# THE CYTOGENETICS OF *THINOPYRUM* HYBRIDS AND AMPHIPLOIDS

R. de V. Pienaar[1], G.M. Littlejohn[1], H.S. Roux[1] and E.R. Sears[2]

(1) Dept. of Genetics, University of Stellenbosch 7600, R.S.A.

(2) Dept. of Agronomy, University of Missouri-~~Columbia~~, Columbia, Mo 65211, U.S.A.

**Summary**

Meiotic analyses of *Triticum durum*/*Thinopyrum distichum* and *T. durum*/*Th. junceiforme* $F_1$-hybrids, amphiploids and backcross hybrids indicated that there is substantial homology between the $J^d_1$ and $J^d_2$ genomes of *Th. distichum* (2n=28), as well as the $J_1$ and $J_2$ genomes of *Th. junceiforme* (2n=28).

When *T. durum*/*Th. distichum*//*T. durum* $BC_1F_1$ hexaploids were crossed with *T. durum*/*Th. elongatum* amphiploids (2n=42), fertile progeny were obtained which showed good meiotic pairing between the $J^e$ genome of *Th. elongatum* (2n=14) and a derived $J^d_{1-2}$ genome from *Th. distichum*. The observed frequency of 2,96 trivalents/PMC in a *Th. distichum*/*Th. elongatum* $F_1$-hybrid (2n=21) also suggests substantial, but not complete homology between the $J^e$ genome of *Th. elongatum* and the $J^d_1$ and $J^d_2$ genomes of *Th. distichum*; the values of the other meiotic configurations were 2,92 univalents, 4,36 bivalents and 0,12 quadrivalents. Colchicine treatment of this hybrid led to the production of six $C_2$ amphiploids (2n=42) and four aneuploids.

A meiotic study of a *Th. distichum*/*Th. junceiforme* $F_1$-hybrid (2n=28) showed average frequencies per PMC of 5,0

univalents, 6,56 bivalents, 1,7 trivalents, 0,88 quadrivalents and 0,22 higher configurations, indicating good, but incomplete homology between the Th. distichum and Th. junceiforme genomes.

**Key words:** Agropyron; Thinopyrum; Triticum; genome analysis; wheat cytogenetics; biosystematics.

## INTRODUCTION

Agropyron has traditionally been the largest genus of the tribe Triticeae, encompassing well over 100 diverse perennial species with one spikelet per node (cf. Dewey, 1984). Most of these species occur in the northern hemisphere, but a few have made their way to the southern hemisphere. The only South African representative of these grasses is coastal wheatgrass, formerly named Agropyron distichum (Thunb.) Beauv.

Many of the Agropyron species proved to be of economic importance as forage grasses, and to constitute a reservoir of genes for enhanced cold, drought and salinity tolerance, disease resistance, high protein content, and other traits that can be transferred to wheat by cytogenetic manipulations (Asay & Dewey, 1983; Cauderon, 1979; Dewey, 1976, 1977; Dvořák et al, 1985; Fedak, 1985; Knott & Dvořák, 1976; Mujeeb-Kazi et al, 1984; Napier & Walton, 1984; Pienaar, 1981; Riley & Law, 1984; Sears, 1981, 1983, 1984; Sharma & Baenziger, 1986; Sharma & Gill, 1983a, b; Simmonds, 1984). These findings led to many hybridization experiments, genome analyses and other cytogenetic investigations in the Triticeae. The wealth of biosystematic information that became available for this tribe made it possible to introduce new classification systems that reflect the phylogeny and biological relationships of

the species. The most recent taxonomic treatments of this tribe, viz. those of Löve (1982, 1984) and Dewey (1984), are both based on genomic relationships, but differ slightly from each other. In this paper we will use Dewey's system, because his treatment of the genus Thinopyrum is more appropriate to our findings.

