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Comparison of the Chromosomes of *Triticum timopheevi* with Related Wheats Using the Techniques of C-banding and in situ Hybridization

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Summary. The chromosomes of the tetraploid wheats *Triticum timopheevi* (Genome AAGG) and *T. araraticum* (Genome AAGG) were C-banded at mitosis. The identity of the banded and unbanded chromosomes was then established by firstly making comparisons with the hexaploid species *T. zhukovskyi* which has the genome formula AAAAGG. Secondly, the meiotic pairing in F_1 hybrids between *T. timopheevi* and diploid wheats was examined by means of C-banding. The results showed that the banded chromosomes belonged to the G genome, while the unbanded chromosomes belonged to the A genome. Only one of the two pairs of satellited chromosomes had strong heterochromatic bands. The relationship between the genomes of *T. timopheevi* and *T. dicoccum* (Genome AABB) was then assessed at meiosis in hybrids between these species, using the techniques of C-banding and in situ hybridisation of a cloned ribosomal RNA gene probe. It was concluded that there were differences both in the amount and distribution of heterochromatin and also translocation differences between the species.

Key words: *Triticum timopheevi* – Chromosomes – C-banding – In situ hybridisation – Heterochromatin – Translocation

Introduction

The tetraploid wheats have been classified into two groups; the *dicoccum* group with the genome formula AABB and the *timopheevi* group with the genome formula AAGG. Over many years, experiments have been carried out to try to determine the relationship between these tetraploid groups and in particular, the relationship between the B- and the G-genome chromosomes.

Much of the work has involved a study of the pairing behaviour at meiosis in F_1 hybrids between *Triticum timopheevi* and various other tetraploid wheats (Lilienfeld and Kihara 1934; Kostoff 1937; Love 1941; Sachs 1953). The conclusions drawn from these experiments were that the A genomes matched fairly well, but that there were some structural differences between the B and G genomes. Later, Wagenaar (1961; 1966), in a more extensive study of a wide range of different *timopheevi* lines, claimed that there was a genetically controlled system in *T. timopheevi* which induced asynapsis in F_1 hybrids, and that this was more important than the structural differences in controlling the meiotic pairing. However, Feldman (1966) again concluded that there were structural differences, on the basis of results obtained by crossing *T. timopheevi* × *Ae. squarrosa* amphiploid (AAGGDD) with telocentric lines of hexaploid wheat (AABBDD).

To try to determine in more detail the nature of any structural differences between the B and G genomes, and the consequences that these differences have on meiotic pairing and chiasma formation, the *timopheevi* and *dicoccum* wheats have been examined by means of C-banding of their chromosomes and in situ hybridisation of a cloned ribosomal RNA gene sequence.

Materials and Methods

1 Plant Stocks

The following accessions from the Plant Breeding Institute, Cambridge, were used in the investigations:

T. timopheevi (2n = 4× = 28) AAGG 1, 2, 3, 4, 5
T. araraticum (2n = 4× = 28) AAGG 1, 2, 2A
T. zhukovskyi (2n = 6× = 42) AAAAGG 1
T. dicoccum (2n = 4× = 28) AABB E5, E13, E23, E16

Other accessions were obtained from the Waite Institute, Adelaide, Australia.

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2 Crosses

The F_1 hybrids obtained by crossing *T. timopheevi* and *T. dicoccum* were grown in an environmental cabinet maintained at 20 °C with continuous illumination.

Hybrids between *T. timopheevi* and the AA-genome diploid species *T. aegilopoides, T. thaoudar, T. monococcum* and *T. urartu* were produced by Dr. K. W. Shepherd at the Waite Institute.

3 Cytology

For both C-banding and in situ studies, root-tips were pretreated with 1-bromonaphthalene for 4 h and 30 min at room temperature and fixed in 1 : 3 acetic alcohol. The meristematic regions were then dissected out in 45% acetic acid and squashed under an acid-washed coverslip. This was removed by the liquid-nitrogen technique. Anthers at metaphase I of meiosis were fixed in 1 : 3 acetic alcohol and dissected out as described by Hutchinson et al. (1980).

The C-banding technique was as described by Seal and Bennett (1981), with the exception that the whole procedure was carried out after the dissection of the tissue. The chromosomes were stained with 20% Leischmann's solution in 1/15 M $NaHPO_4$ pH 6.8.

The technique used for in situ hybridisation is described in detail by Hutchinson et al. (1980), except that preparations were stained with 10% aqueous Giemsa. The radioactive probe used was the tritium-labelled cRNA transcribed by *E. coli* RNA polymerase from plasmid pTA71. This chimaeric plasmid consists of a single wheat ribosomal RNA gene repeating unit in the vector plasmid pAC184 (Gerlach and Bedbrook 1979).

Results

1 C-banding of Mitotic Chromosomes

A *Triticum Timopheevi*

Five different accessions of *T. timopheevi* were C-banded and showed few differences in their banding patterns. Figure 1 shows a composite idiogram together with representative photographs from one of those lines. There are five pairs of chromosomes which are largely unbanded, two pairs with only limited banding and seven pairs which show mostly centromeric bands situated at one or both sides of the centromere, together with some intercalary bands. There is very little telomeric banding. These banding patterns are substantially in agreement with previously published karyotypes for *T. timopheevi* (Zurabishvili *et al.* 1978; Belea and Féjer

