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Studies on the Linkage Relations between the Factors for Endosperm Characters and Sterility in the Rice Plant, with Special Reference to Selective Fertilization

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Introduction

Since the rediscovery of the Mendelian laws of heredity in 1900, many valuable genetical studies have been made on the rice plant in Japan, as well as in India, Java, and other oriental countries, and also in the U. S. of America (IKENO, 1927; MATUURA, 1933). However, comparatively few cases of linkage have been shown definitely, and nothing has been reported till now concerning selective fertilization in the rice plant.

In this paper, the author presents a new instance of linkage associated with selective fertilization, namely, the linkage of sterility and an endosperm character accompanied by selective fertilization. These experiments were begun 1922 and continued until the end of 1925 at the Agricultural Experiment Station General Government of Chôsen, Suigen, Chôsen, Japan.

The author wishes to express his sincerest thanks to Dr. G. DAIKUHARA, the director of the station while the present experiments were carried on, and also to T. LEE and R. SUGIMOTO for their kind assistance. He wishes also to express many thanks to Dr. G. H. SHULL, of Princeton University in U. S. A. for reading the manuscript and allowing the author to use the literature in his laboratory while he was staying at Princeton in the summer of 1927.

Materials

A mutant family No. 1–466, herein designated as SII, the progeny of NC. 1 is the original family of the present experiments. This family was first noted by the author in 1922 in his genetic studies (TAKAHASHI, N. 1923). In order to show the relation between this mutant family and the other families the following table is given:

	Tarobemoti × Tamanisiki		Total
1919 F_1 seeds	NC. 1	NC. 2	2
1920 F_1 plants	1	1	2
1921 F_2 plants	729	177	906
1922 F_3 (number of families)	171 ↓ SII (1–466)	71	241

The new mutant sterile plants are quite different from the fertile plants. The most noticeable feature of these sterile plants is the abnormal structure of the spikelets, as 4–5 percent of the spikelets of one individual plant show one or two large glumes as well as extra paleae beside the normal two. The difference in size of spikelets in the fertile and in the sterile type is not great, the latter being slightly smaller. The grains of sterile plants are very small, about half the size of normal fertile grains and quite irregular.

The height of plants, length of ear, time of shooting, length of awn, and number of ears per plant in both fertile and sterile types in the original family SII are given in Table 1.

As will be seen in the table, both the height of plant and length of ear are much shorter in sterile plants than in fertile plants; the time of shooting of sterile plants is about 3 days later than the fertile plants. The number of culms per plant is also smaller in the sterile than in the fertile type. The number of spikelets per ear of sterile plants averages about half the number found in fertile plants. The fertility of sterile plants averages 17.92 percent and of fertile plants 87.68 percent. Fuller details of fertility and the number of spikelets per ear in both types will be given in a later section (page 41–43).

TABLE 1.

	Fertile	Sterile
Number of plants observed	86	19
Height of plants	100 cm.	86 cm.
Length of ears	21 cm.	16 cm.
Time of shooting	August 22	August 25
Length of awns	Medium	Short
Number of ears per plant	7–8	5–7

It may be supposed that the vitality of the two types would differ considerably, especially under unfavorable conditions. This was found to be the fact and many sterile plants died before harvesting. This difference of survival value in the two types resulted in a remarkable departure from the theoretically expected ratios in these experiments.

For this reason, the data obtained by classification of the growing plants were rationally corrected by using the data obtained from observation of the endosperm generation. Thus, the error caused by the differential survival was reduced to a minimum.

Remarks: For the sake of brevity, the author has used the following abbreviations in this paper.

F_n refers to the generation of pedigree cultures and thus the F_2 shows the original family which was found in the F_3 families of NC. 1.

F_n-*seeds* refers to the endosperm generation and thus, the F_3 *seeds* means the endosperm generation on the F_2 plants corresponding to the F_3 plants generation.

D and d refer to the fertile and sterile types, respectively, and represent the factors for both types.

U and *u* refer to starchy and glutinous endosperm characters or factors, respectively, and thus *Uu* indicates the heterozygotes in respect to endosperm characters.

Experimental Results

1. F_2 generation

As has been said above, the new type of sterile plants appeared in one of the families segregating for the factors *U* and *u*, and it was supposed that the sterile plants which appeared in the original family resulted from a factor *d* mutated from the factor *D*, the constitution of the mother plant having been *DdUu*.

As the new sterile type behaves as a recessive to the fertile type, it may be assumed that the mother plant of SII family was of the fertile type. No sterile plants were observed among the F_2 plants of NC. 1. Table 2 shows the results of segregation in the mutant family SII.

TABLE 2.

Family No.	Total	*D*			*d*			*d*%	*u*%
		U	*Uu*	*u*	*U*	*Uu*	*u*		
SII	103	25	58	1	0	0	19	18.45	19.42

From this, it can be seen that the fertile type is dominant over the sterile type, and that the starchy character is, of course, dominant over the glutinous character. There are two remarkable facts in the hereditary behavior of the two types. In the first place, except for one out of 20, glutinous plants are sterile and the distribution of endosperm characters of the fertile plants, 84 in all, is remarkably different from normal expectation; the fertile starchy plants exceed the fertile glutinous plants in a ratio of 25 to 1, and it can be seen at a glance that there is a linkage between the two factors *D* and *U* in coupling phase. In the second place, the ratios of segregation in both types, taken singly, show marked deviations from the Mendelian expectation, the sterile being only 18.45 percent and the glutinous 19.42 percent instead of the expected 25 percent.

2. F_3 generation

Four different phenotypes of plants were obtained in the previous generation, namely *DU*, *DUu*, *Du* and *du*. Most of these plants were genetically tested by rearing their progenies in this generation.

i. *Progenies of DU-type.*

All of the 25 *DU*-type plants in the F_2 generation were tested and among them 24 families showed constancy for both factors *D* and *U*, the total number of plants being 3,540 and only one family (No. 74) segregated for the normal and sterile types. The proportion of normal and sterile types in the segregating family No. 74 is abnormal, there being 132 fertile and 15 sterile plants, or 10.20 percent sterile.

ii. *Progenies of DUu-type.*

All grains of *DUu*-type plants in the preceding generation were removed from their glumes to observe the ratio of segregation in endosperm characters, and these naked seeds were used for planting. Because of the above treatment the number of plants raised was considerably decreased by the attack of insects or fungus in the seed-beds.

The results obtained from the observation of the plant generation seem rather unsatisfactory. However, the segregations in the endosperm generation observed in the seeds of the previous year serve as a check on the plant generation grown from them. The results of observation in both plant generation and corresponding endosperm generation are shown in Table 3, a and 3, b. The last column of these tables shows percentages of glutinous endosperms on the heterozygous plants in the previous year.

TABLE 3, a.

DDUu segregation in 2 families.

Family No.	Total	*D*			*d*			*d*	F_3-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*		
1	15	2	12	1	0	0	0	6.67	27.00
35	11	2	7	2	0	0	0	18.18	22.00
Total	**26**	**4**	**19**	**3**	**0**	**0**	**0**	**11.54**	**24.90**

a) *DDUu segregation in 2 families.* Table 3, a. shows two families which were segregated for the factors *U* and *u*, and were constant for the factor *D*. Because of the small number of plants observed, it is difficult to distinguish these two families from the other 54 families in Table 3, b. It may be noticed, however, that the segregation of endosperm characters in the previous year is just about the normal ratio, i. e. the glutinous percentage is 24.90. And, as will be seen later, the glutinous percentages in the succeeding generation of these families showed nearly 25 percent and the fertility factor *D* showed constancy.

TABLE 3, b.

DdUu segregation in 54 families.

Family No.	Total	*D*			*d*			*d*%	*u*%	F_3-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*			
3	3	3	0	0	0	0	0			14.60
4	18	7	11	0	0	0	0			9.88
5	47	16	29	0	0	0	2			10.30
6	21	6	15	0	0	0	0			15.40
7	21	8	9	0	0	0	4			20.01
9	7	2	5	0	0	0	0			22.40
10	79	33	43	1	0	0	2			12.64
11	2	2	0	0	0	0	0			8.26
12	10	3	7	0	0	0	0			16.10
14	6	3	3	0	0	0	0			23.20
17	87	31	50	1	0	0	5			13.20
21	10	4	5	0	0	0	1			20.57
22	20	9	9	0	0	0	2			19.60
25	3	2	1	0	0	0	0			22.10
27	7	1	6	0	0	0	0			12.70
28	12	2	8	1	0	0	1			18.60
38	5	2	3	0	0	0	0			18.50
39	27	13	10	0	0	1	3			14.70
41	1	0	1	0	0	0	0			19.90
42	4	2	1	0	0	0	1			9.01
44	21	9	8	1	0	0	3			12.80
46	9	2	7	0	0	0	0			18.10
47	13	3	10	0	0	0	0			13.30
48	15	6	8	0	1	0	0			14.25
49	35	11	18	0	0	0	0			17.85
51	14	7	6	0	1	0	0			11.45
52	43	13	23	1	0	0	5			11.55
53	22	11	11	0	0	0	0			14.05
55	30	15	13	1	0	0	1			18.62
64	20	7	13	0	0	0	0			22.20
66	52	24	21	0	0	0	7			17.20
67	12	4	8	0	0	0	0			13.70
69	4	4	0	0	0	0	0			15.01
70	10	1	6	1	1	0	1			15.35
73	3	1	2	0	0	0	0			18.40
77	18	10	8	0	0	0	0			13.50
86	43	23	20	0	0	0	0			8.15
88	19	10	8	0	0	0	1			7.77
90	2	1	1	0	0	0	0			12.69
92	27	7	16	2	0	0	2			15.20
97	26	11	13	0	0	0	2			14.00
98	20	11	9	0	0	0	0			16.70
99	2	1	1	0	0	0	0			19.90
100	9	4	5	0	0	0	0			15.20
101	45	20	21	1	0	0	3			17.25
102	11	4	6	0	0	0	1			7.30
103	15	7	8	0	0	0	0			18.60
104	11	4	7	0	0	0	0			10.90
105	21	5	15	0	0	0	1			22.00
107	18	8	5	0	0	1	4			18.30
108	6	2	4	0	0	0	0			19.90
110	6	2	4	0	0	0	0			11.47
112	15	4	8	0	1	0	2			12.50
113	18	3	15	0	0	0	0			18.70
Total	1028	404	548	10	4	2	60	6.42	6.81	15.48

b) *DdUu segregation in 54 families.* Inspecting each of 54 families in Table 3, b., it is almost impossible to determine whether the segregating type is the same as in the previous generation. However, in the total number of these families it can see that they belong to the same type as the F_2 generation. In the total number of 1,028 plants, six different phenotypes were obtained, two of which were lacking in the previous generation and the distribution of these types showed again a strong linkage between the factors *D* and *U*.

The percentages of glutinous and sterile plants are significantly low compared with the normal case, namely the glutinous only 6.81 percent and the sterile 6.42 percent. Comparing the glutinous percent 6.81 in the plant generation with the percentage 15.48 in the endosperm generation, there is a difference of 8.67 percent.

iii. *Progenies of Du-type.*

From one *Du*-type plants obtained in the F_2 generation, only three plants were reared. All of these showed only fertile glutinous plants, but because of the small numbers, it can hardly be determined whether the family is constant or not for the factor *D*. The homozygous or heterozygous condition of the factor *D* was not determined in these three plants by means of pedigree culture, but observations of many other families in the same situation as this family, make it more reasonable to consider it a segregating family.

iv. *Progenies of du-type.*

Thirteen families were reared in this generation out of 19 *du*-type plants in the previous generation. The total number of plants counted was 142, all showing glutinous sterile type.

3. F_4 generation

Analysis of different types in the previous generation was not satisfactory because the number of plants and of families were too small. Therefore, a far greater number of families and plants were reared in the F_4 generation.

i. *Progenies of family No. 74.*

In the previous generation, family No. 74 segregated fertile and sterile types showing a marked deficiency of sterile plants. From this family, 41 fertile and 10 sterile-type plants were tested in this generation by raising their progenies. Sixteen out of 41 families showed constancy for the factors *D* and *U*, the total number of plants being 2,962. The

remaining 25 families again showed segregation for fertile and sterile types, there being 3,419 fertile and 483 sterile, or 12.38 percent sterile, which is about one-half that expected on the basis of the Mendelian monohybrid ratio. The minimum percent of sterile was only 2.65 and the maximum 18.97 percent, (See Table 4).

TABLE 4.

DU : *dU* Segregation in 25 families.

Family No.	Total	*DU*	*dU*	*d*%
74- 1	186	159	27	14.52
74- 2	148	125	23	15.54
74- 3	184	168	16	8.70
74- 7	217	193	24	11.06
74- 8	184	174	10	5.43
74- 13	112	96	16	14.29
74- 15	114	100	14	12.29
74- 17	149	126	23	15.44
74- 18	116	94	22	18.97
74- 21	78	66	12	15.38
74- 27	150	136	14	9.33
74- 30	157	128	29	18.47
74- 32	154	132	22	14.28
74- 35	155	135	20	12.90
74- 45	150	135	15	10.00
74- 51	152	139	13	8.55
74- 60	153	136	17	11.11
74- 63	189	184	5	2.65
74- 64	194	165	29	14.95
74- 80	143	129	14	9.79
74- 82	179	154	25	13.97
74-115	175	143	32	18.29
74-122	178	157	21	11.80
74-137	143	124	19	13.29
74-138	142	121	21	14.79
Total	3902	3419	483	12.38

The ratio of constant and segregating families was quite different from that of the F_3 generation where 24 families showed constant and only one family showed segregation. It is evident that there is a strong coupling relation between factors *D* and *U*, because of the marked excess of constant families compared with segregating families in the F_3 gene-

ration. In the present generation, however, one constant and two segregating families for the factors *D* and *d* would be normally expected. The actual ratio showed a slight excess of constant families above the normal expectation.

	Total	*D*-const.	*D* : *d* segregated
Observed	41	16	25
Theoretical (1 : 2)	—	13.67	27.33

The offspring of 10 sterile plants just noted above showed 114 sterile glutinous plants and 4 fertile plants. Three of these fertile plants showed quite long awns, and one had purple awns. It is evident that these four fertile plants resulted from natural hybridization.

ii. *Progenies of families No. 1 and No. 35.*

As already stated above, Families No. 1 and No. 35 in the endosperm generation (in Table 3, a) showed normal segregation with respect to the endosperm characters and it was supposed that these two families in the previous generation showed constancy for the factor *D*. This was definitely ascertained in this generation.

Table 5 shows 17 families derived from the *DUu*-type plants in both families, and the last column shows the percentages of glutinous from corresponding parent plants in the previous year.

Comparing the percentages in endosperm generation with the percentages in the plant generation, it can seen that both are nearly the same, the former being 24.12 percent and the latter 23.28 percent in total, showing a normal Mendelian monohybrid case. With respect to the fertility characters, 16 families showed constancy for the factor *D*, as has been expected, and the family No. 1–5 segregated fertile and sterile types. This is quite an unexpected result. After the inspection of this segregating family No. 1–5, it was found that the sterile plants (designated SIII) are quite different from the SII-type sterile plants in the present experiments.

New SIII-type sterile plants are completely self-sterile under guarded or unguarded conditions and they are slightly taller than the fertile plants in the same family.

Hereditary behavior of SIII-type is also quite different from that of SII-type sterile. There is no linkage between the new sterile character (SIII) and the endosperm characters. Although the segregating ratio

of endosperm characters in the sterile plants is not available because of complete sterility, the segregating ratio in the fertile plants showed nearly the normal ratio, 1:2:1, there being 44 starchy; 98 heterozygous; 39 glutinous plants. The percent of sterile was quite small, only 6.21 for

TABLE 5.

DDUu Segregation in 17 families.

Family No.	Total	*D*			*d*			*d*%	*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*			
1- 1	191	57	92	42	0	0	0	0.0	21.99	28.00
1- 2	188	56	92	40	0	0	0	0.0	21.28	19.58
1- 3	192	45	102	45	0	0	0	0.0	23.44	25.69
1- 5	181	44	98	39	—	(12)*	—	(6.21)	21.55	21.05
1- 6	197	58	85	54	0	0	0	0.0	27.41	20.00
1- 7	187	46	98	43	0	0	0	0.0	22.97	27.27
1- 9	325	77	168	80	0	0	0	0.0	24.62	26.95
1-11	193	57	100	36	0	0	0	0.0	18.65	21.57
1-12	255	78	118	59	0	0	0	0.0	23.14	23.58
1-14	258	79	116	63	0	0	0	0.0	24.42	28.78
1-15	195	54	105	36	0	0	0	0.0	18.46	18.34
35- 1	195	47	101	47	0	0	0	0.0	24.10	21.74
35- 2	193	57	89	47	0	0	0	0.0	24.35	26.25
35- 3	200	54	100	46	0	0	0	0.0	23.00	25.62
35- 4	196	56	94	46	0	0	0	0.0	23.47	21.37
35- 6	195	51	93	51	0	0	0	0.0	26.15	31.16
35- 7	193	53	92	48	0	0	0	0.0	24.74	20.45
Total	3534	969	1743	822	0	0	0	0.0	23.28	24.12

* Completely sterile (new mutants).

the total 193 plants. The cause of the deficiency of the sterile type plants in this family is unknown. It may be supposed that the SIII-type sterile plants resulted from the gene mutation on another pair of chromosomes.

iii. *Progenies of Du-type.*

Two plants of *Du*-type in families No. 1 and No. 35, were tested by raising their offspring in this generation. All of the 221 plants were of *Du*-type.

iv. *Progenies of six types in 54 families* (see Table 3, b)

The situation of these progenies is the same as that of the F_3 generation. The plants were taken from the six phenotypes in the 54 families of the previous generation and a sufficient number of plants were raised in this generation.

a) *Progenies of DU-type.* One hundred families were reared from the *DU*-type plants of five families of the previous generation. Of these 100 families 90 showed constancy for the factors *D* and *U*, all of the 17,189 plants being fertile starchy type. The remaining ten families showed segregation for the factors *D* and *d*, there being 1,717 normal fertile and 231 sterile; the percentage of sterile was only 11.86 (Table 6).

TABLE 6.

DU : *dU* Segregation in ten families.

Family No.	Total	*DU*	*dU*	*d*%
5- 8	190	167	23	12.10
5-15	247	228	19	7.69
17- 4	184	155	29	15.76
17-36	193	154	39	20.21
66-17	194	167	27	13.92
86- 1	201	179	22	10.95
101- 2	191	174	17	8.90
101- 7	166	156	10	6.02
101- 8	190	163	27	14.21
101-15	192	174	18	9.37
Total	1948	1717	231	11.86

Inspecting each family, it can be seen that the deficiency of sterile plants is very significant, the maximum percent being only 20.21 and the minimum 6.02.

b) *Progenies of DUu-type.* Out of 548 individuals of *DUu*-type in 54 segregating families in the previous generation, 281 individuals were genetically tested by raising their progenies in this generation. It is clear that the situation of these families is the same as the 56 families observed in the F_3 generation.

