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Standard karyotype of *Triticum searsii* and its relationship with other S-genome species and common wheat

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Abstract C-banding polymorphism was analyzed in 14 accessions of *Triticum searsii* from Israel, and a generalized idiogram of the species was established. One accession was homozygous for whole arm translocations $T1S^sS{\cdot}4S^sS$ and $T1S^sL{\cdot}4S^sL$. C-banding analysis was also used to identify 7 *T. aestivum* cv 'Chinese Spring'-*T. searsii* disomic chromosome addition lines, 14 ditelosomic chromosome addition lines, 21 disomic whole chromosome, and 31 ditelosomic chromosome substitution lines. The identity of these lines was further confirmed by meiotic pairing analysis. Sporophytic and gametophytic compensation tests were used to determine the homoeologous relationships of the *T. searsii* chromosomes. The results show that the *T. searsii* chromosomes do not compensate well for their wheat homoeologues. The C-banding patterns of *T. searsii* chromosomes are distinct from those of other S-genome species and from the B-genome chromosomes of wheat, indicating that *T. searsii* is not a direct B-genome donor species of *T. turgidum* and *T. aestivum*.

Key words C-banding · *Triticim searsii* · S genome · Substitution lines · *T. aestivum* · B genome

Introduction

Triticum searsii (Feld. & Kis.) Feld. & Kis. (syn. *Aegilops searsii*) is a diploid S-genome species (2n=2x=14, S^sS^s) that is native to the sub-Mediterranean regions of Israel, Jordan, southwestern Syria, and southeastern Lebanon (Feldman and Kislev 1977). *Triticum searsii* belongs to the section *Sitopsis* Zhuk. (syn. *Platystachys* Eig), which also includes the species *T. longissimum* (syn. *Ae. longissima*, 2n=2x=14, S^lS^l), *T. sharonense* (syn. *Ae. sharonensis*, 2n=2x=14, $S^l_{sh}S^l_{sh}$), *T. bicorne* (syn. *Ae. bicornis*, 2n=2x=14, S^bS^b), and *T. speltoides* (syn. *Ae. speltoides*, 2n=2x=14, SS).

S-genome species are involved in the parentage of several tetraploid and hexaploid *Triticum* species, *T. kotschyi* (syn. *Ae. kotschyi*, 2n=4x=28, UUSS), *T. peregrinum* (syn. *Ae. variabilis*, 2n=4x=28, UUSS), and *T. syriacum* (syn. *Ae. crassa*, 2n=6x=42, DDMMSS) (Kimber and Feldman 1987; Kimber and Sears 1987). The S genome is also the probable donor of the B and G genomes of *T. turgidum* (2n=4x=28, AABB), *T. timopheevii* (2n=4x=28, A^tA^tGG), and common wheat, *T. aestivum* (2n=6x=42, AABBDD) (Jiang and Gill 1994a, b; for review, see Kimber 1981). In addition to their evolutionary significance, S-genome species are also a valuable source for resistance to diseases and pests (Tomerlin et al. 1983; Gill et al. 1985; Manisterski et al. 1988; McKendry and Henke 1994).

Recently, a standard karyotype of *T. longissimum* was developed, and its cytogenetic relationship with *T. aestivum* was established (Friebe et al. 1993). Similar analyses of the other S-genome species are necessary to determine their evolutionary relationships with polyploid wheats.

A set of *T. aestivum-T. searsii* disomic chromosome addition, ditelosomic chromosome addition, disomic chromosome substitution, and ditelosomic chromosome substitution lines was produced by one of us (NT). The homoeology of the added *T. searsii* chromosomes was determined by isozyme analysis and morphological characters (Pietro et al. 1988). In the study presented here, C-band polymorphism was analyzed in 14 accessions of *T. searsii* in order to construct a standard karyotype of this species. Furthermore, C-banding analysis was used to confirm the identity of the wheat-*T. searsii* chromosome and telosome addition and substitution lines. The relationship of the *T. searsii* chromosomes with their homoeologues of wheat was determined by analyzing sporophytic and gameto-

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phytic compensation. The results are discussed with respect to the phylogenetic relationships among the S-genome species and the B-genome chromosomes of tetraploid and hexaploid wheat.

Materials and methods

Fourteen accessions of *T. searsii* (Table 1, provided by Dr. M. Feldman, Weizmann Institute, Rehovot, Israel), the amphiploid *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10 (2n=8x=56, AABBDDS^{s}S^s, produced and provided by Dr. M. Feldman), and 7 derived disomic addition, 14 ditelosomic addition, 21 disomic whole chromosome, and 31 ditelosomic substitution lines were analyzed.

