B-chromosome Effects at Meiosis in *Crepis capillaris*

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Introduction

In many species of flowering plants and animals certain individuals within populations may carry a variable number of additional chromosomes over and above the regular diploid or polyploid complement. Aneuploidy is not the explanation, because invariably the extra, and usually smaller chromosomes, are not homologous with any member of the basic complement. For this reason they have been classified as *B-chromosomes* (Randolph 1928), and on the grounds of homologies, are thus differentiated from the basic *A-chromosome* set. Such a simple description however belies a full appreciation of their nature—in many ways they are more fascinating than the A-chromosomes themselves. Not least among their anarchic properties is a non-mendelian system of inheritance. They may behave in an opportunist way during certain critical mitotic divisions, notably in pollen grains and megaspore cells of plants, which not only compensates for their inadequacy (loss) at meiosis, but may even over-compensate and result in their numerical accumulation within individuals and populations. Characteristically they are only present in a proportion of individuals in a population, and where they do occur numbers vary among individuals. Their frequency also varies considerably from population to population within a species, and this has led to the idea that they may be of some adaptive significance. Mitotic instability is common, leading to exclusion from particular tissues and organs. For example in *Aegilops speltoides* (Mendelson and Zohary 1972) and *Xanthisma texanum* (Berger and Witkus 1954) they are absent from the root system. The phenotypic consequences are slight when only low numbers are present, and genetically the effects are of a polygenic nature. High numbers lead to severe infertility and retardation of growth and vigour (Müntzing 1943, Bosemark 1957, Battaglia 1964). The most interesting and possibly the most significant effects have been detected at the cell and nuclear level. B-chromosome influence on A-chromosome behaviour is of particular interest. They are known to alter the frequency and distribution of chiasmata at meiosis (see discussion). This has even been interpreted as their *raison d'être* by some (Hewitt and John 1967), but not by all. Nur (1966, 1969) takes the view that they are positively harmful, in mealy bugs, and are maintained in the populations only on account of their potent accumulation mechanisms.

B-chromosomes are important because they are so widely distributed. According to the latest estimate (Jones 1975) they are known in at least 600 species of flowering plants. Altogether they are represented in 55 families and, relatively

speaking, are just as common in polyploids as they are in diploids. In certain families they are found in as many as 10 per cent of the cytologically known species. Within certain individual species the presence of B-chromosomes may constitute a more normal situation than their absence. Such is the case in certain primitive strains of Korean rye (Müntzing 1957) where plants without B-chromosomes only account for a small fraction (10 per cent) of the population. From a consideration of such cases, and bearing in mind the nature of their effects, it is axiomatic that B-chromosomes form a component of the genetic system that still leaves much to be reckoned with.

Crepis capillaris carries B-chromosomes, over the range 0–5, and quite a lot is already known about their behaviour in this species. Their distribution within the plant is complex. Röthlisberger (1970) has described the situation in some detail, and shown that a rather special mechanism of accumulation is in operation that involves a doubling up of the number of B's in cells destined for the germ line, by a directed non-disjunction of the B's at the particular mitoses co-incident with flower initiation.

The present investigation is addressed to the question of B-chromosome influence on A-chromosome recombination at meiosis. The study is cytological and involves the quantifying of chiasmata at first metaphase in pollen mother cells.

Material and methods

Seeds of *Crepis capillaris* ($2n=2x=6$), with B-chromosomes, were germinated in a seed box and then transplanted individually to five inch pots in an unheated greenhouse. After several weeks, roots emerging from the bases of the pots were screened for chromosome number at c-mitosis. Inflorescences were subsequently fixed in Carnoy's fluid, and pollen mother cells squashed out in acetocarmine for analysis of the chromosomes at first metaphase of meiosis. A sample of twenty pollen mother cells were analysed from each plant.