According to Dewey (1984) all species that possess genomes other than the P genome should be excluded from Agropyron. This resulted in the reduction of the traditional large genus to a small one with no more than 10 species and 19 subspecies. He reclassified the other perennial species of the Triticeae according to their genome constitution, as follows:

Critesion (consists of those species that only have the HH (genome)
Psathyrostachys consists of those species that only have the N genome
Pseudoroegneria consists of those species that only have the S genome
Thinopyrum consists of those species that only have the J(=E) genome
Elytrigia consists of those species that only have the SX* genomes
Leymus consists of those species that only have the JN genomes
Elymus consists of those species that only have the SHY* genomes
Pascopyrum consists of those species that only have the SHJN genomes
(*X and Y designate unspecified genomes of unknown origin)

The genome designations employed above are only some of the symbols proposed by Löve (1982) for the entire tribe in his endeavour to establish a taxonomic system that ~~will~~

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extracted seed proteins (largely the albumins) can augment cytological information to determine genome and species relationships (Moustakas et al., 1986).

The principles involved in circumscribing a genus on genomic grounds involve a three-step process, according to Dewey (1984): **(1)** The determination of the genomic constitution of the type species of a genus. **(2)** The incorporation of all taxa with the same basic genome, or combination of genomes into that genus. **(3)** The exclusion from that genus of all taxa which do not have the same basic genome or combination of genomes as the type species. This

straightforward genomic system of classification requires the accumulation of a vast amount of cytogenetic data from interspecific and intergeneric hybrids as well as haploids. add (3)

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current status of Triticum-Thinopyrum hybridization was recently reviewed by Sharma and Gill (1983).

(3) At present the system appears to serve well for the species formerly included in the genus Agropyron. Whether or not it may have to be modified as additional information about the species accumulates remains to be seen.

Thinopyrum (derived from Greek words meaning 'shore' and 'wheat') ~~was~~ is a genus erected in 1980 by Löve, and is based on the J genome (Löve, 1982). The type species, Th. junceum (L.) Löve (=Agropyron junceum (L.) P.B.; A. junceum ssp. mediterraneum Simonet; Elytrigia juncea (L.) Nevski; Elymus farctus (Viv.) Runemark ex Melderis), is a hexaploid with 2n=42. Löve (1980) included only the six species of the former A. junceum (L.) P.B. complex into Thinopyrum, but Dewey (1984) on genomic grounds found it necessary to include the species of Lophopyrum sensu Löve and part of Elytrigia sensu Löve into this genus, thus expanding it to about 20 species. Lophopyrum elongatum (Host) Löve, the type species of the genus Lophopyrum Löve, is diploid with 2n=14, and is based on the E genome (Löve, 1982). Wang (1985) found that the diploid hybrid between Th. bessarabicum (Savul & Rayss) Löve (2n=14, JJ) and L. elongatum averaged 2.68 univalents; 4,68 bivalents; 0,27 trivalents; 0,27 quadrivalents and 0,01 pentavalents per PMC with a maximum of 7 bivalents per cell. The triploid hybrids between the tetraploid Th. junceiforme (Löve & Löve) Löve ($J_1J_1J_2J_2$) and L. elongatum averaged 2,8 trivalents per PMC with a maximum of 7 trivalents per cell (Cauderon & Saigne, 1961). Dewey (1984) and Wang (1985) regarded this as

sufficient evidence to conclude that the J and E genomes are so closely related that they should be considered variations of the same genome. Dvořák (1981) favoured combining the J and E genome designations under the letter E, but J is the older of the two genome designations, having been applied as early as 1940 by Östergren, and should therefore be given preference according to Dewey (1984). Consequently Wang (1985) changed the E genome designation of L. elongatum to $J^e$ and supported Dewey (1984) in transferring the latter species to the genus Thinopyrum. It is now known as Th. elongatum (Host.) Dewey (=Agropyron elongatum (Host.) Beauv., Elytrigia elongata (Host.) Nevski, Elymus elongatus (Host.) Runemark, Lophopyrum elongatum (Host.) Löve). Since the other Lophopyrum sensu Löve species have the same basic genome as Th. elongatum, they were also transferred to the genus Thinopyrum by Dewey (1984); e.g., the decaploid species Lophopyrum ponticum (Podp.) Löve (=Agropyron elongatum ssp. ruthenicum Beldie, Elytrigia pontica (Podp.) Holub, Elymus elongatus ssp. ponticus (Podp.) Melderis) was renamed Thinopyrum ponticum (Podp.) Barkworth & Dewey.

