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Standard karyotype of *Triticum umbellulatum* and the characterization of derived chromosome addition and translocation lines in common wheat

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Abstract A standard karyotype and a generalized idiogram of *Triticum umbellulatum* (syn. *Aegilops umbellulata*, 2n = 2x = 14) was established based on C-banding analysis of ten accessions of different geographic origin and individual *T. umbellulatum* chromosomes in *T. aestivum* – *T. umbellulatum* chromosome addition lines. Monosomic (MA) and disomic (DA) *T. aestivum* – *T. umbellulatum* chromosome addition lines (DA1U = B, DA2U = D, MA4U = F, DA5U = C, DA6U = A, DA7U = E = G) and telosomic addition lines (DA1US, DA1UL, DA2US, DA2UL, DA4UL, MA5US, (+ iso 5US), DA5UL, DA7US, DA7UL) were analyzed. Line H was established as a disomic addition line for the translocated wheat – *T. umbellulatum* chromosome T2DS·4US. Radiation-induced wheat – *T. umbellulatum* translocation lines resistant to leaf rust (*Lr9*) were identified as T40 = T6BL·6BS-6UL, T41 = T4BL·4BS-6UL, T44 = T2DS·2DL-6UL, T47 = 'Transfer' = T6BS·6BL-6UL and T52 = T7BL·7BS-6UL. Breakpoints and sizes of the transferred *T. umbellulatum* segments in these translocations were determined by *in situ* hybridization analysis using total genomic *T. umbellulatum* DNA as a probe

Key words C-banding · Genomic *in situ* hybridization · *Triticum aestivum* · *T. umbellulatum* · Chromosome addition and translocation

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Introduction

Triticum umbellulatum (Section polyeides; syn. *Aegilops umbellulata*) is a diploid (2n = 2x = 14, genome composition UU) wild relative of cultivated bread wheat, *T. aestivum* (2n = 6x = 42, AABBDD). It is an inbreeder and native to the Mediteranean region including Greece, Turkey, Syria, Iran, Iraq and Russia (Kimber and Feldman 1987). *T. umbellulatum* is involved in the parentage of the polyploid species *T. kotschyi* (syn. *Ae. kotschyi*) (2n = 4x = 28, UUSS), *T. peregrinum* (syn. *Ae. peregrina*, *Ae. variabilis*) (2n = 4x = 28, UUSS), *T. ovatum* (syn. *Ae. ovata*) (2n = 4x = 28, UU*MM*), *T. neglecta* (syn. *Ae. triaristata*) (2n = 4x = 28, UU*MM*), *T. macrochaetum* (syn. *Ae. biuncialis*, *Ae. lorentii*) (2n = 4x = 28, UU*MM*), *T. columnare* (syn. *Ae. columnaris*) (2n = 4x = 28, UU*MM*), *T. triunicale* (syn. *Ae. triuncialis*) (2n = 4x = 28, UU*CC*), *T. juvenale* (syn. *Ae. juvenalis*) (2n = 6x = 42, *DDMMUU*) and *T. recta* (syn. *Ae. triaristata* 6x) (2n = 6x = 42, UU*MMNN*) (Kimber and Feldman 1987; Kimber and Abu Baker 1981; Kimber and Sears 1987; Kimber and Yen 1989; Yen and Kimber 1992).

T. umbellutaum is the source of the leaf rust resistance gene *Lr9* that has been transferred to wheat using radiation treatment (Sears 1956). In addition, it is a source of resistance to powdery mildew, Hessian fly and greenbug (Gill et al. 1985). Kimber (1967) produced a set of *T. aestivum* – *T. umbellulatum* chromosome addition lines, and nine derived telosomic addition lines have been produced by one of us (NT).

C-banding and genomic *in situ* hybridization (GISH) analyses are very powerful tools to detect alien chromatin in wheat (for review see Friebe et al. 1993a,b; Jiang et al. 1994). In the present article we present a generalized idiogram of *T. umbellulatum* based on C-banding analysis of ten different accessions. Furthermore, C-banding and GISH analysis were used to identify wheat – *T. umbellulatum* chromosome addition, telosome addition and translocation lines.

Material and methods

Plant material

Ten accessions of *T. umbellulatum* were analyzed and their origins are given in Table 1. In addition, the amphiploid *T. aestivum* cv 'Chinese Spring' (CS) – *T. umbellulatum* accession no. U2010001 (2n = 56, AABBDDUU), 6 derived disomic chomosome addition lines, DA, (A, B, C, D, E and G), 1 monosomic chromosome addition line, MA, (F) and 1 disomic addition line for a CS – *T. umbellulatum* translocation chromosome (H = CSU-31) were analyzed. The amphiploid and the set of chromosome addition lines were produced and kindly provided by G. Kimber, University of Missouri, and seed smaples of these lines were also obtained from S. M. Reader, Cambridge laboratory. The homoeologous relationships of six of the seven *T. umbellulatum* chromosomes were established by analyzing their meiotic chromosome pairing behavior and their compensation ability in chromosome substitution lines (Chapman and Riley 1970; Athwal and Kimber 1972; Riley et al. 1973; Chapman et al. 1974; Koebner and Shepherd 1987; Reader and Miller 1987) as well as by storage protein (Shephered 1973; Brown et al. 1979; Lawrence and Shephered 1981; Stinissen et al. 1983) and isozyme analyses (Benito et al. 1987). One monotelosomic and 8 ditelosomic CS – *T. umbellulatum* chromosome addition lines that had been produced by one of us (NT) were included in the present analysis.