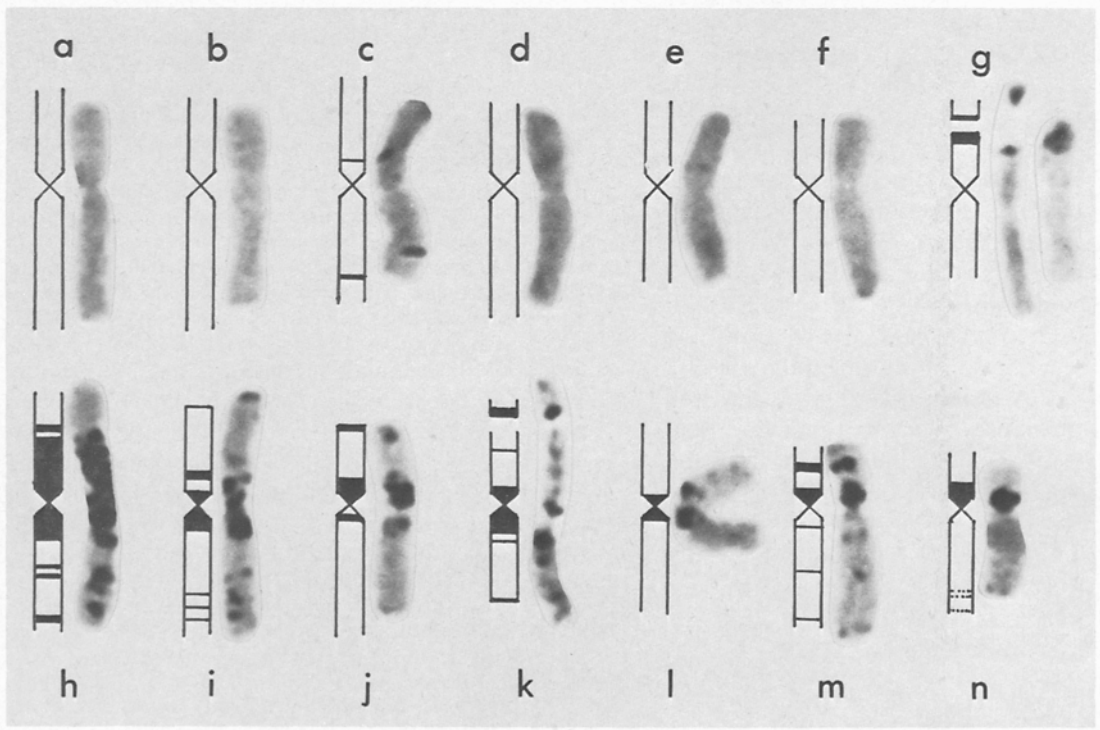

Fig. 1. Idiogram of the C-banded chromosomes of *Triticum timopheevi* together with representational photographs of each banding pattern. The chromosomes are arranged in rows of largely unbanded chromosomes ($a-g$) and banded chromosomes ($h-n$). Within each row, chromosomes are arranged in order of their total lengths. The karyotype is based on Zurabishvili et al. (1978) and was confirmed by measurements of photographs of banded chromosomes. The idiograms were based on the data for many cells measured in four different accessions, and the dotted lines represent bands found only in some accessions. Photographs show the smaller nucleolus organising chromosome (Chromosome *g*) both in the contracted state, and when the secondary constriction is clearly visible

1980). There is, however, one important difference between the karyotype published by Zurabishvili et al. (1978) and the banding patterns shown in Fig. 1. This concerns the banding pattern of one of the satellited chromosomes. *T. timopheevi* has two pairs of nucleolus-organising, satellited chromosomes (Bozzini and Giorgi 1969; Hutchinson and Miller 1982). One pair of these satellited chromosomes shows clear centromeric and interstitial heterochromatin (chromosome k on idiogram, Fig. 1) in agreement with the banding pattern of Zurabishvili et al. (1978). The other, shorter satellited chromosome, however, shows no centromeric banding, and bands only near the secondary constriction (chromosome g, Figs. 1 and 2), unlike the chromosome of Zurabishvili et al. (1978), which is again banded centromerically. It is possible that this difference in results may be due to incorrect identification of the banded chromosomes, or it may represent some degree of polymorphism amongst *T. timopheevi* lines. To test this, and also to broaden the range of genotypes examined, three accessions of *T. araraticum*, which is a wild tetraploid species of the *timopheevi* group, were also C-banded.

B *Triticum araraticum*

The three accessions of *T. araraticum* again showed only minor differences in their banding patterns, and so a composite idiogram, together with representative photographs of one of the lines, is shown in Fig. 2. Although broadly similar to the banding pattern of *T. timopheevi*, *T. araraticum* does nevertheless show some differences, particularly in the centromeric bands of the larger satellited chromosome (chromosome k) and in a heavily banded chromosome (chromosome h, Figs. 1 and 2), and also in some of the intercalary bands on other chromosomes. The shorter satellited chromosome is, however, like the *T. timopheevi* chromosome, only banded near the secondary constriction. Wider variation amongst the *T. araraticum* accessions might have been expected, since many translocation differences are known to exist between different lines of *T. araraticum* (Kawahara and Tanaka 1977).

Various banding studies of hexaploid and tetraploid wheats of the *dicoccum* group have shown that it is the B-genome and 4A chromosomes which show the major C-bands (Gill and Kimber, 1974; Gerlach 1977). Similarly, it might be expected that the banded chromosomes of *T. timopheevi* and *T. araraticum* belong to the G rather than to the A genome. However, the finding in *T. timopheevi* of a pair of satellited chromosomes which are unbanded except for the bands near the secondary constriction throws some doubt on this, since both pairs of satellited chromosomes in *T. timopheevi* are, in Feulgen squashes, morphologically like the nucleolus-organising chromosomes 1B and 6B of the