The "intermediate wheatgrass complex", formerly known as Agropyron intermedium (Host) Beauv. (=Agropyrum glaucum (Desf. ex DC.) Roemer & Schultes), Elymus hispidus (Opiz)Melderis) was transferred to the genus Elytrigia by Nevski (1933) and named Elytrigia intermedia (Host.) Nevski. Löve (1982) concurred with Nevski and retained this name in his treatment of the genus Elytrigia, which also includes Elytrigia repens (L.) Nevski (=Agropyron repens (L.) P. Beauv, Elymus repens (L.) Gould) and other taxa. However, Cauderon (1958) found that the intermediate wheatgrasses have one or more genomes in common with Th. elongatum and Th. junceum, but did not share any genomes with E. repens. Furthermore the octoploid hybrids resulting from crosses between the intermediate wheatgrasses and Th. ponticum have almost complete chromosome pairing and were very fertile

(Lyubimova, 1970). Dewey (1984) considered these findings adequate grounds to transfer the intermediate wheatgrasses from Elytrigia sensu Löve to Thinopyrum sensu Dewey, and these grasses were consequently renamed Thinopyrum intermedium Host.) Barkworth & Dewey. Tzvelev (1976) made a classification of the subspecies of Th. intermedium which is recognized by Dewey (1984).

Thinopyrum sensu Dewey thus consists of three species complexes, each of which was given sectional status in the genus by Dewey (1984). The species of the Th. junceum complex (Th. bessarabicum, Th. distichum, Th. junceiforme, Th. junceum, Th. runemarkii, etc.), which constitute the section Thinopyrum, are maritime grasses, and all bar one grow along the coastlines of the Baltic Sea, Mediterranean Sea and North Sea. The exception is Th. distichum, which is native to South Africa and grows on the shores of the South and South Western Cape. Usually the species of this section are rhizomatous and their spikes have a fragile rachis. They are mostly self-fertilizing grasses. The species of the Th. elongatum complex (Th. elongatum, Th. curvifolium, Th. ponticum, Th. scirpeum, etc.), constitute the section Lophopyrum. Except Th. ponticum, which grows in North America, the species of this section are found in coastal areas around the perimeter of the Mediterranean Sea as well as saline inland sites in the Middle East and European Russia. They are caespitose, self- or cross-pollinating grasses. The third section, Trichophorae, is composed of the species of the Th. intermedium complex (Th. intermedium, Th. gentryi, Th. podperae, etc.) that are adapted to the more favourable inland sites of Europe, the Middle East and Central Asia. These grasses are usually rhizomatous and cross-pollinating.

Thinopyrum have diploid species with 2n=14 (eg., Th. bessarabicum, Th. elongatum), segmental allotetraploids with

Are these all the species? If so, omit the e.g.

2n=28 (eg., Th. curvifolium, Th. distichum, Th. junceiforme, Th. scirpeum), segmental allohexaploids, 2n=42 (eg., Th. intermedium, Th. junceum), complex segmental octoploids with 2n=56 (eg., Th. runemarkii, Th. ponticum ssp. turcicum), and a complex segmental decaploid with 2n=70 (Th. ponticum).

The known genome designations of the various species are:

Th. bessarubicum JJ (Wang, 1985); $J_1J_1$ (Moustakas et al., 1986).

Th. elongatum $J^eJ^e$ (Wang, 1985); EE (Löve, 1982).

Th. junceiforme $J_1J_1J_2J_2$ (Östergren, 1940a; Moustakas, et al., 1986).

Th. curvifolium $J^eJ^eJ^eJ^e$ (Wang, 1985).

Th. junceum $J_1J_1J_2J_2J_3J_3$ (Moustakas et al., 1986)

Th. intermedium $J^eJ^eJ^eJ^eXX$ (Wang, 1985)

Th. runemarkii $J_{(1)}J_{(1)}J_4J_4J_{(4)}J_{(4)}J_6J_6$ (Moustakas et al., 1986).

It is evident that much needs to be done in defining the type of polyploidy and the genomic relationships in Thinopyrum.