Furthermore, a wheat – *T. umbellulatum* chromosome addition line having a gene for resistance to leaf rust (*Lr9*) as well as 5 radiation-inducecd and leaf rust-resistant wheat – *T. umbellulatum* translocation lines (T40, T41, T44, T47 = 'Transfer' and T52) produced by Sears (1956) and obtained from K. Ross, University of Missouri were analyzed.

Table 1 Origins of the *T. umbellulatum* accessions

Accession no.	Origin
TA1825[a]	Turkey
TA11829[a]	Iran
TA1831[a]	Iran
TA1833[a]	Iran
TA1835[a]	Afghanisan
TU24[b]	Turkey
TU31[b]	Turkey
KU8–1[c]	Turkey
KU8–5[c]	Syria
U201001[d]	Unknown

[a] Wheat Genetics Resource Center, Kansas State University, Manhattan, Kan., USA
[b] Obtained from G. Kimber, University of Missouri, Columbia, Mo., USA
[c] Obtained from S. Ohta, Plant Germ plasm Institute, Kyoto University, Kyoto, Japan
[d] Obtained from S. M. Reader, Cambridge Laboratory, Norwich, UK

Cytogenetic analysis

Root tips were pretreated with 0.05% colchicine for 3 h and fixed in 99% ethanol-glacial acetic acid (3:1). Chromosome identification was according to the C-banding technique described by Gill et al. (1991). For GISH analysis the protocol of Jiang et al. (1993) modified from Le et al. (1989) was used. Chromosome measurements were made on 20 C-banded *T. umbellulatum* chromosomes present in the amphiploid CS – *T. umbellulatum* using wheat chromosome 3B as a standard. Breakpoints were determined in ten CS-*T. umbellulatum* translocation chromosomes after C-banding and GISH analysis, and the positions of the break points were calculated as fraction lengths from the centromere (FLs). Microphotographs were taken with a Zeiss photomicroscope III using Kodak Imagelink HQ microfilm 1461.

Results

C-banding polymorphism of *T. umbellulatum*

T. umbellulatum has seven pairs of similarly sized metacentric to submetacentric chromosomes. Chromosomes 1U and 5U are SAT chromosomes and can be identified in phase contrast by the presence of secondary constrictions (Fig. 1a). The secondary constriction is usually more prominent in 1U than in 5U. All *T. umbellulatum*

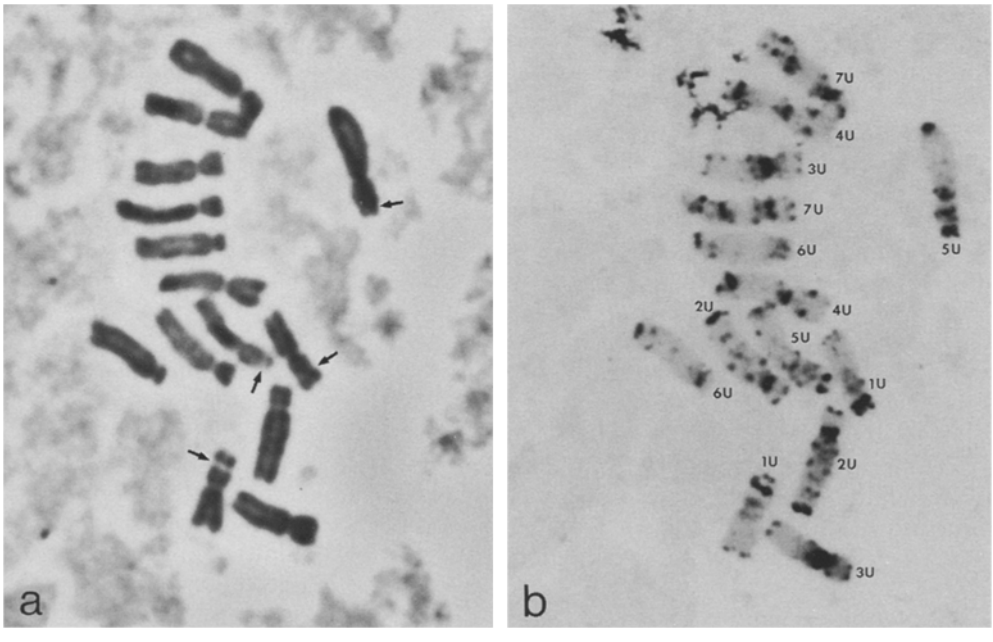


Fig. 1a,b Mitotic metaphase chromosomes of *T. umbellulatum* accession no. U201001. **a** Phase contrast, **b** C-banding (*arrows* point to the secondary constrictions)

