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Synthesis and cytological characterization of trigeneric hybrids involving durum wheat, *Thinopyrum bessarabicum*, and *Lophopyrum elongatum*

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Summary. In an attempt to transfer genes for salt tolerance and other desirable traits from the diploid wheatgrasses, *Thinopyrum bessarabicum* (2n = 2x = 14; JJ genome) and *Lophopyrum elongatum* (2n = 2x = 14; EE genome), into durum wheat cv 'Langdon' (2n = 4x = 28; AABB genomes), trigeneric hybrids with the genomic constitution ABJE were synthesized and cytologically characterized. C-banding analysis of somatic chromosomes of the A, B, J, and E genomes in the same cellular environment revealed distinct banding patterns; each of the 28 chromosomes could be identified. They differed in the total amount of constitutive heterochromatin. Total surface area and C-banded area of each chromosome were calculated. The B genome was the largest in size, followed by the J, A, and E genomes, and its chromosomes were also the most heavily banded. Only 25.8% of the total chromosome complement in 10 ABJE hybrids showed association, with mean arm-pairing frequency (*c*) values from 0.123 to 0.180 and chiasma frequencies from 3.36 to 5.02 per cell. The overall mean pairing was 0.004 ring IV + 0.046 chain IV + 0.236 III + 0.21 ring II + 2.95 rod II + 20.77 I. This is total pairing between chromosomes of different genomes, possibly between A and B, A and J, A and E, B and J, B and E, and J and E, in the presence of apparently functional pairing regulator *Ph1*. Because chromosome pairing in the presence of *Ph1* seldom occurs between A and B, or between J and E, it was inferred that pairing between the wheat chromosomes and alien chromosomes occurred. The trigeneric hybrids with two genomes of wheat and one each of *Thinopyrum* and *Lophopyrum* should be useful in the production of cytogenetic stocks to facilitate the transfer of alien genes into wheat.

Key words: Chromosome pairing – *Ph1* pairing regulator – Genome analysis – Giemsa C-banding – Alien gene transfer

Introduction

Wide hybridization has contributed significantly to the genetic enrichment of common bread wheat (*Triticum aestivum* L. em Thell.) (Sharma and Gill 1983; Brar and Khush 1986). The wheatgrass genera *Thinopyrum* A. Löve and *Lophopyrum* Á. Löve are rich reservoirs of genes for wheat improvement, although they remain largely untapped. *Thinopyrum bessarabicum* (Savul. & Rayss) Á. Löve (2n = 2x = 14; JJ genome) [= *Agropyron bessarabicum* Savul. & Rayss; *Agropyron junceum* ssp. *boreoatlanticum* Simonet & Guinochet; *Elytrigia bessarabica* (Savul. & Rayss) Dubovik] and *Lophopyrum elongatum* (Host) A. Löve (2n = 2x = 14; EE genome) [= *Agropyron elongatum* (Host) Beauv.; *Thinopyrum elongatum* (Host) D. R. Dewey; *Elytrigia elongata* (Host) Nevski] are particularly valuable sources of genes for barley yellow dwarf virus (BYDV) resistance and several other agronomically desirable traits, including salt tolerance (Wyn Jones et al. 1984; Gorham et al. 1986; Dvořák and Ross 1986; Forster et al. 1987). Because salt-affected lands cover about 950 million hectares of the earth's surface (Shannon 1982), the significance of incorporating desirable genes from the E and J genomes into wheat cannot be overemphasized. Moreover, understanding the relationships between these genomes and their pairing affinity with the wheat genomes will help transfer genes into wheat. Such relationships can be ascertained in the wheat background with the functional *Ph1* pairing regulator that suppresses homoeologous pairing (Jauhar and

Crane 1989; Jauhar 1991). The study reported here constitutes the first report of the production and cytological characterization of trigeneric hybrids combining both E and J genomes with the genomes of durum wheat, *Triticum turgidum* L. (2n = 4x = 28; AABB genomes). The basic information obtained here may help wheat improvement programs.

Diploid hybrids (2n = 2x = 14; JE) between *Th. bessarabicum* and *L. elongatum* are completely sterile. However, the derived amphidiploids (2n = 4x = 28; JJEE) have essentially diploid-like pairing and are largely fertile (Jauhar 1988 a, b). The meiotically regular and reproductively stable amphidiploids were crossed with durum wheat, and 35 tetraploid (2n = 4x = 28; ABJE) hybrids were synthesized. The objectives of this study were: (1) to analyze C-banding patterns of uniformly condensed chromosomes of the A, B, E, and J genomes in the same cellular environment and to locate well-defined markers to identify specific chromosomes; and (2) to assess pairing relationships among the chromosomes of these genomes in the presence of *Ph1*. The ultimate aim would be to improve durum wheat by incorporating in it desirable traits from the E and J genomes, and once a desirable durum wheat is produced, to hybridize it with a superior hexaploid wheat to acquire the D genome. Gross morphological characteristics, diagnostic karyotypic features, and details of chromosome pairing and chiasma frequency in 10 trigeneric ABJE hybrids are reported.