Results

1. *Distribution of B-chromosomes between and within plants*

The findings for the numbers of B-chromosomes in root tip cells, and corresponding numbers detected in the pollen mother cells of the anthers at meiosis are summarised in Table 1. The earlier assertion by Röthlisberger (1970), that the number of B-chromosomes entering the germ line cells undergoes a somatic doubling, is confirmed. Plants with only a single B-chromosome in root meristem cells have a majority of two in their pollen mother cells, and those with 2B's in roots have a majority of four at meiosis. Obviously, with such an effective mechanism of numerical accumulation operating in the somatic tissues, there must be a fairly drastic rate of loss of B's if the predominance of 0, 1 and 2B-chromosomes in the population is to be maintained. The causes of this loss are discussed later in the section on B-chromosome behaviour at meiosis.

2. Chiasmata in the A-chromosomes

Mean chiasma frequency

Data for the average number of chiasmata per pollen mother cell (PMC) for the A and B-chromosomes in the five different B-chromosome classes of plants are presented in Table 2 and Fig. 1. As far as the A-chromosomes are concerned it can be seen that the mean PMC chiasma frequency increases with the presence of increasing numbers of B-chromosomes. The regression analysis of variance of mean PMC chiasma frequency against B-class is significant at the five per cent level. There

Table 1. B-chromosome distribution between and within plants

B-Class	Root tip	Pollen mother cell				
		0B	1B	2B	3B	4B
0B	9	9	—	—	—	—
1B	13	—	1	11	1	—
2B	6	—	—	2	1	3

Table 2. The mean chiasma frequencies of the A and B-chromosomes in the five classes of plants

Plant	B-chromosome class and mean chiasma frequencies									
	0B		1B		2B		3B		4B	
	A	B	A	B	A	B	A	B	A	B
1	4.50	—	3.90	—	5.10	1.25	4.70	1.85	5.90	3.60
2	4.40	—	—	—	5.05	0.90	4.64	1.00	5.35	3.05
3	4.35	—	—	—	5.00	0.85	—	—	5.35	2.45
4	4.05	—	—	—	4.75	0.05	—	—	—	—
5	4.00	—	—	—	4.70	0.60	—	—	—	—
6	3.95	—	—	—	4.65	0.75	—	—	—	—
7	3.90	—	—	—	4.65	0.55	—	—	—	—
8	3.85	—	—	—	4.60	0.90	—	—	—	—
9	3.70	—	—	—	4.55	0.55	—	—	—	—
10	—	—	—	—	4.50	0.60	—	—	—	—
11	—	—	—	—	4.40	0.65	—	—	—	—
12	—	—	—	—	4.35	0.35	—	—	—	—
13	—	—	—	—	4.20	0.20	—	—	—	—
Class mean	4.08	—	3.90	—	4.65	0.63	4.68	1.43	5.53	3.03

is therefore a dosage effect of the B's and, in addition, a suggestion of some differential activity relative to odd and even numbered combinations (See discussion).

Chiasma distribution

Variation exists in the chiasma frequencies of different PMC's within individual plants due to environmental and developmental effects. This variation is non-heritable, but Rees and Thompson (1956) have shown that it can also have a genotypic component. A convenient way to measure this variation between PMC's within plants (between cells variance) is to calculate the variance of the chiasma frequencies

Fig. 1. Mean PMC chiasma frequencies of the A-chromosomes plotted against B-chromosome class.

for the twenty PMC's scored in each plant. In the circumstances of the present homogeneous outbreeding population any measurable differences between different B-chromosome classes of plants can then reasonably be accounted for through the presence of the B's themselves. Comparisons of the average variances in the five different classes are presented in Table 3. An analysis of variance confirms that the differences between classes are significant ($P < 0.05$). One possible explanation for this effect of course, is a correlation of these variances with the mean cell chiasma frequencies,

but the regression analysis is not significant, and it seems likely therefore that the differences in cell variances are independent of the chiasma frequency means. The differences must then be attributable to the presence of the B-chromosomes. Apparently the B-chromosomes of *Crepis capillaris* are instrumental in influencing A-chromosome recombination at two levels of control. There are increases in both the mean PMC chiasma frequency and in the variance of the mean PMC chiasma frequencies. In effect, this means that the increase in the numbers of chiasmata attendant upon the presence of increasing numbers of B's is further amplified in some individual pollen mother cells, albeit at the expense of others. There is yet another level of analysis of chiasma distribution that involves an as-