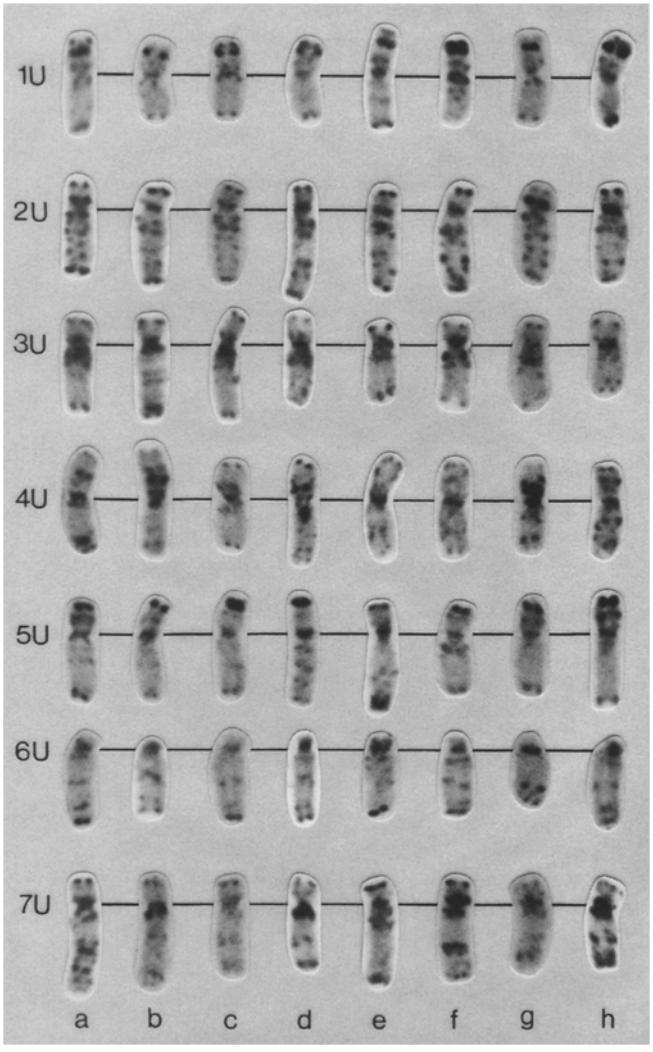


Fig. 2a–h C-banded karyotypes of *T. umbellulatum*. **a** U2010001, **b** TA1825, **c** TA1831, **d** TA1835, **e** TU24, **f** Tu31, **g** KU8–1, **h** KU8–5

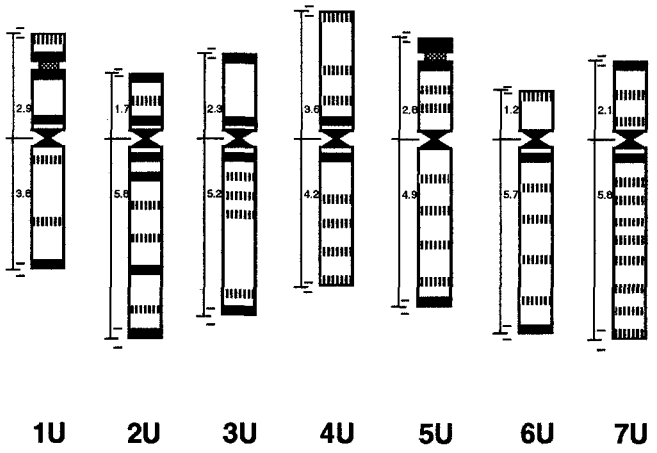


Fig. 3 Generalized idiogram of *T. umbellulatum* (Marker C-bands that are present in all accessions are shown in *black* and C-bands that are present only in some accessions are shown in *hatching*; chromosome arm length data are given in μm and are based on measurements of 20 chromosomes of each *T. umbellulatum* chromsome present in the amphiploid CS-*T. umbellulatum*; standard deviations of the measurements are indicated by *small bars*)

chromosomes have C-bands at the centromeres and, in addition, interstitial and telomeric C-bands, permitting their identification (Fig. 1b). Polymorphism for C-band size and C-band position was only found between the different accessions analyzed (Fig. 2). Monomorphic C-bands, called marker C-bands, were diagnostic for chromosome identification and are indicated by solid bands in the generalized idiogram of *T. umbellulatum* (Fig. 3). Polymorphic C-bands present in some accessions only are shown in hatching. No large structural chromosomal rearrangments were detected in any of the *T. umbellulatum* accessions analyzed.

1) Chromosome 1U (arm ratio L/S: 1.3, L + S: 6.68 ± 1.46 μm, 63% of total 3B length): The SAT chromosome has a secondary constriction in the distal region of the short arm. Marker C-bands are present at both sides of the NOR, in the proximal region of the short arm and at the telomere of the long arm.