The results of observation are shown in Table 7, a, and Table 7, b, in Appendix. Seven families in Table 7, a, show constancy for the factor *D* and segregation for the factors *U* and *u*, there being 364 *DU*, 721 *DUu*

and 306 *Du* plants, i. e. the percentage of glutinous is 22.35 Comparing this percentage with the glutinous percentage 23.34 glutinous endosperms (last column in the Table) there is a slight but statistically excess in the latter. However, it can be easily recognized that the above seven families indicate the normal Mendelian segregation because the three different types of plants are distributed nearly according to the expectation 1 : 2 : 1.

All of the remaining 274 families (Table 7, b) show segregation for both factors *D* and *U*, including six different phenotypes of plants, as has been observed in the previous generations. In each family it can be noticed that all families show a similar type of segregation indicating strong coupling. Putting all together in the form of the ordinary dihybrid ratio gives the following numerical relation. The linkage between

Total	$\overbrace{(U+Uu)}^{D} : \overbrace{u}^{D}$		$\overbrace{(U+Uu)}^{d} : \overbrace{u}^{d}$		*d*%	*u*%	F_2-seeds (*u*%)
51304	43890	441	162	6813	13.59	14.14	17.43

the two characters is obvious and also it can be noticed that the crossover value between the two factors is very low. Using the ordinary formulae for the calculation of linkage intensities, it is impossible to get the theoretical number which fits closely the observed data, because the numbers of both recessive types are too small, the percentage sterile being only 13.59 and the percentage glutinous 14.14. The calculation of linkage intensities will be given later.

Examining each family in Table 7, b, it can be seen that the percentages of sterile plants in all families are definitely lower than the normal expectation 25 percent, showing the maximum 23.00 percent and the minimum 6.05 percent. As to the glutinous percentages in each family, there are marked differences between the percentages of the plant generation and that of the endosperm generation.

TABLE 8.

Du : *du* Segregation in 3 families.

Family No.	Total	*Du*	*du*	*d*%
17- 5	121	98	23	19.01
55- 3	110	90	20	18.18
101-22	115	103	12	10.43
Total	**346**	**291**	**55**	**15.90**

c) *Progenies of Du-type.* 4 out of 10 *Du*-type plants originated in the F_3 generation were reared in this generation. Total 111 plants in one family showed all constancy for *Du*-type and the other three families showed segregation for the fertile and sterile types (Table 8). As seen in Table 8 the total number of plants in the three segregating families was 346, including 55 sterile plants or 15.90 percent sterile type. Again the deficiency of sterile plants is remarkable. Number of families in this generation is insufficient to determine the ratio of constant and segregating families. Many families representing the same situation as the above families will be seen in the next generation.

d) *Progenies of dU-type.* Only four *dU*-type plants were found in the previous generation and from these two families were raised in this generation. The total of 50 plants were of the sterile glutinous type.

e) *Progenies of dUu-type.* Progenies of two *dUu*-type plants found in the previous generation were grown, but unfortunately, all individuals reared from one parent died off before harvesting. Therefore, only one family, No. 39–12, including 17 sterile plants, was obtained. These plants segregated for the endosperm characters, there being 3 *dU*: 13 *dUu*: 3 *du* plants. The percentage of glutinous plants was 17.65. This is a marked deviation from the normal expectation of 25 percent, and the percentage of glutinous in the endosperm generation showed 30.77. Putting together the above two percentages, it can be supposed that the *dUu*-type plants indicate the normal segregation for their endosperm characters in the next generation.

f) *Progenies of du-type.* As has been stated in the preceding sections, a rather large number of *du*-type plants was obtained in the F_2 and F_3 generations. Therefore, in this generation many progenies of *du*-type were raised. From 44 families in the F_3 generation 902 *du*-type plants were grown, and 1,208 of the same type from 40 families in the F_2 generation. Among these, 3 fertile plants appeared, which were supposed to be natural hybrids resulting from pollen carrying the segregation of fertile starchy endosperm characters. From the above results it can be seen that the *du*-type plants bred true in the next generation.

4. F_5 generation

The main purpose of the observation of this generation was to determine the ratio of constant and segregating families in the progenies of different-type plants. Therefore, a considerable number of families were reared and the several questions were cleared up. One or two ears of each individual in the F_4 generation were used to raised the F_5 plants without removing the spikelets from their panicles. After soaking in

cold water for three days, the panicles with spikelets were placed on the seed-beds side by side. The crowding of seedlings resulted in thinner and weaker plants.

In the ordinary rice field, the rows were kept 26 cm. apart, but the plants were set only 18 cm. apart in the row, so that twice as many plants were grown on a given area as are grown in the standard plantation. Consequently, the experimental plants were less vigorous than the plants grown by the standard method. It has been observed that a considerable number of both the fertile and sterile plants died before the time of harvest.

i. *Progenies of DU-type derived from family No. 74, of the* F_4 *generation.*

It will be remembered that the progenies of family No. 74 in the F_4 generation consisted of 16 constant, and 25 segregating families. From the 25 segregating families, 56 *Du*-type plants were tested for their genetical constitution by raising their progenies.

Among the 56 families thus produced, 22 families including a total of 2,772 plants were uniformly *Du*-type. Table 9 presents the remaining 34 segregating families, consisting of 4,071 fertile and 321 sterile plants, or 7.31 percent sterile plants, the minimum percentage of sterile being only 2.27 and the maximum 15.62. In the previous generation, 12.38 percent sterile plants had been found in 25 segregating families.

The difference in percentage of sterile plants in the two generations is remarkable, and it is evident that the modified method of cultivation in this generation affected the number of sterile plants, probably through selective elimination, as many plants died before harvest.

The numerical ratio between constant and segregating families in this generation agrees fairly well with that of the previous generation as follows:

Fn	Total	Constant (*D*)	Segregated (*D* : *d*)
F_4	41	16	25
F_5	56	22	34
Observed	97	38	59
Theoretical (1 : 2)	—	32.33	64.67

There is a slight excess of constant families in both generations.

TABLE 9.

DU : *dU* segregation in 34 families.

Family No.	Total	*DU*	*dU*	*d%*
74-1- 1	124	112	12	9.68
74-1- 3	128	108	20	15.62
74-1- 4	127	123	4	3.15
74-1- 7	158	120	18	13.04
74-1- 8	126	113	13	10.32
74-1-10	127	112	15	11.81
74-1-12	122	106	16	13.11
74-1-13	131	118	13	9.92
74-1-15	132	125	7	5.34
74-1-16	130	122	8	6.15
74-1-19	97	90	7	7.22
74-2- 4	129	120	9	6.98
74-2- 6	122	106	16	13.11
74-2- 7	131	121	10	7.63
74-2- 9	142	125	17	11.97
74-2-10	132	117	15	11.36
74-2-13	121	110	11	9.09
74-2-14	115	110	5	4.35
74-2-15	131	121	10	7.63
74-2-16	126	115	11	8.73
74-2-17	133	126	7	5.26
74-2-18	130	125	5	3.85
74-3- 2	135	126	9	6.67
74-3- 5	132	120	12	9.09
74-3- 6	131	122	9	6.87
74-3- 7	132	129	3	2.27
74-3- 8	125	119	6	4.80
74-3-10	133	130	3	2.26
74-3-12	136	130	6	4.44
74-3-13	130	125	5	3.85
74-3-14	134	129	5	3.73
74-3-16	137	133	4	2.92
74-3-17	136	130	6	4.61
74-3-18	137	133	4	2.92
Total	**4392**	**4069**	**321**	**7.51**

ii. *Progenies of family No. 1–2.*

Family No. 1–2 was constant for the fertility and segregated for the endosperm characters in the previous generation (see Table 5) and it was supposed that this family belonged to the normally segregating group. From this family, 5*DU*, 13 *DUu* and 2 *Du*-type plants were tested genetically by raising their progenies. Five families of the offspring of *DU*-type plants showed 502 *DU*-type and 2 *DUu*-type plants. We may assume that the 2 *DUu* plants are the natural hybrids, and on this assumption we can say that these 5 *DU*-type plants bred true in the next generation. The offspring of 19 *DUu*-type plants segregating for the endosperm characters are shown in Table 10.

TABLE 10.

DU : *DUu* : *Du* segregation in 13 families.

Family No.	Total	*DU*	*DUu*	*Du*	*u*%
1-2- 1	58	16	23	19	32.75
1-2- 2	34	10	11	13	38.24
1-2- 3	103	31	39	33	32.04
1-2- 4	98	19	48	31	31.63
1-2- 5	127	34	68	25	19.68
1-2- 6	132	31	68	33	25.00
1-2- 7	99	28	48	23	23.23
1-2- 8	106	26	54	26	24.53
1-2- 9	105	26	58	21	20.00
1-2-10	125	29	60	36	28.80
1-2-11	124	45	56	23	18.55
1-2-12	122	26	65	31	25.41
1-2-13	128	42	60	26	20.31
Total	**1361**	**363**	**658**	**340**	**24.91**

The total of 1,361 plants consisted of 363 *DU*, 658 *DUu*, 340 *Du*-type plants, or 24.91 percent glutinous. Progenies of 2 *Du*-type plants, of course, bred true; but there occurred 2 *DUu*-type plants beside 188 *Du*-type plants. It can be easily supposed that these 2 *DUu*-type plants resulted from natural hybridization in the previous year.

TABLE 11.

DU : *dU* segregation in 32 families.

Family No.	Total	*DU*	*dU*	*d%*
5-8- 2	135	125	10	7.41
5-8- 3	66	56	10	15.15
5-8- 7	69	67	2	2.90
5-8- 8	64	60	4	6.25
5-8- 9	65	60	5	7.69
5-8-12	63	61	2	3.17
5-8-13	64	63	1	1.56
5-8-15	68	65	3	4.41
5-8-16	69	65	4	5.80
5-8-21	66	62	4	6.06
5-8-22	61	59	2	3.28
5-8-23	64	63	1	1.56
5-8-24	63	60	3	4.76
5-8-25	67	63	4	5.97
5-8-26	67	64	3	4.48
5-8-29	61	56	5	8.20
5-8-30	65	63	2	3.08
5-8-31	65	60	5	7.69
5-8-34	64	58	6	9.37
5-8-35	67	63	4	5.97
5-8-37	64	56	8	12.50
5-8-38	64	55	9	14.06
5-8-39	65	62	3	4.62
5-8-41	66	61	5	7.35
5-8-42	65	63	2	3.08
5-8-43	67	60	7	10.45
5-8-45	65	59	6	9.23
5-8-46	67	63	4	5.97
5-8-47	65	62	3	4.69
5-8-48	65	64	1	1.54
5-8-50	66	64	2	3.03
5-8-51	66	62	4	6.06
Total	**2158**	**2024**	**134**	**6.16**

iii. *Progenies of DU-type derived from family No. 5—8* (see Table 6).

The situation of the progenies of family No. 5–8 is the same as in the case of family No. 74 as stated in the beginning of the F_3 generation. 51 *Du*-type plants were selected from the family and their progenies tested. These progenies consisted of 19 constant families included 1,511 plants and 32 segregating families.

Table 11 shows that the 32 segregating families included 2,024 fertile- and 134 sterile-type plants. The percentages of sterile plants are markedly smaller than the expectation based on the Mendelian ratio, 3 : 1. The percentage sterile averaged only 6.16, ranging from the minimum 1.54 to the maximum 15.15 percent. This is nearly the same ratio obtained in the progenies of family No. 74.

The ratio of constant and segregating families is also the same as in the case of the progenies of family No. 74. There are 19 constant and 32 segregating families, which is a slight excess of constant families based on the normal expectation.

iv. *Progenies derived from plants in families No. 5–26 and No. 67–3.*

a) *Progenies of DU-type.* It was seen in Table 7, b that the family No. 5–26 and 67–3 segregated for the both factors *D* and *U* yielding dihybrid segregation. From these two families 82 *DU*-type plants were selected and their offspring reared. The situation of these progenies is the same as those of the F_3 generation where 24 constant families and 1

TABLE 12.

DU : *dU* segregation in 5 families.

Family No.	Total	*DU*	*dU*	*d%*
5-26-58	94	79	15	15.85
5-26-76	79	76	3	3.80
5-26-88	97	92	5	5.15
5-26-93	82	69	13	15 85
67- 3-95	121	110	11	9.91
Total	473	426	47	9.94

segregating family were obtained in the offspring of *DU*-type plants from the F_2 generation. This ratio was repeated in this generation, there being 77 true-breeding families with a total of 8,370 plants and 5 segregating families. The segregating families contained 426 fertile type and 47 sterile type plants, as shown in Table 12. The percentage sterile in each segregating family was quite small, ranging from minimum 3.80 to maximum 15.85 percent, an average of 9.94 percent.

b) *Progenies of DUu-type.* From 117 *DUu*-type plants in families No. 5–26 and No. 67–3, progenies were grown, and the results are given in Table 13, a and b. The last column in these tables show the percentages of glutinous endosperm of each corresponding plant.

TABLE 13, a.

D (*U* : *Uu* : *u*) segregation in 2 families.

Family No.	Total	*D*			*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*		
67-3-18	121	31	68	22	18.18	17.12
67-3-58	93	24	46	23	24.73	27.15
Total	214	55	114	45	21.03	22.52

As seen in Table 13, a. two families are constant for the factor *D* and segregated for the endosperm characters showing three type of plants namely 55 *DU*: 114 *DUu*: 45 *Du*. The percentage of glutinous plants was 21.03 and the corresponding percentage glutinous in the endosperm generation 22.52 percent. From these results it is evident that these two families show normal segregation with respect to the factors *U* and *u* as has been already noticed in the preceding section.

In Table 13, b (in Appendix) it is seen that the remaining 115 families show segregation for both factors, *D* and *U*. The distribution of the six different types of plants in each family shows nearly the same type of segregation as has been seen in the F_2, F_3 and F_4 generations, exhibiting the characteristic feature of the coupling phase, in that the extreme terms are considerably in excess as compared with the middle terms.

All families show a strong coupling phase and there is no exception representing the repulsion phase. The sterile and glutinous percentages in these families were again considerably lower than might be expected on the basis of normal Mendelian segregation. The total number of plants counted was 11,958, there being 10.25 percent sterile and 11.64 percent glutinous. The percentage of glutinous in the endosperm gene-

ration was 18.28 in total. The difference of percentage of glutinous in plants and in the endosperm generations is remarkably large, namely, 6.64 percent excess in the endosperm generation.

It should be remembered that the difference is mainly caused by the differential survival of both fertile and sterile types of plants in the ordinary rice field, since there was no difference of germinating power between different families in the seed-beds. If the capacity for survival of the fertile and sterile plants had been the same, it should be expected that the percentage of glutinous in the plant generation and that in the endosperm generation would be nearly the same.

c) *Progenies of Du-type.* Only 5 families of offspring of this type were observed in the preceding generation and one in the F_3 generation, one of which showed constant and the other four families segregated for fertile and sterile plants.

On account of the small number of families, the ratio of constant and segregating families can not be determined. In this generation, many families of this type were reared and their genetical constitution demonstrated. Progenies were reared from 120 individuals of the 441 *Du*-type plants (see Table 13, b in Appendix) which were of the same constitution as the *Du*-type plants in the original family SII.

Two families consisting of 238 plants were uniformly *Du*-type and the remaining 118 families, included in Table 14, showed segregation for the fertile and sterile types.

The ratio of constant and segregating families is just reversed in the case of the progenies of *DUu*-type plants. The total number of plants involved in Table 14 (in Appendix) 9,293, including 916 sterile type plants or 9.86 percent sterile.

The remarkable deficiency of sterile plants showed again as in the families segregating for the factors *D* and *d* in the preceding generation.

It can be seen from the foregoing results that the deficiency of sterile plants in the segregating families of the progenies of *DU, DUu* and *Du* plants is always in the same direction and is independent of the endosperm characters. In other words, the deficiency of sterile plants appeared in the offspring of three different endosperm plants (*DU, DUu, Du*) showed nearly the same degree of deviation from the normal segregation of 25 percent.

d) *Progenies of dUu-type.* The *dUu*-type plants obtained in the previous generation numbered 82 (see Table 7, b). A portion of these plants was used for the observation of endosperm and the rest were reared and the character of the plant generation observed. The results are given in Table 15.

TABLE 15.

dU : *dUu* : *du* segregation in 12 families.

Family No.	Total	*D*			*d*			*u*%
		U	*Uu*	*u*	*U*	*Uu*	*u*	
5-13- 78	4	0	0	0	2	1	1	25.00
5-15- 12	9	0	0	0	1	5	3	33.33
5-15-135	6	1?	0	0	0	6	0	0.00
5-20-183	4	0	0	0	1	3	0	0.00
49-13- 89	19	1?	0	0	9	6	4	21.05
49-13-131	5	0	0	0	3	1	1	20.05
52-25-100	26	1?	0	0	9	11	6	23.08
53-17-107	7	0	0	0	4	1	2	28.57
53-20- 19	11	0	0	1?	4	4	3	27.27
53-20- 77	11	0	0	0	0	8	3	27.27
55-19- 17	6	0	0	0	3	2	1	16.66
113-10- 2	24	0	0	0	9	11	4	16.66
Total	132	3?	0	1?	45	59	28	21.21

Although two families produced no *du*-type plants, owing to the small number of individuals available, if the size of family is taken into account, the three types of plants do not deviate too seriously from the 1 : 2 : 1 ratio. A total of 132 plants included 28 sterile glutinous plants or 21.21 percent. In addition to these sterile plants, there appeared four fertile plants, one of which was glutinous and the other three starchy.

It is obvious that these fertile plants resulted from the natural fertilization as mentioned several times in the preceding sections. Therefore, it is possible to say that the ratio of starchy and glutinous characters in the sterile type showed the normal segregation (3 : 1). This fact was also confirmed from direct observation of the endosperm generation, details of which will be given later.

v. *Progenies of Du-type in the offspring of family No 17–5 and 101–22 in the previous generation.*

As has been seen in Table 8, family No. 17–5 and No 101–22 fertile and sterile types were segregated in the F_4 generation. Of the offspring of these two families, 100 *Du*-type plants were reared. It would be

supposed that the ratio of constant and segregating families in the offspring of 100 *Du*-type might be approximately 1 : 2 as in the progenies of *DU*-type. This supposition was fully confirmed, 34 families out of 100 were uniform, including 4,917 fertile glutinous plants, and the remaining 66 families segregated for the fertile and sterile types.

The total number of plants involved in these segrgating families was 7,631, there being of fertile glutinous 6,964 and of sterile glutinous 667, showing only 8.74 percent sterile as seen in Table 16 in Appendix. The deficiency of sterile type plants is again remarkably shown, the degree of deviation being approximately the same in the case of *DU*-type plants.

vi. *Progenies of the offspring of family No. 39–12 in the previous generation.*

It will be recalled that the offspring of family No. 39–12 segregated 3 *dU* : 13 *dUu* : 3 *du* in the F_4 generation. All progenies of these 17 plants were raised in this generation. Three *dU* and *du* plants bred true, of course, whereas 11 *dUu* plants segregated for the endosperm characters as seen in Table 17.

TABLE 17.

dU : *dUu* : *du* segregation in 11 families.

