GENOTYPIC CONTROL OF CHROMOSOME BEHAVIOUR IN RYE

IX. THE EFFECT OF SELECTION ON THE DISJUNCTION FREQUENCY OF INTERCHANGE ASSOCIATIONS

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1. INTRODUCTION

CONTROL exercised by the genotype over the orientation of interchange configurations at first metaphase in structural heterozygotes has been demonstrated by Thompson (1956) and by Rees and Sun (1964). On the basis of genotypic control the expectation is that the frequencies of disjunctional as opposed to non-disjunctional arrangements may be adjusted by selection. Indirect evidence for this is provided by Lawrence (1958), who showed that selection for high seed set among interchange heterozygotes is accompanied, and probably at least partly achieved, by an increase in the frequency of disjunction. The present work is concerned with the effect of selection practised directly upon disjunction frequency. The aims were, first, to determine to what degree one can alter the disjunction frequencies in pollen mother cells (*p.m.c.*) of interchange heterozygotes by selection for high and low disjunction. Second, in view of the relation established between *p.m.c.* chiasma frequency and disjunction in rye (Rees and Sun, *loc. cit.*; see also Darlington, 1937), to investigate the correlated responses of the two characters to the selection.

2. MATERIALS AND METHODS

The plants were derived from a cross between two rye lines, *Line 1* and *Line 3* described by Rees and Sun (1965). An F_1 plant from this cross, heterozygous for two independent interchanges *A* and *B* (see Rees and Sun, *loc. cit.*), was selfed to give an F_2 generation comprising plants heterozygous for both interchanges (Het. *AB*), for the separate interchanges (Het. *A* and Het. *B*), as well as structural homozygotes.

Among heterozygotes in each interchange class i.e. *AB*, *A* and *B*, the plants with highest and lowest disjunction frequencies were self pollinated to start high and low lines in F_3 and subsequent high and low selections were made among the F_3 progeny to continue the lines to F_4 .

The disjunction frequency in the interchange heterozygotes was estimated from twenty *p.m.c.s* and expressed as the proportion of interchange associations arranged in disjunctional fashion. Subsequently these proportions were transformed to angular values to allow for straightforward analyses of variance.

The chiasma frequencies in these plants were scored in the same twenty *p.m.c.* scored for disjunction and the frequency per plant expressed as chiasmata per cell.

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3. RESULTS

Selection: parent offspring correlation. The data on disjunction frequencies for the F_2 parent plants and their F_3 and F_4 derivatives are given in table 1. A simple way of determining whether the selection

TABLE 1

The mean disjunction frequencies (in angular values) of F_1 and F_4 selection lines and of their F_2 ancestors. F_3 and F_4 means based on an average of 5 to 6 plants

Interchange		F_2 Parent	F_3	F_4
Het. A {	High	60.0	63.4	79.56
	Low	45.0	59.1	77.48
Het. B {	High	67.2	71.9	69.40
	Low	47.9	60.4	71.60
Het. AB {	High	77.1	71.6	97.26
	Low	49.3	64.4	67.70

has proved effective is to find out whether the disjunction frequencies of plants in the F_3 and F_4 families are correlated with those of the F_2 plants from which they are descended. For this purpose the mean disjunction frequencies of F_3 and F_4 derivatives were plotted against

FIG. 1.—The average disjunction frequencies (in angular values) of F_3 and F_4 progenies plotted against those of the F_2 parents. Circles Het. A, triangles Het. B and squares Het. AB. Open symbols, low selection lines; blocked symbols, high selection lines.

those of the F_2 parents (fig. 1). The figure shows a strong, positive, correlation between parent and offspring frequencies and a regression analysis confirmed that the correlation is significant ($P = < 0.05$). It will also be observed from the graph that the response is consistent for

the three interchange classes as indeed was confirmed by statistical analysis which showed no significant variation between the interchange types. One concludes therefore that the variation in disjunction between F_2 parents was at least partly of a heritable nature and that the selection practised was effective.

FIG. 2.—(a) The disjunction frequencies in high and low lines in F_2 , F_3 and F_4 for the three interchange classes. Note overall increase in disjunction. (b) The chiasma frequencies of F_2 parents and the mean chiasma frequencies of F_3 and F_4 selection lines. Note the negative correlation between chiasma frequencies in 2b and the disjunction frequencies in 2a. Triangles, low lines; circles high lines.

Asymmetry. Apart from showing a correlation between parents and offspring an effective selection within high and low lines over a number of generations among heterozygous parents normally leads to a divergence between the selection lines such that mean values for high and low lines often transgress those of the original high and low parents. While the selection practised here extends over only two generations it is evident that the progress of selection does not follow this expected pattern. It will be seen from fig. 2a, where the results for each interchange class are plotted separately, that the disjunction frequency increases both in the high and in the low lines. There is throughout a steady and significant increase in disjunction from F_2 to F_4 .