2) Chromosome 2U (L/S: 3.3, L + S: 7.50 ± 0.72 μm, 71% of total 3B length): Proximal marker C-bands are present on both sides of the centromere, 1 in the short and 2 in the long arm. In addition, marker C-bands are present at both telomeres and at an interstitial position in the long arm.

3) Chromosome 3U (L/S: 2.3, L + S: 7.47 ± 0.70 μm, 71% of total 3B length): Marker C-bands are present on both sides of the centromere and at both telomeres.

4) Chromosome 4U (L/S: 1.2, L + S: 7.81 ± 0.48 μm, 74% of total 3B length): Marker C-bands are present on both sides of the centromere. Chromosome 4U shows the largest amount of C-band ploymorphism.

5) Chromosome 5U (L/S: 1.7, L + S: 7.64 ± 0.60 μm, 72% of total 3B length): The SAT chromosome has a secondary constriction in the distal region of the short arm. Marker C-bands are present at the NOR and at both telomeres.

6) Chromosome 6U (L/S: 5.0, L + S: 6.86 ± 0.50 μm, 65% of total 3B length): Marker C-bands are present close to the centromere and at the telomere of the long arm.

7) Chromosome 7U (L/S: 2.8, L + S: 7.82 ± 0.75 μm, 74% of total 3B length): Marker C-bands are present at the telomere of the short arm and close to the centromere in the long arm.

Identification of *T. aestivum* – *T. umbellulatum* chromosome addition and translocation lines

The C-banding patterns of the *T. umbellulatum* chromosomes in the amphiploid CS – *T. umbellulatum* and in the set of related wheat – *T. umbellulatum* chromosome addition lines are identical to those of the corresponding chromosomes present in the *T. umbellulatum* parent accession no. U2010001. Thus, these chromosomes are

not structurally rearranged. Lines A, B, C, D and E = G were identified as DA6U, DA1U, DA5U, DA2U, and DA7U, respectively (Fig. 4). Of the 20 plants of line F analyzed, 5 were identified as being monosomic for chromosome 4U (MA4U), whereas 1 plant was disomic for this chromosome (DA4U). Line H was identified as a disomic addition line for the wheat – *T. umbellulatum* translocation chromosome T2DS·4US with the breakpoint within the centromeric region. Because all other *T. umbellulatum* chromosomes were already assigned to their homoeologous groups, except for the group 3 chromosome, the *T. umbellulatum* chromosome missing in the set of addition lines was designated as 3U. C-banding identified the *T. umbellulatum* telosomes as 1US, 1UL, 2US, 2UL, 4UL, 5US, 5UL, 7US and 7UL. Except for 5US, a monosomic addition line also having an isochromosome 5US, all of the other lines were disomic for the *T. umbellulatum* telosomes.

Radiation-induced wheat – *T. umbellulatum* translocation lines resistant to leaf rust (*Lr9*), T40, T41, T44, T47 and T52, were identified as T6BL·6BS-6UL, T4BL·4BS-6UL, T2DS·2DL-6UL, T6BS·6BL-6UL, and T7BL·7BS-6UL translocation lines, respectively (Figs. 5, 6). The breakpoints and sizes of the transferred *T. umbellulatum* segment were determined by GISH analysis (Table 2).

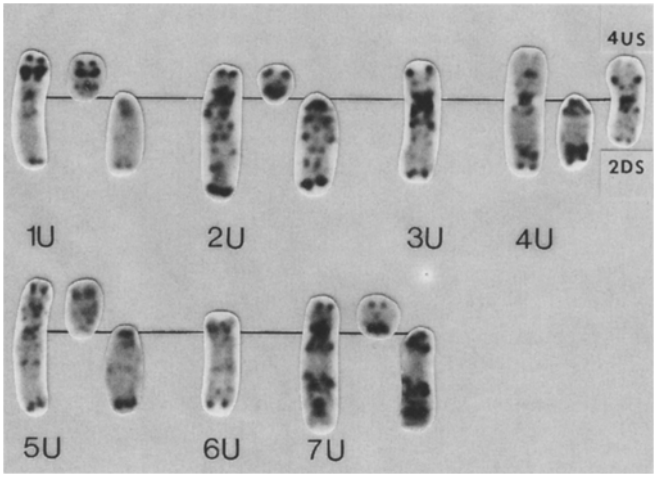
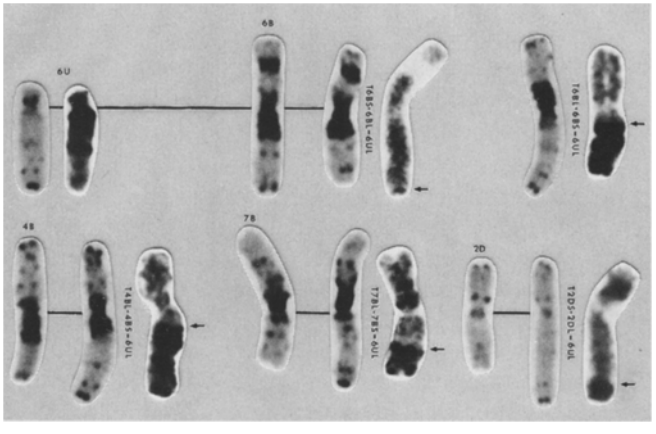


