Theor Appl Genet (1988) 76:118–124

Chromosome elimination and chromosome pairing in tetraploid hybrids of *Hordeum vulgare* × *H. bulbosum*

H. M. Thomas
Welsh Plant Breeding Station, Plas Gogerddan, Aberystwyth SY23 3EB, UK

Received December 7, 1987; Accepted February 6, 1988
Communicated by G. Wenzel

Summary. The C_0 tetraploid counterparts of diploid hybrids of *Hordeum vulgare* × *H. bulbosum* were meiotically analysed, and were found to be chromosomally less stable than the same genotypes had been as diploids. The 14 *bulbosum* chromosomes present in the tetraploid cytotypes were probably eliminated as pairs rather than randomly or one genome at the time. Development of the *vulgare* and *bulbosum* genomes was asynchronous in some hybrids, the *bulbosum* chromosomes appearing less advanced than the *vulgare* chromosomes in the same cell. This appeared to reduce pairing between *bulbosum* homologues and also suppressed homoeologous pairing.

Key words: *Hordeum*, chromosome elimination, chromosome pairing, genome asynchrony

Introduction

In an earlier paper, Thomas and Pickering (1985) demonstrated that chromosome elimination and chromosome pairing in diploid *Hordeum vulgare* × *H. bulbosum* hybrids are genotypically controlled. The chromosome number of a selection of these hybrids was doubled in order to examine the cytology of the same genotypes as tetraploids and make direct comparisons of chromosome elimination and pairing in 2x and 4x cells within a given genotype.

Generally, diploid plants are far more sensitive to aneuploidy than are polyploids, and chromosome loss is usally lethal in diploids. In polyploids, the duplication of genes provides a buffer against the deleterious effects of aneuploidy and they are able to withstand both chromosome gain and loss; polyploidy may also increase the ability of individual cells to withstand chromosome loss. Although Lange (1971) found no obvious differences in chromosome stability between diploid and tetraploid hybrids of *H. vulgare* × *H. bulbosum*, he was not comparing the same genotypes at the different ploidy levels.

The potential amount of pairing in PMCs with reduced numbers of chromosomes obviously depends on the number of chromosomes remaining and more particularly on the number of pairs remaining. Therefore, the study of patterns of chromosome pairing in PMCs with different chromosome numbers should cast light on the order, if any, in which chromosomes are eliminated.

In the amphidiploids under investigation there are two pairs of identical genomes. Each chromosome, therefore, has the opportunity of pairing with its identical homologous partner or with its homoeologous partners. By analysing the chromosome pairing in the tetraploid forms of high and low pairing diploid hybrids, it should be possible to determine if the pairing control described by Thomas and Pickering (1985) simply depresses chiasma frequency or whether it specifically reduces homoeologous pairing. This paper describes such an analysis.

Materials and methods

Tetraploid hybrids were produced by colchicine treatment of the vegetative tillers of diploid hybrids of *H. vulgare* × *H. bulbosum* as described by Thomas and Pickering (1985) following the method of Morgan (1976).

Mitotic chromosome counts were made on metaphases of dividing cells in root-tips from vegetative tillers grown on a culture tank (Morgan 1976). Root-tips were pre-treated in distilled water at 1 °C for 24h, fixed in ethanol-acetic acid (3 : 1) and stained by the Feulgen method. Squash preparations were made in 1% aceto-carmine. For meiotic analyses inflorescences were taken before emergence, fixed in Carnoy's solution (6 : 3 : 1) and anthers squashed in 1% aceto-carmine.

The expected frequencies of 'pairs' of *bulbosum* chromosomes in cells if elimination was random, were determined by a FORTRAN program using a Monte-Carlo method. For instance in a 22 chromosome cell a selection of eight was randomly made from seven pairs (14 chromosomes), and the selection tested for the number of pairs present. The program repeated this 100,000 times, accumulating results and finally converting to percentages (Potter, personal communication). The same was done for other even numbered cells.

