

LINKAGE STUDIES IN RICE¹ *

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INTRODUCTION

According to the chromosome theory, all genes on the same chromosome are linked, unless crossing over takes place. If this postulate is true, we should expect to find no more linkage groups than there are haploid chromosomes in the variety or species in question. Thus far, *Drosophila melanogaster* is the only species in the animal kingdom in which all known genes have been found to fall into one or another of the four linkage groups, each probably corresponding to one of the four haploid chromosomes. In the plant kingdom, *Zea mays* is the only species in which the linkage relations of Mendelian characters have been studied extensively.

In rice, the common species, *Oryza sativa* L., has twenty-four chromosomes (KUWADA 1910, NAKATOMI 1923). We should expect, therefore, to find twelve linkage groups in the common races of rice. Investigations in this respect, however, have just begun. PARNELL (1917) observed the

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association between purple lining of the internode and purple glumes, and also between purple stigma and purple axil, whereas green internode and glumes are associated with purple stigma and axil. He further observed (1922) that purple pericarp color belongs to the same pattern. No satisfactory data, however, have been published regarding the chromosomal relations of the genes responsible for the characters just mentioned. NAGAI (1921) observed close association between the purple awn and the reddish-brown testa. HECTOR (1922) showed that the color of the pericarp is due either to the same factor which is responsible for ligule color or to a factor completely linked with it, and that the fact that a few plants were found with colored ligules and white grains is evidence in favor of the latter view. HECTOR (1922) further found that certain color characters on the vegetative parts of the plant are grouped in patterns or systems which are inherited together, segregating as if they were due to a single factor or due to the same interacting factors. In four cases, however, he observed that some patterns were altered. (1) In the cross Noachur \times Pookhi, the pattern "colored internode and stigma" was altered three times out of 1,199 plants examined, giving three plants in F_2 with "colored stigma and green internode." (2) In the same cross, the pattern "colored leaf-sheath and apiculus" changed twice out of 1,199 plants giving two plants in F_2 with "colored apiculus and green leaf-sheath." (3) In the cross Bailabkri \times Pookhi the pattern "colored leaf-sheath, internode and stigma" was altered twenty-four times out of 4,687 plants examined, giving twenty-four plants with "colored leaf-sheath and stigma but green internode." (4) In the cross Agartollah \times C₂₅, the pattern "colored leaf-sheath, pulvinus, auricles, internode, glumes, apiculus" changed once out of 4,669 plants examined, namely, one plant was found with color in the glumes and apiculus, but with green leaf-sheath, internode, pulvinus and auricles. In all the cases thus far reviewed, while there is some indication of association between certain characters, no linkage group is definitely established.

In three instances, however, the linkage relation seems to be clear. The first of these is between the factor for awn color and the glutinous gene. In the cross, Tamanishiki \times Shinriki, TAKAHASHI (1923) found that the dominant factor for awn color (R) is coupled with the non-glutinous factor (U), giving about twenty-one percent crossing over. The exact percentage of crossing over, however, is not certain, for NAGAI (1926) found 21.7 percent crossing over in one cross and 14.3 percent crossing over in another cross. Of course, the latter case may be concerned with a different factor. The second instance of linkage is given by YAMAGUCHI

(1926) who found that the factor for apiculus color (*S*) is coupled with the non-glutinous gene giving about 20–22 percent crossing over. Just recently, YAMAGUCHI (1927) found that the factor (*F*) for flowering time is also linked with the glutinous gene. The exact locus, however, is not certain.

The present studies were started in the winter of 1924. Some twenty-five factors were studied and their chromosomal relations determined so far as practicable. Since it is not practical to make backcrosses with this plant, the linkage relations were analyzed exclusively from data obtained from the F_2 generation. The varieties used have been briefly described in an earlier paper by the author (CHAO), but a few important characters are pointed out in the following list.

Variety	Characters
100	Glutinous endosperm; awnless; colorless apiculus and glumes.
200	Non-glutinous endosperm; long awn; tawny apiculus and glumes.
300	Glutinous; colorless apiculus, stigma and leaf-sheath.
400	Non-glutinous; colored apiculus, stigma and leaf-sheath.
600	Non-glutinous; colorless apiculus, stigma and leaf-sheath; red brown pericarp; colorless ligule, auricle, and internode; light hull with brown furrows.
800b	Glutinous; colored apiculus, stigma and leaf-sheath; purple pericarp; purple ligule, auricle and internode; light hull without brown furrows.
4269	Glutinous; long spikelet and long glumes; colorless apiculus, stigma and leaf-sheath; colorless ligule, auricle and pulvinus; purple pericarp.
4957	Non-glutinous; short spikelet and short glumes; red apiculus; purple stigma; leaf-sheath purple lined; colorless ligule, auricle and pulvinus; white pericarp.

EXPERIMENTS AND RESULTS

Relation between the awn and the glutinous character

Concerning the inheritance of the awned and awnless character in rice, YAMAGUCHI (1926) reported a simple Mendelian 3:1 ratio. NAGAI (1926) reported three cases, one segregating in a ratio of three awned: one awnless; another segregating in a ratio of one awned: three awnless: and the third, a ratio of fifteen awned: one awnless.

The writer found a case similar to the one last mentioned. The F_1 was fully awned like the awned parent. The F_2 population consisted of four types. One type was fully awned and another fully awnless like the original parents. Of the two new types, one had awns on most of the spikelets, while the other had awns on a few spikelets only, as shown in figure 1. These four types were designated as *fully awned*, *mostly awned*, *rarely awned*, and *fully awnless*, respectively. They occurred in a ratio of

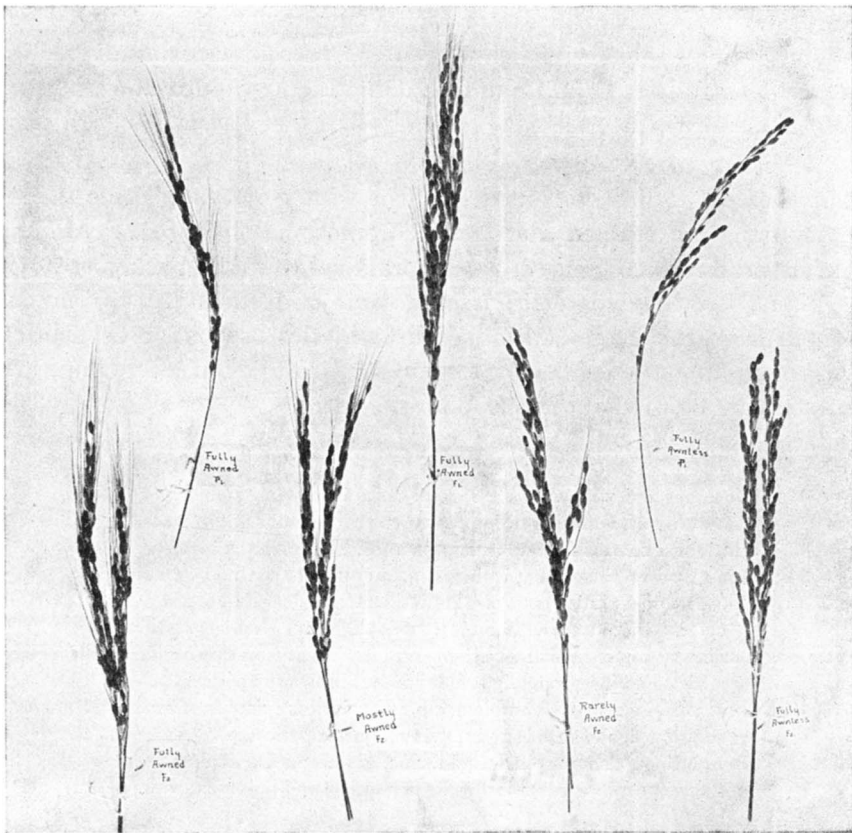


FIGURE 1.—Showing P₁, F₁, and F₂ generations of 101×205, with particular reference to the segregation of the awn character.

12:1:2:1. When all the awned types were classified together, however, the ratio of awned to awnless approaches very closely to 15:1, as shown in table 1.

TABLE 1
Segregation of fifteen awned: one awnless in the F₂ generation of (101×205) D.

PHENOTYPES	OBSERVED	Calculated 12:1:2:1	OBSERVED	Calculated 15:1	DEVIATION
Fully awned	319	326.16	406	407.70	-1.7
Mostly awned	29	27.18			
Rarely awned	58	54.36			
Fully awnless	29	27.18	29	27.18	1.82

$$\frac{\text{Dev. } 1.82}{\text{P. E. } 3.41} = 0.53$$

These facts are explained on the basis of two pairs of factors $A_{n_1}a_{n_1}$ and $A_{n_2}a_{n_2}$, both being concerned with the production of the awn character. A_{n_2} is considered to be weaker in its action than A_{n_1} . So, A_{n_1} can produce the fully awned type with or without A_{n_2} . A_{n_2} in double dose may produce the mostly awned class, but in single dose, it will only produce the rarely awned type. The fully awnless type is due to the double recessive constitution. The interpretation that one of these two factors is weaker in its action than the other is supported by the fact that among the mostly awned and rarely awned types of F_2 plants the frequency of awned spikelets on the early or late panicles of the same plant may vary according to environmental conditions, while among the fully awned or fully awnless types the phenotypic expression is not so easily subject to environmental influence.

These two pairs of factors $A_{n_1}a_{n_1}$ and $A_{n_2}a_{n_2}$ are independent of the glutinous pair, G_1g_1 , as shown in table 2. It is to be noted that among the F_2 population of 434 plants, 349 were non-glutinous and 85 glutinous, showing a deficiency of glutinous grains that is about 3.86 times the probable error.

TABLE 2
Independent segregation between factors $A_{n_1}a_{n_1}$, $A_{n_2}a_{n_2}$ and G_1g_1 .

PHENOTYPES	OBSERVED	Calculated 45:3:15:1	$\frac{(O-C)_2}{C}$
Non-glutinous awned	327	305.10	1.57
Glutinous awned	78	101.70	5.52
Non-glutinous awnless	22	20.34	0.13
Glutinous awnless	7	6.78	0.01
	434	434	7.23 = χ^2

$$P=0.0718$$

The deviation from expectation on the basis of independent segregation is not large, if we take into consideration the significant deficiency of the glutinous plants involved.

