different from those shown by canes of similar stock which are known never to have had mosaic. Slight as the evidence undoubtedly is, it points toward the truth of the second of our hypotheses; that is to say, it is perhaps more probable that sugar-cane plants gain an apparent immunity by reducing the virulence of the mosaic virus than by throwing it off entirely.

[1] East, E. M., and Weston, W. H., Jr., "A Report on the Sugar Cane Mosaic Situation in February, 1924, at Soledad, Cuba," *Harv. Univ. Press*, Cambridge, 1925, pp. 52, plates IX.

CYTOLOGICAL EVIDENCE FOR SEGMENTAL INTERCHANGE BETWEEN NON-HOMOLOGOUS CHROMOSOMES IN MAIZE[1,2]

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Communicated May 11, 1931

During the past few years a number of cases of partial sterility in maize have come to light which appear to involve structural changes in the chromosomes. In one of these, semisterile-1, clear-cut genetic evidence has been secured indicating that the phenomenon is associated with alterations in two linkage groups of the nine which it is now possible to test.[3,4] Burnham[5] reports that at diakinesis in three different semisteriles, -1, -2 and -3, a ring of four chromosomes and eight bivalents occurs. The rings in semisteriles-1 and -3 appear to have one member in common, since crosses between the two lines give some offspring with a group of six chromosomes and seven bivalents. Semisterile-2 in combination with semisterile-1, on the other hand, gives two rings of four chromosomes each plus six bivalents.

Critical genetic evidence regarding the character of the change in the nuclear complement leading to ring formation at diakinesis is not yet forthcoming. It is anticipated that alterations in the composition of certain linkage groups corresponding to the particular chromosomes concerned will be found, and studies to this end are in progress. On the basis of observations on a similar phenomenon in other genera, Belling[6] has brought forward the hypothesis that ring-formation at diakinesis is a consequence of interchange of terminal segments between non-homologous chromosomes. Assuming attachment of homologous ends, a normal and an interchanged chromosome of each pair would give a closed group of four. As Burnham[5] has pointed out, however, a ring might be expected following a simple translocation if a cross-over occurred in the "four-strand" stage.

In a recent paper, Miss McClintock[7] has presented strong cytological evidence for segmental interchange in semisterile-2. The chromosomes affected are the second and third smallest. A study of the early prophase stages, in which the thread-like chromosomes are paired throughout their entire length, revealed a cross-shaped structure in the semisterile plants. One of the pairs of chromosomes in this complex, in the strain employed, possessed characteristic terminal knobs which serve to identify it and the interchange group. Utilizing these morphological features in the analysis, Miss McClintock has shown that the cross-shaped configuration is very probably the result of segmental interchange between the second and third smallest chromosomes.

Our own investigations have been concerned with two other stocks, semisterile-1 and -5. Semisterile-5 is a particularly favorable object for this study in that one of the two pairs of chromosomes in the ring is regularly attached (or closely appressed) to the nucleole at the end which bears satellites.[8] By means of this feature this pair of chromosomes is readily distinguished from the other nine. Semisterile-5 in combination with semisterile-1 shows a ring of six chromosomes and seven bivalents. The two semisteriles, therefore, have one chromosome in common, that corresponding to either the *B-lg* or the *P-br* linkage group.

Portions of the staminate inflorescence from field-grown plants were fixed in a modification of Carnoy's solution which contained 6 parts 95 per cent alcohol, 2 parts glacial acetic acid and 2 parts chloroform. The material was allowed to remain in the fixing fluid for 15–30 minutes and was then transferred to 90 per cent alcohol. After a period of 12–24 hours it was stored in 80 per cent alcohol. The mounts were made in freshly prepared aceto-carmine to which had been added a fourth part of Ehrlich's haematoxylin. After crushing an anther in the stain a cover glass was added to the mount and the slide slightly warmed. The preparations, when sealed by running melted paraffin around the edge of the cover glass, will keep for a month without deterioration. Permanent slides were made in the manner described by Miss McClintock.[9]