Dewey (1984) transferred the South African species A. distichum (cf. Chippindall and Crook, 1976-78) to the section Thinopyrum, because it has all the characteristics of the Th. junceum complex. Although some botanists believed that it was inadvertently brought to South Africa when Phoenecian boats became shipwrecked (Chippindall, personal communication), it is unlike any of the existing species of Europe, the Middle East or Central Asia, and must have evolved on the shores of the Cape Province over a very long period of time. It should therefore be of great interest to archeologists, botanists, cytotaxonomists, and plant breeders to know its genomic relationship with the other species of Thinopyrum and related genera.

Pienaar (1981, 1983) revealed that Th. distichum is a segmental allotetraploid ($X_1X_1X_2X_2$) with two similar genomes of unknown origin that are unlike those of wheat and capable of considerable autosyndetic pairing in its hybrids with the wheats, Triticum turgidum var. durum and T. aestivum var. aestivum. When the T. durum/Th. distichum amphiploids were back-crossed to T. durum and the resulting hexaploids crossed with T. durum/Th. elongatum amphiploids, hybrids were obtained which showed good chromosome pairing (an average of 16,94 bivalents and 0,6 multivalents per PMC with a maximum of 21II per cell) and good fertility (31,8 kernels per spike). This indicated a good resemblance between the Th. distichum and Th. elongatum genomes.

The aim of the present study was to obtain further data on the genomic relationships between Th. distichum, Th. elongatum and Th. junceiforme.

## Materials and Methods

Th. distichum plants were collected from the sand dunes at the high-tide level on the beaches near East London and Gordons Bay, Cape Province. Seeds of Th. elongatum (CS-5-71, originally from France) and Th. junceiforme (PI414667, originally from Greece) were obtained from Dr. D.R. Dewey, Crops Research Laboratory, Logan, Utah, U.S.A. in 1980, and grown in pots in a greenhouse. During the following years various controlled crosses were made between the Th. distichum, Th. elongatum and Th. junceiforme accessions. In 1982 the Triticum durum cultivars Yavaros 79 and Balcarceno Inta were crossed with Th. junceiforme.

Except for ~~the cross~~ Th. distichum x Th. elongatum, which produced one viable kernel, the embryos produced by the

~~other~~ crosses had to be rescued from their endospermless seeds by excising them under sterile conditions 18-20 days after pollination, and culturing them for a few weeks on Difco Orchid Agar (29 g/l) fortified with sucrose (2,8 g/l) at pH 6,5. Seedlings at the three-leaf stage were transplanted into pots in a growth chamber and transferred to a greenhouse after ten days. When the plants began to tiller they were cloned, and some were amphiploidised following the procedure described by Pienaar (1981).

Young spikes at the stage of meiosis were fixed at noon in Carnoy's (6:3:1) fixative for a few days and stored in 70% ethanol at 4°C. Anthers at metaphase I were stained following the Feulgen procedure and squashed in 1% aceto-carmine. The cover-glasses were floated off in a solution consisting of 1 part glacial acetic acid:1 part tertiary butyl alcohol, and passed through two changes of tertiary butyl alcohol for 5 min in each, before mounting in Canada Balsam.

Chromosome counts in root tips were done following a 30-hour cold treatment of the root tips in ice water, fixation in a 3:1 methanol-propionic acid solution for 24 hours, a 30-minutes rinse in distilled water, 6-7 minutes hydrolysis in NHCl at 60°C, 2 hours staining with Feulgen at 4°C, two distilled water rinses, a 1-hour treatment in a solution consisting of 5% pectinase and 1% peptone in pH 4,5 sodium acetate buffer at 37°C, gentle tapping of a meristematic tip in a drop of 1% Rosner aceto carmine on a slide, gentle squashing under a cover glass, warming over a spirit flame for 3-5 seconds, and further squashing.

## Results

The results of the various crosses are given in Table 1. One viable kernel was produced when Th. distichum was crossed with Th. elongatum. It developed into a vigorous perennial plant with 2n=21, and was readily cloned. This hybrid was completely sterile. A few of the cloned plants produced fertile $C_1$ sectors after colchicine treatment, and 13 seeds were obtained. Ten of the seeds germinated to give 6 plants with 42 chromosomes, 3 plants with 41 chromosomes and one plant with 43 chromosomes. This is indicative of some meiotic instability in the amphiploid. The $C_2$ spikes on average had 18 spikelets/spike and each spikelet had 11 florets. The $C_2$ plants were rather infertile and on average produced only 3,4 kernels/spike (range 0-12).

