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RELATION OF THE DIFFERENTIAL FERTILIZATION GENES, *Ga ga*, TO CERTAIN OTHER GENES OF THE *Su-Tu* LINKAGE GROUP OF MAIZE[1]

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The *Ga*, or "gamete" gene of maize can be studied only or principally by its disturbance of normal Mendelian ratios of contrasted characters differentiated by genes linked with it. The amount of this disturbance can be used as a measure of the intensity of linkage between *Ga* and other genes of the *su-Tu* group.

Disturbance of the 3:1 ratio of starchy, *Su*, to sugary, *su*, endosperm has been most studied. In one of the early papers on Mendelian inheritance, CORRENS (1902) reported that, although crosses between most starchy and sugary varieties gave an F_2 ratio of 3:1 for starchy and sugary kernels, a popcorn with pointed kernels, when crossed with sugary races, gave only 16 percent of sugary kernels in F_2. That *Su* and *su* segregated normally was shown by reciprocal crosses of F_1 with the sugary parent, which gave approximately 50 percent sugary kernels. From this CORRENS concluded that the deficiency of sugary kernels in F_2 is due to selective fertilization.

JONES (1924) reported that crosses of rice popcorn with sugary maize gave 16.2 percent sugary kernels in F_2, while other starchy races crossed with sugary gave approximately 25 percent sugary kernels. Backcrosses to sugary gave about 50 percent sugary, as CORRENS had reported. From counts of starchy and sugary kernels on the butt and tip ends of ears, JONES concluded that the mechanism of this selective fertilization was differential pollen-tube growth. The writer (EMERSON 1925) suggested that this assumed differential pollen-tube growth is due not to the *Su su* genes themselves but to some gene linked with *Su*. MANGELSDORF and JONES (1926) called this accessory gene the "gamete" factor, *Ga*. Since *Ga* and *ga* pollen exhibit differential fertilization when the pistils have *Ga* either homozygous or heterozygous the gene is regarded as dominant. Backcrosses of F_1 on the sugary parent carrying the homozygous recessive allelomorph, *ga*, show little or no selective fertilization.

By dividing the silks of *Ga* carrying ears and pollinating those of one side with *Ga* and those of the other side with *ga* pollen, DEMEREC (1929) obtained results which indicate that differential fertilization is due to cross-sterility of *ga* pollen on *Ga* plants. The writer's repeated attempts to de-

[1] Paper No. 200, Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, New York.

termine whether differential fertilization involving *Ga* and *ga* is due to differential pollen-tube growth or to cross-sterility have given somewhat contradictory and, therefore, confusing results. Fortunately an understanding of the mechanism of differential fertilization is not essential in a consideration of the relation of *Ga ga* to other genes of the *su-Tu* linkage group.

CROSSES BETWEEN VARIOUS TYPES OF STARCHY AND OF SUGARY MAIZE

In the course of the writer's studies of the relation of *Ga* and *ga* to the *Su-su* pair, records of crosses of many different types of starchy maize with

TABLE 1

Starchy and sugary kernels obtained from self-pollinated plants of the crosses indicated.

ITEM NUMBER	GENERATION	PERCENT *su* OF PRECEDING GENERATION	NUMBER OF EARS	NUMBER OF KERNELS: STARCHY	SUGARY	TOTAL	PERCENT SUGARY
			Common starchy crossed with common sugary F_1 genotype: *ga Su/ga su*				
1	F_2		834	203,700	68,089	271,789	25.1
2	F_3	F_2 normal	148	31,051	10,173	41,224	24.7
			Rice pop crossed with common sugary F_1 genotype: *Ga Su/ga su*				
3	F_2		363	111,368	19,798	131,166	**15.1**
4			96	26,340	5,009	31,349	**16.0**
5	F_3	F_2 low	81	20,171	6,505	26,676	24.4
6			16	2,858	1,608	4,466	**36.0**
7			52	10,646	2,147	12,793	**16.8**
8		F_3 low	63	14,286	4,681	18,967	24.7
9			6	977	522	1,499	**34.8**
10	F_4	F_3 normal	75	16,526	5,600	22,126	25.3
11			4	272	55	327	**16.8**
12		F_3 high	39	7,501	2,465	9,966	24.7
13			32	6,124	3,669	9,793	**37.5**
			Common starchy crossed with sugary derivatives of rice pop F_1 genotype: *ga Su/Ga su*				
14	F_2		263	60,704	33,775	94,479	**35.7**
15			21	4,994	876	5,870	**14.9**
16	F_3	F_2 high	99	23,067	7,932	30,999	25.6
17			101	19,953	10,820	30,773	**35.2**
			Rice pop crossed with sugary derivatives of rice pop F_1 genotype: *Ga Su/Ga su*				
18	F_2		197	60,670	20,200	80,870	25.0
19	F_3	F_2 normal	9	1,601	550	2,151	25.6

several varieties of sugary maize have accumulated. The starchy types used in these crosses included different varieties of dent, flint, flour, and pop maize and of crosses between them. The sugary types used included several varieties of sweet corn, of crosses between them, and of sugary derivatives from various starchy-sugary crosses. Records of progenies obtained from self-pollination of individuals of various generations of the several crosses are summarized in table 1.

All of these starchy types, except rice pop and derivatives of it, when crossed with any of the sugary lots except derivatives of rice pop, have given normal ratios of starchy to sugary, approximately 25 percent sugary (table 1, items 1, 2). The genotype of heterozygous starchy plants of these crosses is assumed to be *ga Su/ga su*.

In strong contrast to these results are the records of crosses of rice pop and its starchy derivatives with many of the same lots of sugary maize employed in the crosses noted above. Heterozygous starchy plants of these rice pop crosses, *Ga Su/ga su*, have consistently given low percentages of sugary, with perhaps somewhat greater variation than that observed in crosses involving *ga ga*. The average for the F_2 generation was 15.1 percent sugary (table 1, item 3). Some of the starchy derivatives of rice pop were evidently *Ga ga*, for about half of their F_2 progenies had approximately 25 percent sugary while the other half showed a wide departure from 25 percent.