Table 3. Between cell variances for the five classes of plants

	B-class and cell variances				
	0B	1B	2B	3B	4B
Plants	0.789	0.411	0.726	0.642	0.726
	0.779	—	0.892	0.555	0.976
	0.976	—	0.842	—	0.450
	0.471	—	1.039	—	—
	0.421	—	0.642	—	—
	0.576	—	1.503	—	—
	0.516	—	0.660	—	—
	0.661	—	0.884	—	—
	0.432	—	1.208	—	—
	—	—	0.789	—	—
	—	—	0.674	—	—
	—	—	1.186	—	—
	—	—	0.800	—	—
Mean	0.625	0.411	0.911	0.599	0.717

assessment of the variation between individual chromosome *within* PMC's, the so-called *bivalent variance*. For certain comparable PMC chiasma frequency classes, comparisons can be made between average within cell variances, between the different B-chromosome categories of plants. The data are given in Table 4, and it can be shown by regression analysis of variance that the differences between plants with different numbers of B's are not significant. This result of course can also have a positive interpretation viz. the suggestion that changes in chiasma frequency effected by the B's co-ordinately involve all three chromosome pairs within individual cells.

As it happens, the three chromosome pairs of *Crepis capillaris* are sufficiently different on the basis of length and arm ratios for them to be individually analysed in respect of their chiasma frequencies. Table 5 gives the mean chiasma frequency per chromosome pair, for each of the three pairs, in each of the five classes of plants.

Table 4. Bivalent variances for the five classes of plants, for PMC's with 3, 4, 5 and 6 chiasmata

PMC chiasma fre- quency class	B-class and bivalent variances				
	0B	1B	2B	3B	4B
3	0.0953	0.2000	0.0181	0.0000	0.0000
4	0.3333	0.4166	0.3135	0.3333	0.3333
5	0.3333	0.3333	0.3695	0.3717	0.4166
6	0.5000	0.0000	0.2802	0.1665	0.1992
Mean	0.3154	0.2374	0.2528	0.2178	0.2372

Table 5. Mean chiasma frequency per chromosome pair in the five B-classes

Chromosome	B-class and mean chiasma frequency				
	0B	1B	2B	3B	4B
A	1.51	1.20	1.52	1.62	1.90
D	1.13	1.25	1.51	1.40	1.85
C	1.44	1.45	1.64	1.65	1.78

A joint regression analysis of variance using the data from all three pairs is significant ($P < 0.001$) confirming the positive correlation of mean chiasma frequency and B-chromosome number. Moreover there is no significant heterogeneity of the individual regression lines. Each chromosome pair can be represented by the same regression slope, and in addition, the means of the three regression lines do not differ significantly either. Notwithstanding the difference in size between the chromosomes, each pair has the same mean chiasma frequency and the same increase in that mean with each additional dosage of B-chromosomes. The relationship is somewhat surprising in view of the disparity in chromosome lengths. Chromosome C is the shortest one, 2.60μ (in root tip c-mitosis). Chromosomes A and D are 4.84μ and 4.04μ respectively (see Fig. 2.). The question which now arises of course is to what extent this pattern of chiasma distribution in the A-chromosomes is a peculiarity of the B-chromosome effects, and to what extent it represents the normal means by

which changes in chiasma frequency are accommodated? Information on this point can be gained by the same method of analysis, but in this case by making comparisons between cells of differing chiasma frequency class *within* rather than between the different B-chromosome classes. The analysis is summarised in Fig. 3.

Fig. 2. The chromosomes of *Crepis capillaris*. 1, root tip c-mitosis showing 1B. 2, metaphase I in 0B individual. 3, metaphase I in 2B individual. 4, metaphase I in 3B individual.

For each of the four B-chromosome classes (1B is omitted because the data are insufficient) the mean number of chiasmata per chromosome pair, for each of the three pairs, is plotted against a range of cell chiasma frequency classes. In all four classes the joint regressions are significant ($P < 0.01$, 0B; $P < 0.001$ 2B; $P < 0.001$.

