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An Inheritance and Linkage Study of Barley with Special Emphasis on Purple Pigmentation of the Auricle

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AN INHERITANCE AND LINKAGE STUDY OF BARLEY WITH SPECIAL EMPHASIS ON PURPLE PIGMENTATION OF THE AURICLE

by

Devon Lyle Doney

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of the requirements for the degree

of

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Devon Lyle Doney

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INTRODUCTION

New and better adapted varieties of crop plants have resulted from the application of the principles of genetics. Fundamental research in the field of barley genetics has helped the plant breeder in developing better varieties for specific uses and adaptability.

Barley is one of the best cultivated crop plants for making genetic studies. It has a wide range of adaptability, exhibits a host of contrasting genetic characters, is a simple diploid with only seven pairs of chromosomes, and all the cultivated species are interfertile.

The mode of inheritance of nearly 200 characters has been studied, many of whose genes have been mapped and assigned to one of the seven chromosomes.

The inheritance and linkage of the factors responsible for anthocyanin pigmentation in the auricle of barley is the primary purpose of this study.

Other character pairs are included in this study for possible linkages with purple auricle or with each other. These linkages may help materially in mapping genes on their respective chromosome.

A new system of designating the linkage groups and chromosomes with Arabic numbers, adopted by the Fourth Annual Barley Research Worker's Conference, will be followed throughout this study. Comparison of the new and old systems is given in table 1.

Table 1. Correspondence of the various systems of designating chromosomes and linkage groups in barley.

New linkage group and chromosome No.	Previous linkage groups	Key marker gene pairs
1	III - VII[a]	N n, Br br
2	I	V v
3	VI	Uz uz
4	IV	K k
5	II	B b
6	- -	O o
7	V	R r

[a] Kramer, Veryl, and Hanson (21) from translocation experiments found these two groups to be separate arms of the same chromosome.

REVIEW OF LITERATURE

The literature on genetic studies of barley has been reviewed by several workers. One of the most comprehensive reviews was made by Smith (37) who reviewed 1,400 articles, 900 of which are listed in his bibliography. Robertson and co-workers have also published several such reviews (31), (35).

This review will be confined to the gene pairs involved in this study.

Inheritance of Gene Pairs

Factors in chromosomes

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike. The complicated problem of number of kernel rows and fertility of lateral florets was given a reasonable explanation by Woodward (47). Harlan (12), (13) had previously classified cultivated barley into four species on the basis of the fertility of lateral florets. Woodward suggested the number of rows of kernels is determined by an allelic series of four genes. These are designated (V^t) deficiens, (V) weak two-rowed, (V^d) strong two-rowed and (v) six-rowed with dominance incomplete. The fertility of the lateral florets is determined by (i), (I), and (I^h) with dominance in decreasing order as listed.

The (I) series tend to modify the expression of the (V) genes, and sometimes confuse the classification.

Daave (5), Immer and Henderson (17), Tedin (41), Gillis (10), Buckley (4), Neatby (26), Leonard (23), and Robertson (29) have also substantiated Woodwards conclusions on the fertility of the lateral florets.

Normal (E) versus long awned outer (e) glumes. A number of workers have reported the dominance of normal versus long awned outer glumes by a simple Mendelian ratio. Among the workers reporting a single gene difference were Immer and Henderson (17), Robertson, Immer, Wiebe, and Stevens (34), Hor (15), Bose (3), Swenson (38), Heiner (14), Isom (19), Gill (9), Imam (16), and Woodward (48).

Normal (Tr) versus triple (tr) awned. A monofactorial inheritance for normal versus triple awned lemma with triple awns being recessive has been reported by Immer and Henderson (17), Imam (16), Isom (19), Heiner (14) and LeBaron (22). Kasha and Walker (20) reported finding another gene for triple awns in chromosome 3.

Purple (Pr) versus non-purple (pr) straw. A simple Mendelian ratio has been observed by Robertson (20) and Woodward (46). A two factor mode of inheritance has also been suggested by the work of Gill (9), Al-Jibouri (1), Heiner (14), and Imam (16). Woodward (personal communication) suggested that environmental influences can cause a considerable variation in the color expression of purple straw.

Purple (Re_2) versus non-purple (re_2) lemma and pericarp. Buckley (4) reported a single gene inheritance in some crosses but in other crosses he considered the possibility of two complementary genes that inhibit the expression of purple when both are dominant.

Woodward and Thieret (49) obtained 3:1 ratios from crosses in which one parent was purple and one non-purple. In other crosses in which both parents were non-purple 9:7 ratios were observed, indicating a two factor inheritance. Al-Jibouri (1) also obtained a 9:7 ratio from crosses between non-purple parents. Gill (9), Heiner (14), and Imam (16) reported both 3:1 and 9:7 ratios.

Normal (Li) versus liguleless (li). Takashashi (40) obtained good 3:1 ratios in normal versus liguleless crosses. Heiner (14), Iman (16) and LeBaron (22) reported similar results.

Lax (L) versus dense (l) spike. Biffon (2) observed a wide range of spike densities and suggested a quantitative inheritance. Wexelsen (42), (43) classified five different factors that affect spike density and located them in several of the linkage groups. Hor (15), Neatby (26) and Heiner (14) reported monofactorial segregations for a spike density gene located in linkage group 2. Takahashi (40) suggested that there are a number of different factor pairs that affect spike density.

Early (Ea) versus late (ea) maturity. Time of maturity has been reported to be affected by several factors. Woodward (48) and Griffee (11) reported a monogenic inheritance for an early maturity factor pair found in group 2. Frey (7) found one factor for earliness in group 5, while Wexelsen (43) found evidence for one factor pair for earliness in group 1. Neatby (26) reported that several factors affect the expression of earliness.

Factors in chromosome 1

Covered (N) versus naked (n) caryopsis. Buckley (4), Daane (5), Gill (9), Heiner (14), Hor (15), Imam (16), and Neatby (26) have all reported a monogenic mode of inheritance for covered versus naked caryopsis.

Normal (Br) versus brachytic (br) habit. Swenson (38) conducted a very comprehensive study of the growth habit and genetics of the brachytic habit. His results indicated a single recessive gene was responsible for the brachytic habit. Powers (28) and Robertson (31) obtained similar Mendelian ratios.

Factors in chromosome 4

Long (k_1) versus short (k_2) awns. Myler (25) concluded that two gene pairs affected the awn length. Myake and Imai (Smith 37) suggested that in some crosses there were three genes responsible for awn length while in other crosses there was only one factor difference. LeBaron (22) found a 3:1 ratio in crosses between long and short awns.

Normal (Gl) versus glossy (gl) leaf. Ratios of 3:1 have been reported by Immer and Henderson (17), Robertson and Coleman (32), Smith (37), Iman (16) and Heiner (14). Low probability values were obtained in several of these studies. Heiner (14) attributed this to the poor seedling vigor of the glossy leaf plants.

Normal (Z) versus zoned (z) leaf. Immer and Henderson (17) and Heiner (14) reported monogenic ratios for normal versus zoned leaf. Heiner concluded that low probability values often occur because of poor seedling vigor.

