Genet. Res., Camb. (1970), **16**, *pp.* 325–331
With 4 text-figures
Printed in Great Britain

Induced variation in chiasma frequency in Rye in response to phosphate treatments

By M. D. BENNETT* and H. REES
Department of Agricultural Botany, University College of Wales, Aberystwyth

(*Received* 17 *July* 1970)

1. SUMMARY

Plants of two rye genotypes, one highly inbred, the other not, were grown with varying amounts of available mineral phosphate. In two experiments, one using culture solutions, the other a field experiment, the results show an effect of phosphate treatments on mean chiasma frequency at first metaphase in meiocytes. Plants given increased amounts of phosphate showed an increase in chiasma frequency. A similar effect of phosphate on chromosome size and mass at mitotic metaphase in meristems is known and there may be a direct link between chromosome size and chiasma frequency.

2. INTRODUCTION

It is well known that chiasma frequency at meiosis varies in different environments. There is a considerable literature describing the influence upon chiasma frequency of temperature changes (Mather, 1938; Dowrick, 1957; Henderson, 1962; Yanney, 1959), chemical treatments (e.g. colchicine, Barber, 1940) and of ionizing radiation treatments (Mather, 1938; Lawrence, 1961*a*,*b*). Other results (Steffenson, 1957; Law, 1963) show an influence of changes in mineral treatments upon chiasma frequencies and chiasma distributions. Bennett & Rees (1969) have demonstrated large induced changes in chromosome volume and nuclear dry mass in root-tip meristems of rye. It was considered worthwhile, therefore, to investigate whether the induced changes in chromosomes volume in root tips were accompanied by changes in chiasma frequency and chiasma distributions.

3. MATERIALS AND METHODS

(*a*) *Materials*

The investigation was carried out using two types of rye, *Secale cereale*,

$$2n = 2x = 14.$$

These were *P*1, a line derived from the Swedish variety Stalrag by inbreeding for more than 30 generations; and Lovaszpatonai, a commercial variety of Polish origin, obtained from Dunns Seeds Ltd.

* Present address: Plant Breeding Institute, Maris Lane, Trumpington, Cambridge, England.

(*b*) *Methods*

Plants were cultivated in two ways. In the first experiment seeds were germinated at 20 °C on germination pads moistened with distilled water. After 3–4 days seedlings were suspended over large light tight bowls of aerated culture solution maintained at 19–21 °C in a glasshouse with artificial light supplied to maintain a 16 h day length. The culture solutions used, which varied in their phosphorus concentration, are those previously described (Bennett & Rees, 1969). The mineral content of the culture solutions, to the nearest part per million, is

Table 1. *The mineral content of the culture solutions (to the nearest p.p.m.)*

Treatment	P	N	K	Ca	Mg	Na	Cl
High PO_4	40	23	27	39	10	11	—
Normal PO_4	16	23	27	29	10	—	—
No PO_4	—	23	30	29	10	—	21
No minerals	—	—	—	—	—	—	—

Fe, B and Mn supplied as traces.

given in Table 1. In the second experiment plants of the two rye genotypes were grown in a field experiment with two treatments. Plants were either grown on poor field soil which had not received any fertilizer for many years, or on an adjacent plot to which a phosphorus dressing at a rate of 100 units of phosphorus per acre (a normal agricultural dressing) was applied.

In both experiments suitable inflorescences were fixed and the chiasma frequency estimated from squashes of first metaphase of meiosis in pollen mother cells (p.m.c.).

4. RESULTS

(*a*) *Culture solution experiment*

P 1 rye plants were grown in 'high' and 'normal' phosphate culture solutions for 8 weeks. After 3 weeks some plants were transferred from 'high' phosphate treatment to either 'no phosphate' or 'no minerals' treatments. Seven or eight weeks after sowing, inflorescences were fixed and the mean chiasma frequency determined in each plant. The results show (Fig. 1) an increase in chiasma frequency with increasing phosphate supplied in culture solution (Table 2). Analysis of variance shows a significant difference between treatments ($P < 0{\cdot}01$). Chiasma frequencies in plants of the commercial variety Lovaszpatonai grown in three of the culture solutions were also examined (Table 3), and again a significant difference between treatments ($P < 0{\cdot}001$) is seen.

(*b*) *Field experiment*

(i) *Mean chiasma frequency*

Chiasma frequency in p.m.c. was estimated in ten heads of both rye genotypes grown in a field experiment with two levels of phosphate treatment as previously

described in Materials and Methods. The results (Table 4) plotted in Fig. 2 shows a highly significant difference between treatments ($P < 0{\cdot}01$) for both rye genotypes.