3B; $P=0.001$, 4B) and positive. There are no significant heterogeneities of regressions and no significant differences in means either. Evidently the changes in mean chiasma frequencies for the three chromosome pairs brought about by the presence of B-chromosomes has the same operational basis as that which is normally used to effect chiasma frequency changes. The distribution of chiasmata between the three chromosome pairs at different levels of frequency, follows precisely the same pattern in those plants without any B's as it does in those with two, three and four.

Fig. 3. Chiasmata per bivalent (see Fig. 2 for classification) plotted against PMC chiasma frequency class for 0, 2, 3 and 4B classes of plants.

These data for chiasma distribution differ from an earlier description of the situation (Richardson 1935). Richardson made a detailed study of chiasma behaviour in the three bivalents of *C. capillaris* and found that the chiasma frequency was almost directly proportional to chromosome length. Almost invariably Richardson has described the small bivalent as having a single chiasma in its long arm, whereas in our scoring we commonly find the small bivalent with two chiasmata, the same as the longer ones often have (see Fig. 2). Apparently the frequency of chiasmata per unit length of chromosome is much greater in the small bivalent than it is in the other two.

3. *B*-chromosome behaviour

Chiasma frequencies

B-chromosome chiasma frequencies are given in Table 2 and Fig. 4. The PMC chiasma frequency for the B's increases with increasing B-chromosome number, as too does the number of chiasmata per B-chromosome. In plants with 2B's per cell there is an average of 0.3 chiasmata per B-chromosome, and this is raised to an average of 0.7 in plants with 4 B's per cell. The A and B-chromosome chiasma frequencies are, it seems, positively correlated. In the 2 B class for example the regression of the mean B-chromosome chiasma frequency on that of the A's is significant at the five per cent level. The possibility exists therefore of some mutual influence, such that not only do the B's alter the A-chromosome chiasma frequency

Fig. 4. Mean PMC chiasma frequencies of the B-chromosomes ●—● and chiasmata per B-chromosome ○—○ plotted against B-chromosome class.

and distribution, but that the A-chromosome genotype itself (the species is outbreeding) also regulates chiasma formation in the B's. A more detailed analysis has therefore been made in the 2B-chromosome category of plants, of the relation between the A and B-chromosome chiasma frequencies. In Table 6 are given the B/A chiasma frequency ratios for each PMC for each of the thirteen plants scored. The data, transformed to angles for the purposes of analysis of variance, show that there are large and significant differences in the ratio between different 2B plants ($P < 0.001$, LSD at the five per cent level = 157.54). The proportion of chiasmata allocated to the B-chromosome varies in relation to the A-chromosome genotype.

B-chromosome segregation

B-chromosomes generally pair much less effectively than do A-chromosomes in most of the species which have been analysed at meiosis (see Jones 1975). One of the consequences of this irregular meiotic behaviour is that univalent B's get excluded from nuclei and are lost from the reproductive cells. This loss is undoubtedly an important factor, not only in so far as it counteracts the tendency of the B's to accumulate, but also because it constitutes one of the ways by which the frequency of B-chromosomes in natural populations can be adjusted. There is indeed evidence that the rate of loss by meiotic elimination is dependent to some extent on the genotype. In rye, for example, Müntzing (1945) has shown that the elimination of

B's in this very way occurs much more readily in certain strains (Östgöta Gråråg) than in others (Vasa II). Kishikawa (1970) has also demonstrated that varying environmental circumstances can also influence the rate of loss of B's at meiosis in rye. In view of the very effective accumulation mechanism operating in *Crepis capillaris* (see earlier) and the distinctive absence of consequent high numbers in the population plants, it was anticipated that a high level of B-chromosome elimination should be found. For this reason some assessment of the pattern of B-chromosome