Materials and methods

Several meiotically regular, fertile amphidiploids (2n = 4x = 28; JJEE) between *Thinopyrum bessarabicum* and *Lophopyrum elongatum* (Jauhar 1988 b) were crossed with durum wheat cv 'Langdon', as female parent. Crosses were made both in the field and in the greenhouse in July 1988. The wheat spikes were manually emasculated and pollinated with pollen of the amphidiploids. The pollinated individual florets were sprayed with GA_3 (75 mg l^{-1}) 1 day after pollination. Ten to fifteen days after pollination, the developing embryos were cultured on Orchid Agar (Difco) medium. The seedlings were transferred to pots and grown to maturity in the greenhouse. Of the 35 trigeneric hybrids (2n = 4x = 28; ABJE) 10 are described in this report. Nine hybrids (designated with the letter F) were made on the Evans' Farm near Logan (Utah), whereas 1 (designated with GH) was produced in the greenhouse.

For chromosome count and gross chromosome morphology, somatic chromosomes from root tips were stained with aceto-orcein (Jauhar 1991), which allowed the study of details of primary and secondary constrictions. The C-banding technique of Giraldez et al. (1979) was used to identify individual somatic chromosomes of the A, B, J, and E genomes in the hybrids. The total surface area and total banded area of each chromosome were determined from photomicrographs using a Delta T Area Metre (Delta T Devices, Cambridge, England) (Jauhar 1990). Chromosomes of each genome were cut from each of the eight well-spread metaphase plates (e.g., Fig. 3 a) and arranged in a photoidiogram (e.g., Fig. 3 b). Duplicate transparencies of each photoidiogram were then prepared. Total area of each chromosome was determined by blackening each chromosome in one copy with a marker pen and measuring the opaque area with the area meter. The C-banded regions were measured on the second copy of the same idiogram.

For meiotic analysis of unbanded chromosomes, spikes were fixed in freshly prepared Carnoy's fluid containing approximately 1.5 ml of a saturated aqueous solution of ferric chloride per 100 ml of fixative (Jauhar 1975, 1991). Anthers were squashed in 1.5% acetocarmine. Ring and rod configurations were scored at meiotic metaphase I (MI), and the mean arm-pairing frequency (c) was calculated. Mean chiasma frequencies per cell and per bivalent were also scored. In this study, the terms " chromosome pairing" and "chromosome association" are used interchangeably, although the latter may be the preferred term for wide hybrids of the type described here.

Chromosome banding of meiotic chromosomes can be very useful in assessing the degree of pairing relationship between chromosomes of different genomes. However, in the absence of C-banded or otherwise marked chromosomes, an acceptable – although less reliable – substitute is the fitting of numerical models to the observed configuration frequencies. The relative pairing affinities among chromosomes of the constituent genomes of the trigeneric hybrids were assessed by applying mathematical models for tetraploids: the models of Kimber and Alonso (1981) and Crane and Sleper (1989). The proportions of MI associations due to each pairwise combination of the four genomes are represented in descending order by s_1, s_2, s_3, s_4, s_5, and s_6; s_1 represents the MI associations between the two most closely related genomes (Crane and Sleper 1989).

Results

The trigeneric hybrids (2n = 4x = 28; ABJE) between *T. turgidum* and *Th. bessarabicum*/*Lophopyrum elongatum* amphidiploids are perennial, profusely tillering, and vigorous. There was some variation in tillering and vigor among hybrids. The vegetative morphology of the hybrids was closer to the male amphidiploid parent than to wheat. Spike morphology was intermediate between the two parents, as was the density of spikelets (Fig. 1 a). However, awns in the hybrids were greatly suppressed (Fig. 1 b).

All 10 hybrids had 28 chromosomes in somatic cells (Fig. 2). Most well-condensed somatic metaphase plates had only 2 satellited chromosomes instead of the 6 expected (1 from each of the A and B genomes, and 2 from each of the E and J genomes). The reduction in the number of satellites could be due to amphiplasty. However, it was difficult to determine which satellites were visibly expressed.

C-banding of somatic chromosomes of the A, B, E, and J genomes in the same cellular environment showed distinct banding patterns (Fig. 3 a). Figure 3 b shows a photoidiogram of chromosomes of the four genomes; all of the 28 chromosomes are from the same cell (shown in Fig. 3 a). The chromosomes of the E and J genomes (Table 1) are numbered according to Endo and Gill (1984), and their numbering does not reflect their homoe-

