	s	Total	X^2	P
B 478	102	44	146	2.055	.15
B 493	80	29	109	0.149	.70
Total	647	232	879	0.988	.35

Normal versus brachytic plant

Table 12 shows that in the F_2 generation, the plants segregated in a simple ratio of three normal plants to one brachytic, which means that character is simply inherited and depends on a single factor pair (Br br).

Table 12. Segregation of normal versus brachytic plant (Br br) in F_2 generation.

Cross No.	Br	br	Total	X^2	P
B 479	82	25	107	0.153	.70

Normal versus ribbon grass leaves (streaked)

The inheritance of the character pair, normal versus parallel striped leaves, was studied in the cross, B 493. The results of table 13 show that in the F_2 generation there was segregation in a ratio of three normal to one ribbon grass, indicating that the character pair differ by a single factor pair (Rb rb).

Table 13. Segregation of normal versus ribbon grass leaves (Rb rb) in F_2 generation.

Cross No.	Rb	rb	Total	X^2	P
B 493	125	40	165	0.051	.80

Normal versus glaucous sheath and spike

Table 14 gives the segregation of F_2 plants which indicate that normal versus glaucous sheath segregate in a simple monofactorial ratio of three to one.

Table 14. Segregation of normal versus glaucous sheath and spike (Gs gs) in the F_2 generation.

Cross No.	Gs	gs	Total	X^2	P
B 284	70	23	93	0.004	.95
B 328	77	29	106	0.314	.55
B 334	150	56	206	0.524	.50
B 475	180	60	240	0.000	.99
B 476	209	78	287	0.726	.45
B 478	112	34	146	0.228	.70
B 479	79	28	107	0.078	.80
B 481	125	34	159	1.109	.30
B 493	118	47	165	1.069	.30
Total	1120	389	1509	0.488	.50

Long versus short glume hairs

During the study of the character pair, long versus short glume hairs, difficulty was experienced in the classification of the two contrasting characters in F_2. The F_1 plants were intermediate in length for the glume hairs, and in the F_2 generation segregation seemed to be a gradual gradation between the two extremes of the parents. An attempt was made to classify them into two classes, ie., long or short glumes, but a ratio of one long to one short glume hairs usually resulted. Due to uncertainty of the results, all the crosses given below were grown in F_3 generation as a check on the F_2 results. The F_3 lines proved to be of three kinds. One homozygous for long glume hairs, one with short haired glumes, while the third segregated into long and short hair glumes. These three types appeared in approximately a 1 : 2 : 1 ratio. The results show a one factor difference (#3, #2) between long versus short glume hairs.

In the cross B 314 in table 15, the ratio for the long versus short glume hairs is 1 : 3 instead of 3 : 1, as in all the other crosses. Most likely there was a difference in classification of the F_2 in which the intermediate was listed as short glume hairs (no F_3 data on this cross). There is also a possibility that short glume hair has a tendency towards dominance, which did not show up so much in the other crosses. Table 15 gives the segregation in the F_2 generation as determined by F_3.

Table 15. Long versus short glume hair (#3, #2) segregation in the F_2 generation.

Cross No.	#3	#2	Total	X^2	P
B 357	59	22	81	0.202	.70
B 380	141	47	188	0.000	.99
B 475	45	20	65	1.154	.30
B 479	82	25	107	0.153	.70
B 493	120	45	165	0.455	.50
Total	447	159	606	0.495	.50
Cross No.	#2	#3			
B 314	53	15	68	0.314	.55

Blue versus white aleurone

Table 16 gives the segregation of the plants. The results indicate that character pair, blue versus white aleurone, is dependent upon a single factor pair (Bl bl).

Table 16. Segregation of blue versus white aleurone (Bl bl) in the F_2 generation.

Cross No.	Bl	bl	Total	X^2	P
B 314	52	16	68	0.078	.80
B 363	44	16	60	0.089	.80
Total	96	32	128	0.000	.99

Character Pairs Independently Inherited

Following the study of single contrasting characters, a study for independence between pairs was made. In tables which show the character pairs inherited independently, the columns of frequencies for the four classes are headed by the general symbols: XY, Xy, xY, and xy. X^2 was used to test for the character pairs concerned.

The independence of long versus short glume hairs (#3, #2) in relation to the various other characters found in the same crosses is shown in table 17.