Factors in chromosome 7

Rough (R) versus smooth (r) awns. Simple Mendelian ratios for the rough versus smooth awn character have been reported by Daane (5), Wexelsen (43), Hor (15) and Griffee (11). Robertson, Deming and Koonce (33) suggested a two factor inheritance for rough versus smooth awns. Vavilov (Griffee 11) found varying degrees of smoothness on the awns.

Unassigned factor pairs

Purple (Pau) versus non-purple (pau) auricle. Ubisch (Smith 37) reported that red color in the auricle was dominant. Ratios of 3:1 and 10:6 for red to white color were found by Huber (Smith 37). Huber also stated that one gene was responsible for the formation of anthocyanin in the auricle; however, this gene would only express itself in the heterozygous condition or when another intensifier gene was also present in the dominant condition. Grassner and Straib (Smith 37) observed that anthocyanin development could be increased by a deficiency of nitrogen or a high concentration of CO_2. A 3:1 ratio for purple over white was reported by LeBaron (22), who also found close linkage of purple auricle with purple lemma and pericarp. A monogenic ratio was also reported by Murty (24).

Normal (Rb) versus ribbongrass (rb) leaf. The inheritance of ribbongrass has been reported by Robertson, Wiebe, and Shands (35) and Heiner (14) to be influenced by a single recessive gene.

Normal (Gs) versus glossy (gs) stem. Several workers including Immer and Henderson (17), Gill (9), Heiner (14), and LeBaron (22) have reported a monofactorial inheritance for glossy stem.

Normal (Da) versus dehiscent (da) awns. Huber (Smith 37) reported that the dropping of awns at maturity was conditioned by one gene. Tavcar (Smith 37) suggested that while one gene controlled the dropping of awns at maturity in some crosses, two genes determined the deciduousness in other crosses.

Long (Gh) versus short (gh) glume hairs. Single factor pair ratios have been obtained by Hor (16), Al-Jibouri (1), Heiner (4) and Iman (16).

Reported Linkages

Linkages in chromosome 2

Two-rowed (V) versus six-rowed (v) in relation to other factor pairs.

Recombination %	Phase	Authority
	(V v) in relation to (Pr pr)	
20.5 ± 3.4	coupling	Heiner (14)
16.0 ± 2.6	coupling	Woodward (48)
9.0 ± 0.7		Robertson (30)
23.2 ± 2.2	coupling	Iman (16)
12.5 ± 3.3		Gill (9)
13.0 ± 1.2		Gill (9)
9.09		Takahashi, Yamamoto, Jasuda and Itamo (40)
	(V v) in relation to (Re_2 re_2)	
18.6		Buckley (4)
13.2		Woodward (49)
13.0 ± 1.2		Gill (9)
12.5 ± 2.4		Al-Jouri (1)
17.1 ± 0.7	coupling	Woodward (48)
14.0 ± 1.3	coupling	Woodward (48)

(V v) in relation to (Re_2 re_2)

10.0 ± 4.8	repulsion	Woodward (48)
22.1 ±16.3	repulsion	Woodward (48)
15.0 ± 2.2	coupling	Heiner (14)
14.5 ± 6.5	repulsion	Heiner (14)

(V v) in relation to (E e)

24.7		Bose (3)
26.6 ± 0.6		Robertson (34)
28.0 ± 1.2		Immer and Henderson (17)
26.7 ± 1.7		Swenson (39)
27.0 ± 5.7	repulsion	Woodward (48)
26.5 ± 2.0	coupling	Woodward (48)
30.0 ± 4.7	repulsion	Heiner (14)
31.0 ± 2.4	coupling	Heiner (14)
28.1		Takahashi, Yamamoto, Jasuda and Itamo (40)

(V v) in relation to (L l)

40.0		Wexelsen (43)
Correlated		Neatby (26)
41.3 ± 2.6	coupling	Woodward (48)
33.5 ± 3.5	coupling	Heiner (14)
37.6 ± 3.0	coupling	Imam (16)

(V v) in relation to (Tr tr)

30.0		Woodward (48)
41.0		Woodward (48)
39.0 ± 3.0		Immer and Henderson (17)

(V v) in relation to (Li li)

33.3 ± 2.9	coupling	Woodward (48)
39.5 ± 5.4	repulsion	Woodward (48)
43.1 ± 2.7	repulsion	Imam (16)
39.3 ±		Takahashi, Yamamoto, Jasuda and Itamo (40)

(V v) in relation to (Ea ea)

13.5 ± 2.4	coupling	Woodward (48)
42.0		Griffee (11)
correlated		Wexelsen (43)

Purple (Re_2) versus non-purple (re_2) lemma and pericarp in relation to other factor pairs.

Recombination %	Phase	Authority
	(Re_2 re_2) in relation to (L l)	
41.3 ± 2.6	coupling	Woodward (48)
35.0 ± 5.8	coupling	Heiner (14)
36.0 ± 5.9	repulsion	Heiner (14)
46.1 ± 7.2	coupling	Imam (16)
43.1 ± 3.6	coupling	LeBaron (22)
	(Re_2 re_2) in relation to (Pr pr)	
5.5 ± 1.9		Heiner (14)
	(Re_2 re_2) in relation to (Li li)	
40.0 ± 4.8	coupling	Woodward (48)
	(Re_2 re_2) in relation to (Ea ea)	
33.0 ± 3.0	coupling	Woodward (48)

Normal (E) versus long awned (e) outer glumes in relation to other factor pairs.

Recombination %	Phase	Authority
	(E e) in relation to (L l)	
31.5 ± 4.0	repulsion	Woodward (48)
21.2 ± 1.5	coupling	Woodward (48)
42.0 ± 5.9	coupling	LeBaron (22)
18.1 ± 2.5	coupling	Imam (16)
23.0 ± 2.0	coupling	Heiner (14)
	(E e) in relation to (Pr pr)	
32.5 ± 9.0		Gill (9)
13.0 ± 19.7	repulsion	Heiner (14)
34.1		Takahashi, Yamamoto, Jasuda and Itamo (40)

Lax (L) versus dense (l) spike in relation to normal (Li) versus liguleless (li).

Recombination %	Phase	Authority
26.0 ± 6.0	repulsion	Woodward (48)
27.5 ± 3.0	coupling	Woodward (48)

Purple (Pau) versus non-purple (pau) auricle in relation to other factor pairs.

(Pau pau) in relation to (V^t V)

37.9 ± 2.0	repulsion	LeBaron (22)

(Pau pau) in relation (Re_2 re_2)

4.2 ± 0.5	repulsion	LeBaron (22)

Linkages in chromosome 4

Normal (Gl) versus glossy (gl) leaf in relation to normal (Z) versus zoned (z) leaf.

