

NOTES AND COMMENTS

GENETIC CONTROL OF NEOCENTRIC ACTIVITY IN RYE

M. D. HAYWARD*

Department of Genetics, University of Birmingham

Received 24.iii.62

1. INTRODUCTION

The chromosomes form an integral part of the genetic system of an organism (Darlington, 1956): as such, they are not only the bearers of the hereditary material but are themselves subject to genotypic control (Darlington, 1932). Further, like most genetic characters which have been adequately studied, they may be under both major and polygenic control. A number of examples of both types of gene controlled chromosome behaviour have now been established (Rees, 1961). With regard to polygenic control, however, little attempt has been made to elucidate the form of the genetic components involved; though Rees and Thompson (1956) have shown that chiasma frequency in inbred rye is controlled by a system of interacting non-allelic genes.

Neocentric chromosome behaviour was first described in inbred rye by Prakken and Müntzing (1942). Line differences in the occurrence of neocentric or "T end" activity clearly indicated it to be under genotypic control. Subsequent work has confirmed these initial findings (Östergren and Prakken, 1946; Rees, 1955) but as yet there has been no clear indication of the exact nature of the genetic control of this kind of behaviour. The present study was undertaken with this problem specifically in mind.

2. MATERIAL AND METHODS

Two inbred lines of rye derived from those of Rees (1955) were used as the parental material. Neocentric activity was scored in the parents, F_1 's, F_2 's and backcrosses. All generations were grown out and sampled under comparable conditions during the summer of 1961.

For cytological examination, heads were fixed in 1:3 acetic alcohol and subsequent squash preparations were made using acetocarmine. From each plant 100 cells at MI or AI were examined for evidence of unambiguous neocentric behaviour.

3. RESULTS

The number and percentage of plants in each generation which showed neocentric activity are presented in table 1. Within any one plant exhibiting "T end" behaviour, the incidence ranged from 1.21 per cent. of the cells, whilst within a cell, 1.3 of the seven bivalents were involved. There is no evidence of differences between reciprocal crosses for the inheritance of neocentric activity; for instance, the heterogeneity $\chi^2(6)$ for the four backcrosses to each parent is 8.65 ($P = 0.2-0.1$).

* Present address: Welsh Plant Breeding Station, Aberystwyth.

It is apparent from the ratios of normal to plants showing neocentric activity that this character is not under simple major gene control. However, by considering the proportions of plants in each generation which showed neocentric activity, as a continuously varying character, it is possible to

TABLE 1
Number of plants showing neocentric behaviour

Generation	No. of plants per generation		Total no. of plants	Per cent. neocentrics
	With neocentrics	Without neocentrics		
Parents				
P_3	9	16	25	36
P_6	24	1	25	96
F_1				
3×6	0	25	25	
6×3	1	24	25	
	1	49	50	2
F_2				
3×6	14	35	49	
6×3	12	38	50	
	26	73	99	26.26
Backcrosses				
$3 \times (3 \times 6)$	2	8	10	
$3 \times (6 \times 3)$	2	8	10	
$(3 \times 6) \times 3$	0	10	10	
$(6 \times 3) \times 3$	5	5	10	
	9	31	40	22.5
$6 \times (6 \times 3)$	4	6	10	
$6 \times (3 \times 6)$	2	8	10	
$(3 \times 6) \times 6$	2	8	10	
$(6 \times 3) \times 6$	4	6	10	
	12	28	40	30.0

obtain weighted least squares estimates of the components of the mean, m [d] and [h] by a modification of the method of Cavalli (1952) based on the scaling tests of Mather (1949). The modifications involve transformation of the data to angles and the use of the theoretical error for weighting purposes. The values thus obtained are $m = 56.25 \pm 0.583$, [d] = 16.236 ± 0.292 and [h] = -49.45 ± 0.339 ; which closely agree with the observed generation means on the joint scaling test $\chi^2(3) 4.7746 (P = 0.2-0.1)$. The non-significance of this latter item would indicate the absence of any non-allelic interaction detectable on this scale. From the values of the components it would thus appear that neocentric activity in rye is controlled

by a polygenic system. The high negative value for the dominance component h would signify that dominance is for low neocentric activity. Indeed, the high value of this component compared with the additive item d must be considered as either evidence for over-dominance or alternatively, and more simply, the presence in the two lines, of genes for both high and low neocentric activity, *i.e.* the genes must be dispersed.

It has been shown in maize (Rhoades, 1942) that neocentric activity depends upon the presence in the homo- or heterozygous state of an abnormal heterochromatic knob on the long arm of chromosome 10. The controlling genes would therefore appear to be located in or near to this knob. In rye, however, there is no evidence to suggest a specific localisation of the determinant genes. Rhoades (1952) has suggested that in maize it is the interaction of the telomere and the centromere which results in neocentric activity. This interaction possibly involves a specific centromeric substance which, produced in excess in the presence of abnormal 10, flows along the chromosome to the end where it imparts mobile properties. An alternative explanation, which would also account for the activity in rye, is that the controlling genes, whether localised or scattered, divert to the telomeres the necessary potential for centromeric activity. The low incidence of neocentric behaviour both within and between cells, encountered in the present study, may then be taken to indicate possible competition between the centromeres and telomeres for this specific potential.

In summary, neocentric activity in the inbred lines of rye is apparently controlled by a system of polygenes showing dominance but no non-allelic interaction. The mode of action of these is not known, nor probably will it become known until the biophysical processes underlying centromere behaviour are elucidated.

Acknowledgments.—I am greatly indebted to Professor K. Mather and Dr J. L. Jinks for advice and discussion on the interpretation of the data.

4. REFERENCES

- CAVALLI, L. L. 1952. An analysis of linkage in quantitative inheritance. *Quantitative Inheritance* 135-145. H.M.S.O. London.
- DARLINGTON, C. D. 1932. The control of the chromosomes by the genotype and its bearing on some evolutionary problems. *Amer. Nat.*, 96, 25-51.
- DARLINGTON, C. D. 1956. Natural populations and the breakdown of classical genetics. *Proc. Roy. Soc. B.*, 145, 350-364.
- MATHER, K. 1949. *Biometrical Genetics*. Methuen, London.
- ÖSTERGREN, G., AND PRAKKEN, R. 1946. Behaviour on the spindle of actively mobile chromosome ends of rye. *Hereditas*, 32, 473-494.
- PRAKKEN, R., AND MÜNTZING, A. 1942. A meiotic peculiarity in rye, simulating a terminal centromere. *Hereditas*, 28, 442-482.
- REES, H. 1955. Genotypic control of chromosome behaviour in rye. I. Inbred lines. *Heredity*, 9, 93-115.
- REES, H. 1961. Genotypic control of chromosome form and behaviour. *Bot. Rev.*, 27, 288-318.
- REES, H., AND THOMPSON, B. 1956. Genotypic control of chromosome behaviour in rye. III. Chiasma frequency in homozygotes and heterozygotes. *Heredity*, 10, 409-424.
- RHOADES, M. M. 1942. Preferential segregation in maize. *Genetics*, 27, 395-407.
- RHOADES, M. M. 1952. Preferential segregation in maize. *Heterosis*. Ed. Gowen. Iowa State College Press, Ames., 66-80.