1934

Relation of the Differential Fertilization Genes, Ga ga, to Certain Other Genes of the Su-Tu Linkage Group of Maize

R. A. Emerson

University of Nebraska-Lincoln

Follow this and additional works at: http://digitalcommons.unl.edu/agronomyfacpub

Part of the Agricultural Science Commons, Agriculture Commons, Agronomy and Crop Sciences Commons, Botany Commons, Horticulture Commons, Other Plant Sciences Commons, and the Plant Biology Commons

Emerson, R. A., "Relation of the Differential Fertilization Genes, Ga ga, to Certain Other Genes of the Su-Tu Linkage Group of Maize" (1934). Agronomy & Horticulture -- Faculty Publications. 914.

http://digitalcommons.unl.edu/agronomyfacpub/914

This Article is brought to you for free and open access by the Agronomy and Horticulture Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Agronomy & Horticulture -- Faculty Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
RELATION OF THE DIFFERENTIAL FERTILIZATION GENES, \(Ga\) \(ga\), TO CERTAIN OTHER GENES OF THE \(Su-Tu\) LINKAGE GROUP OF MAIZE

R. A. EMERSON

Department of Plant Breeding, Cornell University, Ithaca, New York

Received April 23, 1933

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.

Genetics 19 (1934), pp 137-156.
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>
<thead>
<tr>
<th>Item</th>
<th>Number</th>
<th>Number of preceding generation</th>
<th>Number of kernels</th>
<th>Percentage of starchy</th>
<th>Percentage of sugary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>F2</td>
<td>834</td>
<td>203,700</td>
<td>68,089</td>
<td>271,789</td>
</tr>
<tr>
<td>2</td>
<td>F3</td>
<td>F2 normal</td>
<td>148</td>
<td>31,051</td>
<td>41,224</td>
</tr>
</tbody>
</table>

Rice pop crossed with common sugary

<table>
<thead>
<tr>
<th>F1 genotype: Ga Su/ga su</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Item</th>
<th>Number</th>
<th>Number of preceding generation</th>
<th>Number of kernels</th>
<th>Percentage of starchy</th>
<th>Percentage of sugary</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>F2</td>
<td>363</td>
<td>111,368</td>
<td>19,798</td>
<td>131,166</td>
</tr>
<tr>
<td>4</td>
<td>F4</td>
<td>96</td>
<td>26,340</td>
<td>5,009</td>
<td>31,349</td>
</tr>
<tr>
<td>5</td>
<td>F4 low</td>
<td>81</td>
<td>20,171</td>
<td>6,505</td>
<td>26,676</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>16</td>
<td>2,858</td>
<td>1,608</td>
<td>4,466</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>52</td>
<td>10,646</td>
<td>2,147</td>
<td>12,793</td>
</tr>
<tr>
<td>8</td>
<td>F2 low</td>
<td>63</td>
<td>14,286</td>
<td>4,681</td>
<td>18,967</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>6</td>
<td>977</td>
<td>522</td>
<td>1,499</td>
</tr>
<tr>
<td>10</td>
<td>F4 normal</td>
<td>75</td>
<td>16,526</td>
<td>5,600</td>
<td>22,126</td>
</tr>
<tr>
<td>11</td>
<td>F4 high</td>
<td>4</td>
<td>272</td>
<td>55</td>
<td>327</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td>39</td>
<td>7,501</td>
<td>2,465</td>
<td>9,966</td>
</tr>
<tr>
<td>13</td>
<td></td>
<td>32</td>
<td>6,124</td>
<td>3,669</td>
<td>9,793</td>
</tr>
</tbody>
</table>

Common starchy crossed with sugary derivatives of rice pop

<table>
<thead>
<tr>
<th>F1 genotype: ga Su/Ga su</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Item</th>
<th>Number</th>
<th>Number of preceding generation</th>
<th>Number of kernels</th>
<th>Percentage of starchy</th>
<th>Percentage of sugary</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>F2</td>
<td>263</td>
<td>60,704</td>
<td>33,775</td>
<td>94,479</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td>21</td>
<td>4,994</td>
<td>876</td>
<td>5,870</td>
</tr>
<tr>
<td>16</td>
<td>F4</td>
<td>F4 high</td>
<td>99</td>
<td>23,067</td>
<td>7,932</td>
</tr>
<tr>
<td>17</td>
<td></td>
<td>101</td>
<td>19,953</td>
<td>10,820</td>
<td>30,773</td>
</tr>
</tbody>
</table>