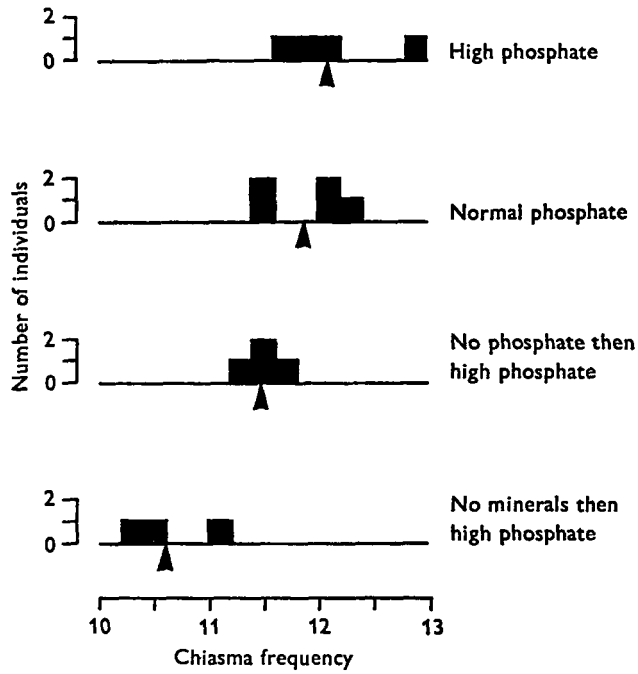

Fig. 1. Chiasma frequencies estimated from 20 p.m.c.'s of *P* 1 rye plants grown in different culture solutions. An average of four plants in each treatment. Arrows indicate means.

Table 2. *The mean chiasma frequency in p.m.c. of* P *1 rye grown in different culture solutions until heading at 8 weeks*

Treatment	High phosphate	Normal phosphate	No phosphate then high phosphate	No minerals then high phosphate
Mean ± S.E.	12·01 ± 0·25	11·88 ± 0·16	11·46 ± 0·08	10·60 ± 0·23

Table 3. *The mean chiasma frequency in p.m.c. of Lovaszpatonai rye grown in different culture solutions until heading at 12 weeks*

Treatment	High phosphate	Normal phosphate
Mean ± S.E.	13·93 ± 0·22	13·08 ± 0·11

(ii) *The between-cell distribution of chiasmata*

Besides the effect of mineral treatments on the *mean* plant chiasma frequency, it is also interesting to compare the effect of the various treatments on the distribution of chiasmata between p.m.c. within plants. It must be emphasized that

such variation between cells is not of a *heritable nature* but rather a reflexion of development response to the treatments given. Variation in the mean chiasma frequency between p.m.c. within a plant cannot be heritable because the p.m.c. are of identical nuclear genotype. It has been shown, however, that the extent of variation in mean chiasma frequency between cells within plants is determined partly by the plant genotype but also by environmental factors (Rees & Thompson, 1956; Dowrick, 1957).

The variation between p.m.c., calculated from the variance of the chiasma frequencies for the 20 p.m.c. scored in each plant of the two types of rye grown in the field experiment is given in Table 4.

Table 4. *The mean chiasma frequency and between-cell variance in plants of the inbred line* P1 *and the commercial variety Lovaszpatonai grown in soil with or without phosphate dressing*

	High phosphate treatment (Poor soil + P_2O_5 dressing)		Low phosphate treatment (Poor soil)	
Rye genotype	Chiasma frequency	Between-cell variance	Chiasma frequency	Between-cell variance
P_1 mean ± S.E.	14·90 ± 0·15	0·0350 ± 0·0026	13·75 ± 0·28	0·0467 ± 0·0044
Lovaszpatonai mean ± S.E.	12·24 ± 0·17	0·0687 ± 0·0072	11·20 ± 0·20	0·0983 ± 0·0095

