GENOTYPIC CONTROL OF CHROMOSOME BEHAVIOUR IN RYE

XI. THE INFLUENCE OF *B* CHROMOSOMES ON MEIOSIS

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Received 5.xi.66

1. INTRODUCTION

Supernumerary, *B*, chromosomes have been reported in nearly 200 species of higher plants. They are especially common in the Gramineae. They occur also in mosses, liverworts, and in many animal species (Battaglia, 1964). It is generally held that *B* chromosomes are of adaptive importance because their occurrence and frequency within a species varies between populations of different origin or habitat. An alternative view, held by the minority (*cf.* Östergren, 1945), is that *B* chromosomes are parasitic and are maintained more or less independently of any adaptive benefit or handicap they confer upon individuals or populations.

In rye, *B* chromosomes are abundant in the Orient (found in more than 90 per cent. of plants in some Japanese populations, Kishikawa, 1965), less frequent in the Middle East (one to thirty per cent. of individuals in Iranian populations, Müntzing, 1957) and rare or, more commonly, absent in European populations (Müntzing, 1954). Their effects on the phenotype in rye are very similar to those reported in other species. Most important of these are:

1. A reduced fertility with increasing number of *B*s.
2. Change in external plant form, *e.g.* a reduction in plant weight and height with an increasing *B* frequency (Müntzing, 1963). Such variation is of an essentially quantitative, *i.e.* continuous, nature and it is virtually impossible to detect the presence, let alone the frequency, of *B*'s, by reference to the external phenotype of individual plants.

As for the structure of *B*'s in rye:

1. They are smaller than the normal, *A*, chromosomes although there is some variation in the size of *B*'s found in different populations (Lima de Faria, 1963).
2. They are slightly heterochromatic and replicate their *DNA* later in interphase than do *A* chromosomes (Darlington and Haque, 1966).
3. At meiosis *B*'s do not pair with *A*'s and, hence, are not homologous with any of these. *B*'s do pair with one another and form chiasmata at meiosis.
4. *B*'s exhibit a polarised non-disjunction at mitosis following both male and female meiosis (Muntzing, 1946; Håkansson, 1948). For this reason the frequency of *B*'s in a population tends to increase, at

least under experimental conditions; but only up to a certain level, above which the plants are completely sterile.

From the standpoint of adaptation one factor to consider is the phenotypic polymorphism directly attributable to the presence or absence of *B*'s in individuals within a population. There is, however, good reason to suppose that such a polymorphism may not be the only, or even the main, factor which could account for their possible adaptive importance. Darlington (1956) has pointed out that *B*'s are rare in tetraploids as compared with diploids. He infers from this that a probable role of *B*'s, in potentially less variable diploids, is the boosting of genetic variability. The recent work by Moss (1966) provides evidence to support this view. He confirms that the presence of *B* chromosomes not only affects directly the growth and development of individuals, in respect of germination and seedling growth, but finds, also, that the presence of *B*'s in parents increases the variability of their progenies, over and above that directly determined by the presence of *B*'s in the progenies themselves.

A possible explanation for this boosting of variability is that *B*'s influence the *release* of variability by genotypic control upon chiasma formation and, hence, upon the degree of genetic recombination at meiosis. Evidence that *B*'s do indeed influence chiasma formation and chiasma frequency in some species has been presented by John and Hewitt (1965). Some preliminary observations by our colleague S. Sun (1964, unpublished) indicated that *B*'s may also affect chiasma formation in rye. The aim of the present work therefore was to examine in detail the effects of *B*'s in rye on the frequency and distribution of chiasmata.

2. MATERIALS AND METHODS

An experimental population of plants with 0-8 *B* chromosomes was initiated in 1961 from crosses between plants of *Secale cereale*, derived from the variety Stälrag, and individuals of *Secale vavilovii* which were found to carry two *B* chromosomes. These " species hybrids " were grown together and allowed to cross pollinate. Cross pollination among the progenies was continued for three subsequent generations in order to build up a range of numbers of *B* chromosomes and, as well, to produce a reasonably homogeneous genetic background in respect of the *A* chromosomes.

In 1965 heads were fixed in Carnoy's fluid and preparations of 1st metaphase of meiosis made by staining with acetocarmine. Twenty pollen mother cells (*p.m.c.*'s) were scored for chiasma frequency in each plant, and where possible a total of ten plants for each class of *B* chromosome were examined. Chiasma frequency is expressed as the mean number of chiasmata per *p.m.c.*

3. CHIASMATA IN A CHROMOSOMES

(A) *Chiasma frequencies*

The complete data for the mean chiasma frequencies of the *A* chromosomes in the nine classes of plants are given in table 1.