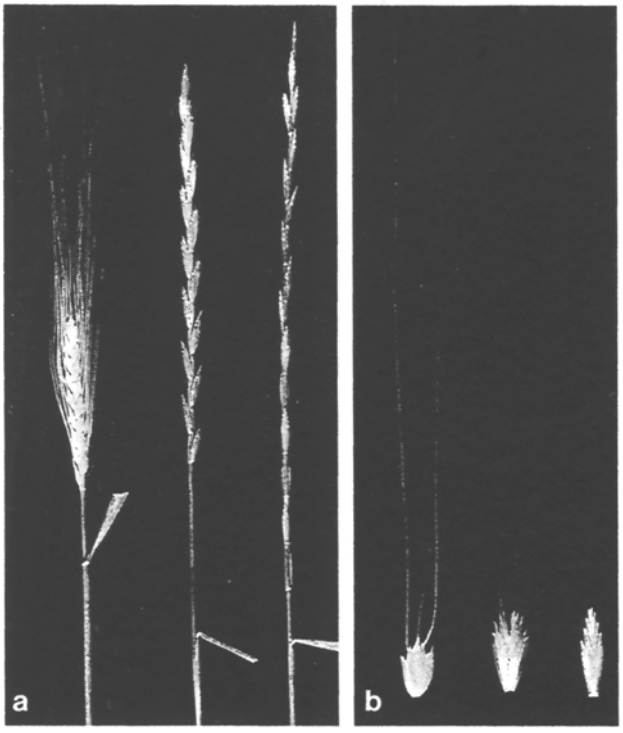

Fig. 1 **a** Spike morphology of the female parent, durum wheat cv 'Langdon' (*left*), trigeneric ABJE hybrid (*center*), and the male parent, *Thinopyrum bessarabicum*/*Lophopyrum elongatum* amphidiploid JJEE (*right*). Note intermediate morphology of the hybrid; awnedness of wheat is highly suppressed. **b** Spikelets of Langdon (*left*), trigeneric hybrid (*center*), and *Th. bessarabicum*/*L. elongatum* amphidiploid (*right*). Note short awns in the hybrid

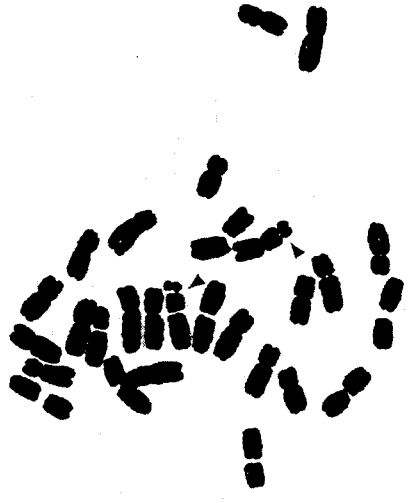

Fig. 2. Twenty-eight somatic chromosomes of the ABJE hybrid. Note that only two satellited chromosomes are noticeable (*arrows*); the remaining four satellites are visibly suppressed

Table 1. Total surface area and C-banded area of the A-, B-, E-, and J-genome chromosomes at somatic metaphase in trigeneric hybrids (ABJE) between *Triticum turgidum* (AABB), *Thinopyrum bessarabicum* (JJ), and *Lophopyrum elongatum* (EE)

Chromosome	Area in arbitrary units[a]		% C-banded area
	Total area	C-banded area	
A-genome chromosomes			
1A	1,168	210	17.98
2A	1,885	465	24.67
3A	2,136	541	25.33
4A	2,108	875	41.51
5A	1,892	355	18.76
6A	1,471	602	40.92
7A	1,573	289	18.37
Total	12,233	3,337	27.28
B-genome chromosomes			
1B	2,465	1,745	70.79
2B	2,136	1,043	48.83
3B	2,796	1,811	64.77
4B	1,986	1,450	73.01
5B	2,507	1,684	67.17
6B	2,562	1,662	64.87
7B	2,160	1,545	71.53
Total	16,612	10,940	65.86
E-genome chromosomes			
Ea	1,646	371	22.54
Eb	1,670	434	25.99
Ec	1,800	527	29.28
Ed	1,694	438	25.86
Ee	1,578	375	23.76
Ef	1,753	490	27.95
Eg	1,592	479	30.09
Total	11,733	3,114	26.54
J-genome chromosomes			
Ja	1,985	646	32.54
Jb	1,927	389	20.19
Jc	2,287	539	23.57
Jd	2,245	274	12.20
Je	2,178	275	12.63
Jf	2,330	654	28.07
Jg	2,046	509	24.88
Total	14,998	3,286	21.91

[a] Average of eight cells

Note: Chromosomes of the E and J genomes are not numbered according to their homoeologous relationships with wheat. They are arranged according to Endo and Gill (1984). The designations 4A and 4B follow the recommendations of the Business Meeting of the 7th Int. Wheat Genet Symp, Cambridge, England, July 1988

ologous relationships with wheat. Thus, 1E in Fig. 3a is Ea of Endo and Gill (1984), 2E is Eb, and so on; similarly 1J is Ja, 2J is Jb, and so on. All individual chromosomes could be identified by their characteristic C-bands. The chromosomes of the A and B genomes were easily identified. The chromosomes of the J genome were characterized by one or two prominent telomeric bands and virtually no interstitial bands (Fig. 3b). In contrast, the