Not only was the F_2 percentage of sugary in these crosses involving *Ga ga* different from that of the crosses involving *ga ga*, but the F_3 behavior also was different. F_3 progenies from *Su-su* F_2's of the latter crosses were all of one class, the percentage of sugary varying about 25 as a mean. The F_3 progenies of *Su-su* F_2's of the *Ga-ga* crosses, on the contrary, fell into three classes with low, normal, and high sugary percentages. The usual variation resulted doubtless in some overlapping of classes, but in general they were readily separable, varying about their respective means of 16.0, 24.4, and 36.0 percent sugary (table 1, items 4, 5, 6).

Heterozygous starchy kernels of the low sugary F_3 class repeated in F_4 the behavior of F_2 starchy kernels in F_3. There were again three fairly distinct classes of progeny with mean percentages of sugary of 16.8, 24.7, and 34.8 (table 1, items 7, 8, 9). Numerically these three classes, with F_3 and F_4 combined, were as 148:144:22 for low, normal, and high sugary, respectively. The high sugary class presumably arises from crossing over, producing the genotype *Ga su/ga Su*, and hence of relatively infrequent occurrence.

The F_4 progenies from *Su-su* plants of the normal sugary F_3 class showed normal sugary only, the mean percentage being 25.3 (table 1, item 10).

The high sugary F_3 lot gave the same three F_4 classes of low, normal, and

high sugary as did the low sugary F_3's. The mean percentages of sugary also were similar, being 16.8, 24.7, and 37.5, respectively (table 1, items 11, 12, 13). But the numerical relation of the low and high classes was reversed, low, normal, and high having the relation of 4:39:32, respectively. Here low sugary is a crossover class, *Ga Su/ga su*.

The normal sugary class in each F_3 and F_4 group must also have come from crossovers resulting in *Ga Su/Ga su*, or *ga Su/ga su*, or both. The latter, however, as will appear from evidence yet to be presented, should be relatively rare. It should, therefore, be readily possible to obtain sugary stocks of the type *Ga su*.

Crosses of all types of starchy maize, *ga Su*, except rice pop and its derivatives, with sugary derivatives of rice pop, *Ga su*, have given consistently high sugary percentages in F_2, with a mean percentage of 35.7 (table 1, item 14). When these sugary derivatives are *Ga ga*, there occur in F_2, of course, both normal and high sugary progenies in nearly equal numbers.

Heterozygous starchy kernels from high sugary ears of F_2 of this cross repeat in F_3 the behavior in F_4 of similar kernels of high sugary F_3 ears of the preceding cross (compare items 11, 12, 13 with 15, 16, 17 of table 1). Here again low, normal, and high sugary classes were observed, the mean percentages of sugary being 14.9, 25.6, and 35.2. The relative number of progenies of the three classes also was of the same general order. These F_4 and F_3 lots together were as 25:138:133 for low, normal, and high sugary, respectively.

Crosses of rice pop or its starchy derivatives, *Ga Su*, with sugary derivatives of rice pop, *Ga su*, have given uniformly normal sugary percentages in F_2 and F_3. Of course, when one or the other parent, or both, had *Ga ga*, the resulting progenies were normal and low, normal and high, or all three together. The percentage of sugary in F_2 was 25.0 and in F_3, with smaller numbers, 25.6 (table 1, items 18, 19).

Both CORRENS (1902) and JONES (1924) reported that crosses of rice pop with various sugary races, showing when selfed a low percentage of sugary kernels, exhibited normal segregation of starchy and sugary, with approximately 50 percent of sugary kernels, when backcrossed reciprocally with the sugary parents. Obviously the sugary parents of these crosses were *ga*, and the results indicated that differential fertilization does not occur when the silks to which *Ga-ga* pollen is applied do not have *Ga*. MANGELSDORF and JONES (1926) backcrossed plants of the genotype *Ga Su/ga su* with the rice pop parent, *Ga Su*, and noted in the following generation the numbers of *Su-Su* and *Su-su* plants. Almost equal numbers of the two classes were observed, 213 *Su Su* and 207 *Su su*, when rice pop furnished the pollen for the backcrosses. When, however, rice pop was used as the female parent of the backcrosses, the ratio of *Su Su* to *Su su*

was 353 to 88. In short, *su* pollen of F_1 plants had functioned in the production of only 20 percent of the kernels.

A more direct test of differential fertilization in backcrosses is obtained by backcrossing to *Ga-su* as well as to *ga-su* plants. Accordingly, a number of plants, which when selfed gave low, normal, or high percentages of sugary, were crossed—some of them reciprocally—with both *ga su* and *Ga su*. The results are presented in table 2.

TABLE 2

Backcrosses of various genotypes involving Ga ga and Su su by and on ga su and Ga su.

CONSTITUTION OF HETEROZYGOTES AND TYPE OF POLLINATION	NUMBER OF HETEROZYGOUS PLANTS	NUMBER OF KERNELS			PERCENT SUGARY
		STARCHY	SUGARY	TOTAL	
ga Su/ga su					
Self-pollinated	50	14,252	4,736	18,988	24.9
Crossed by *ga su* ♂	6	853	807	1,660	48.6
Crossed by *Ga su* ♂	14	1,917	1,798	3,715	48.4
Crossed on *ga su* ♀	41	3,771	3,992	7,763	51.4
Crossed on *Ga su* ♀	50	5,579	5,643	11,222	50.3
Ga Su/Ga su					
Self-pollinated	10	4,272	1,412	5,684	24.8
Crossed by *ga su* ♂	4	581	593	1,174	50.5
Crossed by *Ga su* ♂	3	479	471	950	49.6
Crossed on *ga su* ♀	2	191	214	405	52.8
Crossed on *Ga su* ♀	5	547	573	1,120	51.2
Ga Su/ga su					
Self-pollinated	53	19,498	3,296	22,794	14.5
Crossed by *ga su* ♂	13	2,518	2,451	4,969	49.3
Crossed by *Ga su* ♂	16	3,663	3,535	7,198	49.1
Crossed on *ga su* ♀	45	5,328	5,796	11,124	52.1
Crossed on *Ga su* ♀	44	8,860	3,844	12,704	**30.3**
Ga su/ga Su					
Self-pollinated	24	5,805	3,494	9,299	**37.6**
Crossed by *ga su* ♂	4	541	509	1,050	48.5
Crossed by *Ga su* ♂	11	1,425	1,412	2,837	49.8
Crossed on *ga su* ♀	14	2,010	1,903	3,913	48.6
Crossed on *Ga su* ♀	17	1,768	3,729	5,497	**67.8**

Only two of these backcrosses exhibited large departures from 50 percent sugary kernels. Plants of the genotypes *Ga Su/ga su* and *Ga su/ga Su* when used as pollen parents in crosses with *Ga su* gave respectively 30.3 and 67.8 percent sugary. These are departures in opposite directions from 50 of 19.7 and 17.8, respectively, corresponding to the deviations from 25 percent of 10.5 and 12.6 in the progenies derived from self-pollination.