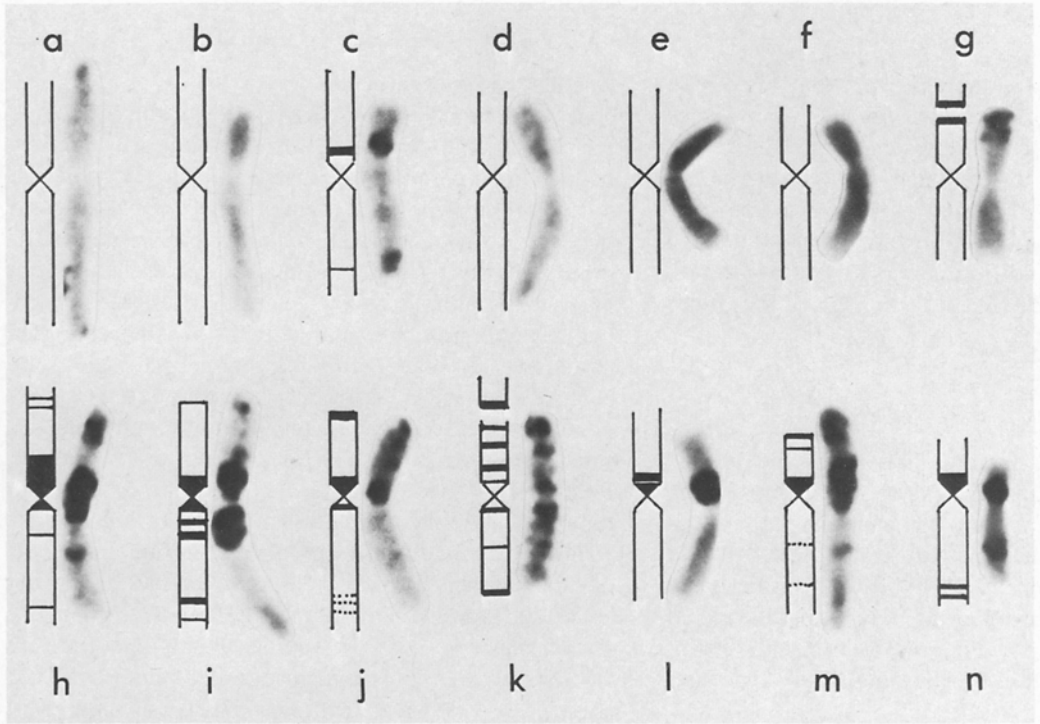

Fig. 2. Composite idiogram together with representative photographs of C-banded chromosomes of *T. araraticum*. The arrangement of the chromosomes is as described in Fig. 1

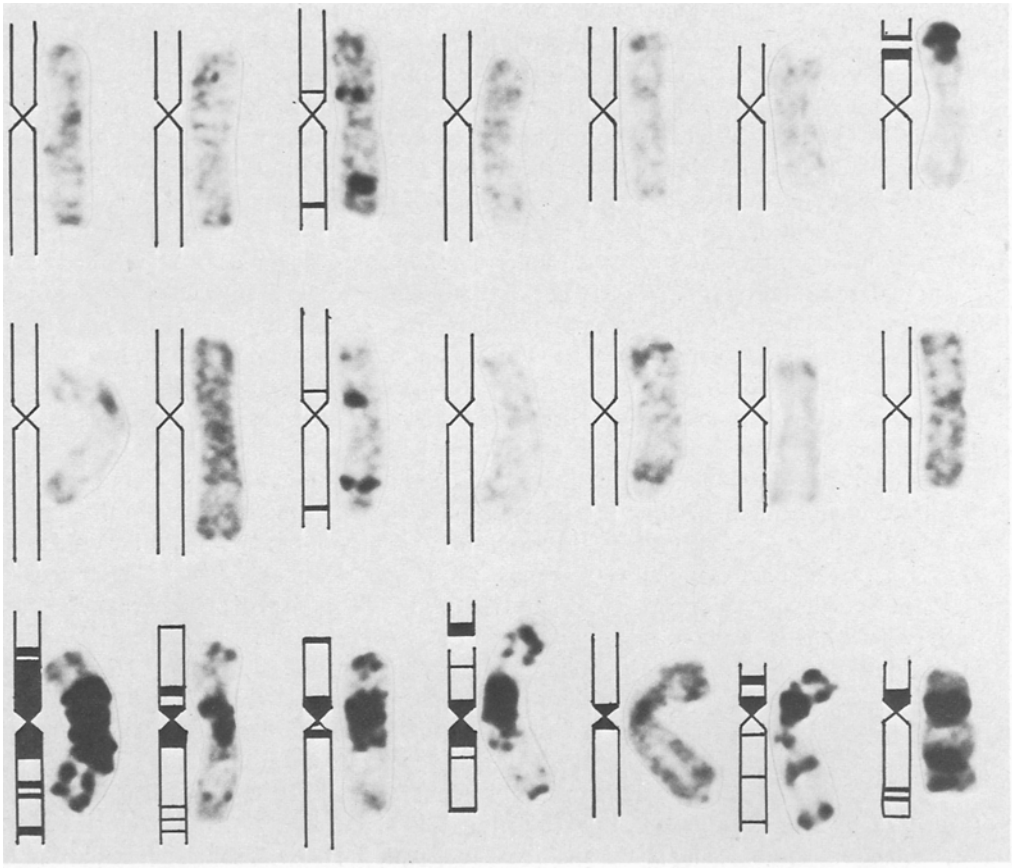

Fig. 3. Idiogram together with representative photographs taken from one cell of the C-banded chromosomes of the hexaploid *T. zhukovskyi*

dicoccum wheats. It was therefore necessary to try to determine which of the *timopheevi* chromosomes belongs to the A genome, and which to the G genome. The first approach to this problem was to examine the banding pattern of *T. zhukovskyi,* which has the genome construction AAAAGG, and is thought to have arisen as an amphiploid from the cross *T. timopheevi* × *T. monococcum* (Bowden 1959; Upadhya and Swaminathan 1963).