Table 17. Character pairs which are inherited independently - F_2 data.

Cross	Character	XY	Xy	xY	xy	X^2	P
B 475	Pr pr vs. #3 #2	32	14	13	6	0.107	.99
B 479	" "	65	19	17	6	0.979	.80
B 493	" "	83	26	37	19	6.647	.10
	Total	180	59	67	31	5.678	.15

Table 17 - (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	V v vs. #3 #2						
B 357		40	19	19	3	2.433	.50
B 380		107	31	34	16	2.108	.50
B 475		30	15	15	5	2.692	.50
B 479		62	16	20	9	1.677	.70
B 493		89	28	31	17	4.772	.20
	Total	328	109	119	50	4.810	.20
	Ea ea vs. #3 #2						
B 380		107	34	34	13	0.236	.95
B 475		110	40	7	5	2.696	.30
B 493		40	18	5	2	3.420	.30
	B b vs. #3 #2						
B 357		43	18	16	4	0.931	.80
	N n vs. #3 #2						
B 357		43	15	16	7	0.931	.80
	N n vs. #2 #3						
B 314		41	11	12	4	0.496	.90
	R r vs. #3 #2						
B 357		45	16	14	6	0.317	.95
B 493		89	36	31	9	1.152	.70
	Total	134	52	45	15	0.923	.80

Table 17 - (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	S s vs. #3 #2						
B 314		39	11	14	4	0.392	.95
B 475		33	14	12	6	1.544	.70
B 493		60	20	21	8	0.259	.95
	Total	132	45	47	18	0.733	.85
	Br br vs. #3 #2						
B 479		60	22	20	3	2.408	.50
	Rb rb vs. #3 #2						
B 493		89	36	31	9	1.152	.90
	Gs gs vs. #3 #2						
B 475		30	14	15	6	3.021	.40
B 479		59	20	23	5	0.879	.85
B 493		84	34	36	11	2.014	.55
	Total	173	68	74	22	3.705	.30
	Bl bl vs. #2 #3						
B 314		40	12	13	3	0.497	.90

In almost all the crosses, the observed frequencies agree very well with theoretical, giving a low X^2 and satisfactory P value. This P value is interpreted as meaning that deviation as large as in individual cases or larger might be expected much more than five times in one hundred trials on the basis of random sampling. In other words, the probabilities are high that all the two factor pairs mentioned above are inherited independently or are located fifty or more genetic units apart.

Independence of the character pair, normal versus glaucous sheath and spikes relation to other characters by crosses is shown in table 18.

Table 18. Independent inheritance of the characters in relation to normal versus glaucous sheath and spike - F_2 data.

Cross	Character	XY	Xy	xY	xy	X^2	P
	Pr pr vs. Gs gs						
B 284		54	18	16	5	0.305	.95
B 328		54	21	22	8	1.108	.80
B 475		135	43	45	17	0.356	.95
B 476		168	51	51	27	4.629	.20
B 478		84	28	28	6	1.142	.80
B 481		101	21	24	13	6.176	.10
B 479		58	26	26	2	5.166	.15
	Total	654	208	212	78	0.926	.80
	Ea ea vs. Gs gs						
B 475		171	9	54	6	1.920	.55
B 493		111	7	42	5	2.848	.40
	Total	282	16	96	11	3.957	.30
	R r vs. Gs gs						
B 284		57	19	14	3	2.598	.45
B 475		135	46	45	14	0.089	.99
B 478		87	26	25	8	0.703	.85
B 493		91	34	27	13	1.540	.70
	Total	370	125	111	38	1.228	.75
	S s vs. Gs gs						
B 475		31	16	13	5	2.309	.50

Table 18 - (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	S s vs. Gs gs						
B 476		106	44	45	11	2.915	.40
B 478		75	27	37	7	4.502	.20
B 493		55	25	23	6	2.086	.55
	Br br vs. Gs gs						
B 479		60	22	19	6	0.315	.95
	V v vs. Gs gs						
B 284		58	15	12	8	3.477	.30
B 475		133	48	47	12	0.918	.80
B 479		54	24	25	4	3.704	.30
B 493		83	34	35	13	2.574	.40
	Total	270	106	107	29	3.708	.30

These data, presented in table 18, indicated that nearly all the pairs of contrasting characters are inherited independently. This is shown by P value ranging from .1 to .9.