Linkage between the $T_v t_v$ pair and the $G_1 g_1$ pair

In this particular material, when the panicle first emerges from the leaf-sheath, the apiculus, the glumes, and the awn, if present, are green like the other parts of the spikelet. As the spikelet is filled up by the developing grain, the three parts concerned gradually develop color through successive shades from Pale Orange Yellow, Light Orange Yellow up to

Tawny (Ridgway) or even brighter and more glassy than Tawny at maturity. This is designated as the "tawny character," and the absence of it is non-tawny or colorless.

In inheritance, the tawny character is completely dominant over non-tawny in the F_1 generation. In the F_2 , the writer obtained a simple 3:1 ratio, as shown in table 3.

TABLE 3
F₂ segregation of tawny non-tawny from the cross (101×205)D.

	TAWNY	NON-TAWNY	TOTAL
Observed	339	99	438
Calculated 3:1	328.5	109.5	438
Deviation		-10.5	

$$\frac{\text{Dev.}}{\text{P.E.}} = \frac{10.5}{6.11} = 1.71$$

Since the tawny color appeared on three parts of the spikelet and no crossing over was noticed in a population of 438 F_2 plants, it is very probable that the tawny character is due to one allelomorph pair of factors rather than to several different genes completely linked. This allelomorph pair is designated as $T_y t_y$.

Breeding data presented in table 4 show that the T_y factor is coupled with the G_1 factor. On the basis of independent segregation, we should

TABLE 4
Coupling between G_1 and T_y
(Gametic ratio $r:s:s:r=4.48:1:1:4.48$)

	NON-GLUTINOUS TAWNY	NON-GLUTINOUS COLORLESS	GLUTINOUS TAWNY	GLUTINOUS COLORLESS	TOTAL
Observed	309	43	30	58	440
Calculated	293.11	36.39	36.39	73.44	440
Deviation	15.89	6.61	-6.39	-15.44	

$$X^2 = 5.05$$

$$P = 0.17$$

expect 247.5 non-glutinous tawny plants, 82.5 non-glutinous colorless plants, 82.5 glutinous tawny plants, and 27.5 glutinous colorless plants.

But the observed data deviated very widely from the expectation. By EMERSON'S (1916) method, the gametic ratio is found to be:

$$r:s:s:r=4.48:1:1:4.48$$

From this, the zygotic ratio is calculated. The percentage of crossing over is about 16.59 percent. Considering the significant deficiency of the glutinous plants involved, the calculated ratios are fairly close to the observed ones.

Relation between the pericarp color and the glutinous character

The pericarp color of rice varies from pure white, grey-brown, red to purple. Several investigators notably THOMPSTONE (1915), PARNELL and AYYANGAR (1917), IKENO (1918), NAGAI (1921), and HECTOR (1922), have reported that red and white colors form a simple Mendelian pair segregating in a 3:1 ratio in F_2 , red being dominant over white. PARNELL *et al* (1917), however, found a case where red and white segregated in a 9:7 ratio. PARNELL (1922) reported that purple and white also form a Mendelian pair segregating in a 3:1 ratio and that purple \times red gave a ratio of 12 purple: 3 red: 1 white in F_2 . KATO and ISHIKAWA (1921) found a case where red \times white gave a ratio of 9 red:3 yellow:4 white. All these facts seem to indicate that there are two factors concerned with the production of pericarp color.

I found that the Chinese Imperial rice has a red pericarp color which also behaved as a simple Mendelian dominant when crossed with a white variety. This allelomorphous pair is designated as $P_{r_1} p_{r_1}$. Further data show that P_{r_1} is independent of the factor G_1 , as shown in table 5.

TABLE 5
Independent segregation between G_1 and P_{r_1} (600 \times 100).

	NON-GLUTINOUS RED PERICARP	NON-GLUTINOUS WHITE PERICARP	GLUTINOUS RED PERICARP	GLUTINOUS WHITE PERICARP	TOTAL
Observed	96	31	37	15	179
Calculated 9:3:3:1	100.62	33.54	33.54	11.18	179
Deviation	-4.62	-2.54	3.46	3.82	

In another cross between 4269 and 4957, the former being purple and the latter white, a ratio of 15 colored:1 colorless was obtained, showing that there are two factors concerned. One of these two genes in this case

is presumably the same as P_{r_1} and the other is designated as P_{r_2} . Both of them are independent of the glutinous gene, as shown in table 6.

TABLE 6
Independent segregation between P_{r_1} and P_{r_2} and g_1 from the cross 4269 × 4957.

	NON-GLUTINOUS COLORED	NON-GLUTINOUS COLORLESS	GLUTINOUS COLORED	GLUTINOUS COLORLESS	TOTAL
Observed	515	36	147	11	709
Calculated 45:15:3:1	498.15	33.21	166.05	11.07	709
Deviation	16.85	2.79	-9.05	-0.07	

Inheritance of glume length and its relation with the g_1 , p_{r_1} , and p_{r_2} factors

At the base of the spikelet there are two small lance-shaped structures called glumes. In common varieties, the glumes are very short, about one-third as long as the lemma and palea. But there are some varieties in which the glumes are as long as the lemma and palea. In inheritance, PARNELL *et al* (1917) and NAGAI (1921) have reported that the short glume is dominant to the long glume giving a simple 3:1 ratio in F_2 .

The writer found a case where the short glume × long glume gave a 15:1 ratio, long glume being recessive, as shown in table 7.

TABLE 7
Segregation for glume length in the cross 4269 (long) × 4957 (short).

	SHORT GLUME	LONG GLUME	TOTAL
Observed	674	43	717
Calculated 15:1	672.15	44.81	717
Deviation		-1.81	

$$\frac{\text{Dev.}}{\text{P.E.}} = \frac{1.81}{4.37} = 0.41$$

Since the observed ratio is remarkably close to 15:1, undoubtedly there are two duplicate factors concerned with the production of the glume length. These two pairs of duplicate genes are designated as G_1g_1 and G_2g_2 .

Further data clearly indicate that g_1 and g_2 are independent of the glutinous gene g_1 , as shown in table 29. The observed data approach the calculated ratios very closely, considering the deficiency of the glutinous plants involved. Furthermore, the duplicate genes G_1 and G_2 have no chromosomal relations with factors P_{r_1} and P_{r_2} , as shown in table 30.

Inheritance of spikelet length and its relation with other characters

The spikelet length varies with different varieties. The variety, 4957, has spikelets varying from 3.5–4.9 mm in length with an average of 4.13 mm. The variety 4269 has spikelets varying from 7.3–10.3 mm in

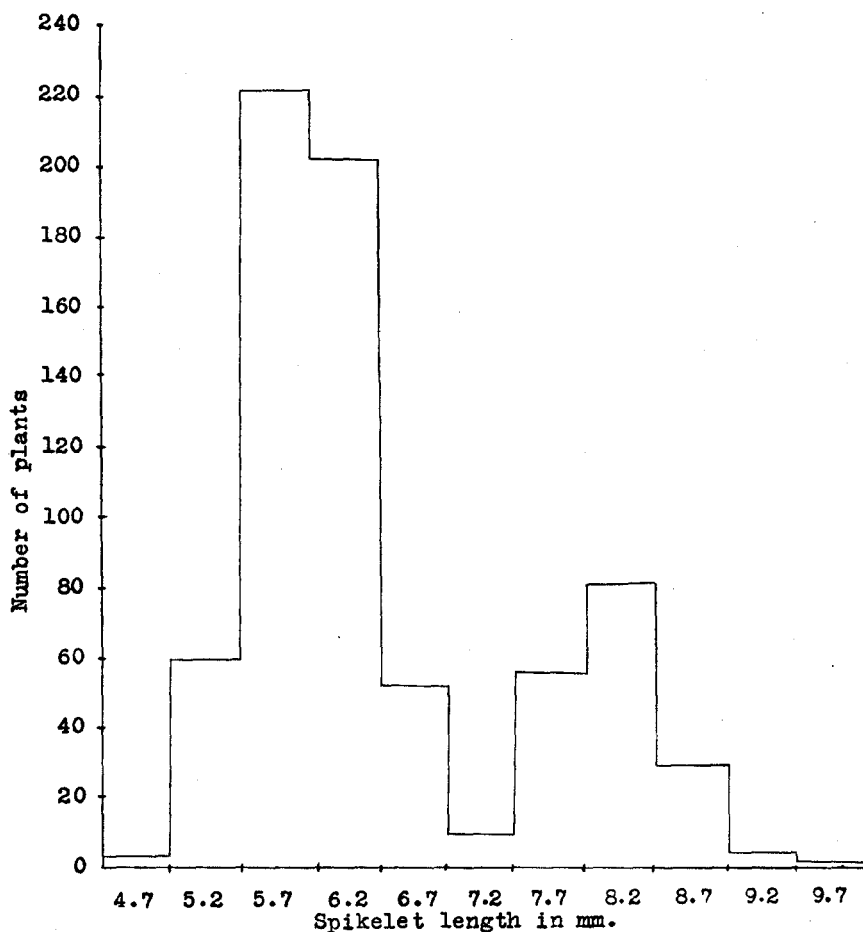


FIGURE 2.—Showing segregation for spikelet length in F_2 of cross 4269 \times 4957.

length with an average of 8.81 mm. The variation within each of these varieties follows a normal frequency curve.

In the cross, 4269 \times 4957, made by the writer at the CROWLEY RICE EXPERIMENT STATION, 1925, ten F_1 plants were obtained, each showing a similar intermediate type of spikelet ranging from 3.9–6.4 mm long with an average of 5.33 mm in length. In the F_2 generation, segregation for the

spikelet length took place, but the spikelets on the same plant were uniform, as expected. Six spikelets taken from the different parts of a panicle in a random fashion were measured and their average length was taken to represent the spikelet length of the plant in question. That this method of sampling actually gives a representative value is proved by the fact that when all the 95 spikelets of a panicle from the plant (Hg_{11}) were measured, their average was 5.66 mm approaching very closely to the respective average lengths of several samples of six spikelets each taken at random from that same panicle, namely 5.86, 5.3, 5.75, 5.64, and 5.66. In a population of 718 F_2 plants, the spikelet length ranged from 4.7 to 9.7 mm, as shown in table 8. When the different class values were plotted against the frequency of each class, we obtained a distinctly bimodal curve (figure 2). Since the dividing point of the two groups on the curve

TABLE 8
Showing segregation for spikelet length in F_2 from the cross 4269×4957.

