

ORISSA UNIVERSITY OF AGRICULTURE AND TECHNOLOGY
Bhubaneswar, India

1. Interchromosomal effects on chiasma formation in maize heterozygous for an inversion and an interchange.

Reduction in crossing over due to inversion heterozygosity in one chromosome is known to enhance crossing over in certain nonhomologous chromosomes in Drosophila. Cytological evidence of such compensation has been reported in maize. The problem is a bit difficult to study in the case of maize, because of a large number of chromosomes. Further, as pointed out by Sinha and Mohapatra (Cytologia, 34:523-527, 1969), the occurrence of the phenomenon may be obscured under certain conditions. We have now obtained further evidence for compensation of the loss of chiasmata in a different stock of maize, heterozygous for both an inversion and an interchange. The conditions under which the phenomenon can be clearly detected have been determined.

Material for the present study was heterozygous for a pericentric inversion in the second chromosome (In 2a) and a reciprocal translocation involving chromosomes 6 and 9 (T6-9b). Chiasmata were recorded at diakinesis separately for each of the following bivalents: the longest (presumably chromosome 1), the second longest (presumably chromosome 2) and the shortest (presumably chromosome 10). Further, the types of configuration (ring, chain or other) of the interchanged chromosomes were also noted along with actual chiasma counts. Chiasma number for the remaining five bivalents as a group was recorded separately. The total number of PMC's studied was divided into suitable groups, as discussed later, according to (1) the number of chiasmata in the second chromosome carrying the inversion and (2) the number of chiasmata in the interchanged chromosomes. This kind of grouping made possible an examination of the probable effect of reduction in chiasmata in one or more of the specified chromosomes on the chiasma frequency in the other chromosomes. This method hopefully should eliminate the possible complicating influence of either segregating genes or environmental variation on chiasmata and their distribution.

The main findings of this study will be presented in two different sections.

I. Differences between PMC's grouped according to chiasma frequency in the second bivalent:

The relevant data presented in Table 1 permit comparison of chiasma frequencies of (a) the longest bivalent, (b) the shortest one and (c) the interchanged chromosomes 6-9 in two distinct classes of PMC's. In one class the second longest, carrying the inversion, had only one chiasma suggesting reduction due to inversion heterozygosity. In the other class there were two chiasmata, indicating little effect of the inversion. Our earlier work (Sinha and Mohapatra, 1969) suggested the utility of studying the problem of compensation in PMC's with a varying number of total chiasmata per nucleus. Hence for a more meaningful comparison, PMC's were further grouped as follows: Gr. 1 or low number (13-14) of chiasmata; Gr. 2 = medium number (15-16) of chiasmata; Gr. 3 = moderately high number (17-18) and Gr. 4 = very high number (above 18). The following salient points may be noted from Table 1:

Table 1

Comparison of chiasma frequencies of specific chromosomes in (1) PMC's with varying number of chiasmata in the second bivalent (carrying inversion) and (2) in different groups with varying number of chiasmata / nucleus.

		Gr. 1 (13-14 chiasmata)	Gr. 2 (15-16 chiasmata)	Gr. 3 (17-18 chiasmata)	Gr. 4 (18 or more chiasmata)	All PMC's pooled together
Chiasma frequency in the 6-9 inter- change.	In Gr. I* cells	3.38	3.62	3.79	4.00	3.58
	In Gr. II** cells	3.08	3.51	3.71	4.00	3.62
Chiasma frequency in the longest bivalent.	In Gr. I cells	1.94	2.06	2.29	2.75	2.09
	In Gr. II Cells	2.00	2.09	2.46	2.82	2.34
Chiasma frequency in the shortest bivalent.	In Gr. I cells	0.97	1.00	1.13	1.25	1.03
	In Gr. II cells	1.00	0.97	1.08	1.36	1.09

*Cells with 1 chiasma in chromosome 2 bivalent.

**Cells with 2 chiasmata in chromosome 2 bivalent.

(i) Only the 6-9 interchange shows increased chiasma frequency along with reduction in the second bivalent. (ii) The increase in the case of the 6-9 interchange is most clearly manifested in the low chiasmata group and is gradually and consistently less evident in the medium and moderately high chiasmata groups. In the very high chiasmata group no difference can be noted. (iii) Considering all the PMC's together, little difference in chiasmata in the 6-9 interchange can be noted between the two classes of PMC's with 1 or 2 chiasmata in the second bivalent. (iv) The longest bivalent (chromosome 1 ?) shows a consistent decrease in chiasmata accompanying reduction in the second longest. This decrease is also seen when all the PMC's are considered together. (v) The shortest bivalent shows a trend similar to the longest, though not as sharp and consistent.

Evidently, all chromosomes do not participate in the compensatory increase, even if it occurs. Further, the detection of this phenomenon may not be possible, if all the PMC's are pooled for analysis.