On examining the last section in the above table, ie., the relation of non-six-row versus six-row and normal versus glaucous sheath, there seems to be some association or weak linkage between the two pairs of characters. On calculating the percentage recombination for the above mentioned crosses, recombination values were found, 37.0 ± 5.0, 45.0 ± 5.1, 36.0± 8.5, 48.5 ± 5.8, respectively. In view of high standard errors attached to each cross and also considering the fact that Gs vs. gs character pair is independent of the character pair Pr vs. pr, located in the same linkage group as the V vs. v (see table 18), it seems that perhaps the two character pairs are independent of each other.

Independence of normal versus ribbon grass and other characters is shown in table 19. In each cross and for every character the observed segregation approached an expected ratio for independence. When tested for goodness of fit, a satisfactory P value was obtained. A fit as bad or worse could be expected way above five out of one hundred trials due to chance alone.

Table 19. Independent inheritance of normal versus ribbon grass in relation to other characters.

Cross	Character	XY	Xy	xY	xy	X^2	P
	Rb rb vs. Rr						
B 493		97	28	28	12	1.022	.90
	Rb rb vs. Ss						
B 493		59	20	23	9	1.641	.80
	Rb rb vs. Vv						
B 493		91	34	26	14	2.445	.50
	Rb rb vs. Ea ea						
B 493		113	9	37	3	0.379	.95

Table 20 shows that early and late heading character is independent of the character pairs rough versus smooth (R r) and long versus short rachilla hairs (S s). A P value of above .5 in the three crosses is a fair fit and a good indication of independence.

Table 20. Independence of early versus late heading in relation to character pairs (R r) and (S s).

Cross	Character	XY	Xy	xY	xy	X^2	P
	Ea ea vs. R r						
B 475		168	57	13	2	1.102	.80
B 493		115	38	10	2	0.814	.85
	Total	283	95	23	4	1.716	.65

Table 20. (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	Ea ea. vs. S s						
B 475		73	28	7	1	1.398	.85

The independence of non-six-rowed versus six-rowed and other characters is shown in table 21. The observed frequencies agree very well with the expected, which in turn shows a low X^2, thus, increasing the probability that each of the two pairs of characters are inherited independently.

Table 21. Non-six-rowed versus six-rowed and other characters, showing independence.

Cross	Character	XY	Xy	xY	xy	X^2	P
	V v vs. B b						
B 223		70	24	21	10	0.880	.80
B 314		36	12	13	5	0.263	.95
B 316		25	5	7	4	1.970	.60
B 357		43	16	18	4	0.931	.80
	Total	174	59	57	23	0.678	.85
	V v vs. R r						
B 326		25	9	10	2	0.531	.90
B 329		39	11	10	4	0.667	.85
B 357		43	16	18	4	0.931	.80
B 475		135	46	46	13	0.311	.95
B 493		89	28	36	12	1.540	.70
	V v vs. S s						
B 314		76	21	27	10	3.154	.40
B 475		32	13	15	5	1.488	.70
B 493		58	17	22	12	4.826	.20

Table 21 - (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	V v vs. Br br						
B 479		62	16	20	9	1.677	.65
	V v vs. K k						
B 316		23	7	10	1	1.710	.65
	V v vs. N n						
B 211		114	40	32	10	1.442	.70
B 314		76	21	27	10	0.026	.99
B 318		30	7	10	4	0.974	.80
B 357		42	17	16	6	0.712	.85
	Total	262	85	85	30	0.122	.99

Table 22 gives the F_2 data of factor pairs, hulled versus naked caryopsis, in relation to other characters. These results indicate that the factor pairs N n and K k, Bl bl, B b, R r, or S s are inherited independently.

Table 22. Independent inheritance of hulled versus naked caryopsis in relation to other characters.