Fig. 4 C-banding patterns of the *T. umbellulatum* chromosomes, telosomes and a wheat – *T. umbellulatum* translocation chromosome present in the CS – *T. umbellulatum* chromosome addition and telosomic addition lines

Fig. 5 C-banding (*left*) and genomic *in situ* hybridization patterns (*right*) of the critical wheat, *T. umbellulatum* and wheat – *T. umbellulatum* translocation chromosomes involved in the radiation-induced leaf rust (*Lr9*)-resistant transfers (*arrows* point to the breakpoints)



Spike morphologies of the *T. aestivum* – *T. umbellulatum* chromosome addition and telosome addition lines

Spikes of the CS – *T. umbellulatum* chromosome addition and telosomic addition lines are shown in Fig. 7. Spikes of DA1U and the ditelosomic additions for the short and long arms are seen to be similar in appearance to those of CS. Spikes of DA2U have awns and tenacious glumes. The ditelosomic addition for 2UL is similar in appearance to the whole chromosome addition, whereas spikes of the ditelosomic addition for the short arm are similar to those of CS. Spikes of he monosomic addition 4U and the ditelosomic addition 4UL are similar to those of CS, and spikes of the disomic addition for the translocation chromosome T2DS·4UL are shorter than those of CS. The spikes of both the disomic addition 5U and the ditelosomic addition 5UL are lax at the base and compact at the top. Spikes of the monoisosomic addition 5US, that should be equivalent to DA5US, are similar to CS. Spikes of both the disomic

Fig. 6 Idiograms of the radiation-induced wheat – *T. umbellulatum* translocation chromosomes. *T. umbellulatum* segments are shown in *light* (unbanded regions) or *dark* (C-banded regions) *hatching*

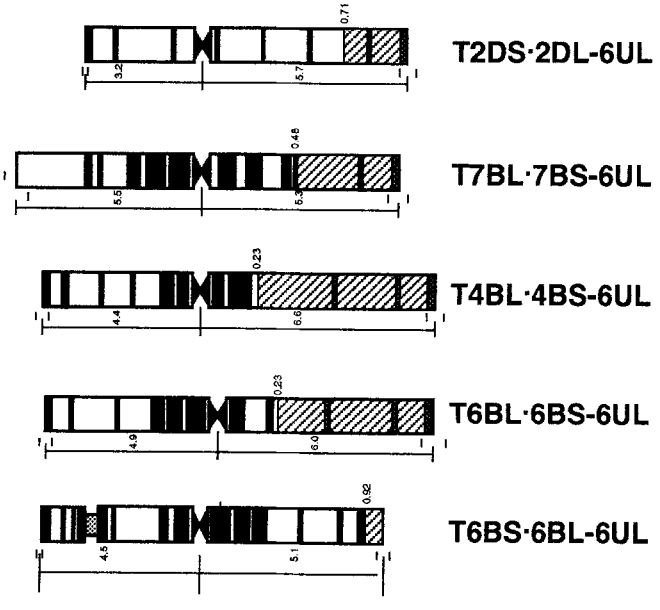


Table 2 Chromosome arm lengths standard deviations (s), arm ratios, translocation breakpoints given as fraction lengths from the centromere, sizes of the transferred *T. umbellulatum* segments and sizes of the missing wheat segments in radiation-induced leaf rust resitant wheat – *T. umbellulatum* translocation lines

Line[a]	Chromosome	Chromosome arm length[b] (s) in μm		Arm ratio L/S	Fraction length of translocation breakpoints	Size of the *T. umbellulatum* segment in μm[c]	Size of the missing wheat segment in μm[d]
		S arm	L arm				
CS	3B	4.06(0.32)	5.82(0.36)	1.4			
DA6U	6U	1.18(0.19)	5.88(0.53)	5.0			
CS	6B	4.68(0.49)	5.18(0.70)	1.1			
T47	T6BS·6BL-6UL	4.48(0.20)	5.08(0.44)	1.1	0.92	0.41(7%)	0.51(10%)
T40	T6BL·6BS-6UL	4.90(0.42)	6.04(0.70)	1.2	0.23	4.65(79%)	3.29(70%)
CS	4B	4.42(0.36)	4.78(0.38)	1.1			
T41	T4BL·4BS-6UL	4.44(0.41)	6.60(0.50)	1.5	0.23	5.08(86%)	2.90(66%)
CS	7B	3.76(0.26)	5.76(0.29)	1.5			
T52	T7BL·7BS-6UL	5.31(0.74)	5.47(0.55)	1.0	0.48	2.84(48%)	1.13(30%)
CS	2D	3.27(0.29)	4.27(0.33)	1.3			
T44	T2DS·2DL-6UL	3.20(0.28)	5.74(0.51)	1.8	0.71	1.66(28%)	0.19(4%)