C *Triticum zhukovskyi*

An idiogram of the banding pattern of the mitotic chromosomes of *T. zhukovskyi* is shown in Fig. 3. The first obvious finding is that the banding patterns do indeed correspond with the patterns expected from a *T. timopheevi* × *T. monococcum* hybrid. This is in agreement with previous cytological data (Upadhaya and Swaminathan 1963) and with a previous examination of the number and position of ribosomal RNA gene sites (Hutchinson and Miller 1982).

Since the haploid A genome is present in four copies in *T. zhukovskyi,* it is possible to determine tentatively whether chromosomes belong to the A or to the G genome. The idiogram (Fig. 3) shows that the only banded chromosome found in four copies is a lightly banded one, chromosome c (Figs. 1 and 3), while all other chromosomes additional to the *timopheevi* complement are unbanded. This implies that, in general, as expected, the A-genome chromosomes have little heterochromatin. It also suggests that all the strongly banded chromosomes, and also the smaller satellited chromosome, belong to the G genome. However, one complication arises here, because there are thus 8 pairs of banded chromosomes (excluding chromsome c). There are two possible explanations for this result. Firstly, it is known that the 4A chromosome of the diploid *T. monococcum* is unbanded (Gill and Kimber 1974), while the 4A chromosome of hexaploid wheats of the *aestivum* group is strongly banded near the centromere, and it may be that the 4A chromosome of *T. timopheevi* is similarly heterochromatic. Secondly, it is known that the rRNA gene clusters of the AA diploid species are located on chromosomes which have very small satellites (Gerlach et al. 1980), unlike both markedly satellited chromosomes of *T. timopheevi*

Table 1. Mean chromosome pairing in Feulgen stained preparations at first metaphase of meiosis in F_1 hybrids between *T. timopheevi* and diploid wheat species. (Ranges in parentheses)

Hybrid	Plant	Number of cells	Pairing configuration				
			I	II	III	IV	V
T. timopheevi × *T. thaoudar*	1	30	7.07 (5 – 10)	4.87 (3 – 6)	0.53 (0 – 2)	0.40 (0 – 1)	0.20 (0 – 1)
	2	30	6.90 (4 – 9)	5.11 (4 – 7)	0.66 (0 – 2)	0.40 (0 – 1)	0.06 (0 – 1)
T. timopheevi × *T. urartu*	1	25	7.40 (5 – 9)	5.24 (4 – 7)	0.52 (0 – 2)	0.20 (0 – 1)	0.16 (0 – 1)
	2	25	7.64 (6 – 10)	5.32 (4 – 7)	0.40 (0 – 1)	0.28 (0 – 1)	0.08 (0 – 1)

(Hutchinson and Miller 1982). The smaller satellited chromosome g of *T. timopheevi* may therefore possibly be involved in a reciprocal translocation between chromosomes of the A and G genomes. To try to find out which of these explanations was most likely, a study was carried out into the meiotic pairing behaviour of F_1 hybrids between *T. timopheevi* and various (AA-genome) diploid wheats.

2 C-banding of Meiotic Chromosomes

A Hybrids Between *T. timopheevi* and Diploid Wheats

Crosses were made between *T. timopheevi* and the diploids *T. aegilopoides. T. thaoudar, T. monococcum* and *T. urartu.* The F_1 hybrids between *T. timopheevi* and *T. aegilopoides* were semi-lethal and therefore could not be analysed.

Table 1 shows the results of a conventional feulgen squash analysis of the pairing between *T. timopheevi* × *T. thaoudar* and *T. timopheevi* × *T. urartu.* Both crosses show a mean of seven or more univalents, and also multivalents involving up to 5 chromosomes, suggesting the presence of translocation heterozygosity.

C-banding analysis of the meiosis in all the hybrids showed that in most cells all the univalents were banded (for example, see Fig. 4). This therefore confirms the expectation that banded chromosomes belong to the G rather than to the A genome.

The second finding was that all crosses showed the presence of a rod bivalent consisting of the smaller satellited chromosome from *T. timopheevi* and an unbanded chromosome (Fig. 4). No multivalents involving the satellited chromosome were observed. This suggests that this satellited chromosome was indeed an A-genome chromosome. However, the possibility of a translocation between an A-genome chromosome and a nucleolus-organising G-genome chromosome cannot be absolutely excluded, since chiasma formation in the region of the secondary constriction is often reduced.

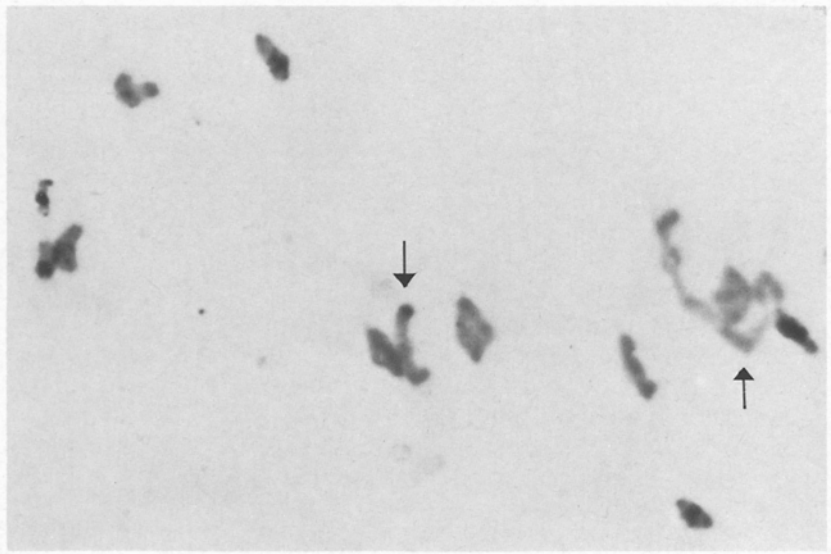

Fig. 4. C-banding of the metaphase I chromosomes of the F_1 hybrid between *T. timopheevi* and *T. urartu.* Arrows indicate the bivalent involving the smaller satellited chromosome, and the multivalent involving a banded chromosome