They show that there is very little variation between the means of the nine classes. A regression analysis of variance shows that the slight

TABLE I

The mean chiasma frequencies of the " A " and " B " chromosomes in the nine classes of plants

Plant	*B* chromosome class																	
	0B		1B		2B		3B		4B		5B		6B		7B		8B	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
1	14·15	...	14·95	...	14·90	1·60	12·30	1·85	11·70	1·95	12·85	2·44	15·85	3·10	15·90	3·50	12·50	4·50
2	16·15	...	11·90	...	12·25	1·25	14·50	1·30	13·35	2·10	13·90	2·00	11·10	3·31	14·65	3·60	15·20	4·83
3	14·25	...	...	...	14·35	1·10	14·10	1·60	13·85	2·35	12·65	3·16	12·00	3·35	10·50	4·33	10·65	5·00
4	...	...	...	...	14·15	0·65	15·90	1·60	13·10	2·05	14·90	2·50	13·55	3·44	9·50	4·50	13·75	4·33
5	...	...	...	...	11·45	1·10	13·35	0·95	14·05	2·11	13·60	3·10	13·30	3·80	...	...	...	...
6	...	...	...	...	13·15	1·15	12·90	1·75	13·10	2·10	11·50	2·55	13·10	3·60	...	...	...	...
7	...	...	...	...	13·25	1·50	13·45	1·70	10·90	2·15	10·10	2·75	14·75	3·69	...	...	...	...
8	...	...	...	...	12·75	1·20	10·80	1·90	12·45	2·50	...	...	11·00	3·83	...	...	...	...
9	...	...	...	...	14·00	1·10	13·10	1·67	12·30	2·65	...	...	13·80	3·69	...	...	...	...
10	...	...	...	...	11·95	1·60	13·50	1·55	11·65	2·40	...	...	13·75	4·12	...	...	...	...
Class mean	14·85	...	13·43	...	13·22	1·23	13·39	1·59	12·64	2·24	12·86	2·64	13·20	3·59	12·64	3·98	13·03	4·67

decrease in means with increasing number of *B*'s is not significant (P = 0·1-0·2).

These results differ from those in other organisms. For example, Hanson (1962) showed that an increasing number of *B* chromosomes considerably enhanced genetic recombination and, hence presumably, the chiasma frequency in chromosome *III* of Maize. More recently John and Hewitt (*loc. cit*) have established that the mean chiasma frequency at spermatogenesis in a grasshopper, *Myrmeleotettix maculatus* (*Thunb.*), is also increased in the presence of *B*'s.

While *B*'s in rye have no effect on mean chiasma frequencies the question arises whether they influence the *distribution* of the chiasmata, either between or within plants. The following sections are concerned with analyses to test this possibility.

(B) *Chiasma distribution*

(a) *Between plants*

A convenient measure of the amount of variation in chiasma frequencies between plants within each *B* chromosome class is the variance of the mean plant chiasma frequencies. Comparisons of the variances can then be made to ascertain differences in the distribution of mean chiasma frequencies within the different classes. The data (table 2) have been analysed by means of a regression analysis of variance. In carrying out this analysis it was, however, important to weight the variances in relation to the number of plants in each class because, clearly, variances calculated from the very few plants in some classes are much less reliable than those based on larger numbers. From the analysis of variance of these weighted data there is a significant regression (P = <0·05). The regression is positive and it follows that the chiasma frequency variation between plants increases with increasing numbers of *B* chromosomes. There are two possible explanations. Firstly, it may be that the chiasma frequencies of plants with many *B*'s are more susceptible to environmental fluctuations, *i.e.* they are developmentally less stable than plants with few or no *B*'s. Secondly, the progenies of plants with many *B*'s are genetically more variable. Clearly plants with most *B*'s are more likely to be descended from parents with high *B* frequencies. That the offspring of the latter are more variable than those of plants with few or no *B*'s conforms exactly to the situation reported by Moss (*loc. cit.*) and may be taken as a further indication of the role of *B*'s as promoters of extra variability.

TABLE 2

The variances of the mean plant chiasma frequencies in the nine classes of plants

B Class	0B	1B	2B	3B	4B	5B	6B	7B	8B
Plant variance	1·270	4·651	1·276	1·808	1·047	2·132	2·324	9·702	3·724

While this second possibility is a most likely one it is, however, realised that there is no way of distinguishing between the two possibilities in the present instance.