From the standpoint of compensation, chromosomes may be divisible into two classes: (1) competitive, that is, capable of showing compensation and (2) non-competitive. The 6-9 interchange behaves as a strongly competitive group, particularly under conditions when the total number of PMC chiasmata is low. In the presence of this competitor, the longest and the shortest bivalents fail to take advantage of compensation.

II. A test of independence of events leading to chiasma formation in chromosome 2 and 6-9 interchange:

The results presented above suggest the possibility that events leading to chiasma formation in the second chromosome and the 6-9 interchange may not be entirely independent. An alternative analysis was adopted to test this point.

The frequencies of single chiasma and double chiasmata in the second bivalent were calculated. Similarly, the frequencies of 2, 3 and 4 chiasmata in the 6-9 interchange were determined. From these figures the probabilities of different combinations of chiasmata in the second and the 6-9 interchanged chromosomes could be worked out. Next a comparison was made between the expected probabilities of these joint events and the observed frequencies. The results presented in Table 2, based on the data on all the PMC's, do not indicate a significant difference between the expected and observed.

Table 2
Frequencies of PMC's with varying numbers of chiasmata
in the second bivalent and the 6-9 interchange.

	4 or > in chr. 6-9 and 2 in chr. 2 (class 1)	3 in chr. 6-9 and 2 in chr. 2 (class 2)	4 in chr. 6-9 and 1 in chr. 2 (class 3)	3 in chr. 6-9 and 1 in chr. 2 (class 4)	2 in chr. 6-9 and 1 in chr. 2 (class 5)
Expected	60.9	27.1	71.7	31.1	11.2
Observed	60.0	26.0	71.0	33.0	12.0

It might be inferred that the events underlying chiasma formation in chromosome 2 are independent of those in chromosomes 6 and 9. Thus, there is apparently no evidence of compensatory chiasma formation in these three chromosomes. It should, however, be recalled that compensation was most clearly suggested in the PMC's showing a low number of chiasmata (vide Table 1). Hence, it should be desirable to undertake the same analysis in the PMC's with a low or medium number of chiasmata. Table 3 contains the results of this analysis.

Table 3
Frequencies of PMC's with varying numbers of chiasmata
in the second bivalent and the 6-9 interchange.
(Only PMC's with 13-16 chiasmata are considered.)

	4 or > in chr. 6-9 and 2 (or rarely 3) in chr. 2 (class 1)	3 in chr. 6-9 and 2 in chr. 2 (class 2)	4 in chr. 6-9 and 1 in chr. 2 (class 3)	3 in chr. 6-9 and 1 in chr. 2 (class 4)	2 in chr. 6-9 and 1 in chr. 2 (class 5)
Observed	24.00	19.00	49.00	29.00	12.00
Expected	47.08	28.86	27.93	17.16	11.97
Deviation (O-E)	-23.08	-9.86	+21.07	+11.84	+0.03
(O-E) ² /E	11.29	3.37	15.89	8.17	

$$\chi^2 = 38.72$$

$$P < 0.005$$

It is evident that deviation in some of the classes has contributed to a high Chi-square value with $P < 0.005$. In fact, class 3 shows the maximum departure from the expected. This class can be called compensatory since a high chiasma frequency in the 6-9 interchange is combined with a low number in the chromosome carrying the inversion. A high deviation from the expected is also observed in class 1, a non-compensating type of combination, in which high chiasma frequencies are observed in chromosome 2 as well as in chromosomes 6-9. There is an excess of PMC's of the class 3 or compensating type; but in the case of class 1, the non-compensating type, the observed frequency of PMC's is much below the expected. Thus, it appears that under conditions leading to low PMC chiasmata, events underlying chiasma formation in the nonhomologous chromosomes may not be entirely independent of each other.

Besides providing an evidence of compensatory chiasma formation, this study further suggests that the phenomenon can be detected easily under conditions rather stringent for chiasma formation.

S. K. Sinha
B. K. Mohapatra

2. The distribution of bivalent chiasmata in maize plants heterozygous for two pericentric inversions.

An investigation was undertaken in maize to determine the effect of inversion heterozygosity on the distribution of chiasmata in maize, since the information on this aspect appears to be meagre.

The material, heterozygous for two pericentric inversions designated Inv. 2a (2S 0.7; 2L 0.8) and Inv. 9a (9S 0.7; 9L 0.9), was synthesized through suitable crosses involving the inversion stocks and a highly inbred line, Ext. 355. Chiasma frequency was studied at diakinesis in PMC's. Data were recorded separately for the longest, the shortest, the sixth and the remaining bivalents. The PMC's were grouped into classes according to chiasmata per PMC. The class-wise distribution of chiasmata was worked out for the longest (presumably chromosome 1), the shortest (presumably chromosome 10) and the sixth bivalent. These distributions were compared with the expected values calculated on the basis of relative pachytene lengths (published data of Rhoades, 1955). Two kinds of