Family No.	Total	*D*			*d*			*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*		
39–12– 1	37	1?	0	0	14	13	10	27.03	27.78
39–12– 2	26	0	0	0	12	13	1	3.85	30.00
39–12– 3	36	1?	0	0	11	17	8	22.22	30.43
39–12– 4	36	0	0	0	8	21	7	19.44	25.00
39–12– 7	45	0	0	0	13	24	8	17.78	13.33
39–12– 8	22	0	1?	0	6	8	8	36.36	7.15
39–12–10	52	1?	0	0	20	22	10	19.23	30.00
39–12–11	29	0	0	0	11	12	6	20.34	20.00
39–12–13	44	0	0	0	23	17	4	9.09	40.00
39–12–14	13	0	0	0	4	6	3	23.08	25.00
39–12–15	40	0	0	0	10	24	6	15.00	44.44
Total	380	3?	1?	0	132	177	71	18.68	26.31

Total number of plants in these segregating families counted 380 and the distribution of three different types of endosperm characters showed 132 *U*: 177 *Uu*: 71 *u*, that is, a percentage of glutinous plants of 18.68. The number of starchy plants shows considerable excess compared with the glutinous plants. However, if we neglect the two families 39–12–2 and 39–12–13, which showed quite small percentages of glutinous plants, the experimental results agree practically with the normal expectation of 1: 2: 1. Further, considering the percentages of glutinous endosperm generation with those of the plant generation, it can easily be recognized that the endosperm character in the sterile plants shows the normal Mendelian expectation, 3: 1.

5. Summary of the results of the pedigree culture

A large series of pedigree cultures has been analysed and practically all possible tests of analysis of different types have now been made and substantiated in every cases. For the sake of simplicity, the main points obtained may be summarized as follows:

i. Fertility, *D*, acts as a dominant character to sterility, *d*, and the starchiness *U*, dominant over the glutinous *u*.

ii. The sterile plants in the progenies of *Dd*-type were definitely fewer than might be expected on the basis of Mendelian monohybrid expectation, especially under unfavorable conditions. The results are summarized in Table 18, a, b, c.

TABLE 18, a.

Segregation of *D* : *d* in the progenies of *DU*-type.

F_n	No. of families	No. of plants observed			*d*%
		Total	*D*	*d*	
F_3	1	147	132	15	10.20
F_4	25	3902	3419	483	12.38
F_5	10	1948	1717	231	11.86
F_5	34	4392	4071	321	7.31
F_5	32	2158	2024	134	6.16
F_5	5	473	426	47	6.69
Total	107	13020	11789	1231	9.45

TABLE 18, b.

Segregation of D : d in the progenies of Du-type.

F_n	No. of families	No. of plants observed			$d\%$
		Total	D	d	
F_4	3	346	291	55	15.90
F_5	118	9293	8377	916	9.86
F_5	66	7631	6964	667	8.74
Total	187	17270	15632	1638	9.48

TABLE 18, c.

Segregation of D : d in the progenies of DUu-type.

F_n	No. of families	No. of plants observed			$d\%$
		Total	D	d	
F_2	1	103	84	19	18.45
F_3	54	1028	926	66	6.42
F_4	274	51304	44331	6973	13.59
F_5	115	11948	10731	1217	10.18
Total	444	64383	56108	8275	12.86

The homozygous double dominant (DD) showed a remarkable excess or deficiency, compared with the heterozygous Dd in the progenies of coupling phase. The results are summarized in Table 19, a, b, c.

TABLE 19, a.

Progenies of DdU-type.

F_n	No. of families	D-constant	D : d segregated
F_3	25	24	1
F_4	100	90	10
F_5	82	77	5
Total	207	191	16

TABLE 19, b.

Progenies of *DdUu*-type.

F_n	No. of families	*D*-constant	*D* : *d* segregated
F_3	56	2	54
F_4	281	7	274
F_5	117	2	115
Total	454	11	443

TABLE 19, c.

Progenies of *Ddu*-type.

F_n	No. of families	*D*-constant	*D* : *d* segregated
F_3	1	1	0
F_4	4	1	3
F_5	120	2	118
Total	125	4	121

Further it was observed that the homozygous double dominant (*DD*) are in excess over the heterozygous (*Dd*) in the progenies of *Dd*-type where no linkage exists between *D* and *U* factor are slightly less than might be expected in a ratio 1 : 2.

The results are summarized in Table 20, a, b.

TABLE 20, a.

Progenies of *DdU*-type.

F_n	No. of families	*D*-constant	*D* : *d* segregated
F_4	41	16	25
F_5	56	22	34
F_5	51	19	32
Total	148	57	91

TABLE 20, b.

Progenies of *Ddu*-type.

F_n	No. of families	*D*-constant	*D* : *d* segregated
F_5	100	34	66

iii. Concerning the endosperm characters, there appeared two cases of segregations: (a) the normal segregation, 3 : 1, in the progenies of *DDUu*- or *ddDu*-type and (b) a remarkable deficiency of the glutinous character in progenies of the *DdUu*-type. The actual results are summarized in Table 21, a, b, c.

TABLE 21, a.

The distribution of endosperm characters in the progenies of *DDUu*-type.

F_n	No. of families	No. of plants observed				*u*%	F_n-seeds (*u*%)
		Total	*U*	*Uu*	u		
F_3	2	26	4	19	3	11.54	24.90
F_4	17	3534	969	1743	822	23.28	24.11
F_4	7	1391	364	721	306	22.35	23.34
F_5	13	1361	363	658	340	24.91	—
F_5	2	214	55	114	45	21.03	22.52
Total	41	6526	1755	3255	1516	23.23	24.12

TABLE 21, b.

The distribution of endosperm characters in the progenies of *ddUu*-type.

F_n	No. of families	No. of plants observed				*u*%	F_n-seeds (*u*%)
		Total	*U*	*Uu*	*u*		
F_4	2	17	3	11	3	17.63	30.30
F_5	12	132	45	59	28	21.21	29.36
F_5	11	380	132	177	71	18.68	26.31
Total	25	529	180	247	102	19.28	28.78

TABLE 21, c.

The distribution of endosperm characters in the progenies of *DdUu*-type.

F_n	No of families	No. of plants observed				u%	F_n-seeds (u%)
		Total	*U*	*Uu*	*u*		
F_2	1	103	25	58	20	19.41	—
F_3	54	1028	408	550	70	6.81	15.48
F_4	274	51304	19616	24434	7254	14.14	17.43
F_5	115	11948	4741	5825	1382	11.57	18.28
Total	444	64383	24790	30867	8726	13,55	16.71

iv. Bi-factorial segregation showed a strong coupling phase between the factors *D* and *U*. All of the 444 lines indicated coupling and none showed the repulsion phase. However, the determination of the linkage intensites was impossible because of the deficiency of both recessive characters. The results are summarized in Table 22.

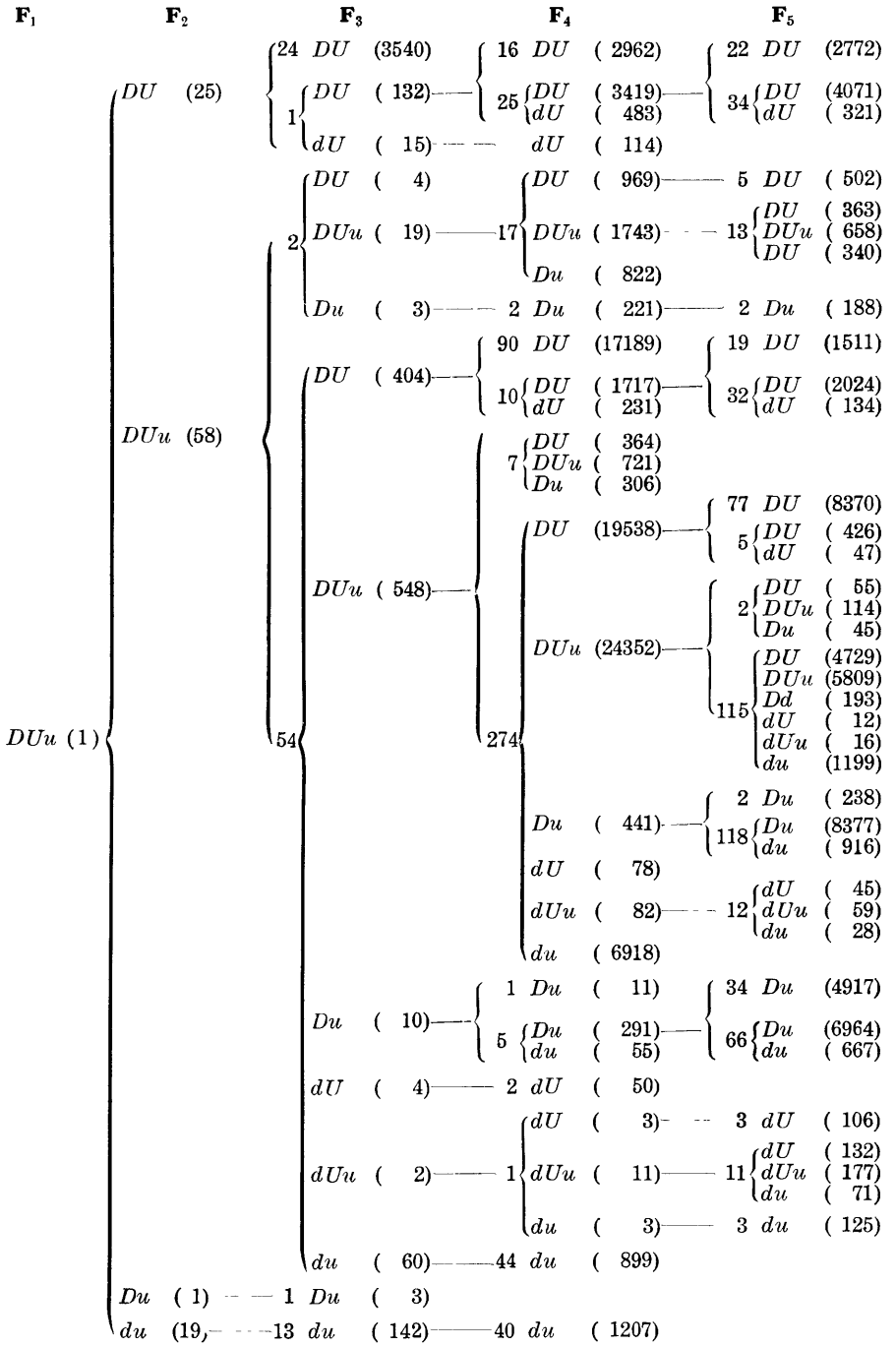
TABLE 22.

The distribution of endosperm characters and sterility in the progenies of *DdUu*-type.

F_n	No. of families	Total	*D*			*d*			d%	u%	F_n-seeds (u%)
			U	*Uu*	*u*	*U*	*Uu*	*u*			
F_2	1	103	25	58	1	0	0	19	18.45	19.41	—
F_3	54	1028	404	548	10	4	2	60	6.42	6.81	15.48
F_4	274	51304	19538	24353	441	78	82	6813	13.59	14.14	17.43
F_5	115	11948	4729	5809	193	12	16	1189	10.18	11.57	18.28
Total	444	64383	24096	30767	645	94	100	8081	12.86	13.55	16.71

v. A diagramatic representation of the pedigree cultures is given in Table 23.

TABLE 23.



Figures in parentheses are the number of plants observed.
Figures not in parentheses are the number of families observed .

6. Further observations on the ratios of starchy to glutinous plants in the progenies of different types of plants

A remarkable deficiency of glutinous character in the progenies of *DdUu*-type plants was observed, whereas the percentage of glutinous the progenies of *DDUu* or *ddUu*-type plants showed approximately 25 percent of the glutinous character. Further discussion of this point will be given in this section.

a) *The glutinous percentages in the progenies of DdUu-type.* Comparing the percentage of glutinous in the plant generation with that of the endosperm generation, there was marked deviation between them. This difference was considered as resulting from the differential power of survival between the fertile and sterile types of plants in the ordinary rice field. Actual number obtained in the endosperm generations and in the plant generations will be compared in Table 24.

TABLE 24.

F_n-seeds	No. of plants observed	No. of grains observed			F_n-seeds (u%)	Plant generation u%
		Total	U	u		
F_3	54	32284	26286	4998	15.48	6.81
F_4	274	31595	26089	5506	17.43	14.14
F_5	115	10765	8797	1968	18.28	11.64
Total	**443**	**74644**	**62172**	**12472**	**16.71**	**10.86**

In addition to the above, the count of starchy and glutinous grains on sister individuals was made to ascertain the percentage glutinous in each generation. Although the progenies of these sister individuals were not raised, it is evident that most individuals belonged to *DdUu*-type and few of them to *DDUu*-type. The results are shown in Table 25.

TABLE 25.

F_n-seeds	No. of plants	No. of grains observed			F_n-seeds (u%)
		Total	U	u	
F_3	2	1428	1230	188	13.87
F_4	267	31267	25496	5771	18.47
F_5	88	8056	6669	1387	17.22
Total	**357**	**40751**	**33395**	**7356**	**18.05**

The total number of grains counted was 40,751, the percentage of glutinous being 18.05. Comparing this percentage with the percentage 16.71 in Table 24, a slight excess is seen in the latter.

However, both percentages are much lower than the normal 25.00 percent expected on the basis of a Mendelian monohybrid segregation.

Summing up the two above results, there are 800 individuals with 115,395 seed-grains in which 17.18 percent were glutinous. The fluctuating variations in percentage of glutinous grains in each individual plant are given in Table 26.

TABLE 26.

Fluctuations of percent glutinous in each *DdUu*-type plant.

(*u*%)	(1)	(2)	Total
3- 4			
5- 6	1		1
7- 8	5	2	7
9-10	19	9	28
11-12	36	29	65
13-14	68	47	115
15-16	72	62	134
17-18	80	59	139
19-20	89	71	160
21-22	49	28	77
23-24	11	29	40
25-26	8	12	20
27-28	3	5	8
29-30	1	4	5
31-32	1		1
33-34			
Total	443	357	800

b) *The percentages of glutinous in the progenies of DDUu-type plants.* As has been stated in the foregoing section, nearly 25 percent glutinous was obtained in the progenies of *DDUu*-type plants, in both plants and endosperm generations. There was, however, a slight deficiency of glutinous character, and the degree of deficiency was slightly higher in the plant generation in comparison with the corresponding endosperm generation. (see Table 21, a, b.)

Whether the endosperm characters segregate exactly according to a monofactorial Mendelian plan of distribution or whether there are always deviations from the normal expectation caused by certain physiological or genetical factors is the most important matter in relation to the present investigation. Therefore, critical observations were made in 1922 and 1925 to confirm the percentages of glutinous plants and endosperm, in the progenies of heterozygotes for the factors *U* and *u*, and homozygous for the factor *D*.

In 1922, 225 heterozygous plants in 8 families of the F_3 of NC. I. were used for this study. These families were the sister families of SII family in which the SII-type sterile characteristic appeared.

In 1925, observations were made also on the descendants of SII-families (Family No. 4–14, 22–2 and 52–19 see Table 7, a) which were split out from the progenies of *DdUu*-type plants.

The fluctuation of variation of glutinous percentages on each individual plant is shown in Table 27.

TABLE 27.

Fluctuations in percentage of glutinous plants of the *DDUu*-type.

(*u*%)	1922	1925	Total
11–12			
13–14	3	1	4
15–16	1	1	2
17–18	2	6	8
19–20	10	13	23
21–22	33	45	78
23–24	80	91	171
25–26	61	75	136
27–28	19	33	52
29–30	12	9	21
31–32	5	5	10
33–34	1	4	5
35–36		1	1
37–38	1		1
Total	225	284	509

As will be seen in the above table, the fluctuation curves show nearly the same order and the three modes are at the same point of ordinates, that is between 23 percent and 25 percent. The total number of seed-grains observed in 1922 and 1925 is seen in the following table.

TABLE 28.

Year	No. of plants	No. of grains observed			(*u*%)
		Total	*U*	*u*	
1922	225	157545	118474	39071	24.90
1925	284	19245	14517	4728	24.57
Total	**509**	**176790**	**133991**	**43799**	**24.77**

From the above experimental results, it can hardly be doubted that the percentage glutinous for the endosperm characters in the heterozygous plants shows the typical Mendelian segregation (3 : 1) expected on a monofactorial basis.

Several workers, however, have suggested that the remarkable deficiency of glutinous character in the offspring of hybrids between starchy and glutinous varieties in rice is similar to the case of waxy or sugary characters in maize, and several explanations have been offered from time to time by the different investigators. PARNELL (1921) called attention to the deficiency of glutinous individuals in the progenies of the hybrids between starchy and glutinous varieties in Indian rice. In conclusion, he stated that the single factor explanation is correct but that some disturbing influence affects the ratio in F_2. He suggested that differential germination and dying off may be responsible for the deficiency of glutinous individuals. BRINK and MACGILLIVRAY (1924) suggested that the deficiency of glutinous grains among rice hybrids is due to selective pollen-tube growth. YAMAGUTI (1926) studying the hybrids between Karasumoti (glutinous) and Sinriki (starchy) offered a bifactorial hypothesis for the starchy and glutinous characters, to explain the deficiency of glutinous plants in his experiments and those of PARNELL (1921). He stated that the starchy character may be represented by two cumulative factors, *H* and *I*, corresponding factors being *h* and *i* for the external form of the glutinous character. Both factors *H*, *I* are responsible for the formation of starchy endosperm but the factor *I* is some what weaker than *H*, therefore, two factors, *H*, *I*, are needed for the expression of the starchy character and the external character of the single factor *I* is glutinous.

From the above assumption, a ratio of 13 starchy to 3 glutinous should be expected in the F_2 generation, or 18.75 percent glutinous.

CHAO (1928) believes, on the contrary, that environmental factors can influence the rate of growth of pollen-tubes containing the recessive factor, as has been suggested by Brink and MACGILLIVRAY (1924).

Recently ENOMOTO (1929) reported on a glutinous variety (Aikokumoti) which gives, on selfing, a few starchy seed-grains. These seed-grains proved to be always heterozygous, giving in the next generation starchy and glutinous offspring in the 3 : 1 ratio (actually 23.77 percent glutinous). The case was considered to be due to a gene mutation from the recessive to the dominant condition. Actually he observed the occurrence of a small percentage (1.04 percent) of starchy pollen-grains in the glutinous plants. It is interesting to present the actual data obtained by different investigators together with those here reported.

All available data are summarized in Table 29 a, b. The data included in Table 29, a, show the results of observations of characters in the endosperm generation, and those in Table 29, b, show those of the plant generation.

A summary of the data in Table 29, a, obtained by several investigators shows that in 265,327 seed-gains there occurred 24.60 percent glutinous grains. The percentages of glutinous grains ranged from 21.84 to 28.49 percent. It is evident that the above results show a typical monofactorial segregation and we need not postulate the bifactorial hypothesis offered by YAMAGUTI (1926) for the data presented in the table.

TABLE 29, a.

Historical summary of endosperm segregation in the heterozygous plants (Uu) of hybrids between starchy and glutinous varieties of rice plants (expected 3 : 1).