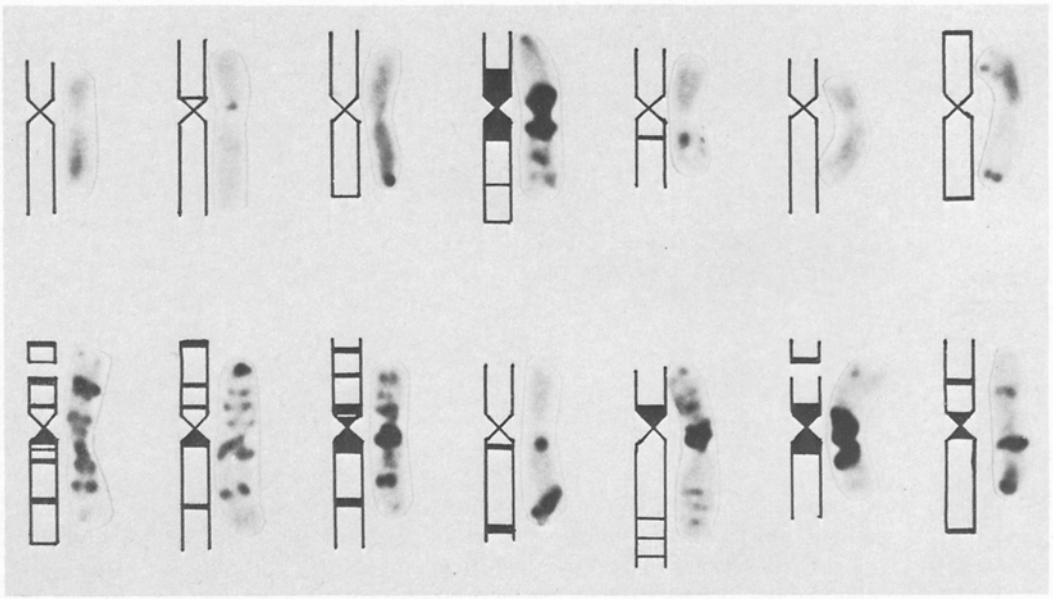

Fig. 5. Composite idiogram together with representative photographs of C-banded chromosomes of *T. dicoccum*. The chromosomes are arranged according to their supposed homology with 1A on the left in the top row and 1B on the left in the bottom row. As telocentric marker stocks of these tetraploid lines were not available, the homologies were based on comparisons with the published idiograms of the hexaploid wheats (Gill and Kimber 1974). The karyotypes are based on Zurabishvili et al. (1978)

Thirdly, multivalents consisting of up to 4 chromosomes were unbanded, suggesting the presence of translocation differences between the A genomes of the diploid species and that of *T. timopheevi*. In quinquivalents, however, the additional chromosome was heavily banded and was identified as chromosome h of *T. timopheevi*. This indicates the presence of an A–G translocation within the *T. timopheevi* relative to the diploid species.

B Hybrids Between *T. timopheevi* and *T. dicoccum*

Crosses were made between different *T. timopheevi* accessions and two *T. dicoccum* accessions. An idiogram of the banding pattern of mitotic chromosomes of *T. dicoccum* (genome AABB) is presented in Fig. 5. This is very similar to previously reported banding patterns (Zurabishvili et al. 1978). Both of the satellited chromosomes are centromerically banded. Only two

Table 2. Mean chromosome pairing at first metaphase of meiosis in F_1 hybrids between *T. timopheevi* and *T. dicoccum*. (Ranges in parentheses)

Cross	Staining technique	Number of cells	Pairing configuration						
			I	II	III	IV	V	VI	VII
T. timopheevi 2 × *T. dicoccum* E13	Feulgen	20	5.40 (1 – 9)	8.00 (5 – 12)	1.50 (0 – 4)	0.40 (0 – 1)	0.10 (0 – 1)	–	–
	Giemsa	20	7.30 (0 – 13)	7.00 (4 – 12)	1.30 (1 – 4)	0.70 (0 – 2)	–	–	–
T. timopheevi 3 × *T. dicoccum* E23	Feulgen	15	7.80 (1 – 11)	6.81 (4 – 10)	1.13 (0 – 2)	0.80 (0 – 3)	–	–	–
	Giemsa	20	7.30 (1 – 14)	6.90 (5 – 9)	1.50 (0 – 4)	0.60 (0 – 2)	–	–	–
T. timopheevi 4 × *T. dicoccum* E13	Feulgen	20	5.80 (3 – 13)	7.20 (3 – 11)	1.05 (0 – 3)	0.65 (0 – 2)	0.10 (0 – 1)	0.20 (0 – 1)	0.05 (0 – 1)
	Giemsa	20	5.85 (3 – 10)	8.00 (5 – 11)	0.80 (0 – 2)	0.50 (0 – 1)	0.15 (0 – 1)	0.05 (0 – 1)	0.10 (0 – 1)