GENERATION	CLASS CENTERS (IN MM) AND FREQUENCIES													NUMBER OF PLANTS	NUMBER OF SPIKELETS
	3.7	4.2	4.7	5.2	5.7	6.2	6.7	7.2	7.7	8.2	8.7	9.2	9.7		
P_1 (4957)	1	3												4	282
P_1 (4269)												4		4	362
F_1				10										10	851
F_2			2	60	222	202	52	9	56	81	29	4	1	718	6 for each plant

is clearly at the class center, 7.2, which is exactly the length of the shortest spikelet of the long parent, and since the longest spikelet of either the short parent or of the F_1 is never over 6.5 mm in length, it appears legitimate to place the nine plants of the class (7.2) in the long group. In so doing, the F_2 population is divided into two phenotypes, one with short spikelets and the other with long spikelets in almost exactly a 3:1 ratio, as shown in table 9.

TABLE 9
Segregation for short and long spikelet in F_2 from 4269×4957.

	SHORT SPIKELET	LONG SPIKELET	TOTAL
Observed	538	180	718
Calculated 3:1	538.5	179.5	718
Deviation		0.5	

The data clearly indicates that the spikelet length, in this material at least, is due to one allelomorph pair of factors which may be designated as $S_p s_p$.

The $S_p s_p$ pair of genes are not linked with the $G_1 g_1$ pair as shown in table 31, nor with $P_{r_1} p_{r_1}$ and $P_{r_2} p_{r_2}$ as shown in table 32.

We have seen, in the preceding pages, that glume length depends upon two independent duplicate factors G_1g_1 and G_2g_2 , the short glume being dominant and that the spikelet length depends on one allelomorphic pair of genes, $S_p s_p$. When the variety, 4957, having short spikelet and short glumes, was crossed with the variety 4269, having long spikelet and long glumes, all F_1 plants had short glumes and intermediate spikelets. In the F_2 generation, two new types occurred in addition to the two grand-parental types, as illustrated in figure 3.

The F_2 population consists of 538 plants having short spikelet and short glumes, one plant having short spikelet and long glumes, 134 plants having long spikelet and short glumes, and 45 plants having long spikelet and long glumes, as shown in table 10. On the basis of three independent factors, we should expect the corresponding classes of F_2 plants to be 504.45, 33.63, 168.15, and 11.21, respectively. But this is not the case; the observed data show a great excess of the two parental types. If we assume that one of the glume factors is the same as the spikelet factor, the calculated ratios would be 12:0:3:1, giving the class frequencies 538.50, having short glumes and short spikelet, none having short spikelet with long glumes, 134.625, having long spikelet with short glumes, and 44.875 having long spikelet and long glumes. The expectation on this assumption fits the observed data very well, except that the single plant with short spikelet and long glumes is not accounted for, as shown in table 10.

TABLE 10
Relation between the glume length (15:1) and the spikelet length (3:1).

PROGENIES	SHORT SPIKELET SHORT GLUME	SHORT SPIKELET LONG GLUME	LONG SPIKELET SHORT GLUME	LONG SPIKELET LONG GLUME	TOTAL
4269×4957A	37	0	3	6	
“ B	48	0	11	4	
“ C	52	1 (CSTG)	13	3	
“ D	58	0	14	5	
“ E	45	0	6	5	
“ F	76	0	22	8	
“ G	68	0	16	5	
“ H	4	0	4	0	
“ I	73	0	18	6	
“ J	77	0	27	3	
Observed	538	1	134	45	718
Independent 45:3:15:1	504.45	33.63	168.15	11.21	717.44
Independent 12:0:3:1	538.50	0	134.625	44.875	718

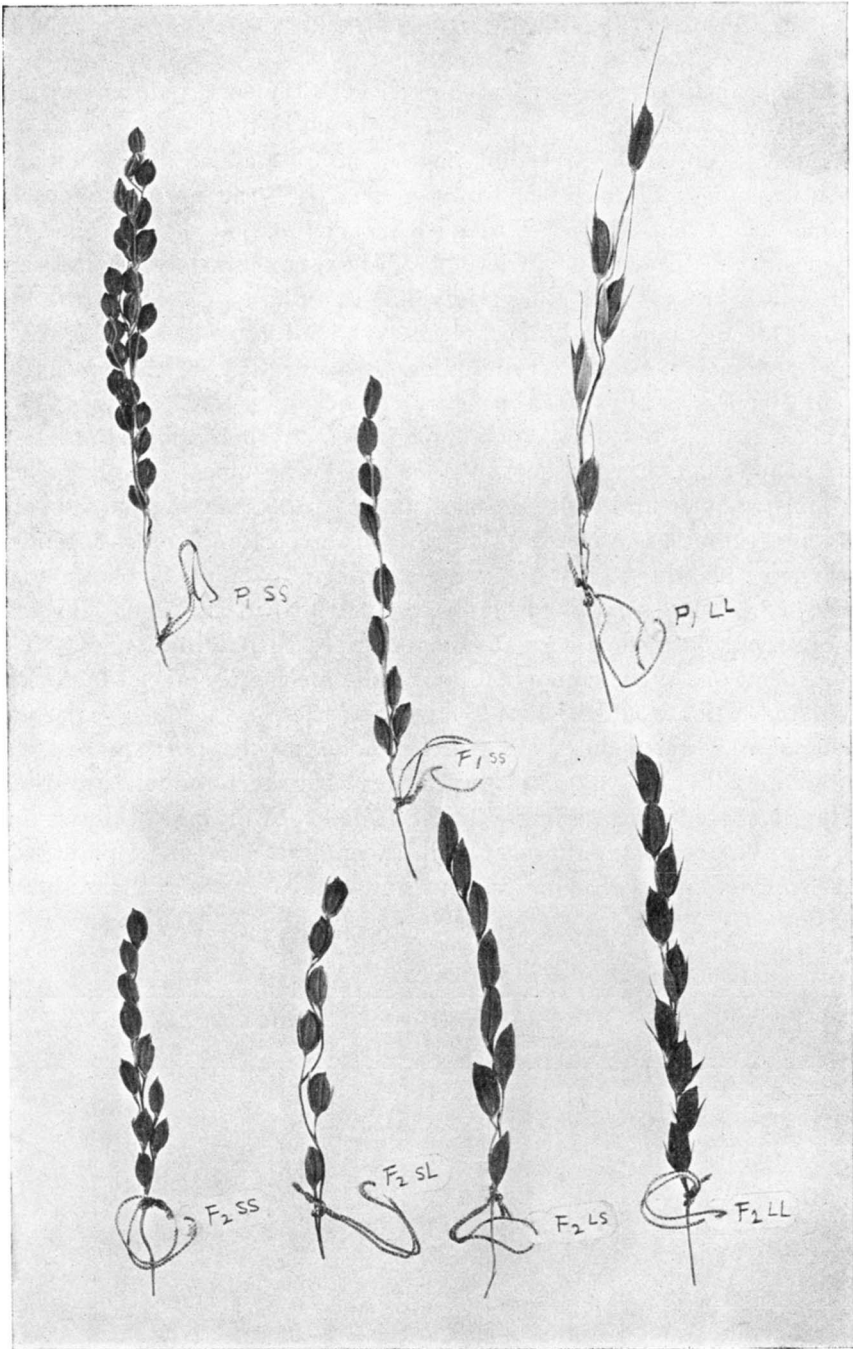


FIGURE 3.— $P_1 ss$ = The paternal parent having short spikelet and short glumes. $P_1 LL$ = The maternal parent, having long spikelet and long glumes. $F_1 ss$ = Hybrid, having short or intermediate spikelet and short glumes. $F_2 ss$ = One of 538 F_2 plants, having short spikelet and short glumes. $F_2 sL$ = The only F_2 plant which had short spikelets and long glumes. This combination is a result of crossing over. $F_2 Ls$ = One of the 134 F_2 plants having long spikelets and short glumes. $F_2 LL$ = One of the 45 plants having long spikelets and long glumes.

The same difficulty occurs if we assume complete linkage between one of the glume factors and the spikelet factor.

So far as the evidence goes, the best explanation, in the writer's opinion, may be obtained on the basis of close linkage between one of the duplicate factors for glume length and the factor for spikelet length. Here, it may be arbitrarily assumed that g_2 is closely linked with s_p . On this assumption, we can calculate the gametic ratio.

If only the factors G_1g_1 and $S_p s_p$ had been concerned in this cross, the F_2 distribution would be represented by the general formula,

$$\frac{a}{3r^2 + 2(s^2 + 2rs)} : \frac{b}{s^2 + 2rs} : \frac{c}{s^2 + 2rs} : \frac{d}{r^2} \quad (1)$$

Where $r:s:s:r$ is any gametic series and $a, b, c,$ and d are the phenotypes, $G_1S_p, G_1s_p, g_1S_p,$ and $g_1s_p,$ respectively.

But when the G_2g_2 pair of genes is also involved, as is the case in this cross, r = the non-crossover gametes $G_1G_2S_p, g_1G_2S_p, G_1g_2s_p,$ and $g_1g_2s_p$; and s = crossover gametes $G_1G_2s_p, g_1G_2s_p, G_1g_2S_p,$ and $g_1g_2S_p$. Combinations of these gametes in all possible ways grouped according to phenotypes may be represented by the general formula,

$$\frac{a}{12r^2 + 11(s^2 + 2rs)} : \frac{b}{3r^2 + 4(s^2 + 2rs)} : \frac{c}{s^2 + 2rs} : \frac{d}{r^2} \quad (2)$$

From formula (2), we get the following four equations:

$$a = 12r^2 + 11(s^2 + 2rs) = \text{Short spikelet and short glumes}$$

$$b = 3r^2 + 4(s^2 + 2rs) = \text{Long spikelet and short glumes}$$

$$c = 2rs + s^2 = \text{Short spikelet and long glumes}$$

$$d = r^2 = \text{Long spikelet and long glumes}$$

From these four equations, we can determine the gametic ratio directly from the observed zygotic series. Thus, we get $a + b + c + d = 16r^2 + 16c$

$$16r^2 = a + b + d - 15c$$

$$r^2 = \frac{a + b + d - 15c}{16}$$

$$r = 0.25\sqrt{a + b + d - 15c} \quad (3)$$

Also,

$$16(s^2 + 2rs) = a + b + c - 15r^2$$

$$s^2 + 2rs = \frac{a + b + c - 15r^2}{16}$$

Adding r^2 (or d) to both sides, we get,

$$r^2 + 2rs + s^2 = \frac{a+b+c+d}{16}$$

$$r+s = 0.25\sqrt{a+b+c+d}$$

$$s = 0.25\sqrt{a+b+c+d-r} \quad (4)$$

By substituting the observed data of the four phenotypes for a , b , c , and d , in the formulae (3) and (4), we get,

$$r = 6.6225$$

$$s = 0.0750$$

If we take $s=1$, the ratio of $\frac{r}{s} = \frac{88.3}{1}$.

