Theor Appl Genet (1990) 80: 523–536



# Multidisciplinary approach to genome analysis in the diploid species, *Thinopyrum bessarabicum* and *Th. elongatum* (*Lophopyrum elongatum*), of the Triticeae *

**P. P. Jauhar**

USDA-ARS, Forage and Range Research, Utah State University, Logan, UT 84322-6300, USA

Received February 15, 1990; Accepted March 23, 1990
Communicated by G. S. Khush

**Summary**. The J and E genome species of the Triticeae are invaluable sources of salt tolerance. The evidence concerning the phyletic relatedness of the J genome of diploid *Thinopyrum bessarabicum* and the E genome of diploid *Th. elongatum* (=*Lophopyrum elongatum*) is discussed. Low level of chromosome pairing between J and E at different ploidy levels, suppression of J-E pairing by the *Ph1* pairing regulator that inhibits homoeologous pairing, complete sterility of the diploid hybrids (JE), karyotypic divergence of the two genomes, differences in total content and distribution of heterochromatin along their chromosomes, and marked differences in gliadin proteins, isozymes, 5S DNA, and rDNA indicate that J and E are distinct genomes. Well-defined biochemical markers have been identified in the two genomes and may be useful in plant breeding. The level of distinction between J and E is comparable to that among the universally accepted homoeologous genomes A, B, and D of wheat. Therefore, the J and E genomes are homoeologous and not homologous, although some workers continue to call them homologous. The previous workers' data on chromosome pairing in diploid hybrids and/or karyotypic differences in the conventionally stained chromosomes do not provide sufficient evidence for the proposed merger of J and E genomes (and, hence, of the genera *Thinopyrum* and *Lophopyrum*) specifically and for establishing genome relationships generally. Extra precautions should be exercised before changing the designation of an established genome and before merging two genera. A uniform, standardized system of genomic nomenclature for the entire Triticeae is proposed, which should benefit cytogeneticists, plant breeders, taxonomists, and evolutionists.

**Key words**: Chromosome pairing – *Ph1* pairing regulator – Isozymes – Gliadins – Biochemical markers

## Introduction

Triticeae is the most important tribe of the family Poaceae. It includes three major cereal crops, wheat, barley, and rye. It is also comprised of several forage grasses that are important sources of genes for wheat improvement. Löve (1982, 1984) delimited genera of this tribe on the basis of their genomic constitution. *Thinopyrum* was established as a new genus to include J-genome-containing species and *Lophopyrum* for E-genome species. Thus, J and E genomes were assigned to these well defined genera. Dewey (1984) largely adopted Löve's (1984) system. However, defining a genus by a specific genome has engendered some controversy (Baum et al. 1987; Kellogg 1989; Seberg 1989) and may not always be practicable. Dewey (1984) considered the J genome of *Thinopyrum* and the E genome of *Lophopyrum* to be closely related and suggested that the two genomes and the two genera should be combined. He used the designation J for both genomes. This merger was based mainly on the observed high frequency of trivalents (mean = 2.76 III per cell; Cauderon and Saigne 1961) in triploid hybrids between tetraploid *Thinopyrum junceiforme* and diploid *Lophopyrum elongatum*, and on the presumed karyotypic similarity (Heneen and Runemark 1972) of J and E genomes.

*Thinopyrum* Löve is an important genus closely allied to the wheat genus *Triticum* L. Dewey's (1984) genomic classification of the tribe Triticeae includes only two diploid species in this genus: *Th. bessarabicum* (2n=2x=14; JJ genome) and *Th. elongatum* (=*Lophopyrum elongatum*) (2n=2x=14; EE). (Some common synonyms of the diploid species are given under 'Materials and

* Cooperative investigations of the USDA-Agricultural Research Service and the Utah Agricultural Experiment Station, Logan, UT 84322, USA. Approved as Journal Paper no. 3832

methods'). Both J and E genomes are important sources of genes for agronomically desirable traits, particularly salt tolerance (Dvořák and Ross 1986; Forster et al. 1987). Information on the degree of relatedness between J and E genomes may, therefore, be important to plant breeders trying to transfer genes from these genomes into wheat. Relationships between the species containing J and E genomes have been investigated by studying chromosome pairing in hybrids between naturally occurring polyploid species and in hybrids between diploid and naturally occurring polyploid species (Cauderon and Saigne 1961; Dvořák 1981; McGuire 1984; Pienaar et al. 1988; Wang and Hsiao 1989). These workers concluded that the J and E genomes are so closely related that they should have the same genomic designation. Therefore, J was changed to $E^J$ by Dvořák (1981), but to $E^b$ by McGuire (1984), so that the original J and E designations were included in the same basic genome symbolized by the letter E. Dewey (1984) retained the designation J for both genomes, arguing that J was the older of the two genome designations, a view essentially endorsed by Pienaar et al. (1988) and Moustakas et al. (1988). Wang (1985) favored the merger of E with J by changing E to $J^e$.

Genome analysis based on the study of chromosome pairing in hybrids between naturally occurring polyploid species is somewhat complicated. Synaptic competition among different genomes that may have been reconstituted (due to prior homoeologous exchanges in the parental complements) can make it difficult to interpret chromosome pairing relationships. Therefore, wherever possible, studying chromosome pairing in hybrids (at different ploidy levels) between diploid species with relatively pure genomes is more useful in assessing genome relationships. Chromosome pairing does not always measure genomic affinity very accurately (Dvořák 1988) and, therefore, a multidisciplinary approach to genome analysis is advisable. Wang (1985) conducted genome analysis based on chromosome pairing in diploid hybrids (JE) between the two diploid species, *Th. bessarabicum* (JJ) and *Th. elongatum* (EE). He observed a mean of 0.01 V + 0.27 IV + 0.27 III + 1.43 ring II + 3.25 rod II + 2.69 I per cell in the diploid hybrids. Based on these meiotic data and karyotypic analysis on conventionally stained mitotic chromosomes of the parental species, Wang concluded that J and E genomes are homologous. Therefore, he merged the two genomes and also supported the merger of *Lophopyrum* (E genome) in the genus *Thinopyrum* (J genome). Analyzing genome relationships in diploid hybrids and using that as a basis for merging established genomes can cause considerable confusion, however.

In this paper, the validity or nonvalidity of genome analysis based on pairing in diploid hybrids is discussed, a multidisciplinary approach to genome analysis is adopted, and the overall problem of deciphering genomic integrity and giving appropriate genomic designation is outlined.

## Materials and methods

Some common synonyms of the diploid species, *Thinopyrum bessarabicum* (2n = 2x = 14; JJ genome) and *Th. elongatum* (2n = 2x = 14; EE genome), are given below.

*Thinopyrum bessarabicum* (Savul. & Rayss) Á. Löve [= *Agropyron bessarabicum* Savul. & Rayss; *Agropyron junceum* ssp. *boreoatlanticum* Simonet & Guinochet; *Elytrigia bessarabica* (Savul. & Rayss) Dubovik; *Elytrigia juncea* ssp. *bessarabica* (Savul. & Rayss) Tzvelev; *Elymus striatulus* Runemark; *Elymus junceus* spp. *bessarabicus* (Savul. & Rayss) Melderis].

*Thinopyrum elongatum* (Host) D. R. Dewey [= *Agropyron elongatum* (Host) Beauv.; *Lophopyrum elongatum* (Host) Á. Löve; *Elytrigia elongata* (Host) Nevski; *Elymus elongatus* (Host) Runemark].

The seed of *Th. bessarabicum* and *Th. elongatum* was kindly supplied by Dr. D. R. Dewey of the USDA Forage and Range Research Laboratory, Logan, UT. Diploid hybrids (2n = 14; JE) between these species, colchicine-induced amphidiploids (2n = 28; JJEE), and a triploid hybrid (2n = 21; JJE) were kindly provided by Dr. R. Wang. Methods of fixation and meiotic analyses described earlier (Jauhar 1975 a, 1988 a) were used. Pollen fertility was determined by their stainability with 1 % cotton blue in lactophenol. Seed set on open-pollinated amphidiploids was determined on an individual spike basis.

The method of Giraldez et al. (1979) was adopted for studying Giemsa C-banding differences between the J and E genomes in the ABJE hybrids, derived by crossing durum wheat (AABB) with *Th. bessarabicum* × *Th. elongatum* amphidiploids (JJEE).

The total area of each chromosome and its banded regions was determined from photomicrographs using a Delta T Area Meter (Delta T Devices, Cambridge, England). Duplicate transparencies of each somatic plate were prepared. The total area of each chromosome was determined by blackening each chromosome in one copy with a marker pen and measuring the opaque areas with the Area Meter. The C-banded regions were measured on the second copy (of the same cell).