Results

Chromosome elimination

Tetraploid PMCs were found in the inflorescences of six hybrids and these are presented in Table 1; cell to cell variation in chromosome number was found in all plants, except that in one anther (anther B) of Domen × Cb 2920/4 (9) all cells had 27 chromosomes. As Table 1 shows, Emir × S1 (3) and Domen × Cb 2920/4 (9) (anther A), the lowest and highest means respectively both differed significantly from the other four hybrids. These four hybrids did not, however, differ significantly from each other. The five Emir hybrids involved three different *bulbosum* lines; when these were grouped by *bulbosum* parent for analysis, no differences were found between *H. bulbosum* parents.

Although Domen × Cb 2920/4 (9) proved to be the most stable of the hybrids at both ploidy levels this relationship did not hold for the other hybrids (Table 1), and there was no significant correlation between mean chromosome numbers of the diploid and tetraploid cytotypes ($r = 0.251$; $df = 4$). All hybrids were, however, less stable as tetraploids than as diploids; on average only 0.4 chromosomes per cell had been eliminated in the diploids whereas in the tetraploids 3.84 chromosomes per cell had been eliminated (Table 1).

It is generally believed that in *H. vulgare* × *H. bulbosum* hybrids, only the *H. bulbosum* chromosomes are lost and Subramanyam and Kasha (1973) offered evidence of this. In the tetraploid hybrid there is the full diploid complement of *H. bulbosum* chromosomes that may be eliminated.

The order, if any, in which individual *bulbosum* chromosomes were eliminated is considered. They were that (a) the chromosomes are eliminated in pairs, or (b) one of the two genomes of *H. bulbosum* is eliminated and then the other, or (c) the elimination of all 14 *bulbosum* chromosomes is completely at random.

As chromosomes are eliminated, potential pairing sites are reduced in number. If the *bulbosum* chromosomes are eliminated as pairs the maximum possible number of bivalents is reduced by one for every two chromosomes eliminated. If the *bulbosum* chromosomes are eliminated one genome at the time, then for the first seven chromosomes eliminated, the maximum possible number of bivalents is reduced by one for each chromosome lost, so that in a 21 chromosome cell, no more than seven bivalents is possible, and there will be at least seven univalents. For the purposes of this exercise, quadrivalents are taken to be equivalent to two bivalents, and trivalents to be the equivalent of one bivalent and one univalent.

The number of bivalents scored in each PMC was compared with the theoretical maximum number of bivalents possible for that cell, depending on the chromosome number and whether the chromosomes were eliminated as pairs or one genome at the time. The number of univalents was compared to the theoretical minimum possible univalents for that cell if chromosomes were eliminated

Table 1. Chromosome numbers of the PMCs of six *H. vulgare* × *H. bulbosum* tetraploid hybrids

Plant	Chromosome no./cell		Number of cells	Chromosome no. in 2x [+]	
	Mean	Range		Mean	Range
Emir × S1 (3)	22.16[a*]	30–13	69	13.45	14–10
Emir × S1 (1)	23.94[b]	27–17	32	13.95	14–13
Emir × Cb 2929/1 (1)	23.95[b]	30–14	150	11.48	14– 7
Emir × Cb 2929/1 (6)	24.15[b]	30–14	82	13.90	14–12
Emir × Cb 2920/4 (11)	24.61[b]	30–19	76	13.25	15–11
Domen × Cb 2920/4 (9) A	27.08[c]	30–23	25	14	–
Domen × Cb 2920/4 (9) B	27	–	25	–	–
Overall	24.16	30–13	459 (total)	13.60	15– 7

[+] Data from Thomas and Pickering (1985)

* Means with a common letter do not differ significantly at the 5% level by t-tests; Domen × Cb 2920/4 (9) 'A' and 'B' are two anthers from the same inflorescence – all PMCs in B contained 27 chromosomes

one genome at the time. All hybrids had some PMCs with more bivalents than the maximum possible if elimination was by genomes; this ranged from 8.33% of PMCs in Domen × Cb 2920/4 (9) to 43.75% of PMCs in Emir × S1 (3). Also, all hybrids had PMCs with fewer univalents than the minimum possible if elimination was by genomes; 25% of PMCs in Domen × Cb 2920/4 (9) to 62.50% of PMCs in Emir × S1 (3) had fewer univalents than possible for this model. Therefore, one genome of *bulbosum* is not eliminated before the other.