For chromosome identification, the C-banding technique described by Gill et al. (1991) was used. Chromosome measurements were made on 20 C-banded *T. searsii* chromosomes present in the amphiploid *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10, using wheat chromosome 3B as a standard. Meiotic chromosome pairing was analyzed in aceto-carmine-stained pollen mother cells (PMC's). Microphotographs were taken with a Zeiss photomicroscope III using Kodak Imagelink HQ microfilm 1461.

Seed set was recorded in disomic and ditelosomic substitution lines after self-pollination. Because the data were obtained from plants grown under different environments, they reflect environmental effects as well as the sporophytic compensation ability of *T. searsii* chromosomes for the homoeologous chromosomes of wheat. Gametophytic compensation of *T. searsii* chromosomes was determined by analyzing the chromosomal constitutions in progenies derived from the cross ♀ 'Chinese Spring'×♂ double monosomics ($20^{II}+2^{I}$), and the data were compared with a 3 (21^{II}):3($20^{II}+2^{I}$):1($21^{II}+1^{I}$) segregation using the chi-square test as described by Dvorák (1980) and Friebe et al. (1993).

Results

C-banding polymorphism

All seven chromosome pairs of *T. searsii* were individually identified on the basis of their C-banding patterns. No variation was observed within the accessions, but C-band polymorphism was detected between the different accessions analyzed (Fig. 1). A generalized idiogram of *T. searsii* was constructed (Fig. 2). Monomorphic C-bands present in all accessions are called marker C-bands and are diagnostic for chromosome identification (Fig. 3).

Chromosome 1S^s (arm ratio L/S: 1.6; total chromosome length L+S: 7.5±0.8 μm=74% of total 3B length): marker C-bands are present at the telomeres of both arms.

Chromosome 2S^s (L/S: 1.3; L+S: 9.3±1.1 μm=91% of total 3B length): marker C-bands are present at the telomeres of both arms in addition to two distally located marker C-bands in the short arm and one distally located marker band in the long arm.

Chromosome 3S^s (L/S: 1.4; L+S: 9.0±1.3 μm=89% of total 3B length): one telomeric marker C-band is present