The asymmetrical distributions shown in fig. 2*a* consequent upon the overall increase in disjunction in both, albeit distinctive, high and low lines is on the face of it surprising and somewhat bizarre. They are, however, readily explained when account is taken of the relations between disjunction and the chiasma frequencies within these selected inbred families.

Inbreeding, chiasma frequency and disjunction. It is well known that forced inbreeding in rye, as in other normally outbreeding species, causes a decrease in *p.m.c.* chiasma frequencies (*e.g.* Lamm, 1936). Because the plants used in the present work were propagated by self-pollination we should therefore expect the chiasma frequencies to

TABLE 2

Mean chiasma frequencies of selection lines in F₃ and F₄. Data from the same plants described in table 1

Interchange		F ₃	F ₄	Mean
High {	A	12.90	12.70	12.05
	B	12.98	12.72	
	AB	12.53	12.48	
Low {	A	13.25	12.85	13.06
	B	13.30	12.95	
	AB	13.04	12.99	
Mean		13.00	12.28	

decrease with the increasing inbreeding. This decrease is in fact found in all lines (table 2 and fig. 2*b*).

The significance of variation in chiasma frequency to the disjunction of interchange configurations has been established (Rees and Sun, 1964). It was shown that the disjunction is strongly and negatively correlated with the chiasma frequency, such that the disjunction frequency is higher in *p.m.c.s* with low chiasma frequencies and *vice versa*. The increase in disjunction shown by *all* the above families from F₂ to F₄ follows clearly as a direct consequence of the drop in their chiasma frequencies.

As a further consequence of the chiasma/disjunction frequency correlation we should also expect low and high chiasma frequencies as correlated responses to selection for high and low disjunction respectively. Such responses are manifested by the data in table 2 and the graphs in fig. 2*b*. In all cases "low" disjunction lines have higher chiasma frequencies than "high" lines. An analysis of variance shows that these chiasma frequency differences are significant ($P = < 0.01$).

To summarise, therefore, the selection was effective in establishing distinct lines with *relatively* high and low disjunction frequencies. At the same time the inbreeding practised during the selection gave rise to

a situation that may best be described in terms of a genetic inertia (see Mather, 1953), where variation in the one character, disjunction, is restricted and, in this case, largely determined by the release of variation in the other, the chiasma frequency.

4. DISCUSSION

The experiment confirms that selection is effective in causing adjustment in the disjunction frequency of interchange configurations, an adjustment that may be of special adaptive significance where interchanges are established in natural populations. It is of interest to observe that interchange heterozygosity in nature is commonly established and maintained in conditions where inbreeding is imposed upon colonising derivatives of a normally outbreeding species (see Lewis and John, 1963). Inbreeding under such circumstances would normally result in lower chiasma frequencies, at least in the initial stages. Lower chiasma frequencies it has been shown lead to higher disjunction frequencies in interchange configurations. Such populations could, therefore, be regarded as showing a pre-adaptation towards a high disjunction and, hence, high fertility of interchange heterozygotes which arise within them.

One other consequence of the chiasma frequency/disjunction correlation is that selection for change in the latter may not only be restricted and limited by adjustment in chiasma frequency but may also be achieved only at the expense of such adjustment. Thus whereas an effective selection for higher disjunction in interchange heterozygotes may in itself promote an increase in fertility the inevitable lowering of the chiasma frequency upon which the high disjunction depends could, in extreme cases, become intolerable were it to result in extensive univalent formation and hence cause infertility by chromosome loss. From the fertility standpoint, therefore, the optimum would appear to be a compromise where the chiasmata decrease to a level which gives the highest disjunction of interchange configurations compatible with regular and effective pairing of the chromosome complement generally.

5. SUMMARY

1. Selection for high and low frequencies of disjunctional arrangements of interchange configurations at first metaphase of meiosis in rye pollen mother cells was effective in giving rise to distinct lines showing relatively high and low disjunction.

2. The effects of selection were, in general, similar and consistent for genotypes heterozygous for interchanges *A*, *B* and for the double heterozygotes, *AB*.

3. The variation in disjunction frequency is negatively correlated with chiasma frequency. Two consequences of this correlation are:

- (a) "High" and "low" disjunction lines have low and high chiasma frequencies respectively—as correlated responses to selection practised for disjunction.

(b) There is, overall, an increase in disjunction frequency throughout the selection experiment. This increased disjunction is directly attributed to the decreasing chiasma frequency due to the inbreeding practised during the selection.

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