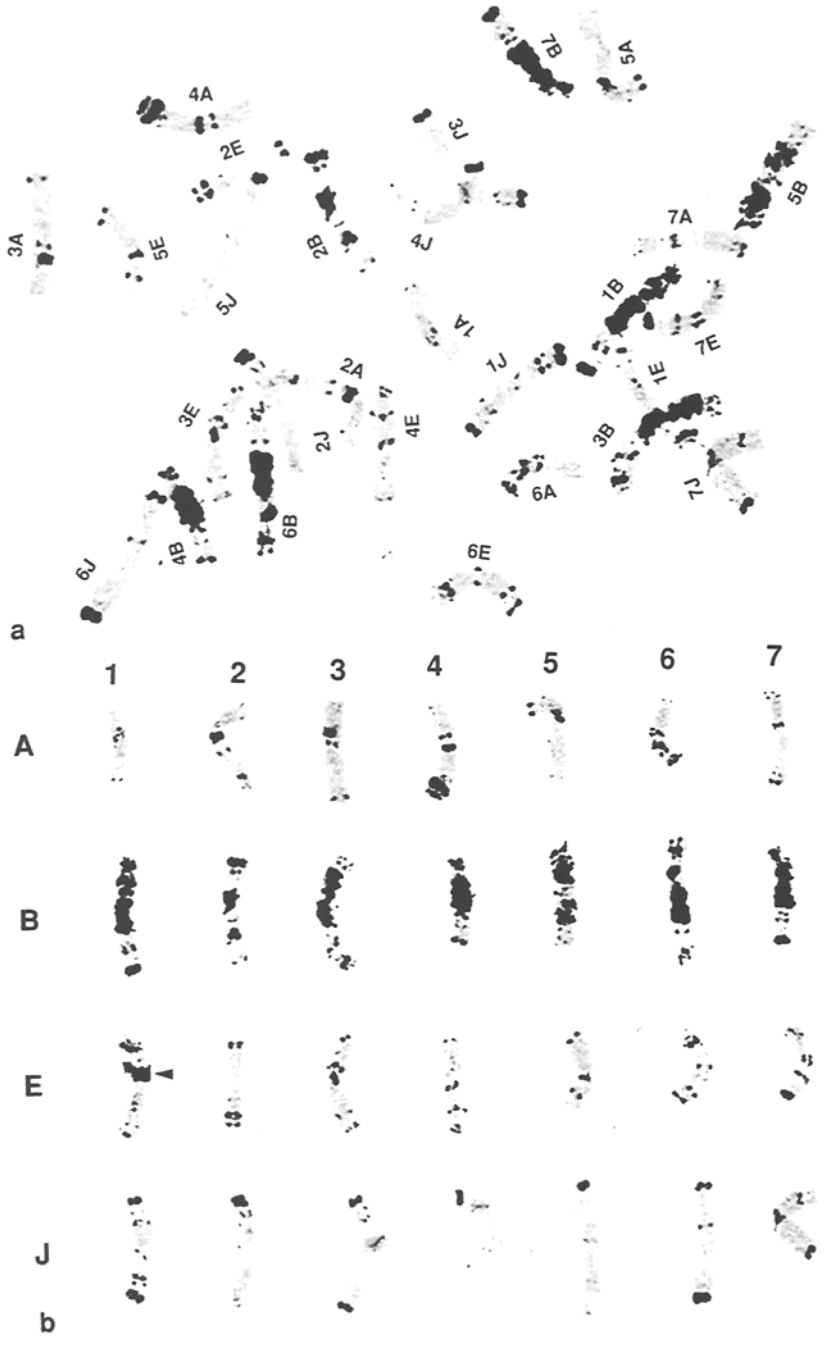

Fig. 3a, b. C-banded somatic chromosomes of the trigeneric ABJE hybrid. Note that each of the 28 chromosomes can be identified on the basis of its diagnostic banding pattern. (For the sake of convenience, chromosomes of each genome are numbered from 1 to 7.) The numbering of chromosomes of the E and J genomes does not relate to their homoeology with wheat chromosomes. They are numbered according to Endo and Gill (1984), *1E* being Ea, *2E* being Eb, *1J* being Ja, *2J* being Jb, and so on (see Table 1). The thick dark region on chromosome 1E is due to an overlap (*arrow*). **a** Twenty-eight chromosomes in a somatic metaphase cell in the same cellular environment. Every chromosome of the A, B, E, and J genomes is identified. **b** Photoidiogram of 28 chromosomes, all from the metaphase cell in **a**. Note the chracteristic bands of different chromosomes and the marked differences in the size and the banding pattern of the J- and E-genome chromosomes

E-genome chromosomes had either small or no terminal bands, but several interstitial bands.

Total surface area and the C-banded area of each of the chromosomes of the four genomes are given in Table 1. The B genome was the largest, followed by J, A, and E; B was 10.76% larger than J, J was 22.60% larger than A, and A was 4.26% larger than E. B was also the most heavily banded genome; nearly two-thirds of the surface area was C-banded (Table 1, Fig. 3b). Chromosome 3B had the largest total surface area, followed by 6B, 5B, 1B, 7B, 2B, and 4B.