Rice pop crossed with sugary derivatives of rice pop

<table>
<thead>
<tr>
<th>F1 genotype: Ga Su/Ga su</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Item</th>
<th>Number</th>
<th>Number of preceding generation</th>
<th>Number of kernels</th>
<th>Percentage of starchy</th>
<th>Percentage of sugary</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>F2</td>
<td>197</td>
<td>60,670</td>
<td>20,200</td>
<td>80,870</td>
</tr>
<tr>
<td>19</td>
<td>F4</td>
<td>F4 normal</td>
<td>9</td>
<td>1,601</td>
<td>2,151</td>
</tr>
</tbody>
</table>
DIFFERENTIAL FERTILIZATION IN MAIZE

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 F2 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 F2 progenies had approximately 25 percent sugary while the other half showed a wide departure from 25 percent.

Not only was the F2 percentage of sugary in these crosses involving Ga ga different from that of the crosses involving ga ga, but the F3 behavior also was different. F3 progenies from Su-su F2's of the latter crosses were all of one class, the percentage of sugary varying about 25 as a mean. The F3 progenies of Su-su F2'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 F3 class repeated in F4 the behavior of F2 starchy kernels in F3. 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 F3 and F4 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 F4 progenies from Su-su plants of the normal sugary F3 class showed normal sugary only, the mean percentage being 25.3 (table 1, item 10). The high sugary F3 lot gave the same three F4 classes of low, normal, and
high sugary as did the low sugary F₃’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 F₃ and F₄ 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 F₂, with a mean percentage of 35.7 (table 1, item 14). When these sugary derivatives are Ga ga, there occur in F₂, of course, both normal and high sugary progenies in nearly equal numbers. Heterozygous starchy kernels from high sugary ears of F₂ of this cross repeat in F₃ the behavior in F₄ of similar kernels of high sugary F₂ 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 F₄ and F₃ 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 F₂ and F₃. 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 F₂ was 25.0 and in F₃, 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.

<table>
<thead>
<tr>
<th>Constitution of Heterozygotes and Type of Pollination</th>
<th>Number of Heterozygous Plants</th>
<th>Number of Kernels</th>
<th>Percent Sugary</th>
</tr>
</thead>
<tbody>
<tr>
<td>( Ga ) ( Su/ga ) su</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Self-pollinated</td>
<td>50</td>
<td>14,252</td>
<td>4,736</td>
</tr>
<tr>
<td>Crossed by ( ga ) su ( \sigma )</td>
<td>6</td>
<td>853</td>
<td>807</td>
</tr>
<tr>
<td>Crossed by ( Ga ) su ( \sigma )</td>
<td>14</td>
<td>1,917</td>
<td>1,798</td>
</tr>
<tr>
<td>Crossed on ( ga ) su ( \varphi )</td>
<td>41</td>
<td>3,771</td>
<td>3,992</td>
</tr>
<tr>
<td>Crossed on ( Ga ) su ( \varphi )</td>
<td>50</td>
<td>5,579</td>
<td>5,643</td>
</tr>
<tr>
<td>( Ga ) ( Su/Ga ) su</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Self-pollinated</td>
<td>10</td>
<td>4,272</td>
<td>1,412</td>
</tr>
<tr>
<td>Crossed by ( ga ) su ( \sigma )</td>
<td>4</td>
<td>581</td>
<td>593</td>
</tr>
<tr>
<td>Crossed by ( Ga ) su ( \sigma )</td>
<td>3</td>
<td>479</td>
<td>471</td>
</tr>
<tr>
<td>Crossed on ( ga ) su ( \varphi )</td>
<td>2</td>
<td>191</td>
<td>214</td>
</tr>
<tr>
<td>Crossed on ( Ga ) su ( \varphi )</td>
<td>5</td>
<td>547</td>
<td>573</td>
</tr>
<tr>
<td>( Ga ) ( Su/ga ) su</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Self-pollinated</td>
<td>53</td>
<td>19,498</td>
<td>3,296</td>
</tr>
<tr>
<td>Crossed by ( ga ) su ( \sigma )</td>
<td>13</td>
<td>2,518</td>
<td>2,451</td>
</tr>
<tr>
<td>Crossed by ( Ga ) su ( \sigma )</td>
<td>16</td>
<td>3,663</td>
<td>3,535</td>
</tr>
<tr>
<td>Crossed on ( ga ) su ( \varphi )</td>
<td>45</td>
<td>5,328</td>
<td>5,796</td>
</tr>
<tr>
<td>Crossed on ( Ga ) su ( \varphi )</td>
<td>44</td>
<td>8,860</td>
<td>3,844</td>
</tr>
<tr>
<td>( Ga ) ( su/ga ) Su</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Self-pollinated</td>
<td>24</td>
<td>5,805</td>
<td>3,494</td>
</tr>
<tr>
<td>Crossed by ( ga ) su ( \sigma )</td>
<td>4</td>
<td>541</td>
<td>509</td>
</tr>
<tr>
<td>Crossed by ( Ga ) su ( \sigma )</td>
<td>11</td>
<td>1,425</td>
<td>1,412</td>
</tr>
<tr>
<td>Crossed on ( ga ) su ( \varphi )</td>
<td>14</td>
<td>2,010</td>
<td>1,903</td>
</tr>
<tr>
<td>Crossed on ( Ga ) su ( \varphi )</td>
<td>17</td>
<td>1,768</td>
<td>3,729</td>
</tr>
</tbody>
</table>