Investigators	No. of seed-grains observed				Materials used
	Total	(*U*)	(*u*)	(*u*%)	
KATO, S. (1910)*	—	—	—	24.11	Shinriki × Karasumoti
,, ,, (?)**	307	286	101	26.10	? ?
IKENO, S. (1914)	7101	5245	1856	26.14	Hiemoti × Akage
,, ,, ,,	7916	5882	2034	21.84	Akage × Hiemoti
YAMAGUTI, Y. (1918)	3642	2798	844	23.17	Karasumoti × Shinriki
PARNELL, R. F. (1921)	6879	5292	1587	23.07	Indian varieties
TAKAHASHI, N. (1923)	184	143	41	22.28	Tarobemoti × Tamanisiki
,, ,, ,,	193	138	55	28.49	Tarobemoti × Wasesinriki
CHAO, L. F. (1928)	57925	44043	13882	23.97	
TAKAHASHI, N. (1935)	157545	118474	39071	24.90	NC. 1
	19245	14517	4728	24.57	*DDUu*-type
	4390	3331	1059	24.12	,, ,,
Total	**265327**	**200149**	**65258**	**24.60**	

* .....from IKENO (1927)
** ....from CHAO (1928)

TABLE 29, b.

Historical summary showing the segregation of endosperm characters in the offspring of hybrids between starchy and glutinous varieties of rice plants (expected 1 : 2 : 1).

Investigators	No. of plants observed				u%	Materials used
	Total	U	Uu	u		
IKENO, S. (1914)	82	28	54	—	—	Owarimoti × Yogore
,, ,,	140	53	87	—	—	Yogore × Owarimoti
PARNELL, F. R. (1921)	27961	9211	13729	5021	(17.92)	Indian varieties
YAMAGUTI, Y. (1921)	441	95	245	101	22.90	Karasumoti × Sinriki
TAKAHASHI, N. (1923)	906	243	455	208	22.96	Tarobemoti × Tamanisiki
,, ,, ,,	1156	275	666	215	(18.60)	Tarobemoti × Wasesinriki
YAMAGUTI, Y. (1926)	1794	463	921	410	22.85	Karasumoti × Sinriki
,, ,, ,,	5084	(3860)		1224	24.08	,, ,,
CHAO, L. F. (1928)	1504	(1176)		328	21.81	
TAKAHASHI, N. (1935)	23114	5918	17374	5722	23.86	
,, ,, (1936)	6526	1755	3255	1516	23.23	*DDUu*-type
Total (1)	68386	(53641)		14645	21.56	
(2)	39269	(29760)		9509	24.22	

Inspecting Table 29, b, it will be found, that all cases without exception, show the deficiency of glutinous plants, and the most significant departures from the normal expectation will be seen in the results of PARNELL and TAKAHASHI (1923). However, the observation of the endosperm generation in the same hybrids (Tarobemoti × Wasesinriki, in Table 29, a) shows 28.49 percent glutinous. If we neglect the results of PARNELL and TAKAHASHI (1923), it will be seen that the percentage of glutinous in a total of 39,269 plants was 24.22 percent.

From the above, we can say that the percentage of glutinous in the hybrids between starchy and glutinous varieties shows more or less lower than 25 percent in the plant generation. Comparing the plant generation with the endosperm generation, there is relatively a more marked deficiency in the plant generation. However, it must be kept in mind that the results of observations in the endosperm generation are more reliable than those of the plant generation. And as to the deficiency of glutinous individuals in the plant generation compared with the endosperm generation, we can suppose several causes for the disturbing effect; for example, the differential germination or power of survival in the different types, etc.

KIESSELBACH and PETERSON (1926) have summarized all the available data on the inheritance of waxy endosperm in maize, including considerable new data of their own. When all the results are combined, there is a deficiency of 1.1 percent from the expected 25 percent when the heterozygote is selfed, 0.7 percent from the expected 50 percent when segregating pollen from the heterozygous plants is applied to the pure recessives. Finally, they conclude that "the evidence at hand seems insufficient to definitely establish the causes or the significance of the deviations herein reviewed."

MANGELSDORF and JONES (1926) have attempted to analyse KEMPTON's data (1919) on the waxy hybrids of maize and they state that "with the evidence of an accessory factor in mind it should be possible to isolate from such crosses as KEMPTON's, some heterozygous waxy lines which regularly give normal ratios, some which give a majority of minus deviations and other a majority of plus deviations."

In the case of rice plants as shown in the above tables, no such explanation is needed as that offered for maize plants, since the data presented in Table 29, a, clearly show a monohybrid segregation and the author believes that the endosperm characters in rice plants segregate in a typical Mendelian monohybrid manner.

c) *Distribution of starchy and glutinous characters in the progenies of the ddUu-type plants.* Mention has been already made in this paper that the grains of sterile plants are very small and irregular compared

TABLE 30, a.

Ratio of starchy and glutinous in the ears of *ddUu*-type plants.

F_n-seeds	No. of plants observed	No. of grains observed			F_n-seeds (u%)
		Total	U	u	
F_4	2	33	23	10	30.30
F_5	39	807	570	237	29.36
F_5	11	171	126	45	26.31
Total	**52**	**1011**	**719**	**295**	**28.78**

with the grains of fertile types, so that the observations of endosperm characters were not accomplished so easily. Moreover, the number of plants or grains observed was small compared with the number in the fertile type. Therefore, the results obtained are more or less unreliable and are not comparable with those of fertile type. It is very interesting.

nevertheless, that there is a rather marked excess of glutinous grains in the endosperm generations of *ddUu*-types. It was considered in the foregoing section that this excess resulted merely from errors of observation, but further consideration of this point will be discussed in this section, including other new data. The results in the endosperm generations are summarized in Table 30, a.

In 52 plants bearing 1,011 seed-grains the percentage glutinous was 28.78. This is a marked excess of glutinous grains comapred with the 25 percent expected. From this it might be assumed that the combination of *u*-pollen and *u*-eggs on the sterile plants takes place much more easily than the combination of *U*-pollen and *U*-eggs. In other words, it suggests that there may be some relation between the sporophytogenesis and gameto-

TABLE 30, b.

Distribution of starchy and glutinous characters in the progenies of *dUu*-type plants.

F_n	No of families	No. of plants observed				*u*%
		Total	*U*	*Uu*	*u*	
F_4	2	17	3	11	3	17.63
F_5	12	132	45	59	28	21.21
F_5	11	380	132	177	71	18.68
Total	25	529	180	247	102	19.28

genesis which disturbs the independent combination of the genes at fertilization. The data presented in Table 30, b, obtained in the plant generations show that the above consideration is merely a supposition and that we can not draw a definite conclusion.

The total of 529 plants includes the three types, starchy heterozygous and glutinous, and shows the percentage of glutinous plants to be 19.28 percent.

7. The correction of the data obtained from the observation of the plant generation, by the data obtained from the observation of corresponding endosperm generation

It was confirmed that the plants heterozygous for both factor *D* and *U* always segregate in six different phenotypes in the next generation and the deficiency of recessive types is exceedingly large in both characters, glutinous endosperm and sterility, though their ratio should be 25 percent, theoretically.

As to the endosperm characters, observation was made both on the plant generation and on the corresponding endosperm generation. As already stated in the above section, the observation on the endosperm generation is the more accurate one, just as in the case of waxy or sugary maize. Practically no errors of classification can have effected the ratios of starchy and glutinous segregation in the endosperm generation. On the other hand, the observation in the plant generation is a rather unreliable one because of the disturbing effects of environment.

As has been shown in the foregoing sections, the percentages of glutinous plants is always less than those of the endosperm generation, and in the more extreme cases remarkable differences were found between the percentage glutinous in the endosperm generation and its corresponding plant generation. The greatest difference was found in the F_3 generation where the cultivation was not adequately carried out, the difference of two observations showing 8.67 percent. In the F_4 generation, there was a much smaller difference, 3.29 percent, between endosperm and plant generation and in the F_5 generation the difference of the two observations was again large, 6.71 percent.

It should be remembered that the most precise precautions were taken for the cultivation of F_4 plants and that the cultivation of F_5 plants was largely modified from the standard plantation method. From the above, it is evident that the main causes of decrease in the percentages of glutinous plants is the differences of survival between the fertile and sterile type under unfavorable conditions.

If the above supposition be corrrect, it is possible to correct the data obtained from the observations in the plant generation depending upon the data from the endosperm generation, thus getting more accurate data by avoiding errors caused by the differential survival of fertile and sterile types of plants in the rice field. The corrected data fit more closely to the theoretical expectation, of course, than the original data. An example to illustrate the method of correction follows. To simplify the calculation, the total number was represented by per 10,000 (see Table 22). The original data thus reduced is as follows.

Total	D			d			d%	u%	(u%)	Dev.
	U	Uu	u	U	Uu	u				
10000	3836	4778	100	15	16	1255	12.86	13.55	16.71	3.16

There is a difference of 3.16 percent between the percentage of glutinous in endosperm and that of the plant generation. This difference

means a decrease in number of sterile plants, therefore, the corrected sterile percent is 15.97 found by adding 3.16 to the original sterile percent 12.86.

However, there are two kinds of sterile types (15*dU*, 16*dUu*) beside the homozygous sterile type 1,255 plants. If we suppose these three kinds of sterile types have the same survival value in the rice field, in other words, if there is no selective elimination between them, then it follows that the decreased number in these three types would be proportional to their actual numbers. Consequently, the corrected numbers for three types as follows:

	d			*d*%	*u*%	(*u*%)
	U	*Uu*	*u*			
Original	15	16	1255	12.81	13.55	16.71
Correction	4	4	308	3.16	3.16	
Corrected	**19**	**20**	**1563**	**15.97**	**16.71**	

Besides the above, there are 100 homozygous glutinous plants among fertile types. Adding this 100 glutinous plants to the corrected sterile plants 1,563 gives 1,663 glutinous plants. However, the number of glutinous plants should be kept 16.71 percent in total. Thus, (100 + 8) is the corrected fertile glutinous plants.

Now we will consider the number of *DU* and *DUu*-type plants. The corrected percentage of sterile is 15.97, therefore, the percentage of fertile plants should be changed to

$$100-15.97 = 84.03 \text{ percent.}$$

However, the corrected percentage of fertile glutinous 1.08, percent, must be stand for the glutinous percent of total number without changing its ratio. Consequently, the 82.95 percent (84.03–1.08) for the sum of *DU* and *DUu* percentages will be obtained. The proportion of *DU* to *DUu* among the corrected percentage 82.95 should be kept without changing their relation. Thus, the corrected number for both types are as follows:

$$\begin{array}{r} 3836 \\ 4778 \\ \hline 8414 \end{array} \qquad \frac{3836 \times 8295}{8414} = 3692 \quad \text{for} \quad DU$$

$$\frac{4778 \times 8295}{8414} = 4598 \quad \text{for} \quad DUu$$

The corrected numbers for the six different types together with the original data are shown in Table 31. It will be seen in the table that the corrected data in each generation fit more closely to the corrected total numbers than those of the original numbers to their original total numbers.

In the following sections, these corrected numbers are used for the calculation of theoretical numbers.

TABLE 31.

Comparison of the original and corrected data in each generation (per 10,000).

F_n		D			d			$d\%$	$u\%$
		U	Uu	u	U	Uu	u		
F_2	Original	2437	5631	97	0	0	1845	18.45	18.42
	Corrected	—	—	—	—	—	—	—	—
F_3	Original	3930	5331	97	37	19	584	6.42	6.81
	Corrected	3529	4748	175	92	44	1373	15.09	15.48
	Deviation	+411	+544	−78	−55	−25	−789	−8.67	−8.67
F_4	Original	3808	4747	86	15	16	1328	13.59	14.14
	Corrected	3658	4560	94	19	20	1649	16.88	17.43
	Deviation	+159	+187	−8	−4	−4	−321	−3.29	−3.29
F_5	Original	3958	4862	162	10	13	995	10.18	11.57
	Corrected	3588	4407	177	17	21	1651	16.89	18.28
	Deviation	+370	+455	−15	−7	−8	−656	−6.71	−6.71
Total	Original	3836	4778	100	15	16	1255	12.86	13.55
	Corrected	3692	4598	108	19	20	1563	16.02	16.71
	Deviation	+144	+180	−8	−4	−4	−308	−3.16	−3.16

In addition to the above segregating families, there were several segregating families for the fertile and sterile types. For those families, the above correction was applied to correct the ratio of segregation for the sterility character.

From the tables 18, a, b, it can be noticed that the percentages of sterile plants in the progenies of both *DU* and *Du*-type, are nearly the same, and the deviations from the normal segregation (3 : 1) are quite large, as has been noticed also in the progenies of *DUu*-type.

Comparing the percentages of sterile plants in the progenies of *DU* and *Du* with those of sterile plants in the progenies of *DUu*-type, the former are seen to be significantly smaller than the latter; namely, in total number the latter is 12.86 percent and the former 9.47 percent. It is evident that this difference is caused by the difference of distribution of families in each generation. Because most of the progenies of *DUu*--type plants were obtained in the F_4 generation where the most precise precau-

tions were taken in cultivation. On the other hand, the most of progenies of *DU* and *Du*-types were cultivated in the F_5 generation in which the modified method of cultivation was adopted. The differences in capacity for survival in the fertile and sterile types in each generation is assumed to be as follows:

F_3 . . . . . 8.67%
F_4 . . . . . 3.29% See Table 31.
F_5 . . . . . 6.71%
In total 3.16%

If we add these differences in power of survival, in each generation, to d percent of corresponding generation, the corrected percentages of sterile plants are more uniform than the original percentages.

TABLE 32.

F_n	Number of families	Total number of plants observed	Observed d%	Corrected d%	Correction %
F_3	1	147	10.20	18.87	8.67
F_4	25	3902	12.36	15.67	3.29
F_5	10	1948	11.86	18.57	6.71
F_5	34	4392	7.31	14.02	6.71
F_5	32	2158	6.16	12.87	6.71
F_5	5	473	9.67	15.40	6.71
			Mean.....	15.76	

TABLE 33.

F_n	Number of families	Total number of plants observed	Observed d%	Corrected d%	Correction %
F_4	3	346	15.90	19.19	3.29
F_5	118	9293	9.86	16.57	6.71
F_5	66	7631	8.74	15.45	6.71
			Mean.....	17.07	

From the above corrected data, it can be seen that the mean percent of sterile plants in the progenies of *DU*-type plants shows 15.76 whereas in the progenies of *Du*-type, the percentage sterile is 17.07. In the total of both progenies, the percentage sterile was 16.42, which is very close to the percentage of sterile, 16.02, of *DdUu*-type plants.

8. Fertility of various types in the fertile and sterile plants

On examining the foregoing data, it can be seen that there are two kinds of segregation with respect to endosperm characters, one of which approximates the 3 : 1 ratio and the other shows a remarkable deficiency of glutinous plants. Similarly, the segregation of fertile and sterile types always shows a deficiency of sterile plants even in the different progenies, and the deficiencies are approximately of the same amount. Furthermore the number of constant families in the progenies of fertile type show a slight excess in all cases. The above facts indicate that the heterozygous condition for the factor *D* is in some way connected with the causes which tend to increase the proportion of homozygous dominant individuals. No selective difference was found in the viability of the seeds of different fertile type plants. The percentages of germination in the rice were just as high in the seed borne by plants heterozygous for the mutated factor (*d*) as in those of homozygous fertile plants. Therefore, counts were made of fertile spikelets on the panicles of different types of plants to find out the causes of deficiency of sterile plants or of glutinous plants.

Observations were carried out mostly in the F_3 generation and the results in the F_2 generation were added.

Six different types of plants in the F_3 generation were *DU, DUu. Du, dU, dUu, du.*

In the progenies of the first types, constant and segregating families for fertility were obtained in the next generation and these three phenotypes were sorted for the six genotypes after the observation of their progenies.

The nine different genotypes examined are as follows:

1. *DDUU*
2. *DDUu*
3. *DDuu*
4. *DdUU*
5. *DdUu*
6. *Dduu*
7. *ddUU*
8. *ddUu*
9. *dduu*

If the factor *d* affects the zygotic generation, causing the death of the embryo, it should result in a definite correlation between their genetic constitution and the percentage fertile. No such correlation was found between the factorial constitution and fertility among the different fertrile plants, as shown in Table 34. The average percentage of fertility of *DDUU, DDUu, DDuu*-types was 88.16 and that of *DdUU, DdUu* and *Dduu*-type plants was 87.37 percent. The difference of these two percentages is not significant because the percentages of sterile types from fertile parents are very low compared with the fertile types.

TABLE 34.

Fertility of various types.

	Genotypes	F_n	Number of individuals	Number of spikelets				
				Total	F	S	F%	per ear
1	*DDUU*	F_3	2	271	223	48	82.29	135 50
	,,	F_3	90	12161	10583	1578	87.02	135.12
	,,	F_3	304	40317	35858	4459	88.94	132.62
2	*DDUu*	F_2	2	1340	1239	101	92.46	167.50
	,,	F_3	19	3054	2496	558	81.73	160.74
	,,	F_3	7	947	809	138	85.43	135.29
3	*DDuu*	F_3	3	507	456	51	89.94	169.00
	,,	F_3	1	214	181	33	94.58	214.00
4	*DdUU*	F_3	10	1232	1045	187	84.82	123.20
5	*DdUu*	F_2	41	26145	23879	2266	91.33	113.67
	,,	F_3	274	38035	32653	5382	85.85	138.81
	,,	F_3	267	37201	32064	5137	86.19	139.33
6	*Dduu*	F_3	3	512	465	47	90.82	170.67
	,,	F_3	6	1073	974	99	90.77	178.83
7	*ddUU*	F_3	15	851	88	761	10.34	56.73
	,,	F_3	4	320	43	277	13.44	80.00
8	*ddUu*	F_3	2	126	33	93	26.19	63.00
9	*dduu*	F_2	19	5842	807	5035	13.81	64.91
	,,	F_3	60	4584	738	3746	16.10	76.40
	,,	F_3	143	10160	2145	8015	21.11	71.05

The percentages of fertile plants of *ddUU*, *ddUu* and *dduu*-type were 11.19, 26.19 and 17.92, respectively, there being an average of 17.61 percent. The number of spikelets per ear of sterile plants was also considerably less than in the fertile types. Comparison of the fertile and sterile types is summarized in Table 35.

TABLE 35.

Types	Number of plants observed	Total number of spikelets observed	Fertility %	Number of spikelets per ear
DD	428	58811	88.16	133.51
Dd	591	104198	87.37	131.90
dd	243	21883	17.61	69.69

It is evident that the factor *d* is not the cause of the zygotic lethal on the heterozygous plants, and its double dose, *dd*, affects the fertility and the number of spikelets per ear, besides weakening the plants.

9. Observation of pollen-grains

From the observation of germinating power of different fertile types of seed-grains in the seed-beds and the count of fertile spikelets on the panicles of different types of plants, it was confirmed that a zygotic lethal does not explain the present case. Therefore, one is naturally inclined to think of a gametic lethal to explain the abnormal segregation.

Observations of pollen-grains were made on the different types of plants, and it was found that all the pollen-grains on the fertile type of plants were distinctly sound and showed practically no admixture of aborted pollen-grains. As to the sterile types, only the pollen-grains on the *du*-type plants were examined. The pollen-grains on the *du*-type plants are mostly aborted and irregularly developed. From this, it can be supposed that the pollen-grains on the sterile plants are incomplete and mostly aborted, so that they can not fertilize their endosperms fully.

