the order of the central of \( G \) must be finite and hence \( g \) is finite. That is, there is only a finite number of groups which contain a fixed number, greater than zero, of complete sets of non-invariant conjugate operators. From the theorem at the close of the preceding paragraph it results that there is an infinite number of groups such that each group contains one and only one complete set of non-invariant conjugate subgroups.

When \( G \) contains three and only three complete sets of non-invariant conjugate operators it results that one of the three numbers \( g_1, g_2, g_3 \) is at most as large as 4. If this smallest number is 2 then \( G \) is the dihedral group of order 10. When it is 3 then the central of \( G \) must be the identity as this is obviously always true when at least one of the numbers \( g_1, g_2, \ldots, g_n \) is a prime number. Hence the order of \( G \) is 12 and \( G \) is the tetrahedral group. Finally, when the smallest of the three numbers \( g_1, g_2, g_3 \) is 4 then each of them is 4 and \( G \) is either the octic group or the quaternion group. There are therefore four and only four groups which have the property that each of them contains three and only three complete sets of non-invariant conjugate operators, viz., the dihedral group of order 10, the tetrahedral group, the octic group and the quaternion group.


**LINKAGE VALUES IN AN INTERCHANGE COMPLEX IN ZEA**

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A translocation between non-homologous chromosomes may be either simple or reciprocal. In a simple translocation one chromosome is the donor and a second chromosome the recipient of a piece of the first, but in a reciprocal translocation pieces of chromatin are interchanged between the two chromosomes. Another name for reciprocal translocation is segmental interchange.

The first suggestion of segmental interchange was of a cytological nature and was made by Belling and Blakeslee\(^1\) in their study of chromosome pairing in certain trisomic races in Datura. This hypothesis was later successfully applied by many investigators to explain unusual genetical and cytological behavior in such diverse forms as Stizolobium, Pisum, Oenothera, Zea and Drosophila.

Brink\(^2\) and Brink and Burnham\(^3\) reported a case of semi-sterility in maize. They advanced the hypothesis that the abortion of half the
eggs and pollen was caused by a simple or reciprocal translocation between two non-homologous chromosomes. Brink found that the P-br and b-lg linkage groups were involved. He reported, however, no linkage between factors in the P-br chromosome with factors in the b-lg chromosome in cultures segregating for genes in these groups and for semi-sterility. Burnham further substantiated the hypothesis of a segmental interchange by showing that semi-sterile individuals had a ring of four chromosomes at diakinesis. This case of semi-sterility was designated semi-sterile-1. McClintock first supplied a cogent demonstration of a segmental interchange by her determination of the location of the point of breakage between two non-homologous chromosomes in semi-sterile-2.

The purpose of this paper is to report the results obtained in the analysis of another semi-sterile, called semi-sterile-4. Genetical data of a nature not previously reported are presented. The genetical data and cytological behavior may be regarded as conclusive evidence of the occurrence of a segmental interchange.

Genetic tests have shown that the b-lg and pr-v2 chromosomes are involved. The percentages of crossing-over of genes located in these two linkage groups with the locus of the break or interchange are given in table 1.

<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>PERCENTAGES OF CROSSING-OVER BETWEEN GENES IN THE b-lg AND pr-v2 CHROMOSOMES AND THE LOCUS OF THE BREAK</th>
</tr>
</thead>
<tbody>
<tr>
<td>b-lg CHROMOSOME</td>
<td>pr-v2 CHROMOSOME</td>
</tr>
<tr>
<td>ts1-break = 4.0 ± 1.20</td>
<td>pr-break = 18.3 ± 1.19</td>
</tr>
<tr>
<td>b-break = 22.1 ± 0.94</td>
<td>v2-break = 46.3 ± 1.15</td>
</tr>
<tr>
<td>ig-break = 47.3 ± 1.49</td>
<td></td>
</tr>
</tbody>
</table>

These data show that the locus of the break in the b-lg chromosome was very close to ts1 which occupies the left-most region in the known genetic map. It is impossible to tell from the present data whether the break in the b-lg chromosome took place to the left or right of the ts1 locus. In the pr-v2 chromosome, if the locus of v2 be considered to be to the right of pr, then the break took place 18 units to the left of pr in what is at present an unmapped portion of the chromosome. The standard crossover values and the values found in the segmental interchange are given in table 2.

<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>PERCENTAGES OF CROSSING-OVER IN NORMAL LINES AND IN LINES WITH THE SEGMENTAL INTERCHANGE FOR FACTORS IN THE b-lg AND pr-v2 LINKAGE GROUPS</th>
</tr>
</thead>
<tbody>
<tr>
<td>NORMAL CROSSOVER VALUES</td>
<td>INTERCHANGE CROSS-OVER VALUES</td>
</tr>
<tr>
<td>ts1-b = 23 ± %</td>
<td>ts1-b = 21 ± %</td>
</tr>
<tr>
<td>ts1-lg = 40 ± %</td>
<td>ts1-lg = 40 ± %</td>
</tr>
<tr>
<td>b-lg = 35 ± %</td>
<td>b-lg = 34 ± %</td>
</tr>
<tr>
<td>pr-v2 = 42 ± %</td>
<td>pr-v2 = 44 ± %</td>
</tr>
</tbody>
</table>
The data in table 2 show that crossing-over in plants with the interchange is of the same order as in normal lines, since the values found are surprisingly close to the standard distances.

