THE ORIENTATION OF MULTIPLE ASSOCIATIONS RESULTING FROM INTERCHANGE HETEROZYGOSITY

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INTERCHANGE complexes in which the frequency of the different orientations at metaphase I departs from the random expectation have often been reported (see DARLINGTON 1937, BURNHAM 1956). Most frequently an excess of the alternate orientation, and a deficiency of one or both of the adjacent arrangements, has been found. It is unlikely that interchange heterozygosity will become incorporated into the genetic system of most species unless a reasonably high frequency of disjunction is achieved immediately after the interchange event (DARLINGTON 1939, 1958). Thus the types of factors giving rise to such directed segregation (BURNHAM 1956) have particular evolutionary significance.

A number of these factors have been suggested, including centromere position, sizes of the interchanged segments in relation to one another and to the chromosomes, relative sizes of the chromosomes, and the number and position of chiasmata (see DARLINGTON 1937, BURNHAM 1956). For this reason species possessing equal sized metacentric chromosomes each with two terminal or subterminal chiasmata at metaphase have been described as preadapted for interchange heterozygosity (DARLINGTON 1939, 1958; JOHN and LEWIS 1959). It would appear, however, that while such chromosome morphology and behavior is, in most species, necessary for a high disjunction frequency, it is not always sufficient. BURNHAM (1956) points out that in a number of cases a high frequency of the alternate orientation might be expected, but that this is not found. A similar conclusion may be drawn from the differences in disjunction frequency of the same two independent interchanges, in three lines of rye brought about by segregation (THOMPSON 1956) and selection (LAWRENCE 1958) of a number of genes influencing this character. The differences do not appear to be due to changes in either the number or position of chiasmata (LAWRENCE, unpublished).

Rings and chains had the same disjunction frequency and few associations had more than four chiasmata. The small differences in the position of the terminally and subterminally located chiasmata appeared to have no influence on orientation. The nature of this genetically controlled mechanism (or mechanisms) is unknown, but may be concerned with the mechanical flexibility of chromosomes or a direct control of centromere behavior.

In the different families of rye described by THOMPSON (1956) and LAWRENCE (1958), the proportion of associations showing the alternate orientation varied between less than 50 percent to nearly 90 percent. However the F_1 plant in which

the two interchanges were first observed had a disjunction frequency of nearly 90 percent. If orientation in rye, and presumably in other species, is not entirely determined by chromosome morphology together with the number and position of chiasmata, the question remains of why directed segregation is found—i.e., why the genetic constitution gives rise to a high, rather than low, disjunction frequency. In some material, selection subsequent to the interchange event may be responsible, but in others this possibility can be excluded (irradiated materials: CATCHESIDE 1954; GARBER and DHILLON 1962).

The orientation of radiation-induced interchange rings and chains of four has been further studied using four inbred lines of rye, from material described by REES (1955), and the six hybrids between them. A number of young flowering plants of each genotype were irradiated in air with 200 rads of Co^{60} gamma rays, and inflorescences from each plant fixed in acetic-alcohol (1:3) 6 to 8 days later. The induced interchanges were observed in pollen mother cells at metaphase I. These cells were irradiated during or after the last premeiotic mitoses, and therefore the majority of the associations of four observed in any one plant represent independent interchange events.

From Table 1 it can be seen that in these large samples the proportion of interchanges showing the alternate orientation is high in all families, varying between 68 percent and 82 percent. Data from replicate plants within families, from reciprocal families, and from different fixation dates are all homogeneous. A chi-square test also fails to reveal any heterogeneity between the families, but the presence of small family differences is suggested by a significant ($P = 0.05-0.01$) $W'r/Wr$ regression (HAYMAN 1958). This regression cannot be significant in the absence of dominance variation between the lines. The disjunction frequency of rings and chains of four did not differ significantly, and results from the two classes were therefore pooled. All chiasmata were close to the ends of the chromosomes at metaphase. Further, disjunction frequency was not correlated with the proportion of paired arms having terminal chiasmata in normal cells. Unless the localization and terminalization of chiasmata in the associations is unrelated to that in normal bivalents, differences between the lines in this respect were of little importance. It is possible that variation between the families in preferred points of exchange contribute towards the variation in disjunction frequency, but no obvious differences could be observed. The majority of the interchanges ap-

TABLE 1

Proportions of associations of four with alternate orientation in the four inbred lines (underlined) and their six hybrids. In the brackets are the total number of interchanges observed, and the number of plants scored, respectively

Line	1	5	13	18
1	<u>0.767</u> (90,5)	0.735(98,6)	0.747(75,5)	0.766(137,10)
5		<u>0.726</u> (73,5)	0.816(125,7)	0.677(136,10)
13			<u>0.793</u> (29,3)	0.818(77,7)
18				<u>0.762</u> (42,5)

peared equal. The results therefore support the earlier work (THOMPSON 1956, LAWRENCE 1958) in two respects: first, in probably showing genetic control of disjunction frequency; and second, in demonstrating that newly arising interchanges in rye have a marked tendency to assume the alternate orientation at metaphase I.

High disjunction frequencies are not however, as mentioned earlier, characteristic of all rye genotypes, and therefore it must be concluded that the four randomly chosen inbred lines of rye all have genotypes promoting high disjunction. Since it is unlikely that such lines were chosen by chance, two alternative explanations for these results can be considered. First, the influence on orientation may merely be a secondary effect of genetically controlled factors whose primary effects are of selective importance in normal, noninterchange, individuals. The high disjunction frequencies observed would in this case be a purely fortuitous occurrence. Second, rye populations may have been directly subject to selection for high disjunction in interchange heterozygotes. At first sight the first alternative appears the more attractive. The lack of inbreeding depression in the present results, and its presence in the previous findings (LAWRENCE 1958) may be explained in this manner, though correlated response during inbreeding (DARLINGTON and MATHER 1949) may also explain the difference. Further, interchanges do not appear to be common in rye populations (BURNHAM 1956). It is possible, however, that rye, as well as other preadapted species, may have acquired, over many generations, a gene system promoting high disjunction frequency in interchange heterozygotes by a process analogous to FISHER's (1930) theory of the evolution of dominance. During long periods, interchange must be a very common event, and although each structural rearrangement may be quickly removed from the population, their continued occurrence would give rise to a small but persistent selection pressure tending to increase the alternate orientation. Since there appears to be one gene system controlling orientation in the cell, the selection pressure would be larger than that involved in the evolution of dominance.

It is not possible to distinguish between these two alternative hypotheses in the present results, and clearly more information must be obtained before this is possible. However, the conclusion that such genetical preadaptation of species is a product of selection and not a fortuitous event, is more in keeping with the known properties of the genetic system.

SUMMARY

Among the many factors thought to influence the orientation of multiple associations in interchange heterozygotes, previous evidence suggests that there is a genetically controlled mechanism (or mechanisms) which is distinct from that varying the position and number of chiasmata. In rye, variation between 50 percent and 90 percent disjunction frequency has been ascribed to this mechanism. Nevertheless, in this species, directed segregation has been found in newly arising interchanges, suggesting that the genetic constitution has been selected to give a high disjunction frequency. Two alternative explanations for these findings were considered. First, the influence on orientation may be a secondary effect of factors whose primary effect is of selective importance in normal, non-interchange individuals. Second, direct selection for a high disjunction frequency may have occurred in a manner analogous to FISHER's theory of the evolution of dominance.

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