[a] DA = disomic addition; CS = *T. aestivum* cv 'Chinese Spring'
[b] Total chromosome length of chromosome 6U corresponds to 71% of the total chromosome length of 3B of CS
[c] Percentage of the corresponding *T. umbellulatum* chromosome arm is given in parentheses
[d] Percentage of the corresponding wheat chromosome are given in parentheses

Fig. 7 Spike morphologies of the CS – *T. umbellulatum* chromosome addition and telosomic addition lines. From *left to right, upper row: T. umbellulatuum*, CS, CS – *T. umbellulatum* amphiploid, DA1U, DA1US, DA1UL, DA2U, DA2US, DA2UL, MA4U, DAT2DS·4US, DA4UL; *lower row*: DA5U, MA5US +iso 5US, DA5UL, DA6U, DA7U, DA7US, DA7UL

addition 7U and the ditelosomic addition 7UL are more lax at the base than those of CS, and spikes of DA7US are similar to those of CS.

Discussion

T. umbellulatum has two pairs of nucleolus organizer regions (NORs) that were identified earlier by the presence of secondary constrictions (Chennaveeraiah 1966), by *in situ* hybridization using a ribosomal DNA probe (Teoh et al. 1983) and by Ag-NOR-banding (Cermeno et al. 1984). *T. umbellulatum* SAT chromosomes have been previously identified as being 1U and 5U, and it has been shown that these chromosomes partially inactivate the NORs on wheat chromosomes 1B, 6B and 5D (Martini et al. 1982; Lacadena and Cermeno 1985).

The C-banding patterns of the *T. umbellulatum* chromosomes presented here are similar to the C- and N-banding patterns of this species reported earlier (Gill 1981; Jewell and Driscoll 1983; Teoh and Hutchinson 1983; Cermeno et al. 1984). However, in earlier studies only one *T. umbellulatum* accession was analyzed, and no information was available with respect to C-band

polymorphisms. The present study describes the variation in C-banding patterns observed in ten different *T. umbellulatum* accessions and establishes a generalized idiogram of this species.

Whereas no variation in C-banding patterns was observed within the *T. umbellulatum* accessions analyzed, polymorphism for C-band size and C-band position was observed between the different accessions; however, this did not prevent chromosome identification. No large structural rearrangements detectable by C-banding analysis were found in any of the *T. umbellulatum* accessions analyzed. This situation is similar to the one found in *T. dichasians* (syn. *Ae. caudata*, *Ae. markgrafii*) and *T. longissimum* (syn. *Ae. longissima*), where C-banding analysis did not detect large rearrangements in 19 and 17 of the accessions analyzed, respectively (Friebe et al. 1992a,b). However, in *T. tauschii* (syn. *Ae. squarrosa*) 2 out of 16 accessions and in *T. searsii* (*Ae. searsii*) 1 out of 14 accessions analyzed were found to be homozygous for reciprocal tanslocations involving complete chromosome arms (Friebe et al. 1992b and unpublished). Translocations have also been found in other *Triticum* species (Kawahara 1986, 1987, 1988, 1990; Badaeva et al. 1993).

Chromosomes 1U, 2U, 5U, 6U and 7U were verified as disomic addition lines, whereas 4U is maintained in the monosomic condition. Not addition line was found for chromosome 3U. The C-banding pattern of this chromosome was established and will permit the isolation of this chromosome from the wheat-*T. umbellulatum* amphiploid. Chromosmes 1U, 2U, 5U and 7U are also available as wheat – *T. umbellulatum* substitution lines (Shepherd and Islam 1988). Furthermore, C-banding analysis was used to identify 1 monotelosomic and 8 ditelosomic addition lines (DA1US, DA1UL, DA2US, DA2UL, DA4UL, MA5US (+ iso 5US), DA5UL, DA7US, DA7UL).

Line H was identified as a disomic addition line for the wheat – *T. umbellulatum* translocation chromosome T2DS·4US. Plants of this line show poor vigor, whereas plants that are disomic for the long arm of chromosome 4U only show slightly reduced seed set compared with those of CS. Plants disomic for the complete chromosome 4U can be recovered in progenies of monosomic plants but die before reaching maturity. This suggests that the short arm of chromosome 4U has a gene(s) conditioning poor plant vigor when transferred into a wheat background.

Sears (1956) was first in transferring a gene for resistance to leaf rust, *Lr9*, from a group 6 *T. umbellulatum* chromosome to wheat by using radiation treatment. At least 17 different wheat – *T. umbellulatum* translocations were recovered in his experiment, but only 5 of them have been maintained and were avilable for the present analyis.The C-banding patterns of the group 6 *T. umbellulatum* chromosome having *Lr9* is identical to the corresponding chromosome in the set of 'Chinese Spring' – *T. umbellulatum* chromosome addition lines although it is of different origin. GISH analysis using total genomic *T. umbellulatum* DNA as probe revealed that the proximal half of 6UL shows stronger hybridization than the distal half of this chromosome arm. This result suggests that the proximal half of 6UL has a higher amount of highly repetitive DNA that is related to the U genome than the distal half, making it difficult to detect small translocations in the latter region.