Table 6. B/A ratio (degrees) for each PMC in 13 plants of 2B class

PMC	Plant												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	26.6	0	26.6	0	26.6	39.2	0	30.0	30.0	24.1	0	0
2	24.1	0	0	0	30.0	0	45.0	0	0	24.1	30.0	0	35.3
3	26.6	26.6	0	26.6	24.1	0	24.1	0	45.0	24.1	30.0	24.1	0
4	35.3	0	0	24.1	0	30.0	24.1	30.0	30.0	26.6	0	30.0	35.3
5	26.6	30.0	0	26.6	0	0	26.6	0	26.6	0	0	30.0	30.0
6	30.0	0	0	30.0	30.0	24.1	30.0	0	0	24.1	30.0	24.1	0
7	24.1	30.0	0	26.6	26.6	0	35.3	0	0	30.0	0	30.0	26.6
8	0	30.0	0	24.1	26.6	0	24.1	0	0	26.6	26.6	30.0	30.0
9	0	30.0	0	0	35.3	35.3	30.0	0	0	24.1	30.0	30.0	0
10	0	30.0	0	24.1	26.6	24.1	26.6	35.3	0	26.6	30.0	26.6	0
11	0	35.3	0	26.6	24.1	26.6	26.6	0	26.6	24.1	32.3	30.0	0
12	30.0	24.1	0	0	30.0	26.6	30.0	0	26.6	30.0	24.1	22.2	0
13	0	0	0	0	0	24.1	39.2	0	30.0	26.6	30.0	24.1	0
14	0	30.0	0	0	0	26.6	30.0	0	35.3	26.6	26.6	30.0	0
15	0	0	30.0	26.6	30.0	30.0	35.3	26.6	30.0	0	0	26.6	39.2
16	0	0	0	0	30.0	0	26.6	30.0	30.0	35.3	26.6	26.6	0
17	0	0	0	26.6	0	26.6	24.1	0	26.6	26.6	30.0	24.1	0
18	30.0	30.0	0	0	30.0	45.0	24.1	0	0	24.1	26.6	26.6	0
19	26.6	0	0	26.6	26.6	30.0	24.1	0	0	0	35.3	24.1	0
20	26.6	0	0	0	30.0	26.6	30.0	0	0	30.0	45.0	26.6	0
Total	279.9	322.6	30.0	315.1	399.9	402.2	595.0	121.9	336.7	459.5	477.2	485.7	196.4

Table 7. B-chromosome pairing configurations at MI

	II	I+I	III	II+I	I+I+I	IV	III+I	II+I+I	II+II	Total
2B	155	105	—	—	—	—	—	—	—	260
3B	—	—	29	9	2	—	—	—	—	40
4B	—	—	—	—	—	41	9	1	9	60

segregation at meiosis was made. Data for the pairing configurations at first metaphase appear in Table 7. There is no pairing at all between the B and A-chromosomes. As the B's are all structurally homologous with one another they are able to form multivalents with a maximum valency equal to the highest number of B's present. According to Table 7 it appears that in fact the B's have a preference for multivalent associations, and this may account for the increase in mean chiasmata per B with the increasing numbers. None the less univalents are very common, and these it must be presumed, lead to a substantial rate of loss at meiosis. In the 2 B

class, for example, 40 per cent of the PMC's showed the B's unpaired. In the 4 B class there were fewer PMC's, 16.7 per cent, containing univalents. In some of these PMC's the univalents can segregate successfully at AI, even though they are unpaired, and become included in the telophase nuclei. B-chromosomes which fail to be included in telophase nuclei at either the first or second division can be witnessed as micronuclei in the terads. In the 2 B class 27.6 per cent of the tetrads showed micronuclei in the cytoplasm. There were 49.5 and 23.5 per cent in the 3 B and 4 B plants respectively. Clearly the B-chromosomes in this species do suffer a high rate of meiotic elimination.