To identify genome-specific gliadin (prolamine) markers for use in our breeding programs, two accessions each of diploid *Th. bessarabicum* (MA-96-41-85 and MB-6-16-30) and diploid *Th. elongatum* (MA-95-1-85 and MA-99-56-65) were studied by gel electrophoresis. Native seed gliadins were extracted by the procedure described by Konarev et al. (1981). Twenty-five microliter aliquots of the sample extracts were loaded into the wells of 180 mm × 120 mm × 1.5 mm vertical polyacrylamide gels (pH = 3.2). Separations of 5 ½ h were run in an LKB Model 2001 Vertical Electrophoresis System at 30 mA.

Euphaploids (2n = 3x = 21; ABD genomes) with and without *Ph1* pairing regulator were extracted by crossing wheat cultivars with barley (*Hordeum vulgare* L.). The *ph1b*-euhaploid was produced by crossing *ph1b ph1b* mutant of 'Chinese Spring' with 'Luther' barley; the *Ph1*-euhaploid was derived by crossing normal 'Chinese Spring' with 'Luther'. Chromosome pairing relationships among the A, B, and D genomes were studied both in the presence and in the absence of *Ph1*.

## Results and discussion

### *Pairing in diploid hybrids and genome analysis*

Diploid hybrids contain only two sets of chromosomes and, hence, conditions for preferential pairing do not

**Table 1.** Chromosome pairing in three diploid ($2n=2x=14$) hybrids of perennial Triticeae

| Hybrid | Genomes | Mean and range of chromosome associations | | | | | | $c$ | Ref. |
|---|---|---|---|---|---|---|---|---|---|
| | | IV | III | II | | | I | | |
| | | | | Ring | Rod | Total | | | |
| *Pseudoroegneria spicata* × *Th. bessarabicum* | SJ | 0.14 (0–1) | 0.24 (0–1) | 1.42 (0–4) | 2.77 (0–6) | 4.19 (1–7) | 4.34 (0–9) | 0.47 | Wang 1988 |
| *Th. elongatum* × *P. spicata* | ES ($J^eS$) | – | 0.05 (0–1) | 0.08 (0–2) | 2.27 (0–6) | 2.35 (0–6) | 9.13 (2–14) | 0.18 | Wang 1986 |
| *Th. bessarabicum* × *Th. elongatum* | JE($JJ^e$) | 0.27 (0–2) | 0.27 (0–2) | 1.43 (0–5) | 3.25 (0–7) | 4.68 (1–7) | 2.69 (0–12) | 0.54 | Wang 1985 |

The genomic designations in the parentheses are given by Wang (1985, 1986)

exist. Analyzing chromosome pairing in diploid hybrids is, therefore, somewhat analogous to conducting an experiment without a control; the two genomes have only two options; either to pair or not to pair with each other. Chromosome association under these conditions is not necessarily a function of homology. Chromosomes seem to have an inherent tendency to pair. In the absence of their own homologous partners, they may pair with less related (homoeologous) or even nonhomologous chromosomes, as illustrated by chromosome pairing in numerous monoploids and polyhaploids, e.g., monoploids of barley (Sadasivaiah and Kasha 1971, 1973), monoploids of pearl millet (Powell et al. 1975, Jauhar 1981), and polyhaploids (ABD) of wheat when the pairing regulator is missing or disabled (Riley and Chapman 1958; Kimber and Riley 1963; P.P. Jauhar, O. Riera-Lizarazu, W. G. Dewey, B. S. Gill, C. F. Crane, and J. H. Bennett unpublished results; see also Table 3). And the pairing persists until metaphase I in several cases.

Most cytogeneticists do not rely on chromosome pairing in diploid hybrids as a means of genome analysis. For example, Kimber and Feldman (1987) state that hybrids between diploid species are "essentially useless" for genome analysis. A similar position on diploid analysis is outlined in Jauhar (1988a). In any case, chromosome pairing in diploid hybrids is weak evidence of genomic relationship.

### *Chromosome pairing in some diploid hybrids of perennial Triticeae*

Studying genome relationships based on pairing in diploid hybrids may lead to erroneous conclusions. Table 1, for example, gives chromosome pairing data in three diploid hybrids, SJ, ES, and JE of the Triticeae. The SJ hybrids have almost the same frequency of ring bivalents as the JE hybrids. If this pattern of pairing can be interpreted to show that J and E genomes are homologous (Wang 1985), what does it indicate about the relationship between S and J, which show essentially similar pairing? If J is changed to $J^e$ (Wang 1985), should S be changed to $J^s$? Moreover, if J and E are indeed homologous or very closely related, should they pair very differently with the same parent, *Pseudoroegneria spicata*? If J = E, and J is also equal to S, shouldn't E be equal or nearly equal to S? These examples show the weakness of diploid pairing in genome analysis.

### *Chromosome pairing in diploid hybrids between established homoeologous genomes*

Chromosome pairing relationships among A, B, and D genomes of wheat have been thoroughly studied. Homoeologous relationships among the three genomes were well established by nullisomic-tetrasomic compensation (Sears 1954, 1966). Genetic homoeologies identified by nulli-tetra compensation tests have also been cytologically demonstrated (Riley and Kempanna 1963; Riley and Chapman 1966; Feldman and Avivi 1984). Chromosome pairing in some diploid hybrids between putative progenitors of wheat are given in Table 2. Pairing in AD and AB hybrids (Table 2) is essentially similar to that in JE and SJ hybrids (Table 1). The frequency of ring bivalents between J and E genomes is lower than that between well-accepted homoeologous, distinct genomes A and D, or A and B. The J and E genomes are therefore best considered as distinct genomes. Lower mean arm pairing frequency ($c$) values have also been reported for some AD and AB hybrids, but the examples in Table 2 were selected to show that pairing in diploid hybrids may lead to erroneous conclusions about genome relationships. When a large number of hybrids between various accessions of *Thinopyrum bessarabicum* and *Th. elongatum* are studied, lower $c$ values than recorded in Table 1 may be found. It is therefore advisable to study several accessions whenever possible.

If the data on JE hybrids (Table 1) call for the merger of the two genomes, should the data on AD and AB

**Table 2.** Chromosome pairing in selected diploid hybrids between putative diploid progenitors of breadwheat

| Hybrid | Genomic constitution | No. of cells | IV | III | II | | | I | *c* | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Ring | Rod | Total | | | |
| *Triticum monococcum* × *Aegilops squarrosa* | AD | 50 | 0.08 (0–1) | 0.20 (0–1) | 1.58 (0–4) | 3.28 (0–6) | 4.86 (1–7) | 3.36 (0–10) | 0.506 | Sears 1941 |
| *Ae. speltoides*[a] *ligustica I* × *T. monococcum* | AB | 50 | 0.02 (0–1) | 0.18 (0–2) | 2.44 (0–5) | 3.84 (0–6) | 6.28 (1–7) | 0.82 (0–4) | 0.653 | Sears 1941 |
| *Ae. speltoides*[a] × *Ae. squarrosa* | BD | 50 | – | 0.46 (0–3) | 0.18 (0–2) | 3.28 (1–6) | 3.46 (0–6) | 5.70 (1–10) | 0.326 | Kimber and Riley 1963 |

[a] *Aegilops speltoides* is now believed to have the S genome (Kimber and Feldman 1987), which is entirely different from the S genome of *Pseudoroegneria*. Nevertheless, this may be a source of confusion to Triticeae cytogeneticists and breeders. However, the genome in *Ae. speltoides* is probably the B genome or very close to the B genome of hexaploid breadwheat

**Table 3.** Chromosome pairing in polyhaploids ($2n=3x=21$) with and without *Ph1* and in nulli-*5B* haploids ($2n=3x-1=20$) of breadwheat var. 'Chinese Spring'

| Haploid and genomic constitution | No. of cells | IV | | | III | II | | | I | Xma freq. | *c* | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Ring | Chain | Total | | Ring | Rod | Total | | | | |
| Euhaploid ABD with *Ph1* | 100 | – | – | – | 0.02 | 0.02 | 0.81 | 0.83 | 19.28 | 0.89 | 0.064 | This study |
| Euhaploid ABD without *Ph1* | 50 | 0.04 | 0.08 | 0.12 | 1.16 | 1.54[a] | 2.92 | 4.46 | 8.04 | 9.08 | 0.623 | This study |
| Nullihaploid ABD-5B | 75 | | | 0.02 | 0.86 | 0.96 | 3.20 | 4.16 | 9.02 | 6.90 | 0.493 | Riley and Chapman 1958 |

[a] Banding analysis showed that these ring bivalents were formed between the A and D genomes

hybrids (Table 2) and on ABD triploids (Table 3; see section below) justify the merger of A, B, and D into one genomic designation?