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.
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 \( De \, de_1 \). 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° 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.  

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 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 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, 17.8 percent de, 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 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 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 and 29.6 for Ga and su, the combined map distances of which are about 70.8. 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.

---

* The frequency distribution reported by MANGELSDORF and JONES (1926) of 601 De, Su, 238 De, su, 247 de, Su, 64 de, 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,
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 De₁ to de₁ 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:

<table>
<thead>
<tr>
<th>Su Su</th>
<th>Ga Su/Ga Su = p r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Su su</td>
<td>Ga Su/ga Su = (p+q)rs = p r² + (p+q)rs + q s²</td>
</tr>
<tr>
<td></td>
<td>ga Su/ga Su = q s²</td>
</tr>
</tbody>
</table>

Total Su Su and su su = (p+q) r² + 2(p+q) rs + (p+q) s²
DIFFERENTIAL FERTILIZATION IN MAIZE

$Su \; su$

$Ga \; Su/Ga \; su = 2p \; rs$

$ga \; Su/ga \; su = 2q \; rs$

$Ga \; Su/ga \; su = (p+q)r^2$

$Ga \; su/ga \; Su = (p+q)s^2$

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:

<table>
<thead>
<tr>
<th>Progenies</th>
<th>Parent ears</th>
<th>Low sugary</th>
<th>Normal sugary</th>
<th>High sugary</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low sugary</td>
<td>148</td>
<td>144</td>
<td>22</td>
<td></td>
<td>314</td>
</tr>
<tr>
<td>High sugary</td>
<td>25</td>
<td>138</td>
<td>133</td>
<td></td>
<td>296</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Like parent ear</th>
<th>Reverse of parent ear</th>
<th>Total</th>
<th>Value of χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>281 282</td>
<td>47</td>
<td>610</td>
<td></td>
</tr>
</tbody>
</table>

Calculated for recombination percentage of—

<table>
<thead>
<tr>
<th>percentage of—</th>
<th>Like parent ear</th>
<th>Reverse of parent ear</th>
<th>Total</th>
<th>Value of χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
<td>316</td>
<td>246</td>
<td>48</td>
<td>610</td>
</tr>
<tr>
<td>29</td>
<td>307</td>
<td>252</td>
<td>51</td>
<td>610</td>
</tr>
<tr>
<td>30</td>
<td>299</td>
<td>256</td>
<td>55</td>
<td>610</td>
</tr>
<tr>
<td>31</td>
<td>290</td>
<td>261</td>
<td>59</td>
<td>610</td>
</tr>
<tr>
<td>32</td>
<td>282</td>
<td>266</td>
<td>62</td>
<td>610</td>
</tr>
<tr>
<td>33</td>
<td>271</td>
<td>271</td>
<td>68</td>
<td>610</td>
</tr>
</tbody>
</table>