To see if the *bulbosum* chromosomes were eliminated as pairs, or randomly, the frequencies of cells with different numbers of bivalents were recorded for all 26, 24, 22 and 20 chromosome cells. Cells with less than 20 chromosomes were excluded because of their low incidence. The data for all the hybrids were used in these calculations. It is assumed that the 14 *vulgare* chromosomes are always present. Therefore, by substracting seven from the number of bivalents for each cell, the numbers of *bulbosum* bivalents were found and these are presented in Table 2. The method of determining the expected number of pairs was described earlier.

As can be seen in Table 2, there were more cells recorded with reduced pairing than expected in all classes except the 20 chromosome class. In the 26 chromosome class, whatever the order of elimination, the *bulbosum* complement of 12 chromosomes must consist of either six pairs, or five pairs and two single chromosomes. The presence of cells with less than five bivalents in this class is therefore caused by desynapsis (or asynapsis) of homologous chromosomes, and there are therefore more pairs of *bulbosum* chromosomes present than recorded in many of the cells in the 26 chromosome class. For the same reason it follows that there are likely to be more pairs present than bivalents recorded in the other chromosome classes. Even so, there are also more cells recorded with maximum or near maximum pairing than expected, particularly cells with 4 pairs of *bulbosum* chromosomes in the 24 chromosome and 22 chromosome classes, and cells with two and three pairs in the 20 chromosome class (Table 2).

The random selection programme predicted that only 7.8%, 2.1%, 1.1% and 1.2% of PMCs in the 26, 24, 22 and 20 chromosome classes respectively would have all the chromosomes present as pairs. This means that with the number of PMCs analysed, 23 to 61 per class, the expected number of cells with complete pairing was small. It was necessary to pool categories to perform χ^2 tests with the result that there was only one degree of freedom for each chromosome class. Nevertheless there were significantly more pairs of chromosomes in 20 and 24 chromosome PMCs than expected if elimination was random. Whether 'pairs' are eliminated in a particular order cannot be determined, but in one cell a pair of satellite chromosomes could be recognised as being the second pair lost (Fig. 1).

Chromosome pairing

As a measure of overall chromosome pairing, independent of chromosome number, the number of chiasmata per chromosome was calculated for each cell. There was a significant difference between plants for this character ($P<0.05$) but the plants could not be grouped into high and low pairing types, and there was no relationship between this character and the *H. bulbosum* parent involved (Table 3). There was no correlation between the

Table 2. Frequencies of PMCs with different numbers of pairs of *bulbosum* chromosomes, i.e. pairs in excess of seven, in even numbered chromosomes classes; expected observations based on 100,000 random selections

Chromosome no.	No. of bulbosum chromosomes		Frequencies of PMCs with the following no. of pairs							Total no. of PMCs	Total χ^2
			0	1	2	3	4	5	6		
26	12	O	0	0	2	6	11	37	6	62	0.3516
		E	0	0	0	0	0	56.242	4.758		(N.S.)
		χ^2					0.0274		0.3242		
24	10	O	0	0	5	16	27	1		49	4.1664
		E	0	0	0	27.391	20.580	1.029			($P<0.05$)
		χ^2				1.4912		2.6752			
22	8	O	1	3	16	7	4			31	0.5921
		E	0	4.650	17.298	8.711	0.341				(N.S)
		χ^2		0.1729		0.4192					
20	6	O	1	11	9	2				23	3.9697
		E	3.427	12.926	6.394	0.276					($P<0.05$)
		χ^2	1.1587		2.8109						

