GENOTYPIC CONTROL OF CHROMOSOME BEHAVIOUR IN RYE

VI. SELECTION FOR DISJUNCTION FREQUENCY

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I. INTRODUCTION

It has been shown (Thompson, 1956) that the frequency of disjunctional separation of the chromosomes in rings and chains formed at meiosis in an interchange heterozygote is subject to the control of the genotype. One would expect, therefore, that the disjunction frequency could be changed by selection, and indeed if the differences found between characteristic disjunction frequencies of closely related species (*e.g.* in *Oenothera*, Cleland, 1926; Kulkarni, 1929) are genetic, they suggest that selection may in fact bring about such a change. The following account offers direct evidence of the effect on this character of selection among genotypes within a species.

FIG. 1.—*Pedigree of material.* P_2 and P_8 are inbred lines. The parents and each number in F_1 and F_2 represent a single plant. In F_3 and subsequent generations each number represents a family which arose from a single plant self-pollinated in the preceding generation.

2. MATERIAL AND METHOD

The material used is that described by Thompson (*l.c.*). Two independent interchanges are involved, and these can be distinguished at diplotene in heterozygotes, though not at metaphase. Interchange A includes the nucleolar chromosome, and interchange B contains slightly unequal chromosomes.

The interchanges were found in an F_1 plant from a cross between two inbred lines of rye. This doubly heterozygous F_1 plant was selfed; and among the F_2 plants three double heterozygotes were used to start three lines, each maintained by self-pollinating one double heterozygote in every generation. The pedigree is shown in fig. 1.

3. SELECTION

During the breeding programme, from F_3 onwards, the aim was to grow families of twenty-five plants, each family being obtained by selfing, where available, three heads on a single plant. Not all plants gave this number of seed, and thus there was selection for high seed set between plants within a family. In so far as the variation in self-fertility was due to differences in disjunction frequency, and was heritable, we might expect an increase in the frequency of disjunctive associations in subsequent generations. No selection was practised in the F_2 because the single plants in each line were chosen without reference to their seed set.

TABLE 1

The maximum likelihood estimates of mean disjunction frequency for interchange A (p_a) and interchange B (p_b) in the three lines and the number of plants involved in these estimates. The pooled estimate is obtained from data summed over the three lines. The three F_2 plants used to start the lines were not scored separately from other F_2 plants

	line (1)			line (2)			line (3)			Pooled estimate		
	p_a	p_b	No. of plants	p_a	p_b	No. of plants	p_a	p_b	No. of plants	p_a	p_b	No. of plants
F_1	...	...	...	...	...	...	...	...	...	0.88	0.88	2
F_2	...	...	...	...	...	...	...	...	...	0.66	0.55	11
F_3	0.56	0.47	7	0.75	0.67	17	0.74	0.82	14	0.71	0.69	38
F_4	0.67	0.76	26	0.82	0.79	26	0.80	0.87	14	0.77	0.79	66
F_5	0.69	0.63	11	0.84	0.81	9	0.75	0.75	5	0.78	0.71	25
F_6	0.67	0.78	9	0.86	0.79	27	0.81	0.78	29	0.80	0.79	65

4. RESULTS AND ANALYSES

As a result of segregation in the double heterozygote, selfed to produce succeeding generations, each family may be classified into four types with respect to the interchanges.

- (i) Plants heterozygous for both interchanges (Class AB).
- (ii) Plants heterozygous for A interchange, homozygous for B (Class A).
- (iii) Plants heterozygous for B interchange, homozygous for A (Class B).
- (iv) Plants homozygous for both interchanges (Class O).

The mean disjunction frequency for interchange A may then be obtained by pooling data from all plants in class A. A similar procedure will give the mean frequency of disjunction for interchange B. However, it will be seen that information about these values is also contained in the double heterozygotes (Class AB), but since the two interchanges are indistinguishable at metaphase this information is not readily extracted. Efficient estimates, taking into account observations from the three classes (A, B, and AB), may be obtained by the method of maximum likelihood (Thompson, *l.c.*). In all, two hundred

and seven plants are involved. These estimates, and the joint estimates over the three lines in each generation, are given in table 1.

FIG. 2.—Disjunction frequency plotted against generation.

These estimates have also been plotted against generation in fig. 2.

In the graph it will be seen that from F_3 onwards the disjunction frequency in general increased for both A and B interchanges. We

TABLE 2

Regression analysis of variance. (Disjunction frequency on generation)

	Item	N	M.S.	V.R.	P
(i)	Mean regression	1	0.02627	6.4	0.05-0.01
(ii)	Heterogeneity in regressions of lines	2	0.00982	2.4	0.2-0.1
(iii)	Heterogeneity in regressions of interchanges	1	0.00002	...	...
(iv)	Heterogeneity in means of lines	2	0.05034	12.2	<0.001
(v)	Heterogeneity in means of interchanges	1	0.00003	...	...
	Error	16	0.00412	...	...
	Total	23	...	...	...

must, however, analyse the data in more detail and test the significance of this increase. This has been done by means of an analysis of variance based on the regression of disjunction frequency on generation. The result of this analysis is shown in table 2. Since no selection

was practised on the F_2 , only data from generations subsequent to this are analysed.

Item (i) in table 2 shows that there is a significant joint regression over the three lines and for both interchanges. ($P = 0.05-0.01$). Furthermore, as the hypothesis demands, this regression is positive ($b = +0.0296$). There can be little doubt therefore, that the disjunction frequency has increased from F_3 to F_6 . From this we can conclude that selection for high seed set resulted indirectly in an increase in disjunction.

Two alternative explanations for these trends must be considered. Firstly, the change could be due to seasonal influence. However, it is extremely unlikely that the seasons 1953 to 1956 were so progressively and increasingly favourable to higher disjunction. Secondly, the results could be explained as an accessory of inbreeding depression. This can be ruled out by comparing the F_1 and F_2 values. The F_1 had a higher disjunction frequency than any generation in all lines. The F_2 had a low disjunction frequency, generally lower than other generations.

It will be seen that though there is no evidence in these data of differences in the rate of response to selection between the three lines, they show marked differences in their mean disjunction frequencies (table 2, items (ii) and (iv)), whereas the two interchanges apparently not only behave similarly, but have the same mean values (table 2, items (iii) and (v)). The striking differences in the means of lines support Thompson's earlier findings in F_3 and F_4 , which he attributes to segregation for genes controlling the character, and show moreover that the divergence in lines has been maintained. In these data the consistently uniform behaviour of the two interchanges in all lines suggest that they are controlled by the same genic system and respond similarly to it (*cf.* Thompson *l.c.*).

5. CONCLUSIONS AND SUMMARY

During an inbreeding programme the disjunction frequency of interchange heterozygotes increased by about 10 per cent. from F_3 to F_6 . This increase resulted indirectly from selection within families for high self-fertility. No doubt in natural populations which contain interchanges either floating as in *Campanula* (Darlington and Gairdner, 1937) or fixed, as in *Oenothera* and *Rhoeo*, such selection has been of great importance in their survival. It may equally well explain the very high disjunction frequencies found recently in populations of cockroaches (Lewis and John, 1957).

A marked difference between lines in the material supports the earlier findings of Thompson. No differences between interchanges was observed, suggesting that they are controlled by the same genic system and respond similarly to it.

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