GENOTYPIC CONTROL OF CHROMOSOME BEHAVIOUR IN RYE

IV. THE ORIGIN OF NEW VARIATION

HUBERT REES

Department of Genetics, University of Birmingham

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1. INTRODUCTION

It is generally recognised that the pattern and the efficiency of chromosome behaviour within a population has been achieved under the influence of natural selection acting upon heritable variation arising in chromosome behaviour. This implies that new chromosome variation is continually being exposed, largely, it may be supposed, as the result of segregation and recombination of genes controlling the chromosomes. It is with the origin of such new variation that this investigation is mainly concerned.

In order to show experimentally that recombination can give rise to new forms of chromosome behaviour two homozygous inbred lines were crossed, and the derivatives of the hybrid were compared with the parents for evidence of new recombinant forms. A brief statement of some of the results has appeared in an earlier paper (Rees, 1955*b*). More complete data are now available and are discussed in the following account. While the main concern is with the origin of new forms of chromosome behaviour, the results have, at the same time, provided information about the nature of the gene systems controlling the chromosomes in heredity, in regard to their properties of recombination, and also about the way in which these genes act in controlling chromosome behaviour during development.

2. MATERIAL AND CHARACTERS

P₂ and P₅ (derived from the Swedish variety Stålråg) were the two inbred parental lines used. Both have been inbred by selfing for more than twenty generations, and as the following and other evidence indicates, they are virtually true breeding. Their cytology is described in detail elsewhere (Rees, 1955*a*). Two characters are dealt with (see plate I). They are :—

- (1) *chiasma frequency*, expressed as the average per bivalent from scoring 20 p.m.c. in each plant.
- (2) *pre-meiotic errors*. These result in p.m.c. containing extra nuclei or micro-nuclei whose chromosomes are frequently broken and invariably retarded at the early stages of meiosis. Usually less than 2 per cent. of cells in the affected plants are involved. In the parent lines they occur in P₅ but not in P₂.

A pedigree of the families derived from crossing P₂ and P₅ is represented in fig. 1. The scoring commenced with the F₃ generation—for two reasons. In the first place structural abnormalities such as pre-meiotic errors are generally rare or absent in the more heterozygous F₁ and F₂. These errors, and others which affect chromosome pairing, emerge with increasing unbalance of the more homozygous genotypes in later generations of inbreeding (fig. 2). In the second place, of course, family comparisons are possible from F₃ onwards, and where

TABLE 1
The chiasma frequencies in P₂ and P₅ over three years

1952		1953		1954	
P ₂	P ₅	P ₂	P ₅	P ₂	P ₅
1.79	1.41	1.54	1.64	1.90	1.66
2.01	1.54	1.68	1.70	1.91	1.69
2.04	1.69	1.86	1.74	1.94	1.74
2.04	1.74	1.87	1.77	1.96	1.76
2.08	1.76	1.88	1.79	1.98	1.79
				2.01	1.81

Item	SS	N	MS	VR	P
Years	0.0573	2	0.0287	2.70	0.10—0.05
Lines	0.3330	1	0.3330	31.42	<0.001
Years/lines	0.1321	2	0.0661	6.24	<0.01
Error	0.2762	26	0.0106	...	...
Total	0.7986	31	...	...	...

any differences occur between F₃ families and parents their heritability can subsequently be verified in the following two generations. Altogether more than 200 plants are involved.

3. CHIASMA FREQUENCY

For all families and lines the average frequencies for each year are given in fig. 3. The full data are not produced in order to save space.

Year to year variation. Although the parent lines are homozygous, the chiasma frequencies vary, sometimes considerably, between plants within lines grown in the same season. It has been shown that the *amount* of variation exhibited tends to be characteristic of a line and to differ between lines (Rees and Thompson, 1956). It is worth inquiring therefore to what extent the chiasma frequency of lines may vary from one season to the other, and whether any seasonal effect is the same for all lines. The complete data for P₂ and P₅ are given in table 1; and below is an analysis of variance based on these figures. The analysis shows that between lines the differences are significant, whereas between years they are not. It will be seen also that the interaction item for years and lines is significant. From this

FIG. 1.—The history of the material. Scoring covers the three years from 1952 to 1954.