Table 8. Summary of B-chromosome effects on A-chromosome recombination
(+ increase, — decrease, 0 no change)

Species	Chiasma frequency	Cell variance	Bivalent variance	Reference
<i>Aegilops speltoides</i>	—			Zarchi, Simchen, Hillel and Schapp 1972
<i>Brachycome lineariloba</i>	0	0		Carter and Smith-White 1972
<i>Crepis capillaris</i>	+	+	0	This paper
<i>Festuca mairei</i>	+			Malik and Tripathi 1970
<i>Listera ovata</i>	+			Vosa and Barlow 1972
<i>Lolium perenne</i>	—		+	Cameron and Rees 1967
<i>Najas marina</i>	—			Viinikka 1973
<i>Parthenium argentatum</i>	0			Catchside 1950
<i>Pennisetum typhoides</i>	+			Pantula and Manga 1972
<i>Puschkinia libanotica</i>	+	change in chiasma distribution		Barlow and Vosa 1970
<i>Secale cereale</i>	+*, 0	+	+	*Zecevic and Paunovic 1969 Jones and Rees 1967
<i>Zea mays</i>	+	+		Ayonoadu and Rees 1968
<i>Melanoplus differentialis differentialis</i>	+			Abdel-Hameed, Rootham and Flinn 1970
<i>Melanoplus femur-rubrum</i>	0	+		Stephens and Bregman 1972
<i>Myrmeleotettix maculatus</i>	+	+		Barker 1960, John and Hewitt 1965 (ab), Hewitt and John 1967, Hewitt and Brown 1970
<i>Tettigidea lateralis</i>		change in chiasma distribution		Fontana and Vickery 1973

Discussion

B-chromosome effects on A-chromosome recombination were first described by Barker (1960), who reported increases in the mean cell chiasma frequencies in B-chromosome carrying male grasshoppers of the species *Myrmeleotettix maculatus*. John and Hewitt (1965 a b) subsequently carried out a more detailed analysis in grasshoppers from several populations and established effects on the 'between cells variance', as well as on the mean chiasma frequency. In plants, Jones and Rees (1967) found that in an experimental B-chromosome rye population, the B's had no effect on mean PMC chiasma frequencies, but there were increases in both the 'between' and the 'within' cell variances. Similar cytological analyses have now been

completed in several species of both plants and animals. The results of these analyses are summarised in Table 8. Only rarely are the B-chromosomes without some measurable effect on chiasma frequency or distribution. Genetical analysis using marker genes, have confirmed the cytological findings in *Zea mays* (Hanson 1969). Mean chiasma frequencies seem to respond to the presence of B-chromosomes by showing an increase, a decrease, or no change at all. Variances likewise are either increased, or, as in the case of *Puschkinia* (cell variance), reduced. In three species to date, including the present one, account has been taken of the response of individual A-chromosomes to the presence of B's. *Myrmeleotettix maculatus* has long (L), medium (M) and short (S) bivalents in its A-chromosome complement, and it is the L and M bivalents which accommodate the extra chiasmata in those cells which show an increase in their frequency. In *Puschkinia libanotica* the degree to which the frequency of chiasmata is raised in each bivalent, is related to the length of the bivalent. Shorter bivalents show a smaller increase than longer ones. In *Crepis capillaris* additional chiasmata are distributed to all three bivalents, even though one of them is much the shorter. As already mentioned, this situation is at variance with an earlier investigation (not involving B-chromosomes), in which the numbers of chiasmata found in each bivalent were proportional to bivalent length. In the present material the short subterminal chromosome appears to form more chiasmata, two is quite common, than one might have expected. This particular relationship between chiasma frequency and chromosome length is also quite independent of the existence of the B-chromosomes.