On the basis of the segmental interchange hypothesis, the ring-forming group in semisterile individuals comprises two normal chromosomes (one of each pair) and two chromosomes which are complementary to each other as a result of having exchanged terminal segments. In the open spireme stage in normal plants, the members of a chromosome pair are closely associated throughout their whole length, homologous portions presumably lying in juxtaposition. At this stage the interchange complex would be expected to form a cross-shaped figure since each of the complementary chromosomes should synapse for a part of its length with one normal chromosome and for the remainder of its length with the other normal chromosome. On the basis of a simple translocation a linear configuration

or a T-shaped structure should occur, depending upon whether the detached segment was affixed in its new position by the broken or the free end.

Examination of a number of preparations in the open spireme stage and the stages immediately following reveals that semisterile-5 plants regularly show a cross-shaped chromosome complex attached by one end to the nucleole (Fig. 1). Several figures obtained were sufficiently clear to permit of analysis. One arm of the cross, bearing statellites, is affixed to the nucleole. The other three arms show a definite size relationship to each other, one being comparatively short, another of medium length and the third longer. The arm of medium length always lies opposite the attached arm.

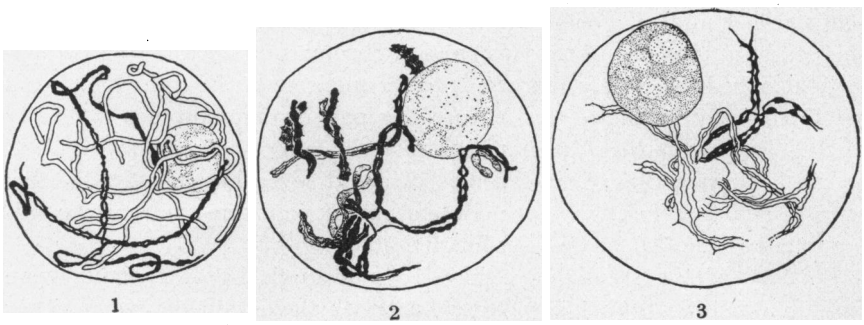

Figure 1.—Nucleus of a microspore mother cell of semisterile-5 shortly after the open spireme stage. The cross-shaped figure with one arm attached to the nucleole is clearly apparent. ×775.

Figure 2.—Early diakinesis in semisterile-5 showing eight bivalents and the cross-shaped figure beginning to open into a ring. The arm opposite the attached one turns downward and therefore appears foreshortened in the figure. ×1450.

Figure 3.—Nucleus of microspore mother cell of semisterile-1 shortly after synizesis. The cross-shaped figure shows an exchange of partners. ×1450.

Six cross-shaped figures at stages from the open spireme to mid-diakinesis were measured. The lengths of the three arms, taking the one opposite the attached end as unity, were as follows:

0.5	1.0	1.3
0.5	1.0	1.4
0.6	1.0	1.6
0.7	1.0	1.5
0.4	1.0	1.9
0.4	1.0	1.4

At very early diakinesis eight bivalent chromosomes and the cross-shaped complex may be recognized, as shown in figure 2. In this figure the arm opposite the attached one turns downward at the end for a distance

of about 6μ and consequently appears foreshortened in the drawing. At this stage the regions of spindle fibre attachment appear as short hyaline areas in the four chromosomes which later form the ring. In normal plants the spindle fiber attachment on the satellite chromosome appears to be at a point about one-quarter of the length of the chromosome from the satellite end. In the interchange complex, therefore, it is the longer chromosome attached to the nucleole which is the normal satellite chromosome of the set; and the chromosome opposite this is the normal member of the other pair in the group. The interchange appears to have involved approximately two-thirds of the satellite chromosome and about one-third of the other chromosome entering into the ring. These relations are depicted diagrammatically in figure 4.