FIG. 2.—Graphs showing the average chiasma frequencies and the proportions of plants showing pre-meiotic errors in F₁, F₂ and F₃ generations from a cross between P₂ and P₅. With increasing homozygosis the chiasma frequency falls and the proportion of plants showing pre-meiotic errors rises.

FIG. 3.—The mean chiasma frequencies of the families and lines. The order of families is the same as in fig. 1.

it is concluded that the response to different growing conditions from year to year is not the same for the two lines, P₂ in this case being more variable between years.

Segregation and recombination. The differences in chiasma frequencies between families within F₃, F₄ and F₅ are highly significant, the probability values being less than 0.001 in each instance. Regression

FIG. 4.—*a, b.* Graphs showing regressions between the proportions (in angles) of plants with pre-meiotic errors in related families in F₃, F₄ and F₅ respectively. *c, d.* The regressions for the mean chiasma frequencies of the families.

analyses between parent and offspring families, F₃ and F₄, F₄ and F₅, prove that these differences are genotypically controlled. The regressions (fig. 4) are significant at the 0.001 level.*

Family 10 and its derivatives are of particular interest in that, considered over the three years, they have significantly lower chiasma frequencies than either parent. These families with chiasma frequencies transgressing the parental values must have arisen as indicated previously (Rees, 1955*b*) by recombination. Equally evident from

* For calculating the regression between F₃ and F₄ families the data for sister families in F₄ were pooled.

fig. 3 is the wide range of chiasma frequencies in the families which have resulted from segregation and recombination. The values make up a more or less continuous series, from lower than the "low" parent to as high as the "high" parent.

4. PRE-MEIOTIC ERRORS

The expression of this character within anthers is entirely different from chiasma frequency and is such that the abnormal and normal cells develop side by side. Furthermore in some anthers all the p.m.c. are normal while in other anthers of the same plant some p.m.c. are abnormal. Consequently even in the homozygous parent P₅ not all the plants are scored as showing the abnormality. For purposes of comparison therefore the measure adopted for pre-meiotic errors has been the proportion of plants affected in the line or family. These proportions were then transformed to angles for statistical analyses. The angular values are presented in fig. 5.

FIG. 5.—The proportions (as angular values) of plants in lines and families showing pre-meiotic errors.

Firstly, no significant difference was found between inbred P₅ plants grown in different years. Secondly, it will be seen that a whole range of differing families appear in the derivatives of the P₂/P₅ cross. As for chiasma frequency, regression analyses between parent and offspring families confirm the heritability of these differences (see fig. 4). Again as for chiasma frequency one sub-line, *viz.* family (46) and its derivatives, are of particular interest from the point of view of recombination and the origin of new chromosome variation. In these families the proportion of plants which show pre-meiotic errors is significantly higher than in the affected P₅ parents over the same period ($P = 0.05$). Evidently the new variation has arisen by recombination of the genes affecting the penetrance of the pre-meiotic errors.

That family 46 and its derivatives represent entirely new forms is confirmed when these are compared with P₅ in respect of the *proportions of abnormal p.m.c.* within anthers, *i.e.* in terms of expressivity. The proportions have in fact been calculated for all plants from the scoring of about 200 cells in each. As percentages the family averages for

affected plants appear in fig. 6. For the parent P₅ the average is about 1 per cent. in each of the three years, 2 per cent. being the highest value for any one plant. In contrast families descended from 46 have plant averages of up to 4 per cent. abnormal cells, with 8 and 9 per cent. abnormal in some F₄ and F₅ individuals. Using the percentages (transformation makes virtually no difference to such small values) a regression between F₄ families and those related to them in F₅ is significant at the 5 per cent. level; and thereby establishes heritability of the degree of the abnormality expressed within anthers.

In anthers where the relative frequency of abnormal p.m.c. is very high it is clear even in squash preparations that the abnormal cells tend to be localised in groups, but exactly where in the anthers these groups occur is not known. Comparable examples of localisation of pre-meiotic errors are reported by Darlington and Haque (1955), and also by Holden and Mota (1956).

FIG. 6.—The average percentages of p.m.c. showing pre-meiotic errors in the affected plants in lines and families. Note the relatively high values in 46 and its descendants.