Cross	Character	XY	Xy	xY	xy	X^2	P
	Nn vs. Kk						
B 314		76	27	26	5	1.536	.70
B 316		26	6	7	2	.929	.80
B 463		32	15	10	3	1.629	.70
	Total	134	48	43	10	1.898	.60
	N n vs. Bl bl						
B 314		40	13	12	3	0.497	.90
B 463		31	13	10	3	0.668	.85
	Total	71	26	22	6	0.796	.85

Table 22 - (Continued)

Cross	Character	XY	Xy	xY	xy	X^2	P
	N n vs. B b						
B 314		37	14	11	4	0.370	.95
B 316		23	9	7	2	0.409	.95
B 357		44	14	17	6	0.536	.90
	Total	104	37	35	12	0.123	.99
	N n vs. R r						
B 357		44	14	17	6	0.536	.90
B 314		79	24	24	7	0.501	.90

Independence of the character pair, long versus short rachilla hair, to the other character is shown in the table 23. In most of the crosses, the X^2 value is relatively low, indicating a good fit for independence.

Table 23. Long versus short rachilla hair and other characters, showing independence.

Cross	Character	XY	Xy	xY	xy	X^2	P
	S s vs. Pr pr						
B 475		34	13	12	6	1.161	.70
B 476		101	49	45	11	6.020	.10
B 479		79	23	33	11	2.359	.50
	Total	214	85	90	28	4.325	.20
	S s vs. B b						
B 314		39	14	9	4	1.232	.80
	S s vs. K k						
B 314		79	24	23	8	0.421	.95
	S s vs. Bl bl						
B 314		42	11	8	5	2.525	.50

Table 24 gives F_2 data for the factor pairs, purple versus smooth awns (R r) and normal versus brachytic plant (Br br). The P value of .70 in the first case and .45 in the second case shows a fair fit. It can be concluded that these factor pairs are independently inherited.

Table 24. Independence of purple versus white glumes and pericarp in relation to rough versus smooth awns and normal versus brachytic character.

Cross	Character	XY	Xy	xY	xy	X^2	P
	Pr pr vs. R r						
B 284		61	11	15	6	4.166	.20
B 475		133	45	48	14	0.296	.95
B 478		87	25	26	8	0.703	.85
Total		281	81	89	28	1.494	.70
	Pr pr vs. Br br						
B 479		67	17	15	8	2.774	.45

Segregation of black versus white pericarp in relation to rough versus smooth awns (R r) and hooded versus awned (K k) is presented in table 25. In no case is the P value less than .80 which shows a good fit. The probabilities are, therefore, high that these two factor pairs are inherited independently.

Table 25. Black versus white pericarp (B b) in relation to rough and smooth awn (R r) and hooded versus awned (K k), showing independence.

Cross	Character	XY	Xy	xY	xy	X^2	P
	B b vs. R r						
B 357		45	16	16	4	0.317	.95
	B b vs. K k						
B 314		36	12	15	3	0.909	.80
B 316		25	6	8	2	0.756	.85
	Total	61	18	23	5	1.079	.80

Table 26 shows the inheritance of early versus late heading (Ea ea) in relation to non-six-rowed versus six-rowed (V v) and purple versus white straw. When tested for goodness of fit, maximum X^2 value was 2.880 with a corresponding P value of .50. It can be concluded that these characters are inherited independently. A worse fit than this could be expected due to chance alone in one out of two trials.

Table 26. Independent inheritance of early versus late heading in relation to non-six-rowed versus six-rowed and purple versus white straw.

Cross	Character	XY	Xy	xY	xy	X^2	P
	Ea ea vs. V v						
B 380		137	48	51	12	1.319	.70
B 475		172	53	9	6	2.050	.50
B 493		107	46	10	2	2.880	.50
	Ea ea vs. P p						
B 380		99	86	39	24	1.413	.70

<u>Segregation of Character Pairs That Showed Correlation and Possible Linkage</u>

The inter-relation of character pairs that showed considerable deviation from theoretical independent segregation is given in the following table.

Table 27. Character pairs which showed linkage.