*Chromosome pairing in wheat polyhaploids with and without Ph1 and in 5B nullihaploids*

The A, B, and D genomes in hexaploid wheat are in essentially the same state as those of the original diploids from which they were derived (Riley 1960). However, the affinity between equivalent chromosomes of these homoeologous genomes is suppressed mainly by the genetic activity of the *Ph1* locus on chromosome 5B (Okamoto 1957; Riley and Chapman 1958; Sears and Okamoto 1958; Sears 1976). Therefore, chromosome pairing relationships among A, B, and D can be studied in ABD euhaploids ($2n=3x=21$) in which *Ph1* is disabled, or in nullihaploids ($2n=3x-1=20$) which lack chromosome 5B (Table 3). Clearly, there is very little pairing in ABD euhaploids with *Ph1* intact (Fig. 1 a). In the polyhaploid derived from the mutant *ph1b ph1b*, which lacks the pairing regulator, chiasma frequency per cell increased almost ten fold, and in the nullihaploid it increased almost eight fold.

The application of the Alonso-Kimber (1981) model showed the optimized genomic structure of ABD euhaploid without *Ph1* to be 2:1. The proportions of metaphase I (MI) associations due to each pairwise combination of genomes, represented in decreasing order by $s_1$, $s_2$, and $s_3$ (as used by Crane and Sleper 1989), were 0.749, 0.125, and 0.125, respectively. The value of $s_1$, represents the proportion of MI associations between two most closely related genomes. These genomes are A and D, because our N-banding analysis of meiotic chromosomes showed that most MI associations, i.e., almost 75%, were between A and D genomes. Details will be published elsewhere. The established homoeologous genomes A and D formed several ring bivalents (Fig. 1 b), ranging up to five per cell. These data are consistent with the formation of a high frequency of ring bivalents in AD diploid hybrids (Table 2). It is interesting that some AB diploid hybrids also show very good pairing, almost as good or better than that in AD hybrids (Table 2). However, when conditions for preferential pairing exist, such as in ABD euhaploids without *Ph1*, A and D pair preferentially, indicating that these genomes are closer to each other than either one is to B. These selected exam-

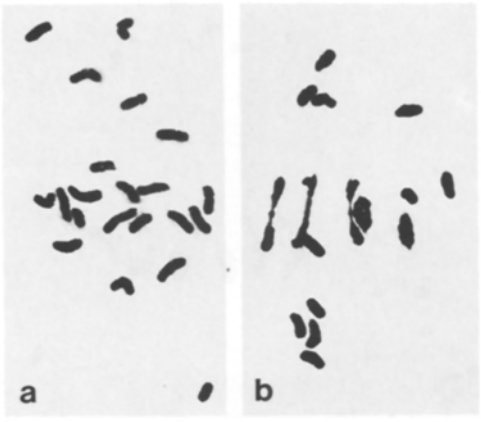


**Fig. 1 a, b.** Chromosome pairing at metaphase I in *Ph1*- and *ph1b*-euhaploids ($2n=3x=21$; ABD) of breadwheat. **a** *Ph1*-haploid showing 21 I; there is no pairing among the A, B, D genomes in the presence of the *Ph1* pairing regulator. **b** *ph1b*-haploid with 2 ring II + 3 rod II + 11 I; note substantial homoeologous pairing in the absence of the pairing regulator. Heteromorphic bivalents are noticeable

ples again show the weakness of diploid pairing as a means of studying genome relationships.

*Is diploid pairing valid for genome analysis?*

Wang (1989) maintains that pairing in diploid hybrids is valid for genome analysis in the perennial Triticeae, but not in the annual Triticeae. Why the principles of cytogenetics and chromosome pairing should apply differently to perennial and annual members of the same tribe is not clear, however. Perhaps the discrepancy is related to the breeding system, but then the perennials and annuals both contain autogamous and allogamous species. Wang has accumulated a large body of published and unpublished data and compared the mean arm binding frequencies ($c$ values) in diploid hybrids in perennial Triticeae with the relative affinities between most closely related genomes ($x$ values) in what he calls corresponding triploids and tetraploids. He found that the two values were "highly positively correlated" and, therefore, concluded that pairing in diploid hybrids is valid for genome analysis.

Wang has in several cases compared synthetic autoallotriploids involving diploid species and the triploids synthesized by crossing diploids with naturally occurring tetraploids. These comparisons may not be valid for the following reasons. (1) It is not certain which genomes are represented in some natural polyploids, because different standards and methods of genome analysis were applied by different researchers. For example, the genomic constitution of tetraploid *Thinopyrum junceiforme* was considered to be $J_1J_1J_2J_2$ by Dewey (1984) and Pienaar et al. (1988). Wang (1989) accepted the genomic formula JJJJ, but later changed it to $JJJ^eJ^e$ (= JJEE) (Wang and Hsiao 1989). The chromosome pairing data of Mujeeb-Kazi et al. (1987) can be interpreted to show that the genomic constitution of *Th. junceiforme* is probably JJJJ, or at least closer to autotetraploidy than to JJEE. (2) Naturally occurring polyploids may have developed a genetic control of chromosome pairing (e.g., Sears 1976; Jauhar 1975a, b). If so, the pairing patterns in synthetic hybrids involving such polyploids may be entirely different than in hybrids obtained by crossing a diploid species and its synthetic autopolyploid, although both hybrids may have the same or similar genomic composition. The polyhaploids derived from natural polyploids must also be used with the same caution. (3) During the course of evolution, naturally occurring polyploids may have undergone homoeologous recombinations between the constituent genomes, which may alter the pattern of chromosome pairing in their hybrids with one another and with their ancestral diploids.

Moreover, Wang (1989) has often compared very distinct genomes such as P and S, S and N, S and H, J and N, J and R, S and R, H and R, etc. Very little pairing occurs between these genomes, either at the diploid or autoallotriploid level. Therefore, data from these combinations could erroneously appear to indicate that genome analysis based on pairing in diploid hybrids is valid. To avoid these problems and to assure valid comparisons, chromosome pairing should be studied not only in diploid hybrids, such as AB, between diploid species AA and BB, but also in autoallotriploids AAB and ABB derived by crossing a synthetic autotetraploid of one species (AAAA or BBBB) with a diploid of the other (BB or AA), and in amphidiploids AABB produced by crossing synthetic autotetraploids (AAAA and BBBB) of the two species. Bivalent frequency in diploid hybrids should then be compared to trivalent frequency in autoallotriploids and quadrivalent (or quadrivalent + trivalent) frequency in the amphidiploids, using the statistical techniques employed by Wang (1989). Diploid pairing may certainly prove valid for genome analysis in some cases, e.g., between *Lolium multiflorum* and *L. perenne*, where the diploid hybrids show high pairing and are fertile (Breese et al. 1975; Jauhar 1975c), but not in others, e.g., between *Thinopyrum bessarabicum* and *Th. elongatum* (Jauhar 1988a). Genome analysis is of paramount importance because scientists in other disciplines (e.g., plant breeders, taxonomists, and evolutionists) may receive guidance from this work. Therefore, genome relationships should not be assessed merely on the basis of pairing in diploid hybrids.

*Use of autoallotriploids and amphidiploids in genome analysis*

The rationale of using autoallotriploids in genome analysis is to create conditions for preferential pairing between

genomes to ascertain their relative affinities. Such conditions are lacking in diploid hybrids and, hence, sound inferences regarding genome relationships cannot be drawn (see also section on wheat polyhaploids above). For example, on the basis of chromosome pairing in diploid hybrids (JE) between *Thinopyrum bessarabicum* (JJ) and *Th. elongatum* (EE), it was concluded that J and E are very closely related (Wang 1985). What is very close? The question of closeness can be addressed by introducing an extra dose of either J or E from the diploid parent into the same cellular environment. Chromosome pairing can then be studied in JJE and JEE autoallotriploids as well as in JJEE amphidiploids [1]. The degree of preferential pairing in these hybrids will provide another means of evaluating the degree of closeness or differentiation between J and E. In the JJE triploid, for example, an extra dose of J genome serves as a control for measuring the pairing relationship between J and E. Jauhar (1988a) not only analyzed chromosome pairing in JE hybrids, but also in a JJE autoallotriploid and several JJEE amphidiploids. The diploid hybrids had a mean association of < 0.01 V + 0.30 IV + 0.28 III + 1.88 ring II + 3.10 rod II + 1.97 I with 8.36 chiasmata per cell, and were completely sterile. In several cells, chromosomes were loosely associated, which Jauhar (1988a) called chromosome 'dating' rather than pairing. Such loose 'pairing' may not lead to genetic recombination and chiasma formation (Orellana 1985).