TABLE 1

Th. distichum crossed more readily with Th. junceiforme (Table 1), but the kernels were inviable and the embryos had to be rescued by the embryo-culture method. Five mature perennial plants were obtained with 2n=28, but they were not as vigorous as the Th. distichum/Th. elongatum hybrid, and produced poorly developed spikes which were completely sterile. No fertile amphiploids could be obtained with colchicine treatment. The reciprocal cross yielded some seed, but these were without viable embryos.

The two Triticum durum cultivars Balcarceno Inta and Yavaros 79 both crossed much more readily with Th. junceum (Table 1) than with Th. distichum (Pienaar, 1981). Again the hybrid embryos had to be rescued from the endospermless seeds. Nine hybrid plants with 2n=28 were obtained. These were completely sterile. The Yavaros 79/Th. junceiforme hybrid produced fertile sectors after colchicine treatment. Chromosome counts were obtained on eleven $C_2$ seedlings; seven had 55 chromosomes, three had 56 chromosomes and one had 57 chromosomes. These results were similar to those

Table 1. Crossing results involving *Thinopyrum distichum* (2n=28), *Th. elongatum* (2n=14), *Th. junceiforme* (2n=28), and *Triticum turgidum* var. *durum* (2n=28).

| Cross | No. of pollinated florets | No. of kernels set | No. of embyros excised | No. of successful cultures | Mature plants |
|---|---|---|---|---|---|
| 1. *Th. distichum* X *Th. elongatum* | 66 | 1 (kernel was viable) | | | 1 |
| 2. *Th. distichum* X *Th. junceiforme* | 130 | 51 | 39 | 9 | 5 |
| 3. *Th. junceiforme* X *Th. distichum* | 84 | 17 | 0 | 0 | 0 |
| 4. *T. durum* cv. Balcarceno Inta X *Th. junceiforme* | 22 | 6 | 6 | 3 | 3 |
| 5. *T. durum* cv.'Yavaros 79' X *Th. junceiforme* | 84 | 10 | 10 | 6 | 6 |

obtained with the T. durum/Th. distichum amphiploids (Pienaar, 1983). The Yavaros 79/Th. junceiforme $C_2$ amphiploid plants with 2n=56, on average had 12,3 spikelets/spike, four florets/spikelet, and produced 14,8 kernels/spike. ~~It~~ They were thus more fertile than the T. durum/Th. distichum $C_2$ amphiploids, which averaged 8,5 kernels/spike. However, the latter amphiploids were much larger and more vigorous than the Yavaros 79/Th. junceiforme amphiploid, they back-crossed more readily with T. durum, and their $BC_1F_1$ progeny were more fertile than those of the Yavaros 79/Th. junceiforme//Yavaros 79 $BC_1F_1$ plants, viz. 14,2 kernels/spike against 4,7 kernels/spike, respectively.

The meiotic results of three of the hybrids listed in Table 1 (hybrids 1, 2 and 5) are given in Table 2 (hybrids 3, 4 and 5) and compared with the results obtained previously with other hybrids, viz. Th. bessarabicum/Th. elongatum (Wang, 1985), Th. junceiforme/Th. elongatum (Cauderon & Saigne, 1961), T. durum/Th. junceiforme (Östergren, 1940b), T. durum/Th. distichum (Pienaar, 1981) T. aestivum/Th. distichum (Pienaar, 1981), and T. durum/Th. elongatum amphiploid/3/T. durum/Th. distichum amphiploid//T. durum (Pienaar, 1983).

TABLE 2

Nearly all the ring bivalents of the Th. distichum/Th. elongatum hybrid involved pairs of short chromosomes, and many of the trivalents consisted of one long and two short chromosomes. The short pairs were probably those of Th. distichum.