Cross No.	Character	XY	Xy	xY	xy	X^2	P	% Recombination
	Pr pr vs. V v							
B 209		150	20	16	37	70.285	less than .01	17.8 ± 2.8
B 284		66	6	7	14	24.864	less than .01	14.5 ± 4.0
B 326		31	3	3	9	21.401	less than .01	12.5 ± 5.2
B 329		40	8	4	10	16.566	less than .01	19.0 ± 5.6
B 475		168	10	13	49	125.111	less than .01	10.0 ± 2.0
B 479		77	7	1	22	66.374	less than .01	5.5 ± 2.2
B 493		105	4	14	44	142.621	less than .01	8.0 ± 2.19
	Total	637	58	58	185	453.10	less than .01	13.0 ± 1.2
B 253		312	155	31	122	100.768	less than .01	6.0 ± 1.5
	P p vs. V v							
B 380		128	10	60	50	47.870	less than .01	12.5 ± 3.3
	P p vs. E e							
B 380		96	42	92	18	6.624	.08	25.0 ± 13.7
	V v vs. E e							
B 380		137	51	51	9	4.215	.20	39.5 ± 5.29
	Ea ea vs. E e							
B 380		134	51	54	9	4.587	.20	38.5 ± 5.33
	E a ea vs. Pr pr							
B 475		170	8	55	7	3.793	.30	32.5 ± 9.0
B 493		96	10	54	2	10.458	.02	33.5 ± 15.3
	K k vs. Z z							
B 362		34	14	22	4	6.240	.10	38.0 ± 9.7
	K k vs. Bl bl							
B 314		45	7	7	9	11.686	less than .01	24.0 ± 6.1
B 443		51	15	15	16	17.638	less than .01	33.0 ± 6.0
B 463		27	13	17	3	4.711	.10	36.0 ± 7.7
	R r vs. S s							
B 475		36	18	11	0			
B 478		69	44	33	0			

Table 27 - (Continued)

Cross No.	Character	XY	Xy	xY	xy	X^2	P	% Recombination
B 493	R r vs. S s	58	25	22	4			
	Total	163	87	66	4	27.155	less than .01	22.5 $\pm$ 2.7

An examination of table 27 shows the values of P were very low. It indicates a poor fit for independent inheritance. In other words, there is likely a linkage between the two contrasting factor pairs.

Data in table 27 indicated that the factor pair (V v) for non-six-row versus six-row is linked with the factor pair (Pr pr) for purple versus white glumes and pericarp with about 13.0 $\pm$ 1.2 per cent crossing over. All the crosses involved were in the coupling phase. Recombination value for the total was found which gave a X^2 value of 453.10 making P much less than .01.

In the cross B 253, in which two complementary factors were involved for the purple pigmentation, the character pair purple versus colorless, white glume and pericarp is associated with (V v) non-six-row versus six-row giving a recombination of 6.0 $\pm$ 1.5 per cent.

Purple versus colorless straw (P p) was found to be correlated with the contrasting pairs, (V v) for non-six-row versus six-row and (E e) normal versus long awned outer glume with recombination values of 12.5 $\pm$ 3.3 and 25.0 $\pm$ 13.7, respectively.

Normal vs. long awned outer glume, when tested for independence in relation to (V v) for non-six-row versus six-row and (Ea ea) for early versus late heading, gave a X^2 of 4.215 and 4.587, respectively. P values in the two cases were about .20. No doubt, P is not low enough to suggest association, yet on examining the data in the table, there seems to be a weak linkage between the above mentioned characters. The crossing over value, when calculated by the product method, was 39.5 ± 5.29 per cent in the first case and 38.5 ± 5.33 per cent in the second.

In crosses B 475 and B 493 there was a correlation between the factor pairs early versus late heading and purple versus white glumes and pericarp. The first cross is in the coupling phase, while the second is in repulsion. In the repulsion cross, the recombination fraction was .335 ± .156, while in the coupling cross, it was .325 ± .090. To combine these two, we may take the weighted average, using the amount of information supplied by each cross. The amount of information is the reciprocal of the square of the standard error. For the repulsion cross this will be $1/(.156)^2 = 75$, and for the coupling cross, $1/(.09)^2 = 123$. The weighted average of the recombination fraction will be $[(.335 \times 75) + (.325 \times 123)] \;/\; (75 + 123) = .328$ or 32.8 per cent recombination. The S. E. of this average percentage recombination will be the square root of the reciprocal of the total amount of information supplied by both crosses or $\sqrt{1/(75 + 123)} = .071$ or 7.1 per cent.

Factor pair K k, for hooded versus awned was linked with Z z, for normal versus zoned leaf with a recombination value of 38.0 ± 9.7 per cent.

The crossing over value of K k, for hooded versus awned and Bl bl, for blue versus white aleurone, was checked in three crosses, B 314, B 443, and B 463. The values were 24.0 ± 6.1 per cent, 33.0 ± 6.0 per cent, and 36.0 ± 7.7 per cent, respectively. The three estimates were combined to get a weighted average, in the same way as described previously. The result was 30.4 ± 4.07 per cent.