Recombination %	Phase	Authority
33.0 ± 0.05		Immer and Henderson (17)
9.3 ± 0.51	repulsion	Woodward (48)
14.0 ± 5.3	coupling	Woodward (48)

MATERIALS AND METHODS

The crosses used in this study were furnished by Dr. R. W. Woodward. Several crosses involving purple versus non-purple auricle, and other contrasting characters were made in 1957. F_1 plants were grown in 1958 and the seed from each F_1 plant was space planted in 35 foot rows in 1959. Characters in F_2 which were identifiable only in immature plants were labeled by tying the recessives with an assigned colored string. Labeling was done when each character was best exhibited to facilitate classification at maturity. These characters included glossy stem, glossy leaf, zoned leaf, ribbongrass, grandpa, purple auricle, purple straw, and purple lemma and pericarp. Each family was pulled when mature and the plants classified separately.

Two crosses were carried through the F_3 in 1960. Each F_2 plant was represented by a five foot F_3 row. The characters were classified throughout the season as they were most readily identified with follow ups on each from time to time.

Two additional crosses of similar nature were made in 1959. The seed from these crosses was grown in California as F_1's that winter and planted in F_2 the following spring. Classification of these crosses was performed the same as previously described for F_2 populations. Heads from each plant were saved, after being numbered for future reference.

The material was first analyzed for inheritance of individual factor pairs. Dihybrid combinations were then studied for independence or association. Chi-square values were calculated, as a test for goodness of fit, for each factor pair and for each dihybrid combination. The probability values for chi-square were taken from Ostle (27). Recombination values were computed for both F_2 and F_3 populations by the Fisher product method as described by Immer (18).

Characters used in this study and their gene symbol.

Linkage Group 2

Two-rowed versus six-rowed	V v
Deficiens versus two-rowed	V^t v
Normal versus triple awned	Tr tr
Normal versus long awned outer glumes	E e
Purple versus non-purple straw	Pr pr
Purple versus non-purple lemma and pericarp	Re_2 re2
Lax versus dense spike	L l
Early versus late maturity	Ea ea
Normal versus liguleless	Li li
Non-dehiscent versus dehiscent awns	Da da

Linkage Group 1

Covered versus naked caryopsis	N n

Linkage Group 4

Long versus short awns	k_1 k_2
Normal versus zoned leaf	Z z
Normal versus glossy leaf	Gl gl

Linkage Group 5

Black versus non-black lemma and pericarp	B b

Linkage Group 7

Rough versus smooth awns	R r
Long versus short rachilla hairs	S s

Factor pairs unassigned

Purple versus non-purple auricle	Pau pau*
Normal versus glossy stem	Gs gs
Long versus short glume hairs	Gh gh
Normal versus ribbongrass	Rb rb
Normal versus grandpa	Gp gp

*Symbol suggested by author

Barley crosses, parents and segregating factor pairs used in this study

Cross	Parents	Segregating factor pairs
B1747	T942	V - e - z - gl - Tr - R - rb - Gp
	B1257-21	v - E - Z - GL - tr - r - Rb - gp
B1753	P #100	pr - pau - k_2 - n - e
	T188	Pr - Pau - k_1 - N - E
B1755	T957	Pr - Pau - Gs - N - S
	B1239-25	pr - pau - gs - n - s
B1757	T957	da-Pr- Pau-Br-Gs-V-R-Gh-re_2-l-Ea
	T119	Da-pr- pau-br-gs-V^t-r-gh-Re_2-L-ea
B1769	T357	Li - b - V - E - L - Pr - Re_2 - Pau
	T945	li - B - V^t - e - l - pr - re_2 - pau
B1840	T357	Li - b - V - E - L - Pr - Re_2 - Pau
	T945	li - B - V^t - e - l - pr - re_2 - pau

EXPERIMENTAL RESULTS

The experimental results from this study are presented in the following sequence: The inheritance of independent segregating factor pairs, factor pairs showing linkage, and factor pairs showing independence. Special emphasis was placed on the purple auricle character in an attempt to determine the inheritance and position of the gene conditioning it.

Inheritance of Segregating Characters

Factors in linkage group 2

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v). These three genes (V^t), (V) and (v) have been shown to be allels of the same loci, and will be considered in this section although the results will be presented in separate tables.

Data from table 1 and 2 indicate a monofactorial mode of inheritance for deficiens versus two-rowed spikes. Cross B1757 was grown in F_3 because of classification difficulty in F_2. The good fit in F_3 shown in table 2 indicates the low P value in F_2 was due to misclassification.

Two-rowed versus six-rowed has been reported as due to a single gene difference. Cross B1747 was grown in F_3 because of classification difficulties, but low P values were obtained in both F_2 and F_3. The data for two-rowed versus six-rowed are in table 3. No explanation seems evident for the excess of six-rowed plants although this cross was observed to have some seeding mortality.

Table 2. Segregation of deficiens (V^t) versus two-rowed (V) in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	V^t	V	Total	X^2	P
B 1757	329	152	481	10.67	$< .01$
B 1840	699	238	937	.04	.7- .8
B 1769	333	103	436	.44	.5- .6
Sum of 3 chi-squares				12.114	.01
Total	1361	493	1854	2.587	.10-.20
Interaction				9.527	$< .01$

Table 3. Segregation of deficiens (V^t) versus two-rowed (V) in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	V^tV^t	V^tV	VV	Total	X^2	P
B 1757	113	238	129	480	1.085	.5-.7

Table 4. Segregation of two-rowed (V) versus six-rowed (V) in F_2 and F_3 generation. Chi-square and P values are based on 3:1 ratio.

Cross No.	V	v	Total	X^2	P
B 1747 (F_2)	399	203	602	23.00	$< .01$
B 1747 (F_3)	367^a	203	570	33.585	$< .01$

[a] Segregation F_3 rows were combined in this total.

Normal (E) versus long awned outer (e) glumes. The segregation of normal versus long awned outer glumes is shown in table 4. Data from individual crosses support a single factor difference. Every cross is low for the expected recessive character, resulting in a low P value for the combined total. In some previous crosses the heterozygous plants have shown a tendency for long awned outer glumes.

Purple (Pr) versus non-purple (pr) straw. Data shown in table 5 indicates a single factor pair responsible for the inheritance of purple versus non-purple straw. The higher interaction and better fit for the total than for individual crosses suggest that this character varies considerable. Cross B1757 segregated in a 3:1 ratio in F_2 but when grown in F_3 purple pigmentation was observed in varying intensities in all the plants. F_3 rows from cross B1757 were classified according to color intensity and a 1:2:1 ratio was obtained as recorded in table 6. It has been noted by Woodward (personal communication) that enviromental conditions, especially extreme heat, soil or fertility spots can cause a marked variation in the color expression.

Purple (Re_2) versus non-purple (re_2) lemma and pericarp. The inheritance of purple versus non-purple lemma and pericarp appears to be controlled by a single gene as the data from table 7 and 8 indicate. Two genes have been found to be involved in some crosses when two shite parents gave a purple F_1 (49).

Normal (Li) versus liguleless (li). The data in table 9 suggests a monofactorial inheritance for normal versus liguleless. This is supported by the previously reported literature.

Table 5. Segregation of normal (E) versus long-awned (e) outer glume in F_2 and F_3 generations. Chi-square and P values are based on a 3:1 ratio.