It is generally conceded that the mechanism of these B-chromosome effects remains an enigma, while opinions differ as to their significance. A much favoured view is that the B-chromosomes have an adaptive role to play in regulating the release of variability by adjusting the frequency and distribution of chiasmata at meiosis (John and Hewitt 1965 a b, Jones and Rees 1967). One of the objections to this view, however, is that the system is too burdensome to the species, especially in plants, where the associated effects on vigour and fertility can be severely depressive. On the other hand, as Hewitt and John (1967) have pointed out, the alternative method, of selection for genes or gene combinations producing the same effects would require many generations before the system could become operative, and many more again to render it inoperative should circumstances so demand. B-chromosome effects, which can incidentally, also be achieved by other forms of 'supernumerary' chromosome material (John 1973), are effective immediately in the individuals to which they are transmitted. In some plant species, e. g. rye (Moss 1966), there is good evidence to show that B-chromosome containing individuals, and the progenies of B-chromosome containing individuals, are indeed more variable than those lacking in B-chromosomes. Rhoades and Dempsey (1972) have recently advanced an alternative suggestion that the consequences of B-chromosomes to recombination are nothing more than manifestations of a basic change in cell function. Certainly B's do have very fundamental effects, such as a lengthening of the mitotic cycle time (Ayonoadu and Rees 1968). This, Rhoades has argued, would significantly alter cell conditions, including those pertaining at the time when the critical molecular events associated with recombination are taking place. The B-chromosomes are to

be looked upon as 'accidents' of evolution, perpetuated by advantageous mechanisms of heredity which foster their own multiplication and survival. This view commands respect, but finds conflict with experimental evidence of a different kind produced by Rees and Hutchinson (1973), which shows quite clearly that selection procedures can be applied to B-chromosome populations of *Lolium perenne* that can change the population B-frequency even within the span of one generation. Differential mortality of 0B and plus B individuals under conditions of severe environmental stress can result in an increase in the proportion of individuals with B-chromosomes. Kishikawa (1970) has also demonstrated mechanisms of selection in rye, such that B-frequencies are altered in the progenies of plants grown in different environments, by variations in the transmission rates of the B's.

There are other effects of B-chromosomes at meiosis, which are of a much more dramatic nature, and which result from experimental hybridisations between different species. In the crosses *Triticum aestivum* $\times$ *Aegilops mutica* (Mochizuki 1964, Dover and Riley 1972), *Lolium temulentum* $\times$ *Lolium perenne* (Evans and Macefield 1972, 1973) and *Lolium perenne* $\times$ *Festuca arundinacea* (Bowman and Thomas 1973), B-chromosomes introduced from one of the parental species can cause a suppression of homoeologous pairing between the chromosome from the different parental genomes. These effects are pertinent to the present discussion in so far as they may ultimately be of use as an experimental system for determining the mode of action of B's on chromosome pairing and chiasma formation at meiosis.

Finally, there is yet another intriguing B-chromosome effect on the behaviour of the A-chromosomes at meiosis, which could also have some potential as an experimental device, and this concerns the differential activities of odd and even numbered combinations of B's. In *Crepis capillaris* the chiasma frequency means of the A-chromosomes were disproportionately increased by the even numbered B-combinations. Although these particular differences in *Crepis* were not amenable to a statistical analysis, there is every reason to believe that they are genuine, because there is now a catalogue of such "odds and evens" effects relating to several character differences in several different species. In rye (Jones and Rees 1967), the cell variances showed the same 'zig-zag' relationship, so that there was a disproportionate increase in the variances of the odd numbered classes. In *Listera ovata*, where both male and female meioses have been examined, it is the odd numbered B-combinations which show the highest increases in mean chiasmata—the opposite to the situation in *Crepis*. The operational basis of these differences in odd and even numbered B-chromosome combinations is not really understood at all. Speculations have been made (Jones and Rees 1969) that since B's are often inherited in such a manner that even numbered classes predominate in the population, there may be some functional advantage in having them present in pairs, as opposed to odd numbers. Somatic chromosomes are known to form associations at interphase (Feldman, Mella-Sampayo and Avivi 1972) and it may be that B-chromosomes do so as well.

Abstract

Analysis of chromosome behaviour at meiosis in *Crepis capillaris*, $2n=2x=6+$

B-chromosomes, shows that the B-chromosomes influence the frequency and distribution of chiasmata in the A-chromosomes. The mean chiasma frequency of the A's is increased by the presence of one to four B's, so too is the variance of the chiasma frequency mean between the pollen mother cells within plants. The A-chromosome bivalents differ in length, but all have similar mean chiasma frequencies, and they are all influenced to the same extent. Some data are also presented on the meiotic behaviour of the B-chromosomes themselves. Many of them get eliminated as micronuclei.

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