5. THE TWO CHARACTERS

Recombination so far has been considered only in respect of genes affecting the two characters separately. For chiasma frequency and also for pre-meiotic errors new variants were shown to arise through recombination. When the two characters are considered together, as in fig. 7, it is seen that a wide range of forms emerges, and families with high or low chiasma frequencies turn up, either with or without pre-meiotic errors in p.m.c. There is thus no doubt of the recombination of the genes controlling the two characters in a number of ways. It also would appear from the graph that these two particular characters are inherited independently of one another.

6. DISCUSSION

The expectation of discovering new chromosome variation resulting from gene recombination has been fully justified by the results described. These, in conjunction with earlier evidence, *e.g.* Maeda (1937) and Peto (1933) enable us to visualise how natural selection acting upon the variation arising in this way determines the behaviour pattern of the chromosomes in a population. This pattern we might expect to vary adaptively from one environment to another. As yet,

unfortunately, not much information is available concerning such variation in wild populations within species. But what information there is amply confirms this (*cf.* Darlington, 1956).

From a developmental point of view it may be noted that the two characters dealt with show variation even between the p.m.c. of the same anther, but they do so in very different ways. For chiasma frequency there is no sharp distinction between cells with few and

FIG. 7.—Proportions (in angles on the vertical scale) of plants in F_8 families with pre-meiotic errors plotted against mean chiasma frequencies of the families. Parent lines for the same year are included. Note the wide range of types in F_8 resulting from segregation and recombination. The two characters appear to be independent in inheritance.

many chiasmata, and whether the plant frequency is high or low the p.m.c. tissues are qualitatively more or less homogeneous. At the same time there is a range of p.m.c. chiasma frequencies within an anther, thereby causing, in respect of the amount of recombination, a variety in the gametes produced. This variety, it has been shown, is genetically controlled (Rees and Thompson, 1956).

Variety with regard to pre-meiotic errors within anthers is of an entirely different kind. Two sharply distinguished types of cells develop side by side and where increased expressivity of the character was achieved this resulted in even more pronounced qualitative

heterogeneity of the p.m.c. tissue. Such a divergence in development, *e.g.* in P₅, in what normally constitutes a homogeneous tissue, is instructive from the point of view of development generally. As Darlington and Haque (1955) have pointed out with reference to a comparable case in *Allium*, the development of the two kinds of p.m.c. represents, in simple form, the problem of differentiation. When viewed from the standpoint of normal development of a simple or complex organ, divergence between cell types is the first essential, accomplished no doubt as the above authors suggest with the aid of diffusion barriers between the different kinds of cells. The second essential is that the components of the organ, being complementary to one another, are in such proportions as to confer, collectively, greatest efficiency to the organ and to the phenotype generally. Consequently the differentiation during development of the organ is achieved in such a way, or at such a time, that the tissues comprise well defined fractions of the whole. The achievement of the right proportions, it may be assumed, is the result of natural selection, which of course implies that the tissue proportions are genetically determined and show heritable variation. The rye results presented above show, albeit in connection with an abnormal organ, how this heritable variation in the relative amounts of the component tissues can arise by recombination. In the parental line P₅ it is seen that one class of cells comprises 1 per cent., whereas in the F₄ and F₅ derivatives this class constitutes up to 9 per cent. of p.m.c. Thus, at cell level, exactly the same capacity of adjustment in developmental pathways is indicated as has been demonstrated for more elaborate levels of organisation, *e.g.* the symmetry of eyes and other body parts in *Drosophila* (*cf.* Waddington, 1942, Mather, 1953).

7. SUMMARY

1. A cross was made between two inbred lines of rye differing in two characters, (*a*) chiasma frequency, and (*b*) a structural abnormality resulting from pre-meiotic errors. In the F₃ and later derivatives of the hybrid between the lines, recombination was demonstrated for genes controlling chiasma frequency, and for genes affecting the penetrance and expressivity of pre-meiotic errors. Recombination is also demonstrated for the two characters considered jointly, the results indicating they are inherited independently.

2. The effect of year to year variation in chiasma frequency is not the same for the two inbred lines.

3. Heritable variation in the proportions of p.m.c. showing pre-meiotic errors indicates how, in normal organs, the relative amounts of the component tissues may be adjusted under natural selection.

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Plate

1. The results, at MI, of pre-meiotic errors. Seven normal bivalents, extra bivalents, univalents and fragments.
- 2, 3. MI in p.m.c.'s of an "asynaptic" family derived by recombination of genes controlling chiasma formation. Only two bivalents in 2, none in 3.

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