O = observed; E = expected

Table 3. Chiasmata per chromosome in the tetraploids and chiasmata per pairable chromosome in the diploid counterparts

Hybrids	Emir × S1 (1)	Emir × Cb 2929/1 (1)	Emir × Cb 2920/4 (11)	Domen × Cb 2920/4 (9)	Emir × Cb 2929/1 (6)	Emir × S1 (3)
Means	0.7848[a+]	0.7856[ab]	0.7894[ab]	0.8172[ab]	0.8202[b]	0.8213[b]
Means in diploids*	0.1346	0.1614	0.5445	0.3821	0.3878	0.1302

* Data from Thomas and Pickering, 1985
[+] (Means with a common letter are not significantly different at the 5% level by t-test)

Table 4. Mean number of multivalents (quadrivalents + trivalents) in tetraploid (26–28 chromosome) cells

Emir × Cb 2929/1 (1)	Emir × S1 (3)	Emir × Cb 2929/1 (6)	Emir × S1 (1)	Emir × Cb 2920/4 (11)	Domen × Cb 2920/4 (9)
0.7544	0.8889	0.9677	1.1429	1.4783	1.7955

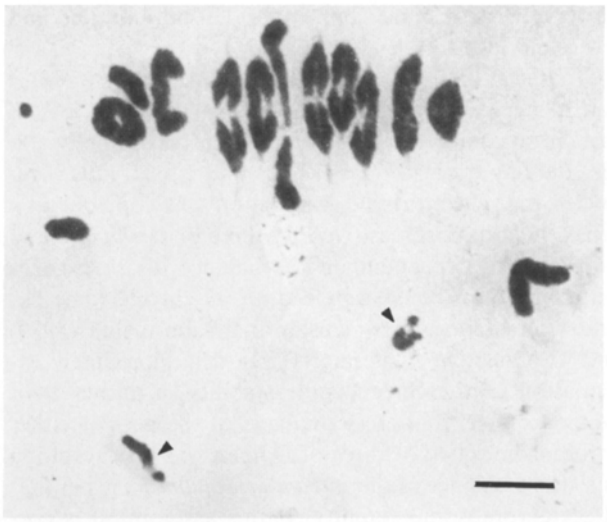

Fig. 1. First metaphase of Emir × Cb 2929/1 (1); arrows indicate two degraded chromosomes with satellites; bar represents 10 μm

mean chiasmata per chromosome in the tetraploids and the mean chiasmata per pairable chromosome recorded by Thomas and Pickering (1985) in the diploid counterparts and reproduced in Table 3 ($r = -0.098$; $df = 4$).

The mean pairing configurations for each class of chromosome number in each of the six tetraploid hybrids are presented in detail elsewhere (Thomas 1987). Although the number of multivalents recorded was generally small, cells with up to six multivalents were occasionally scored: in Domen × Cb 2920/4 one cell had three quadrivalents and three trivalents. More commonly, however 0–2 multivalents were recorded.

In each of the six hybrids the frequency of multivalents did not vary between 28, 27 and 26 chromosome cells. Therefore, these classes were pooled as circa tetraploid cells and the frequencies of cells with different numbers of multivalents were calculated for each hybrid. The mean number of multivalents per tetraploid cell for each plant are presented in Table 4. A χ^2 analysis showed a highly significant difference between four of the hybrids ($P < 0.001$) – the two hybrids involving Cb 2920/4 had higher multivalent frequencies than the two hybrids involving Cb 2929/1. Plants with the same *bulbosum* parent did not differ from each other. Emir × S1 (1) and Emir × S1 (3) could not be included in the analysis as few tetraploid cells were recorded in these plants.

When the mean numbers of multivalents (Table 4) are related to the mean chiasmata per chromosome (Table 3) it is clear that there is no correlation between them ($r = -0.241$; $df = 4$). When the mean number of multivalents are compared with the chiasmata per pairable chromosome recorded in the original diploid cytotypes of each plant reproduced in Table 3 there is again no significant correlation ($r = 0.642$; $df = 4$).