The total of the three crosses, B 475, B 478, and B 493, gave a recombination percentage of 22.5 ± 2.7 between the character pairs R r, for rough versus smooth awn and S s for long versus short rachilla hair.

Possible new associations

During the study of the inheritance and inter-relation of character pairs, a wide deviation in F_2 segregation from the expected ratio was often found. Table 28 is made up of the few character pairs suggesting association among them and possible linkage.

Table 28. Characters in barley showing correlations.

Cross No.	Character	XY	Xy	xY	xy	X^2	P	% Recombination
B 314	K k vs. #2 #3	43	8	10	7	4.732	.2	32.5 ± 7.17
B 465	K k vs. #3 #2	94	20	24	18	11.293	.01	33.5 ± 4.8
B 380	P p vs. #3 #2	84	11	54	36	22.145	less than .01	20.5 ± 4.2
B 493	R b rb vs. Gs gs	84	41	34	6	6.216	.10	36.0 ± 6.6

The character pair #3 #2 for long versus short glume hair was found to be independent of the linkage groups, I, II, III, V, and VII, (see table 17). Table 28 indicated that the contrasting pair seem to be associated with factor pair K k, for hooded versus awned found in linkage group IV, with a recombination value of 32.5 ± 7.17 per cent and 33.5 ± 4.8 per cent, in the crosses, B 314 and B 465, respectively. As indicated previously, it is likely that the intermediate segregates for glume hairs in the cross, B 314, were classed as short glume hairs instead of long glume hairs, as was done in all the others crossed included for its study. But the over-all picture for the crossing over studies did not change due to these irregular cases.

Cross B 380 included the relationship of P p, for purple versus white straw to long versus short glume hairs (#3, #2). When tested for independence, a X^2 value of 22.1 was obtained with a P value less than .01. It is a poor fit for independent inheritance. Recombination percentage, as found with the help of Immer and Burnham's table (17), was equivalent to 20.5 ± 4.2 per cent. It should be remembered that the factor pair P p, for purple versus white straw was found to be linked with V v, for non-six-row versus six-row (see table 27). Perhaps one of the complementary factors for the purple color is located in linkage group IV and the other in linkage group I.

The character pair Gs gs, for normal versus glaucous sheath and spike, was found to be independent of linkage groups, I, IV, V, and VII, (see tables 17 and 18). Cross 380 (table 28) shows association for the factor pairs Gs gs for normal versus glaucous sheath and spike in relation to Rb rb, for normal versus ribbon grass leaves. The percentage recombination was about 36.0 ± 6.6 per cent. The location of Rb rb for normal versus ribbon grass, has not yet been fixed. During this study, the character pair Rb rb was found to be independent of #3 #2, R r, S s, V v, and Ea ea. (See tables 17 and 19).

DISCUSSION

One handicap in barley linkage studies has been the lack of adequate known genes in at least four of the chromosomes. When the few known genes lie close to each other as do the three albino genes in linkage group VI, a new factor pair may appear to be independent of them when in reality it is located in the same chromosome, but fifty or more genetic units from the nearest located gene.

Studies on the inheritance of the two characters, #3, #2, and Rb rb, for long versus short glume hairs and normal versus ribbon grass leaves, not reported in the literature previously, showed definitely that there is a single factor difference in their inheritance.

Segregation of the character pair (Pr pr) for purple versus white pericarp and glume, in F_2 generation of nine crosses (table 2) indicated a one factor difference, a result in accordance with earlier workers. In one cross, # 253 (table 2), two complementary factors were found to be responsible for the expression of purple. Also, in case of contrasting pairs (P p) for purple versus white straw, two complementary factors were necessary to account for its expression. Previously, Robertson (30) has reported one factor difference for the later character pair.

In the present study, semi-smooth and smooth awns were grouped in one class and rough awns in the other. Using this method, the character pair, rough vs. smooth awns appears to depend on a single factor difference. But, after examining the work done by other investigators, where degrees of barbing are considered, the most logical explanation of rough awns is on the basis of two main factor differences. When the main factor R is present, a fully rough awn results, when the second main factor R_1 is present, in the absence of R, a semi-smooth awn results, and when both are absent ($r\ r_1$)

a smooth awn is produced. When either R R or R_1 R_1 is involved in a cross with r r_1, a 3 : 1 ratio is the result. This can be explained on the basis of two independently inherited factors, with R being epistatic to R_1.

