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Suppression of Multivalent Formation by B Chromosomes in Natural and Artificial Autopolyploids of Scurvy-Grass (*Cochlearia* L.)

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Summary. In diploid *Cochlearia pyrenaica*, its established natural autotetraploid *C. officinalis*, and their newly induced autotetraploid and auto-octoploid derivatives, B chromosomes change the normal pattern of chromosome association by suppressing homologous pairing. Frequency of bivalents increases at the expense of multivalents from lower to higher numbers of B chromosomes. The reduction of multivalents due to the direct influence of the B chromosomes, independent of pollen mother cell chiasma frequency, is suggested as being related to the mechanism that prevents A/B chromosome pairing.

Key words: *Chochlearia pyrenaica* – Newly induced autopolyploids – Established natural autopolyploids – B chromosomes – Multivalent suppression

Introduction

The restriction of meiotic pairing in homeologous chromosomes has been shown to be under the control of B chromosomes in diploid and tetraploid interspecific hybrids of *Lolium*, *Festuca* and *Briza* (Evans and Macefield 1972, 1974; Bowman and Thomas 1973; Murray 1978). The influence of B chromosomes on homologous chromosome pairing in autotetraploids is also known in *Lolium perenne* (Macefield and Evans 1976). However, such findings on the restriction of homeologous and homologous chromosome pairing have been hitherto confined within a family Gramineae. The effects of B chromosomes in these plants are also far from uniform: some involve drastic reduction in chromosome pairing, whereas others are relatively mild.

In the present investigations, the effects of B chromosomes on the pairing of homologous chromosomes at meiosis in three different ploidy levels of *Cochlearia*, family Cruciferae, were studied. The diploid *C. pyrenaica* and its established natural autotetraploid derivative *C. officinalis* were chosen. In addition, their synthetic autotetraploids and auto-octoploids were produced for a comparative study of the influence of B chromosomes.

Materials and Methods

The plants of diploid *C. pyrenaica* and its established natural autotetraploid derivative *C. officinalis* were collected from naturally growing populations in Durham (England) and Caernarvon (Wales). These species were also obtained as seed from the University Botanic Gardens of Murmansk (U.S.S.R.), Oslo (Norway) and Munich (Germany). Autotetraploids and auto-octoploids were produced by the application of aqueous colchicine on both the germinating seed and seedling stages of these species, as described earlier (Gupta 1980). All these plants of diploid, newly induced autotetraploid, established natural autotetraploid and newly induced auto-octoploid origins were grown to maturity under glasshouse conditions (15 ± 2°C, 14 h photoperiod and 10 ± 2°C, 10 h dark). Cytological preparations were made from pollen mother cell (PMC) squashes by the usual iron-acetocarmine technique. Frequencies of chiasmata and various chromosome configurations were scored at first metaphase of meiosis in 20 PMCs of each plant, and in a total 6-10 plants for each class of B chromosomes.

Results

The present studies reveal 2-4 B chromosomes in diploid plants, 4-8 B chromosomes in newly induced autotetraploids, 0-1 B chromosome in established natural autotetraploids and 0-2 B chromosomes in newly induced auto-octoploids. The B chromosomes are euchromatic and show no evidence of pairing with the A chromosomes in any of these cochlearias.

The frequencies of chiasmata and various chromosome configurations were examined in both the diploids and in the various autopolyploids. The data are presented in Table 1. It is clear from this Table that the pattern of chromosome association is markedly affected, a result of the B chromosomes, at the 4x and 8x levels. In the presence of the B

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Table 1. Mean chromosome configurations and chiasma frequency at different numbers of B chromosomes in diploid *C. pyrenaica*, its established natural autotetraploid *C. officinalis*, and their newly induced autotetraploid and auto-octoploid derivatives