(*b*) *Within plants*

(i) *Between p.m.c.* Chiasma frequency variation between *p.m.c.*'s within a plant must of course be of non-heritable or developmental origin because the *p.m.c.* are of identical nuclear genotype. It has been shown, however, that the range of such variation is at least partly determined by the plant genotype (Rees and Thompson, 1956). This variation between *p.m.c.*'s (between cells variance) is readily measured by calculating the variance of the chiasma frequencies for the twenty *p.m.c.*'s scored in each plant. Comparisons between the average variances in the nine different classes were then made to see if the *B* chromosomes had any effect upon the chiasma frequency variation between *p.m.c.*'s within plants. From the data, represented in fig. 1, it is quite evident that the variances increase with increasing numbers of *B*'s. A regression analysis of variance confirms the positive correlation between the variances and the number of *B*'s per plant ($P = < 0 \cdot 001$).

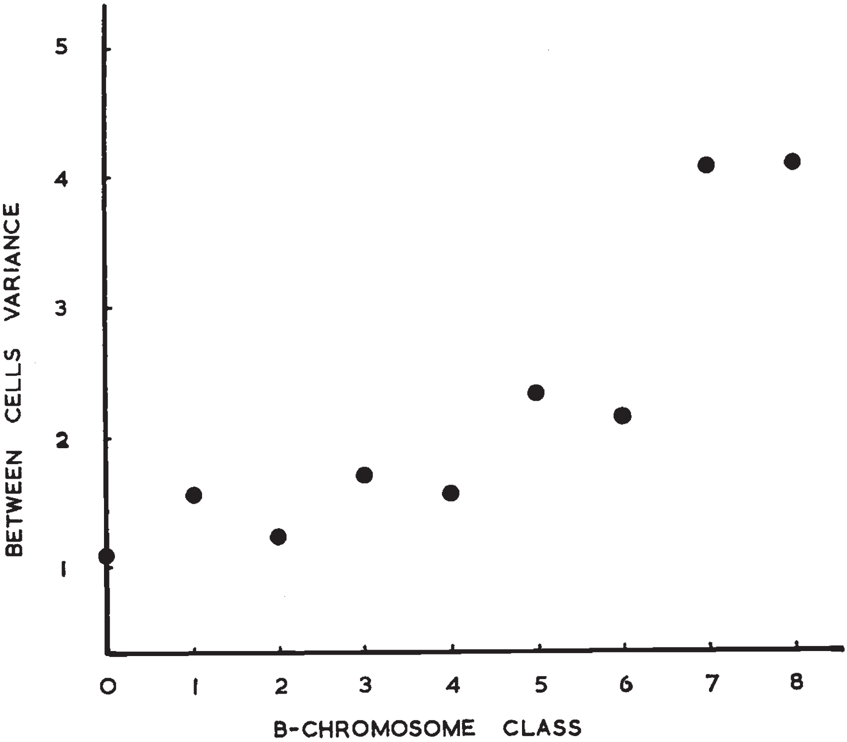

FIG. 1.—Mean " cell variances " within plants plotted against the number of *B*'s per plant.

It is worth noting that in rye the variation between *p.m.c.*'s is often partly dependent upon the mean plant chiasma frequencies (Rees and Thompson, *loc. cit.*). In the present case there is no significant variation in mean chiasma frequencies between the different *B* classes, which indicates that *B*'s influence the amount of variation between *p.m.c.*'s quite independently of the mean chiasma frequency. A regression analysis of variance of the mean variances between *p.m.c.*'s on the mean plant chiasma frequencies for each class confirms that variation between *p.m.c.*'s is independent of the means. The regression is not significant (P = 0·05-0·10).

(ii) *Within p.m.c.*'s. The distribution of chiasmata between the different bivalents within *p.m.c.*'s will depend, amongst other things, upon differences in chromosome length and upon chromosome structural changes. In the present material the chromosome complement is similar for all families except for the variation in the number of *B* chromosomes. For comparisons the variation within *p.m.c.*'s (bivalent variance) was calculated as the variance of the chiasma frequencies within the twenty *p.m.c.*'s scored in each plant. In making these comparisons, however, it has been borne in mind that the average plant variances within *p.m.c.*'s are, in rye, correlated with the mean plant chiasma frequencies (Rees and Thompson, *loc. cit.*). A convenient and effective way to eliminate possible confusion of this variation due to chiasma frequency is to compare the variation between bivalents in *p.m.c.*'s of similar chiasma frequencies in the different *B* chromosome classes (see Jones and Rees, 1964). The data on the mean variances for *p.m.c.*'s with 11, 12, 13 and 14 chiasmata—which are represented in plants of all classes—are plotted in fig. 2.