By substituting the values of r and s in the four equations, we obtain the expected frequencies of the four phenotypes, which fit the observed data unusually closely, as shown in table 11.

TABLE 11
Showing coupling between g_2 and s_p (crossover = 1.11 percent).

	SHORT SPIKELET SHORT GLUMES	LONG SPIKELET SHORT GLUMES	SHORT SPIKELET LONG GLUMES	LONG SPIKELET LONG GLUMES	TOTAL
Observed	538	134	1	45	718
Calculated (linkage)	537.5	135.63	0.99	43.87	
Deviation	0.5	-1.63	0.01	1.13	

$$X^2 = 0.0533. \quad \text{When } X^2 = 1, P = .801253$$

Since this is a coupling phase, the crossover between g_2 and s_p will be,

$$\frac{s}{r-s} \times 100 = 1.11 \text{ percent.}$$

Inheritance of the apiculus color and its relation with other characters

The apex of the lemma and palea is colored in many varieties. This localized color spot at the upper tip of the spikelet is here spoken of as the apiculus color. The inheritance of this character has been studied by several investigators. HECTOR obtained a ratio of three colored apiculus to one colorless in 1913 and another ratio of 27:37 in 1916. Besides, HECTOR (1922) reported two new conditions, one of which segregated in a 9:7 ratio and the other in a 15:1 ratio.

In crosses between different varieties, the writer obtained various ratios in the F_2 generations, namely, 3:1, 9:7, 15:1, 27:37, and 162:94, indicating that there are at least four genetic factors responsible for the production of the apiculus color. The data are presented in table 12.

TABLE 12
Showing segregation of colored and colorless apiculus in different ratios in F_2 populations of different crosses.

	CROSSES AND THE PARENTAL TYPES	F_1	F_2 SEGREGATION		CLOSEST RATIO	EXPECTED F_2		DEVIATION	SYMBOLS
			Colored	Colorless		Colored	Colorless		
1	Colorless \times colored 300 \times 400	Colored	77	65	9:7	79.83	62.09	2.91	CC A_{p_1}, A_{p_2}
2	Colorless \times colorless 300 \times 600	Colored	356	499	27:37	360.45	493.95	5.05	Cc A_{p_1}, A_{p_3}
3	Colorless \times colored 600 \times 400	Colored	330	190	162:94	328.86	190.82	-0.82	A_{p_1}, Cc A_{p_2}, A_{p_3}
4	Colored \times colorless 800 \times 600	Colored	255	22	15:1	259.65	17.31	4.69	A_{p_5}, A_{p_6}
5	Colorless \times colored 4269 \times 4957	Colored	567	176	3:1	557.25	183.75	7.75	A_{p_4}

That variety 300, though colorless, actually carries some factor is shown by the fact that when it was crossed with another colorless variety 600 (see cross No. 2), the F_1 had colored apiculus. In the F_2 , a ratio of 27:37 was observed, showing at least three factors were involved. This situation may be explained, if the two parental types have the following genetic constitutions:

$$300 = g_1 g_1 CC a_{p_1} a_{p_1} a_{p_2} a_{p_2} a_{p_3} a_{p_3} a_{p_4} a_{p_4} \text{ (glutinous colorless)}$$

$$600 = G_1 G_1 cc A_{p_1} A_{p_1} A_{p_2} A_{p_2} A_{p_3} A_{p_3} A_{p_4} A_{p_4} \text{ (non-glutinous colorless)}$$

Where A_{p_1}, A_{p_3} and C are complimentary factors for apiculus color.

In cross No. 1 (300 \times 400) the 9:7 ratio clearly indicates that two factors are concerned in the production of the apiculus color, these being designated as A_{p_1} and A_{p_2} . The situation can be explained by assuming the genetic constitutions of the parents as follows:

$$\text{Parent 300} = g_1 g_1 CC a_{p_1} a_{p_1} a_{p_2} a_{p_2}$$

$$\text{Parent 400} = G_1 G_1 CC A_{p_1} A_{p_1} A_{p_2} A_{p_2}$$

Where C = chromogen, and A_{p_1} and A_{p_2} are complementary for the apiculus color.

That the variety 600 actually carries at least one apiculus factor differing from those in the variety 400 is proved by cross No. 3, which gave a ratio of 162:94, showing that four factors are involved. The situation may be explained on the bases of the foregoing genetic constitutions assumed for varieties 400 and 600, respectively.

Cross No. 4 gave a ratio of 15:1, showing that there are two factors involved, each of them alone producing apiculus color. These factors may be designated as A_{p_5} and A_{p_6} . As no further crosses were made, the assumption must be considered as a tentative one.

Cross No. 5 gave a simple 3:1 ratio, showing that only one factor pair was involved. This factor pair is different from A_{p_1} , A_{p_2} , and A_{p_3} , in that none of the latter alone can produce the apiculus color. Furthermore, this new factor is linked with the glutinous gene as will be shown later. This gene is designated as A_{p_4} . It may be that one of the two duplicate factors involved in cross No. 4 is the same as A_{p_4} .

Factors A_{p_1} and A_{p_2} are independent of the glutinous gene as shown in table 13.

TABLE 13
Showing independent segregation between factors A_{p_1} , A_{p_2} and g_1 (307×410).

	COLORED APEX NON-GLUTINOUS	COLORLESS APEX NON-GLUTINOUS	COLORED APEX GLUTINOUS	COLORLESS APEX GLUTINOUS	TOTAL
Observed	65	51	12	14	142
Calculated 27:21:9:7	59.67	46.41	19.89	15.47	142
Deviation	5.33	4.59	-7.89	-1.47	

As mentioned above, A_{p_4} is linked with the glutinous gene as shown in table 14. On the independent Mendelian basis, the expected frequencies should be 417.87 colored non-glutinous, 139.29 colored glutinous, and 46.43 colorless glutinous. But this is far from the observed data which clearly indicate coupling between a_{p_4} and g_1 . On the latter basis, the

TABLE 14
Showing coupling between a_{p_4} and g_1 from F_2 of 4269×4957.

	COLORED APEX NON-GLUTINOUS	COLORLESS APEX NON-GLUTINOUS	COLORED APEX GLUTINOUS	COLORLESS APEX GLUTINOUS	TOTAL
Observed	491	90	76	86	743
Calculated	474.17	83.16	83.16	102.62	743
Deviation	16.83	6.84	-7.16	-16.62	

$$X^2 = 4.46. \quad P = 0.22.$$

gametic ratio is found from EMERSON'S (1916) formula, $r=10.13$, and $s=3.5$. The crossover is, therefore, about 22.34 percent.

The large deviation is clearly due to the deficiency of the glutinous plants, the latter being 2.98 times the probable error.

Further data show that A_{p4} is independent of the factors P_{r1} and P_{r2} , G_1 and G_2 , and S_p , as is seen in tables 33, 34, and 35 respectively.

Relation between stigma color and other characters

In some varieties, the stigma is colorless, and in others it is colored with an intensity varying from pale red to dark purple. In inheritance, colored and colorless stigma segregate in different ratios according to the material used. HECTOR (1916, 1922) reported cases of 3:1, 9:7, 27:37, and 81:175 ratios, showing that there are at least five factors responsible for the production of stigma color.

The writer obtained two cases, one segregating in a 3:1 ratio, and the other, 9:7, as shown in table 15.

TABLE 15
Showing segregation of stigma color.

CASE	CROSSES COLORLESS X PURPLE	F ₁	F ₂ SEGREGATION		CLOS- EST RATIO	F ₂ EXPECTED		DEVI- ATION	DEV. P. E.	SYMBOLS
			Colored	Colorless		Colored	Colorless			
1	307X410	Colored	101	41	3:1	106.5	35.5	5.5	1.58	
2	4269X4957 (ABFGI)	Colored	242	179	9:7	236.79	184.17	5.17	0.75	$S_{a1} S_{a2}$

In the first case, the factor is probably the same as A_{p1} (or A_{p2}), because in the same F₂ population arising from the same cross, the apiculus color alone segregated in a 9:7 ratio (see table 12) whereas a 9:3:4 ratio was observed when both apiculus and stigma were considered at the same time, as shown in table 16.

TABLE 16
Showing F₂ segregation for apex and stigma color (307X410).

	COLORED STIGMA	COLORED STIGMA	COLORLESS STIGMA	COLORLESS STIGMA	TOTAL
	COLORED APEX	COLORLESS APEX	COLORED APEX	COLORLESS APEX	
Observed	77	24	0	32	142
Calculated 9:3:4	79.83	26.61	0	35.48	142
Deviation	-2.83	-2.61	0	3.48	

In the second case, there are clearly two separate factors for the production of the stigma color. These are designated as S_{a_1} and S_{a_2} . They are complementary to each other. One of them is linked with the glutinous gene, g_1 . For the sake of convenience, the linkage may be arbitrarily assumed to be between s_{a_1} and g_1 . The data are presented in table 17.

TABLE 17
Showing linkage between s_{a_1} and g_1 in F_2 generation from the cross 4269×4957.

	NON-GLUTINOUS PURPLE STIGMA	NON-GLUTINOUS COLORLESS STIGMA	GLUTINOUS PURPLE STIGMA	GLUTINOUS COLORLESS STIGMA	TOTAL
Observed	210	100	32	79	421
Independent 27:21:9:7	177.39	137.97	59.13	45.99	421
Linkage	210.23	105.45	26.53	78.69	421
Deviation	-0.23	-5.45	5.47	0.31	

$$X^2 = 1.4094. \quad P = 0.707564.$$

BRUNSON'S (1924) modified formulae

$$r = \sqrt{\frac{(AB + 3ab) - (Ab + aB)}{18}}$$

$$s = \frac{1}{4} \sqrt{AB + Ab + aB + ab} - r$$

were used in calculating the intensity of the linkage between s_{a_1} and g_1 . The gametic ratio is $r = 4.18$ and $s = 0.95$. Since this is a coupling phase, the percentage of crossing over is obtained from the formula $\frac{s}{r+s}$, namely 18.51 percent.