A count was made, also, of starchy and glutinous pollen-grains on the heterozygous plants for endosperm characters, using the iodine test as adopted by PARNELL (1921). It will be recalled that there are two kinds of heterozygous plants, i. e. *DDUu* and *DdUu*. The offspring of *DDUu* plants show always normal segregation in the next generation and the ratio of functional gametes on the heterozygous plants must be 1 : 1. On the other hand, the segregation in the progenies of *DdUu*-type plants shows marked departure from the normal Mendelian expectation; both recessive forms in the six phenotypes showed considerable deficiency.

A large number of pollen-grains were counted to obtain the ratio of starchy and glutinous on the *DdUu*-type plants. For this purpose, 26 *DDUu*-type plants were selected from the following three families;

Family No. 1–2–1, 1–2–2, 1–2–9 (see Table 10).

These families showed all fertile-type plants. After harvesting, it was confirmed that the distribution of the three types (*U* : *Uu* : *u*) occurred in the expected 1 : 2 : 1 ratio the actual numbers being 52 *U* : 91 *Uu* : 53*u*. The total number of pollen-grains counted in 26 *Uu*-type plants in the above families was 33,159. Among these, 16,530 pollen-grains stained yellowish brown and 16,629 stained blue. This is 49.85 percent glutinous grains and 50.15 percent starchy. The observed ratio fits closely the expectation based on the monohybrid Mendelian segregation.

The count of pollen-grain from the *DdUu*-type plants was made on 55 heterozygous plants belong to the following seven families:

Family No. 5–26–3, –4, –9, 67–3–10, –11, 57, 59 (see Table 13, b). These seven families showed the same of segregation, and it is evident that most of the *DUu*-type plants in these families were *DdUu* plants.

The total number of pollen-grains counted in these seven families was 47,076, there being 24,111 starchy and 21,668 glutinous grains, that is, 47.33 percent glutinous. This percentage is slightly less than that from the *DDUu*-type plants. It is not known whether this discrepancy resulted from errors of observation or from other causes; but it will be shown later, that 32 percent glutinous instead of 47.33 percent should be expected on the basis of the gametes which functioned at the time of fertilization.

Beside the above observations, counts of pollen-grains were made on the plants heterozygous for starchy and glutinous characters from the F_2 families of the hybrids between Sôtô (starchy) and Tarobemoti (glutinous) varieties.

A count was made on 13 segregating plants, resulting in 1,699 pollen-grains stained blue and 1,708 stained yellowish brown. This is 49.87 percent starchy and 50.13 percent glutinous. The three above results are summarized in Table 36, a.

TABLE 36, a.

Results of observation on the pollen-grains.

Type of plants	Number of plants	Number of pollen-grains			
		Total	*U*	*u*	*u*%
DDUu	26	33159	16629	16530	49.85
DdUu	55	45779	24111	21668	47.33
DDUu	13	3407	1689	1708	50.13
Total	94	82345	42439	39906	48.46

The variation in percentage of glutinous grains in the above three groups of plants is given in Table 36, b.

As will be seen in the fluctuation table, the variation of glutinous percentages range from 42 to 57 percent. The ranges of variation of percentages in the three groups of plants are more or less different, and the range of percentages of *DDUu*-type is smallest and that of *DdUu*-type is largest.

However, the total number of frequencies in each type is not adequate for a statistical comparison of their fluctuations. On this point, PARNELL

(1921) has made a count of pollen-grains in eighteen anthers from three F_1 plants of hybrids between certain starchy and glutinous varieties of Indian rice. He states that there was some variation in the proportions of starchy and glutinous grains and that the ratio was rather more uniform for anthers in the same flower than for different flowers of the same plants. The percentages of glutinous grains varied from 48.2

TABLE 36, b.

u%	*DDUu*	*DdUu*	*DDUu*	Total
42		2		2
43		0	1	1
44		3	0	3
45		7	0	7
46		8	0	8
47	1	11	0	12
48	2	10	2	14
49	4	5	2	11
50	9	6	2	17
51	5	0	2	7
52	2	2	1	5
53	3	0	3	6
54		0		0
55		0		0
56		0		0
57		1		1
Total	26	55	13	94

to 56.8 percent, the average being 51.9 percent. CHAO (1928) also counted the pollen-grains on six heterozygous plants and obtained 49.78 percent glutinous.

Comparing their results with the present case, slight departures are found in both, but it can hardly be doubted that the segregation of starchy and glutinous characters in the gametic generation shows the theoretical expectation of Mendelian law of segregation, 1:1. Therefore, in this experiment, it is evident that the factor *d* is not a gametic lethal in the usual sense. How, then, may we explain the discrepancy between the gametic segregations and the corresponding zygotic segregations?

The author has made, as yet, no observations of pollen-tube growth or development in the styles of rice flowers. It is suspected that the factor *d* affects the development of pollentubes which bear the same factor thus disturbing the free combination of eggs and sperms of the different genotypes. This supposition agrees fairly well with the deviations of the zygotic generation. This point will be given further consideration in the following section.

Explanation of the Experimental Results

In the diagrammatic representation of pedigree cultures (Table 23), if the deviation of sterile and glutinous plants are left out of consideration, the main line of hereditary behavior of endosperm character and sterility will be seen to belong to a bifactorial Mendelian case accompanied by a strong coupling between two of the factors. Factors *D* and *d* are responsible for the external form of fertile and sterile types, respectively; the genetic constitutions of the normal fertile type, therefore, *DD* and *Dd*, *D* being dominant to *d*. At the same time, *U* and *u* are concerned in the character of endosperms, *U* relating to the starchy character, and *u* to the glutinous, so that *U* is dominant to *u* with respect to endosperm characters.

As regards the deficiency of zygotic (*dd*) two assumptions would be possible, one of them is the disturbance of the gametic ratio caused by the factor *d*, and the other is the death of zygotes of the *dd* type after fertilization.

I have shown in this paper that zygotic lethal effect is not indicated in the present case. This leads to the conclusion that the causes of deficiency must be found in gametogenesis, either as incompatibility or a gametic lethal. But this would also lead to a disturbance the normal ratio of endosperm characters. Assuming the bifactorial constitution to be *DdUu*, and further assuming that one of these factors is linked with a factor *L* and causes the deficiency of the recessive characters, will not explain the present case; for if the lethal factors *L* and *l* were linked with the factors *D* and *d*, then it would follow that these lethal factors would be linked with *U* and *u* factors in cases where the factors *D* or *d* are homozygous. No deficiency or excess of glutinous endosperms was found in the segregation of endosperm characters where the factors *D* or *d* are homozygous. Consequently, the author believes there is no lethal factor or any other factors than the above two factors *D* and *U*, as far as the two characters are concerned.

Of course, it might be considered that the factor *L* is linked absolutely with the factor *D*. This consideration is also not adequate for the present

experiments, because there was no gametic lethal or elimination in the pollen-grains or endosperms on the *Dd*-type plants.

We may now pass on to the theoretical numbers of expectation in the F_2 generation and the calculation of linkage intensities. It is of distinct advantage to backcross the heterozygotes to the double recessives for the calculation of linkage intensities, since the gametic ratio can then be determined directly from the zygotic ratio. In some plants, as Zea or Nicotiana, for example, backcrosses are easily and readily made, but in the rice plants the practical difficulties attending artificial hybridization are too great to admit of backcrosses in sufficiently large numbers. The calculation of linkage intensities in this plant, therefore, is confined to the F_2 distribution following self-fertilization.

EMERSON (1916) has developed formulae for calculation of the gametic ratio directly from any given zygotic series representing dihybrid distributions. WOODWORTH (1923) devised the formulae from EMERSON's formula for the calculation of linkage intensities where duplicate factors are concerned. ALBERTS (1925) has given us the numerical relations in the calculation of linkage intensities. HALDANE (1919, a, b) and COLLINS (1924) also have given us a very accurate method of calculating linkage intensities from the zygotic series. It is evident that these formulae, devised by several investigators, are based on the case where no disturbances occur in the gametic stages nor the zygotic generation, that is on cases in which there has been random mating of equal numbers of gametes.

Thus, the above formulae are not suitable for the present experiments. MANGELSDORF and JONES (1926) have given the zygotic ratios accompanying gametic disturbances and linkage. However, they do not give formulae for general use. To estimate the linkage values and the functional gametic ratio for the present experiments, new formulae have been devised. These formulae are useful for the calculations of theoretical numbers where the Mendelian segregation is modified by selective fertilization or when there is linkage with a gametic lethal.

Estimation of crossover values between two factors one of which is a cause of disturbance of the gametic ratio

The presence of gametophyte factors which disturb the equality in which two kinds of gametes are presented at fertilization, brings up entirely new problems in Mendelian segregation. The amount of crossing over and the relative effectiveness of the accessory factor or factors are two variables which determine the amount of deviation from the normal ratio. Three causes may be assumed to show the same deviation for

the recessive character as were caused by the accessory factor. The first case is that in which the gametic ratio at the time of fertilization is equally disturbed in both the pollen-grains and endosperms. The second case is that in which gametic ratio at the fertilization is disturbed by only one of gametes, pollen-grains or endosperms. In the third case the disturbance occurs in both gametes in different amounts which together make up the total amount of deviation from the normal expectation.

In each case, it may be expected that another character which is linked with the accessory factor will show a different numerical ratio. Furthermore, the ratio of constant and segregating families in the F_3 generation may be expected to differ in each case. In the present case, there was no selective elimination in the zygotic generation and the fertility of fertile homozygous, *DD* and of heterozygous *Dd* plants is nearly the same. Consequently, it can be supposed that the gametic ratio at fertilization has been disturbed only by the pollen-grains. The second case will then be considered, in which the disturbance of the gametic ratio at fertilization is confined only to the male gametes (pollen-grains).

As has been mentioned above the factors U and u are linked with the factors D and d according to the following factorial constitution.

$$\frac{D}{d} \quad \frac{U}{u}$$

Suppose x is the crossover value between the factors D and U, then the following four values of x, will be conceivable.

$x = 0.00$, complete linkage
$x = 0.50$, nocrossing over
$x > 0.50$, coupling
$x < 0.50$, repulsion

The proportion of functional gametes in the pollen-grains and endosperms are as follows:

Kinds of gametes	Proportion of gametes bearing U and u			Proportion of gametes bearing D and d		
	U	:	u	D	:	d
Pollen grains	1	:	1	$1+z$	:	$1-z$
Endosperms	1	:	1	1	:	1

The ratio in which D and d gametes occur at fertilization may range from 1:1 to 1:0, namely as follows:

$z = 0$ No disturbing effect on the gametic ratio.

$z > 0$ Partial non-functioning of gametes which bear the factor d.

$z = 1$ Complete non-functioning of gametes which bear the factor d.

From the above categories, the following gametic series in both pollen-grains and endosperms at the time of fertilization of *DdUu* plants will be obtained.

Pollen-grains $\frac{1}{2}(1-x)\{(1+z)DU+(1-z)du\}+\frac{1}{2}x\{(1+z)Du+(1-z)dU\}$

Endosperms $\frac{1}{2}(1-x)\ (DU+du)+\frac{1}{2}x\ (Du+dU)$

After the self fertilization of the above gametes, the kind of zygotes is as follows:

$$\begin{aligned}
&\tfrac{1}{4}(1-x)^2\ \{(1+z)DDUU+(1-z)DdUu+(1+z)DdUu+(1-z)dduu\}\\
&+\tfrac{1}{4}(1-x)x\{(1+z)DDUu+(1-z)DdUU+(1+z)Dduu+(1-z)ddUu\}\\
&+\tfrac{1}{4}(1-x)x\{(1+z)DDUu+(1-z)Dduu+(1+z)DdUu+(1-z)ddUu\}\\
&+\tfrac{1}{4}x^2\{(1+z)DDuu+(1-z)DdUu+(1+z)DdUu+(1-z)ddUu\}
\end{aligned}$$

From the above, the formulae of different phenotypes will be given as follows:

Phenotypes	Proportion
DU	$3+z-x\ (2-x+xz)$
Du	$x\ (2-x+xz)$
dU	$x\ (2-x+xz-2z)$
du	$1-z-x\ (2-x+xz-2z)$

In these formulae, the values of x and z are so taken that they may agree most closely with the experimental results. The theoretical numbers thus obtained are compared with the observed numbers in the F_2 generation (Table 37, a).

As will be seen in the above calculations, the sterile percentages are confined by the values of z and there is closest agreement where z is taken as 0.36 and the crossover value x as 0.022, showing the percentage sterile 16.00 and percentage glutinous 16.39.

However, the $d(U+Uu)$ term in the observed number does not agree with the theoretical number. This discrepancy might be caused by an error in sorting the different endosperms in the sterile plants.

As already stated, the sorting of the three types in the sterile plants has not been made so easily, therefore, it would be supposed that the

some of *dUu*-type plants would be placed into the *dU*-type. If the *d* (*U* + *Uu*) type plants are added to the *du*-type plants, the observed numbers agree more closely with the theoretical numbers.

TABLE 37, a.

	D		*d*			
	(*U*+*Uu*)	(*u*)	(*U*+*Uu*)	(*u*)	*d*%	*u*%
Observed number	8290	108	39	1563	16.02	16.71
Theoretical number						
x : *z*						
0.020 : 0.33	8226	99	66	1609	16.75	17.08
0.022 : 0.33	8216	109	73	1602	16.75	17.11
0.024 : 0.33	8206	119	79	1596	16.75	17.15
0.020 : 0.36	8301	99	63	1537	16.00	16.36
0.022 : 0.36	8291	109	70	1530	16.00	16.39
0.024 : 0.36	8281	119	76	1524	16.00	16.43
0.020 : 0.39	8376	99	60	1465	15.25	15.64
0.022 : 0.39	8366	109	66	1459	15.25	15.68
0.024 : 0.39	8356	119	72	1453	15.25	15.72

Passing on to the numerical relations of constant and segregating families in the F_3 generation, the proportion of constant and segregating families with respect to *D*- and *d*-factors in the F_3 generation are shown as follows:

$$\frac{DD}{DD+Dd}\ (UU) \ldots\ldots\ \frac{(1-x)(1+z)}{1+z+(1-z)x}\ \%$$

$$\frac{DD}{DD+2Dd}\ (Uu) \ldots\ldots\ \frac{(1-x)(1+z)x}{1-(1-x)(1-z)x}\ \%$$

$$\frac{DD}{DD+Dd}\ (uu) \ldots\ldots\ \frac{(1+z)x}{2-(1-z)x}\ \%$$

$$\frac{DD}{DD+Dd}\ (U+Uu+u) \ldots\ \frac{1+z}{3+z}\ \%$$

Theoretical numbers were calculated by substituting the values $x = 0.022$ and $z = 0.36$ in the formulae.

Comparison of the observed and the theoretical numbers are given in Table 37, b (see also Table 19, a, b, c, and Table 20, a, b).

The fit of the theoretical numbers to the observed numbers is very high in each case.

As has been shown in the foregoing section, all 443 segregating families indicated the coupling phase and no repulsion phase appeared.

How many times can we expect the repulsion phase in the present experiments?

TABLE 37, b.

	Total	Type of family		Deviation
		DDUU	*DdUU*	
Observed number	207	191	16	
Observed percent		92.27	7.73	
Theoretical percent		96.80	3.20	4.53
		DDUu	*DdUu*	
Observed number	454	11	443	
Observed percent		2.42	97.58	
Theoretical percent		2.97	97.03	0.55
		DDuu	*Dduu*	
Observed number	125	4	121	
Observed percent		3.20	96.80	
Theoretical percent		1.51	98.49	1.69
		DDUU	*DdUU*	
Observed number	148	57	91	
Observed percent		38.51	61.49	
Theoretical percent		37.88	62.12	0.73
		DDuu	*Dduu*	
Observed number	100	34	66	
Observed percent		34.00	66.00	
Theoretical percent		37.88	62.12	3.88

The calculation for the ratio of coupling and repulsion phases was made by the formulae devised in the present experiments. The ratio of the coupling and repulsion phases is independent of the values of z. Therefore, the ratio is the same as in the normal case where the accessory factor is not considered. Among 1964 families, only one repulsion family is to be expected. It is no wonder that no repulsion family appeared among 443 coupling families in the present experiments. The number

Total number of families	Coupling families		Repulsion families
1964	1963	:	1

of families reared is too small to permit a reasonable expectation of the occurrence of the repulsion phase, when there is so small a crossover value as 2.2 percent.

It is interesting, however, to calculate the theoretical number of double recessives in the F_2 generation, in the repulsion phase.

Substituting 0.022 for $(1-x)$, and 0.36 for z, the following theoretical numbers are obtained:

Total No.	D			d		$d\%$	$u\%$
	$(U+Uu)$	:	(u)	$(U+Uu)$	: (u)		
1000	5040		3360	1599	1	16.00	33.61

A considerable excess of glutinous character from the normal Mendelian expectation should be expected in the repulsion family. On the other hand, the percentage of sterile plants will be the same as has been shown in the coupling phase.

Conclusion and Discussion of Related Works

From the data presented in this paper, it is evident that there exists a strong linkage between the factors U and D, the latter of which affects the proportion in which the gametes are presented at fertilization, whatever other effects it may produce. It is more probable that the factor D affects the pollen-grains in a differential manner and does not affect the endosperms. Thus, the number of sterile plants in the segregating families showed a remarkable deficiency from the normal expectation and the segregation of endosperm characters were of two different types, one normal 3 : 1, the other deficient in the percentage of glutinous plants or grains. An excess of glutinous individuals was to be expected in the repulsion phase, but no case of this kind was observed.

It seems that two ways of modification of Mendelian ratio are concerned, namely, by selective fertilization and linkage. In the first, the deviation is always in the same direction from the Mendelian ratio depending upon the amount of disturbing effect of its factor in the gametic generation. This deviation is not changed by the other factor or factors which are linked with the accessory factor. And the deficiency in the zygotic generation caused in this way is always of the same amount, independently of the other factor or factors. In the second, there are three types of segregation, one of which is the normal 3 : 1 and the other

two being higher and lower than the normal expectation, according to the coupling and repulsion phases, respectively.

The deviation of recessive characters depends not alone upon the disturbing effect of the other factor, but upon the amount of the crossover value between the two factors. It was clearly shown in the experimental results that the deviation of the glutinous character is not caused by the factor *U* or *u* but by the factor *d* which is linked with *u*. Therefore, the segregation of endosperm characters in the hybrids in which the factor *d* is not presented, showed the normal segregation, 3 : 1. It was emphasized that as the amount of crossing over and the degree of disturbing effect in the gametic generation cause by the accessory factor or factors might be expected in any degree, the modification of Mendelian ratio should be expected in any degree.

Here we met the foundanental importance of selective fertilization and the linkage on the genetic theories. Suppose, for example, that three factors are concerned in fertilization and that two of these are duplicate factors for one character, and suppose also, that these three factors are linked together to a certain degree, the offspring of such hybrids will not show the normal segregation expected on the basis of the Mendelian ratio for independent traits. Further, it can be supposed that two of more factors might affect the gametic ratio at the time of fertilization just as multiple Mendelian factors may coöperate in a common zygotic expression. It is hardly imaginable how far such factors may modify the Mendelian ratio, and it can be seen that the present case is a rather simple one from the point of view of selective fertilization accompanying linkage.