Some of the cultures segregating for semi-sterility were also segregating for the factor \( b \) in the \( b\)-lg group and the factors \( pr \) and \( v_4 \) in the \( pr-v_4 \) linkage group. The data in table 1 show the locus of \( b \) to be approximately 22 units from the locus of the break in the \( b\)-lg chromosome and \( pr \) to be about 18 units from the break in the \( pr-v_4 \) chromosome, so a linkage between \( b \) and \( pr \) is expected in those families segregating for the two genes and for semi-sterility. If no double crossovers occur the two factors should be 40 \( \pm \) units apart. The value obtained was 31 \( \pm \) percent of crossing-over. The loci of \( b \) and \( v_4 \) showed random assortment which is in agreement with the data as \( v_4 \) was 46 \( \pm \) crossover units from the break.

The genetically determined constitution of the four chromosomes forming a ring at diakinesis may be diagrammed as in figure 1.

These four chromosomes in the mid-prophase of the first meiotic division form a quadripartite figure which may be represented as in figure 2, disregarding all loci save those of \( pr \), \( v_2 \) and \( b \).

Let the distance from \( Pr \) to the break be called region 1 and let the distance from \( B \) to the break be region 2. As functional gametes are formed only when alternate chromosomes in the ring pass to the same pole, the following types of gametes are possible:

Non-crossover gametes: \( pr \) \( b \) normal chromosomes
\( Pr \) \( B \) interchanged chromosomes

Region 1 crossovers: \( pr \) \( B \) interchanged chromosomes
\( Pr \) \( b \) normal chromosomes

Region 2 crossovers: \( pr \) \( B \) normal chromosomes
\( Pr \) \( b \) interchanged chromosomes
Regions 1 and 2 crossover............. \( pr \) \( b \) interchanged chromosomes

\[
Pr B \quad \text{normal} \quad \text{chromosomes}
\]

Since the plants carrying the interchange complex shown in figure 2 were crossed with \( pr \) \( b \) plants from normal lines, the gametic and zygotic frequencies were the same. If a crossover in region 1 does not interfere with a crossover in region 2 the number of observed double crossovers should be equal to the calculated number with no interference. Actually a coincidence value of 1.1 was found which indicates the absence of interference among two of the four arms of the interchange complex. The detailed data will be published later.

The cytological observations are as follows: Semi-sterile-4 plants show a ring of four chromosomes at diakinesis.† When semi-sterile-4 plants are crossed with races trisomic for the two chromosomes, respectively, the 21 chromosome plants carrying the interchange show chains of five chromosomes. Semi-sterile-4 crossed with semi-sterile-1 gives a ring of six chromosomes according to expectations, since the \( b-lg \) chromosome is common to both cases of segmental interchange. Prophase figures of the interchange complex of semi-sterile-4, first found by Miss Harriet Creighton, show the interchange to be approximately an equal one. The genetic data indicate that the interchange took place toward the left end of both chromosomes. The cytological figures confirm this. Unfortunately it has been impossible to distinguish the insertion regions in the figures, and since the interchange was equal no identification could be made of the specific chromosomes in the interchange complex. No exact measurements have been made of the relative lengths of the interchanged pieces and the normal chromosomes but there are considerable portions in the left ends of the \( b-lg \) and \( pr-v_2 \) chromosomes which are, as yet, unmarked by mutant genes.

Summary.—The analysis of a segmental interchange involving the \( b-lg \) and \( pr-v_2 \) chromosomes in Zea is reported. The percentages of crossing-over between \( ts_1 \), \( b \) and \( lg \) with the point of interchange in the \( b-lg \) chromosome are 4, 22 and 47, respectively. The loci of \( pr \) and \( v_2 \) are 18 and 46 crossover units distant from the break in the \( pr-v_2 \) chromosome.

Cultures segregating for the genes \( b \) and \( pr \) and for the interchanged chromosomes show approximately 31 per cent of crossing-over between \( b \) and \( pr \).

The frequency of double crossovers between \( b \), the point of interchange, and \( pr \) indicate the absence of interference in crossing over.

* Paper No. 180 from the Department of Plant Breeding, Cornell University, Ithaca, N. Y.

† I wish to offer my sincere appreciation to Dr. Barbara McClintock who found semi-sterile-4 in her cultures and generously turned it over for analysis. Dr. McClintock has succeeded (unpublished data) in isolating trisomic races for the \( b-lg \) and \( pr-v_2 \)
MODIFICATION OF MENDELIAN RATIOS IN MAIZE BY MECHANICAL SEPARATION OF GYMMETES

By P. C. MANGELSDORF

Texas Agricultural Experiment Station

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For a number of years the writer, in collaboration with Dr. D. F. Jones and Dr. W. R. Singleton, has been studying the inheritance of a peculiar condition in maize known as "high sugary." Plants of this stock, which are heterozygous for the well-known recessive character, sugary endosperm, produce about 66 per cent of sugary seeds when self-pollinated instead of the expected 25 per cent. When the heterozygote is backcrossed on the recessive, approximately 94 per cent of the seeds, instead of the usual 50 per cent, are sugary. The ability to produce these aberrant ratios is inherited but is transmitted through only about 15 per cent of the ovules and about one per cent of the functional pollen.

All plants which produce high sugary ratios have variable pollen. Measurements of the pollen grains show that the distribution, with respect to length, is bi-modal. Approximately half of the grains are smaller than normal, though quite sound and well packed with reserves, while the remainder are normal. The gene or other condition responsible for the production of tiny pollen is located in the third chromosome, to the left of sugary, and the crossing-over is approximately six per cent. Other characters in this linkage group, including defective endosperm de₆₉, tunicate ear Tu, tassel seed Ts₆, and a newly discovered allelomorph of sugary, are also affected.

We may assume that in "high sugary" plants, which are heterozygous for sugary, the normal pollen grains all carry the gene for sugary except six per cent of crossovers, while the tiny grains all carry starchy genes except the six per cent of crossovers. We may assume further that the tiny pollen grains do not function in competition with normal grains;