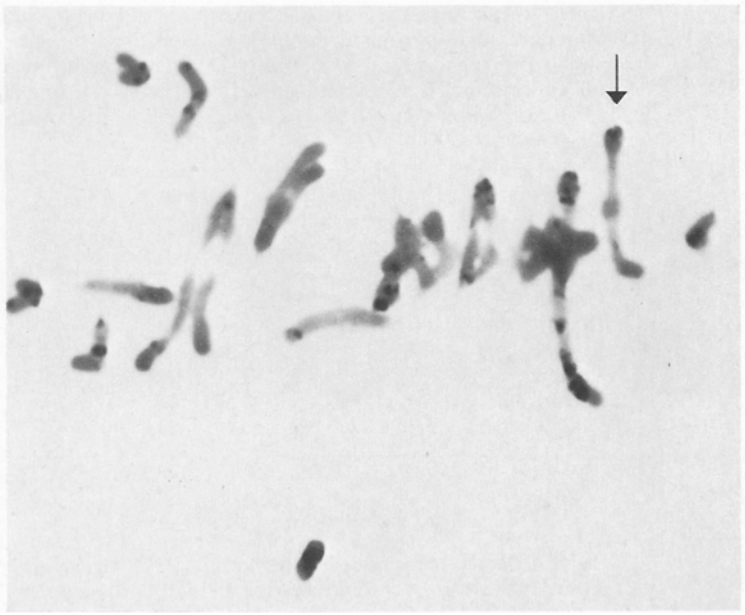

Fig. 6. C-banding of the metaphase I chromosomes of the F_1 hybrid between *T. timopheevi* and *T. dicoccum*. The smaller satellited chromosome is arrowed

pairs of chromosomes were completely unbanded, the other A-genome chromosomes showing slight banding. This suggests that not only are the B and G chromosomes differentiated but also that the A-genome chromosomes differ in these two tetraploid species.

The pairing behaviour at meiosis in the *T. timopheevi* × *T. dicoccum* hybrids was examined in two ways. Firstly by means of a conventional feulgen squash technique, and secondly by C-banding. The pairing data (Table 2) showed a reasonable correlation for the different techniques, and was in the same range as previously reported results (Lilienfeld and Kihara 1934; Kostoff 1937; Sachs 1953).

Figure 6 shows a typical C-banded meiotic preparation. Although some chromosomes can be identified easily by their banding patterns, other chromosomes, especially those with centromeric labelling, are difficult to identify positively. The identification is further confused by the presence of multivalents consisting of banded and unbanded chromosomes. Chromosomes were therefore simply classified as banded (B/G genome) or unbanded/lightly banded (A genome). The smaller nucleolus-organising chromosome of *T. timopheevi* was distinct enough to be clearly identified in each cell.

The results (Table 3) show that most of the univalents are banded. This confirms earlier suggestions that the B and G genomes are less closely related than the A genomes. However, both banded and unbanded bivalents were found. No bivalent was observed which consisted of one banded and one unbanded chromosome, indicating that the pairing was indeed specific. There are slightly more unbanded bivalents (mean frequency per cell 4.25) than banded ones (mean frequency per cell 3.10), and in addition most of the labelled bivalents are of the rod, rather than the ring type, again suggesting a closer relationship between the A-genome chromosomes than between the B- and G-genome chromosomes, despite the banding heterozygosity between the *T. timopheevi* and *T. dicoccum* mentioned above. It should be noted also that the two chromosomes involved in bivalent formation often had different amounts of heterochromatin, resulting in heteropycnic bivalents (Fig. 6).

The multivalents are rather more difficult to interpret. Table 3 shows the number of banded chromosomes involved in each multivalent. Firstly, the results show that there are a number of trivalents and quadrivalents in which all chromosomes are unbanded. This indicates the presence of translocation differences between the A-genome chromosomes. Secondly, Table 3 shows that only one of the 109 multivalents scored involved three banded chromosomes and probably represents a misclassification of one of the lightly banded A-genome chromosomes from *T. dicoccum*. All other multivalents involve either one, or at the most, two banded chromosomes. This indicates that there are translocations between A- and either B- or G-genome chromosomes, but not within the B/G group. However, the possibility of some multivalents being produced by homoeologous pairing due to an imbalance in the pairing control system cannot be completely dismissed.

Finally, the analysis showed that the smaller satellited chromosome from *T. timopheevi* paired with an unbanded chromosome in 87% of cells. There were, however, occasional trivalents that included the small

satellited chromosome (3% of cells), and so this chromosome was investigated further by the technique of in situ hybridisation of a cloned ribosomal RNA gene sequence.

C In situ Hybridisation

Previous studies of *T. timopheevi* and *T. dicoccum* have shown 2 pairs of ribosomal RNA gene clusters to be present (Hutchinson and Miller 1982). In situ hybridisation of the ribosomal RNA gene probe to the F_1 hybrids at meiosis has confirmed that there are four ribosomal RNA gene clusters, two from the *T. timopheevi* parent and two from the *T. dicoccum* parent. As illustrated in Fig. 7, it is also possible to show that although two chromosomes with rRNA gene sites do pair together in many cells, the other two chromosomes with rRNA gene sites only pair with unlabelled chromosomes. The data showing pairing frequencies are given in Table 4. The different chromosomes were identified on the basis of their morphology and also by counting the number of silver grains on each chromosome. In *T. aestivum*, it is known that most ribosomal RNA genes are located on chromosomes 1B and 6B (Flavell and O'Dell 1976), and it might be assumed that a similar situation would occur in *T. dicoccum*. Since silver grain number is proportional to gene number (Miller et al. 1980), it is possible to get estimates for the numbers of ribosomal RNA genes located on the chromosomes. The mean number of silver grains found on the satellited chromosomes which pair together is 11.16 ± 0.37, while the mean number of grains found on

Table 3. The percentage of each configuration occurring with various numbers of banded chromosomes in the F_1 hybrids between *T. timopheevi* and *T. dicoccum*. Data are averaged over all crosses, and exclude configurations involving the smaller satellited chromosome of *T. timopheevi*, which were classified separately