The JJE triploid had a mean configuration of < 0.01 VI + 0.06 IV + 1.53 III + 4.27 ring II + 1.19 rod II + 5.20 I with 13.45 chiasmata per cell (Jauhar 1988a). Thus, chromosomes of the duplicated genome JJ showed preferential pairing and formed mostly ring bivalents with two or three chiasmata each, whereas chromosomes of the E genome remained largely unpaired und were characteristically small (Fig. 2a and b); in 250 pollen mother cells, 49 showed 7 II + 7 I (Fig. 2a), and as many as 77 had 1 III + 6 II + 6 I (Fig. 2b). If J and E were homologous or 'essentially homologous' (Wang and Hsiao 1989), such cells showing complete or very high preferentiality of pairing would not be observed. The degree of preferential pairing was even stronger in the JJEE amphidiploids, which had predominantly bivalent pairing with up to 14 ring bivalents in some cells, and were largely fertile. Figure 3a and b, for example, shows complete preferentiality of pairing and normal meiosis. The mean pairing was 0.02 VI + 0.55 IV + 0.26 III + 8.11 ring II + 3.64 rod II + 1.42 I, with a total of 22.41 chiasmata per cell. The JJ and EE genomes generally maintained their meiotic integrity in the amphidiploids whose chiasma frequency was similar to the sum total of that of the parental complements. Based on this pattern of chromosome pairing in hybrids at different ploidy levels as well as the sterility of the diploid hybrids, Jauhar (1988a) concluded that J and E are distinct, homoeologous genomes.

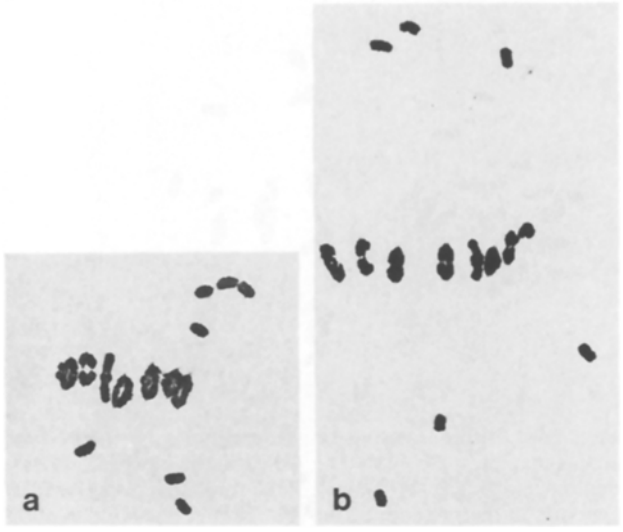


**Fig. 2a, b.** Chromosome pairing at metaphase I in autoallotriploid hybrids ($2n=3x=21$; JJE) between diploid *Thinopyrum bessarabicum* (JJ) and diploid *Th. elongatum* (EE). **a** 6 ring II + 1 rod II + 7 I; note complete preferential pairing between J-J chromosomes; and unpaired, small E-genome chromosomes. **b** 1 III + 5 ring II + 1 rod II + 6 I; note high preferentiality of J-J pairing, and small E-genome univalents

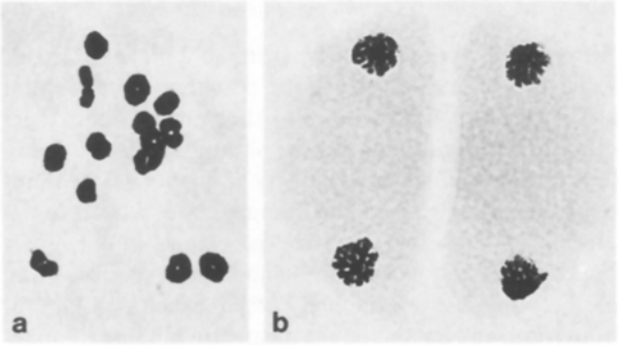


**Fig. 3a, b.** Diploid-like meiosis in the amphidiploids ($2n=4x=28$; JJEE) between diploid *Th. bessarabicum* and diploid *Th. elongatum*. **a** Metaphase I with 13 ring II + 1 rod II; note complete preferentiality of pairing. **b** Telophase II reflecting regular divisions I and II of meiosis

### *Genomic differentiation in relation to stability of amphidiploids*

All seven amphidiploids (2n = 28; JJEE) studied showed essentially diploid-like pairing (Jauhar 1988a). Their pol-

[1] For studying chromosome pairing relationships, the best way to synthesize autoallotriploids will be by crossing a synthetic autotetraploid of one species with the diploid of the other. Similarly, amphidiploids JJEE should be synthesized by crossing colchicine-induced autotetraploids of the two species (JJJJ and EEEE)

len fertility varied from 75% to 92%, whereas the seed fertility ranged between 52% and 67.5%. This level of fertility for raw synthetic amphidiploids can be considered high.

The fertility of an amphidiploid will depend upon the degree of differentiation of the constituent genomes and, hence, on the degree of pairing in the diploid hybrid from which the amphidiploid is derived. There is generally a close inverse relationship between 2x pairing and 4x fertility (Sears 1941) and between 2x chiasma frequency and 4x bivalent frequency (Jackson 1982). Jackson (1982) found a highly negative correlation between chiasma frequency in diploid hybrids and bivalent frequency in the derived amphidiploids in annual Triticeae ($r = -0.9642$, $p < 0.0001$). Thus, a lower chiasma frequency at the 2x level yielded more bivalents and fewer quadrivalents at the 4x level. It is reasonable to conclude, therefore, that diploid-like pairing (Fig. 3a) and high pollen and seed fertility of JJEE amphidiploids stem primarily from distinctiveness of the two genomes. Meiotic and reproductive stability of the amphidiploids is a reflection of poor pairing in the JE hybrids, which form only 8.36 chiasmata per cell.

In view of the divergence of J and E genomes, the merger of *Lophopyrum* (E genome) with *Thinopyrum* (J genome) is not justified (Jauhar 1988a; Jauhar and Crane 1989).

*Pairing between J and E genomes in the presence of Ph1*

*Ph1* is the major pairing regulator in wheat. Pairing or lack of pairing between two genomes in the presence of *Ph1* can, therefore, provide a crucial test of their relationship. Because the *Ph1* locus of wheat suppresses homoeologous pairing, the degree of homologous and homoeologous pairing can be ascertained. As discussed above, the JJEE amphidiploids show diploid-like pairing (Fig. 3a) with a low frequency of multivalents. Although there is no direct evidence for the presence of a *Ph1*-like major pairing regulator in the JJEE amphidiploids, segregation in multivalent frequency observed among the progeny of some amphidiploids could be due to segregation of diploidizing genes (Jauhar 1988b). Even if a *Ph1*-like regulator exists, the J and E genomes must have a certain degree of differentiation (equivalent at least to homoeology between the two genomes) for the pairing regulator to act upon. The J and E are therefore best treated as distinct, homoeologous genomes[2].

Forster and Miller (1989) investigated the pairing relationship of J and E genomes in the wheat (AABBDD) background. They studied chromosome pairing in the AABBDDJE hybrids, derived by crossing wheat/*Th. bessarabicum* (AABBDDJJ) and wheat/*Th. elongatum* (AABBDDEE) amphidiploids. The AABBDDJE hybrids showed mostly 21 II + 14 I. In 120 microsporocytes, the mean pairing was 0.02 IV + 16.80 ring II + 3.98 rod II + 14.32 I. Clearly, the J and E genome chromosomes do not pair in the presence of *Ph1* gene, which inhibits pairing between homoeologues. Because in the same cellular environment the homologous chromosomes show complete pairing, forming almost 21 II, and the chromosomes of J and E genomes consistently remain unpaired, it may be concluded that J and E are homoeologous at best (see also the last section on genomic designation). Similarly, Jauhar and Bickford (1989) found that *Ph1* drastically reduces pairing between J and E in the ABJE hybrids synthesized by crossing tetraploid wheat (AABB) and JJEE amphidiploids. For example, Fig. 4a and b showes 28 univalents and 3 II + 22 I, respectively. Only about 26% of the complement paired in ABJE hybrids; this is the sum total of pairing between A and B, A and J, A and E, B and J, B and E, and J and E. This pairing is much lower than that observed in the diploid JE hybrids in which nearly 86% of the complement paired. Although it is not fully known how much genomic differentiation is required for the *Ph1* regulator to operate, these studies show that J and E are by no means homologous, or at least the degree of relationship between these genomes is not close enough to pass the discrimination limits of the pairing regulator.

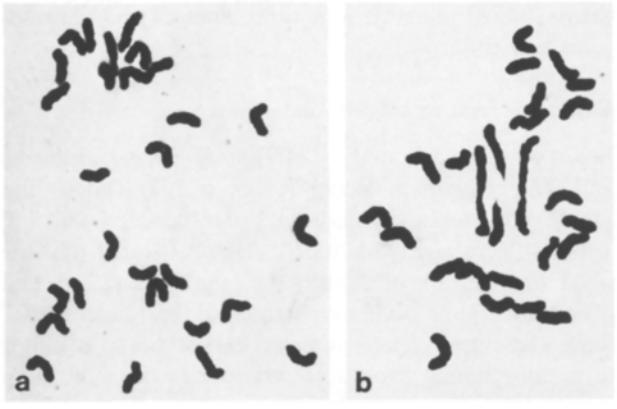


**Fig. 4a, b.** Chromosome pairing in trispecific hybrids between durum wheat (*Triticum turgidum*; AABB), *Thinopyrum bessarabicum* (JJ), and *Th. elongatum* (EE). **a** 28 I; note the complete absence of homoeologous pairing among the A, B, J, and E genomes in the presence of *Ph1* pairing regulator. **b** 3 rod II and 22 I; note heteromorphic bivalents

*Evidence from karyotype analysis*

Genome evolution can be attributed to changes in structure, organization, sequence composition, and size of chromosomes (Flavell 1982). Among these factors which lead to genomic evolution and differentiation, two can be

[2] Kellogg (1989) also concluded that they are best considered as separate evolutionary lines

easily studied, namely, structural changes and chromosome size.