Data from the same cross show factors s_{a_1} and s_{a_2} are independent of p_{r_1} , p_{r_2} , g_1 , g_2 and sp as shown in tables 36, 37, and 38.

The exact relation between the stigma color and the apiculus color in this particular cross is not determined. As described above, a_{p_4} is coupled with g_1 , giving about 22.34 percent crossing over; and s_{a_1} is also linked with g_1 , giving 18.51 percent crossing over. When the apiculus color and the stigma color were involved at the same time, a new situation arose, as shown in table 18.

The zygotic ratios calculated on the basis of three independent factors do not fit the observed ratio at all. There are, then, only two alternative explanations for the situation, namely, complete linkage between a_{p_4} and s_{a_1} , or a_{p_4} being the same factor as s_{a_1} . Since both alternatives give identical

zygotic ratio (9:3:0:4), it is impossible to decide which alternative is correct. It may be mentioned, however, that one plant (FSt 68) which is not counted in table 18 had purple stigma with a doubtful apiculus color, because the latter was under a question mark (?) in the original notebook.

TABLE 18
Relation between a_{p_4} and s_{a_1} .

	COLORED APEX PURPLE STIGMA	COLORED APEX COLORLESS STIGMA	COLORLESS APEX PURPLE STIGMA	COLORLESS APEX COLORLESS STIGMA	TOTAL
Observed	243	64	1 (FSt 68?)	117	424
Calculated 27:21:9:7	178.74	139.02	59.58	46.34	424
Complete linkage 9:3:0:4	238.5	79.5	0	106.0	424
Deviation	4.5	-15.5	0	11.0	

Although a_{p_4} and s_{a_1} have different crossover values with the glutinous gene, the difference is only 3.83 percent. Since both alternatives are possible, the question must be left open for the present.

Relation between the leaf-sheath color and other characters

The leaf-sheath color when present may be either self red or purple, or merely consisting of colored stripes varying in intensity. There are several genetic factors responsible for its production. PARNELL (1917) found a case where colored and colorless leaf-sheath segregated in a simple 3:1 ratio. HECTOR (1916, 1922) reported four cases segregating in 3:1, 9:7 27:37, and 15:1, respectively.

The writer has obtained two kinds of ratios, namely, 9:7 and 15:1, as shown in table 19.

TABLE 19
Showing F_2 segregation for leaf-sheath color.

CASE	CROSSES	F_1	F_2 SEGREGATION		CLOSEST RATIO	Expected		DEVIATION	SYMBOLS
			Colored	Colorless		Colored	Colorless		
1	4269 × 4957 (colorless × colored)	Colored	204	139	9:7	192.87	147.01	-8.01	$L_{S_1} L_{S_2}$
2	800b ₅ × 625 (colored × colorless)	Colored	266	14	15:1	262.5	17.5	-2.05	$L_{S_3} L_{S_4}$

These data indicate that there are at least four factors which are concerned with the production of leaf-sheath color. In the first case, there must be two complementary factors, whose presence is necessary for the expression of color. These factors are designated as L_{S_1} and L_{S_2} . In the

second case, there must be two duplicate factors each of which alone can produce color. These are designated as L_{s_3} and L_{s_4} .

In the first cross, one of the complementary factors is linked with the glutinous gene. The linkage may be arbitrarily assumed to be between l_{s_1} and g_1 . The gametic ratio is calculated by BRUNSON'S formulae,

$$r = \sqrt{\frac{AB + 3ab - (Ab + aB)}{18}} = 3.73$$

$$s = \frac{1}{4} \sqrt{AB + Ab + aB + ab} - r = 0.90$$

The crossing over = $\frac{s}{r+s} \times 100 = 19.43$ percent. By substituting the values of r and s in the following equations, we get the zygotic ratios,

$$AB = 9r^2 + 12rs + 6s^2 = \text{colored sheath non-glutinous}$$

$$Ab = 6rs + 3s^2 = \text{colored sheath glutinous}$$

$$aB = 3r^2 + 12rs + 6s^2 = \text{colorless sheath non-glutinous}$$

$$ab = 4r^2 + 2rs + s^2 = \text{colorless sheath glutinous}$$

The calculated zygotic ratios fit the observed ratios very well considering the deficiency of glutinous plants, as shown in table 20.

TABLE 20
Showing coupling between l_{s_1} and g_1 .

	COLORED SHEATH NON-GLUTINOUS	COLORED SHEATH GLUTINOUS	COLORLESS SHEATH NON-GLUTINOUS	COLORLESS SHEATH GLUTINOUS	TOTAL
Observed	179	25	80	59	343
Calculated 27:9:21:7	144.72	48.24	112.56	37.52	343
Linkage (19.43% crossing over)	170.36	22.57	88.88	63.18	343
Deviation	8.64	2.43	-8.88	-4.18	

Data obtained from the same cross indicate that l_{s_1} , l_{s_2} are independent of the factors p_{r_1} , p_{r_2} , g_1 , g_2 , and s_p , as shown in tables 39, 40 and 41.

l_{s_1} is closely linked with a_{p_4} as shown in table 21. Since a_{p_4} is coupled with g_1 , giving 22.34 percent crossing over, and since l_{s_1} is also linked with g_1 , giving 19.43 percent crossing over, the order of the three genes on the glutinous chromosome would appear to be,

a_{p_4}	l_{s_1}	22.34 percent	g_1
		19.43 percent	

Linkage between stigma color and leaf-sheath color

As described above, in the F_2 generation of the cross, 4269×4957, the stigma color alone segregated in a ratio of 9 colored:7 colorless, and the leaf-sheath color also segregated in a 9:7 ratio. One of the two complemen-

TABLE 21
Showing linkage between a_{p_4} and l_{s_1} in F_2 (4269×4957).

	COLORED APICULUS PURPLE SHEATH	COLORED APICULUS COLORLESS SHEATH	COLORLESS APEX PURPLE SHEATH	COLORLESS APEX COLORLESS SHEATH	TOTAL
Observed	205	43	(BS_{t_3}) 1	98	347
<i>Expected 27:21:9:7</i>	146.34	113.82	48.78	37.94	346.88
Deviation	58.66	-50.82	-47.78	60.06	

tary factors for stigma color is linked with the glutinous gene, giving 18.71 percent crossing over. One of the two complementary genes for the production of the leaf-sheath color is also linked with g_1 , giving 19:43 percent crossing over. When the stigma color and the leaf-sheath color are considered at the same time, a very close linkage between the two characters is revealed, as shown in table 22a, where the calculated zygotic ratios on the basis of four independent factors are shown to be very far from the observed frequencies.

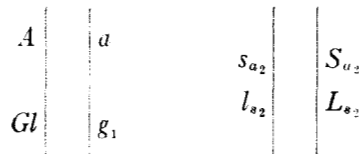
TABLE 22a
Showing close linkage between the stigma color and the leaf-sheath color.

PROGENIES	PURPLE STIGMA PURPLE SHEATH	PURPLE STIGMA COLORLESS SHEATH	COLORLESS STIGMA PURPLE SHEATH	COLORLESS STIGMA COLORLESS SHEATH	TOTAL
4269×4957B	34	2	4	23	
4269×4957D	46	3	2	29	
4269×4957F	52	4	3	44	
4269×4957I	57	0	6	37	
Observed	189	9	15	133	346
<i>Calculated on 4 independent factors</i>	109.35	85.05	85.05	66.15	
<i>3 independent factors</i>	145.97	48.66	48.66	102.72	

Since the stigma and the leaf-sheath give about the same percentage of crossing over with the glutinous gene, the difference being 0.72 percent, it is possible that the two characters have one factor in common. Most probably s_{a_1} is the same factor as l_{s_1} . For the sake of simplicity, this common factor is designated as A . Until further data demonstrate that the s_{a_1} and l_{s_1} are actually two separate entities, factor A will be considered

as a common gene which has a manifold effect conditioning stigma color as well as leaf-sheath color. On this hypothesis, then, A is complementary with S_{a_2} for stigma color and A is also complementary with L_{s_2} for leaf-sheath color.

Since the calculated ratios on the basis that A , S_{a_2} and L_{s_2} are independent factors do not fit the observed frequencies, S_{a_2} and L_{s_2} must be coupled. The situation may be represented by the following diagram:



If $r:s:s:r$ represents any gametic series between the two linked factors, s_{a_2} and l_{s_2} , the non-crossover classes may be represented by the following equations:

$$\begin{aligned}
 A S_{a_2} L_{s_2} &= 3[3r^2 + 2(s^2 + 2rs)] = 9r^2 + 12rs + 6s^2 \\
 a S_{a_2} L_{s_2} &= 3r^2 + 2(s^2 + 2rs) = 3r^2 + 4rs + 2s^2 \\
 A s_{a_2} l_{s_2} &= (3r^2) = 3r^2 \\
 a s_{a_2} l_{s_2} &= (r^2) = r^2
 \end{aligned}$$

On the other hand, the cross over classes may be represented as follows

$$\begin{aligned}
 A s_{a_2} L_{s_2} &= 3(s^2 + 2rs) = 6rs + 3s^2 \\
 A S_{a_2} l_{s_2} &= 3(s^2 + 2rs) = 6rs + 3s^2 \\
 a S_{a_2} l_{s_2} &= (s^2 + 2rs) = 2rs + s^2 \\
 a s_{a_2} L_{s_2} &= (s^2 + 2rs) = 2rs + s^2
 \end{aligned}$$