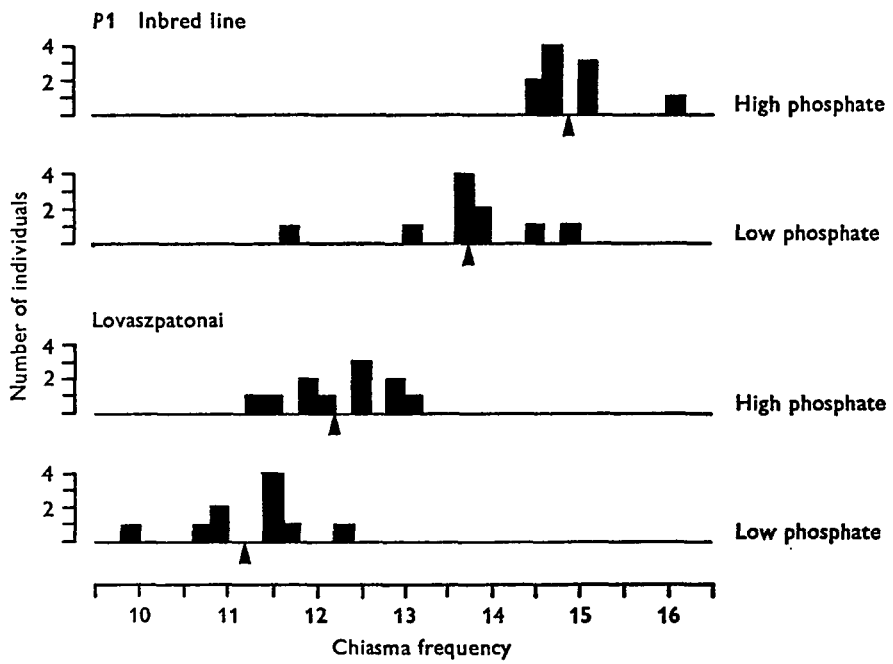

Fig. 2. Chiasma frequency estimated from 20 p.m.c.'s of Lovaszpatonai and *P*1 inbred line rye, grown in a field experiment with or without addition of 100 units of phosphorus/acre. Arrows indicate means.

https://doi.org/10.1017/S0016672300002585 Published online by Cambridge University Press

An analysis of variance of the average differences in between-cell variances shows a significant variation due to treatment ($P < 0{\cdot}001$). While this analysis confirms an influence of treatment upon the extent of developmental variation within plants it is, however, necessary to consider whether this influence upon chiasma distribution is related to variation in mean chiasma frequency. Rees & Thompson (loc. cit.) and Dowrick (loc. cit.) have shown these two characters to be closely correlated. Plotting the average between cell variances against the mean chiasma frequencies (Fig. 3) for both rye types in both treatments reveals a close negative correlation. The regression is significant ($P < 0{\cdot}05$). While there is an influence of treatment upon chiasma distribution the effect is clearly not independent of that on chiasma mean.

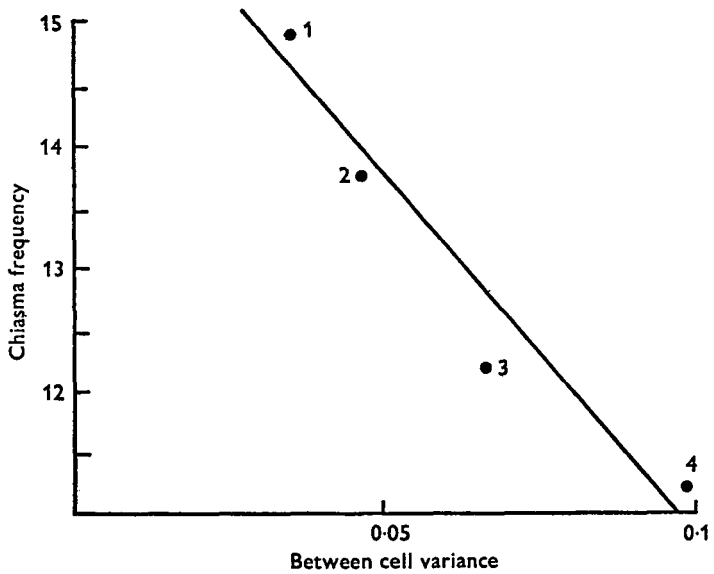

Fig. 3. Regression line calculated for mean chiasma frequency plotted against the mean between cell variance.

	Treatment	Genotype
Key:	(1) High phosphate	*P* 1 inbred line
	(2) Low phosphate	
	(3) High phosphate	Lovaszpatonai
	(4) Low phosphate	

5. DISCUSSION

The results show an effect on chiasma frequency due to different phosphate treatments. An increase in the phosphate available to the plant is accompanied by an increase in mean chiasma frequency in p.m.c. Concerning the mechanism by which this effect is produced, it is worth noting that there is a well-established relationship between chromosome length and the number of chiasmata (Mather, 1938). It is known (Bennett & Rees, 1969) that the mineral solutions which pro-

duce change in mean chiasma frequency also induce large changes in chromosome volume and mass in shoot and root meristems. It is not inconceivable, therefore, that the treatments inducing large chromosome size also directly promote high chiasma frequencies. Fig. 4 shows the result of plotting the chiasma frequencies against the chromosome volume in root meristem cells of the same plants at the same age. A regression analysis for these data shows that the line obtained is significant at the 5 % level. While a causal relationship between induced change in chromosome size and mean chiasmata is not inconceivable, it is not, of course, in any way proven by this work.