The first and third terms, r² and s², 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, χ² = 6.1 and P = 0.048. A considerably better fit is shown by the distribution calculated for 31 percent recombination, χ² = 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:

<table>
<thead>
<tr>
<th>Parent ears</th>
<th>Progenies</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Su Su</td>
<td>Su su</td>
<td>su su</td>
</tr>
<tr>
<td>Low sugary</td>
<td>34.6</td>
<td>50.0</td>
<td>15.4</td>
</tr>
<tr>
<td>Normal sugary</td>
<td>25.0</td>
<td>50.0</td>
<td>25.0</td>
</tr>
<tr>
<td>High sugary</td>
<td>14.3</td>
<td>50.0</td>
<td>35.7</td>
</tr>
</tbody>
</table>

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:

<table>
<thead>
<tr>
<th>Parent ears</th>
<th>Progenies</th>
<th></th>
<th></th>
<th></th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Su Su</td>
<td>Su su</td>
<td>Total</td>
<td>Su Su</td>
<td></td>
</tr>
<tr>
<td>Low sugary—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>227</td>
<td>352</td>
<td>579</td>
<td>39.2</td>
<td></td>
</tr>
<tr>
<td>Calculated</td>
<td>237</td>
<td>342</td>
<td>579</td>
<td>40.9</td>
<td></td>
</tr>
<tr>
<td>Difference</td>
<td>-10</td>
<td>+10</td>
<td>0</td>
<td>-1.7</td>
<td></td>
</tr>
<tr>
<td>Normal sugary—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>98</td>
<td>210</td>
<td>308</td>
<td>31.8</td>
<td></td>
</tr>
<tr>
<td>Calculated</td>
<td>103</td>
<td>205</td>
<td>308</td>
<td>33.3</td>
<td></td>
</tr>
<tr>
<td>Difference</td>
<td>-5</td>
<td>+5</td>
<td>0</td>
<td>-1.5</td>
<td></td>
</tr>
<tr>
<td>High sugary—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>94</td>
<td>353</td>
<td>447</td>
<td>21.0</td>
<td></td>
</tr>
<tr>
<td>Calculated</td>
<td>99</td>
<td>348</td>
<td>447</td>
<td>22.2</td>
<td></td>
</tr>
<tr>
<td>Difference</td>
<td>-5</td>
<td>+5</td>
<td>0</td>
<td>-1.2</td>
<td></td>
</tr>
</tbody>
</table>

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, \textit{de}_1, and in a low defective lot with 1022 kernels 16.8 percent were \textit{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 \textit{de}_1 kernels. On the assumption that no \textit{ga} pollen functions on \textit{Ga} silks, this percentage should result from 35.6 percent of recombination between \textit{Ga ga} and \textit{De}_1 \textit{de}_1. The percentage of recombination calculated on the basis of 4 percent of effective \textit{ga} pollen is 34.3. It may be concluded, then, that the recombination value is not far from 35 percent.

Another defective, \textit{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 \textit{ga} pollen, respectively. The recombination value for \textit{Ga ga} and \textit{De}_{16} \textit{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 \textit{de}_1 and \textit{su}. WENTZ (1925) reported a recombination percentage of 3.2 for \textit{de}_{16} and \textit{su} calculated from counts of 28,276 kernels. Since the writer's records indicate approximately 29 percent of recombination between \textit{Ga} and \textit{su}, the order of these genes is probably: \textit{de}_1, \textit{Ga}, \textit{su}, \textit{de}_{16}.

Tassel seed-5 plants with sun-red plant color, \textit{ga} \textit{Ts}_5 \textit{B}, were crossed with rice pop which was dilute sun-red and had normal tassels, \textit{Ga} \textit{ts}_5 \textit{b}. Pollen of the \textit{F}_1 plants was applied to silks of plants having the genotypes \textit{ga} \textit{ts}_5 \textit{b} and \textit{Ga} \textit{ts}_5 \textit{b}, with the following results:

<table>
<thead>
<tr>
<th>Backcross Progeny</th>
<th>\textit{T}_5 \textit{s}</th>
<th>\textit{ts}_5</th>
<th>Total</th>
<th>Percent \textit{T}_5 \textit{s}</th>
<th>Percent \textit{b}</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{ga} \textit{ts}_5 \textit{b}</td>
<td>401</td>
<td>449</td>
<td>850</td>
<td>47.2</td>
<td>45.3</td>
</tr>
<tr>
<td>\textit{Ga} \textit{ts}_5 \textit{b}</td>
<td>244</td>
<td>570</td>
<td>814</td>
<td>30.0</td>
<td>47.4</td>
</tr>
</tbody>
</table>

Although there was a deficiency of \textit{T}_5 \textit{s} in the progeny of the backcross on \textit{ga} \textit{ts}_5 \textit{b}, it is less than that of the recessive, \textit{b}. When the \textit{F}_1 was backcrossed on \textit{Ga} \textit{ts}_5 \textit{b}, however, the deficiency of \textit{T}_5 \textit{s} was much more while that of \textit{b} was less than for the other backcross. The \textit{B}-\textit{b} pair is known to belong to another linkage group and the percentage of \textit{b}-plants, therefore, should not be disturbed by \textit{Ga}. The gene \textit{T}_5 \textit{s} is known to belong to the \textit{su}-\textit{T}u group. With no functioning \textit{ga} pollen, the percent of \textit{T}_5 \textit{s} should be the percent of recombination between \textit{Ga} and \textit{T}_5 \textit{s}.
DIFFERENTIAL FERTILIZATION IN MAIZE

Table 4
Backcrosses of ga ts5 su/ga Ts5 Su and Ga ts5 su/ga Ts5 Su on ga ts5 su and Ga ts5 su.

<table>
<thead>
<tr>
<th>GENOTYPE OF F1 AND OF PARENT OF BACKCROSS</th>
<th>NUMBER OF INDIVIDUALS</th>
<th>RECOMBINATIONS</th>
<th>PERCENTAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Su Ts5 Su ts5 Su Ts5 su Ts5 Su ts5 Su</td>
<td>Su Ts5 Su Ts5 Su ts5 Su</td>
<td>Su Ts5 Su Ts5 Su ts5 Su</td>
</tr>
<tr>
<td>F1 ga ts5 su ga Ts5 Su</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1—ga ts5 su</td>
<td>158 22 28 155</td>
<td>363</td>
<td>50 13.6 50.4 51.2</td>
</tr>
<tr>
<td>2—Ga ts5 su</td>
<td>161 28 21 154</td>
<td>364</td>
<td>49 13.5 48.1 50.0</td>
</tr>
<tr>
<td>F1 ga ts5 su b Ga ts5 Su b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3—ga ts5 su b</td>
<td>213 38 42 232</td>
<td>525</td>
<td>80 15.2 52.2 48.6 48.0</td>
</tr>
<tr>
<td>4—Ga ts5 su b</td>
<td>167 107 28 624</td>
<td>926</td>
<td>135 14.6 70.4 21.1 47.4</td>
</tr>
<tr>
<td>Total</td>
<td>699 195 119 1165 2178</td>
<td>314</td>
<td>14.4</td>
</tr>
</tbody>
</table>

Common starchy tassel seed-5 plants, ga Ts5 Su, were crossed both with common sugary, ga ts5 su, and with sugary derivatives of rice pop, Ga ts5 su. The F1's of both lots were then backcrossed on ga ts5 su and on Ga ts5 su. As for the crosses noted above, some of the F1'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, Ts5 or b, except for the backcross Ga ts5 su×Ga ts5 su/ga Ts5 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 Ts5. These wide deviations from 50 percent, however, did not disturb the percentage of recombination between su and Ts5 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 Ts5, 21.1, indicate, with no functioning ga pollen, percentages of recombination of 29.6 for Ga su and 21.1 for Ga Ts5; or, with 4 percent functioning ga pollen, 27.8 and 18.5, respectively. The recombination percentages may be taken, therefore, as 14 for su Ts5, 20 for Ga Ts5, and 29 for Ga su, and the order of the genes as Ga Ts5 su.