Factor pair (#3 #2) for long versus short glume hairs was found to be independent of the genes in linkage groups I, II, III, V, and VII. Glume hairs were found to be associated with (K k) for hoods versus awns, a factor pair in the IV linkage group. Glume hairs also suggested linkage with the factor pair (Pc pC), for purple versus white straw, meaning, therefore, that one of the factor pairs for purple pigment might be located in the linkage group IV.

Factor pair (Gs gs) for normal versus glossy stems, which is not yet located, was found to be independent of linkage groups I, V, and VII. Immer and Henderson (18) reported it to be independent of the linkage groups I, II, III, and IV. From the above two statements, it can be inferred that the factor pair is either located in the linkage group VI or in other groups, it being some fifty or more genetic units apart from the known factor pairs with which it was compared. In the present study, the character pair was found to be associated with the factor pair (Rb rb) for normal versus ribbon grass leaves, a pair, the location of which is also unknown. The later contrasting pair was found to be independent of linkage groups I and V.

Recombination percentage for the character pairs Pr pr and V v agreed with the results of Myler (26) and Woodward (47). Linkage intensity between the factor pairs P p and V v reported in this paper, is in harmony with the work of Robertson (30).

There was some variation in the linkage relationships of the factor pairs K k vs. Z z, K k vs. Bl bl, R r vs. S s, and V v vs. E e, as compared to the result of other investigators. Unless synthetic stocks, the parents with characters in proper combinations are built up, such variation in linkage studies will likely continue.

SUMMARY

The inheritance and inter-relation of sixteen barley character pairs were studied. In some of the crosses a check was made on the F_2 results by studying the segregation in F_3.

In the F_2 progeny the following character pairs exhibited a single factor difference in their inheritance:

Normal versus long awned outer glume	(E e)
Purple versus white glumes and pericarp	(Pr pr)
Non-six-row versus six-row	(V v)
Early versus late heading	(Ea ea)
Black versus white pericarp	(B b)
Hulled versus naked caryopsis	(N n)
Green versus zoned leaf	(Z z)
Hooded versus awned	(K k)
Rough versus smooth awned	(R r)
Long versus short haired rachilla	(S s)
Normal versus brachytic	(Br br)
Normal versus ribbon grass	(Rb rb)
Normal versus glaucous sheath	(Gs gs)
Long versus short glume hair	(#3 #2)
Blue versus white aleurone	(Bl bl)

The segregation of the F_2 plants for the following factor pairs can be best explained on a two factor difference.

Purple versus white glumes and pericarp	(Prc, prC)
Purple versus white straw	(Pc, pC)
Early versus late heading	($Ea\ Ea_1$, $ea\ ea_1$)

Independent inheritance was found between the following pairs of characters:

#3 #2 and Pr pr, V v, Ea ea, B b, N n, R r, S s, Br br, Rb rb, and Gs gs

Gs gs and Pr pr, Ea ea, S s, Br br, and V v

Rb rb and R r, S s, V v, Ea ea

Ea ea and R r, S s, V v, and P p

V v and B b, R r, S s, Br br, K k, and N n

N n and K k, Bl bl, B b, R r, and S s

S s and Pr pr, B b, K k, Bl bl

Pr pr and R r, Br br

B b and R r and K k

The character pairs that showed linkage are listed below. The percentage recombinations with probable error in each case is presented.

Pr pr vs. V v	13.0 ± 1.2
P p vs. V v	12.5 ± 3.3
P p vs. E e	25.0 ± 13.7
Ea ea vs. Pr pr	32.8 ± 7.1
Ea ea vs. E e	38.5 ± 5.33
V v vs. E e	39.5 ± 5.29
K k vs. Z z	38.0 ± 9.7
K k vs. Bl bl	30.4 ± 4.07
R r vs. S s	22.5 ± 2.7

Possible linkages were found in the following:

K k vs. #3 #2	33.5 ± 4.8
Pc PC vs. #3 #2	20.5 ±4.2
Rb rb vs. Gs gs	36.0 ± 6.6

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