The poorly developed spikes of the Th. distichum/Th. junceiforme hybrids made it difficult to obtain microsporocytes at metaphase I, and only 50 cells could be analysed. ~~These plants were sterile.~~

Table 2. Average chromosome associations and ranges at metaphase I of meiosis in PMC's of the hybrids involving *Thinopyrum bessarabicum* (2n=14), *Th. elongatum* (2n=14), *Th. distichum* (2n=28), *Th. junceiforme* (2n=28), *Triticum durum* (2n=28) and *T. aestivum* (2n=42).

| Cross | 2n, and Genomes | No. of PMC's | Univalents | Bivalents | | | Multivalents | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Rod | Ring | Total | III | IV | V+ |
| 1* *Th. bessarabicum*/*Th. elongatum* | 14 $JJ^e$ | 526 | 2,68 (0-12) | 3,24 (0-7) | 1,43 (0-5) | 4,68 | 0,27 (0-2) | 0,27 (0-2) | 0,001 (0-1) |
| 2* *Th. junceiforme*/*Th. elongatum* | 21 $J_1J_2J^e$ | 100 | 3,40 (0-7) | - | - | 4,50 (0-9) | 2,76 (0-7) | 0,08 (0-1) | - |
| 3. *Th. distichum*/*Th. elongatum* | 21 $J^d_1J^d_2J^e$ | 50 | 2,92 (1-6) | 1,58 (0-4) | 2,78 (0-6) | 4,36 (0-8) | 2,96 (0-7) | 0,12 (0-1) | - - |
| 4. *T. distichum*/*Th. junceiforme* | 28 $J^d_1J^d_2J_1J_2$ | 50 | 5,0 (1-8) | 2,98 (1-7) | 3,58 (1-7) | 6,56 (4-11) | 1,7 (0-6) | 0,88 (0-3) | 0,2 (0-2 |
| 5. *T. durum* cv. Yavaros 79/*Th. junceiforme* | 28 $ABJ_1J_2$ | 50 | 14,42 (8-24) | 6,6 (1-10) | 0,28 (0-2) | 6,44 (1-10) | 0,22 (0-2) | - - | - - |
| 6* *T. durum* cv. Rivet's Bearded/*Th. junceiforme* | 28 $ABJ_1J_2$ | 50 | 18,40 (14-28) | - | - | 4,80 (0-7) | - | - | - |
| 7* *T. durum* cv. Nordum/*Th. distichum* | 28 $ABJ^d_1J^d_2$ | 200 | 14,12 (6-26) | 3,55 (0-7) | 1,26 (0-4) | 4,81 (1-9) | 0,38 (0-2) | 0,75 (0-2) | 0,02 (0-1) |
| 8* *T. aestivum* cv. Inia 66/*Th. distichum* | 35 $ABDJ^d_1J^d_2$ | 300 | 23,78 (15-35) | 4,05 (0-9) | 0,60 (0-4) | 4,65 (0-10) | 0,44 (0-2) | 0,15 (0-1) | 0 |
| 9* *T. durum* cv. Calvin/*Th. distichum*//Calvin | 42 $AABBJ^d_1J^d_2$ | 100 | 3,18 (0-8) | 4,42 (0-10) | 14,40 (10-18) | 18,82 (16-21) | 0,12 (0-1) | 0,19 (0-1) | 0 |
| 10* *T. durum*/*Th. elongatum*/3/*T. durum*/*Th. distichum*//*T. durum* | 42 $AABBJ^eJ^d$ | 300 | 0,06 (0-22) | 4,79 (0-12) | 12,14 (5-18) | 16,94 (10-21) | 0,37 (0-3) | 0,23 (0-1) | 0,003 (0-1) |

* **(1)** Wang (1985); **(2)** Cauderon & Saigne (1961); **(6)** Östergren (1940b); **(7) & (8)** Pienaar (1981); **(9) & (10)** Pienaar (1983)

Just as the $J_1$ and $J_2$ genomes of Th. junceiforme rarely pair with each other in Th. junceiforme itself, so do they apparently fail to pair regularly in the T. durum/Th. junceiforme amphiploid. Such pairing would result in quadrivalents, trivalents and univalents. The cytological preparations of the amphiploid did not permit scoring for quadrivalent and trivalent formation, but the frequency of univalents was rather low, with only 13 of 100 PMC's scored having one or more. It probably has a fairly normal meiosis.