Before discussing the relevant data, let us consider the relation of gametic lethals or gametic elimination to selective fertilization. According to MORGAN (1919), gametic lethal factors are those that destroy eggs or pollen cells that contain such factors. BELLING (1918) and MOHR (1926) make similar statements, and BELLING emphasizes the gametic sublethal (semi-lethal) beside the gametic lethal. He states that "there may be selective partial elimination of pollen-grains or embryo-sacs by sublethal factors, though this has not yet been proved for any one case."

It will have been noted that in the present experiments, any gametic lethal or elimination has not been observed. Although the pollen-grains might be remain on the styles without the development of pollen-tubes, these pollen-grains appeared completely sound and no one can distinguish two kinds of pollen-grains from the different types of plants *DDUu* and *DdUu*. It is safe to say that these pollen-grains are completely formed and apparently normal in development up to the time of fertilization, but the pollen-tube growth is retarded by the factor *d* in a certain degree thus causing the selective action at the time of fertilization. Of course,

the results obtained are the same as in the case of a gametic semi-lethal.

Therefore, if we assume the retarding of pollen-tube growth by the factor *d* in the present experiment, the gametic lethal defined as an actual elimination of gametes is not necessary for the explanation of selective fertilization. As stated by JONES (1924) it is only a matter of degree between selective elimination of gametes and selective ability to fertilize. From germ cells which are unable to complete development on account of their particular inheritance to those which appear normal but are unable to function perfectly under any circumstance, is only a step. It can hardly doubted that the present case is one of selective fertilization, caused by one or more Mendelian factors, whatever may be the manner of their action.

Several instances have been reported in rice plants where the gametic generation has been disturbed by a certain factor or factors. TERAO (1921) and ISHIKAWA (1927) have found a certain semi-sterile type of rice. The semi-sterile plants, in which about one-half of the spikelets are barren, appeared in certain varieties of rice which had been otherwise constantly fertile. The mode of inheritance of semi-sterility is as follows: each semi-sterile plant segregates into fertiles and semi-steriles, the former breeding true and the latter repeating the same mode of segregation in later generations. The mode of inheritance in this case is the same as that found by BELLING (1914) in the semi-sterility of Stizolobium, although different interpretations are given by these authors. The situation of the present experiments is quite different from their experiments. In their cases the gametic lethal factor affects the endosperm and its action is complete, so that the heterozygous plants show the semi-sterile condition, whereas in the present experiments the action of gametic factor is partial, the fertility of sterile plants quite small, and the action of the gametic factor is supposedly limited to the pollen-grains.

NAGAI (1926, a, b, c, d) in his studies of mutations in rice plants reported several types of sterility and their genetical behaviors. He obtained a marked deficiency or excess of sterile plants in the segregating families and considered that some unknown factors tend to disturb the normal distribution of different kinds of gametes, operating at least in part as the chief causes of deficiency in the zygotic generation. He did not postulated "selective fertilization" as the explanation of his experiments, and stated that "no experimental evidence has yet been obtained to give a definite conclusion." He explained the deficiency of recessive types by the hypothesis offered by TERAO (1917, 1921, 1922), namely, transformability of factors. The numerical relations, however, are different from TERAO's cases and no mosaic form appeared which might be interpreted as due to factor mutations in the somatic cells, nor the

reversion phenomena in the recessive types. From his data it seems that certainly one or two more factors are acting to disturb the gametic ratio, as has been stated by him, and the present author is inclined to assume selective fertilization and linkage between such disturbing factors or other factors rather than a transformation of one factor into another.

Thus, if we postulate the crossover mutation in his case, according to SHULL's (1923) suggestions, it might be possible to solve the problems presented by at least a part of NAGAI's experiments. Of course, the author can hardly analyse NAGAI's data without handling the same materials, because if selective fertilization and linkage be assumed, the expected phenomena in the zygotic generation would be very complex, as stated elsewhere in this paper. Beside the above instances in rice plants, many cases of selective fertilization have been reported in the plant and animal kingdoms and it can hardly be doubted that such a selection of viable gametes in some combinations is a rather general phenomenon, causing deviations from the normal expectation. A fairly complete bibliographic survey is given in the monograph by JONES (1928) and therefore, the author has attempt to review here only a few instances which seem most related to the present experiments.

The first careful studies in which selective fertilization was certainly presented were reported by CORRENS (1917, 1918, 1921, 1922, 1923). He investigated the sex inheritance in the dioecious *Lychnis dioica* L., *Lychnis alba* Nill and *Rumex acetosa* L., where the male plants are interpreted as heterozygous (*Ff*) and produce two types of pollen-grains; male-determining (*f*) and female-determining (*F*). In the F_1 generation of a normal cross (*FF* × *Ff*) CORRENS does not obtained the expected sex ratio 1 *FF*: 1 *Ff*, but a deficiency of male *Ff* was due to slower rate of growth of pollen-tubes carrying the male determiners *f* as compared with those carrying the female determiners *F*. In this case, therefore, it is the pollen with the constitution *F* which is better able than the pollen type *f* to function in the tissue of female plants *FF*.

HERIBERT NILSSON (1920) found an excess of red-nerved plants in the offspring of crosses made with the pollen of a heterozygous red-nerved *Oenothera Lamarckiana* of the constitution *Rr* on either heterozygous red-nerved plants, *Rr*, or homozygous white-nerved plants, *rr*. According to him, a back cross of the type *Rr* × *rr* gives the typical Mendelian segregation, 1 : 1, and the reciprocal cross *rr* × *Rr* showed too large proportion of red-nerved plants. He has investigated the rate of growth of pollen-tubes by cutting off the base of style at certain intervals of time after pollination. And he has observed that the *R*-tubes grow more rapidly than the *r*-tubes, and consequently fertilize a number of eggs before the *r* tubes arrive.

All the red-nerved plants are heterozygous *Rr*. The combination *RR* cannot be produced, consequently a segregation in the ratio $2Rr : 1rr$ is to be expected. However, he obtained too many *Rr* plants. No elimination of *RR* zygotes takes place, but there is a repulsion between the *R*-gametes, " a prohibition" according to him. All the *R* eggs are fertilized by the *r*-pollen. The replacement of the *R* pollen by *r* pollen in fertilization of the *R* eggs receives the name "substitution". In this way a ratio $(2Rr + 1rR)$ to (rr), or 3 : 1, is obtained.

HERIBERT NILSSON (1923) found definitely that the comparative abundance in fertilization of red-nerved *R* gametes over white-nerved *r*, is due to a more rapid rate of pollen-tube growth and the formation of more pollen-tubes than are necessary to fertilize all of the available eggs. Evidence of differential growth-rates was secured from transecting Oenothera styles at intervals of from 20 to 30 hours after pollination. Early-produced capsules gave mainly red-nerved offspring. The cause of non-appearance was rather the non-union of the *R* gametes than the non-viability of *RR* seed, as advanced by RENNER (1922), whose crossing data, when critically examined, indicate a heterozygous condition of the *R* factor, rather than a homozygous condition, which should be postulated if a definite conclusion is to be drawn relative to the non-viability hypothesis.

In 1924 HERIBERT NILSSON reported further complex results of Oenothera crosses. An *Oenothera Lamarckiana* which had colorless leaf-veins was crossed with pollen from *O. biennis* which has a factor for red leaf-veins. In the F_1 337 and in F_2 164, in total, were red-nerved. However, in F_3 and subsequent generations, some white-veined plants appeared, in proportions which did not fit the ratio for normal diploid plants, on the suppositions, (1), that no homozygous red-veined plants ever appear, and (2), that the pollen-grains with the factor for red are of quicker growth. In some of these families of F_3 and later generations, he observed large amounts of segregation, ranging from a remarkable deficiency to a remarkable excess of white-veined plants.

It is interesting that the same situation was found in wheat. NILSSON-EHLE (1921) observed that in the progenies of speltoid heterozygotes, originated through mutation of normal wheat, there are always great numberical aberrations from the ordinary Mendelian segregation (1 normal : 2 heterozygous : 1 mutant) the mutant always being present in too small proportion. Three speltoid series of different behaviors are described and discussed. The working hypothesis suggested is that in the *B* and *C* series, besides elimination of male speltoid gametes, partial heterogamy occurs in which there is differential distribution of the *A* (normal gametes) and an allele (speltoid gametes) according as *A* in the diploid cell as introduced by an ovule (Aa) or by a pollen cell (aA),

as shown by SAUNDERS (1911) in the case of white and cream plastids in Matthiola. Reasons are given for identifying partial heterogamy with partial sex-linkage in wheat.

HALLQUIST (1923) has reported a mutant type of barley showing that defective chlorophyl and dwarfing is dependent upon a simple recessive factor. The percentages of defective, however, were statistically less than expected, and could not be accounted for by differential germination of seed producing normal plants as compared those producing the mutant type. Progeny tests, using the proportion of homozygous normal to heterozygous in a cross of such types, showed that normal segregation occurred in endosperms. But in pollen-grains, evidence seemed to indicate that there was an elimination of some of the pollen-grains which carried the factor for defective chlorophyl.

From the above reported cases, it can be seen that differential activity of gametes causes selective fertilization. In Nicotiana, another case of selection of gametes according to their constitution was published by EAST and MANGELSDORF (1925, 1926). The pollen-grains functioned only on plants which did not contain the same factor as that carried by the pollen-grain. These authors found special sterility factors acting in such a manner that pollen-tubes carrying a factor identical with a factor of the tissue in which they were growing failed normally to fertilize eggs. These sterility factors represented a series of multiple alleles involving three factors S_1, S_2, S_3, etc. For instance, normally in the offspring of a cross of an S_1S_2 plant with an S_1S_3 plant only the S_1S_3 and S_2S_3 combinations appeared, S_1 pollen having failed to function on an S_1S_2 plant. Similarly, in the cross $S_1S_2 \times S_2S_3$ the combination with S_2 pollen was lacking; while in the cross $S_2S_3 \times S_1S_3$ the S_3 pollen was ineffective.

EAST (1919) has demonstrated that in a mixture of compatible and incompatible pollen-grains placed on the stigmas of self-sterile Nicotianas the compatible pollen-grains alone function.

Thus in the above case there is complete selective fertilization in favor of pollen-grains from dissimilar plants. It seems quite likely that factors affecting the rate of pollen-tube growth are not uncommon, resulting in partial or complete selective fertilization.

The instances cited above, treat only the factor or factors which cause the selective fertilization and not the effect on the distribution of another factor or factors which might lie on the same chromosome pair.

Any linkage of viable characters with such pollen-tube growth factors must obviously result in disturbed ratios, the degree of disturbance depending upon the closeness of linkage and the degree of inhibition of pollen-tube growth as already discussed.

Until now two cases have been reported, in which the situation is

similar to that in the present experiments. EMERSON (1924) in his sugar maize experiments, suggested that the differential rate of pollen-tube growth is not due to the *Su*-factor itself but to an accessory factor on the same chromosome. The details have not yet been published, but he has shown that he obtained three types of segregation in the F_3 generation, namely 15, 35 and the normal 25 percent, and the results of the backcrosses are different in both crosses, one showing 50 : 50, another, 70 : 30 (100 : 43). It is interesting that his results are nearly the same as in the present experiments, even in the numerical relation, but he did not show the crossover values or the type of segregation of other factor or factors which might be linked with the factor *Su*.

MANGELSDORF and JONES (1926) have given a detailed discussion of this point and the present results are in harmony with them. They have observed an excess of recessive character (*de*) in the F_2 generation and in the F_3 generation, they have observed three types of segregation, namely six families are high with an average 32.4 percent recessives, four are low with 16.8 percent recessives and eight are normal with 25.2 percent recessives. They explained these aberrant recessive types by assuming that *de* is linked with a factor *Ga*, which has its expression in the gametophyte generation, stimulating the rate of pollen-tube growth. Such linkage will show, in the coupling phase, an excess of recessives; in the repulsion phase, a deficiency. The same hypothesis was applied in the case of crosses in the sugary Rice pop corn (JONES 1924), where the deficiency of sugary character was 16.2 percent in the F_2 generation. Furthermore, they analyzed KEMPTON's data (1919) and COULTER's data (1925) from the same point of view and suggested that in both cases the presence of a gametophyte factor caused the modified Mendelian ratio.

Comparing their results in maize with the present experiments in rice plants, it would be seen the situation is quite the same. Their hypothetical factor (*Ga*) corresponds to the factor *D* in the present experiments. However, the amount of disturbing effect on the pollen-tube growth and the crossing over values are different in the each case. They assumed that the gametes bearing factor *Ga* accomplish fertilization 4.1 times as frequently as the gametes bearing *ga* and the crossing over values between the factor *Ga* and *de* is 24.3 percent and between *Ga* and *su* is 21.2 percent. In the present case, it was assumed that the factor *D* accomplishes fertilization only 1.5 times as frequently as the gametes bearing *d* and the crossing over value between the factor *D* and *U* is quite small, namely only 2.2 percent. The most striking contrast is that they did not observed any zygotic expression of the factor (*ga*), while in the present experiments, it was observed that there is a remarkable effect of the factor *d* on the zygotic generation causing remarkable weakness

and sterility. In other words, the factor *d* which affects the gametic generation is the same factor which affects the zygotic generation. On this point, the present results harmonize with CORRENS's dioecious plants, HERIBERT NILSSON's Oenothera or EAST's Nicotiana cases where the factor or the factors affecting the pollen-tube growth also affect the expressions of the zygotic generation.

BRINK (1927) referring to MANGELSDORF and JONES's (1926) results, stated that "it is only the circumstance that the waxy gene occupies a locus in chromosome 1, adjacent to a particular factor affecting pollen-tube growth, that is responsible for the frequently observed irregular ratios." However, there is no reason to suppose that the gametophyte factor or factors must express their effects in the zygotic generation.

Finally, reference will be made to Nicotiana cases published by BRIEGER and MANGELSDORF (1926). As stated in the beginning of this section, the situation of Nicotiana is apparently different from the other cases because the pollen-tube growth is so strongly inhibited that it results in the total absence of one segregated class. BRIEGER and MANGELSDORF have observed a linkage between self-sterility factors S_1, S_2, S_3, discussed above, and certain flower color factors in Nicotiana crosses. They made crossing experiments by using three kinds of self-sterile strains, consisting of S_1S_3, S_2S_3 and S_1S_2, respectively, and having flower color factors *Cc* and *Ii*. The homozygous recessive whites (*C*) were used as male parents, that is, when *C* and *c* ovules were fertilized by *c* pollen, the resulting progenies showed white and colored plants in equal numbers. In the reciprocal crosses where the white plants (*cc*) were used as female parents and the heterozygous colored plants (*Cc*) were used as male parents, the proportion of colored to white in the progenies showed quite different results, whereas crosses involving the ivory color (*ii*) gave nearly the same results in both reciprocal crosses. These differences in reciprocal crosses in respect of the basic color factor *Cc* and sterility factors S_1, S_2, S_3 are explained by assuming linkage between the factors *C* and S_1, S_2, S_3 with a crossover value of approximately 18 percent.

The experimental results show the promising importance on this line of study for the sterility problems.

Summary

1. Among one of several families segregating for starchy (*U*) and glutinous character (*u*) in the F_3 generation of hybrids between a starchy and a glutionus variety of rice, several sterile plants appeared, which were supposed to be the result of a gene mutation in the previous gene-

ration; the factors *D* and *d* are responsible for the external form of fertility and of sterility, respectively.

2. After pedigree tests of a considerable number of families in the following four generations it was assumed that the factor *D* lies on the same pair of homologous chromosomes in which the factor *U* is found. The crossover percentage between them was assumed to be approximately 2.2 percent.

3. The ratio of sterile plants in the segregating families was rationally corrected by using the data from the corresponding endosperm generation. However, the corrected sterile percentages in the progenies of heterozygous (*Dd*) showed definitely less than might be expected on the basis of Mendelian monohybrid expectation, namely 16.02 percent in the progenies of *DdUu*-type and 16.42 percent in the progenies of *Dd*-type. Further it was observed that the homozygous double dominants (*DD*) are in excess and the heterozygotes (*Dd*) are slightly less than might be expected on the basis of the normal ratio 1 : 2.

4. Concerning the endosperm characters, again, a marked deficiency of glutinous individuals was obtained in the progenies of *DdUu* type; the total number of plants oberved was 64,383, of which only 16.71 percent were glutinous plants (as determined by observations on the endosperm generation). It is suggested that an excess of glutinous individuals (theoretically 33.61 percent) should be expected in the repulsion phase.

5. A considerable number of endosperms were inspected in the control experiments and it was confirmed that the endosperm character of heterozygous rice plants segregates in the typical monohybrid Mendelian ratio, 3 : 1.

The results obtained by several investigators are summarized and compared with the present experimental results. There is a slight deficiency in the results obtained in the plant generations but the endosperm generations show the percentage of glutinous nearly 25 percent (observed 24.60 percent).

6. In order to discover the causes of the deficiency of sterile plants and of glutinous individuals in the progenies of heterozygotes, inspection of fertility in various types of plants has been made. The types of *DDUU*, *DDUu* and *DdUu* were found to exhibit nearly the same degree of fertility and the number of spikelets per ear in the above three types of plants were likewise nearly the same. On the other hand, the fertility of *ddUU*, *ddUu* and *dduu* type plants averaged only 17.00 percent, and the number of spikelets was only about half as great as the number on fertile type plants.

7. The observation of germinating power of different types of seeds (*DDUU*, *DdUU*, *DDUu*, and *DdUu*) in the seed-beds of the F_4 generation showed no selective elimination.

8. Pollen-grains from the *DdUu*-type plants were examined microscopically and it was found that there is no pollen abortion in the fertile type of plants, all pollen-grains being quite normal and sound.

After treatment with an iodin solution, the number of starchy and glutionus pollen-grains were found to be of nearly equal numbers, 1 : 1 which would be expected on the basis of Mendelian segregation.

9. From the results of pedigree cultures and the observation of pollen-grains, germinating power and fertility, it was suspected that the factor *d* causes a disturbance of the gametic ratio at the time of fertilization. And if it be supposed that the factor *d* disturbs the pollen-grains only partially, the theoretical numbers agree closely with the observed facts.

10. It is assumed that the male gametes bearing the factor *D* accomplish fertilization 1.5 times as frequently as *d* bearing gametes, the proportion at the time of fertilization being 100 *D* : 64 *d*.

11. It is emphasized that if the effect of a genetic factor in the gametes and the amount of crossing over are variable in any case, various forms of modified Mendelian ratios will be expected.

12. A few reported results of other investigators are reviewed from the standpoint of selective fertilization and linkage.

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Appendix

TABLE 7, a.

DU : *DUu* : *Du* segregation in 7 families.

Family No.	Total	*D*			*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*		
4-14	185	47	94	44	23.78	25.00
17- 6	189	44	93	52	27.51	21.93
17-71	181	51	93	37	20.44	17.02
22- 2	257	75	125	57	22.18	32.29
52-19	195	46	100	49	25.13	28.91
52-29	194	64	98	32	16.49	25.00
66- 9	190	37	118	35	18.42	14.81
Total	1391	364	721	306	22.35	23.34

TABLE 7, b.

DdUu segregation in 274 families.