RELATION OF LINKAGE OF *Ga ga* WITH OTHER GENES AND OF THE PERCENT OF FUNCTIONING *Ga* AND *ga* POLLEN TO DISTORTED RATIOS

It has been assumed that the differential fertilization genes *Ga ga* disturb the normal *Su-su* ratios because of linkage of these genes. Obviously the magnitude of the disturbance of ratios of dominant to recessive genes is related to the intensity of linkage between them and the *Ga ga* pair. If there were no such linkage the disturbing effect of *Ga ga* would be zero and their existence unsuspected. That they do not distort ratios of genes in linkage groups other than the *su-Tu* group was shown by adding to the genotypes *Ga Su/ga su* and *Ga su/ga Su* certain well known aleurone, endosperm, and plant-color genes in a heterozygous condition.

That the distortion of ratios of dominant to recessive is related also to the percentage of *Ga* and *ga* pollen that functions in fertilization is equally obvious. If *Ga* and *ga* pollen each fertilized 50 percent of the kernels, no disturbance of the ratios of other dominant and recessive genes would result no matter how close the linkage between them and *Ga ga*. This is what occurs when *Ga ga* pollen is used on *ga* plants. *Ga* and *ga* are not, in such cases, differential fertilization genes.

It has been pointed out by MANGELSDORF and JONES (1926) that any given deviation from a normal Mendelian ratio might be due to any one of many different combinations of linkage intensity and percentage of functioning *Ga* and *ga* pollen. If, therefore, we knew the percentages of *Ga* and *ga* pollen effective in fertilization, we could readily determine the percentage of recombination necessary to produce an observed deviation from the normal Mendelian ratio.

MANGELSDORF and JONES (1926) made such an evaluation of the relative effectiveness of *Ga* and *ga* pollen on *Ga* silks. Two curves were constructed, one from the observed percentage of sugary kernels, 16.2, and the other from the observed percentage of defective, de_1, kernels, 17.2, on self-pollinated plants heterozygous for *Ga ga* and for *Su su* or De_1 de_1. The curve for percentage of sugary was so constructed that, at any point on it, the ordinate, read as recombination percentage between *Ga* and *su*, and the abscissa, read as percentage of functioning *ga* pollen, should give the observed percentage of sugary. The curve for percentage of defective kernels was constructed in the same way. The problem was then to determine at what point on the axis of abscissas an ordinate could be erected to intersect the two curves at points whose recombination values, converted into map distance and combined, would equal the map distance corresponding to the observed recombination percentage between *su* and de_1. The recombination percentage for *su* and de_1 was taken as 39[2] corre-

sponding to a map distance of approximately 50. Since the ordinate found best to fit this value intersected the axis of abscissas at approximately 19.6 percent of functioning *ga* pollen, the percentages of recombination were indicated to be 21.2 for *Ga* and *su* and 24.3 for *Ga* and de_1.

From the published data of MANGELSDORF and JONES (1926) with the addition of more recent unpublished data by the same authors involving a total of 14,677 kernels, the recombination percentage of de_1 and *su* is calculated as approximately 47. This corresponds to a map distance of 75 units according to HALDANE'S (1919) table; and the present indication is that the actual map distance between de_1 and *su* is somewhat more than 75 units. The percentages of defective in a total of 4518 kernels on high defective ears and in a total of 1022 kernels on low defective ears (MANGELSDORF and JONES 1926) were respectively 32.0 and 16.8. The weighted mean departure from 25 percent is 7.2, corresponding to an average of 17.8 percent defectives. The data presented in table 1 show 15.4 percent sugary in a total of 181,505 kernels on ears of the low sugary class and 35.7 percent in 141,010 kernels on ears of the high sugary class. The deviations from 25 percent are, therefore, 9.6 and 10.7, respectively. The weighted average deviation is 10.2, corresponding to a percent of sugary of 14.8.

On the basis of these data, namely, 47 percent of recombination between *su* and de_1, 17.8 percent de_1, and 14.8 percent sugary, the method of MANGELSDORF and JONES (1926), with the aid of their table 9, gives as the percentage of functioning *ga* pollen on *Ga* silks 2.5, and as the recombination percentages between *Ga* and de_1 34.9, and between *Ga* and *su* 28.5. The corresponding map distances are 42.4 and 32.6 totaling 75 which is taken as the map distance for 47 percent recombination between de_1 and *su*. Since the actual map distance is probably greater, rather than less, than 75, it is interesting to note that this method of calculation gives, for zero percent of functioning *ga* pollen, recombination percentages of 35.6 for *Ga* and de_1 and 29.6 for *Ga* and *su*, the combined map distances of which are about 78.0. In so far, therefore, as this method is at all reliable, it may be concluded that the percentage of functioning *ga* pollen in competition with *Ga* pollen on *Ga* silks is from zero to 2.5.

A more direct method for an evaluation of the relative effectiveness of *Ga* and *ga* pollen on *Ga* silks is the pollination of *Ga* plants with a known mixture of *Ga* and *ga* pollen. In such a mechanical mixture of pollen, one variable is eliminated, namely, the crossovers between *Ga ga* and genes linked with them, which occur in the hybrid mixture of pollen of a heterozygous plant.