## Discussions and Conclusions

The analysis of the meiotic data of two Th. bessarabicum/Th. elongatum hybrids (Table 2, hybrid 1) led Wang (1985) to conclude that the hybrids have two similar but non-identical genomes, J and $J^e$. On the ~~grounds~~ basis of karyotype analyses and electrophoretic investigations of seed proteins, Moustakas & Coucoli (1982) and Moustakas et al. (1986) are of the opinion that the J genome of Th. bessarabicum is identical to one of the two genomes of Th. junceiforme. These two genomes were named $J_1$ and $J_2$ by Östergren (1940a) on the grounds of autosyndetic pairing between the $J_1$ and $J_2$ genomes in a Th. junceiforme/Elymus repens hybrid. Cauderon and Saigne (1961) and Heneen (1963) supported the findings of Östergren and concluded that Th. junceiforme and E. repens have no genomes in common; i.e., $J \neq S \neq H \neq Y$.

The meiotic analysis of the two T. durum/Th. junceiforme $F_1$ hybrids which revealed bivalent averages of 6,44 and 4,80/PMC (Table 2, hybrids 5 and 6) confirmed the high incidence of autosyndesis between the chromosomes of the $J_1$ and $J_2$ genomes of Th. junceiforme, since the homoeologous chromosomes of the A and B genomes according to Kihara (1936) and Lacadena & Ramos (1968) rarely undergo synapsis.

In the triploid hybrid, Th. junceiforme/Th. elongatum, of Cauderon & Saigne (1961) the two genomes of Th. junceiforme paired autosyndetically, as well as allosyndetically with the Th. elongatum genome to produce a maximum of seven trivalents per PMC and averages of 2,76 trivalents, 4,50 bivalents and 3,40 univalents per cell (Table 2, hybrid 2). If the three sets were identical and all chromosomes were metacentric, the averages per PMC would have been 4,67 trivalents, 2,33 bivalents and 2,33 univalents. However, some Thinopyrum chromosomes are submetacentric to acrocentric and/or shorter than the rest (Hsiao et al., 1986). This reduces the chances of trivalent formation and increases the averages of the bivalents and univalents per PMC. The attained pairing configurations are therefore indicative of great similarity between the three genomes.

From the above observations it can be concluded that the genomes of the two diploid species Th. bessarabicum and Th. elongatum are not only similar to each other, but also similar to the two nearly identical genomes of the near-autotetraploid (or segmental allotetraploid), Th. junceiforme. The latter species probably arose as an autopolyploid whose two genomes underwent some differentiation or diploidization (Cauderon, 1958; Charpentier et al., 1986). Until a meiotic analysis of the hybrid between Th. junceiforme and Th. bessarabicum can prove that the $J_1$ genome of the former species is identical to the J genome of the latter species, the designations of Östergren (1940), Wang (1985) and Moustakas et al. (1986) should be retained; i.e., JJ for Th. bessarabicum, $J^eJ^e$ for Th. elongatum, and $\hat{J}_1J_1J_2J_2$ for Th. junceiforme.

As mentioned in the "Introduction", Pienaar (1981, 1983) found much autosyndetic pairing between the chromosomes of the two genomes of Th. distichum in the presence of the

wheat genomes (Table 2, hybrids 7, 8 and 9). After deducting the expected meiotic configurations of the wheat genomes, the averages per PMC of the synaptic configurations involving the two Th. distichum genomes were 0,12 univalents, 4,81 bivalents, 0,38 trivalents and 0,75 quadrivalents in the tetraploid hybrid (~~Table 2,~~ hybrid 7); 2,78 univalents, 4,65 bivalents, 0,44 trivalents and 0,15 quadrivalents in the pentaploid hybrid (~~Table 2,~~ hybrid 8); and 3,18 univalents, 4,82 bivalents, 0,12 trivalents and 0,19 quadrivalents in the hexaploid hybrid (~~Table 2,~~ hybrid 9). As the number of wheat genomes in the hybrids increases, the number of multivalents produced by the two Th. distichum genomes decreases and the number of univalents increases. The number of bivalents, is, however, always at least 4,65 per cell. According to the definition given in the "Introduction", the two Th. distichum genomes are therefore not distinct, but variants of the same genome. Thus, Th. distichum can also be regarded as a segmental allotetraploid like Th. junceiforme, but its two genomes are less similar to each other than are the $J_1$ and $J_2$ genomes of the latter species, whose pairing configurations averaged 6,44 bivalents and 0,22 trivalents in a similar hybrid (Table 2, hybrid 5).