Family No.	Total	*D*			*d*			*d*%	*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*			
4- 1	191	84	88	4	0	0	15	7.85	9.95	15.66
4- 2	194	70	88	2	0	0	34	17.53	18.56	13.82
4- 4	191	65	104	2	1	0	19	10.47	10.99	18.05
4- 5	193	80	91	0	0	0	22	11.40	11.40	22.54
4- 7	193	66	90	2	0	0	35	18.14	19.17	17.31
4- 9	258	120	108	3	0	0	27	10.17	11.63	14.78
4-13	192	64	91	2	0	0	35	18.23	19.27	16.78
4-18	192	72	92	2	0	0	26	13.54	14.58	14.93
5- 3	200	64	108	0	0	0	28	14.00	14.00	17.93
5- 6	200	88	85	3	1	0	23	12.00	13.00	17.50
5- 7	185	60	91	1	2	1	30	17.84	16.76	9.83
5-13	170	66	84	2	0	1	17	10.59	11.18	20.00
5-14	189	66	84	2	0	0	37	19.58	20.63	11.05
5-16	188	88	80	1	0	0	19	10.11	10.64	13.04
5-17	197	91	81	2	0	0	23	11.68	12.69	14.40
5-18	176	74	75	0	1	0	26	15.34	14.77	13.59
5-20	189	82	93	0	0	0	14	7.45	7.45	13.94
5-21	188	84	75	2	0	0	27	14.36	15.43	10.10
5-25	187	77	88	0	0	0	22	11.76	11.76	19.40
5-26	195	72	104	1	0	2	16	9.23	8.72	17.29
5-27	195	80	88	0	0	0	27	13.85	13.85	20.18
5-32	183	90	67	0	1	0	25	14.21	13.66	8.33
5-33	193	75	96	2	0	0	20	10.36	11.40	20.80
5-34	194	91	86	1	0	0	16	8.25	8.76	10.92
5-36	191	78	85	1	0	0	27	14.14	14.66	9.66
5-37	192	100	75	2	0	0	15	7.81	8.85	18.65
5-41	195	85	80	1	1	0	28	14.87	15.38	14.03
5-43	192	75	100	0	0	0	17	8.85	8.85	18.35
5-44	198	100	78	2	0	0	18	9.09	10.10	18.23

TABLE 7, b (*continued*)

Family No.	Total	*D*			*d*			*d*%	*u*%	F_4-seeds (*u*%)
		U	*Uu*	*u*	*U*	*Uu*	*u*			
5–45	184	70	85	3	0	0	26	14.13	15.76	20.84
5–46	175	76	83	2	0	0	14	8.00	9.14	19.28
5–47	186	78	85	0	0	2	21	12.37	11.29	15.07
6– 1	189	79	82	4	0	1	23	12.70	14.29	18.85
6–10	126	41	69	0	0	0	16	12.70	12.70	14.17
6–17	179	71	77	5	0	2	24	14.53	16.20	19.69
6–18	183	73	90	0	1	0	19	10.93	10.38	13.21
6–21	124	40	66	1	1	0	16	13.71	13.71	20.33
10– 1	193	94	75	3	0	0	21	10.88	12.44	15.66
10– 3	199	75	100	2	0	0	22	11.06	12.06	11.54
10– 8	188	101	63	1	0	0	23	12.23	12.77	18.52
10–11	139	70	55	0	0	0	14	10.07	10.07	9.09
10–18	195	104	66	0	0	0	25	12.82	12.82	10.96
10–20	172	79	66	3	0	0	24	13.95	15.70	17.19
10–27	140	46	68	0	2	0	24	18.57	17.14	14.66
10–31	128	42	61	2	0	0	23	17.97	19.53	15.07
10–37	230	130	60	2	0	0	38	16.52	17.39	16.34
10–45	195	73	98	0	0	0	24	12.31	12.31	15.65
10–46	194	77	94	2	0	0	21	10.82	11.86	11.11
10–47	194	70	102	1	0	0	21	10.82	11.34	20.25
10–50	196	70	102	0	0	0	24	13.47	13.47	14.18
10–55	193	85	86	1	0	0	21	10.88	11.40	12.04
10–58	194	68	93	3	0	0	30	15.46	17.01	11.59
10–62	154	66	75	1	0	0	12	7.79	8.44	20.37
10–76	158	62	70	0	0	1	25	16.46	15.82	10.38
17– 1	196	76	94	4	0	0	22	11.22	12.24	20.51
17– 3	190	78	88	2	0	0	22	11.58	12.63	12.50
17– 7	180	66	81	1	0	1	31	17.78	17.78	18.92
17– 9	187	60	98	2	0	0	27	14.44	15.51	13.56
17–10	169	64	81	0	0	0	24	14.20	14.20	16.03
17–13	187	67	89	2	0	1	28	15.51	16.04	16.50
17–14	115	49	50	0	0	0	16	13.91	13.91	21.05
17–15	238	130	89	1	0	0	18	7.56	7.98	16.95
17–17	193	71	91	1	0	0	30	15.54	16.06	20.98
17–18	155	56	73	1	0	0	25	16.13	16.77	15.13
17–21	184	73	90	2	0	0	19	10.33	11.41	19.27
17–23	184	61	97	1	0	0	25	13.59	14.13	21.99
17–24	190	62	100	2	0	0	26	13.68	14.74	18.17
17–27	195	75	100	1	0	0	19	9.74	10.26	15.38
17–30	190	68	97	1	0	0	24	12.63	13.16	18.97
17–37	159	49	80	3	0	0	27	16.98	18.87	12.10
17–32	188	68	91	2	0	0	27	14.36	15.43	20.88
17–39	186	73	94	0	0	0	19	10.22	10.22	18.48
17–40	169	77	65	2	0	0	25	14.79	15.98	13.68
17–41	191	61	101	2	0	0	27	14.14	15.18	19.11
17–43	181	70	88	1	0	0	22	12.15	12.71	17.27
17–44	165	58	75	2	1	0	29	18.18	18.79	16.53
17–45	240	97	115	0	0	0	28	11.67	11.67	20.00
17–49	140	56	68	0	0	0	16	12.90	12.90	14.73
17–54	239	76	115	3	0	0	45	18.83	20.08	15.24
17–56	175	68	85	0	1	0	21	12.57	12.00	11.30
17–58	167	64	87	1	0	0	15	8.98	9.58	14.52
17–59	178	67	85	2	0	2	22	13.48	13.48	22.33
17–61	185	68	92	1	0	0	24	12.97	13.51	24.78
17–62	190	90	79	1	0	0	20	10.53	11.05	22.11
17–63	178	61	90	1	0	0	26	14.61	15.17	14.74
17–65	178	60	97	2	0	0	19	10.67	11.80	20.31

TABLE 7, b (*continued*)

Family No.	Total	D			d			d%	u%	F_1-seeds (u%)
		U	Uu	u	U	Uu	u			
17-66	171	59	80	3	0	0	29	16.96	18.71	20.86
17-69	184	71	81	2	0	0	30	16.30	17.39	14.29
17-72	182	79	90	2	0	0	11	6.04	7.14	24.82
17-75	178	76	83	1	0	0	18	10.11	10.67	18.31
17-77	181	62	92	2	0	1	24	13.81	14.36	15.00
17-79	183	70	90	0	0	0	23	12.57	12.57	18.71
17-81	173	55	93	0	0	0	25	14.45	14.45	17.82
17-84	191	72	97	2	0	0	20	10.47	11.52	20.83
17-85	189	67	98	3	1	1	19	11.11	11.64	19.32
17-86	183	70	80	1	0	0	32	17.48	18.03	13.33
17-87	183	61	93	2	0	1	26	14.75	15.30	17.39
22- 1	298	132	132	2	0	0	32	10.74	11.41	20.00
22- 3	190	73	92	2	0	0	23	12.10	13.16	17.30
22-12	176	38	106	7	1	0	24	14.02	17.61	26.19
22-13	199	57	106	0	1	0	36	18.59	18.09	14.63
22-15	195	60	104	1	2	2	26	15.38	13.85	17.78
22-16	188	67	97	3	0	0	21	11.17	12.77	22.82
22-19	193	68	91	3	1	0	30	16.06	17.10	18.82
22-20	186	61	100	1	1	4	19	12.90	10.75	20.00
49- 1	168	56	86	2	0	0	32	10.74	11.41	20.00
49- 2	177	60	89	1	0	1	26	15.25	15.25	14.95
49- 3	175	61	92	0	0	0	22	12.57	12.57	21.93
49- 4	183	55	100	0	0	0	28	15.30	15.30	14.28
49- 6	184	55	102	2	0	0	25	13.59	14.67	26.19
49- 7	95	34	43	1	0	0	17	17.89	18.95	13.83
49- 8	221	80	108	1	1	0	31	14.48	14.48	19.41
49-11	242	89	121	0	0	0	32	13.22	13.22	19.47
49-12	179	55	94	3	1	0	26	15.08	16.20	14.71
49-13	181	70	80	4	0	2	25	14.02	16.02	16.67
49-19	180	57	95	2	0	0	26	14.44	15.56	22.62
49-20	184	56	95	2	0	0	31	16.85	17.98	13.98
49-21	180	67	95	1	0	1	16	9.44	9.44	22.22
49-22	187	67	94	1	0	0	25	13.37	13.90	10.49
49-24	181	57	97	0	0	0	27	14.02	14.02	12.50
49-31	181	64	95	1	1	0	20	11.60	11.60	17.10
49-32	167	45	95	1	0	0	26	15.57	16.17	22.76
52- 4	200	76	99	1	1	0	23	12.00	12.00	14.18
52- 5	199	75	98	1	0	1	24	12.56	12.56	12.37
52- 6	192	81	89	4	0	0	18	9.37	11.46	12.50
52- 7	196	68	98	1	0	0	29	14.80	15.31	15.79
52- 8	197	67	103	1	2	0	24	13.20	12.69	14.60
52-18	196	80	95	0	0	0	21	10.71	10.71	12.27
52-20	197	72	97	0	1	0	27	14.21	13.71	13.53
52-21	172	71	79	1	1	0	20	12.21	12.21	12.40
52-22	179	60	90	2	0	0	27	15.08	16.20	15.00
52-25	195	70	99	2	0	2	22	12.31	12.31	27.34
52-26	185	70	79	3	0	0	33	17.84	19.46	16.81
52-27	199	89	86	2	0	1	21	11.06	11.56	17.69
52-28	197	85	79	2	1	0	30	15.74	16.24	14.29
52-30	197	81	85	1	0	0	30	15.46	15.98	21.74
52-34	198	87	84	2	2	1	22	12.63	12.12	13.59
52-35	194	95	73	2	0	0	24	12.37	13.40	17.39
52-36	197	80	77	1	0	0	39	19.80	20.30	20.41
52-38	169	62	78	4	0	1	24	14.79	16.57	20.43
52-39	194	60	103	1	0	0	30	15.46	15.98	15.89
52-40	193	78	87	1	0	0	27	13.99	14.51	18.18
52-42	194	81	90	2	1	0	20	10.82	11.34	16.67

TABLE 7, b (*continued*)

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
53- 6	190	75	89	1	1	0	24	13.16	13.16	10.77
53- 7	191	62	96	1	0	0	32	16.75	17.28	30.10
53-14	189	73	83	1	0	0	32	16.93	17.46	24.73
53-17	139	50	63	1	3	2	20	17.99	15.11	23.40
53-20	177	63	89	1	0	2	22	13.56	12.99	12.13
53-22	181	52	97	0	0	0	32	17.68	17.68	23.21
55- 7	175	63	85	2	0	0	25	14.29	15.43	21.09
55- 8	182	63	88	0	0	0	31	17.03	17.03	15.96
55- 9	178	76	79	3	0	0	20	11.24	12.92	19.99
55-10	174	75	77	1	1	0	20	12.07	12.07	18.36
55-17	179	71	78	0	0	0	30	16.76	16.76	25.64
55-19	177	63	78	5	0	1	30	17.51	19.77	17.89
55 20	179	80	82	1	1	0	15	8.94	8.94	26.19
55-24	175	62	97	2	0	0	14	8.00	9.14	27.45
55-27	182	72	92	1	0	0	17	9.34	9.88	17.12
64- 1	198	66	103	2	0	4	27	15.66	14.39	18.39
64- 2	195	63	98	2	0	0	32	16.41	17.44	19.80
64- 3	192	60	98	1	1	1	31	17.19	16.67	20.00
64- 4	191	52	108	0	0	1	30	16.23	15.71	22.14
64- 5	192	65	97	0	0	0	30	15.71	15.71	17.07
64- 8	187	66	97	0	0	1	23	12.83	12 30	15.86
64- 9	195	75	91	3	0	0	26	13.33	14.87	18.18
64-14	194	63	94	5	0	0	32	16.49	19.07	19.69
64-19	192	67	105	0	0	1	19	10.42	9.90	20.80
64-20	197	65	102	2	1	0	27	14.21	14.72	16.09
66- 2	175	64	82	0	0	0	29	16.57	16.57	16.92
66- 5	190	60	91	2	0	0	37	14.21	15.26	16.00
66-10	192	60	108	2	0	0	22	11.46	12.50	16.17
66-13	191	73	87	4	0	0	27	14.14	16.23	12.60
66-14	189	65	93	2	1	0	28	15.34	15.87	19.13
66-15	243	95	117	3	0	0	28	11 52	12.76	15.90
66-19	166	90	64	2	0	0	10	6.02	7.23	16.83
66-20	180	69	85	0	1	0	25	14.44	13.89	21.65
66-24	252	89	130	0	1	0	32	13.10	12.70	18.18
66-30	305	109	155	7	0	1	33	11.15	13.11	20.00
66-31	244	104	114	5	2	0	19	8.61	9.84	20.80
66-42	160	79	60	2	0	0	19	11.87	13.12	17.52
66-43	179	63	85	2	0	0	29	16.20	17.32	12.85
66-48	181	59	90	3	0	1	28	16.02	17.13	15.03
66-49	175	68	81	2	0	1	23	13.71	14.29	22.02
66-51	174	63	78	1	1	0	31	18.39	19.39	19.54
66-52	180	67	91	4	1	1	16	10.00	11.11	15.56
67- 3	189	79	94	0	0	0	16	8.47	8.47	15.27
67- 4	208	87	105	2	0	1	13	5.73	7.21	20.72
67- 9	182	75	90	0	1	0	16	9.34	8.79	22.58
67-11	186	81	72	3	0	0	30	15.31	16.84	14.85
67-12	182	62	85	3	0	2	30	17.58	18.13	16.88
86- 7	188	66	89	2	0	2	29	15.49	15.49	14.63
86- 8	194	71	84	3	0	0	36	18.56	20.10	20.69
86-11	188	75	77	3	0	0	33	17.55	19.15	15.00
86-17	192	76	84	1	0	0	31	16.15	16.67	22.12
86-19	188	65	90	4	0	0	29	15.43	17.55	10.00
86-22	197	66	100	4	1	0	26	13.71	15.23	11.83
86-25	265	104	129	2	0	0	30	11.71	12.07	13 91
86-26	196	67	107	1	0	0	21	10.71	11.22	12.38
86-31	190	64	93	1	0	0	32	16 84	17.37	17.65
86-32	198	89	82	0	0	0	27	13.64	13.64	22.83

TABLE 7, b (*continued*)

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
86-35	194	77	81	2	1	1	32	17.53	17.53	15.69
86-36	200	67	100	2	0	1	29	15.50	15.50	14.04
86-37	192	70	90	2	0	0	30	15.62	16.67	24.42
86-40	196	70	98	1	0	0	27	13.78	14.29	16.03
86-41	200	83	87	7	0	0	23	11.50	15.00	16.15
86-43	192	66	90	4	0	0	32	16.67	18.75	22.58
88- 2	197	81	83	2	0	0	31	15.74	16.75	15.96
88- 4	197	88	78	1	0	0	30	15.23	15.74	17.97
88- 6	198	91	73	5	0	0	24	12.12	14.65	11.54
88-10	199	78	93	1	0	0	27	13.57	14.07	6.82
88-11	184	62	87	3	11	1	20	17.39	12.50	16.66
88-12	193	80	88	3	0	0	22	11.40	12.95	15.93
88-18	186	79	81	3	0	1	22	12.87	13.44	13.56
92- 6	185	77	82	0	1	0	25	14.05	13.51	14.78
92-12	191	84	91	1	0	1	14	7.85	7.85	20.93
92-15	195	91	86	2	0	2	14	8.21	8.21	12.00
92-16	189	78	85	2	2	0	22	12.70	12.70	19.72
92-17	185	70	92	1	0	0	22	11.89	12.43	14.29
92-20	181	65	90	3	0	0	23	12.71	14.36	21.71
92-24	195	72	88	2	0	2	31	16.92	16.92	20.80
97- 1	160	72	74	0	0	0	14	8.75	8.75	15.52
97- 8	169	90	60	0	1	1	17	11.24	10.65	20.63
97- 9	254	113	115	0	1	0	25	10.24	9.84	18.80
97-10	176	75	85	1	0	1	14	8.52	8.52	13.14
97-13	188	88	78	1	0	0	21	11.17	11.70	18.52
97-14	189	74	88	2	0	0	25	13.23	14.29	14.29
97-15	188	91	68	0	0	0	29	15.43	15.43	25.61
97-19	188	73	90	0	0	0	25	13.30	13.30	21.85
97-20	188	84	86	1	0	0	17	9.04	9.57	15.52
97-21	172	82	64	4	0	0	22	12.79	15.12	16.81
97-23	181	78	80	0	0	0	23	12.71	12.71	16.89
97-26	194	73	95	1	0	0	25	12.89	13.40	15.60
101- 3	184	61	91	0	0	0	32	17.39	17.39	12.24
101- 4	181	76	80	5	0	0	20	11.05	13.81	20.31
101- 5	153	55	71	0	0	0	27	17.65	17.65	18.79
101- 9	178	58	85	1	2	0	32	19.10	18.54	16.22
101-10	186	79	82	1	0	0	24	12.90	13.44	10.67
101-11	169	65	87	0	0	1	16	10.06	9.47	14.93
101-12	181	69	90	1	0	0	21	11.60	12.15	20.71
101-16	177	60	85	2	0	0	30	16.95	18.08	20.00
101-17	192	75	79	4	0	0	34	17.71	19.79	31.25
101-18	185	55	97	1	0	0	32	17.30	17.84	15.89
101-19	178	73	82	2	0	0	21	11.80	12.92	11.50
101-20	177	50	100	2	1	0	24	14.12	14.69	18.75
101-23	178	80	75	4	0	0	19	10.67	12.92	14.86
101-24	180	75	77	2	0	1	25	14.44	15.00	21.74
101-28	188	82	85	0	0	0	21	11.17	11.17	25.56
101-33	172	76	76	2	1	0	17	10.47	11.05	11.21
101-34	164	64	80	2	1	1	16	10.98	10.98	17.91
101-35	178	59	95	0	1	0	23	13.48	12.92	19.88
101-40	182	70	80	1	0	2	29	17.03	16.48	17.02
101-41	169	64	78	0	0	0	27	15.98	15.98	24.66
101-42	181	60	83	1	0	1	36	20.44	30.44	19.40
102- 4	186	60	82	1	0	0	43	23.12	23.66	13.44
102- 8	191	68	87	2	1	0	33	17.80	18.32	18.71
102- 9	106	33	45	7	0	0	21	19.81	26.43	16.03
102-10	196	52	93	2	3	0	46	25.00	24.49	17.11

TABLE 7, b (*continued*)

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
104- 3	193	66	98	1	0	0	28	14.51	15.03	15.46
104- 5	191	69	93	0	0	0	29	15.18	15.18	23.75
104- 7	194	68	101	1	0	1	23	12.37	12.37	16.55
104- 8	191	70	95	1	0	0	25	13 09	13.61	13.42
104- 9	175	63	86	1	0	2	23	14.29	13.71	26.27
104-10	317	97	173	1	0	0	46	14.51	14.83	16.67
113- 2	174	52	92	1	0	1	28	16.67	16.67	17.56
113- 3	179	44	100	2	0	1	31	17.82	18.44	18.49
113- 4	181	57	92	3	0	0	29	16.02	17.68	14.29
113- 8	184	68	99	2	0	0	15	8.15	9.24	21.87
113- 9	180	58	88	2	1	0	31	17.71	18.33	15.97
113-10	177	57	98	1	0	2	19	11.86	11.30	20.20
113-11	172	53	87	2	1	0	29	17.44	18.02	20.39
113-12	173	56	86	3	0	0	28	16.18	17.92	22.78
113-14	184	59	95	1	0	2	27	15.76	15.22	19.58
113-16	174	62	85	0	0	0	27	15.52	15.52	17.96
113-17	238	76	125	1	0	0	36	15.13	15.55	27.17
Total	**51304**	**19538**	**24352**	**411**	**78**	**82**	**6813**	**13.59**	**14.14**	**17.43**

TABLE 13, b.