*Structural repatterning of karyotypes*

Based on karotypic analysis of *Thinopyrum bessarabicum* and *Th. elongatum*, Wang (1985, p. 727) stated that "three of the seven chromosomes (numbers 3, 4, and 7 in Table 2) were nearly identical". He also stated that the remaining four chromosomes, i.e., numbers 1, 2, 5, and 6, had undergone "extensive structural rearrangements." Since structural repatterning of karyotypes is a major force in genomic evolution and species differentiation (Grant 1981; Flavell 1982), it is inconsistent with Wang's hypothesis (Wang 1985; Wang and Hsiao 1989) that the J genome of *Th. bessarabicum* and E genome of *Th. elongatum* are 'essentially homologous'.

*Chromosome size differences*

According to Table 2 in Wang's (1985) paper, every chromosome of the J genome is considerably larger than the corresponding chromosome of the E genome. Thus, chromosomes 1, 2, 3, 4, 5, 6, and 7 of *Th. bessarabicum* are 12.4%, 15.0%, 18.8%, 15.3%, 17.2%, 12.0%, and 16.6% larger, respectively, than the 'corresponding' chromosomes of *Th. elongatum*. Overall, the length of the somatic metaphase genome of *Th bessarabicum* is 15.3% larger than that of *Th. elongatum*. C-banding also shows the size differences very clearly (Fig. 5). Such size differences exist between well-recognized homoeologous genomes. For example, the B genome of wheat is 10.9% larger than the A genome, whereas the A genome is 15.3% larger than the D genome (Gill 1987). Thus, the above data show that the size difference between the J and E genomes is of the same level as between the A and D genomes.

Chromosomes 3, 4, and 7 of the two species are not 'nearly identical' as stated by Wang (1985). The satellited region of chromosome 4 of *Th. bessarabicum* is much larger than the satellited region of the corresponding chromosome of *Th. elongatum* (Fig. 2 in Wang 1985). Wang and other proponents of the merger of J and E genomes have misquoted Heneen and Runemark (1972) as stating that these genomes are very similar karyotypically. On the contrary, Heneen and Runemark (1972, p. 427) stated that *Elymus striatulus* (= *Thinopyrum bessarabicum*) and *E. elongatus* (= *Th. elongatum*) differ in the morphology of the satellited chromosomes as well as in the size and centromeric position of the other chromosomes. C-banding also shows very clear size differences between the J- and E-genome chromosomes (Table 4; Fig. 5).

The formation of asymmetrical multivalents and heteromorphic bivalents in the JE hybrids (Wang 1985; Jauhar 1988a) is evidence of karyotypic divergence. Although Wang reported only one heteromorphic bivalent in any single cell, Jauhar recorded at least two distinctly heteromorphic bivalents in many PMCs (Fig. 2b, c, e and f; Jauhar 1988a). Heteromorphic bivalents are, in fact, evident in Figs. 4, 7, 8, and 9 in Wang (1985). Formation of univalents of different sizes (Fig. 2a in Jauhar 1988a; Fig. 4 in Wang 1985) further shows the differentiation of the two genomes.

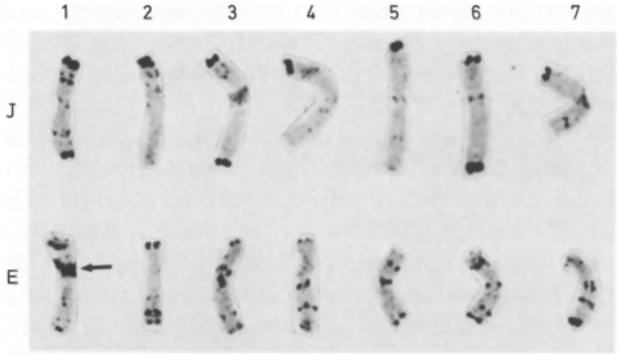


**Fig. 5.** C-banding patterns of J and E genome chromosomes. Note distinct size differences between the two genomes, prominent telomeric bands on J-genome chromosomes, and several interstitial bands on E-genome chromosomes. The thick dark region on chromosome *1E* is due to an overlap (*arrow*)

*Evidence from C-banding*

The C-banding patterns of the J and E genomes are very distinct (Endo and Gill 1984; Jauhar and Bickford 1989; Fig. 5). Clear C-banding differences were observed between the J and E genomes in the same cellular environment in ABJE hybrids derived by crossing durum wheat (AABB) with *Th. bessarabicum* × *Th. elongatum* amphidiploids (JJEE). Individual somatic chromosomes of the J and E genomes as well as of the A and B genomes can be identified by their diagnostic C-banding patterns (Jauhar and Bickford 1989). Table 4 gives the relative sizes of individual J- and E-genome chromosomes and their C-banded regions.

Total chromatin area of the J genome was 24.8% larger than the E genome. However, the proportion of the C-band positive region was 23.3% of the total complement of the J genome and 26.6% of the E genome. Because the E genome is considerably smaller than the J genome, in absolute terms, the banded area in the J genome was only 9.4% more than in the E genome.

Not only was the total heterochromatin more in the J genome than in the E genome, but the distribution of heterochromatin along their chromosomes was also different. The J genome of *Th. bessarabicum* is characterized by prominent terminal bands, whereas the E genome of *Th. elongatum* has either small or no terminal bands but several interstitial bands (Fig. 5). These features indicate

**Table 4.** Total surface area and C-banded area of the J- and E-genome chromosomes

| Chromosome | Total area in arbitrary units | Total C-banded area in arbitrary units | % C-banded area |
|---|---|---|---|
| *1J* | 225 | 86 | 38.22 |
| *2J* | 215 | 45 | 20.93 |
| *3J* | 253 | 62 | 24.51 |
| *4J* | 241 | 30 | 12.45 |
| *5J* | 246 | 31 | 12.60 |
| *6J* | 243 | 74 | 30.45 |
| *7J* | 224 | 56 | 25.00 |
| Total | 1647 | 384 | 23.32 |
| *1E* | 195 | 50 | 25.64 |
| *2E* | 183 | 47 | 25.68 |
| *3E* | 201 | 59 | 29.35 |
| *4E* | 198 | 46 | 23.23 |
| *5E* | 166 | 42 | 25.30 |
| *6E* | 186 | 52 | 27.96 |
| *7E* | 190 | 55 | 28.95 |
| Total | 1319 | 351 | 26.61 |

Note: Chromosomes are not numbered according to their homoeologous relationships with wheat; they are arranged according to Endo and Gill (1984), *1J* being J(A), and *1E* being E(A), and so on

differences in biochemical organization of the chromosomes of the two genomes. In situ hybridization using two repeated DNA sequence probes from rye also revealed that the J and E genomes are differentiated (Lapitan et al. 1987).

*Karyotype, genome analysis, and homoeologous relationships*

Karyotypic analysis on conventionally stained, condensed somatic chromosomes has been used for genome analysis by some cytogeneticists (e.g., Wang 1985). However, the measurement of condensed chromosomes at somatic metaphase may involve considerable error and it is not always easy to identify unequivocally the different chromosomes and their homologous partners. The satellited chromosomes can be identified, but amphiplasty[3] can mask the nucleolar organizing regions in hybrids between different species (Lacadena et al. 1984). Therefore, karyotypic analysis as a means of determining phylogenetic relationships may have severe limitations (Kimber and Feldman 1987). Based on chromosome measurements, Wang (1985) inferred that "chromosomes 1 and 2 of *Th. bessarabicum* might be homoeologous to chromosomes 2 and 1 of *Th. elongatum*, respectively". However, homoeologous relationships cannot be determined by chromosome measurements alone.