Configuration	Number of banded chromosomes					
	0	1	2	3	4	5
Univalent	11.49	88.51				
Rod bivalent	16.56	0	83.44			
Ring bivalent	77.90	0	22.10			
Trivalent	51.29	29.88	17.50	1.33		
Quadrivalent	20.00	37.46	42.54	0	0	
Quinquivalent	0	33.33	66.67	0	0	0

Table 4. Results of hybridising the ribosomal RNA gene probe in situ to the meiotic chromosomes of the F_1 hybrid between *T. timopheevi* and *T. dicoccum*. Data show the percentage of cells which occur in each configuration, together with their pattern of labelling

	Univalents	Bivalents			
		Rings	Rods		
T. timopheevi – smaller satellited chromosome	6	–	–	–	94
T. dicoccum – chromosome 1B	44	–	–	–	56
chromosomes 6B and 6G	42	14	16	28	–

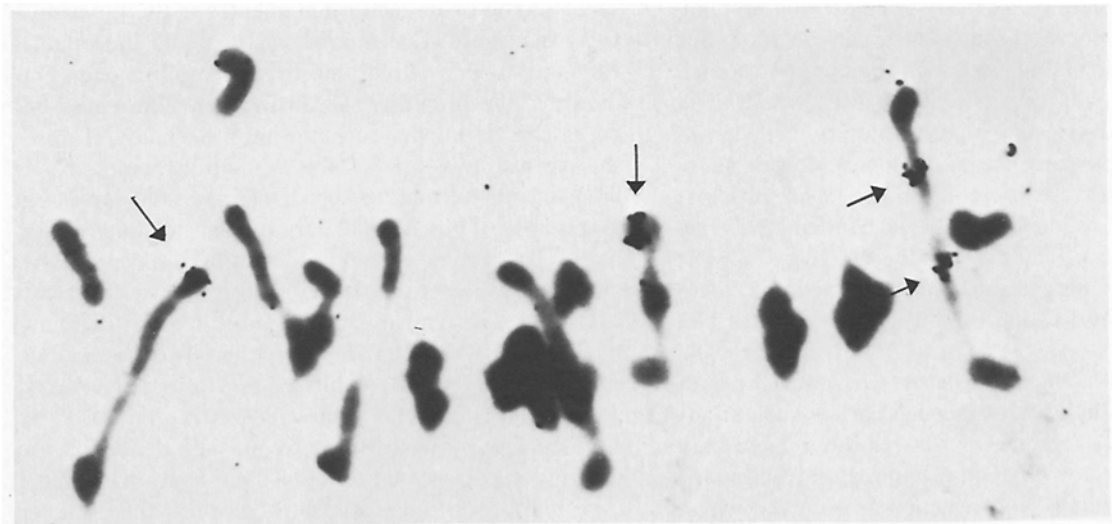

Fig. 7. In situ hybridisation of the cloned ribosomal RNA gene probe to the metaphase I chromosomes of the F_1 hybrid between *T. timopheevi* and *T. dicoccum*. The ribosomal RNA gene clusters are arrowed. 145,000 c.p.m. of probe were applied per slide, and the slides exposed for two weeks

the other *T. dicoccum* satellited chromosome is 7.34 ± 0.39. If the ratio of these counts ($11.16/7.34 = 1.52$) is compared with the ratio of the number of genes found on chromosomes 6B and 1B of *T. aestivum* ($6550/4450 = 1.47$, data from Flavell and O'Dell 1979), there is a very close correlation ($\chi^2 = 0.47$, $P = 0.50$). This may therefore be used to identify tentatively the chromosomes which pair together as chromosomes 6B and 6G. This tentative identification is supported by evidence from Sears (1975), who showed that chromosome 6B of *T. aestivum* may be substituted for by the 6G chromosome of *T. timopheevi.* The *T.dicoccum* labelled chromosome which pairs with an unlabelled chromosome must therefore be chromosome 1B. This identification is supported by Feldman (1966), who showed that in the crosses between the *T. timopheevi* × *Ae. squarrosa* amphiploid and wheat telocentric lines, the *T. timopheevi* chromosome which paired with the 1BL wheat telocentric was not satellited. It therefore seems likely that, as suggested earlier, there is a translocation between the A and G genomes in *T. timopheevi* which involves a satellited chromosome.

Discussion

The origins and evolution of the polyploid wheats and the relationship of genomes within species have been studied in detail for many years. The basis for much of the work has been a comparison of both the morphology of the chromosomes at mitosis and the pairing behaviour, in particular hybrids, of chromosomes at meiosis. In the present comparison of the tetraploid wheats *T. timopheevi* and *T. dicoccum,* both these approaches have been used, but with the added advantage that individual chromosomes would be identified by means of the techniques of C-banding and in situ hybridisation. It has been possible to show that there are at least two types of structural difference distinguishing both the A genomes from each other and also the B from the G genome.

The first kind of structural variation observed in the *T. timopheevi* and *T. dicoccum* chromosomes concerned the size and distribution of heterochromatic bands. There were differences between the A genomes, but these were relatively small, and appeared to have little effect on pairing and chiasma formation. The B and G genomes, however, paired less well, and even where bivalents were formed, the mean chiasma frequency per bivalent (1.24) was lower than in the A-genome bivalents (1.80). As there were marked differences in the distribution of heterochromatin between the B and G genomes, this may indicate that the heterochromatin caused the reduced chiasma frequency. Indeed, heterochromatin has been shown to influence crossing over in a number of organisms (review by John and Miklos 1979). In comparisons between different varieties of wheat, heterochromatic differences have also been suggested as a cause of reduced chiasma formation in B-genome bivalents relative to A- and D-genome bivalents (Dvořák and McGuire 1981). However, as shown in Fig. 7, some B/G bivalents were formed in which the paired chromosomes were markedly different in their heterochromatic content. In addition, most chiasmata in the wheats are localised towards the ends of the chromosomes, while the heterochromatin is largely centromeric or interstitial. This would appear to suggest that, although differences in heterochromatin may be implicated in the reduced crossing over, this is not the complete story.