If the percentages of recombination between Ga su and between Ga Ts5 were calculated from the percentages of su and of Ts5 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 F1 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 Ts₅ 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:

<table>
<thead>
<tr>
<th>Genotype of F₁</th>
<th>Backcross progeny</th>
</tr>
</thead>
<tbody>
<tr>
<td>Su Tu</td>
<td>Su tu</td>
</tr>
<tr>
<td>su Tu</td>
<td>su tu</td>
</tr>
<tr>
<td>Total</td>
<td></td>
</tr>
<tr>
<td>Ga Su tu/ga su Tu</td>
<td>281</td>
</tr>
<tr>
<td></td>
<td>552</td>
</tr>
<tr>
<td></td>
<td>188</td>
</tr>
<tr>
<td></td>
<td>92</td>
</tr>
<tr>
<td></td>
<td>1113</td>
</tr>
</tbody>
</table>

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:

\[ de₁, Ga 35, de₁ su 47, de₁₆ Ga 34, de₁₆ su 3, Ga su 29, Ga Ts₅ 20, Ga Tu 42, su Ts₅ 14, su Tu 29. \]

The order of the genes and their approximate spacing, therefore, is apparently as follows:

\[ de₁ 35 Ga 20 Ts₅ 14 su 3 de₁₆ 26 Tu. \]

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

\[ N = \text{the total number of individuals} \]

\[ w = \text{the number of non-crossovers} \]

\[ x = \text{the number of single crossovers in region 1} \]
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:

<table>
<thead>
<tr>
<th>Su Tu</th>
<th>Su tu</th>
<th>su Tu</th>
<th>su tu</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>281</td>
<td>552</td>
<td>188</td>
<td>92</td>
<td>1113</td>
</tr>
</tbody>
</table>

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 F1 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 F1 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 F1 genotypes, leaving as possibilities only these two:

\[ \text{Ga Su tu} \quad \text{and} \quad \text{Su Ga tu} \]

These will be considered in the order given. Then:

\[ \begin{align*}
  & Su Tu = py + qz = 281 \\
  & su tu = qy + pz = 92 \\
  \hline
  & y + z = 373 \\
  & y = 373 - z \\
  & z = 373 - y
\end{align*} \]

Substituting for y in the Su Tu equation,

\[ \begin{align*}
  p(373 - z) + qz &= 281 \\
  373p - pz + qz &= 281 \\
  (p - q)z &= 373p - 281 \\
  z &= (373p - 281)/p - q \\
  &= 77.08/0.92 = 83.78 \\
  z/N &= 83.78/1113 = 7.5 \text{ percent.}
\end{align*} \]
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,
\[
\begin{align*}
Su \ tu &= pw + qx = 552 \\
-su \ Tu &= qw + px = 188 \\
\end{align*}
\]
\[
\begin{align*}
w + x &= 740 \\
w &= 740 - x \\
x &= 740 - w.
\end{align*}
\]

Substituting in the \( Su \ tu \) equation for \( w \) and for \( x \) and solving,
\[
\begin{align*}
p (740 - x) + qx &= 552 \\
pw + q (740 - w) &= 552 \\
x &= 172.17, \ x/N = 15.5 \text{ percent} \\
w &= 567.83.
\end{align*}
\]

The recombination percentages are:
\[
\begin{align*}
Ga \ Su &= 15.5 + 7.5 = 23.0 \\
Su \ Tu &= 26.0 + 7.5 = 33.5 \\
Ga \ Tu &= 15.5 + 26.0 = 41.5.
\end{align*}
\]

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:
\[
\begin{align*}
Su \ Tu &= py + qz = y = 281, \ y/N = 25.2 \text{ percent} \\
su \ tu &= qy + pz = z = 92, \ z/N = 8.3 \text{ percent} \\
Su \ tu &= pw + qx = w = 552. \\
su \ Tu &= qw + px = x = 182, \ x/N = 16.9 \text{ percent}.
\end{align*}
\]

Three-point tables can be constructed from these data from \( Ga \ su \ tu \times Ga \ Su \ tu / ga \ su \ Tu \), as follows:
Differential Fertilization in Maize