Chromosome pairing and chiasma frequency in PMCs of 10 hybrids are given in Table 2, and representative cells are shown in Figs. 4a-f. A large proportion of the chromosome complement remained unpaired, resulting in *c* values of only 0.123–0.180 and chiasma frequencies of 3.36–5.02. In a total of 517 PMCs, only 25.8% of the complement showed chiasmatic association, limited mostly to rod bivalent formation. Some of the rod bivalents were distinctly heteromorphic (Figs. 4b, f) and tended to undergo precocious disjunction. Some of the trivalents (Fig. 4f) and quadrivalents (Fig. 4d) were also

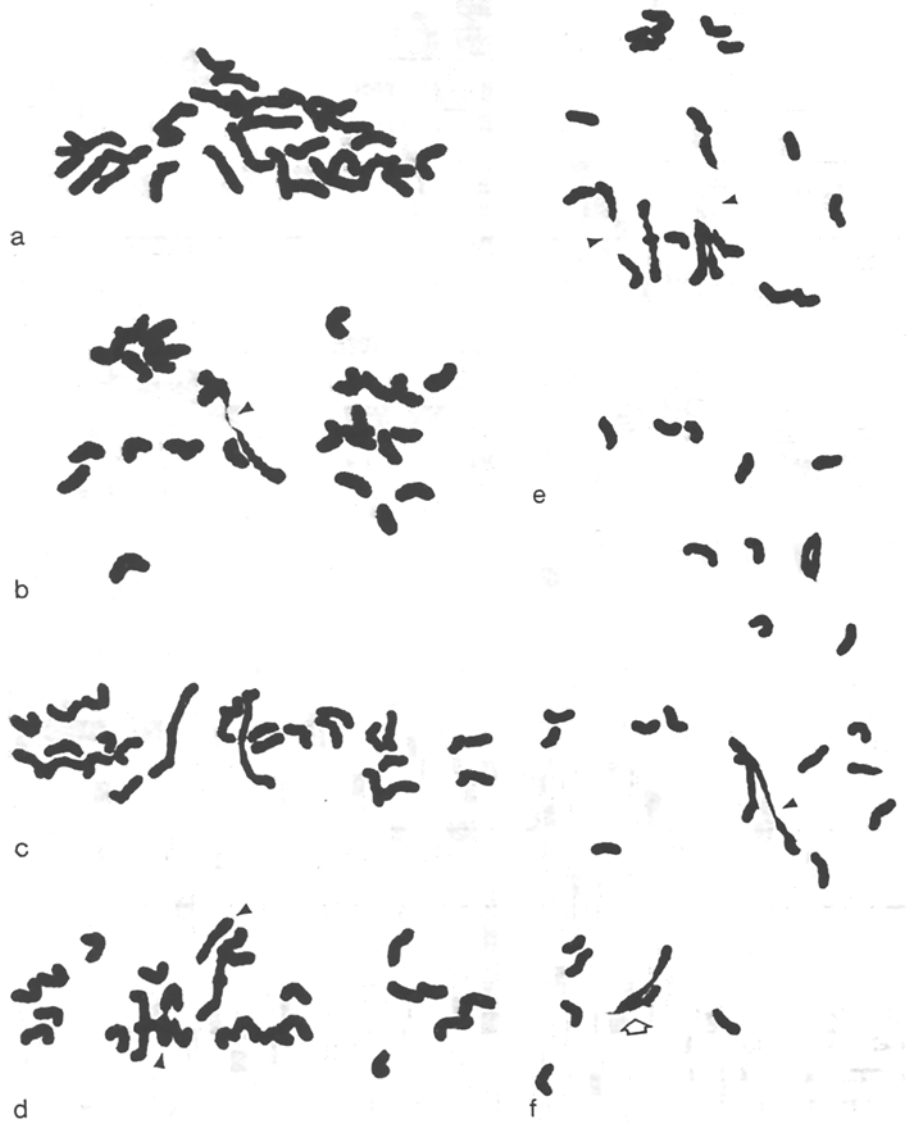

Fig. 4a–f. Chromosome association in representative PMCs of the trigeneric hybrids ($2n=4x=28$; ABJE genomes). Intergenomic pairing often produces heteromorphic configurations. **a** Early metaphase I with 28 I. Note total absence of pairing among chromosomes of the A, B, E, and J genomes. **b** Metaphase I with 1 II + 26 I. Note conspicuous heteromorphy of the rod bivalent (*arrow*). **c** Metaphase I with 2 rod II + 24 I. Note peculiar rods. **d** Metaphase I showing 1 IV + 2 rod II + 20 I. Note heteromorphy of the quadrivalent (marked by *arrows*). Two univalents overlap with one rod bivalent. **e** Metaanaphase I showing 1 III + 3 rod II + 19 I. Note that two rods have already disjoined (*arrows*). **f** Metaphase I with 1 III + 1 ring II + 2 rod II + 19 I. Note the heteromorphic trivalent (open arrow) and a heteromorphic rod bivalent (*solid arrow*)

heteromorphic and probably involved intergenomic chromosome pairing. The hybrids had indehiscent anthers, although pollen stainability ranged from 5% to 14%. They may have some female fertility to facilitate their backcrossing to wheat.