[2] The frequency distribution reported by MANGELSDORF and JONES (1926) of 601 De_1 *Su*, 238 De_1 *su*, 247 de_1 *Su*, 64 de_1 *su* gives a recombination percentage of 44.0 as computed by aid of IMMER'S (1930) tables.

Such pollen-mixture tests were reported by MANGELSDORF and JONES (1926) but not used for the purpose of determining the relative effectiveness of *Ga* and *ga* pollen in hybrid mixtures. A mixture of pollen of rice pop, *Ga Su*, with pollen of a variety of sugary maize, *ga su*, was applied to the silks of both of the types that furnished the pollen. The starchy type had white and the sugary type yellow endosperms, so that the kernels resulting from cross-pollination could be distinguished from those resulting from self-pollination. From the pollination of the sugary plants 6435 kernels were obtained of which 4233, or 65.8 percent, were sugary. This indicates that there was an abundance of viable *ga-su* pollen in the mixture. The same pollen mixture used on rice pop gave a total of 12,690 kernels of which only 75, or 0.59 percent, were yellow. In short, *ga* pollen functioned in competition with *Ga* pollen on *Ga* silks in the production of only a little more than one-half of one percent of the kernels.

Similar tests by DEMEREC (1929) gave almost identical results. Pollen from *ga* plants with purple aleurone and shrunken endosperm was mixed with pollen from *Ga*, (popcorn) plants with colorless aleurone and non-shrunken endosperm, each type thus having one dominant and one recessive character by which kernels produced by cross-pollination could be distinguished from those produced by self-pollination. Pollination of *ga* plants with this mixture resulted in 1189 kernels of which 654, or 55.0 percent, were fertilized with *ga* pollen. Pollination of *Ga* plants with the same mixture gave 1690 kernels of which only 13, or 0.77 percent, were fertilized with *ga* pollen. Silks of *Ga* plants pollinated with pollen from several different varieties of *ga* plants, without competition from *Ga* pollen, resulted in the production of only 39 kernels on ears estimated to have had 7090 ovules, a percentage of only 0.55.

The writer's tests with mechanical mixtures of *Ga* and *ga* pollen were conducted because of the bearing they were expected to have on the problem of the relative effectiveness of *Ga* and *ga* pollen in hybrid mixtures. Endosperm color and composition were used to identify kernels resulting from the different kinds of pollen. In all but one test mixtures of only two kinds of pollen were used, one carrying *Ga* and the other *ga*, while in the one test four kinds of pollen were mixed, involving all the four combinations of *Ga* and *ga* with *Su* and *su*. In half of the tests the pollen mixtures were applied to *ga su* and *Ga su* silks only, while in the other half they were put on *ga Su* and *Ga Su* as well. In each test approximately equal quantities of the different kinds of pollen were mixed thoroughly, then divided, and each part applied at once to one or other of the kinds of plants to be pollinated. Since it is impossible to be certain that any mixture contains equal numbers of viable pollen grains, of the stocks used, all mixtures were used on *ga* plants, on which no differential fertilization is expected,

TABLE 3
Summary of tests of pollen mixtures applied to maize silks of different genotypes.

NUMBER OF TESTS SUMMARIZED	POLLEN MIXTURE	GENOTYPE OF SILKS	GENOTYPE OF KERNELS PRODUCED: NUMBER			PERCENT	
			Ga	*ga*	TOTAL	*su*	*ga*
			Su	*su*			
3	*Ga Su+ga su*	*ga su*	1,089	1,627	2,716	59.9	59.9
		Ga su	1,958	85	2,043	4.2	**4.2**
			su	*Su*			
4	*Ga su+ga Su*	*ga su*	968	1,044	2,012	48.1	51.9
		Ga su	3,261	94	3,355	97.2	**2.8**
			su	*su*			
1	*Ga su+ga su*	*ga su*	208	270	478	..	56.5
		Ga su	727	41	768	..	**5.3**
			Su	*Su*			
2	*Ga Su+ga Su*	*ga su*	344	132	476	..	27.7
		Ga su	1,707	10	1,717	..	**0.6**
		ga Su	477	320	797	..	40.2
		Ga Su	1,447	24	1,471	..	**1.6**
			su	*Su*			
2	*Ga su+ga Su*	*ga su*	185	67	252	73.4	26.6
		Ga su	1,185	18	1,203	98.5	**1.5**
			Su	*Su*			
		ga Su	576	177	753	..	23.5
		Ga Su	670	25	695	..	**3.6**
			Su	*su*			
3	*Ga Su+ga su*	*ga su*	371	653	1,024	63.8	63.8
		Ga su	1,909	99	2,008	4.9	**4.9**
			Su	*Su*			
		ga Su	476	644	1,120	..	57.5
		Ga Su	797	71	868	..	**8.2**
			Su+su	*Su+su*			
1	*Ga Su+ga su* + *Ga su+ga Su*	*ga su*	605	1,029	1,634	..	63.0
		Ga su	2,478	186	2,664	..	**7.0**
			Su	*Su*			
		ga Su	348	523	871	..	60.0
		Ga Su	201	21	222	..	**9.5**
			Ga	*ga*			
16	*Ga+ga*	*ga*	5,647	6,486	12,133	..	53.5
		Ga	16,340	674	17,014	..	**3.96**

in order to determine quantitatively the actual composition of the mixtures used in the tests with *Ga* plants. The results of these tests are summarized in table 3.

It will be noted that the percentages of kernels fertilized by *ga* pollen on *ga* plants varied from 23.5 to 63.8 with an average, for the 12,133 ker-

nels, of a little more than 50. In strong contrast to these results, *ga* pollen functioned on *Ga* plants in the production of from 0.6 to 9.5 percent of the kernels, with an average, for the 17,014 kernels, of only about 4.0 percent. The 4 percent of functioning *ga* pollen on *Ga* plants shown by these tests is greater than indicated by similar tests of MANGELSDORF and JONES and of DEMEREC which showed only about 0.6 and 0.8 respectively. It is also somewhat in excess of the 2.5 percent calculated from deviations from 3:1 ratios of De_1 to de_1 and *Su* to *su* by the method of MANGELSDORF and JONES (1926). The conclusion to be drawn from all these tests is that on the average *ga* pollen on *Ga* plants functions in the production of from almost zero to about 4 percent of the kernels.