Our C-banding and GISH analysis confirmed earlier reports (Sears 1956, 1961) and identified these lines as T40 = T6BL·6BS-6UL, T41 = T4BL·4BS-6UL, T44 = T2DS·2DL-6UL, T47 = T6BS·6BL-6UL and T52 = T7BL·7BS-6UL; further, it allowed us to determine the breakpoints and sizes of the transferred *T. umbellulatum* segments in these translocations. All transfers were identified as terminal translocations. Absence of the terminal C-band in the 6BL-6UL arm of the 'Tranfer'-translocation (T47) is mostly likely caused by the loss of this region in the orignianl 6UL arm. Meiotic pairing analysis revealed that the T6BS·6BL-6UL translocation chromosome only pairs in 12% of the pollen mother cells with the complete chromosome 6U, whereas meiotic pairing of the other wheat – *T. umbellulatum* translocation chromosomes was normal (Sears 1956). A similar reduction in the amount of meiotic pairing has also been observed in deletion stocks of wheat (Curtis et al. 1991 and our own unpublished data), indicating that homology at the chromosome ends is essential for normal meiotic pairing and recombination.

The T6BS·6BL-6UL translocation chromosome present in line T47 has the smallest *T. umbellulatum* segment and is the only radiation-induced translocation in which homoeologous chromosome arms are involved. Thus, the transferred *T. umbellulatum* segment can compensate for the missing 6BL segment, resulting in good gametophytic compensation (Sears 1966). However, restriction fragment length polymorphism (RFLP) analysis recently revealed evidence that at least chromosomes 4U and 6U are structurally rearranged compared to those of wheat (Chen et al. unpublished). Further work is under way to confirm the homoeology of all U genome chromosomes.

The basic karyotype information on *T. umbellulatum* presented here will allow a more detailed analysis of the evolutionary relationships of polyploid U genome species and will be also useful for transferring further genes of interest from this species to wheat.

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References

Athwal RS, Kimber G (1972) The pairing of an alien chromosome with homoeologous chromosomes of wheat. Can J Genet Cytol 14: 325–333

Badaeva ED, Gill BS, Badaev NS, Kawahara T, Filatenko AM (1993) Chromosomal rearrangements and the process of intraspecific diversity in *Triticum araraticum*. In: Proc 8th Int Wheat Genet Symp. Beijing, (in press)

Benito C, Figueiras AM, Gonzáles-Jaen MT (1987) Location of genes coding isozyme markers on *Aegilops umbellulata* chromosomes adds data on homoeology. Theor Appl Genet 73: 581–588

Brown JWS, Kemble RJ, Law CN (1979) Control of endosperm proteins in *Triticum aestivum* (var 'Chinese Spring') and *Aegilops umbellulata* by homoeologous group 1 chromosomes. Genetics 93:189–200

Cermeno MC, Orellana J, Santos JL, Lacadena JR (1984) Nucleolar activity and competition (amphiplasty) in the genus *Aegilops*. Heredity 53:603–611

Chennaveeraiah MS (1966) Karyomorphologic and cytotaxonomic studies in *Aegilops*. Acta Hortic Gotob 23:85–178

Chapman V, Riley R (1970) Homoeologous meiotic chromosome pairing in *Triticum aestivum* in which chromosome 5B is replaced by an alien homoeologue. Nature 226:367–377

Chapman V, Riley R, Miller TE (1974) Alien chromosome addition and substitution lines. In: Annual Report of the Plant Breeding Institute, Cambridge, pp 125–126

Curtis CA, Lukaszewski AJ, Chrzastek J (1991) Metaphase-I pairing of deficent chromosomes and genetic mapping of deficiency breakpoints in common wheat. Genome 34:553–560

Friebe B, Schubert V, Blüthner WD, Hammer K (1992a) C-banding pattern and polymorphism of *Aegilpos caudata* and chromosomal constitutions of the amphiploid *T. aestivum – Ae. caudata* and six derived chromosome addition lines. Theor Appl Genet 83: 589–596

Friebe B, Mukai Y, Gill BS (1992b) C-banding polymorphisms in several accessions of *Triticum tauschii* (*Aegilops squarrosa*). Genome 35:192–199

Friebe B, Jiang J, Raupp JW, Gill BS (1993a) Molecular cytogenetic analysis of radiation-induced alien genetic transfers in wheat. In: Proc 8th Int Wheat Genet Symp. Beijing (in press)

Friebe B, Tuleen N, Jiang J, Gill BS (1993b) Standard karyotype of *Triticum longissimum* and its cytogenetic relationship with *T. aestivum*. Genome 36:731–742

Gill BS (1981) Evolutionary relationships based on heterochromatin bands in six species of the Triticinae. J Hered 72:391–394

Gill BS, Sharma HC, Raupp WJ, Browder LE, Hatchett JH, Harvey TL, Moseman JG, Waines JG (1985) Evaluation of *Aegilops* species for resistance to wheat powdery mildew, wheat leaf rust, Hessian fly and greenbug. Plant Dis 69:314–316