It is difficult to assess the degree of association between chromosomes of any two genomes in the ABJE hybrids. Only 25.8% of the complement paired homoeologously, which is the total pairing between chromosomes of different genomes, possibly of A and B, A and J, A and E, B and J, B and E, and J and E. The application of mathematical models to meiotic data in 9 hybrids (all those listed in Table 2, except F88-123-12) produced varied results because the c values were very low. On the basis of the Kimber-Alonso (1981) models, 4 hybrids (F88-122-1a, F88-123-3a, F88-124-3, and F88-124-5) conformed best to a 2:2 structure with x between 0.799 and 0.843, while the remaining 5 fitted a 2:1:1 structure with x between 0.796 and 0.972. Under the Crane-Sleper (1989) model, there was considerable variation in s_1 through to s_6. Two hybrids (F88-123-3a and F88-124-3) reached a 4:0 solution in all acceptably close fits, whereas all the remaining hybrids approached 2:1:1 solutions. However, numerical analysis of the sum of the 10 hybrids revealed a 2:1:1 genomic structure.

Discussion

The pioneering work of Sears (1956), in which a chromosome segment carrying a leaf-rust resistance gene was transferred from *Aegilops umbellulata* into common

Table 2. Chromosome pairing in trigeneric hybrids (ABJE) involving *Triticum turgidum* (AABB), *Thinopyrum bessarabicum* (JJ), and *Lophopyrum elongatum* (EE)

Hybrid[a]	Chromosome number 2n	Number of cells scored	Mean and range of chromosome configurations at metaphase I											Chiasma frequency	
			IV			III			II			I	*c*		
			Ring	Chain	Total	Fry. pan	Chain	Total	Ring	Rod	total			Per cell	Per II
F88-122-1a	28	50	–	0.02 (0-1)	0.02 (0-1)	–	0.26 (0-2)	0.26 (0-2)	0.10 (0-1)	3.06 (0-7)	3.16 (0-7)	20.82 (14-28)	0.137	3.60 (0-8)	1.03 (1-2)
F88-122-18	28	50	–	0.14 (0-2)	0.14 (0-2)	–	0.16 (0-1)	0.16 (0-1)	0.28 (0-2)	2.56 (0-6)	2.84 (0-7)	21.30 (14-28)	0.138	3.65 (0-9)	1.22 (1-2)
F88-122-25a	28	50	0.02 (0-1)	0.02 (0-1)	0.04 (0-1)	0.02 (0-1)	0.18 (0-1)	0.20 (0-1)	0.54 (0-2)	2.70 (0-5)	3.24 (0-6)	20.76 (16-28)	0.154	4.32 (0-7)	1.17 (1-2)
F88-123-3a	28	50	–	0.02 (0-1)	0.02 (0-1)	–	0.22 (0-2)	0.22 (0-2)	0.02 (0-1)	2.90 (0-6)	2.92 (0-6)	21.42 (16-28)	0.123	3.44 (0-7)	1.01 (1-2)
F88-123-6	28	42	–	0.05 (0-1)	0.05 (0-1)	–	0.26 (0-1)	0.26 (0-1)	0.36 (0-2)	3.31 (0-6)	3.67 (0-6)	19.69 (16-28)	0.168	4.69 (0-8)	1.10 (1-2)
F88-123-12	28	25	0.04 (0-1)	0.08 (0-1)	0.12 (0-1)	–	0.08 (0-1)	0.08 (0-1)	–	2.92 (0-5)	2.92 (0-5)	21.44 (28-28)	0.124	3.36 (0-5)	1.00 (1-2)
F88-124-3	28	100	–	0.03 (0-1)	0.03 (0-1)	–	0.23 (0-2)	0.23 (0-2)	0.06 (0-1)	2.92 (0-8)	2.98 (0-8)	21.23 (12-28)	0.128	3.59 (0-9)	1.02 (1-2)
F88-124-5	28	50	–	0.04 (0-1)	0.04 (0-2)	–	0.32 (0-2)	0.32 (0-2)	0.32 (0-2)	3.64 (0-7)	3.96 (0-7)	18.96 (11-28)	0.180	5.02 (0-9)	1.08 (1-2)
F88-152	28	50	–	0.04 (0-1)	0.04 (0-1)	–	0.26 (0-2)	0.26 (0-2)	0.28 (0-2)	2.62 (0-5)	2.90 (0-5)	21.26 (17-28)	0.136	3.86 (0-7)	1.10 (1-2)
GH88-164	28	50	–	0.06 (0-1)	0.06 (0-1)	0.02 (0-1)	0.28 (0-1)	0.30 (0-1)	0.18 (0-1)	2.98 (0-6)	3.16 (0-6)	20.54 (13-28)	0.147	4.14 (0-8)	1.06 (1-2)
Mean of 10 hybrids	28	517	0.004	0.046	0.050	0.004	0.232	0.236	0.21	2.95	3.16	20.77	0.143	3.96	1.07

[a] F, Evans' Farm; GH, Greenhouse

wheat, heralded an era of utilization of wild gene resources by chromosomal manipulation (Brar and Khush 1986; Khush and Brar 1988). The E genome of *Lophopyrum* and J genome of *Thinopyrum* have been separately incorporated into durum wheat (Jenkins and Mochizuki 1957; Jauhar 1991). However, the present study reports the simultaneous addition of both genomes to durum wheat, thus making it possible to study the karyotypic features and pairing relationships among chromosomes of the A, B, E, and J genomes in the same cellular environment in the trigeneric ABJE hybrids.