Since either stigma color or leaf-sheath color needs two complementary factors ($A S_{a_2}$ or $A L_{s_2}$) for its expression, the five classes ($a S_{a_2} L_{s_2}$, $A s_{a_2} l_{s_2}$, $a s_{a_2} l_{s_2}$, $a S_{a_2} l_{s_2}$, $a s_{a_2} L_{s_2}$) are thrown into the same phenotypic group. By this regrouping, the four phenotypic classes are represented by the four equations:

$$\begin{aligned}
 XY &= 9r^2 + 12rs + 6s^2 && \text{Purple stigma and purple sheath} \\
 Xy &= 6rs + 3s^2 && \text{Purple stigma and colorless sheath} \\
 xY &= 6rs + 3s^2 && \text{Colorless stigma and purple sheath} \\
 xy &= 7r^2 + 8rs + rs^2 && \text{Colorless stigma and colorless sheath}
 \end{aligned}$$

Where X =purple stigma, x =colorless stigma, Y =purple sheath and y =colorless sheath. From these equations, we get:

$$XY + xy = 16r^2 + 20rs + 10s^2 \tag{A}$$

$$Xy + xY = 12rs + 6s^2 \tag{B}$$

Dividing both (A) and (B) by 2, we get

$$\frac{XY+xy}{2} = 8r^2 - 10rs + 5s^2 \quad (C)$$

$$\frac{Xy+xY}{2} = 6rs + 3s^2 \quad (D)$$

Multiplying (C) by 3, and (D) by 5, we get

$$24r^2 = \frac{3}{2}(XY+xy) - \frac{5}{2}(Xy+xY)$$

$$r = \sqrt{\frac{\frac{3}{2}(XY+xy) - \frac{5}{2}(Xy+xY)}{24}} \quad (1)$$

Also,

$$XY+Xy+xY+xy = 16(r^2+2rs+s^2)$$

Taking the square roots, we get

$$4(r+s) = \sqrt{XY+Xy+xY+xy}$$

$$s = \frac{1}{4}\sqrt{XY+Xy+xY+xy} - r \quad (2)$$

From (1) and (2), we can calculate the gametic ratio, this being:

$$r = 4.19$$

$$s = 0.46$$

Since this is a coupling case, the percentage of crossing over =

$$\frac{0.46}{4.19+0.46} \times 100 = 9.8 \text{ percent}$$

Substituting the calculated values of r and s in the four original equations representing the four F_2 phenotypic classes, we get the frequencies quite similar to the observed ones, as shown in table 22b:

TABLE 22b
Showing close linkage between sa_2 and ls_2 .

	PURPLE STIGMA PURPLE LEAF-SHEATH	PURPLE STIGMA COLORLESS SHEATH	COLORLESS STIGMA PURPLE SHEATH	COLORLESS STIGMA COLORLESS SHEATH
Observed	189	9	15	133
Calculated	182.68	12.19	12.19	138.88
Deviation	6.32	-3.19	2.81	-5.88

$$X^2 = 1.947$$

$$P = .584536$$

Relation between ligule color and other characters

The ligule is a structure that projects out at the juncture of the leaf-blade and the leaf-sheath. In some varieties, this structure has a deep purple color. In inheritance, the ligule color depends on several factors for its expression. HECTOR (1922) reported two cases, one segregating in 9:7 ratio and the other segregating in 27:37 ratio.

The writer has obtained a ratio of 27 purple: 37 green in the cross, 4269×4957, as shown in table 23.

TABLE 23
Showing segregation for ligule color.

	LIGULE PURPLE	LIGULE GREEN	TOTAL
Observed	109	148	257
Calculated 27:37	108.41	148.55	257
Deviation	0.59	-0.55	

The data clearly show that three factors are concerned in the production of ligule color in this case. These factors are designated as l_{g1} , l_{g2} , and l_{g3} . These three genes are probably independent of the factors g_1 , g_2 , and s_p , as shown in tables 24, 42, and 43.

TABLE 24
Showing independent segregation of g_1 , l_{g1} , l_{g2} , and l_{g3} .

PROGENIES	NON-GLUTINOUS PURPLE LIGULE	NON-GLUTINOUS GREEN LIGULE	GLUTINOUS PURPLE LIGULE	GLUTINOUS GREEN LIGULE	TOTAL
4269×4957A	21	15	2	9	
4269×4957B	18	26	4	15	
4269×4957C	33	27	4	5	
4269×4957D	23	42	4	9	
Observed	95	110	14	38	257
Calculated 81:111:27:37	81.32	111.44	27.11	37.15	
Deviation	13.68	-1.44	-13.11	0.85	

Relation between ligule color and pericarp color

As mentioned above, the pericarp color in this cross is due to two duplicate factors which have been designated as P_{r1} and P_{r2} . When the ligule color and the pericarp color are considered at the same time, a new situation appears, as shown in table 25.

As shown in table 25, there is only one individual in the class "purple ligule and colorless pericarp" from four progenies. It is possible that some of the ligule factors are closely linked with the pericarp genes, and the rare occurrence of this class is due to linkage and the small population.

TABLE 25
Showing relation between p_{r1} , p_{r2} , l_{o1} , l_{o2} , and l_{o3} .

PROGENIES	PURPLE LIGULE COLORED PERICARP	PURPLE LIGULE COLORLESS PERICARP	GREEN LIGULE COLORED PERICARP	GREEN LIGULE COLORLESS PERICARP	TOTAL
4269×4957A	21	(Agl ₆) 1	20	4	255
4269×4957B	22	0	36	5	
4269×4957C	38	0	27	3	
4269×4957D	26	0	48	4	
Observed	107	1	131	16	
Calculated 108:0:132:16	108	0	132	16	
Deviation	-1	1	-1	0	

On the other hand, it is equally possible that one of the ligule genes is the same as one of the pericarp factors, and the single individual may be due to contamination. Indeed, the calculated ratios (108:0:132:16) on the latter basis fit the observed ratios remarkably well. However, the question must be left open for the present. Earlier investigations (HECTOR 1922) have shown a similar situation.

Relation of hull color to other characters

The term "hull" here used includes the lemma and palea which enclose the grain within. There are different colors either extended entirely over the hull such as "dark gold, ripening gold, and ripening straw," or restricted to certain portions of the hull, such as "dark furrows, piebald gold, tipped gold, patchy gold, mottled gold, and granular furrows" (PARNELL 1922). The character with which we are immediately concerned here is the ripening black color. The hull is first green as usual, but when the grains reach maturity, the hull turns black. PARNELL (1917) reported two cases of a similar condition, one segregating in a 3:1 ratio and the other 9:7.

The writer crossed two non-black varieties (800b₅×625), the F₁ spikelets at first had green hull which later changed black or sooty black (Ridgway). The F₂ plants segregated in a ratio of approximately 9 black : 7 non-black, as shown in table 26, where the data for this and other characters involved in the same cross (800b₅×625) are presented together.

TABLE 26

Showing segregation for colors of hull, internode, leaf-sheath, apiculus, and pericarp.

	DESCRIPTION	F ₁ SEGREGATION		CLOSEST RATIO	F ₂ EXPECTATION		DEV.	SYMBOLS
						P. E.		
Hull	Black <i>versus</i> non-black	115	103	9:7	122.76	95.48	1.52	$h_1 h_2$
Internode	Colored <i>versus</i> colorless	142	117	9:7	145.13	112.88	0.76	$In_1 In_2$
Leaf-sheath	Purple <i>versus</i> colorless	266	14	15:1	262.5	17.5	0.91	$ls_3 ls_4$
Apiculus	Colored <i>versus</i> colorless	255	22	15:1	259.65	17.31	1.72	$ap_6 ap_6$
Pericarp	Colored <i>versus</i> colorless	199	19	15:1	203.42	13.56	2.25	$pr_1 pr_2$

The data clearly show that there are two complementary factors for the production of the black hull. These are designated as H_1 and H_2 . Both these genes are independent of the factors I_{n_1} , I_{n_2} , L_{s_3} , L_{s_4} , A_{p_5} , A_{p_6} , P_{r_1} , and P_{r_2} , as shown in tables 27, 28, 44, and 45.

TABLE 27

Showing independent segregation between h_1 , h_2 , i_{n_1} , and i_{n_2} .

	BLACK HULL COLORED INTER- NODE	BLACK HULL COLORLESS INTERNODE	NON-BLACK COLORED INTERNODE	NON-BLACK COLORLESS INTERNODE	TOTAL
Observed	63	47	44	57	211
Calculated 81:63:63:49	66.74	51.91	51.91	40.38	210.94
Deviation	-3.74	-4.91	-7.91	16.62	

The large deviation of the observed frequencies may be due to the small population, because at least 256 individuals are necessary to make the ratios barely even.

TABLE 28

Showing independent segregation between h_1 , h_2 , l_{s_3} , and l_{s_4} .

	BLACK HULL PURPLE SHEATH	NON-BLACK HULL PURPLE SHEATH	BLACK HULL COLORLESS SHEATH	COLORLESS HULL COLORLESS SHEATH	TOTAL
Observed	111	97	3	6	217
Calculated 135:105:9:7	114.75	89.25	7.65	5.95	217
Deviation	-3.75	7.75	-4.65	0.05	

DISCUSSION OF RESULTS

In the foregoing pages, data have been presented to show the behavior and chromosomal relations of twenty-five or more genetic factors affecting one or another part of the plant. To facilitate further discussion, we may outline the established genes and their behavior as follows:

FACTORS	CHARACTERS FOR WHICH THE FACTORS ARE RESPONSIBLE	RATIOS
$G_1 g_1$	The non-glutinous and glutinous pair	3:1
$A_{n1} a_{n1}$ $A_{n2} a_{n2}$	Duplicate factors for the production of awns Independent of $G_1 g_1$ pair	15:1
$T_v t_v$	For the tawny color on the awn, apex and glumes Linked with $G_1 g_1$ —crossover = 16.59 percent	3:1
$P_{r1} p_{r1}$ $P_{r2} p_{r2}$	Duplicate factors for pericarp color Independent of g_1	15:1
$G_1 g_1$ $G_2 g_2$	Duplicate factors for the glume length Independent of g_{11} , p_{r1} and p_{r2}	15:1
$S_p s_p$	Factor pair for spikelet length Independent of g_{11} , p_{r1} , p_{r2} and g_1 Closely linked with g_2 —crossing over 1.11 percent	3:1
$A_{p1} a_{p1}$ $A_{p2} a_{p2}$	Complementary factors for apiculus color Independent of g_1	9:7
$A_{p3} a_{p3}$	A third factor for apiculus color	(27:37)
$A_{p4} a_{p4}$	Factor for apiculus color Linked with g_1 —crossing over = 22.34 percent Independent of p_{r1} , p_{r2} , g_1 , and s_p	3:1
$A_{p5} a_{p5}$ $A_{p6} a_{p6}$	Duplicate factors for the apiculus color	15:1
$S_{a1} s_{a1}$ $S_{a2} s_{a2}$	Complementary factors for the stigma color S_{a1} is linked with g_1 —crossover = 18.51 percent Independent of p_{r1} , p_{r2} , g_1 , g_2 and s_p s_{a1} may be the same factor as a_{p4} or closely linked with a_{p4}	9:7
$L_{s1} l_{s1}$ $L_{s2} l_{s2}$	Complementary factors for the leaf-sheath color l_{s1} is linked with g_1 —crossover = 19.43 percent They are independent of p_{r1} , p_{r2} , g_1 , g_2 and s_p l_{s2} is closely linked with s_{a2} —crossing over 9.8 percent	9:7