Gill BS, Friebe B, Endo TR (1991) Standard karyotype and nomenclature system for description of chromosome bands and structural aberrations in wheat (*Triticum aestivum*). Genome 34:830–839

Jewell DC, Driscoll CJ (1983) The addition of *Aegilops variabilis* chromosomes to *Triticum aestivum* and their identification. Can J Genet Cytol 25:76–84

Jiang J, Friebe B, Dhaliwal HS, Martin TJ, Gill BS (1993) Molecular cytogenetic analysis of *Agropyron elongatum* chromatin in wheat germplasm specifying resistance to wheat streak mosaic virus. Theor Appl Genet 86:41–48

Jiang J, Friebe B, Gill BS (1994) Recent advances in alien gene transfer in wheat. Euphytica 73:199–212

Kawahara T (1986) Difference in structural variability of genomes in *Triticum* and *Aegilops*. Wheat Inf Serv 63:42–43

Kawahara T (1987) Identification of reciprocal translocation types in the emmer wheats. III. Six chromosome types in *Triticum dicoccoides*. Jpn J Genet 62:197–204

Kawahara T (1988) Variation in chromosome structures in *Aegilops kotschyi* Boiss. and *Ae. variabilis* Eig. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp. Bath Press, Bath, UK, pp 99–104

Kawahara T (1990) Spontaneous translocation in the wild diploid wheat, *Triticum boeoticum* Boiss. Jpn J Genet 65:221–223

Kimber G (1967) The addition of the chromosomes of *Aegilops umbellulata* to *Triticum aestivum* (var 'Chinese Spring'). Genet Res 9:111–114

Kimber G, Abu Baker M (1981) The genomic relationships of *Triticum dichasians* and *T. umbellulatum*. Z Pflanzenzuecht 87:265–273

Kimber G, Feldman M (1987) Wild wheat. An introduction. Spec Rep 353, Coll Agric Univ Missouri, Columbia, Mo

Kimber G, Sears ER (1987) Evolution in the genus *Triticum* and the origin of cultivated wheat. In: Heyne EG (ed) Wheat and wheat improvement. Am Soc Agron Monogr 13, Madison Wis., pp 154–164

Kimber G, Yen Y (1989) Hybrids involving wheat relatives and autotetraploid *Triticum umbellulatum*. Genome 32:1–5

Koebner RMD, Shepherd KW (1987) Allosyndetic recombination between a chromosome of *Aegilops umbellulata* and wheat chromosomes. Heredity 59:33–45

Lacadena JR, Cermeno MC (1985) Nucleolus organizer competition in *Triticum aestivum – Aegilops umbellulata* chromosome addition lines. Theor Appl Genet 71:278–283

Lawrence GJ, Shepherd KW (1981) Chromosomal location of genes controlling seed proteins in species related to wheat. Theor Appl Genet 59:25–31

Le HT, Armstrong KC, Miki B (1989) Detection of rye DNA in wheat-rye hybrids and wheat translocation stocks using total genomic DNA as probe. Plant Mol Biol Rep 7:150–158

Martini G, O'Dell M, Flavell RB (1982) Partial inactivation of wheat nucleolus organizer by the nucleolus organizer chromosomes from *Aegilops umbellulata*. Chromosoma 84:687–700

Reader SM, Miller TE (1987) The simultaneous substitution of two pairs of chromosomes from two alien species in *Triticum aestivum* cv 'Chinese Spring' Cereal Res Commun 15:39–42

Riley R, Chapman V, Miller TE (1973) The determination of meiotic pairing. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, Mo., pp 731–738

Sears ER (1956) The transfer of leaf rust resistance from *Aegilops umbellulata* to wheat. Brookhaven Symp Biol 9:1–22

Sears ER (1961) Identification of the wheat chromosome carrying leaf rust resistance from *Aegilops umbellulata*. Wheat Inf Serv 12:12–13

Sears ER (1966) Chromosome mapping with the aid of telocentrics. In: MacKey J (ed) Proc 2nd Int Wheat Genet Symp. Hereditas Suppl Vol 2, pp 553–560

Shepherd KW (1973) Homoeology of wheat and alien chromosomes controlling endosperm protein phenotypes. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, Mo., pp 745–760

Shepherd KW, Islam AKMR (1988) Fourth compendium of wheat-alien chromosome lines. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, Bath Press, Bath, UK, pp 1373–1398

Stinissen HM, Peumnans WJ, Law CN, Payne PI (1983) Control of lectins in *Triticum aestivum* and *Aegilops umbellulata* by homoeologous group 1 chromosomes. Theor Appl Genet 67:53–58

Teoh SB, Hutchinson J (1983) Interspecific variation of C-banded chromosomes of diploid *Aegilops* species. Theor Appl Genet 65:31–40

Teoh SB, Hutchinson J, Miller TE (1983) A comparison of the chromosomal distribution of cloned repetitive DNA sequences in different *Aegilops* species. Heredity 51:635–641

Yen Y, Kimber G (1992) Genomic relationships of N-genome *Triticum* species. Genome 35:962–966