B chromosome class	Chromosome configurations						Total chromosomes in multivalents	Chiasma frequency per	
	I	II	III	IV	VI	VIII		cell	chromosome
Diploid (2n=12)									
2B	–	6.00 ± 0.00	–	–	–	–	–	9.10 ± 0.03	0.758
4B	–	6.00 ± 0.00	–	–	–	–	–	8.95 ± 0.05	0.746
Induced autotetraploid (2n=24)									
4B	0.54 ± 0.07	8.64 ± 0.32	0.36 ± 0.08	1.27 ± 0.12	–	–	6.16	15.09 ± 0.22	0.629
6B	0.78 ± 0.05	9.39 ± 0.27	0.15 ± 0.05	1.00 ± 0.09	–	–	4.45	15.24 ± 0.17	0.635
8B	2.53 ± 0.14	8.73 ± 0.49	0.27 ± 0.06	0.80 ± 0.07	–	–	4.01	13.63 ± 0.36	0.568
Established natural autotetraploid (2n=24)									
0B	0.07 ± 0.001	10.18 ± 0.05	–	0.89 ± 0.03	–	–	3.56	15.70 ± 0.07	0.654
1B	0.31 ± 0.002	10.31 ± 0.02	–	0.77 ± 0.01	–	–	3.08	15.38 ± 0.04	0.641
Induced auto-octoploid (2n=48)									
0B	0.75 ± 0.06	13.37 ± 0.42	0.50 ± 0.09	2.00 ± 0.19	0.52 ± 0.05	1.00 ± 0.08	20.62	29.04 ± 0.41	0.605
1B	0.88 ± 0.11	17.10 ± 0.39	0.42 ± 0.10	1.67 ± 0.13	0.50 ± 0.02	0.25 ± 0.03	12.94	28.27 ± 0.52	0.589
2B	1.26 ± 0.09	19.12 ± 0.35	0.40 ± 0.05	1.25 ± 0.08	0.10 ± 0.005	0.20 ± 0.01	8.40	28.85 ± 0.37	0.601

chromosomes the frequency of trivalents, quadrivalents, hexavalents and octovalents decrease significantly. Differences are also greater ($P < 0.01$; d-test) when the number of Bs increase. The frequency of bivalents increases coincidentally with certain univalents at the expense of these multivalents in both autotetraploids and auto-octoploids. Furthermore, the suppression of multivalents caused by B chromosomes is found to be higher in the auto-octoploids as compared to the autotetraploids (Table 1).

When the established natural and newly induced autotetraploids are compared, the former shows a high frequency of bivalents and very low frequencies of quadrivalents and univalents whereas in the latter, multivalents (quadrivalents and trivalents) are present in a high number. In both kinds of autotetraploids, the frequencies of bivalents increase at the expense of multivalents from lower to higher numbers of B chromosomes. Thus, an overall pattern appears in the induced autotetraploids, natural autotetraploids and induced auto-octoploids: plants without or with low number of B chromosomes have more multivalents and fewer bivalents than those containing high number of B chromosomes.

In general, there is only a slight decrease in chiasma frequency with increasing numbers of B chromosomes (Table 1), but the difference is significant ($d = 2.047$; $P < 0.05$) only in the 8B class where the univalent frequency is relatively very high. The relationship between various chromosome configurations amongst the six sets of four and eight homologous and distribution of chiasmata are not clearly visible as the individual sets are indistinguishable at meiosis. In order to estimate the independence of the variation in multivalent frequency from chiasma frequency, the average frequency of chromosomes in multivalents against specific cell chiasma frequency was plotted with no B chromosomes (in induced autotetraploids, lowest number of Bs) and with different numbers of Bs (Fig. 1). Multivalent frequency remains almost the same with increasing chiasma frequency in every class of B chromosomes and the regressions are non-significant.

Discussion

From the above findings it is clear that B chromosomes are responsible for altering the pairing pattern of A chromosomes in the different kinds of auto-polyploids of *Cochlearia*. The effect of B chromosomes in these autopolyploids is such that there is a significant increase in the frequency of bivalents at the expense of multivalents. Univalents also increase with increasing frequency of B chromosomes, but because they appear in very low frequencies (0.29-10.5%) chromosome segregation is normally unaffected.