Kimber and Alonso (1981) presented a method for making a mathematical assessment of the relative affinities of the genomes in tetraploid hybrids. Cells with 28 chromosomes were recorded in only four of the hybrids and Kimber and Alonso's method was applied to the mean pairing of the 28 chromosome cells for each of these plants. Two of the hybrids – Emir × Cb 2929/1 (1) and Emir × Cb 2920/4 (11) – fitted the 2 : 1 : 1 model more closely than they did the 2 : 2.

A feature of meiosis in many PMCs analysed was the presence of chromosomes at different stages within the cell. While some bivalents were at late metaphase I others were at pro-metaphase, not yet orientated on the metaphase plate (Fig. 2). This phenomenon which will be referred to as genome asynchrony, was found in

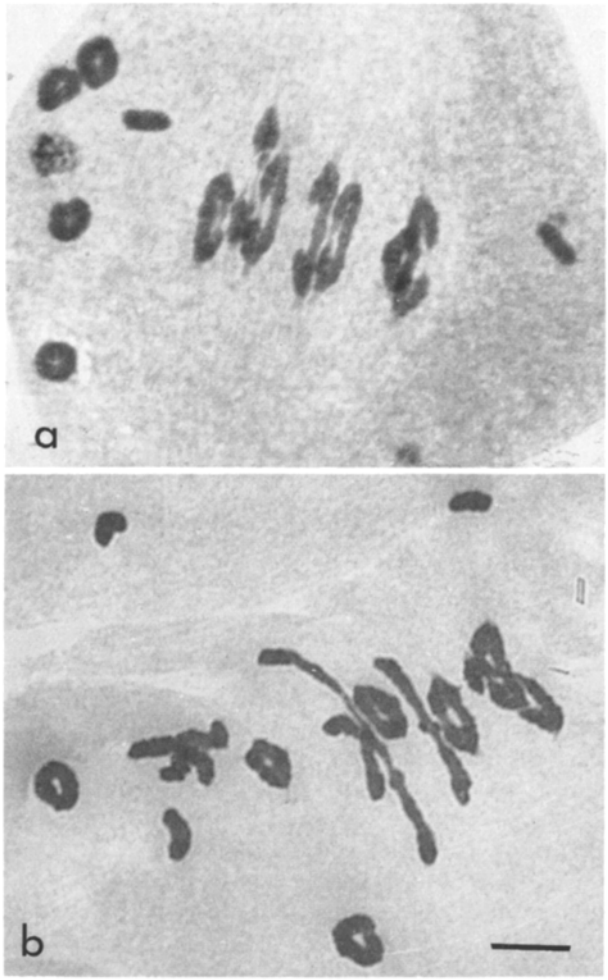

Fig. 2 a and b. Genome asynchrony at first metaphase of **a** Emir × Cb 2929/1 (1), and **b** Emir × Cb 2929/1 (6); bar represents 10 μm

cells irrespective of their chromosome number. In Emir × Cb 2929/1 (1) and Emir × S1 (1) 50% and 60% respectively of PMCs were judged to have chromosomes that could be classified into two groups according to stage. Most commonly, the more advanced set consisted of seven bivalents, the remainder of the chromosomes being bivalents and univalents (Fig. 2). In some PMCs, and particularly in Emir × Cb 2929/1 (6) while chromosome development was asynchronous, they most often could not be clearly separated into groups of retarded and advanced. In these cells chromosomes ranged in some instances from diakenesis or pro-metaphase through to the onset of anaphase with chromosomes at the various intermediate stages. No genome asynchrony was found in PMCs of either Emir × Cb 2920/4(11) or Domen × Cb 2920/4 (9).