The fact that all of the 10 hybrids studied had 28 chromosomes shows the meiotic stability of the parental *Th. bessarabicum*/*L. elongatum* amphidiploids (JJEE; 2n=4x=28), which is consistent with earlier reports (Jauhar 1988a, b). The C-banding analysis confirmed that the trigeneric hybrids had 7 chromosomes from each of the A, B, E, and J genomes; each chromosome could be identified by its diagnostic banding pattern. The A and B genomes of wheat have been shown to be distinct by several workers (Gill 1987). Individual chromosomes of the E and J genomes also differed in the amount and distribution of constitutive heterochromatin (Table 1), which indicate possible differences in their biochemical organization. The E and J genomes have been shown to be distinct, homoeologous genomes (Jauhar 1988a, 1990). The unique banding patterns of the 28 chromosomes will be useful in identifying the whole or recombinant chromosomes in the hybrid progeny. The value of C-banding as a tool to identify wheat-rye translocations has been demonstrated (Gill and Kimber 1977; Lukaszewski and Gustafson 1983).

The hybrids afforded an opportunity to study size differences among somatic chromosomes of the A, B, E, and J genomes in the same metaphase cell, where they underwent the same degree of condensation; there is no allocycly between chromosomes of these genomes. The relative sizes of chromosomes may provide insights into the possible donors of different genomes to polyploids and aid phylogenetic studies (Nishikawa 1970; Nishikawa and Furuta 1979; Furuta et al. 1986; Flavell et al. 1987). The B genome is the largest and the most heavily banded of the four genomes (Table 1). However, because the C-banded heterochromatic regions generally appear broader than the euchromatic regions of chromosomes, the B genome's large size in the present study may

reflect this "error," i.e., chromosome size was based on both length and breadth, instead of length alone as in previous studies. Thus, the B genome (of durum wheat) was 10.76% larger than J, 35.8% larger than A (of durum wheat), and 41.58% larger than E (Table 1). Gill (1987) found that in hexaploid bread wheat var 'Chinese Spring', the B genome was 10.9% longer than the A genome. Sears (1954) measured chromosomes at meiosis and found that the B genome was 15.15% longer at metaphase I and 21.68% longer at telophase II than the A genome. However, the measurement error at meiotic stages may exceed that at somatic metaphase.

In the durum complement, chromosome 3B was the largest, followed by 6B, 5B, 1B, 7B, 2B, and 4B. Sears (1954) ranked the B-genome chromosomes as 3B>2B>5B>6B>1B>7B>4B at metaphase I and 3B>5B>2B>1B>6B>4B>7B at telophase II. However, Gill's (1987) ranking was 3B>2B>6B>7B>5B>4B>1B. In durum, the ranking of A-genome chromosomes was 3A>4A>5A>2A>7A>6A>1A, again somewhat different than how Sears (1954) or Gill (1987) ranked the A-genome chromosomes of 'Chinese Spring'.

The fact that only 25.8% of the total chromosome complement in the 10 ABJE hybrids associated (limited largely to rod bivalent formation, Table 2) shows low homology among chromosomes of the constituent genomes, although some intergenomic pairing must have occurred. Heteromorphic bivalents, trivalents, and quadrivalents probably resulted from intergenomic pairing. There was probably little if any intragenomic (nonhomologous) pairing, although autosyndetic pairing can occur in monoploids, where chromosomes have no other synaptic choice.