The autopolyploids of both artificial and natural origins

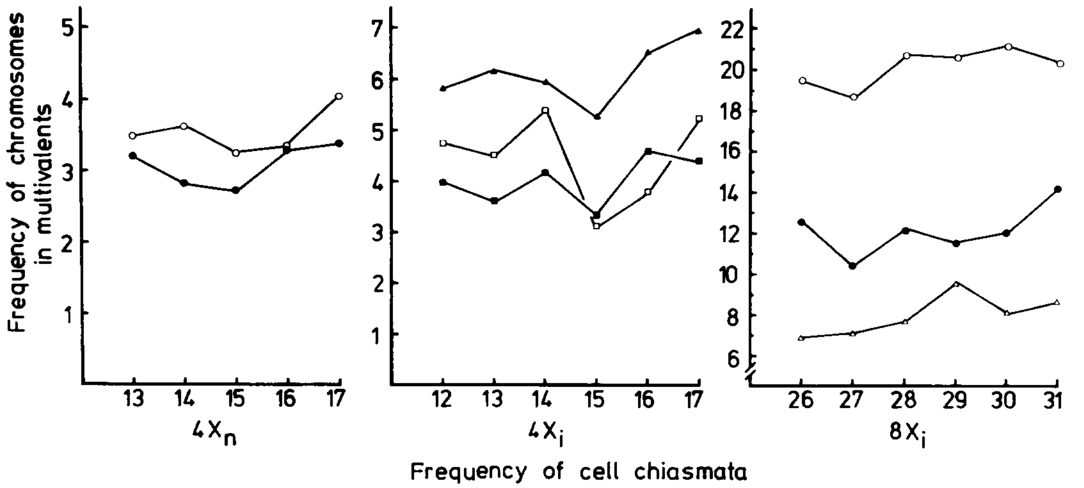

Fig. 1. Independence of the variation in multivalent frequency with cell chiasma frequency in established natural autotetraploid ($4x_n$), induced autotetraploid ($4x_i$) and induced auto-octoploid ($8x_i$) cochlearias. Mean frequency of chromosomes in multivalent configurations in PMCs of specific chiasma frequency at different classes of B chromosomes. ○–○, 0B; ●–●, 1B; △–△, 2Bs; ▲–▲, 4Bs; □–□, 6Bs; ■–■, 8Bs

show slight and normally nonsignificant reduction in chiasma frequency, both per chromosome as well as per cell, from lower to higher numbers of B chromosomes, whilst at the same time multivalents reduce significantly. It is obvious from Figure 1 that multivalent frequency does not change with increasing chiasma frequency at any class of B chromosomes. Therefore, it can be suggested that in *Cochlearia* the B chromosomes alter both the level of chromosome association and the level of chiasma formation, but independently of each other. These findings are in agreement with the results of Macefield and Evans (1976) in *Lolium perenne*, where frequency of chiasmata and multivalent formation were usually in reverse order.

The mechanism for the reduction of multivalents due to direct influence of the B chromosomes, independent of PMC chiasma frequency, in the different kinds of autopolyploids is worth speculating on. It is unanimously accepted that B chromosomes evolve from A chromosomes, but they never pair with them. For preventing this A/B chromosome pairing, a locus or loci might be responsible that is controlled from the B chromosomes. This locus or loci of the B chromosomes, if it prevents homologous pairing between A and B chromosomes, might also act to suppress the pairing of homologous chromosomes to some extent. In the cochlearias, it seems that a dosage effect of pairing control loci of B chromosomes increases the suppression of homologous pairing of A chromosomes. Therefore, the situation is such that the frequency of bivalents increases along with some univalents at the expense of multivalents from lower to higher numbers of B chromosomes.

The suppression of multivalent formation in autopolyploids is clearly of significance in plant breeding. It may well be possible to use B chromosomes to restore fertility by achieving regularity and stability in the meiotic system of freshly induced autopolyploids, at least in those plants where *Cochlearia*-like B chromosomes are present.

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