Cross No.	E	e	Total	X^2	P
B 1747 (F_2)	481	125	606	5.964	.01-.02
B 1747 (F_3)	441[a]	126	567	2.118	.10-.20
B 1753 (F_2)	434	95	529	13.830	.01
B 1769 (F_2)	332	104	436	.305	.50-.60
B 1840 (F_2)	726	211	937	2.508	.10-.20
Sum of 4 chi-squares				22.607	<.01
Total	1973	535	2508	18.000	<.01
Interaction				4.607	.01-.05

[a] F_3 segregating rows were combined with F_3 homozygous dominant rows. F_3 was not included in totals.

Table 6. Segregation of purple (Pr) versus non-purple (pr) straw in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Pr	pr	Total	X^2	P
B 1753	362	167	529	12.366	.01
B 1755	117	32	149	.898	.30-.40
B 1757	386	95	481	6.940	.005-.01
B 1769	337	99	436	1.223	.20-.30
B 1840	654	286	940	14.757	.01
Sum of 5 chi-squares				36.184	< .01
Total	1856	679	2535	4.259	.02-.05
Interaction				31.925	<.01

Table 7. Segregation of purple (Pr) versus non-purple (pr) straw in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	PrPr	Prpr	prpr	Total	X^2	P
B 1757	144	224	112	480	6.400	.02-.05

Table 8. Segregation of purple (Re2) versus non-purple (re2) lemma and pericarp in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Re2	re2	Total	X^2	P
B 1757	391	90	481	9.330	<.01
B 1769	326	110	436	.012	.90-.95
B 1840	701	237	938	.028	.80-.90
Sum of 3 chi-squares				9.370	.02-.05
Total	1418	437	1855	2.095	.10-.20
Interaction				7.275	<.01

Table 9. Segregation of purple (Re2) versus non-purple (re2) lemma and pericarp in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	Re2Re2	Re2re2	re2re2	Total	X^2	P
B 1757	120	236	124	480	.200	.90-.95

Normal (Tr) versus triple (tr) awns. The segregation of normal versus triple awns is found in table 10. These data support a monogenic mode of inheritance for this character.

Lax (L) versus dense (l) spike. The segregation data for lax versus dense spike are shown in tables 11 and 12. Cross B1747 was classified as lax, medium and club for spike density, but when the medium was combined with the lax class a 3:1 ratio was obtained. The F_3 data found in table 12 indicate a single factor pair to be responsible for this character.

Early (Ea) versus late (ea) maturity. Cross B1757 was the only cross segregating for early versus late maturity. Both monogenic (48) (45) and multigenic (26) modes of inheritance have been reported for this character. The data in table 13 indicate a single factor pair was responsible in this cross. This character is extremely variable depending on the latitude elevation and time of seeding.

Non-dehiscent (Da) versus dehiscent (da) awns. The classification of decidious awns was made from F_3 rows of cross B1757. The proportion of awns dropped at maturity varied considerable from row to row. Rows in which a large majority of the awns had fallen at maturity were classified as dehiscent and the remaining rows as non-dehiscent even though some of the plants within a row had shed their awns. The data are recorded in table 14. From this classification the data suggest a complementary type of inheritance in which two genes are involved, each contributing to the decidiousness.

Table 10. Segregation of normal (Li) versus liguleless (li) in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Li	li	Total	X^2	P
B 1769	321	115	436	.440	.05-.60
B 1840	742	196	938	8.226	$<$.01
Sum of 2 chi-squares				8.666	.01-.02
Total	1063	311	1374	4.233	.02-.05
Interaction				4.433	.02-.05

Table 11. Segregation of normal (Tr) versus triple (tr) awns in F_2 and F_3 generations. Chi-square values are based on a 3:1 ratio.

Cross No.	Tr	tr	Total	X^2	P
B 1747 (F_2)	309	90	399	1.33	.20-.30
B 1747 (F_3)	436	132	568	.938	.30-.40

Table 12. Segregation of lax (L) versus dense (l) spike in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	L	l	Total	X^2	P
B 1747	447[a]	125	572	3.021	.05-.10
B 1769	340	96	436	2.067	.10-.20
B 1840	709	228	937	.215	.60-.70
Sum of 3 chi-squares				5.303	.10-.20
Total	1496	449	1945	3.756	.05-.10
Interaction				1.547	.20-.30

[a] Plants classified as having a medium spike density were included in this total.

Table 13. Segregation of lax (L) versus dense (l) spike in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	LL	Ll	Total	X^2	P
B 1757	120	236	480	.200	.90-.95

Table 14. Segregation of early (Ea) versus late (ea) maturity in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	EaEa	Eaea	Total	X^2	P
B 1757	104	261	480	4.178	.10-.20

Factors in linkage group 1

Normal (Br) versus brachytic (br) habit. The data for normal versus brachytic habit are presented in table 15. These data suggest a monofactorial mode of inheritance although the probability value is low in both F_2 and F_3 crosses. No explanation is available for this low value.

Covered (N) versus naked (n) caryopsis. Table 16 contains the data for the segregation of covered versus naked caryopsis. These data support others who have suggested a single gene inheritance hypothesis. The small number of plants in cross B1755 could be responsible for the low probability value obtained.

Factors in linkage group 4

Long (k_1) versus short (k_2) awns. A single gene difference for long versus short awns is suggested by the data found in table 17.

Normal (Gl) versus glossy (gl) leaf. The results of the segregation of normal versus glossy leaf are presented in table 18. A very low probability value is obtained for the expected 3:1 ratio. High seedling mortality of homozygous recessives might serve as an explanation for the low P value.

Normal (Z) versus zoned (z) leaf. The expected 3:1 ratio for normal versus zoned leaf was not observed as shown in table 19. Zoned leaf not only reduces the vigor of the plants but also results in high seedling mortality for homozygous recessives. Thus, many plants that are homozygous for zoned leaf are lost and this could explain the poor fit.

Table 15. Segregation of non-dehiscent (Da) versus dehiscent (da) awns in F_3 generation. Chi-square and P values are based on a 15:1 ratio.

Cross No.	Da	da	Total	X^2	P
B 1757	448	32	480	.142	.70-.80

Table 16. Segregation of normal (Br) versus brachytic (br) in F_2 and F_3 generations. Chi-square and P values for F_2 are based on a 3:1 ratio. Those for F_3 are based on a 1:2:1 ratio.

Cross No.	Br	br	Total	X^2	P
B 1757 (F_2)	389	92	481	8 - 7	<.01

Cross No.	BrBr	Brbr	brbr	Total	X^2	P
B 1757 (F_3)	127	257	96	480	6.412	.02-.05

Table 17. Segregation of covered (N) versus naked (n) caryopsis in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	N	n	Total	X^2	P
B 1753	395	134	539	.040	.80-.90
B 1755	102	47	149	3.595	.05-.10
Sum of 2 chi-square				3.635	.10-.20
Total	497	181	678	.920	.30-.40
Interaction				2.715	.10

Table 18. Segregation of long (k_1) versus short (k_2) awns in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	k1	k2	Total	X^2	P
B 1753	408	121	529	1.22	.20-.30

Table 19. Segregation of normal (Gl) versus glossy (gl) leaf in F_2 and F_3 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Gl	gl	Total	X^2	P
B 1747 (F_2)	572	65	637	74.09	<.01
B 1747 (F_3)	531[a]	38	569	58.08	<.01

[a] Segregation F_3 rows are included in this total.