The observed homoeologous pairing occurred in the presence of one dose of an apparently functional *Ph1*, which normally suppresses pairing between homoeologues. With unmarked chromosomes, it is difficult to determine the amount of pairing between any two genomes. Chromosomes of the A and B genomes show very little pairing in polyhaploids of durum wheat (Jauhar 1991). Moreover, only 13.67% of the complement of an ABJ hybrid between durum wheat and *Th. bessarabicum* shows association (Jauhar 1991). Therefore, the additional pairing in the ABJE hybrids was probably caused by the E genome. The 7 chromosomes of the E genome show close genetic correspondence to the seven homoeologous groups of common bread wheat (Dvořák 1980) and are probably also homoeologous to the chromosomes of the J genome (Jauhar 1990). Some pairing occurs between chromosomes of A and J, and/or B and J, in the presence of *Ph1* in the ABJ hybrid (Jauhar 1991); the additional pairing in the ABJE hybrids probably involved chromosomes of J and E, A and E, and/or B and E, assuming that *Ph1* is equally functional in these hybrids. However, the E genome has certain genes that either promote or suppress homoeologous pairing (Dvořák 1987; Charpentier et al. 1988). Thus, the haploids of 'Chinese Spring' with added telosome 5EL, either in the monotelosomic or ditelosomic state, had more chiasmata per cell than euhaploids of 'Chinese Spring' (Dvořák 1987). The simultaneous presence of promoters and suppressors in the balanced genome of diploid *L. elongatum* probably has no overall effect on chromosome pairing. The low level of pairing in the ABE hybrids between *L. elongatum* and durum wheat (Jenkins and Mochizuki 1957; Mujeeb-Kazi and Rodriguez 1981) is consistent with this hypothesis[1]. In these hybrids, the formation of only 0.3–2.6 bivalents indicates that the E genome did not counteract the effect of *Ph1*. Because the chromosomes of A and B genomes seldom pair in the presence of *Ph1* (Jauhar 1991), the formation of 2.6 bivalents in the ABE hybrids (Jenkins and Mochizuki 1957) would suggest some pairing of the chromosomes of A and B with those of E.

Although some pairing probably occurs between chromosomes of the A and J, B and J, A and E, and B and E genomes, the amount of pairing cannot be quantified in the absence of banded chromosomes. This pairing between the wheat and alien chromosomes, albeit low, is a welcome feature from the breeding standpoint. Chromosomes of the J and E genomes do not pair in the presence of *Ph1*. In the AABBDDJE hybrids derived by crossing 'Chinese Spring' wheat/*Th. bessarabicum* (AABBDDJJ) and 'Chinese Spring' wheat/*L. elongatum* (AABBDDEE) amphidiploids (Forster and Miller 1989), the homologous chromosomes of wheat consistently paired to form 21 bivalents (mostly rings), but chromosomes of the J and E genomes remained as 14 univalents. Because *Ph1* seems to be functional in the ABJE hybrids also (even though one dose of *Ph1* in these hybrids may not be as effective as two doses in the AABBDDJE hybrids), it may be inferred that chromosomes of the J and E genomes probably show little pairing with each other (Jauhar and Bickford 1989), although they might show some pairing with chromosomes of the A and B genomes.

Mathematical models (Kimber and Alonso 1981; Crane and Sleper 1989) can help assess the pattern of genomic affinity in hybrids. These models allow the calculation of similarities between genomes as reflected in the proportions of MI associations due to each possible pairwise combination of genomes. However, with such low *c* values, the meiotic configurations (ring II, III, chain IV, and ring IV) that bear the information about the shape of genomic structure are infrequent (Table 2) and, therefore, the solutions to any numerical model are only suggestive, not definitive.

[1] It may be noted that monosomic additions of *L. elongatum* chromosomes to hexaploid bread wheat also show low pairing (Dvořák and Knott 1974).

Under the Kimber-Alonso (1981) and the Crane-Sleper (1989) models, most hybrids approached the 2:1:1 pattern of genomic affinity, although s_1, s_2, s_3, s_4, s_5, and s_6 (representing MI associations between different genomic combinations, possibly between A and B, A and J, A and E, B and J, B and E, and J and E; in no particular order) varied considerably. Moreover, pairing was only marginally preferential. It is difficult to ascertain which two genomes, if any, were the most similar in the presence of *Ph1*. It is probably not the A and B genomes. Chromosomes of the J and E genomes show substantial pairing in diploid hybrids (Jauhar 1988a), but they fail to pair in the presence of *Ph1* (Forster and Miller 1989). Therefore, the J and E genomes also cannot be considered to be the closest in terms of pairing affinity unless *Ph1* is somehow disabled or weakened due to the presence of alien genomes. Chromosomes of other distinct genomes (e.g., A and B, and A and D of wheat) do show good pairing in diploid hybrids, but seldom pair in the presence of *Ph1* (Sears 1941; Jauhar 1990).

The distinctiveness of the J and E genomes, at least in terms of the pairing behavior of their chromosomes in the presence of *Ph1*, and their low pairing with the chromosomes of the A and B genomes have a bearing on the strategy to be adopted to transfer desirable genes from *Thinopyrum* and *Lophopyrum* into wheat. The use of the *ph1c* mutant of durum wheat should help promote intergenomic pairing and, hence, intergeneric gene transfers. However, it is significant that a certain degree of pairing occurs between wheat chromosomes and alien chromosomes even in the presence of *Ph1* in the trigeneric hybrids. This pairing could facilitate intergeneric transfer of characters through a series of backcrosses onto wheat, although it is going to be a lengthy procedure. The diagnostic banding patterns of each of the 28 chromosomes should facilitate the identification in the hybrids or their derivatives of recombinant chromosomes or any translocation products that may arise due to spontaneous interchanges or homoeologous pairing. Thus, the synthesis of trigeneric hybrids with two genomes of wheat and one each of *Thinopyrum* and *Lophopyrum* is an important first step in the production of cytogenetic stocks to facilitate the transfer of alien genes into wheat.

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