It is apparent that the chiasma frequency variation between bivalents increases in *p.m.c.*'s of plants with increasing numbers of *B* chromosomes, the increase being quite independent of *p.m.c.* chiasma frequency. A regression analysis of variance confirms the highly significant correlation. The joint regression is significant at the 0·1 per cent. level.

(iii) *Within bivalents.* All chromosomes of the rye complement have median or sub-median centromeres, and normally the chiasmata are more or less equally distributed between the two arms so that bivalents with two chiasmata tend to be rings. Rods with two chiasmata in one arm are rare. To determine whether *B* chromosomes influence the distribution of chiasmata between arms an estimate was made of the proportion of rod bivalents with two chiasmata in one arm in plants in each of the *B* chromosome classes (fig. 3). It is clear that the distribution of chiasmata between arms becomes increasingly asymmetrical with an increasing frequency of *B*'s. A regression analysis shows that the increase is significant ($P<0·05$). *B* chromosomes therefore influence the distribution of chiasmata not only between *p.m.c.*'s, and between bivalents within *p.m.c.*'s, but also between different regions of the chromosomes within each bivalent.

Mechanism. There is no doubt from the analyses above that *B*

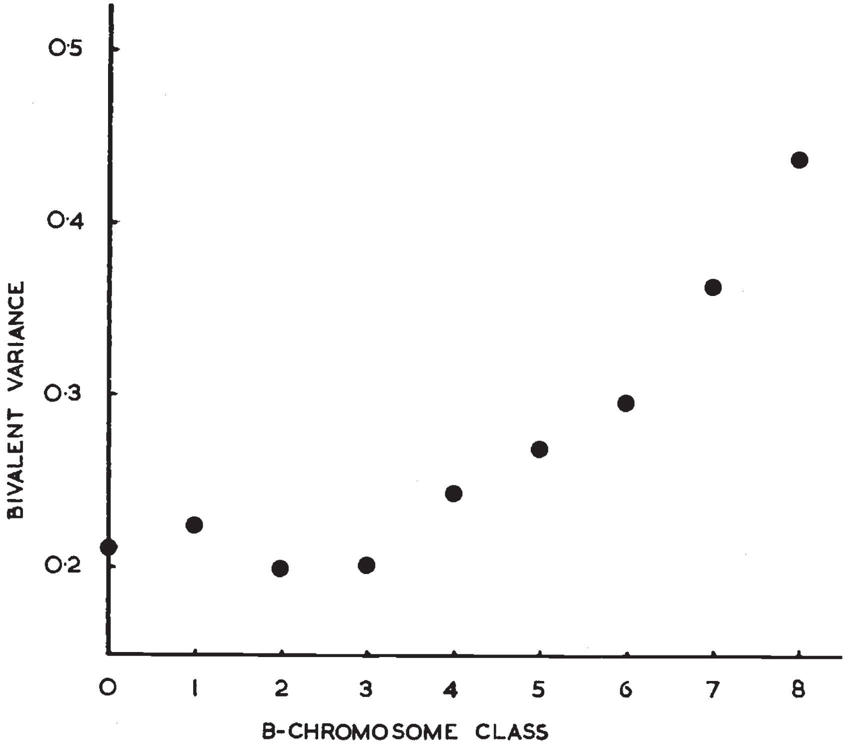

FIG. 2.—The mean "bivalent variance" for *p.m.c.*'s with 11, 12, 13 and 14 chiasmata, plotted against the number of *B*'s per plant.