Table 20. Segregation of normal (Z) versus zoned (z) leaf in F_2 and F_3 generations. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Z	z	Total	X^2	P
B 1747 (F_2)	559	53	612	86.57	<.01
B 1747 (F_3)	556[a]	26	582	130.00	<.01

[a] Segregation F_3 rows are included in this total.

Factors in linkage group 5

Black (B) versus non-black (b) lemma and pericarp. Table 20 presents data suggesting a single gene difference between black versus non-black lemma and pericarp. This is in agreement with findings of numerous other workers.

Factors in Linkage group 7

Rough (R) versus smooth (r) awns. A good 3:1 ratio suggesting a single factor pair difference was found for rough versus smooth awns. The data are presented in tables 21 and 22.

Long (S) versus short (s) rachilla hairs. A single gene difference is suggested for the inheritance of long versus short rachilla hairs as shown in table 23.

Unassigned factor pairs

Purple (Pau) versus non-purple (pau) auricle. The data for the segregation of purple versus non-purple auricle are shown in tables 24 and 25. These data suggest a single factor pair inheritance for purple versus non-purple auricle. Cross B1755 had a low P value, but the small population may be the contributing cause. Cross B1757 had a low probability value in F_2 but the F_3 gave a good fit for a monogenic mode of inheritance, indicating misclassification of the F_2 progeny.

Normal (Rb) versus ribbongrass (rb) leaf. Table 26 shows the data for the segregation of normal versus ribbongrass. A single factor pair is suggested although a very poor fit was obtained in the F_2 progeny.

Normal (Gp) versus grandpa (gp). Data on segregation of normal versus grandpa are presented in table 27. High seedling

Table 21. Segregation of black (B) versus non-black (b) lemma and pericarp in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	B	b	Total	X^2	P
B 1769	330	106	436	.110	.70-.80
B 1840	694	244	938	.569	.40-.50
Sum of 2 chi-square				.679	.70-.80
Total	1024	350	1374	.164	.60-.70
Interaction				.515	.40-.50

Table 22. Segregation of rough (R) versus smooth (r) awns in F_2 and F_3 generations. Chi-square and P values are based on a 3:1 ratio.

Cross No.	R	r	Total	X^2	P
B 1747 (F_2)	358	125	483	.176	.6-.7
B 1757 (F_2)	360	121	481	.008	.90-.95
B 1747 (F_3)	431[a]	137	568	.235	.6-.7
Sum of 2 chi-square				.184	.80-.90
Total	718	246	964	.136	.70-.80
Interaction				.048	.80-.90

[a] Segregation F_3 rows were combined in this total. F_3 was not included in totals.

Table 23. Segregation of rough (R) versus smooth (r) awns in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	RR	Rr	rr	Total	X^2	P
B 1757	120	248	112	480	.80	.6-.7

Table 24. Segregation of long (S) versus short (s) rachilla hairs in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	S	s	Total	X^2	P
B 1747	368	115	483	.298	.6-.7
B 1755	108	41	149	.575	.4-.5
Sum of 2 chi-square				.873	.6-.7
Total	476	156	632	.0337	.8-.9
Interaction				.839	.3-.4

Table 25. Segregation of purple (Pau) versus non-purple (pau) auricle in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Pau	pau	Total	X^2	P
B 1753	393	136	529	.16	.60-.70
B 1755	123	26	149	4.35	.02-.05
B 1757	384	97	481	5.87	.01-.02
B 1769	246	75	321	.4162	.5-.6
B 1840	565	179	744	.3512	.5-.6
Sum of chi-square				11.474	.02-.05
Total	1711	513	2224	4.433	.02-.05
Interaction				7.041	<.01

mortality, late maturity and poor seed set were observed for the homozygous recessive plants. Only the homozygous dominant and segregating F_3 rows were classified for the grandpa character to determine its inheritance. The inheritance and chi-square values were therefore computed on a 2:1 ratio. A monofactorial mode of inheritance was suggested from this analysis, while no such relationship was observed in F_2. Many previous crosses fit the monofactorial hypothesis fairly well.

Normal (Gs) versus glossy (gs) stem. The data on tables 28 and 29 indicate a single gene difference for the inheritance of normal versus glossy stem.

Long (Gh) versus short (gh) glume hairs. The data for the segregation of long versus short glume hairs are presented in tables 30 and 31. Cross B1747 indicates a two factor mode of inheritance, while the data from cross B1840 sheds very little light on the mode of inheritance. A great deal of difficulty was encountered in the classification of glume hairs in B1840 and B1757. B1757 was grown in F_3 of which the data found in table 31 indicates that a single factor pair is responsible.

Table 26. Segregation of purple (Pau) versus non-purple (pau) auricle in F_3 generation. Chi-s quare and P values are based on a 1:2:1 ratio.

Cross No.	Pau Pau	Pau pau	pau pau	Total	X^2	P
B 1757	119	243	118	480	.079	.95-97

Table 27. Segregation of normal (Rb) versus ribbongrass (rb) in F_2 and F_3 generations. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Rb	rb	Total	X^2	P
B 1747 (F_2)	542	93	635	35.65	<.01
B 1747 (F_3)	430[a]	139	569	.084	.7-.8

[a] Segregation F_3 rows were included in this total.

Table 28. Segregation of normal (Gp) versus grandpa (gp) in F_2 and F_3 generation. Chi-square and P values for F_2 are based on a 3:1 ratio. Those for F_3 are based on a 2:1 ratio.

Cross No.	Gp	gp	Total	X^2	P
B 1747 (F_2)	528	109	637	20.96	<.01
Cross No.	GpGp	Gpgp	Total	X^2	P
B 1747 (F_3)	184	307	491	2.71	<.10

Table 29. Segregation of normal (Gs) versus glossy (gs) stem in F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross No.	Gs	gs	Total	X^2	P
B 1755	116	33	149	.575	.4-.5
B 1757	373	108	481	1.67	.2
Sum of 2 chi-squares				2.245	.25-.3
Total	489	141	630	2.17	.1-.2
Interaction				.075	.7-.8

Table 30. Segregation of normal (Gs) versus glossy (gs) stem in F_3 generation. Chi-square and P values are based on a 1:2:1 ratio.

Cross No.	GsGs	Gsgs	gsgs	Total	X^2	P
B 1757	113	250	117	480	.899	.6-.7

Table 31. Segregation of long (Gh] versus short (gh) glune hair in F_2 generation. Chi-square and P values are based on 3:1 ratio.