The substantial amount of autosyndesis between the two Th. distichum genomes in the presence of the wheat genomes, was also evident in the absence of the wheat genomes (Table 2, hybrids 3 and 4). It was therefore not induced by the wheat genomes. The Th. distichum/Th. elongatum triploid hybrid in fact averaged 2,96 univalents, 4,36 bivalents, ~~and~~ 2,94 trivalents and 0,12 quadrivalents per PMC. The trivalent frequency of 2,96 per cell was more than half the frequency of the 4,67 trivalents per cell that would be expected if the two genomes of Th. distichum and the $J^e$ genome of Th. elongatum were completely homologous and if pairing in one arm did not effect pairing in the other arm. The observed frequency, therefore, suggests substantial homology between

the genomes of the two species. The two Th. distichum genomes can therefore be regarded as variants of the basic J genome. Their similarity to the $J^e$ genome is as close as the $J_1$ and $J_2$ genomes of Th. junceiforme are to each other (compare Table 2, hybrids 2 and 3). It is therefore recommended that the two Th. distichum genomes be designated $J^d_1$ and $J^d_2$.

The T. durum/Th. distichum amphiploid//T. durum $BC_1F_1$ hexaploid when crossed with the T. durum/Th. elongatum amphiploid of Jenkins & Mochizuki (1957), gave rise to the complex hybrid listed in Table 2 as hybrid 10. If the above genome designations ~~is~~ are applied, its genome constitution is $AABBJ^dJ^e$; the $J^d$ genome partly consists of $J^d_1$ and partly of $J^d_2$ chromosomes. The PMC's of this hybrid on average had 2,94 bivalents and 0,6 multivalents in excess of the 14 bivalents produced by the A and B genomes. These extra associations are due to synaptic pairing between the $J^d$ and $J^e$ genomes. This again points to some similarity between the genomes of Th. elongatum and Th. distichum.

The Th. distichum/Th. junceiforme tetraploid hybrid did not live up to expectations. It flowered late in the season and produced poorly developed spikes. The 50 analisable PMC's ~~on~~ averaged ~~had~~ 6,56 bivalents (Table 2, hybrid 4), which is less than the expected 11,25 bivalents (i.e., the combined bivalent frequency of 6,44 produced by the $J_1$ and $J_2$ genomes in the hybrid listed in Table 2 as hybrid 5, and the bivalent frequency of 4,81 produced by the $J^d_1$ and $J^d_2$ genomes in the hybrid listed in Table 2 as hybrid 7). On the other hand, the high average of 2,8 multivalents/PMC, which ranged up to 6 (Table 2, hybrid 4), is indicative of substantial homology between the Th. distichum and Th. junceiforme genomes.

The similarity between the J, $J_1$, $J_2$, $J^d_1$, $J^d_2$ and $J^e$ genomes of the various species in the section Thinopyrum will make

it possible to obtain recombined chromosomes consisting of the best segments of two or more homologues of the J-genome series. Some of these may be better for chromosome substitution work in wheat-breeding programmes than the original chromosomes. The applicability of the pivotal-genome concept (proposed by Zohary and Feldman, 1962) to produce new, reshuffled genomes from two or more genomes, was demonstrated in the T. durum/Th. elongatum amphiploid/3/T. durum/Th. distichum amphiploid//T. durum hybrid (Table 2, hybrid 10). Fully fertile plants with 2n=42 were selected in the $F_3$ and subsequent generations that had a balanced, reshuffled $J^{d-e}$ genome pair, consisting partly of Th. distichum and partly of Th. elongatum chromosomes, in addition to the T. durum genomes which served as pivotal genomes. This material may serve as valuable intermediates to transfer genes for important traits from Thinopyrum to wheat using the techniques proposed by Kimber (1984a,b) and Sears (1983).

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