4. SUMMARY

1. The interrelationship between the total chiasma frequency in the standard chromosomes and that in the heterochromatic supernumerary chromosomes was studied in plants with 2, 3 or 4 extra chromosomes.

2. There was a highly significant positive correlation in plants with two supernumeraries, while in plants with 3 and 4 B's the correlations were insignificant.

3. The average correlation for all the synaptic plants with B's was +0.15 and highly significant.

4. The homogeneity of correlations at both intra- and inter-group levels indicates a more general occurrence of these correlations.

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THE INFLUENCE OF B CHROMOSOMES ON MEIOSIS IN *LOLIUM*

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1. INTRODUCTION

REPORTS during the past few years show that supernumerary, *B* chromosomes occur in numerous species, both plant and animal. They are especially prevalent in diploid Angiosperms. While the *B* chromosomes undoubtedly influence development of the phenotype and thereby effect measurable changes in external morphology it is still not clear what adaptive role they play that would account for their widespread distribution and hence, presumed, adaptive importance. John and Hewitt (1965*a, b*) have suggested that *B*'s may serve as regulators of recombination at meiosis. In

FIG. 1.—Chiasma frequency distributions in *Lolium* plants with *oB*, *1B* or *2B* chromosomes (▲ = mean chiasma frequency). Data from 20 pollen mother cells in each plant.

this connection they showed that the mean chiasma frequencies at first metaphase in spermatocytes of the grasshopper, *Myrmeleotettix maculatus* (Thunb.) were considerably and significantly higher in individuals carrying *B*'s (15.68 per cell) than in those without (14.23 per cell). Further, Hanson (1962) showed an increase in recombination between four gene markers on chromosome 3 of maize that was directly proportional to the number of *B*'s carried. A different, but relevant, effect of *B*'s on recombination has been reported also by Jones and Rees (1967) who showed that the *distribution*, as distinct from the frequency, of crossing over varies in relation to the number of *B*'s carried by rye plants.

We have recently found *B* chromosomes in perennial rye grass (*Lolium perenne* $2n = 14$) populations derived from Algeria. In a population of 150 derived by open pollination over two generations, 2 plants had 3*B*'s, 18 had 2*B*'s, 27 had 1*B* and the remainder none. Mean plant chiasma frequencies in the different *B* classes are given in fig. 1. From the histograms it is clear that the mean chiasma frequencies differ between the different *B* categories. The mean frequency is highest for plants with none and decreases progressively with one and two *B*'s. The differences are significant ($P = < 0.05$). There is no doubt that *B*'s influence the chiasma frequencies in pollen mother cells and comparisons we made among other populations involving the same *B* chromosomes have fully confirmed these results. It will be observed that the rye grass *B*'s, unlike those in the grasshopper and in maize, serve to depress rather than to increase the recombination.

2. CHIASMA DISTRIBUTION

In rye, *B* chromosomes have a pronounced influence on the *distribution* as distinct from the frequency of chiasmata within pollen mother cells (Rees and Jones, *loc. cit.*). Whereas in a normal diploid the chiasmata are more or less evenly shared between the bivalents, in the presence of *B*'s they are distributed in a highly asymmetric fashion such that some bivalents have unusually many, up to 4 or 5, and others few, or even none. In statistical terms the effect of *B*'s is to increase the variance of the bivalent chiasma frequency within pollen mother cells. In the present rye grass material, a similar influence of *B*'s is manifested by the data presented in fig. 2. Over a wide range of chiasma frequencies (9-14) the bivalent variance within cells increases progressively with increasing *B* frequency.

3. CONCLUSION

It is clear from these results that *B* chromosomes in *Lolium* affect both the frequency and the distribution of chiasmata in pollen mother cells. As already mentioned, however, the *B*'s in *Lolium*, in contrast to those in other species, reduce rather than increase the chiasma frequencies. This contrast in no way detracts from the general proposition of John and Hewitt that *B* chromosomes may serve to regulate, in adaptive fashion, the amount of recombination at meiosis (see also Jones and Rees, *loc. cit.*). On the contrary the *Lolium* results indicate that *B* chromosomes may regulate recombination in a restrictive as well as an expansive manner. There is, however, one confusing feature of the *Lolium* results that is worth noting. A reduction in chiasma frequency, due to *B*'s would theoretically decrease the rate of release of variability and hence promote a relative uniformity among the genotypes of gametes and progeny. In this respect the *B*'s may be said to

conserve variability as between parents and offspring. The asymmetric distribution of chiasmata, also due to *B*'s, would in contrast be expected to produce gametes with unusual, even novel gene combinations, and hence serve to promote a diversity of genotypes among gametes and offspring.

FIG. 2.—Mean variances in chiasma frequency between bivalents within pollen mother cells of different chiasma frequencies in plants with 0, 1 and 2*B* chromosomes.

Unless it be assumed that the lowering of the chiasma frequency may only be achieved in this case at the expense of some irregularity in pairing and hence in chiasma distribution it is by no means clear, from an adaptive standpoint, how these two apparently conflicting consequences are to be reconciled.

4. SUMMARY

In *Lolium*, *B* chromosomes reduce the mean chiasma frequency of the *A* bivalents but they increase the variance of the *A* bivalent chiasma frequency within pollen mother cells.

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