Inability to determine the percentage of functioning *ga* pollen more closely affects very little the results of calculations of linkage intensity between *Ga ga* and *Su su*. Thus, the recombination percentage with zero percent of functioning *ga* pollen is 29.6, with 2.5 percent 28.5 and with 4.0 percent 27.8. Duplicate linkage tests involving other genes often give results as diverse as these.

With no functioning *ga* pollen, the percentage of sugary or of starchy kernels in a backcross on *Ga su* plants should equal the percentage of recombination. Table 2 shows 30.3 percent sugary from *Ga su*×*Ga Su/ga su* and 67.8 percent sugary, or 32.2 percent starchy from *Ga su*×*Ga su/ga Su*. The weighted average of these records is 30.9 percent for a total of 18,201 kernels. This is only 1.3 greater than the percentage of recombination calculated, on the basis of no functioning *ga* pollen, from the data given in table 1 involving 322,515 kernels.

Since, with the methods so far discussed, it is necessary to evaluate the relative effectiveness of *Ga* and *ga* pollen before recombination percentages can be determined, a method that is independent of *Ga ga* may be of interest. If r:s:s:r be taken as the gametic series for any percentage of crossing over and p and q as the respective percentages of effective *Ga* and *ga* pollen, the several genotypes resulting from self-pollination of *Ga Su/ga su* or *Ga su/ga Su* should occur with the frequencies shown below:

Su Su—

$$\left.\begin{array}{l} Ga\ Su/Ga\ Su = p\ r^2 \\ Ga\ Su/ga\ Su = (p+q)rs \\ ga\ Su/ga\ Su = q\ s^2 \end{array}\right\} = p\ r^2 + (p+q)rs + q\ s^2$$

su su—

$$\left.\begin{array}{l} Ga\ su/Ga\ su = p\ s^2 \\ Ga\ su/ga\ su = (p+q)rs \\ ga\ su/ga\ su = q\ r^2 \end{array}\right\} = q\ r^2 + (p+q)rs + p\ s^2$$

Total *Su Su* and *su su* $= (p+q)\ r^2 + 2(p+q)\ rs + (p+q)\ s^2$

Su su

$$\left.\begin{array}{l} Ga\ Su/Ga\ \ su = 2p\ rs \\ ga\ \ Su/ga\ \ su = 2q\ rs \\ Ga\ \ Su/ga\ \ su = (p+q)r^2 \\ Ga\ \ su/ga\ \ Su = (p+q)\ s^2 \end{array}\right\} = (p+q)\ r^2 + 2(p+q)\ rs + (p+q)\ s^2$$

From this theoretical frequency distribution, it may be noted that the *Su-su* genotypes which should produce low, normal, and high sugary percentages have the following frequencies, respectively: $(p+q)r^2:2(p+q)rs:(p+q)s^2$, or, when simplified, $r^2:2rs:s^2$. In the coupling phase of linkage between *Ga ga* and *Su su*, giving rise to a low sugary percentage, $r>s$; in the repulsion phase, resulting in high sugary, $r<s$. With a given percentage of crossing over, the values of r and s are reversed in coupling and repulsion. Therefore, the value of the first and the third terms of the frequency distribution, $r^2+2rs+s^2$, are reversed while the value of the second term remains constant for coupling and repulsion phases of linkage.

The relative values of the three terms depend not alone on the linkage phase, but also on the intensity of linkage. As crossing over approaches 50 percent, $r=1$ and $s=1$, these values approach 1:2:1; as crossing over percentage approaches zero, $r=1$ and $s=0$ or $r=0$ and $s=1$, the values approach 1:0:0 or 0:0:1. The relative numbers of progenies showing low, normal, and high sugary percentages produced from *Su su* kernels of low sugary and of high sugary ears should, therefore, give an indication of the percentage of crossing over between *Ga ga* and *Su su* without involving the problem of the ratio of functioning *Ga* to *ga* pollen.

Table 1 shows that, from *Su su* kernels of low sugary and from high sugary ears, there were produced a total of 610 progenies exhibiting low, normal, and high sugary percentages in the following numbers:

	Progenies			
Parent ears	Low sugary	Normal sugary	High sugary	Total
Low sugary	148	144	22	314
High sugary	25	138	133	296

As indicated above, the first and third terms are reversed in coupling and repulsion phases of linkage. When rearranged so that the first term consists of the individuals that are like their respective parent ears, the observed distribution is as given below. For comparison, distributions calculated on the basis of various percentages of crossing over are included.

		Deviation from 25 percent sugary				
		Like parent ear	None	Reverse of parent ear	Total	Value of χ^2
Observed		281	282	47	610	
Calculated for recombination percentage of—	28	316	246	48	610	9.2
	29	307	252	51	610	6.1
	30	299	256	55	610	4.9
	31	290	261	59	610	4.4
	32	282	266	62	610	4.5
	33	271	271	68	610	7.3

The first and third terms, r^2 and s^2, of the observed distribution, give 16.76 and 6.86 as values of r and s, respectively, or a crossover percentage of 29.0. It will be recalled that, from the percentage of sugary seeds given in table 1 and by the method of MANGELSDORF and JONES (1926), the percentage of functioning *ga* pollen was calculated as 2.5 and the percent of recombination between *Ga* and *su* as 28.5. The frequency distribution, calculated from 29 percent recombination, does not give a good fit with the observed distribution, $\chi^2=6.1$ and $P=0.048$. A considerably better fit is shown by the distribution calculated for 31 percent recombination, $\chi^2=4.4$, $P=0.114$. This is approximately the recombination percentage, 30.9, given by the backcross data of table 2, when calculated on the basis of no functioning *ga* pollen.

The method here under consideration is independent of the relative effectiveness of *Ga* and *ga* pollen. Its principal disadvantage is the impracticability of dealing with large numbers. None of the frequency distributions calculated by this method fits very well the observed distribution. But do calculated frequency distributions based on the percentage of sugary kernels fit observed frequencies well? When the percentages of starchy and sugary kernels alone are used, conclusions are based on two classes where three exist, namely, *Su Su*, *Su su*, and *su su*.