<table>
<thead>
<tr>
<th>PERCENTAGE OF FUNCTIONING Ga AND gs POLLEN, p AND q</th>
<th>SINGLE CROSVERS, REGION 1</th>
<th>SINGLE CROSVERS, REGION 2</th>
<th>DOUBLE CROSVERS</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ga Su Tu ga su Tu</td>
<td>Ga Su Tu ga Su Tu</td>
<td>Ga Su Tu ga su Tu</td>
<td>Ga Su Tu ga Su Tu</td>
<td></td>
</tr>
<tr>
<td>p=0.96, q=0.04</td>
<td>545 23</td>
<td>165 7</td>
<td>278 12</td>
<td>80 3</td>
</tr>
<tr>
<td>568</td>
<td>172</td>
<td>290</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>15.47</td>
<td>25.99</td>
<td>7.53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>percent</td>
<td>percent</td>
<td>percent</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Ga Su Tu</th>
<th>Ga su Tu</th>
<th>Ga Su Tu</th>
<th>Ga su tu</th>
</tr>
</thead>
<tbody>
<tr>
<td>p=1, q=0</td>
<td>552</td>
<td>188</td>
<td>281</td>
</tr>
<tr>
<td>16.89</td>
<td>25.25</td>
<td>8.26</td>
<td></td>
</tr>
<tr>
<td>percent</td>
<td>percent</td>
<td>percent</td>
<td></td>
</tr>
</tbody>
</table>

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 ts6 su × Ga ts6 su / ga Ts8 Su (table 4, backcross 4) are arranged in the following three-point table:

<table>
<thead>
<tr>
<th>PERCENTAGE OF FUNCTIONING Ga AND gs POLLEN, p AND q</th>
<th>SINGLE CROSVERS, REGION 1</th>
<th>SINGLE CROSVERS, REGION 2</th>
<th>DOUBLE CROSVERS</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ga ts6 su ga Ts6 Su</td>
<td>Ga Ts6 Su ga ts6 su</td>
<td>Ga ts6 Su ga Ts6 su</td>
<td>Ga Ts6 Su ga ts6 su</td>
<td></td>
</tr>
<tr>
<td>p=0.96, q=0.04</td>
<td>618 26</td>
<td>141 6</td>
<td>106 4</td>
<td>24 1</td>
</tr>
<tr>
<td>644</td>
<td>147</td>
<td>110</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>15.87</td>
<td>11.88</td>
<td>2.70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>percent</td>
<td>percent</td>
<td>percent</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Recombination percentages: Ga Ts6 18.57, Ts6 su 14.58, Ga Ts6 27.75
Coincidence = 0.9972

<table>
<thead>
<tr>
<th>Ga ts6 su</th>
<th>Ga Ts6 Su</th>
<th>Ga ts6 Su</th>
<th>Ga Ts6 su</th>
</tr>
</thead>
<tbody>
<tr>
<td>p=1, q=0</td>
<td>624</td>
<td>167</td>
<td>107</td>
</tr>
<tr>
<td>18.03</td>
<td>11.56</td>
<td>3.02</td>
<td></td>
</tr>
<tr>
<td>percent</td>
<td>percent</td>
<td>percent</td>
<td></td>
</tr>
</tbody>
</table>

Recombination percentages: Ga Ts6 21.05, Ts6 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 Ts6 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 Ts5-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.

<table>
<thead>
<tr>
<th>Functioning ga pollen</th>
<th>Zero percent</th>
<th>4 percent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deviation</td>
<td>3-point</td>
</tr>
<tr>
<td></td>
<td>method</td>
<td>method</td>
</tr>
<tr>
<td>su-Tu data</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ga su</td>
<td>25.2</td>
<td>25.2</td>
</tr>
<tr>
<td>Ga Tu</td>
<td>42.1</td>
<td>42.1</td>
</tr>
<tr>
<td>Ts5-su data</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ga Ts5</td>
<td>21.1</td>
<td>21.1</td>
</tr>
<tr>
<td>Ga su</td>
<td>29.6</td>
<td>29.6</td>
</tr>
</tbody>
</table>

**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 De1 de1, De16 de16, Su su are reviewed, and data are presented on the relations of Ga ga to Su su, Ts5 ts5, 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: de1 35 Ga 20 Ts5 14 su 3 de16 26 Tu.

**LITERATURE CITED**


EYSTER, W. H., 1921 The linkage relations between the factors for tunicate ear and sugary endosperm in maize. Genetics 6: 209-240.

HALDANE, J. B. S., 1919 The combination of linkage values and calculation of distances between loci of linked factors. J. Genet. 8: 299-309.