FACTORS	CHARACTERS FOR WHICH THE FACTORS ARE RESPONSIBLE	RATIOS
$L_{s3} l_{s3}$ $L_{s4} l_{s4}$	Duplicate factors for the leaf-sheath color	15:1
$L_{g1} l_{g1}$ $L_{g2} l_{g2}$ $L_{g3} l_{g3}$	Complementary factors for the ligule color They are independent of g_1, g_2 and s_p l_{g3} may be the same factor as p_{r2} or completely linked with it	27:37
$H_1 h_1$ $H_2 h_2$	Complementary factors for the black hull Independent of $l_{s3}, l_{s4}, a_{p6}, p_{r1}$ and p_{r2}	9:7
$I_{n1} i_{n1}$ $I_{n2} i_{n2}$	Complementary factors for the internode color They are independent of h_1 and h_2	9:7

While the results outlined above are self-explanatory, a few of them may be briefly discussed with advantage. First of all, it is interesting to note that the awn, being a sporophytic character, should be either present or absent on all the spikelets of the same plant in the F_2 generation. Contrary to this expectation, two new types have appeared. One type has most of the spikelets awned, and the other has only a few spikelets awned, the remaining spikelets of the same panicle being awnless, as shown in figure 1. These new types and the original grand-parental types occur in about a 12:1:2:1 ratio. The observed frequencies have been explained on the basis of two duplicate factors. The awn may be conceived of as an extension of the central nerve of the lemma. The gene, A_{n1} , extends the central nerve either in single or double dose with or without A_{n2} . The gene A_{n2} is of similar nature, but it is weaker in activity; so, the double doses may extend most of the central nerves, while the single dose may extend just a few of them. Environmental conditions may also enter in, thus influencing the action of A_{n2} during the morphogenesis of the spikelets and particularly of the awn. As the spikelets on the top of the panicle and those on the lower part do not develop at the same time, we can easily see the differential action of the gene under different conditions in the extension of the awn. It is interesting to note that in the "mostly awned" and "rarely awned" classes, usually it is the spikelets at the lower part of the panicle whose awns are not extended.

Factorially, the case may be represented as follows:

$$\left. \begin{array}{l} 1 A_{n1} A_{n1} A_{n2} A_{n2} \\ 2 A_{n1} A_{n1} A_{n2} a_{n2} \\ 2 A_{n1} a_{n1} A_{n2} A_{n2} \\ 4 A_{n1} a_{n1} A_{n2} a_{n2} \\ 1 A_{n1} A_{n1} a_{n2} a_{n2} \\ 2 A_{n1} a_{n1} a_{n2} a_{n2} \end{array} \right\} = 12 \text{ fully awned}$$

- 1 $a_{n_1} a_{n_1} A_{n_2} A_{n_2} = 1$ mostly awned
 2 $a_{n_1} a_{n_1} A_{n_2} a_{n_2} = 2$ rarely awned
 1 $a_{n_1} a_{n_1} a_{n_2} a_{n_2} = 1$ wholly awnless

Several factors have been shown to lie on the glutinous chromosome. T_v is coupled with G_1 , giving 16.59 percent crossing over. a_{p_4} is linked with g_1 , giving 22.34 percent crossing over. l_{s_1} is also coupled with g_1 , giving 19.43 percent crossing over. These constitute the first linkage group which may be expressed in the following diagram:

$$\overline{a_{p_4} \quad l_{s_1} \quad t_v(?) \quad g_1 \quad t_v(?)}$$

Whether t_v is on the left or right hand side of g_1 is not known at present. It may be noted that s_{a_1} is also linked with g_1 , giving about 18.51 percent crossing over. However, whether s_{a_1} is the same factor as l_{s_1} , or a separate gene closely linked with l_{s_1} remains to be determined. It may be further noted that TAKAHASHI's factor (R) for awn color and YAMAGUCHI's factor (S) for apiculus color are also in the same linkage group, though their exact loci cannot be stated. It is possible that (S) is the same factor as s_{p_1} .

The second linkage group constitutes two factors, namely, s_p and g_2 . The glume length depends on two duplicate factors, g_1 and g_2 , segregating in a 15:1 ratio long glume being recessive. The spikelet length depends on a simple factor pair, $S_p s_p$, long spikelet being recessive. The factors g_2 and s_p are coupled, giving 1.11 percent crossing over. That the short spikelet factor, S_p , is coupled with one of the duplicate glume genes (G_2) is beyond doubt. It is of interest to note, however, that on the basis of 1.11 percent crossing over, only 0.99 or one plant in a population of 718 individuals is expected to have short spikelets and long glumes, and one such individual has been obtained as shown in figure 3 (F_2 SL). That this individual is a crossover is proved by the fact that there is no such variety in my stock that has short spikelets and long glumes, thus eliminating any error through contamination. It may further be pointed out that if the observed crossover plant had not appeared, the data (see table 10) could be explained equally well on the basis of 12:0:3:1 ratio by assuming that one of the duplicate glume factors is the same as the S_p factor for the spikelet length. The difficulty, however, is that on this assumption, it must follow that the long spikelet plant must necessarily have long glumes also. But this is not the case.

The third linkage group consists of s_{a_2} and l_{s_2} . The purple stigma in this case depends upon the presence of two dominant complementary factors, namely, S_{a_1} and S_{a_2} . The purple leaf-sheath also depends on two comple-

mentary factors, L_{s_1} and L_{s_2} . Since both L_{s_1} and S_{a_1} are linked with G_1 , giving about the same percentage of crossing over, L_{s_1} and S_{a_1} may be the same factor. For the sake of convenience, a common factor (A) is assumed to represent both L_{s_1} and S_{a_1} , though the assumption must await further verification. It is certain, however, that linkage does exist between the characters, no matter what assumption we may make. The observed frequencies cannot be explained on the independent segregation of either four or three factors, as shown in table 22a. It appears that only on the assumption of a close linkage between S_{a_2} and L_{s_2} can we explain the observed frequencies. In so doing, the crossing over value is found to be 9.8 percent between s_{a_2} and l_{s_2} . The calculated zygotic ratios on this basis fit the observed frequencies closely.

Thus far, three linkage groups have been established beyond doubt. A fourth group is indicated by the data presented in table 25. The observed frequencies can be explained by two alternatives. One is that one of the pericarp factors is the same as one of the three ligule factors, thus giving a ratio of 108:0:132:16 on the basis of four factors, that is the two characters have one factor in common. The other alternative is that one of the pericarp factors is completely or very closely linked with one of the three ligule factors. The occurrence of one individual having "purple ligule and colorless pericarp," which cannot be accounted for by the first alternative, favors the second view. In this connection, the writer takes the liberty to rearrange HECTOR'S (1922) data in the following table for comparison with his own results:

	PURPLE LIGULE COLORED PERICARP	PURPLE LIGULE COLORLESS PERICARP	COLORLESS LIGULE COLORED PERICARP	COLORLESS LIGULE COLORLESS PERICARP	TOTAL
Observed (Hector)	1220	6	951	730	2907
Observed (Chao)	107	1	131	16	255

It must be noted, however, that though the two sets of observed frequencies are similar in nature, they are not exactly comparable. For in HECTOR'S case, the color of the pericarp depends on one factor pair segregating in a 3:1 ratio, while in the present case, the pericarp color is due to duplicate factors segregating in a 15:1 ratio. The common feature in both cases is that on the assumption of a common factor for both pericarp and ligule color, these few exceptions having "purple ligule and colorless pericarp" can not be accounted for. On the other hand, these exceptional individuals tend to support the view that one of the ligule

factors is closely linked with one of the factors responsible for the pericarp color.

Finally, it is interesting to note that so many of the characters studied are due to duplicate genes. This is of particular interest in view of the fact that all the varieties used have twenty-four chromosomes.

SUMMARY

1. Data have been presented to show the Mendelian behavior and chromosomal relations of twenty-five or more genetic factors which affect one or another part of rice plants.

2. Of the twelve characters studied, five are due to duplicate genes, each segregating in a ratio of 15:1.

3. Through the study of the interrelations between these twenty-five genes, three linkage groups have been established beyond doubt and possibly a fourth group is also indicated.

4. The first linkage group consists of four or five factors, namely, g_l, a_{p4}, l_{s1}, t_y , and possibly s_{a1} .

5. There is 16.59 percent crossing over between g_l and t_y ; 18.51 percent between g_l and s_{a1} , 19.43 percent between g_l and l_{s1} , and 22.34 percent between g_l and a_{p4} . In addition a_{p4} is very closely linked with l_{s1} .

6. The second linkage group consists of two genes, namely, s_p and g_2 . The glume length depends on duplicate factors, g_1 and g_2 , segregating in a 15:1 ratio, long glume being recessive. The spikelet length depends on a simple factor pair, $S_p s_p$, long spikelet being recessive. One of the duplicate genes, presumably g_2 , is coupled with s_p , giving 1.11 percent crossing over.

7. The third linkage group consists of s_{a2} and l_{s2} . Purple stigma in this case depends upon the presence of two dominant complementary factors, namely, S_{a1} and S_{a2} . Purple leaf-sheath also depends on two complementary factors, L_{s1} and L_{s2} . Between these two characters, there is close linkage. Only on the assumption of coupling between S_{a2} and L_{s2} can the observed frequencies be explained. BRUNSON'S method for calculating linkage intensities involving complementary factors is further modified for the present case. The crossing over value is found to be 9.8 percent between s_{a2} and l_{s2} .