Genome asynchrony was found not to exclude the formation of multivalents in any given cell. In Emir × Cb 2929/1 (1) and Emir × S1 (1) – the plants with the greatest genome asynchrony – multivalents were recorded as frequently in asynchronous as synchronous cells. On a plant level, however, one of these two plants had the lowest multivalent frequencies in tetraploid cells of all six hybrids (Table 4) while Emir × Cb 2920/4 (11) and Domen × Cb 2920/4 (9), showing no signs of genome asynchrony had the highest multivalent frequencies.

Discussion

Chromosome elimination

If the significant difference between Emir × S1(3) – the least stable hybrid, and the other four Emir hybrids is genotypic, then it is difficult to equate this with the chromosome stability of the same plants as diploids (Thomas and Pickering 1985). Although chromosome number was not tested statistically in the diploids, Emir × S1 (3) was not the least stable of the six. Domen × Cb 2920/4 (9), however, was the most stable hybrid at both diploid and tetraploid levels.

In one anther of Domen × Cb 2920/4 (9) all the PMCs had 27 chromosomes. This means that after the loss of one chromosome the tissue became chromosomally stable. Barclay et al. (1972) and Ho and Kasha (1975) reported that chromosome elimination was controlled by genes on chromosomes two and three of *H. vulgare* and stability was dependent on the balance of these genes with genes in *H. bulbosum*. Stable, 27 chromosome hybrids were reported by Kasha and Sadasivaiah (1971) and Thomas and Pickering (1983). The most likely explanation of the chromosome stability in anther B of Domen × Cb 2920/4 (9) is that one of the pair of either chromosomes two or three of Domen was lost, resulting in a stable balance of the *vulgare* and *bulbosum* genes that affect chromosome stability. If this assumption is correct, it provides evidence that *H. vulgare* chromosomes can be lost from hybrid cells though this may be exceptional.

Chromosome loss in the tetraploids was 9.6 times greater than in the diploids. Loss of chromosomes is rarely tolerated in diploids, where recessive alleles would be exposed, and while monosomics and even nullisomics are frequently found in polyploids, monosomic plants have been found in only a few diploid species (Khush 1973).

An attempt was made to determine the order, if any, in which the chromosomes were eliminated. Although some authors have described *H. vulgare–H. bulbosum* hybrids from which *vulgare* chromosomes have been eliminated (e.g. Fukuyama and Takahashi 1976), and in this study from Domen × Cb 2920/4 (9), this is probably rare and the assumption that most PMCs contained 14 *vulgare* chromosomes is probably a safe one. The data

clearly demonstrate that one *bulbosum* genome is not eliminated before the other. It has been more difficult to show whether the chromosomes are eliminated randomly or as pairs. The small percentage of PMCs with maximum pairs expected and the small number of chromosomes per class, means that both the expected and observed numbers of cells with the different frequencies of pairs are small in many instances. The difficulties are further compounded by pairing failure between *bulbosum* homologues. This makes the experiment less sensitive, as one cannot determine in the lower chromosome number classes whether cells contain 'single' *bulbosum* chromosome or unpaired 'pairs'. Despite these difficulties, the frequencies of cells with the maximum or near maximum possible pairs points to elimination being non-random.

Finch (1983) was able to determine the order of elimination of the haploid set of *H. vulgare* chromosomes from the endosperm nuclei of a hybrid between diploid *H. marinum* and diploid *H. vulgare*. In the present experiment there is no means of establishing whether the pairs are eliminated in any order, but it is difficult to visualize a system where chromosomes are eliminated as pairs but not in any particular sequence. In the PMC featured in Figure 1 there are two chromosomes that are being, or have been, eliminated, and they both appear to be satellite chromosomes. Although the *bulbosum* NOR is not normally expressed in the hybrid karyotype, Finch (1983) found that the satellite was clearly visible in eliminated chromosomes. From what we see in Fig. 1 the *bulbosum* satellite chromosomes are eliminated as a pair from the tetraploid and as there are only 24 chromosomes remaining in the cell, these were the second pair to be shed.