(*DdUu*) segregation in 115 families.

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
5-26- 1	106	44	49	3	0	0	10	9.43	12.26	19.67
5-26- 2	97	35	54	0	0	0	8	8.25	8.25	18.02
5-26- 3	111	48	54	0	1	0	8	8.11	7.21	19.85
5-26- 4	118	80	30	0	1	0	7	6.78	5.93	16.13
5-26- 5	107	33	61	4	0	0	9	8.41	12.15	22.22
5-26- 6	117	46	54	1	1	0	15	13.68	13.68	15.05
5-26- 7	84	33	36	3	0	0	12	14.29	17.86	18.00
5-26- 8	103	41	52	3	0	0	7	6.80	9.71	21.92
5-26- 9	101	41	52	0	0	0	8	7.92	7.92	18.18
5-26-10	125	48	58	2	0	0	17	13.60	15.20	9.47
5-26-11	88	34	38	1	0	0	15	17.05	18.18	20.00
5-26-12	93	33	45	2	0	0	13	13.98	16.13	9.72
5-26-13	62	19	37	0	0	0	6	9.68	9.68	12.06
5-26-14	102	32	54	0	0	1	15	15.69	14.71	18.82
5-26-15	108	42	54	1	0	0	11	10.10	11.11	21.28
5-26-16	103	33	59	0	0	0	11	10.68	10.68	22.33
5-26-17	110	46	50	1	0	0	13	11.82	12 73	16.67
5-26-18	108	40	60	2	0	0	6	5.56	7.41	14.55
5-26-19	115	50	51	2	0	0	12	10.43	12.17	17.39
5-26-20	84	28	45	2	0	0	9	7.14	13.10	19.00
5-26-21	107	37	53	2	0	0	15	14.02	15.89	16.67
5-26-22	96	33	52	3	0	0	8	8.33	11.46	19.69
5-26-23	111	45	54	1	0	0	11	9.91	10.81	21.18
5-26-24	107	44	48	3	0	1	11	12.15	13.08	18.80
5-26-25	100	31	57	0	0	0	12	12.00	12.00	19.28
5-26-26	103	37	57	1	0	0	8	7.77	8.84	20.21

TABLE 13, b (*continued*)

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
5-26-27	96	26	59	2	1	0	8	9.38	10.42	20.49
5-26-28	125	34	80	0	0	0	11	8.80	8.80	18.28
5-26-29	58	10	38	1	0	0	9	15.52	17.24	22.06
5-26-30	114	44	57	1	0	0	12	10.53	11.40	13.51
5-26-31	96	37	42	1	0	0	16	16.67	17.71	17.20
5-26-32	117	48	59	1	0	0	9	7.69	8.55	14.87
5-26-33	128	54	57	3	0	0	14	10.94	13.28	14.78
5-26-34	63	27	29	1	0	0	6	9.51	11.11	21.43
5-26-35	95	33	49	0	0	0	13	13.68	13.68	17.39
5-26-36	67	27	26	1	0	0	13	19.40	20.90	21.28
5-26-37	110	40	56	1	0	0	13	11.82	12.73	18.81
5-26-38	111	44	54	5	0	2	6	7.21	9.91	21.74
5-26-39	115	41	60	4	0	0	10	8.70	12.17	19.59
5-26-40	106	36	56	1	0	0	13	12.26	13.21	19.15
5-26-41	131	49	73	0	0	0	9	6.87	6.87	11.34
5-26-42	62	27	25	1	0	0	9	14.52	16.13	20.00
5-26-43	99	39	55	2	0	0	3	3.03	5.05	22.61
5-26-44	47	24	18	0	0	0	5	10.64	10.64	18.28
5-26-45	116	48	60	1	0	0	7	6.03	6.90	16.25
5-26-46	119	44	65	2	0	0	8	6.72	8.40	19.35
5-26-47	65	21	39	1	0	0	4	6.15	7.69	12.86
5-26-48	57	22	22	1	0	0	12	21.05	22.81	20.39
5-26-49	121	52	52	2	0	0	15	12.40	14.05	19.44
5-26-50	108	85	20	0	0	0	3	2.91	2.91	20.99
5-26-51	112	44	58	3	0	0	7	6.25	9.93	20·83
5-26-52	110	40	53	2	0	0	15	13.64	15.45	22.89
5-26-53	110	41	53	2	0	0	14	12.73	14.55	20.00
5-26-54	106	37	55	3	1	0	10	9.43	12.26	18.42
5-26-55	100	32	48	0	1	0	19	20.00	19.00	21.18
5-26-56	127	54	52	2	0	1	18	14.96	15.75	19.59
5-26-57	106	48	43	1	0	1	13	13.21	13.21	19.63
5-26-58	113	38	61	2	0	1	11	10.62	11.50	16.04
67- 3- 1	128	32	80	5	0	0	11	8.59	12.56	19.05
67- 3- 2	82	37	36	2	0	1	6	8.54	9.76	20.00
67- 3- 3	115	42	61	3	0	1	8	7.83	9.59	13.82
67- 3- 4	111	40	57	3	0	0	11	9.93	12.61	22.99
67- 3- 5	119	42	66	3	0	0	8	6.72	9 24	20.19
67- 3- 6	112	45	54	2	0	0	11	9.82	11.61	15.65
67- 3- 7	77	16	49	2	0	0	10	12.99	15.58	19.35
67- 3- 8	108	36	55	6	0	0	11	10.19	15.74	18.89
67- 3- 9	60	25	29	1	0	0	5	8.33	10.00	14.67
67- 3-10	117	50	56	0	0	0	11	9.41	9.41	14.93
67- 3-11	67	32	28	0	0	0	7	10.45	10.45	17.24
67- 3-12	119	44	64	2	0	0	9	7.56	9.24	17.65
67- 3-13	114	41	63	1	0	1	8	7.89	7.89	16.48
67- 3-14	118	44	60	0	0	0	14	11.87	11.87	10.21
67- 3-15	117	58	53	1	0	1	4	4.17	4.17	16.67
67- 3-16	120	55	58	2	0	0	5	4.17	5.83	15.22
67- 3-17	121	56	49	4	0	0	12	9.92	13.22	14.41
67- 3-19	120	69	42	1	0	0	8	6.67	7.50	13.86
67- 3-20	123	56	55	1	1	0	10	8.94	8.94	13.08
67- 3-21	119	50	56	1	0	0	12	10.08	10.92	23.81
67- 3-22	115	50	46	1	0	1	17	15.65	15.65	20.93
67- 3-23	121	40	61	5	0	0	15	12.40	16.53	22.81
67- 3-24	121	44	64	4	0	0	9	7.44	10.74	21.74
67- 3-25	88	30	41	3	0	0	14	15.91	19.32	20.41
67- 3-26	83	34	35	4	0	0	10	12.05	16.87	14.89

TABLE 13, b (*continued*)

Family No.	Total	D			d			d%	u%	F_4-seeds (u%)
		U	Uu	u	U	Uu	u			
67- 3-27	76	30	38	1	0	0	7	9.21	10.53	20.00
67- 3-28	119	50	50	1	0	0	18	15.13	15.27	22.89
67- 3-29	121	82	29	1	1	0	8	7.44	7.44	16.50
67- 3-30	114	52	53	3	0	0	6	5.26	7.89	14.96
67- 3-31	119	52	56	0	1	1	9	9.24	7.56	14.77
67- 3-32	116	40	60	0	0	0	16	13.79	13.79	18.52
67- 3-33	118	57	47	4	0	0	10	8.47	11.86	20.83
67- 3-34	93	40	43	0	0	0	10	10.75	10.75	20.79
67- 3-35	118	38	64	1	0	0	15	12.71	13.56	16.67
67- 3-36	114	43	57	4	0	0	10	8.77	12.28	24.21
67- 3-37	54	18	27	1	0	0	8	14.81	16.67	17.48
67- 3-38	108	33	63	0	0	0	12	11.11	11.11	10.75
67- 3-39	120	43	53	4	0	0	20	16.67	20.00	21.59
67- 3-40	124	44	64	3	1	0	12	10.48	12.10	17.65
67- 3-41	119	45	61	3	0	0	10	8.40	10.92	26.53
67- 3-42	87	44	32	1	0	0	10	11.49	12.64	18.37
67- 3-43	118	69	41	0	0	0	8	6.78	6.78	17.81
67- 3-44	112	42	58	1	0	0	11	9.82	10.71	16.00
67- 3-45	60	20	25	1	0	0	14	23.33	26.00	22.80
67- 3-46	54	22	24	1	0	0	7	12.96	14.81	19.78
67- 3-47	110	40	63	1	0	1	5	5.45	5.45	19.54
67- 3-48	107	40	52	0	1	0	14	14.02	13.08	17.35
67- 3-49	120	54	54	1	0	0	11	9.17	10.00	12.62
67- 3-50	65	27	32	2	0	0	4	6.15	9.23	20.51
67- 3-51	120	37	67	3	0	0	13	10.83	13.33	21.36
67- 3-52	116	46	54	3	0	1	12	11.21	12.93	19.10
67- 3-53	117	75	37	2	0	0	3	2.56	4.27	22.12
67- 3-54	123	44	64	2	0	1	12	10.57	11.38	20.83
67- 3-55	123	40	62	3	0	0	18	14.63	17.07	14.29
67- 3-56	119	52	58	0	1	0	8	7.56	6.72	12.22
67- 3-57	105	24	65	3	0	0	13	12.38	15.24	14 61
67- 3-58	98	39	50	2	0	0	7	7.14	9.18	19.72
Total	**11958**	**4720**	**5809**	**193**	**12**	**16**	**1199**	**10.26**	**11.64**	**18.28**

TABLE 14.

Du : *du* segregation in 118 families.

Family No.	Total	*Du*	*du*	*d%*	Family No.	Total	*Du*	*du*	*d%*
4- 1- 7	122	116	6	4.92	4- 9-180	91	83	8	8.79
4- 1- 88	122	110	12	9.84	4- 9-220	132	120	12	9.09
4- 1-154	131	119	12	9.16	4-13- 2	117	103	14	11.97
4- 1-189	108	95	13	12.04	4-13-107	136	111	25	18.38
4- 2- 12	127	107	20	15.75	4-18- 95	127	109	18	14.17
4- 2- 77	114	105	9	7.89	4-18-132	118	106	12	10.17
4- 4- 98	133	116	17	12.78	5- 6- 65	126	111	15	11.90
4- 4-157	114	106	8	7.02	5- 6- 97	137	113	24	17.52
4- 7- 3	111	102	9	8.11	5- 7-131	119	104	15	12.61
4- 7-159	120	109	11	9.17	5-13- 37	110	99	11	10.00
4- 9-153	56	44	12	21.43	5-13-105	109	97	12	11.01

TABLE 14 (*continued*)

Family No.	Total	*Du*	*du*	*d%*	Family No.	Total	*Du*	*du*	*d%*
5-14- 21	115	101	14	12.17	66-15-177	119	107	12	10.08
5-14- 82	118	103	15	12.71	66-19- 71	124	114	10	8.06
5-16- 88	111	100	11	9.91	66-19- 93	121	107	14	11.57
5-17-101	117	97	20	17.09	66-30- 17	112	100	12	10.71
5-17-139	109	93	16	14.68	66-30- 29	116	104	12	10.34
5-21- 4	114	101	13	11.40	66-30- 45	118	103	15	12.71
5-21-181	124	111	13	10.48	66-30- 87	121	112	9	7.44
5-33- 86	127	110	17	13.39	66-30-100	86	73	13	15.12
5-33-107	121	106	15	12.40	66-31- 10	117	102	15	12.82
5-34- 94	118	104	14	11.86	66-31- 22	118	104	14	11.86
5-36- 63	112	98	14	12.50	66-31- 91	121	111	10	8.26
5-37- 19	119	103	16	13.45	66-31-107	121	107	14	11.57
5-37- 87	119	109	10	8.40	66-31-153	121	113	8	6.61
5-41- 13	122	115	7	5.74	86- 7- 4	118	111	7	5.93
5-44-101	119	115	4	3.36	86- 7- 70	121	109	12	9.92
5-44-177	119	113	6	5.04	86- 8- 3	120	106	14	11.67
5-45- 2	114	103	11	9.65	86- 8- 25	108	94	14	12.96
5-45- 77	118	110	8	6.78	86- 8-109	118	103	15	12.71
5-45- 79	121	113	8	6.61	86-11-115	118	103	15	12.71
5-46- 93	115	107	8	6.96	86-11-150	117	106	11	9.40
5-46-111	118	101	17	14.41	86-11-184	114	95	19	16.67
17- 1- 75	119	112	7	5.88	86-17- 5	117	105	12	10.26
17- 1- 89	114	109	5	4.39	86-19- 55	117	98	19	16.24
17- 1-102	116	105	11	9.48	86-19- 72	114	100	14	12.28
17- 1-180	113	102	11	9.73	86-19-103	121	104	17	14.05
17- 3- 15	113	105	8	7.08	86-22- 1	118	106	12	10.17
17- 3- 55	116	111	5	4.31	86-22- 32	118	106	12	10.17
17- 7- 22	123	114	9	7.32	86-22- 66	118	109	9	7.63
17- 9-152	117	110	7	5.98	86-22- 69	109	94	15	15.76
17- 9-177	120	113	7	5.83	86-25- 17	112	105	7	6.25
17-13-154	111	100	11	9.91	86-25- 88	117	109	8	6.84
17-13-184	112	100	12	10.71	86-25-107	120	103	17	14.17
17-15- 2	126	113	13	10.32	86-31- 14	126	114	12	9.52
17-17-111	113	102	11	9.73	86-35-192	111	97	14	12.61
17-18- 56	116	107	9	7.76	86-35-194	119	95	24	20.17
17-21- 77	120	108	12	10.00	86-36- 3	120	101	19	15.83
17-21-163	123	101	22	17.89	86-36-107	116	110	6	5.17
66- 5- 11	104	98	6	5.77	101- 4- 80	112	96	16	14.29
66- 5-107	122	115	7	5.74	101- 4-153	113	101	12	10.62
66-10- 17	120	107	13	10.83	101- 4-167	114	98	16	14.04
66-10- 32	114	106	8	7.02	101- 4-179	124	113	11	8.87
66-13- 79	93	87	6	6.45	101- 9- 19	111	99	12	10.81
66-13- 98	133	124	9	6.77	101-10- 53	116	103	13	11.21
66-13-125	104	99	5	4.81	101-12- 68	120	112	8	6.67
66-13-187	119	110	9	7.56	101-16- 7	100	96	4	4.00
66-14- 65	120	111	9	7.50	101-16- 94	118	110	8	6.78
66-14- 78	120	106	14	11.67	101-24- 52	110	101	9	8.18
66-15-101	123	111	12	9.76	101-24-175	103	88	15	14.56
					Total	9293	8377	916	9.86

TABLE 16.

Du : *du* segregation in 66 families.

Family No.	Total	*Du*	*du*	*d*%	Family No.	Total	*Du*	*du*	*d*%
17- 5- 1	128	119	9	7.03	101-22- 3	111	105	6	5.41
17- 5- 2	117	107	10	8.55	101-22- 4	114	111	3	2.63
17- 5- 5	117	112	5	4.27	101-22- 8	110	102	8	7.27
17- 5- 7	115	109	6	5.22	101-22- 9	112	98	14	12.50
17- 5- 8	119	116	3	2.52	101-22-12	110	96	14	12.73
17- 5- 9	113	103	10	8.85	101-22-13	116	105	11	9.48
17- 5-10	115	102	13	11.30	101-22-14	115	100	15	13.04
17- 5-12	118	109	9	7.63	101-22-16	116	106	10	8.62
17- 5-13	118	114	4	3.39	101-22-17	106	96	10	9.43
17- 5-14	115	106	9	7.83	101-22-21	115	108	7	6.09
17- 5-16	114	106	8	7.02	101-22-22	104	100	4	3.85
17- 5-17	110	105	5	4.55	101-22-23	116	106	10	8.62
17- 5-18	124	114	10	8.06	101-22-24	114	107	7	6.14
17- 5-19	112	97	15	13.39	101-22-25	109	96	13	11.03
17- 5-21	115	99	16	13.91	101-22-26	93	76	17	18.23
17- 5-22	134	122	12	8.96	101-22-27	118	109	9	7.63
17- 5-23	112	97	15	13.39	101-22-28	107	97	10	9.35
17- 5-24	117	100	17	14.53	101-22-29	124	111	13	10.48
17- 5-30	111	104	7	6.31	101-22-30	126	112	14	11.11
17- 5-34	109	103	6	5.50	101-22-32	133	124	9	6.77
17- 5-35	109	97	12	11.01	101-22-34	118	104	14	11.86
17- 5-37	107	97	10	9.35	101-22-35	112	98	14	12.50
17- 5-38	110	100	10	9.09	101-22-36	126	111	15	11.90
17- 5-39	113	111	2	1.77	101-22-37	123	106	17	13.82
17- 5-41	113	108	5	4.42	101-22-38	129	122	7	5.43
17- 5-42	114	108	6	5.26	101-22-41	116	105	11	9.48
17- 5-43	114	106	8	7.02	101-22-42	125	117	8	6.40
17- 5-45	106	94	12	11.32	101-22-43	124	112	12	9.68
17- 5-46	109	107	2	1.83	101-22-44	129	114	15	11.63
17- 5-48	119	110	9	7.56	101-22-47	100	93	7	7.00
17- 5-49	116	102	14	12.07	101-22-48	118	104	14	11.86
101-22- 1	108	93	15	13.08	101-22-49	132	118	14	10.61
101-22- 2	111	103	8	7.21	101-22-51	128	115	13	10.16
Total						7631	6964	667	8.74

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