Since, as shown by the theoretical frequency distribution given above, the heterozygous, *Su su*, kernels equal the sum of the homozygous kernels, *Su Su* and *su su*, any values of r, s, and p, q which result in a deviation upward or downward from 25 percent *su su* should bring about an inverse deviation downward or upward from 25 percent *Su Su*. The low sugary lots of table 1 averaged 15.4 percent sugary, the normal sugary lots 25.0 percent sugary, and the high sugary lots 35.7 percent sugary. From

starchy kernels of low, normal, and high sugary ears, therefore, the three classes should have the following relation:

Parent ears	Progenies			
	Su Su	*Su su*	*su su*	Total
Low sugary	34.6	50.0	15.4	100.0
Normal sugary	25.0	50.0	25.0	100.0
High sugary	14.3	50.0	35.7	100.0

The percentages of homozygous starchy among all starchy kernels of the low, normal, and high sugary lots, therefore, should be, respectively, 40.9, 33.3, and 22.2. A comparison of calculated frequencies, based on these percentages, with observed frequencies is as follows:

Parent ears	Progenies			
	Su Su	*Su su*	Total	Percent *Su Su*
Low sugary—				
Observed	227	352	579	39.2
Calculated	237	342	579	40.9
Difference	−10	+10	0	−1.7
Normal sugary—				
Observed	98	210	308	31.8
Calculated	103	205	308	33.3
Difference	−5	+5	0	−1.5
High sugary—				
Observed	94	353	447	21.0
Calculated	99	348	447	22.2
Difference	−5	+5	0	−1.2

This comparison shows a remarkably close fit of observed frequencies with frequencies calculated from the percentages of sugary kernels. It would seem, therefore, that methods of calculating linkage intensity between *Ga ga* and *Su su*, based on observed percentages of sugary kernels, should give reliable results.

RELATION OF *Ga ga* TO GENES OTHER THAN *Su su*

As noted earlier in this paper, records published by MANGELSDORF and JONES (1926) show that in a high defective lot of maize with a total of

4518 kernels 32.0 percent were defective, de_1, and in a low defective lot with 1022 kernels 16.8 percent were de_1. Rice pop, or a derivative of it, was involved in both of these lots. The weighted mean deviation from 25 percent of the two lots is 7.2, corresponding to an average percentage of 17.8 de_1 kernels. On the assumption that no *ga* pollen functions on *Ga* silks, this percentage should result from 35.6 percent of recombination between *Ga ga* and De_1 de_1. The percentage of recombination calculated on the basis of 4 percent of effective *ga* pollen is 34.3. It may be concluded, then, that the recombination value is not far from 35 percent.

Another defective, de_{16}, when crossed with a derivative of rice pop, showed a marked deviation from the usual 25 percent defective (WENTZ 1925). In a total of 1784 kernels 17.3 percent were defective. This corresponds to recombination percentages of 34.6 and 33.2 with zero and with 4 percent of effective *ga* pollen, respectively. The recombination value for *Ga ga* and De_{16} de_{16}, therefore, may be given as approximately 34 percent.

As indicated earlier in this paper, the records of MANGELSDORF and JONES, including 14,677 kernels, indicate a recombination percentage of about 47 for de_1 and *su*. WENTZ (1925) reported a recombination percentage of 3.2 for de_{16} and *su* calculated from counts of 28,276 kernels. Since the writer's records indicate approximately 29 percent of recombination between *Ga* and *su*, the order of these genes is probably: de_1, *Ga*, *su*, de_{16}.

Tassel seed-5 plants with sun-red plant color, *ga* Ts_5 *B*, were crossed with rice pop which was dilute sun-red and had normal tassels, *Ga* ts_5 *b*. Pollen of the F_1 plants was applied to silks of plants having the genotypes *ga* ts_5 *b* and *Ga* ts_5 *b*, with the following results:

F_1 Backcrossed on	Backcross Progeny Ts_5	ts_5	Total	Percent Ts_5	Percent *b*
ga ts_5 *b*	401	449	850	47.2	45.3
Ga ts_5 *b*	244	570	814	30.0	47.4

Although there was a deficiency of Ts_5 in the progeny of the backcross on *ga* ts_5 *b*, it is less than that of the recessive, *b*. When the F_1 was backcrossed on *Ga* ts_5 *b*, however, the deficiency of Ts_5 was much more while that of *b* was less than for the other backcross. The *B*-*b* pair is known to belong to another linkage group and the percentage of *b*-plants, therefore, should not be disturbed by *Ga*. The gene Ts_5 is known to belong to the *su*-*Tu* group. With no functioning *ga* pollen, the percent of Ts_5 should be the percent of recombination between *Ga* and Ts_5.

TABLE 4

Backcrosses of ga ts_5 su/ga Ts_5 Su and Ga ts_5 su/ga Ts_5 Su on ga ts_5 su and Ga ts_5 su.

GENOTYPE OF F_1 AND OF ♀ PARENT OF BACKCROSS	NUMBER OF INDIVIDUALS					RECOMBINATIONS		PERCENTAGE		
	Su Ts_5	*Su ts_5*	*su Ts_5*	*su ts_5*	TOTAL	NUMBER	PERCENT	*su*	*Ts_5*	*b*
F_1 $\frac{ga\ ts_5\ su}{ga\ Ts_5\ Su}$										
1—*ga ts_5 su*	158	22	28	155	363	50	13.6	50.4	51.2	..
2—*Ga ts_5 su*	161	28	21	154	364	49	13.5	48.1	50.0	..
F_1 $\frac{Ga\ ts_5\ su\ b}{ga\ Ts_5\ Su\ B}$										
3—*ga ts_5 su b*	213	38	42	232	525	80	15.2	52.2	48.6	48.0
4—*Ga ts_5 su b*	167	107	28	624	926	135	14.6	70.4	21.1	47.4
Total	699	195	119	1165	2178	314	14.4	..	..	..