The second, and most obvious of the differences distinguishing the *T. timopheevi* and *T. dicoccum* chromosomes are the translocations which exist within the A genomes and between the A and B or G genomes. One translocation which was investigated in detail involves a nucleolus-organising chromosome of *T. timopheevi.* This shows a banding pattern and pairing behaviour which indicates that there has been a translocation within *T. timopheevi* between a satellited G- and an A-genome chromosome. Nucleolus-organising chromosomes are readily identified in conventional Feulgen squash preparations and are often used for making comparisons between genomes. The finding that one of the satellited chromosomes of *T. timopheevi* is not, as expected, a typical G-genome chromosome, illustrates the dangers of making evolutionary studies based on limited data. The added dimension of the more detailed chromosome mapping obtained by the C-banding and in situ hybridisation techniques should provide additional information in any future debate about the origins of polyploid species.

Literature

Belea, A.; Fejér, O. (1980): Evolution of wheat (*Triticum* L.) in respect to recent research. Acta. Agron. Acad. Sci. Hung. **29,** 306–315

Bowden, M.W. (1959): The taxonomy and nomenclature of wheats, barley and ryes and their wild relatives. Can. J. Bot. **37,** 657–684

Bozzini, A.; Giorgi, B. (1969): Karyotype analysis in *Triticum.* II. Analysis of *T. araraticum* Jakubz. and *T. timopheevi* Zhuk. and their relationships with other tetraploid wheats. Caryologia **22,** 260–268

Dvořák, J.; McGuire, P.E. (1981): Non-structural chromosome differentiation among wheat cultivars, with special reference to differentiation of chromosomes in related species. Genetics **97,** 391–414

Feldman, M. (1966): Identification of unpaired chromosomes in F_1 hybrids involving *T. aestivum* and *T. timopheevi.* Can. J. Genet. Cytol. **8,** 144–151

Flavell, R. B.; O'Dell, M. (1976): Ribosomal RNA genes on homoeologous chromosomes of groups 5 and 6 in hexaploid wheat. Heredity **37,** 377–385

Flavell, R.B.; O'Dell, M. (1979): The genetic control of nucleolus formation in wheat. Chromosoma **71,** 135–152

Gerlach, W.L. (1977): N-banded karyotypes of wheat species. Chromosoma **62,** 49–56

Gerlach, W.L.; Bedbrook, (1979): Cloning and characterization of ribosomal RNA genes from wheat and barley. Nucleic Acids Res. **7,** 1869–1886

Gerlach, W.L.; Miller, T.E. Flavell, R.B. (1980): The nucleolus organizers of diploid wheats revealed by in situ hybridisation. Theor. Appl. Genet. **58,** 97–100

Gill, B.S.; Kimber, G. (1974): Giemsa C-banding and the evolution of wheat. Proc. Natl. Acad. Sci. USA **71,** 4086–4090

Hutchinson, J.; Chapman, V.; Miller T.E. (1980): Chromosome pairing at meiosis in hybrids between *Aegilops* and *Secale* species: A study by in situ hybridisation using cloned DNA. Heredity **45,** 245–254

Hutchinson, J.; Miller, T.E. (1982): The nucleolar organisers of tetraploid and hexaploid wheats revealed by in situ hybridisation. Theor. Appl. Genet. **61,** 285–288

John, B.; Miklos, G.L.G. (1979): Functional aspects of satellite DNA and heterochromatin. Int. Rev. Cytol. **58,** 1–114

Kawahara, J.; Tanaka, M. (1977): Six chromosome types in *Triticum araraticum* Jakubz. differing with reciprocal translocations. Japn. J. Genet. **52,** 261–267

Kostoff, D. (1937): Chromosome behaviour in *Triticum* hybrids and allied genera. Proc. Indian Acad. Sci. **5,** 231–236

Lilienfeld, F.; Kihara, H. (1934): Genomeanalyse bei *Triticum* u. *Aegilops* V. *Triticum timopheevi.* Cytologia **6,** 87–122

Love, R.M. (1941): Chromosome behaviour in F_1 wheat hybrids. I Pentaploids. Can. J. Research **19,** 351–369

Miller, T.E.; Gerlach, W.L.; Flavell, R.B. (1980): Nucleolus organiser variation in wheat and rye revealed by in situ hybridisation. Heredity **45,** 377–382

Sachs, L. (1953): Chromosome behaviour with species hybrids with *Triticum timopheevi.* Heredity **7,** 49–58

Seal, A.G.; Bennett, M.D. (1981): The rye genome in winter hexaploid triticales. Can. J. Genet. Cytol. **23,** 647–653

Sears, E.R. (1975): A *Triticum timopheevi* chromosome homoeologous to *T. aestivum* chromosome 6B. In: XII Int. Bot. Congr. **II,** p. 512

Upadhya, M.D.; Swaminathan, M.S. (1963): Genome analysis in *Triticum zhukovskyi,* a new hexaploid wheat. Chromosoma **14,** 589–600

Wagenaar, E.B. (1966): Studies on the genome constitution of of metaphase I in hybrids between *T. timopheevi* and *T. durum.* Can. J. Bot. **39,** 81–108

Wagenaar, E.B. (1966): Studies on the genome constitution of *T. timopheevi* II The *timopheevi* complex and its origin. Evolution **20,** 150–164

Zurabishvili, T.G.; Badaev, N.S.; Iordansky, A.B. (1978): Linear differentiation of cereal chromosomes II. Polyploid wheats. Theor. Appl. Genet. **51,** 201–210

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