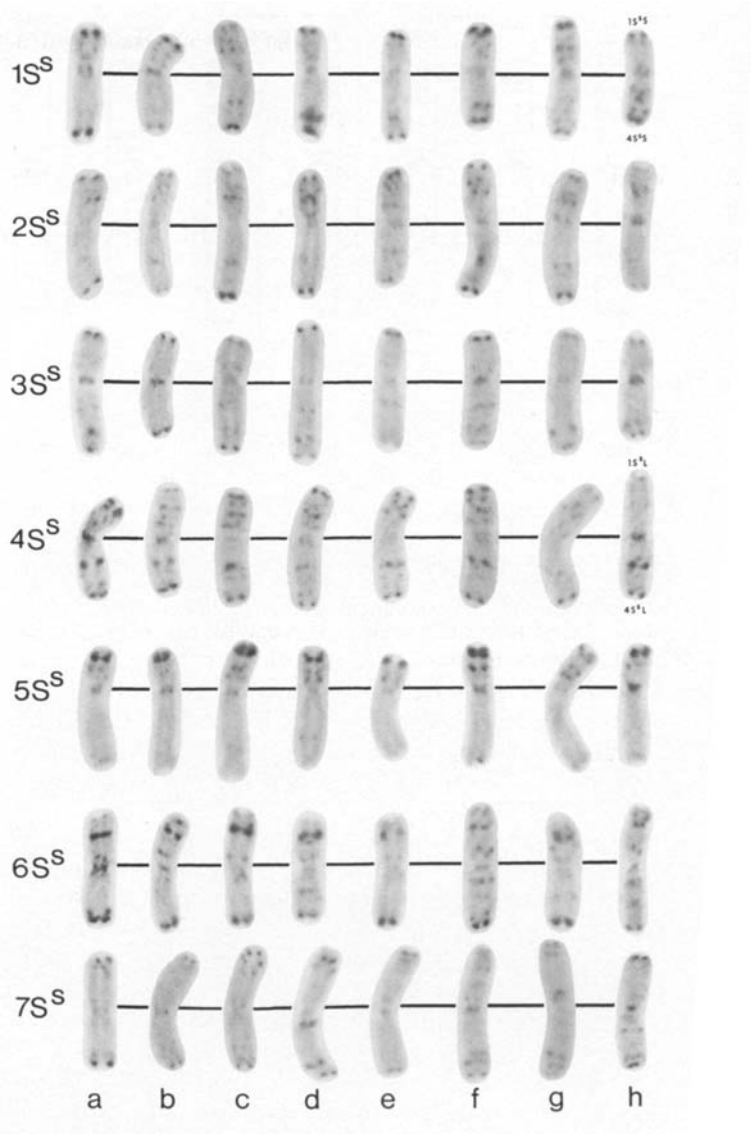

Fig. 1a–h C-banded karyotypes of *T. searsii*. **a** TE10, **b** TE07, **c** TE08, **d** TE18, **e** TE20, **f** TE23, **g** TE30, **h** TE09, all homozygous for the translocated chromosomes T1S^{s}S·4S^{s}S and T1S^{s}L·4S^{s}L

Table 1 Origin of the *T. searsii* accessions

Accession no.	Origin
TE03	Yattir, 1 km NE of the park watchman's house, Israel
TE05	East of Kurza, Hebron-Beer-Sheva, Israel
TE07	Kufar Fajer, E of Gush Etzion, Israel
TE08	South of Daharia, Hebron Beer-Sheva Road, Israel
TE09	4 km E. of Taiyiba, E of Ramala, Israel
TE10	1 km E. of Taiyiba, 15 km E. of Ramala, Samaria, Israel
TE17	Ramtha, Syria (obtained from Tanaka)
TE18	Gabagib, Syria (obtained from Dr. M. Tanaka)
TE20	Turkemiya-Dhahiriya Road, Israel
TE21	Between Bene-Na'im and Qiryat-Arba, Israel
TE23	North of Hevel-Yattir, Israel
TE24	North of Hevel-Yattir, Israel
TE27	Netiv hàlamed Hé-Gush Etzion Road, Israel
TE30	Unknown (obtained from Dr. T. E. Miller)

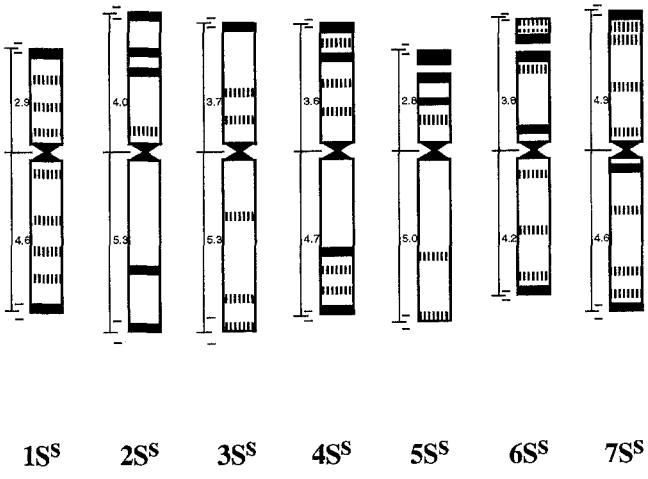

Fig. 2 Generalized idiogram of *T. searsii*. Marker C-bands present in all accessions are shown in *black* and C-bands that are present only in some accessions are *hatched*. Chromosome arm length data are given in micrometres and are based on 20 chromosomes of each *T. searsii* chromosome present in the amphiploid *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10. Standard deviations of the measurements are indicated by *small bars*

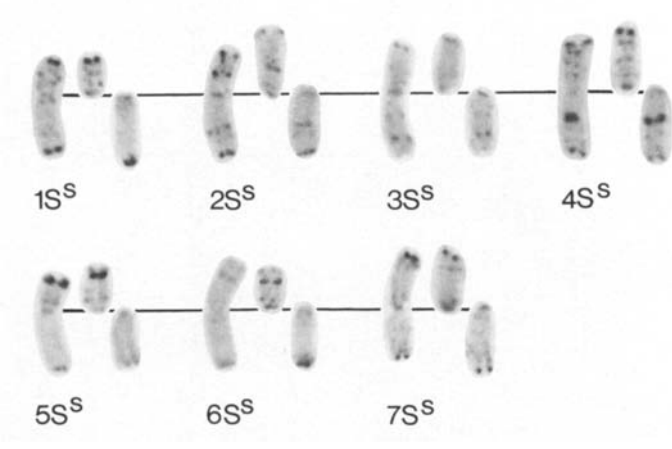

Fig. 3 C-banding patterns of the *T. searsii* chromosomes and telosomes present in the *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10 chromosome and telosome addition lines

at the telomere of the short arm, and additional bands may be present in both arms.