Cross No.	Gh	gh	Total	X^2	P
B 1747	292	189	481	3.73[a]	05. 0 .10
B 1757	321	160	481	16.89	$<$ .01
B 1840	472	244	716	30.33	$<$.01

[a] Chi-square based on a 9:7 ratio.

Table 32. Segregation of long (Gh) ve rsus short (gh) glune hair in F_3 generation. Chi-square and P values are based on a 1:21 ratio.

Cross No.	GhGh	Ghgh	ghgh	Total	X^2	P
B 1757	129	219	132	480	3.712	.10-.20

Dihybrid Combinations Showing Linkage

The inheritance of gene pairs showing linkage is the main concern of this section. The linkage of purple auricle with other factor pairs receives special attention. Recombination percentages for F_3 populations were computed by combining the F_3 segregation with the homozygous dominant progeny, and using the product method to calculate the percentages.

Linkages found in chromosome 2.

Purple (Pau) versus non-purple (pau) auricle in relation to other factor pairs. The linkage of purple versus non-purple auricle in relation to other factor pairs is found in table 33. This table gives data that suggest the association of (Pau pau) in relation to (Pr pr), (Re_2 re_2) and (V^t V). Some relationship was found with purple auricle and lax versus dense spike, however, (Ll) segregated independent of (Re_2 re_2) and (V^t V).

Four crosses with similar recombinations value were combined to give a total recombination value of 13.0 ± .895 for (Pau pau) in relation to (Pr pr). One of these crosses was tested for classification accuracy by growing F_3's of genotype (pau pau pr pr). The F_3 progeny verified the F_2 classification with only one exception. Some degree of expression of purple straw was found in every F_3 row of cross B1757, hence very little confidence can be placed in the associations of the purple straw character in this cross.

The relation of (Pau pau) to (Re_2 re_2) ranged in recombination values from 15.5 ± 4.43 to 33.5 ± 1.94. A better fit was obtained from cross B1757 in F_3 than in F_2, therefore, more confidence could be placed on the F_3 data. The F_3 recombination value in B1757 was 15.5 ± 4.43 for (Pau pau) in relation to (Pr pr).

The F_3 results of (Pau pau) and (V^t V) in cross B1757 gave a recombination value of 28.0 ± 4.15 which was very close to that obtained for the F_2. Two other crosses, however, gave independent segregation for the same gene pairs. No explanation seems apparent for these two rather contradictory associations except for the fact that the color expression for purple auricle was much better in cross B1757.

Deficiens (V^t) versis two-rowed (V) spike in relation to other factor Pairs. Table 34 presents the data to support linkage of deficiens versus two-rowed spike in relation to (Re_2 re_2) and (Li li). The recombination values are in agreement with that obtained by other workers. More confidence could be placed in the F_3 which gave a recombination value for (V^t V) in relation to (Re_2 re_2) of 15.0 ± 1.79.

Purple (Re_2) versus non-purple (re_2) lemma and pericarp in relation to other factor pairs. The data found in table 35 suggest purple versus non-purple lemma and pericarp to be in the same linkage group as (Pr pr), (Ee) and (Li li). The recombination values for the relation of (Re_2 re_2) to (Ee) and (Re_2 re_2) to (Li li) are in agreement with previous findings.

Cross B1757 gave independent segregation for the relation of (Re_2 re_2) to (Pr pr) in both the F_2 and F_3 generations.

Table 33. Purple (Pau) versus non-purple (pau) auricle in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	XY	Xy	xY	xy	Total	X^2	P	Recomb. Percent
		(Pau, pau) in relation to (Pr, pr)							
4 crosses F_2	Coupling	1172	165	63	343	1743	831.0	<.01	13.0 ± .895
B 1757 F_2	Coupling	333	51	53	44	481	44.12	<.01	28.5 ± 2.51
B 1757 F_3	Coupling	287	73	76	45	480	13.96	<.01	38.5 ± 2.96
		(Pau, pau) in relation to (Re_2, re_2)							
B 1757 F_2	Repulsion	298	86	93	4	481	25.7	<.01	25.0 ± 4.23
B 1757 F_3	Repulsion	240	121	115	3	480	28.5	<.01	15.5 ± 4.43
2 crosses F_2	Coupling	699	112	162	90	1065	63.57	<.01	37.5 ± 1.94
		(Pau, pau) in relation to (L, l)							
2 crosses F_2	Coupling	678	133	130	112	1065	104.57	<.01	30.0 ± 1.74
B 1757 F_3	Repulsion	258	104	98	20	480	6.75	.05-.10	40.5 ± 3.76
		(Pau, pau) in relation to (V^t, V)							
2 crosses F_2	Repulsion	605	206	158	94	1065	28.3	<.01	58.0 ± 2.09
B 1757 F_2	Repulsion	243	141	86	11	481	43.8	<.01	29.7 ± 4.10
B 1757 F_3	Repulsion	245	119	108	10	480	16.6	<.01	28.0 ± 4.15

Table 34. Deficiens (V^t) versus two-rowed (V) spike in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	XY	Xy	xY	xy	Total	X^2	P	Recomb. Percent
		(V^t, V) in relation to (Re_2, re_2)							
2 crosses F_2	Repulsion	719	313	307	34	1373	57.13	<.01	32.0 ± 2.39
B 1757 F_2	Coupling	303	26	88	64	481	88.1	<.01	24.0 ± 2.29
B 1757 F_3	Coupling	319	32	37	92	480	205.6	<.01	15.0 ± 1.79
		(V^t, V) in relation to (Li, li)							
2 crosses F_2	Repulsion	760	272	302	39	1373	17.42	<.01	36.0 ± 2.32

Table 35. Purple (Re_2) versus non-purple (re_2) lemma and pericarp in relation to other factor pairs. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	XY	Xy	xY	xy	Total	X^2	P	Recomb. Percent
		(Re_2, re_2) in relation to (Pr, pr)							
2 crosses F_2	Coupling	838	189	151	196	1376	207.7	<.01	28.0 ± 1.47
B 1757 F_2	Repulsion	316	75	70	20	481	18.1	<.01	52.5 ± 3.32
B 1757 F_3	Repulsion	278	78	90	24	480	3.04	.3-.4	49.5 ± 3.44
		(Re_2, re_2) in relation to (E, e)							
2 crosses F_2	Coupling	836	190	222	125	1373	45.2	<.01	37.8 ± 1.74
		(Re_2, re_2) in relation to (Li, li)							
2 crosses F_2	Coupling	857	170	206	141	1373	83.9	<.01	33.5 ± 1.67

Two other crosses gave a combined recombination value of 28.0 ± 1.47 for the same two gene pairs. Here again the relationship of (Pr pr) in B1757 could not be considered to be reliable.

Purple (Pr) versus non-purple (pr) straw in relation to lax (L) versus dense (l) spike. Purple versus non-purple straw in relation to lax versus dense spike as shown in table 36 gave a recombination value of 30.0 ± 1.53. Other workers have reported similar results.