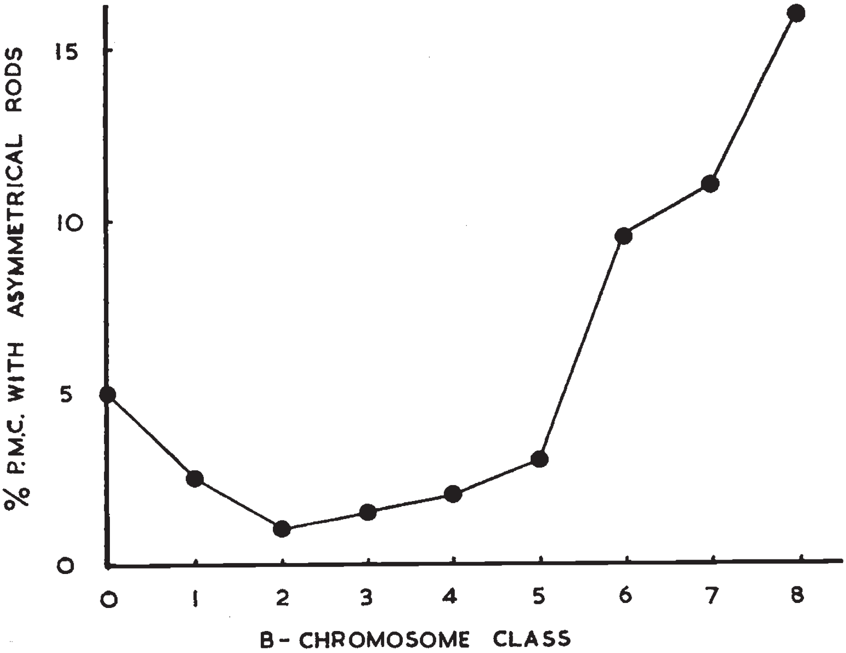

FIG. 3.—The percentage of *p.m.c.*'s with asymmetrical rod bivalents, plotted against the number of *B*'s.

chromosomes affect the distribution of chiasmata between *A* chromosomes at meiosis. However, before one can attribute this effect to genotypic control exercised upon chiasma formation by *B* chromosomes one must consider another possible explanation, that is a simple mechanical interference by *B* chromosomes on the regular pairing of *A*'s during prophase of meiosis; in other words, the possibility of *B*'s " getting in the way " of *A*'s during initial pairing. If this were so it would be expected that the *p.m.c.*'s with the high numbers of *B*'s would also show a lowering of the chiasma frequency overall. As has been pointed out there is no significant decrease in *p.m.c.* chiasma frequency with high *B*'s. On the contrary, it will be seen (fig. 6) that *p.m.c.*'s with the highest chiasma frequencies, up to eighteen and more, occur in those plants with high numbers of *B*'s. It is, therefore, at least improbable that *B*'s affect, in any direct mechanical sense, the pairing and chiasma formation in *A*'s. One must conclude therefore that the influence exerted by *B*'s upon the chiasma distribution in *A*'s is in the nature of a genic, or genotypic, control.

4. CHIASMATA IN B CHROMOSOMES

The results so far have dealt exclusively with chiasma formation in the *A* chromosomes. It remains now to look at the frequency and distribution of chiasmata in the *B* chromosomes, from two, particular, points of view:

(i) Possible interference in chiasma formation between the *A* and *B* chromosomes.

(ii) The influence of the *A* chromosome genotype upon *B* chromosome behaviour.

Interference. The chiasma frequencies of *B* chromosomes appear, along with those of the *A*'s, in table 1.

(a) *Between B classes.* As will be seen from table 1 and fig. 4, the total chiasma frequency of *B*'s per *p.m.c.* increases with increasing *B* frequency. The increase is slightly uneven in that the chiasma frequencies for odd numbers of *B*'s appear to be disproportionately low as compared with those for even numbers, most probably a reflection of a relatively less effective pachytene pairing where odd numbers of *B*'s are involved. Despite this uneveness the total *B* chiasma frequency is, overall, more or less directly proportional to the number of *B*'s.

It will be recalled that the mean chiasma frequency of *A*'s was unaffected by variation in the number of *B*'s. The increase in the total *B* chiasma frequency with increasing *B* frequency is consequently achieved independently of the chiasma frequency of *A*'s. From this kind of comparison, therefore, there is no suggestion of interference in chiasma formation between the *A* add *B* chromosomes.

Figure 4 also shows that *the chiasma frequency per B chromosome* is constant (about 0·57) over the whole range of *B* classes. Thus, with each additional *B* chromosome the total *p.m.c.* chiasma frequency increases by about 0·57—an increase that is entirely taken up by the *B* chromosomes themselves. Evidently there is no effective competition for this extra chiasma allocation on the part of the *A*'s. On Mather's (1939) view this may be perfectly well interpreted to mean that the *p.m.c.* chiasma frequency is below the " upper limit " and hence not inducive of competition between *A*'s and *B*'s. Alternatively one could suppose that the requirements and conditions for chiasma formation in *A*'s and *B*'s were so different as to preclude competition between them or of showing any other correlation in their chiasma frequencies. The evidence of Darlington (1933) on *B* chiasma frequency, however, is against this view. So also is the following evidence concerning the detailed relationship between *A* and *B* chiasma frequencies between plants within the different *B* classes.