Chromosome pairing

Hazarika and Rees (1967) found that genes in rye that suppress chiasma frequency in the diploid did the same in the auto-tetraploid and by restricting chiasmata in the auto-tetraploid also reduced the frequency of multivalents. The Ph gene on chromosome 5B of wheat acts in a more precise way in that it does not suppress chiasma formation as such but restricts chiasma formation to homologous associations only. In the hybrid *Triticum aestivum* × *Aegilops longissima*, Riley and Chapman (1963) discovered that while 5B reduced chiasma frequency in the hybrid it actually increased chiasma frequency in the amphiploid while still reducing multivalent frequency.

In the material under study here there is clearly no relationship between the chiasma frequencies of the hybrids at the different ploidy levels. There is also no relationship between chiasma frequency in the tetraploid and multivalent formation. Multivalent formation is, therefore, not suppressed by a restriction of the chiasmata available. There is also not a significant correlation between the chiasma frequencies of the diploids and multivalent formation in the tetraploids. However, the significantly higher frequency of multivalents in the hybrids involving *H. bulbosum* Cb 2920/4 matches the higher chiasma frequencies in the diploid hybrids; contrary to that stated by Thomas and Pickering (1985) the chiasma frequencies of diploid hybrids involving Cb 2920/4 were significantly higher than those involving Cb 2929/1 (Thomas 1987). It may therefore be that a larger experiment would have shown a significant correlation between chiasma frequencies in the diploids and multivalent frequencies in the tetraploids, and the existence of a Ph-like gene in *H. bulbosum*.

The chromosome pairing data from the 28 chromosome cells of four of the hybrids were subjected to the mathematical analysis of Kimber and Alonso (1981). All four tetraploids were produced by doubling the chromosome number of the diploid interspecific hybrids by the application of colchicine, therefore, the two *vulgare* genomes were identical, as were the two *bulbosum* genomes and the tetraploids must have been the 2:2 type. It is somewhat surprising, therefore, that two of the four hybrids tested fitted the 2:1:1 model the best. This means that the pairing between one pair of genomes is greater than the pairing between the other pair of genomes. In those cells showing genome asynchrony, the fourteen *vulgare* chromosomes paired as seven bivalents and it was the less advanced *bulbosum* chromosomes that were not fully paired and found as a mixture of bivalents and univalents. The Kimber and Alonso test confirms that the two pairs of genomes do not synapse to the same extent even in Emir × Cb 2920/4 (11) where no genome asynchrony was seen.

The difference in the duration of meiosis in the two species may be the cause of failure of these chromosomes to pair. To the author's knowledge, the meiotic timing of *H. bulbosum* has not been measured. However, the asynchrony seen between the genomes at MI in the present study strongly indicates that there are differences in the meiotic times of the two species that have not been reconciled in the hybrid. The chiasmate pairing seen at MI is the consequence of two events that take place during meiotic prophase, chromosome synapsis and then chiasma formation between the synapsed chromosomes. If the bulbosum chromosomes lag behind the *vulgare* chromosomes in development at zygotene, it may be that they will not have completed synapsis when chiasma formation occurs at pachytene and as a result some chromosome associations will become desynaptic. This would lead to PMCs at metaphase I containing seven *vulgare* bivalents with at least some of the *bulbosum* chromosomes remaining as univalents.

Differences in the duration of meiosis was one of several reasons suggested by Fedak (1985) for the re-

duced pairing he found in a *Hordeum* × *Secale* amphiploid; in that amphiploid, however, the frequency of univalents was the same in both sets of chromosomes. Stutz (1962) describes precocious chromosomes at pachytene and diplotene and lagging chromosomes during anaphases I and II to be indicative of 'asynchronous meiotic rhythm of the parental chromosomes' in two *Secale* × *Triticum* amphidiploids. Pohler and Clauss (1984) found that in some PMCs of their *Hordeum* × *Secale* amphidiploid, rye bivalents still showed the shape of diakenesis bivalents at metaphase I and that univalents were mainly rye chromosomes. They concluded that the unadapted high time need of the rye genome may impair the potency of rye chromosomes for homologous and homoeologous pairing.