*Can J and E genomes be considered homologous based on ring bivalent formation?*

Some cytogeneticists do not make a clear distinction between homoeologous and homologous pairing. Wang (1985), for example, states: "Up to five ring bivalents occurred in the diploid hybrids between *T. bessarabicum* and *T. elongatum* (Table 3), indicating the presence of five pairs of homologous chromosomes." The formation of ring bivalents does not necessarily mean homologous pairing. Ring bivalents can form between well-established homoeologus chromosomes, e.g., between the chromosomes of A and D, and A and B genomes (Tables 2 and 3; Fig. 1b) or sometimes even between nonhomologous chromosomes, as in monoploids of barley (Sadasivaiah and Kasha 1971). Moreover, based on 1.16 and 1.86 ring bivalents per cell in the two diploid JE hybrids and 2.75 and 3.28 trivalents in JJE triploids (Wang and Hsiao 1989), it is difficult to infer that J and E genomes are homologous. If they are indeed homologous, as many as 12 of the 14 chromosomes should not remain unpaired in the diploid hybrids (Table 3 in Wang 1985). If the JJE triploid hybrid obtained by crossing diploid *Th. bessarabicum* (unreduced gamete) and diploid *Th. elongatum* forms a mean of 3.28 III per cell, the diploid JE hybrids should show much better pairing (higher ring bivalent frequency) than that observed by Wang (1985) or Jauhar (1988a), because no pairing competition is involved at the diploid level. Whether this triploid is indeed JJE perhaps needs to be confirmed, preferably by C-banding, because the J genome has diagnostic, easily, discernible telomeric bands. Wang and Hsiao (1989) determined the genomic constitution of the triploid hybrid to be JJE based on "the characteristic satellited chromosomes" of the J and E genomes, although earlier Wang (1989, p. 187) stated that there were no differences in the satellited chromosomes of the two genomes.

*Evidence from isozyme patterns, 5S DNA, and rDNA*

McIntyre (1988), McIntyre et al. (1988), and Scoles et al. (1988) evaluated genome relationships in the tribe Triticeae using DNA-DNA hybridizations, DNA analysis of the *Nor*-loci, 5S DNA sequence information, and isozyme electrophoresis. McIntyre (1988) concluded that "the E and J genomes are clearly distinct in terms of isozymes, 5S DNA, and rDNA". Her isozyme data showed that "the E and J genome species are readily distinguishable from each other, and the E genome species are less closely related to the J genome species than to the A, B and D genome species". Isozyme differences

[3] Amphiplasty is the term originally used by Navashin (1928) to denote morphological changes in chromosomes following interspecific hybridization

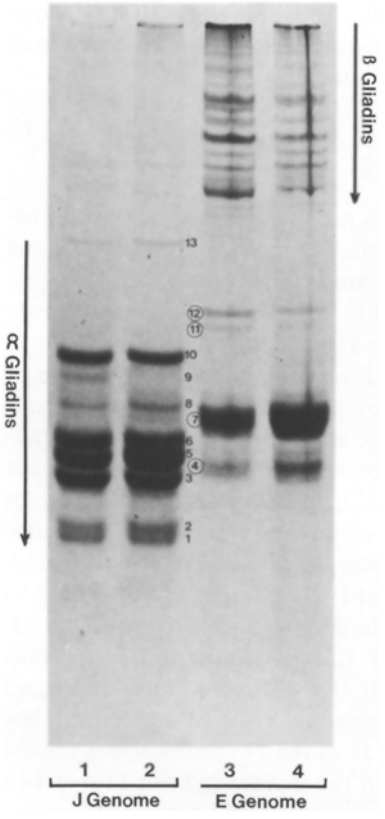


**Fig. 6.** Electrophoretogram comparing 5 1/2 h profiles for native gliadin proteins extracted from seeds of two accessions each of diploid *Thinopyrum bessarabicum* (J genome) (*lanes 1 and 2*) and diploid *Th. elongatum* (E genome) (*lanes 3 and 4*). *Circle α numbers* indicate α gliadin bands unique to the E genome; *uncircled numbers* denote α gliadins diagnostic of the J genome. The β gliadins are virtually absent in the J genome. Note prominent α gliadin bands 1, 2, 3, 5, 6, 8, and 10 in the J genome and α gliadin bands 4, 7, 11, and 12 in the E genome

are known to be useful in elucidating species relationships (Nishikawa 1983).

*Evidence from gliadin electrophoresis*

Electrophoretic similarity of seed gliadin proteins is believed to provide a direct measure of species affinity (Konarev 1983; Metakovsky et al. 1989), because these storage proteins are not influenced by environmental factors (Damania et al. 1983).

Two major (α and β) groups of gliadin proteins are shown based on their relative mobilities (Konarev et al. 1981). In the present study, the α-gliadins were present in higher concentrations and produced unique banding patterns that can be used to differentiate the J genome of diploid *Th. bessarabicum* and the E genome of diploid *Th. elongatum*. An electrophoretogram comparing profiles for native gliadin proteins extracted from the seeds of two accessions each of *Th. bessarabicum* and *Th. elongatum* is shown in Fig. 6. The gliadin profiles were very similar within a species, but very different between species. The banding pattern for the J genome (lanes 1 and 2) differs markedly from that of the E genome (lanes 3 and 4).

The J genome shows predominantly fast-moving α-gliadins, whereas the E genome is rich in β-gliadins with low relative mobilities (Fig. 6). No α-protein bands were common between the two genomes; β-proteins were present in only minute concentrations in the J genome. The α-gliadin bands 1, 2, 3, 5, 6, 8, and 10 were prominent in the J genome, but were altogether missing in the E genome. Similarly, the minor band α-13 was present only in the J genome. On the other hand, the E genome has a prominent α-gliadin band 4 and a very dense band 7, which are both lacking in the J genome. These differences seem to be large enough to be of generic level rather than of species level.

The major α-gliadin bands 1, 2, 3, 5, 6, 8, and 10 are characteristic of all accessions of diploid *Th. bessarabicum* (J genome) in our germplasm collection at Logan. The minor band α-12 and the dense band α-7 were present in all our accessions of diploid *Th. elongatum* (E genome); the prominent band α-7 was particularly diagnostic. These genomes are regularly used as sources of genes for wheat improvement. Their gliadin profiles may, therefore, prove to be useful biochemical markers in wheat breeding and forage breeding programs.

*The problem of genomic designation in the Triticeae*

Genomic affinities may vary from complete homology, on the one hand, to nonhomology, on the other, with various intergrades of partial homology or homoeology between the two extremes. Because there is a continuum of genomic differences from the single-point mutation to no greater nucleotide sequence similarity than expected by chance, each worker will have some arbitrary dividing line between same, similar, and dissimilar genomes. The definition of sameness will in fact lie in the experience of the beholder. Assessing genome relationships between the diploid species *Thinopyrum bessarabicum* (JJ genome) and *Th. elongatum* (EE) has particularly engendered some debate. Some workers (e.g., Wang 1985) feel that J and E are essentially homologous and recommend their merger under one genomic designation. Admittedly, assigning a separate letter to each genome in the Triticeae is problematic, because probably there are or will be more genomes than the 26 letters in the English alphabet. Assigning duplicate genome designations in the same tribe, e.g., S for the genus *Pseudoroegneria* (Dewey 1984) and also for the diploid *Triticum* species of section Sitopsis (Kimber and Feldman 1987) is confusing (see also Table 2).

An alternative procedure would be to group closely related genomes by giving them the same letter designation but different superscripts or subscripts. This may be attempted first on the basis of *c* (the mean arm-binding frequency) of diploid hybrids between two taxa and then confirmed by other methods of genome analysis (Jauhar and Crane 1989). After all, in diploid hybrids, *c* is the only available meiotic measure of genomic similarity (unfortunately, the *c* value is a measure only of paired arms of chromosomes and not actual chiasma frequency), whereas in polyploid hybrids pairing preferentiality is also relevant. Although the *c* values of hybrids are affected not only by genomic affinity but also by arm ratio and chiasma interference, it may be useful to consider *c* in genomic designations; at least it may serve as a useful starting point. If *c* is considered in genomic classification, a higher *c* value will need to be set for giving two genomes a common symbol. Of course, an arbitrary *c* value will need to be set as a standard for genomic designation. For example, if $c \geq 0.850$ in a diploid hybrid, it is generally (not always) reasonable to give the parental genomes the same designation. If in diploid hybrids, *c* lies between 0.75 and 0.84, the genomes could be designated by the same letter but qualified by different numerical subscripts, e.g., $A_1$, $A_2$, $A_3$, etc. If *c* in the diploid hybrid is between 0.65 and 0.74, the genomes could be given the same letter but different alphabetical superscripts, e.g. $A^a$, $A^b$, $A^c$, etc. For lower *c*, the genomes probably require different letters.

However, some precautions will need to be taken in genomic nomenclature.

(1) In cases where a high *c* value is due largely to extensive translocation multivalents, and not ring bivalents, a researcher will need to use his/her own judgement in genomic designations.

(2) The presence of a large number of univalents due to desynapsis/asynapsis will need to be considered. However, the phenomena of desynapsis and asynapsis are generally rare and not difficult to recognize.

(3) The genomic assignments with the subscripts and superscripts suggested above should be given with a full realization that the genomes are related but distinct and that their amphidiploids are not autopolyploids.