8. A fourth linkage group is indicated between p_{r1} or p_{r2} and one of the three complementary factors for purple ligule color.

9. Factors g_1 and g_2 are independent of g_l, p_{r1} , and p_{r2} .

10. The factor s_p is independent of g_l, p_{r1}, p_{r2} .

11. Factors a_{p_1} and a_{p_2} are independent of g_1 .
12. Gene a_{p_4} is independent of p_{r_1} , p_{r_2} , g_1 , g_2 , and s_p .
13. Factors s_{a_1} and s_{a_2} are independent of p_{r_1} , p_{r_2} , g_1 , g_2 , and s_p .
14. Factors l_{g_1} and l_{g_2} are independent of p_{r_1} , p_{r_2} , g_1 , g_2 , and s_p .
15. Factors l_{g_1} , l_{g_2} , and l_{g_3} are independent of g_1 , g_1 , g_2 , and s_p .
16. Factors h_1 and h_2 are independent of i_{n_1} , i_{n_2} , l_{g_3} , l_{g_4} , a_{p_5} , a_{p_6} , p_{r_1} , and p_{r_2} .

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APPENDIX—TABLES 29-45

TABLE 29

Independent segregation between G_1 , G_2 and G_1 from the cross (4269×4957).

PHENOTYPES	OBSERVED	Calculated 45:3:15:1	DEVIATION	$\frac{(O-C)^2}{C}$
Non-glutinous short glume	525	504	21	0.87
Non-glutinous long glume	34	33.6	0.4	0.05
Glutinous short glume	146	168	-26	2.88
Glutinous long glume	12	11.2	0.8	0.05
Total	717	717		3.85 = X^2

 $P=0.2810$

TABLE 30

Independent segregation between G_1 , G_2 and P_{r1} , P_{r2} from the cross (4269×4957).

	SHORT GLUME COLORED PERICARP	SHORT GLUME COLORLESS PERICARP	LONG GLUME COLORED PERICARP	LONG GLUME COLORLESS PERICARP	TOTAL
Observed	590	46	42	1	679
Calculated 225:15:15:1	596.25	39.75	39.75	2.85	679
	-6.25	6.25	2.25	-1.65	

 $P=0.495$

TABLE 31
Independent segregation between $S_p s_p$ and $G_1 g_1$ in F_2 .

	SHORT SPIKELET NON-GLUTINOUS	SHORT SPIKELET GLUTINOUS	LONG SPIKELET NON-GLUTINOUS	LONG SPIKELET GLUTINOUS	TOTAL
Observed	417	118	138	40	713
Calculated 9:3:3:1	400.5	133.5	133.5	44.5	713
Deviation	15.5	-15.5	4.5	-4.5	

$X^2=4.34$. $P=0.2309$.

The deviation is apparently due to the large deficiency of glutinous grains.

TABLE 32
Independent segregation between factors s_p , p_{r_1} , and p_{r_2} (Ratio 45:4:15:1).

PHENOTYPES	OBSERVED	Calculated	$\frac{(O-C)^2}{C}$
Short spikelet, colored pericarp	505	501.75	0.02
Short, colorless	32	33.45	0.06
Long, colored	169	167.25	0.01
Long, colorless	8	11.15	0.89
	714	714.0	0.98 = X^2

When $X^2=1$, $P=0.8013$.

TABLE 33
Showing independent segregation between A_{p_4} and p_{r_1} and p_{r_2} .

	COLORED APEX COLORED PERICARP	COLORLESS APEX COLORED PERICARP	COLORED APEX COLORLESS PERICARP	COLORLESS APEX COLORLESS PERICARP	TOTAL
Observed	500	162	38	9	709
Calculated 45:15:3:1	498.15	166.05	33.21	11.07	709
Deviation	1.85	-4.05	5.21	-2.07	

$X^2=0.982$. $P=0.801253$ when $X^2=1$.

TABLE 34
Showing independent segregation between a_{p_4} and g_1 and g_2 .

	COLORED APEX SHORT GLUMES	COLORLESS APEX SHORT GLUMES	COLORED APEX LONG GLUMES	COLORLESS APEX LONG GLUMES	TOTAL
Observed	525	146	25	16	712
Calculated 45:15:3:1	500.40	166.80	33.36	11.12	712
Deviation	24.55	-20.80	-8.36	4.88	

$X^2=7.839$. $P=0.0418$.

The cause of the deviation is unknown.

TABLE 35

Showing independent segregation between A_{p_4} and s_p .

	COLORED APEX SHORT SPIKELET	COLORLESS APEX SHORT SPIKELET	COLORED APEX LONG SPIKELET	COLORLESS APEX LONG SPIKELET	TOTAL
Observed	428	133	139	43	743
<i>Calculated 9:3:3:1</i>	417.87	-139.29	139.29	46.43	
Deviation	10.13	-6.29	-0.29	-3.43	

$$X^2=0.788 \quad P=0.801253 \text{ when } X^2=1.$$

TABLE 36

Showing independent segregation between s_{a_1} , s_{a_2} and p_{r_1} , p_{r_2} .

	PURPLE STIGMA COLORED PERICARP	COLORLESS STIGMA, COLORED PERICARP	PURPLE STIGMA COLORLESS PERICARP	COLORLESS STIGMA, COLOR- LESS PERICARP	TOTAL
Observed	204	158	27	8	397
<i>Calculated 135:105:9:7</i>	209.25	162.75	13.95	10.85	397
Deviation	-5.25	-4.75	13.05	-2.85	

The deviation is probably due to the small number of plants.

TABLE 37

Showing independent segregation between s_{a_1} , s_{a_2} and g_1 , g_2 .

	PURPLE STIGMA COLORED PERICARP	COLORLESS STIGMA, COLORED PERICARP	PURPLE STIGMA COLORLESS PERICARP	COLORLESS STIGMA, COLOR- LESS PERICARP	TOTAL
Observed	227	163	12	16	418
<i>Calculated 135:105:9:7</i>	220.32	171.36	14.68	11.42	418
Deviation	6.68	-8.36	-2.68	4.58	

$$X^2=2.92. \quad P=0.405996.$$

TABLE 38

Showing independent segregation between s_{a_1} , s_{a_2} and s_p .

	PURPLE STIGMA SHORT SPIKELET	COLORLESS STIGMA, SHORT SPIKELET	PURPLE STIGMA LONG SPIKELET	COLORLESS STIGMA, LONG SPIKELET	TOTAL
Observed	189	130	53	49	421
<i>Calculated 27:21:9:7</i>	177.39	137.97	59.13	45.99	421
Deviation	11.61	-7.97	-5.13	3.01	

$$X=1.85. \quad P=0.6067.$$

TABLE 39
Showing independent segregation between L_{s_1} , l_{s_2} and p_{r_1} , p_{r_2} (4269 × 4957).

	COLORED PERICARP COLORED SHEATH	COLORED PERICARP COLORLESS SHEATH	COLORLESS PERICARP COLORED SHEATH	COLORLESS PERICARP COLORLESS SHEATH	TOTAL
Observed	179	134	19	4	336
Calculated 135:105:9:7	177.12	137.76	11.80	9.18	336
Deviation	1.88	-3.76	7.20	-5.18	

The deviation is probably due to the small number of plants.

TABLE 40
Showing independent segregation for l_{s_1} , l_{s_2} , g_1 and g_2 .

	COLORED LEAF SHEATH SHORT GLUMES	COLORLESS SHEATH SHORT GLUMES	COLORED SHEATH LONG GLUMES	COLORLESS SHEATH LONG GLUMES	TOTAL
Observed	192	128	11	11	342
Calculated 135:105:9:7	180.22	140.17	12.01	9.35	342
Deviation	11.78	-12.17	-1.01	1.65	

$X^2 = 2.7$. $P = 0.4458$.

TABLE 41
Showing independent segregation for l_{s_1} , l_{s_2} and s_p .

	COLORED LEAF SHEATH SHORT SPIKELET	COLORLESS SHEATH, SHORT SPIKELET	COLORED SHEATH LONG SPIKELET	COLORLESS SHEATH, LONG SPIKELET	TOTAL
Observed	154	100	50	39	343
Calculated 27:21:9:7	144.72	112.56	48.24	37.52	343
Deviation	9.28	-12.56	1.76	1.48	

$X^2 = 2.1$. $P = 0.5543$.

TABLE 42
Showing independent segregation of g_1 , g_2 , l_{g_1} , l_{g_2} and l_{g_3} .

	PURPLE LIGULE SHORT GLUMES	PURPLE LIGULE LONG GLUMES	GREEN LIGULE SHORT GLUMES	GREEN LIGULE LONG GLUMES	TOTAL
Observed	104	5	134	13	256
Calculated (5 factors)	101.25	6.75	138.75	9.25	256
Deviation	2.75	-1.75	-4.75	3.75	

Ratio = 405:27:555:37

TABLE 43

Showing independent segregation between l_{01} , l_{02} , l_{03} and s_p .

	PURPLE LIGULE SHORT SPIKELET	PURPLE LIGULE LONG SPIKELET	GREEN LIGULE SHORT SPIKELET	GREEN LIGULE LONG SPIKELET	TOTAL
Observed	87	21	108	40	256
Calculated 81:27:111:37	81	27	111	37	256
Deviation	6	-6	-3	3	

$$X^2 = 2.09, \quad P = 0.5561.$$

TABLE 44

Showing independent segregation between h_1 , h_2 , a_{p_6} and a_{p_8} .

	BLACK HULL COLORED APICULUS	NON-BLACK COLORED APEX	BLACK HULL COLORLESS APEX	NON-BLACK COLORLESS APEX	TOTAL
Observed	109	92	5	12	218
Calculated 135:105:9:7	114.75	89.25	7.65	5.95	218
Deviation	-5.75	2.75	-2.65	6.05	

The deviation is probably due to the small number of plants.

TABLE 45

Showing independent segregation between h_1 , h_2 , p_{r_1} and p_{r_2} .

	BLACK HULL COLORED PERICARP	NON-BLACK COLORED PERICARP	BLACK HULL COLORLESS PERICARP	NON-BLACK COLORLESS PERICARP	TOTAL
Observed	106	89	7	13	215
Calculated 135:105:9:7	113.4	88.2	7.56	5.88	215
Deviation	-7.4	0.8	-0.56	7.12	

The deviation is probably due to the small number of plants.