Genome asynchrony may also be responsible for the different frequencies of multivalents among the six tetraploid hybrids studied here. If, at zygotene the *vulgare* chromosomes begin to synapse before the *bulbosum* chromosomes, then they may exclude the *bulbosum* chromosomes from taking part in the pairing configuration and, by default, the *bulbosum* chromosomes must either pair amongst themselves to form bivalents or remain unpaired.

Acknowledgements. I am indebted to my ex-colleague R. A. Pickering for the hybrids used, to Dr. H. Thomas for his guidance, to J. F. Potter for devising the computer program on random elimination and my other colleagues for their willing help.

References

Barclay IR, Shepherd KW, Sparrow DHB (1972) Chromosome elimination in *Hordeum vulgare–Hordeum bulbosum* hybrids. Bienn Rep (1970–1971), Waite Agric Res Inst, University Adelaide, Australia, pp 39–40

Fedak G (1985) Cytogenetics of a hybrid and amphiploid between *Hordeum pubiflorum* and *Secale africanum*. Can J Genet Cytol 27:1–5

Finch RA (1983) Tissue-specific elimination of alternative whole parental genomes in one barley hybrid. Chromosoma 88:386–393

Fukuyama T, Takahashi R (1976) A study of the interspecific hybrid, *Hordeum bulbosum* (4x) × *H. vulgare* (4x), with special reference to dihaploid frequency. In: Gaul H (ed) Barley genetics III. Thiemig, München, pp 351–360

Hazarika MH, Rees H (1967) Genotypic control of chromosome behaviour in rye. X. Chromosome pairing and fertility in autotetraploids. Heredity 22:317–332

Ho KM, Kasha KJ (1975) Genetic control of chromosome elimination during haploid formation in barley. Genetics 81:263–275

Kasha KJ, Sadasiviah RS (1971) Genome relationships between *H. vulgare* L. and *H. bulbosum* L. Chromosoma 35:264–287

Khush GS (1973) Cytogenetics of aneuploids. Academic Press, New York London

Kimber G, Alonso LC (1981) The analysis of meiosis in hybrids. III. Tetraploid hybrids. Can J Genet Cytol 23:235–254

Lange W (1971) Crosses between *Hordeum vulgare* L. and *H. bulbosum* L. II. Elimination of chromosomes in hybrid tissues. Euphytica 20:181–194

Morgan WG (1976) A technique for the production of polyploids in grasses. Euphytica 25:443–446

Pohler W, Clauss E (1984) Differences in chromosome stability, chromosome pairing, and rhythm of nuclear division between the parental genomes in an amphidiploid hybrid from the cross *Hordeum vulgare* L. × *Secale montanum* Guss. Arch Züchtungsforsch 14:215–224

Riley R, Chapman V (1963) The effects of the deficiency of chromosome V(5B) of *Triticum aestivum* on the meiosis of synthetic amphiploids. Heredity 18:473–484

Stutz HC (1962) Asynchronous meiotic chromosome rhythm as a cause of sterility in *Triticale*. (Abstract) Genetics 47:988

Subrahmanyam NC, Kasha KJ (1973) Gene expression in haploid and hybrid progeny from crosses between *Hordeum vulgare* and *H. bulbosum*. Crop Sci 13:749–750

Thomas HM (1987) Cytogenetic studies of some interspecific hybrids and aneuploids in *Hordeum*. MSc Thesis, Aberystwyth, Wales

Thomas HM, Pickering RA (1983) Chromosome elimination in *Hordeum vulgare* × *H. bulbosum* hybrids. 2. Chromosome behaviour in secondary hybrids. Theor Appl Genet 66: 141–146

Thomas HM, Pickering RA (1985) The influence of parental genotype on the chromosome behavior of *Hordeum vulgare* × *H. bulbosum* diploid hybrids. Theor Appl Genet 71: 437–442