Common starchy tassel seed-5 plants, *ga Ts_5 Su*, were crossed both with common sugary, *ga ts_5 su*, and with sugary derivatives of rice pop, *Ga ts_5 su*. The F_1's of both lots were then backcrossed on *ga ts_5 su* and on *Ga ts_5 su*. As for the crosses noted above, some of the F_1's were *B b*. The results are presented in table 4. The data reported in this table exhibit no wide departure from the expected 50 percent of *su*, Ts_5 or *b*, except for the backcross *Ga ts_5 su*×*Ga ts_5 su/ga Ts_5 Su* (table 4, backcross 4). For that cross 70.4 percent of the plants were produced from *su* kernels, and 21.1 percent of the plants were Ts_5. These wide deviations from 50 percent, however, did not disturb the percentage of recombination between *su* and Ts_5 which is 14.6 for this culture and 14.4 for the average of all four cultures. The percentages of *su*, 70.4, and of Ts_5, 21.1, indicate, with no functioning *ga* pollen, percentages of recombination of 29.6 for *Ga su* and 21.1 for *Ga* Ts_5; or, with 4 percent functioning *ga* pollen, 27.8 and 18.5, respectively. The recombination percentages may be taken, therefore, as 14 for *su* Ts_5, 20 for *Ga* Ts_5, and 29 for *Ga su*, and the order of the genes as *Ga* Ts_5 *su*.

If the percentages of recombination between *Ga su* and between *Ga* Ts_5 were calculated from the percentages of *su* and of Ts_5 observed in backcross 3 of table 4, 52.2 and 48.6, their respective values would be found to be 47.8 and 48.6. But the pollen for backcross 3 was taken from the same F_1 plants as that for backcross 4 from which the values 29.6 and 21.1 are calculated. Since the pollen for backcross 3 was applied to *ga* silks, *ga* as well as *Ga* pollen should have functioned in the production of 50 percent of the kernels. As the percentage of functioning *ga* pollen approaches 50,

the deviations from normal percentages of *su* or Ts_5 approach zero; and, with zero deviation, 50 percent of recombination is indicated for any percentage of functioning *ga* gametes from zero to 50. These calculations, therefore, reveal just what was to have been expected.

EYSTER (1921) reported 29 percent of recombination between sugary and tunicate, *Tu*. The writer has backcross data from 4206 individuals, involving both coupling and repulsion phases of linkage, which also indicate 29 as the percentage of recombination. A cross of common sugary tunicate, *ga su Tu*, with rice pop, *Ga Su tu*, backcrossed on *Ga su tu* plants, gave the following distribution:

Genotype of F_1	Backcross progeny *Su Tu*	*Su tu*	*su Tu*	*su tu*	*Total*
Ga Su tu/ga su Tu	281	552	188	92	1113

These data show 33.5 percent of recombination between *su* and *Tu*, and 25.2 percent *su* and 42.1 percent *Tu*. These percentages, with no effective *ga* pollen, become the percentages of recombination between *Ga* and *su* and between *Ga* and *Tu*, respectively. With 4 percent functioning *ga* pollen, the respective percentages are 23.0 and 41.4. The order of these genes, therefore, is *Ga su Tu*.

The several combinations of the six genes considered here have been shown by two-point tests to have approximately the following percentages of crossing over:

de_1 *Ga* 35, de_1 *su* 47, de_{16} *Ga* 34, de_{16} *su* 3, *Ga su* 29, *Ga* Ts_5 20, *Ga Tu* 42, *su* Ts_5 14, *su Tu* 29. The order of the genes and their approximate spacing, therefore, is apparently as follows:

de_1 35 *Ga* 20 Ts_5 14 *su* 3 de_{16} 26 *Tu*.

THREE-POINT TESTS INVOLVING *Ga ga*

Backcross data involving two other genes linked with *Ga* can be arranged in three-point tables from which can be determined the percentages of crossing over between any two of the three genes and the coincidence of crossing over. It is, however, essential to know, at least approximately, the percentages of functioning *Ga* and *ga* pollen. It has been shown, both by the method of MANGELSDORF and JONES (1926) and by the method of mixed pollen, that *ga* pollen in competition with *Ga* pollen on *Ga* silks functions in the fertilization of from 0 to 4 percent of the kernels. Both these percentages, therefore, will be used in the examples to be given here.

For any order of the three genes, let

N = the total number of individuals

w = the number of non-crossovers

x = the number of single crossovers in region 1

y = the number of single crossovers in region 2
z = the number of double crossovers
p = the percentage of functioning *Ga* pollen
q = the percentage of functioning *ga* pollen.

The data presented earlier for *Ga su Tu* will be used in illustrating the method under consideration. The observed frequency distribution is:

Su Tu	*Su tu*	*su Tu*	*su tu*	Total
281	552	188	92	1113

These data will be considered first on the assumption that 4 percent of *ga* pollen functions. It is known from the parents crossed to produce the F_1 generation whether *Ga* is linked with the dominant or recessive member of the *Su su* and *Tu tu* pairs, but, for purposes of illustration, this information will be disregarded. Since the observed frequencies show that *Su* and *tu* individuals are in excess of *su* and *Tu* ones, respectively, *Ga* must be linked with *Su* and *tu*, and *ga* with *su* and *Tu*. This eliminates all but three of the twelve possible F_1 genotypes. The observed frequencies show also that the ratio of *Su*:*su* deviates much more from the normal 1:1 ratio than does the ratio of *Tu*:*tu*. This indicates that *Ga ga* must be closer to *Su su* than to *Tu tu*; and this fact eliminates one of the three F_1 genotypes, leaving as possibilities only these two:

$$\frac{Ga\ Su\ tu}{ga\ su\ Tu} \quad \text{and} \quad \frac{Su\ Ga\ tu}{su\ ga\ Tu}.$$

These will be considered in the order given. Then:

$$Su\ Tu = py + qz = 281$$
$$su\ tu = qy + pz = \ \ 92$$
$$y + z = 373$$
$$y = 373 - z$$
$$z = 373 - y.$$

Substituting for y in the *Su Tu* equation,

$$p(373 - z) + qz = 281$$
$$373p - pz + qz = 281$$
$$(p - q)z = 373p - 281$$
$$z = (373p - 281)/p - q$$
$$= 77.08/0.92 = 83.78$$
$$z/N = 83.78/1113 = 7.5 \text{ percent.}$$

Substituting for z in the *Su Tu* equation and solving,

$$py+q\ (373-y)=281$$
$$y=289.22,\ y/N=26.0 \text{ percent}$$

Similarly,

$$\begin{aligned} Su\ tu &= pw+qx=552 \\ su\ Tu &= qw+px=188 \\ \hline w+\ x &= 740 \\ w &= 740-x \\ x &= 740-w. \end{aligned}$$

Substituting in the *Su tu* equation for w and for x and solving,

$$p\ (740-x)+qx=552$$
$$pw+q\ (740-w)=552$$
$$x=172.17,\ x/N=15.5 \text{ percent}$$
$$w=567.83.$$

The recombination percentages are:

Ga Su	15.5+ 7.5=23.0
Su Tu	26.0+ 7.5=33.5
Ga Tu	15.5+26.0=41.5.