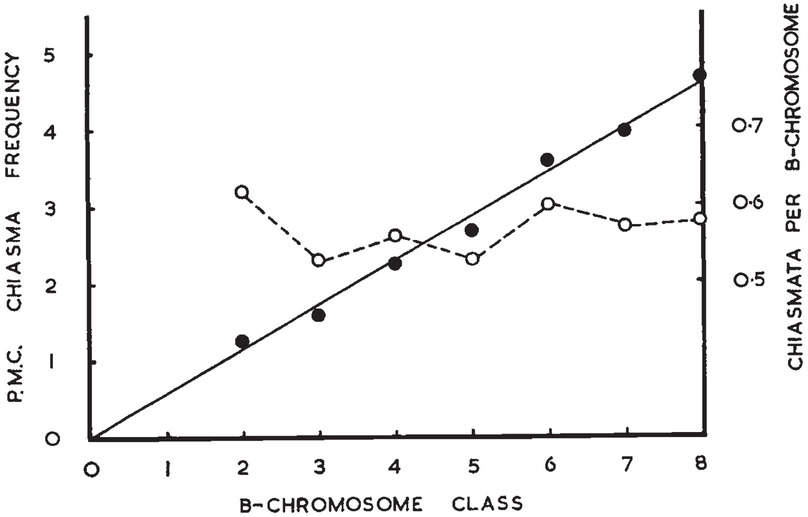

FIG. 4.—Mean *p.m.c.* chiasma frequencies of the *B* chromosomes (solid line), and the mean number of chiasmata per *B* chromosome (dotted line), plotted against the number of *B*'s.

(b) *Within classes.* In table 1 the results indicate that within all classes an increase in *A* chiasma frequency per plant is accompanied by an increase in the *B* chiasma frequency. A joint regression analysis of variance of *B* chiasma frequency on that of the *A*'s for plants within all classes appears in table 3. It will be observed that the regression is highly significant ($P = <0·001$) and consistent for all classes. The analysis confirms that the chiasma frequencies in *A*'s and *B*'s are not entirely independent but are positively correlated. From this one must also conclude that the same factors influence the variation in chiasma frequency in both *A* and *B* chromosomes.

To summarise it is clear that while there is no evidence of competition for chiasmata between *A*'s and *B*'s, their chiasma frequencies do not vary entirely independently of one another; they are to some degree correlated, but showing a positive rather than negative interference in chiasma frequencies.

TABLE 3

The joint regression analysis of variance of B chiasma frequency on that of the A's for plants within all classes

Item	S.S.	d.f.	V.	V.R.	P.
Total regression	1·386	54	...	...	...
Joint regression	1·134	1	1·134	15·32	0·001
Heterogeneity	0·252	6	0·042	0·568	N.S.
Error	3·497	47	0·074	...	...

The influence of A's on B's. While the *B* chromosomes throughout these populations are identical the *A* chromosomes sets are not. They represent genetically heterozygous and heterogeneous combinationssuch as one expects in all outbreeding populations. It is worth while inquiring, therefore, whether the *B* chromosomes, in respect of chiasma formation, are in any way influenced by the genetic differences vested in *A* chromosomes of different individuals. In the first place the results above which show a positive correlation in the chiasma frequencies of *A*'s and *B*'s are in themselves indicative of the influence of *A* chromosomes on the chiasma frequencies of *B*'s because any

TABLE 4

The B/A ratio (in degrees) for each p.m.c. in the ten plants of the 4B class

p.m.c.	1	2	3	4	5	6	7	8	9	10
1	26·6	22·2	35·3	26·6	26·6	22·2	23·1	23·1	23·1	16·8
2	24·1	23·1	25·2	25·2	24·1	22·2	23·1	27·6	22·2	26·6
3	23·1	28·7	21·4	24·1	23·1	22·2	24·1	27·6	22·2	24·1
4	28·7	27·6	30·0	22·2	23·1	22·2	23·1	23·1	24·1	24·1
5	35·3	26·6	22·2	25·2	22·2	22·2	24·1	21·4	22·2	33·2
6	30·0	26·6	23·1	26·6	24·1	22·2	23·1	27·6	24·1	24·1
7	25·2	23·1	24·1	28·1	24·1	22·2	22·2	23·1	30·0	24·1
8	23·1	23·1	24·1	25·2	23·1	22·2	22·2	23·1	30·0	24·1
9	25·2	25·2	28·7	24·1	24·1	22·2	28·7	27·6	22·2	25·2
10	23·1	31·5	30·0	28·1	27·6	22·2	21·4	28·7	27·6	25·2
11	22·2	24·1	24·1	25·2	22·2	21·4	23·1	23·1	28·7	23·1
12	24·1	15·5	25·2	25·2	23·1	21·4	22·2	30·0	26·6	31·5
13	23·1	24·1	26·6	30·0	22·2	32·3	23·1	20·7	23·1	31·5
14	17·5	26·6	23·1	22·2	33·2	22·2	24·1	22·2	26·6	27·6
15	25·2	30·0	24·1	23·1	22·2	23·1	27·6	26·6	28·7	30·0
16	18·4	23·1	21·4	28·1	22·2	24·1	25·2	26·6	27·6	30·0
17	24·1	23·1	30·0	26·6	26·6	22·2	27·6	23·1	28·7	24·1
18	24·1	22·2	23·1	24·1	25·2	22·2	23·1	27·6	33·7	37·8
19	23·1	26·6	30·0	31·5	27·6	20·7	23·1	22·2	33·7	30·0
20	25·2	15·5	23·1	26·6	28·7	22·2	22·2	28·7	28·7	28·7
Totals	491·4	488·5	514·8	518·0	495·3	453·8	477·3	502·0	526·9	539·9