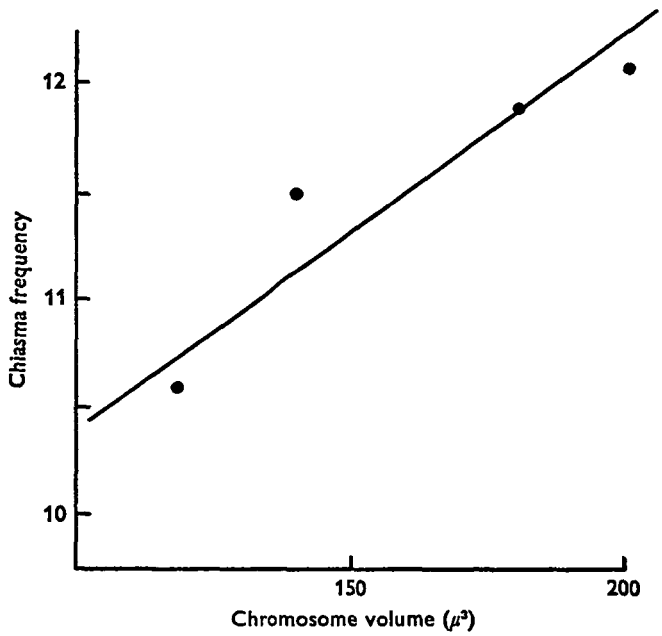

Fig. 4. The mean chiasma frequency at first metaphase in pollen mother cells plotted against the volume of metaphase chromosomes in root tip meristems of *P* 1 rye plants.

It is important to note that the variation in chiasma frequency seen as the result of the various mineral treatments is 'normal'. There are no disruptive effects of the treatments as are seen for instance when X-rays are used. In all cases the plants were morphologically and physiologically normal and meiosis was also normal.

It is not unreasonable to suggest that plant breeders should take advantage of the effects of minerals in altering chiasma frequency and, hence, genetic recombination. In theory it would be possible to generate an increased, and possibly useful, degree of heritable variation amongst progenies of heterozygous genotypes in a way that, in contrast with X-rays and other such agents, has no drastic effect either on the chromosome structure or on the mitotic index.

REFERENCES

BARBER, H. N. (1940). The suppression of meiosis and the origin of diplochromosomes. *Proceedings of the Royal Society London*, B **128**, 170–185.

BENNETT, M. D. & REES, H. (1969). Induced and development variation in chromosomes of meristematic cells. *Chromosoma* **27**, 226–244.

DOWRICK, G. J. (1957). The influence of temperature on meiosis. *Heredity* **11**, 37–49.

HENDERSON, S. A. (1962). Temperature and chiasma formation in *Schistocerca gregaria*. II. Cytological effects at 40 °C and the mechanism of heat induced univalence. *Chromosoma* **16**, 192–221.

LAW, C. N. (1963). Effects of potassium on chiasma frequency and recombination. *Genetica* **33**, 313–329.

LAWRENCE, C. W. (1961*a*). The effect of the irradiation of different stages in microsporogenesis on chiasma frequency. *Heredity* **16**, 83–89.

LAWRENCE, C. W. (1961*b*). The effect of radiation on chiasma formation in *Tradescantia*. *Radiation Botany* **1**, 92–96.

MATHER, K. (1938). Crossing over. *Biological Reviews* **13**, 252–292.

REES, H. & THOMPSON, J. B. (1956). Genotypic control of chromosome behaviour in rye. III. Chiasma frequency in homozygotes and heterozygotes. *Heredity* **10**, 409–424.

STEFFENSON, D. (1957). Effects of various cation imbalances on the frequency of X-ray induced chromosomal aberrations in *Tradescantia*. *Genetics* **42**, 239–252.

WILSON, J. Y. (1959). Changes in the distribution of chiasma in response to experimental factors in Bluebell, *Endymion nonscriptus* (L) Garch. *Genetica* **30**, 417–434.