The genotype chosen for illustration, *Ga Su tu/ga su Tu*, is in agreement with the calculated recombination percentages. When the other of the two supposedly possible genotypes, *Su Ga tu/su ga Tu*, is chosen, identically the same recombination percentages are obtained by the method of calculation used here, but such an arrangement of the genes is impossible with the recombination percentages found.

On the assumption that no *ga* pollen functions, the calculation of cross-over percentages is greatly simplified. On that assumption, p=1 and q=0, and the equations become:

$$Su\ Tu=py+qz=y=281.\ y/N=25.2 \text{ percent}$$
$$su\ tu=qy+pz=z=92.\ z/N=8.3 \text{ percent}$$
$$Su\ tu=pw+qx=w=552.$$
$$su\ Tu=qw+px=x=182.\ x/N=16.9 \text{ percent.}$$

Three-point tables can be constructed from these data from *Ga su tu*× *Ga Su tu/ga su Tu*, as follows:

PERCENTAGE OF FUNCTIONING *Ga* AND *ga* POLLEN, p AND q	NON-CROSSOVERS		SINGLE CROSSOVERS, REGION 1		SINGLE CROSSOVERS, REGION 2		DOUBLE CROSSOVERS		TOTAL
	Ga Su tu	*ga su Tu*	*Ga su Tu*	*ga Su tu*	*Ga Su Tu*	*ga su tu*	*Ga su tu*	*ga Su Tu*	
	pw	qw	px	qx	py	qy	pz	qz	N
p=0.96, q=0.04	545	23	165	7	278	12	80	3	1113
	568		172		290		83		
			15.47 percent		25.99 percent		7.53 percent		

Recombination percentages: *Ga Su* 23.00, *Su Tu* 33.52, *Ga Tu* 41.46
Coincidence = 0.9767

	Ga Su tu	*Ga su Tu*	*Ga Su Tu*	*Ga su tu*	
	w	x	y	z	
p=1, q=0	552	188	281	92	1113
		16.89 percent	25.25 percent	8.26 percent	

Recombination percentages: *Ga Su* 25.15, *Su Tu* 33.51, *Ga Tu* 42.14
Coincidence = 0.9801

In the same way, the data from *Ga* ts_5 *su*×*Ga* ts_5 *su*/*ga* Ts_5 *Su* (table 4, backcross 4) are arranged in the following three-point table:

PERCENTAGE OF FUNCTIONING *Ga* AND *ga* POLLEN, p AND q	NON-CROSSOVERS		SINGLE CROSSOVERS, REGION 1		SINGLE CROSSOVERS, REGION 2		DOUBLE CROSSOVERS		TOTAL
	Ga ts_5 *su*	*ga* Ts_5 *Su*	*Ga* Ts_5 *Su*	*ga* ts_5 *su*	*Ga* ts_5 *Su*	*ga* Ts_5 *su*	*Ga* Ts_5 *su*	*ga* ts_5 *Su*	
	pw	qw	px	qx	py	qy	pz	qz	N
p=0.96, q=0.04	618	26	141	6	106	4	24	1	926
	644		147		110		25		
			15.87 percent		11.88 percent		2.70 percent		

Recombination percentages: *Ga* Ts_5 18.57, Ts_5 *su* 14.58, *Ga su* 27.75
Coincidence = 0.9972

	Ga ts_5 *su*	*Ga* Ts_5 *Su*	*Ga* ts_5 *Su*	*Ga* Ts_5 *su*	
	w	x	y	z	
p=1, q=0	624	167	107	28	926
		18.03 percent	11.56 percent	3.02 percent	

Recombination percentages: *Ga* Ts_5 21.05, Ts_5 *su* 14.58, *Ga su* 29.59
Coincidence = 0.9840

That coincidence of crossing over is practically unity, even for the relatively short map distances involved in the data for *Ga* Ts_5 *su*, suggests

the possibility that *Ga* and *su* may be on opposite sides of the spindle fiber insertion region.

It is of interest to compare the percentages of recombination for these *su-Tu* and Ts_5-*su* data as calculated by this three-point method with those determined directly from a chart based on deviations from normal ratios and constructed by the method of Mangelsdorf and Jones (1926). The comparison is given below both for zero and for 4 percent of functioning *ga* pollen.

	Functioning *ga* pollen			
	Zero percent		4 percent	
	Deviation method	3-point method	Deviation method	3-point method
su-Tu data				
Ga su	25.2	25.2	23.0	23.0
Ga Tu	42.1	42.1	41.4	41.5
Ts_5-*su* data				
Ga Ts_5	21.1	21.1	18.5	18.6
Ga su	29.6	29.6	27.8	27.8

SUMMARY

The effect of the genes *Ga ga* in causing deviations from normal 3:1 and 1:1 ratios is discussed, the results of other investigators showing the relation of *Ga ga* to De_1 de_1, De_{16} de_{16}, *Su su* are reviewed, and data are presented on the relations of *Ga ga* to *Su su*, Ts_5 ts_5, and *Tu tu*. Methods of evaluating the effectiveness of *Ga ga* and of determining recombination percentages are discussed. The relations of the six genes considered are summarized in terms of their linear order and approximate spacing on the genetic map, as follows: de_1 35 *Ga* 20 Ts_5 14 *su* 3 de_{16} 26 *Tu*.

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