(4) The origin of the material, whenever known, should also be considered. For example, if a known tetrasomic of wheat forms 22II in most cells, we know that factors other than homology also govern bivalent formation among the four homologous chromosomes. On the other hand, if the chromosomes of *Secale cereale* ($R^c$ genome) and *S. montanum* ($R^m$ genome) do not pair in the presence of *Ph1* (Riley and Miller 1970), other lines of evidence such as their amphidiploid pairing (Chapman 1984), banding patterns, chromosome morphology and, more importantly, fertility of their diploid hybrids should also be considered. Khush and Stebbins (1961) demonstrated that *S. cereale* differs from *S. montanum* by two reciprocal translocations; the fixation of translocations was facilitated by the adaptive superiority of the translocation heterozygotes and rearrangement homozygotes. Considering all these features, it is not unlikely that $R^c$ and $R^m$ are homoeologous genomes, which deserve different superscripts.

(5) In addition to *c* values, other biosystematic criteria should also be considered when possible. Morphology is easy to study, and isozyme techniques are also well established in biosystematics. While these traits might be more subject to convergent evolution and interpopulational variation than meiotic pairing, they offer evidence that taxonomic entities actually do or do not exchange genes.

(6) The fertility of diploid hybrids between taxa should be considered because it is a very important trait for assessing genome relationships. If diploid hybrids between two taxa have good pairing (e.g., $c \geq 0.85$) and are fertile, e.g., *Lolium multiflorum* × *L. perenne* hybrids (Jauhar 1975c), then the genomes are the same or very similar and deserve the same designation. If diploid hybrids have good pairing (e.g., $c \geq 0.85$) but are sterile, e.g., *Lolium perenne* × *Festuca pratensis* hybrids (Jauhar 1975c), the genomes may be designated by the same letter because the sterility of the diploid hybrids may be due to genetic and not chromosomal factors. On the other hand, if diploid hybrids have $c \leq 0.65$ and are completely sterile, e.g., *Thinopyrum bessarabicum* × *Th. elongatum* hybrids (Wang 1985; Jauhar 1988a, b), the genomes are best given separate letters. They may be given the same letter but different superscripts, provided the same standard of genomic designation is applied throughout the Triticeae, both perennial and annual. This is important because several perennial members of the Triticeae are used by wheat and barley breeders.

Some subjectivity is inevitable in genomic designations but breeders, cytogeneticists, taxonomists, and evolutionists will all benefit if a uniform standardized system of nomenclature can be found. Also, before changing the designation of an established genome in the Triticeae, the matter may be referred to an international committee of the type that exists for wheat. It took several years of careful deliberations before the designation of wheat chromosome 4A was changed to 4B and vice versa. This ideal may not be achievable for the entire Triticeae in the near future, but we should aim for it.

## Conclusions

*Thinopyrum bessarabicum* (JJ) and *Th. elongatum* (*Lophopyrum elongatum*) (EE) are morphologically distinct, reproductively isolated species and occupy differ-

ent ecological habitats. The former is a rhizomatous grass with fragile rachis and grows in shoreline coastal habitats, whereas the latter is predominantly caespitose, and grows on saline inland as well as coastal sites. They were therefore included under different species complexes, the *Th. junceum* complex and the *Th. elongatum* complex, respectively, within the genus *Thinopyrum* (Dewey 1984). *Th. bessarabicum* and *Th. elongatum* differ with respect to anatomical features (J. K. Jarvie and M. E. Barkworth, personal communication), karyotypic features (Heneen and Runemark 1972; Wang 1985; Jauhar 1988a), C-banding patterns of their karyotypes (Endo and Gill 1984; Jauhar and Bickford 1989), and in situ hybridization patterns with two repeated DNA sequence probes (Lapitan et al. 1987). Thus, the two species have diverged considerably over the course of evolution and their genomes have undergone considerable differentiation, as reflected in their heterochromatin patterns. The chromosomes of the two genomes have differentiated to the point that they largely engage in preferential pairing in JJE autoallotriploids and JJEE amphidiploids, particularly in the latter (Jauhar 1988a, b). The degree of precision with which they recognize their own homologous partners shows the distinctiveness of the two genomes. In terms of isozymes, 5S DNA sequence, and rDNA also the J and E genomes are clearly distinct (McIntyre 1988) and their gliadin patterns are also very different. Well-defined biochemical markers of potential value in plant breeding were identified in the J and E genomes in the present study. Based on the chromosome pairing relationships, Jauhar (1988a) concluded that J and E are distinct, homoeologus genomes, a conclusion borne out by the fact that the J and E genome chromosomes do not pair in the wheat background, in AABBDDJE hybrids (Forster and Miller (1989), or in ABJE hybrids in the presence of the *Ph1* regulator that inhibits homoeologous pairing. Thus, the level of distinction between J and E is probably similar to that among the universally recognized homoeologous genomes A, B, and D of wheat.

The evidence available to date shows that the J genome of *Thinopyrum bessarabicum* and the E genome of *Th. elongatum* (*Lophopyrum elongatum*) are best treated as distinct genomes, as done by Löve (1982, 1984). The merger of the genera *Thinopyrum* and *Lophopyrum* is also unwarranted. The J and E genomes may well be related in the sense that they probably arose from a common progenitor, but they have diverged sufficiently during the course of evolution that the genomes should not be merged. The A, B, and D genomes of wheat are closely related as well. They are probably versions of the same genome. Are we going to merge them? A uniform, standardized system of genomic nomenclature for the tribe Triticeae is proposed, which should benefit breeders, cytogeneticists, taxonomists, and evolutionists.

**Note added in proof**

Wang and Hsiao (1989) studied the effect of temperature on chromosome pairing in JEE triploids by fixing spikes on different dates in March to June. The authors reported a drop in the mean trivalent frequency from 2.60 to 2.10 per cell and attributed this decline to changes in temperature. However, the authors did not record (or at least have not reported in their paper) the ambient temperatures on or before the dates the cytological materials were fixed. Even if the temperatures on the days of fixation were different, it should be remembered that chromosome pairing and chiasma formation are initiated much before the onset of metaphase I – the stage at which the chromosome configurations are normally studied. Therefore, to ascertain the effect of temperature on chromosome pairing, one must grow the experimental plants in a replicated experiment under controlled conditions, such as in growth chambers, where temperature and other environmental parameters can be controlled precisely at least during the entire reproductive phase of the plant.

*Acknowledgements.* I am grateful to Prof B. Gill, J. Dvořák, R. Jackson, and Drs. C. Crane and J. Chatterton for critically reviewing the manuscript and for several useful comments.

## References

Alonso LC, Kimber G (1981) The analysis of meiosis in hybrids. II. Triploid hybrids. Can J Genet Cytol 23:221–234

Baum BR, Estes JR, Gupta PK (1987) Assessment of the genomic system of classification in the Triticeae. Am J Bot 74:1388–1395

Breese EL, Stephens DE, Thomas AC (1975) Tetraploid hybrid ryegrasses: Allopolyploidy in action. In: Nüesch B (ed) Proc EUCARPIA Conf Polyploidy Fodder Plants. Reckenholz, Zürich, pp 46–49

Cauderon Y, Saigne B (1961) New interspecific and intergeneric hybrids involving *Agropyron*. Wheat Inf Serv 12:13–14

Chapman CGD (1984) Does preferential pairing occur in *Secale cereale* × *S. montanum* tetraploid hybrids? Heredity 52:317–322

Crane CF, Sleper DA (1989) A model of meiotic chromosome association in triploids. Genome 32:82–98

Damania AB, Porceddu E, Jackson MT (1983) A rapid method for the evaluation of variation in germplasm collections of cereals using polyacrylamide gel electrophoresis. Euphytica 32:877–883

Dewey DR (1984) The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. Stadler Genet Symp 16:209–279

Dvořák J (1981) Genome relationships among *Elytrigia* (=*Agropyron*) *elongata*, *E. stipifolia*, "*E. elongata* 4x", *E. caespitosa*, *E. intermedia*, and "*E. elongata* 10x." Can J Genet Cytol 23:481–492

Dvořák J (1988) Cytogenetical and molecular inferences about the evolution of wheat. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, vol 1. Institute of Plant Science Research, Cambridge, England, pp 187–192

Dvořák J, Ross K (1986) Expression of tolerance of $Na^+$, $K^+$, $Mg^{2+}$, $Cl^-$, and $SO_4^{2-}$ ions and sea water in the amphiploid of *Triticum aestivum* × *Elytrigia elongata*. Crop Sci 26:658–660

Endo TR, Gill BS (1984) The heterochromatin distribution and genome evolution in diploid species of *Elymus* and *Agropyron*. Can J Genet Cytol 26:669–678

Feldman M, Avivi L (1984) Ordered arrangement of chromosomes in wheat. Chromosomes Today 8:181–189

Flavell RB (1982) Sequence amplification, deletion and rearrangement: Major sources of variation during species divergence. In: Dover GA, Flavell RB (eds) Genome evolution. Academic Press, London, pp 301–323

Forster BP, Gorham J, Miller TE (1987) Salt tolerance of an amphiploid between *Triticum aestivum* and *Agropyron junceum*. Plant Breed 98:1–8

Forster BP, Miller TE (1989) Genome relationship between *Thinopyrum bessarabicum* and *Th. elongatum*. Genome 32:930–931