heritable variation between plants can only be attributed to genetic differences between their *A* chromosome sets. The chiasma frequency variation between plants in respect of *B*'s, albeit correlated with that of the *A*'s, must consequently be determined by differences in the *A* genotype. This conclusion is subject to one important reservation, namely, that not all the chiasma frequency variation between plants of different *A* genotype will be of a heritable nature and hence attributable to genotypic control by *A* chromosomes. At least part will be caused by environmental fluctuation. Unfortunately there is no way of distinguishing between the two causes from the present data.

Another possible way in which the *A* chromosomes might be expected to influence the *B*'s is by determining differences in the relative distributions of chiasmata as between the *A* and *B* sets in different individuals. For this purpose a comparison was made of the ratio of the chiasma frequencies in the *B* and *A* chromosomes in different individuals of a representative group, namely 4*B*. If this ratio varies between different individuals there would be grounds for attributing this variation to differences in the genotype of the *A* chromosomes. The ratios for the 20 *p.m.c.*'s for each of the 4*B* plants are given in table 4. It will be seen that the $\frac{B}{A}$ ratio varies to some degree both within and between plants and an analysis of variance shows a significant variation between plants. This is further evidence therefore that the *proportion* of chiasmata allocated to *B*'s varies in relation to the genotype of the *A*'s.

5. FERTILITY AND RECOMBINATION

Fertility. It is well established that fertility in rye decreases with increasing numbers of *B* chromosomes (Müntzing, 1943). This is true also for the present material (fig. 5). The question arises as to whether the reduced fertility is a direct consequence of the abnormal distribution of chiasmata at meiosis that was shown to depend on *B* chromosomes. Such increased variation in chiasma frequency between *p.m.c.*'s and between bivalents within *p.m.c.*'s effected by *B* chromosomes would be expected to produce an abnormally high frequency of univalents. In the first place, the increased variation in chiasma frequencies between *p.m.c.*'s will lead to an abnormally high proportion of *p.m.c.*'s with very low chiasma frequencies and hence with univalents. In the second place, the abnormal distribution of chiasmata within *p.m.c.*'s, even where the frequency is high, leaves a disproportionate number of chromosomes unpaired, *i.e.* as univalents at first metaphase (fig. 6). An increase in univalents would of course contribute to infertility. That univalents do in fact increase with increasing *B* frequency is confirmed in fig. 5. It may be concluded therefore that in part at least the reduced fertility is a direct result of the cytological disturbances earlier attributed to the *B* chromosomes. At the same time, however, it is quite clear from fig. 5 that the univalent frequency in *p.m.c.'s* is far too low to account entirely for the reduction in fertility. Unless the influence of *B*'s upon meiotic behaviour are very different on the female side it must be inferred that much of the reduced fertility results from the influence of *B*'s upon the development of the gametes, the embryo or the endosperm. There is, in fact, good evidence that *B*'s affect pollen development. They cause spindle abnormalities at the first pollen grain mitosis (Håkanson, 1957).

Recombination. In a diploid heterozygote the release of variability at meiosis depends largely upon the frequency and distribution of chiasmata and hence of crossing over and recombination. As has been shown *B* chromosomes have no influence on the mean chiasma frequencies of rye plants. They do, however, influence the distribution of chiasmata. They do so in a number of ways with, theoretically, different consequences to the release of genetic variation by recombination.