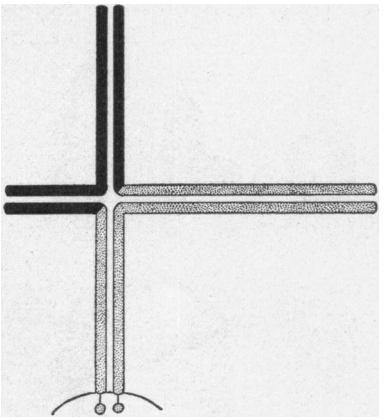

FIGURE 4

A diagrammatic representation of the cross-shaped figure found in semisterile-5. Taking the length of the arm opposite the satellites as unity, the lengths of the two laterals are approximately 0.5 and 1.5.

At the first meiotic division three types of distribution of the chromosomes in the semisterile-5 ring are observed. Adjacent chromosomes of approximately the same size may go to the same pole (Fig. 5a), adjacent chromosomes of different sizes may assort together (Fig. 5b) or alternate chromosomes may pass to the same pole (Fig. 5c). Only the spores resulting from the last type of distribution will be functional since the others lack at least a portion of one chromosome. Counts show about 50 per cent aborted pollen in semisterile-5 plants. This means that in approximately half the cases alternate chromosomes in the ring assort together.

While semisterile-1 is a less favorable object for cytological study on account of the absence of easily distinguishable morphological features in the chromosomes concerned, some evidence has been obtained that its behavior is also due to segmental interchange between non-homologous chromosomes. By means of breeding tests it has been possible to show in this case that the chromosomes affected correspond to the *B-lg* and *P-br* linkage groups. Burnham[5] has reported the occurrence of a chromosome ring plus eight bivalents in this stock, an observation amply confirmed by our own studies.

In early diakinesis figures the interchange complex in semisterile-1 is easily recognized inasmuch as the group of four chromosomes comes to lie at one side of the nucleus and apart from the remaining bivalents. Four

arms consisting of paired strands can be seen. One of the arms is composed of a row of three chromatic bodies. Since neither pair of chromosomes concerned in semisterile-1 is easily identified, it is difficult to trace the cross-shaped structure in the early prophase stages. In figure 3 is shown, however, a very early spireme stage in which a configuration occurs suggesting segmental interchange. The cross-shaped structure is made up of four arms, each arm being composed of paired strands. At the midpoint of this synaptic complex two of the strands exchange partners. Here, as in several early diakinesis figures of semisterile-1 which we have observed, one of the arms consists of a row of three paired chromatic bodies. It seems probable that this configuration is the precursor of the ring seen at diakinesis, but the evidence is less decisive than that bearing on semisterile-5.

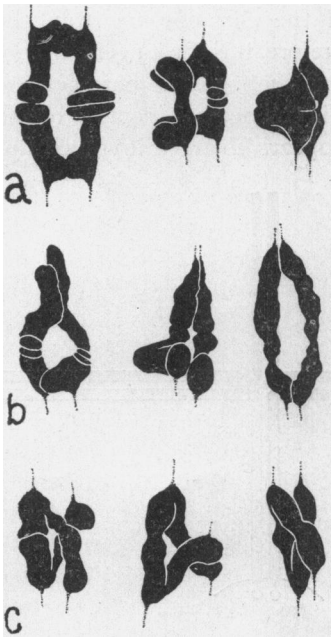

FIGURE 5

Chromosome rings from heterotypic equatorial plates of semisterile-5 showing the distribution of the component chromosomes: a, adjacent chromosomes of unequal size going to the same pole; b, adjacent chromosomes of about the same size going to the same pole; c, alternate chromosomes going to the same pole. ×1450.

[1] Papers from the Department of Genetics, Agricultural Experiment Station, University of Wisconsin, No. 122. Published with the approval of the Director of the Station.

[2] The authors desire to express their appreciation for the assistance received from the Research Fund of the University of Wisconsin, and through a grant-in-aid from the NATIONAL RESEARCH COUNCIL.

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