Gill BS (1987) Chromosome banding methods, standard chromosome band nomenclature, and applications in cytogenetic analysis. In: Heyne EG (ed) Wheat and wheat improvement, 2nd edn. American Society of Agronomy, Madison, Wisconsin, pp 243–254

Giraldez R, Cermeño MC, Orellana J (1979) Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye. Z Pflanzenzuecht 83:40–48

Grant V (1981) Plant speciation, 2nd edn. Columbia University Press, New York

Heneen WK, Runemark H (1972) Chromosomal polymorphism in isolated populations of *Elymus (Agropyron)* in the Aegean. I. *Elymus striatulus* sp. nov. Bot Not 125:419–429

Jackson RC (1982) Polyploidy and diploidy: new perspectives on chromosome pairing and its evolutionary implications. Am J Bot 69:1512–1523

Jauhar PP (1975a) Genetic regulation of diploid-like chromosome pairing in the hexaploid species, *Festuca arundinacea* Schreb. and *F. rubra* L. (Gramineae). Chromosoma 52:363–382

Jauhar PP (1975b) Polyploidy, genetic control of chromosome pairing, and evolution in the *Festuca-Lolium* complex. Heredity 35:430

Jauhar PP (1975c) Chromosome relationships between *Lolium* and *Festuca* (Gramineae). Chromosoma 52:103–121

Jauhar PP (1981) Cytogenetics of pearl millet. Adv Agron 34:407–479

Jauhar PP (1988a) A reassessment of genome relationships between *Thinopyrum bessarabicum* and *T. elongatum* of the Triticeae. Genome 30:903–914

Jauhar PP (1988b) Meiotic and reproductive stability of *Thinopyrum bessarabicum* × *Th. elongatum* amphidiploids: Their potential as sources of genes for wheat improvement. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, vol 1. Institute of Plant Science Research, Cambridge, England, pp 323–328

Jauhar PP, Bickford IW (1989) Chromosome pairing in trispecific hybrids between durum wheat and *Thinopyrum*: Its breeding implications. Agron Abstracts, American Society of Agronomy, Madison, Wisconsin, p. 87

Jauhar PP, Crane CF (1989) An evaluation of Baum et al's assessment of the genomic system of classification in the Triticeae. Am J Bot 76:571–576

Kellogg EA (1989) Comments on genomic genera in the Triticeae (Poaceae). Am J Bot 76:796–805

Khush GS, Stebbins GL (1961) Cytogenetic and evolutionary studies in *Secale*. I. Some new data on the ancestry of *S. cereale*. Am J Bot 48:723–730

Kimber G, Feldman M (1987) Wild wheat: an introduction. Special Rep. 353. University of Missouri, Columbia

Kimber G, Riley R (1963) The relationships of the diploid progenitors of hexaploid wheat. Can J Genet Cytol 5:83–88

Konarev VG (1983) The nature and origin of wheat genomes on the data of grain protein immunochemistry and electrophoresis. In: Proc 6th Int. Wheat Genet Symp, Kyoto, Japan, pp 65–75

Konarev VG, Gavriljuk IP, Gubareva NK, Choroshajlov HG (1981) Electrophoretic and serological methods in seed testing. Seed Sci Technol 9:807–817

Lacadena JR, Cermeño MC, Orellana J, Santos JL (1984) Evidence for wheat-rye nucleolar competition (amphiplasty) in triticale by silver-staining procedure. Theor Appl Genet 67:207–213

Lapitan NLV, Gill BS, Sears RG (1987) Genomic and phylogenetic relationships among rye and perennial species in the Triticeae. Crop Sci 27:682–687

Löve Á (1982) Generic evolution of the wheatgrasses. Biol Zentralbl 101:199–212

Löve Á (1984) Conspectus of the Triticeae. Feddes Repert Z Bot Taxon Geobot 95:425–521

McGuire PE (1984) Chromosome pairing in triploid and tetraploid hybrids in *Elytrigia* (Triticeae: Poaceae). Can J Genet Cytol 26:519–522

McIntyre CL (1988) Variation at isozyme loci in Triticeae. Plant Syst Evol 160:123–142

McIntyre CL, Clarke BC, Appels R (1988) Amplification and dispersion of repeated DNA sequences in the Triticeae. Plant Syst Evol 160:39–59

Metakovsky EV, Kudryavtsev AM, Iakobashvili ZA, Novoselskaya AY (1989) Analysis of phylogenetic relations of durum, carthlicum and common wheats by means of comparison of alleles of gliadin-coding loci. Theor Appl Genet 77:881–887

Moustakas M, Symeonidis L, Ouzounidou G (1988) Genome relationships in the *Elytrigia* group of the genus *Agropyron* (Poaceae) as indicated by seed protein electrophoresis. Plant Syst Evol 161:147–153

Mujeeb-Kazi A, Roldan S, Suh DY, Sitch LA, Farooq S (1987) Production and cytogenetic analysis of hybrids between *Triticum aestivum* and some caespitose *Agropyron* species. Genome 29:537–553

Navashin MS (1928) "Amphiplasty" – a new karyological phenomenon. Z Indukt Abstamm Vererbungsl Suppl 2: 1148–1152

Nishikawa K (1983) Species relationship of wheat and its putative ancestors as viewed from isozyme variation. In: Proc 6th Int Wheat Genet Symp, Kyoto, Japan, pp 59–63

Okamoto M (1957) Asynaptic effect of chromosome V. Wheat Inf Serv 5:6

Orellana J (1985) Most of the homoeologous pairing at metaphase I in wheat-rye hybrids is not chiasmatic. Genetics 111:917–931

Pienaar R de V, Littlejohn GM, Sears ER (1988) Genomic relationships in *Thinopyrum*. S Afr J Bot 54:541–550

Powell JB, Hanna WW, Burton GW (1975) Origin, cytology, and reproductive characteristics of haploids in pearl millet. Crop Sci 15:389–392

Riley R (1960) The diploidisation of polyploid wheat. Heredity 15:407–429

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Riley R, Chapman V (1966) Estimates of the homoeology of wheat chromosomes by measurements of differential affinity at meiosis. In: Riley R, Lewis KR (eds) Chromosome manipulations and plant genetics. Oliver and Boyd Ltd, Edinburgh, London, pp 46–58

Riley R, Kempanna C (1963) The homoeologous nature of the non-homologous meiotic pairing in *Triticum aestivum* deficient for chromosome V (5B). Heredity 18:287–306

Riley R, Miller TE (1970) Meiotic chromosome pairing in *Triticale*. Nature 227:82–83

Sadasivaiah RS, Kasha KJ (1971) Meiosis in haploid barley – An interpretation of non-homologous chromosome associations. Chromosoma 35:247–263

Sadasivaiah RS, Kasha KJ (1973) Non-homologous associations of haploid barley chromosomes in the cytoplasm of *Hordeum bulbosum* L. Can J Genet Cytol 15:45–52

Scoles GJ, Gill BS, Xin Z-Y, Clarke BC, McIntyre CL, Chapman C, Appels R (1988) Frequent duplication and deletion events in the 5S RNA genes and the associated spacer regions of the Triticeae. Plant Syst Evol 160:105–122

Sears ER (1941) Chromosome pairing and fertility in hybrids and amphidiploids in the *Triticinae*. Mo Agric Exp Stn Res Bull 337:20 pp.

Sears ER (1954) The aneuploids of common wheat. Mo Agric Exp Stn Res Bull 572:58 pp.

Sears ER (1966) Nullisomic-tetrasomic combinations in hexaploid wheat. In: Riley R, Lewis KR (eds) Chromosome manipulations and plant genetics. Oliver and Boyd Ltd, Edinburgh, London, pp 29–45

Sears ER (1976) Genetic control of chromosome pairing in wheat. Annu Rev Genet 10:31–51

Sears ER, Okamoto M (1958) Intergenomic chromosome relationships in hexaploid wheat. Proc 10th Int Congr Genet 2:258–259

Seberg O (1989) Genome analysis, phylogeny, and classification. Plant Syst Evol 166:159–171

Wang RR-C (1985) Genome analysis of *Thinopyrum bessarabicum* and *T. elongatum*. Can J Genet Cytol 27:722–728

Wang RR-C (1986) Diploid perennial intergeneric hybrids in the tribe Triticeae. II. Hybrids of *Thinopyrum elongatum* with *Pseudoroegneria spicata* and *Critesion violaceum*. Biol Zentralbl 105:361–368

Wang RR-C (1988) Diploid perennial intergeneric hybrids in the tribe Triticeae. IV. Hybrids among *Thinopyrum bessarabicum*, *Pseudoroegneria spicata*, and *Secale montanum*. Genome 30:356–360

Wang RR-C (1989) An assessment of genome analysis based on chromosome pairing in hybrids of perennial Triticeae. Genome 32:179–189

Wang RR-C, Hsiao C (1989) Genome relationship between *Thinopyrum bessarabicum* and *T. elongatum*: revisited. Genome 32:802–809