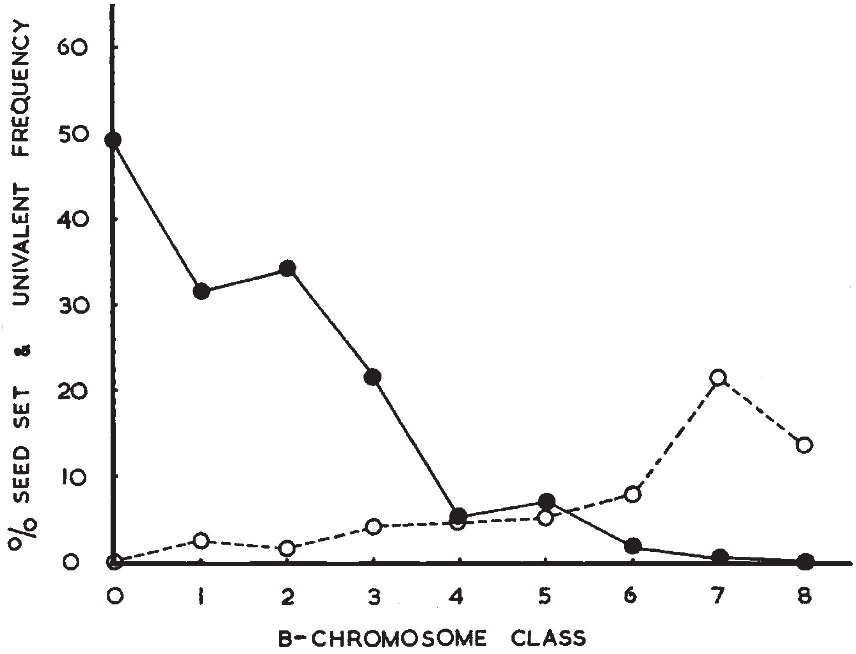

Fig. 5.—Fertility, expressed as percentage seed set (solid line), and univalent frequency, as the mean percentage *p.m.c.*'s with univalents (dotted line), plotted against the number of *B*'s per plant.

1. *Between p.m.c.*'s. The increased variation in chiasma frequencies between *p.m.c.*'s due to *B*'s should result in gametes whose genotypes derive from, on the one hand, less and on the other, more recombination than normal. One would expect, in consequence, an increased range of variability among the progeny.

2. *Within p.m.c.'s* (a) *Between chromosomes.* The effect of *B*'s in increasing the chiasma frequency variation between bivalents within *p.m.c.*'s would be to concentrate recombination in some chromosomes

and hence in certain groups of genes of the complement at the expense of others. This again one should expect to result in novel recombinant gametes and hence in a wider range of genotypes among the progenies of *B* chromosome plants.

(b) *Within chromosomes.* The highly asymmetrical distribution of chiasmata reported between different regions of the chromosomes must, as in 2(a) above, lead to a disproportionate concentration of recombination among some linkage groups and for this reason also lead us to expect a greater and novel range of recombinant gametes, and, consequently, an increased variability among the progeny of *B* chromosome plants.

FIG. 6.—First metaphase in *p.m.c.*'s without *B*'s (A), and with eight *B*'s (B). The *B* chromosomes are drawn in outline only, and figures for chiasma frequencies of the *A* chromosomes are given alongside each *p.m.c.* Note in (B) the greater range of chiasma frequency variation both between *p.m.c.*'s and between bivalents within *p.m.c.*'s.

Reference was made earlier to Darlington's concept that *B* chromosomes play an important adaptive role by promoting extra genetic variability in diploid populations, and to the experimental evidence to support this view provided by Moss (*loc. cit.*). The present work, coupled with that of John and Hewitt (*loc. cit.*), suggests that the control exercised by *B*'s upon chromosome behaviour provides the mechanisms by which the control over variability is achieved, *viz.* by changes in the frequencies and in the distributions of chiasmata at meiosis.

6. SUMMARY

An investigation of the effects of *B* chromosomes on meiosis in rye *p.m.c.*'s showed that:

1. *B* chromosomes have no significant effect on the mean chiasma frequency of the *A* chromosomes.
2. The variation in *A* chiasma frequencies *between p.m.c.*'s within plants increases with increasing numbers of *B*'s.
3. The chiasma frequency variation between *A* bivalents *within p.m.c.'s* also increases with increasing *B* frequency.
4. The distribution of chiasmata between the chromosome arms of *A* bivalents becomes increasingly asymmetrical with an increasing frequency of *B*'s.
5. There is no evidence of competition for chiasmata between *A* and *B* chromosomes. They show a positive rather than a negative interference in chiasma frequency.
6. It is probable that the behaviour of *B* chromosomes at meiosis is influenced by the *A* chromosome genotype.
7. The reduced fertility in plants with high numbers of *B* chromosomes is partly, but by no means entirely, accounted for by the occurrence of univalent *A* chromosomes resulting from abnormal chiasma distributions due to the presence of *B*'s.
8. It is argued that the control exercised by *B* chromosomes over the *distribution* of chiasmata between and within *p.m.c.*'s in rye influences the pattern of recombination and thereby effects an increase in the rate of release of variability to the offspring.

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