Two-rowed (V) versus six-rowed (v) spike in relation to normal (E) versus long awned outer (e) glumes. The relation of two-rowed versus six-rowed spike to normal versus long awned outer glumes is shown in table 37. These two gene pairs have been reported to be linked. A recombination value of 23.5 ± 3.93 was obtained, which is in agreement with other workers.

Linkages found in chromosome 4

Normal (Z) versus zoned (z) leaf in relation to normal (Gl) versus glossy (gl) leaf. The data for the relation of (Z z) to (Gl gl) are presented in table 38. Close linkage was found in both F_2 and F_3 generations. Recombination values of 8.5 ± 1.16 for F_2 and 12.5 ± 1.55 for F_3 were obtained.

Linkages found in chromosome 7

Rough (R) versus smooth (r) awns in relation to long (S) versus short (s) rachilla hairs. Table 39 gives the data for the relation of rough versus smooth awns to long versus short rachilla hairs. Recombination values of 21.0 ± 2.13 for F_2 and 16.5 ± 4.13 for F_3 were obtained, indicating linkage between these two factor pairs.

Table 36. Purple (Pr) versus non-purple (pr) straw in relation to lax (L) versus dense (l) spike. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	Pr L	Pr l	pr L	pr l	Total	X^2	P	Recomb. Percent
2 crosses F_2	Coupling	838	150	211	174	1373	148.3	<.01	30.0 ± 1.53

Table 37. Two-rowed (V) versus six-rowed (v) spike in relation to normal (E) versus long awned (e) outer glumes. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	VE	Ve	vE	ve	Total	X^2	P	Recomb. R Percent
B 1757 F_3	Repulsion	395	62	46	64	567	86.2	<.01	23.5 ± 3.92

Table 38. Normal (Z) versus zoned (z) leaf in relation to normal (Gl) versus glossy (gl) leaf. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	ZGl	Zgl	zGl	zgl	Total	X^2	P	Recomb. Percent
B 1747 F_2	Coupling	561	23	11	42	637	288.6	$<.01$	8.5 ± 1.16
B 1747 F_3	Coupling	282	29	44	180	535	370.6[a]	$<.01$	12.5 ± 1.55

[a] Based on a 4:2:2:1 ratio

Table 39. Rough (R) versus smooth (r) awns in relation to long (S) versus short (s) rachilla hairs. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	RS	Rs	rS	rs	Total	X^2	P	Recomb. Percent
B 1747 F_2	Coupling	248	34	120	81	482	133.3	$<.01$	21.0 ± 2.13
B 1747 F_3	Coupling	69	2	17	10	98	20.5	$<.01$	16.5 ± 4.13

Linkages found in chromosome 1

Normal (Br) versus brachytic (br) habit in relation to other factor pairs. The data in table 40 show the relation of normal versus brachytic habit to other factor pairs. These data suggest a possible linkage between the factor pairs (Br br) to (Gh gh) and (Br br) to (Ea ea). (Br br) has been placed in chromosome 1, but (Gh gh) is still unassigned. The recombination value for (Br br) in relation to (Gh gh) was 38.0 ± 2.94. Earliness genes have been reported to be in several of the chromosomes. The recombination value of 30.0 ± 2.60 for (Br br) and (Ea ea) suggests the possibility of this earliness gene to be in chromosome 1.

New linkages suggested

Normal (Rb) versus ribbongrass (rb) in relation to other factor pairs. Table 41 gives the data for the relation of normal versus ribbongrass leaf to other factor pairs. A recombination value of 22.0 ± 2.17 was obtained for (Rb rb) and (Gp gp), suggesting a linkage between these two factor pairs. It was difficult to detect the ribbongrass character when the grandpa character was present, so these data were computed from F_3 segregating and homozygous dominant rows. A possible relationship was suggested for (Rb rb) and (Tr tr) by a recombination value of 35.5 ± 3.67.

Normal (Gs) versus glossy (gs) stem in relation to early (Ea) versus late (ea) maturity. The data for the relation of normal versus glossy stem to early versus late maturity are given in table 42. These two characters gave a recombination value of 36.5 ± 2.87, which suggests linkage.

Table 40. Normal (Br) versus brachytic (br) habit in relation to other factor pairs in F_3 generation. Chi-square and P values are based on a 9:3:3:1 ratio.

Cross	Phase	XY	Xy	xY	xy	Total	X^2	P	Recomb. Percent
		(Br, br) in relation to (Gh, gh)							
B 1757	Coupling	293	91	55	41	480	12.93	<.01	38.0 ± 2.94
		(Br, br) in relation to (Ea, ea)							
B 1757	Coupling	316	68	49	47	480	41.1	<.01	30.5 ± 2.60

Table 41. Normal (Rb) versus ribbongrass (rb) leaf in relation to other factor pairs in F_3 generation. Chi-square and P values are based on a 6:2:3:1 ratio.

Cross	Phase	XY	Xy	xY	xy	Total	X^2	P	Recomb. Percent
		(Rb, rb) in relation to (Gp, gp)							
B 1747	Repulsion	273	82	34	10	491	134.8	<.01	22.0 ± 2.17
		(Rb, rb) in relation to (Tr, tr)							
B 1747	Repulsion	313	117	123	16	569	15.94	<.01	35.5 ± 3.67

Table 42. Normal (Gs) versus glossy (gs) stem in relation to early (Ea) versus late (ea) maturity. Chi-square and P values are based on a 7:3:3:1 ratio.

Cross	Phase	GsEa	Gsea	gsEa	gsea	Total	X^2	P	Recomb. Percent
Gr1757 F_3	Coupling	294	69	71	46	480	19.58	<.01	36.5 ± 2.87

Factor Pairs Showing Independence

The following dihybrid combinations were found to show independent recombinations:

Purple (Pau) versus non-purple (pau) auricle in relation to:

Rough versus smooth awns	R, r
Normal versus brachytic habit	Br, br
Normal versus glossy stem	Gs, gs
Long versus short glume hairs	Gh, gh
Normal versus long awned outer glumes	E, e
Early versus late maturity	Ea, ea
Covered versus naked caryopsis	N, n
Long versus short rachilla hairs	S, s
Black versus non-black lemma and pericarp	B, b

Normal (Gs) versus glossy (gs) stem in relation to:

Purple versus non-purple straw	Pr, pr
Normal versus brachytic habit	Br, br
Long versus short glume hairs	Gh, gh
Purple versus non-purple lemma and pericarp	Re_2, re_2
Lax versus dense spike	L, l
Deficiens ve rsus two-rowed spike	V^t, V
Rough versus smooth awns	R, r

Long (Gh) versus short (gh) glume hairs in relation to:

Purple versus non-purple straw	Pr, pr
Purple versus non-purple lemma and pericarp	Re_2, re_2
Lax versus dense spike	L, l
Early versus late maturity	Ea, ea
Deficiens versus two-rowed spike	V^t, V
Rough versus smooth awns	R, r

Rough (R) versus smooth (r) awns in relation to:

Deficiens versus two-rowed spike	V^t, V
Two-rowed versus six-rowed spike	V, v
Purple versus non-purple straw	Pr, pr
Normal versus brachytic habit	Br, br
Purple versus non-purple lemma and pericarp	Re_2, re_2
Lax versus dense spike	L, l
Early versus late maturity	Ea, ea
Normal versus long awned outer glumes	E, e
Normal versus triple awns	T, t

Normal (Br) versus brachytic (br) habit in relation to:

Deficiens versus two-rowed spike	V^t, V
Purple versus non-purple straw	Pr, pr
Purple versus non-purple lemma and pericarp	Re_2, re_2
Lax versus dense spike	L, l

Black (B) versus non-black (b) lemma and pericarp in relation to:

Deficiens versus two-rowed spike	V^t, V
Normal versus long awned outer glume	E, e
Purple versus non-purple lemma and pericarp	Re_2, re_2
Lax versus dense spike	L, l
Normal versus liguleless	Li, li

Covered (N) versus naked (n) caryopsis in relation to:

Normal versus long awned outer glumes	E, e
Long versus short rachilla hairs	S, s

Normal (Tr) versus triple (tr) awns in relation to:

Normal versus long awned outer glumes	E, e

Normal (Gp) versus grandpa (gp) in relation to:

Two-rowed versus six-rowed spike	V, v
Rough versus smooth awns	R, r
Normal versus long awned outer glumes	E, e
Normal versus triple awns	Tr, tr

Normal (Gl) versus glossy (gl) leaf in relation to:

Two-rowed versus six-rowed spike	V, v
Rough versus smooth awns	R, r
Normal versus long awned outer glumes	E, e
Normal versus triple awns	Tr, tr
Normal versus grandpa	Gp, gp

Normal (Z) versus zoned (z) leaf in relation to:

Two-rowed versus six-rowed spike	V, v
Rough versus smooth awns	R, r
Normal versus long awned outer glumes	E, e
Normal versus triple awns	Tr, tr
Normal versus grandpa	Gp, gp

The two crosses in which (Pau pau) and (N n) were segregating gave very low probability values. The recombination values for these two crosses were 60.0 ± 3.60 and 32.0 ± 4.80, but when the two were combined a recombination value of 59.5 ± 3.17 was found. The great variation between these two crosses suggests misclassification or differential mortality.

The gene pairs (Tr tr) and (E e) have been placed in the same linkage group by other workers. From the data in this study (Tr tr) was found to segregate independently of (E e). A plausable explanation might be the fact that their position might be well over 50 crossover units apart, which would show independent segregation.

Gene pairs (L l), (Ea ea) and (Tr tr) were found to segregate independently of (Re_2 re_2), (V^t V) and (Li li), all of which have been reported to be in linkage group 2. However, (L l), (Ea ea) and (Tr tr) have also been reported in other linkage groups. These three gene pairs involved in this study do not appear to be in linkage group 2.

Contrary to the results of other workers (Pr pr) showed independence to (Li li), (E e) and (V^t V). These have all been previously placed in chromosome 2. However, some degree of coloration appeared in most of the progeny as was previously pointed out. Thus, the relationship of (Pr pr) to other factor pairs could not be considered too reliable.

SUMMARY

Six F_2 crosses, two of which were grown in F_3, were studied for the inheritance of character pairs. These were in turn studied for their independence or associations with each other.

The following characters showed simple Mendilian inheritance: Pau, Pr, Re_2, L, Ea, Br, Vt, Tr, E, Gh, Gs, K_1, N, B, S, R, Gp, Rb, Z, and Gl.

A two factor pair difference was suggested for Da. One cross indicated a two factor pair difference for Gh.

The following factor pairs showed independence:

Pau in relation to R, Br, Gs, Gh, E, Ea, N, S and B.
Gs in relation to Pr, Br, Gh, Re_2, L, V^t, R, N and S.
Gh in relation to Pr, Re_2, L, Ea, V^t and R.
R in relation to V^t, Pr, Br, Re_2, L, Ea, E and Tr.
Br in relation to V^t, Pr, Re_2 and L.
B in relation to V^t, E, Pr, Re_2, L and Li.
N in relation to E and S.
Tr in relation to E.
V^t in relation to Pr, L, Ea, and Tr.
Re_2 in relation to L and Ea.
Pr in relation to Li and E.
Z in relation to V, R, E, Tr and Gp.
L in relation to Ea, E, and Li.
Rb in relation to R, V, E, Tr, Z and Gl.
Gp in relation to V, R, E and Tr.

Linkages

Linkages found in chromosome 2

Gene Pairs (in relation to)	Recom. percent	Phase	Progeny
Pau pau : Pr pr	13.0 ± .895	coup. (F_2)	1743
Pau pau : Re_2 re_2	25.0 ± 4.23	rep. (F_2)	481
Pau pau : Re_2 re_2	15.5 ± 4.43	rep. (F_3)	480
Pau pau : Re_2 re_2	37.5 ± 1.94	coup. (F_2)	1065
Pau pau : L l	30.0 ± 1.74	coup. (F_2)	1065
Pau pau : L l	40.5 ± 3.67	rep. (F_3)	480
Pau pau : V^t V	29.7 ± 4.10	rep. (F_2)	481
Pau pau : V^t V	28.0 ± 4.15	rep. (F_2)	480
V^t V : Re_2 re_2	32.0 ± 2.39	rep. (F_2)	1373
V^t V : Re_2 re_2	24.0 ± 2.29	coup. (F_2)	481
V^t V : Re_2 re_2	15.0 ± 1.79	coup. (F_3)	480
V^t V : Li li	36.0 ± 2.32	rep. (F_2)	1373
Re_2 re_2 : Pr pr	28.0 ± 1.47	coup. (F_2)	1376
Re_2 re_2 : E e	37.8 ± 1.74	coup. (F_2)	1373
Re_2 re_2 : Li li	33.5 ± 1.67	coup. (F_2)	1373
Pr pr : L l	30.0 ± 1.53	coup. (F_2)	1373
V v : E e	23.5 ± 3.92	rep. (F_3)	567

Linkages found in chromosome 4

Z z : Gl gl	8.5 ± 1.16	coup. (F_2)	639
Z z : Gl gl	12.5 ± 1.55	coup. (F_3)	535

Linkages found in chromosome 7

R r : S s	21.0 ± 2.13	coup. (F_2)	482
R r : S s	16.5 ± 4.13	coup. (F_3)	98

Linkages found in chromosome 1

Br br : Gh gh	38.0 ± 2.94	coup. (F_3)	480
Br br : Ea ea	30.5 ± 2.60	coup. (F_3)	480

New linkages suggested

Rb rb : Gp gp	22.0 ± 2.17	rep. (F_3)	491
Rb rb : Tr tr	35.5 ± 3.67	rep. (F_3)	569
Gs gs : Ea ea	36.5 ± 2.87	coup. (F_3)	480

Purple auricle was found to located in chromosome 2 associated with (Pr pr), (Re_2 re_2) and (V^t V). The exact position of this gene was not determined. The (tr) character involved in this study failed to show linkage with other factors of chromosome 2. The gene responsible for triple awns has been previously assigned to chromosome 2.

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