Chromosome $4S^s$ (L/S: 1.3; L+S: 8.3±0.8 μm=82% of total 3B length): the short arm has one distally located and a telomeric marker C-band, and one interstitial and a telomeric maker C-band is present in the long arm.

Chromosome $5S^s$ (L/S: 1.8; L+S: 7.8±0.6 μm=77% of total 3B length): SAT chromosome with a distally located secondary constriction in the short arm. Marker C-bands are present at the telomere and in the middle of the short arm.

Chromosome $6S^s$ (L/S: 1.1; L+S: 8.0±0.6 μm=79% of total 3B length): SAT chromosome with a distally located secondary constriction in the short arm. The satellite of $6S^s$ is larger than that of $5S^s$. Diagnostic bands include one proximally located and the marker C-band associated with the secondary constriction in the short arm and a telomeric marker C-band in the long arm.

Chromosome $7S^s$ (L/S: 1.1; L+S: 8.9±0.8 μm=87% of total 3B length): marker C-bands are present at the telomeres of both arms and close to the centromere in the long arm.

One accession, TE09, was found to be homozygous for a reciprocal translocation involving complete chromosome arms with the translocated chromosomes $T1S^sS{\cdot}4S^sS$ and $T1S^sL{\cdot}4S^sL$ (Fig. 1h).

Identification of *T. aestivum-T. searsii* chromosome and telosome addition and substitution lines

C-banding was used to identify 7 disomic chromosome addition, 14 ditelosomic addition, 21 whole chromosome, and 31 ditelosomic substitution lines [missing so far: $2S^sS$ (2B), $2S^sS$ (2D), $2S^sL$ (2A), $2S^sL$ (2B), $3S^sS$ (3B), $4S^sL$ (4A), $4S^sL$ (4B), $5S^sS$ (5D), and$7S^sL$ (7D)]. The tentative ditelosomic substitutions $2S^sL$(2A), $3S^sS$(3B), $4S^sL$(4A), and $4S^sL$(4B) were produced but did not set self seeds. The C-banding patterns of the *T. searsii* chromosomes and telosomes present in the set of *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10 addition and substitution lines are similar to the chromosomes of the original accession TE10.

The identity of the whole chromosome addition and substitution lines was also confirmed by meiotic pairing analysis. $22^{II}+6^{I}$ meiotic configurations were usually observed in F_1 hybrids of testcrosses of the disomic *T. searsii* addition lines with the *T. aestivum* cv 'Chinese Spring'-*T. searsii* no.TE10 amphiploid. The F_1s between the disomic *T. searsii* substitution lines and 'Chinese Spring' wheat paired as $20^{II}+2^{I}$, whereas in crosses with the appropriate 'Chinese Spring' ditelosomic lines (i.e., $DS5S^s(5A)$×DT5AL) the F_1s paired as $20^{II}+1^{I}+t^{I}$. The cross with 'Chinese Spring' confirmed that these are whole chromosome substitutions, and the cross with the ditelosomic lines was used to confirm the substitution for that specific chromosome. The F_1 of the cross $DS1S^s(1D)$×DT1DL paired as $18^{II}+1^{IV}+1^{I}+t^{I}$, indicating the presence of a wheat-wheat translocation. C-banding analysis detected the presence of a translocation smaller than a complete arm involving 2AS and an unidentified wheat chromosome in line $DS1S^s(1D)$.

Meiotic pairing analysis of *T. searsii* chromosomes and telosomes with their *T. longissimum* and *T. sharonense* homoeologues

Limited meiotic pairing data showed that the *T. searsii* chromosomes $1S^s$, $2S^s$, $5S^s$ and $7S^s$ do pair with the *T. longissimum* chromosome arms $1S^lL$ (12%), $2S^lS$ (18%), $5S^lL$ (13%), and $7S^lL$ (17%), respectively (Table 2). $4S^sL$ (1%) and $4S^lS$ (19%) pair with $4S^l_{sh}$ of *T. sharonense*. No pairing was observed between $4S^s/4S^lS$ and $6S^s/6S^lS$ and between $4S^l_{sh}$ and $4S^lL$ or $7S^lS$.

Table 2 Meiotic pairing of *T. searsii* chromosomes and telosomes with their *T. longissimum* and *T. sharonense* homoeologues in F_1 hybrids of crosses between disomic substitution lines (DS)

Cross combination	Meiotic pairing configuration	
	Number of PMC's with $20^{II} + 1^{I} + t^{I}$	Number of PMC's with $20^{II} + t1^{II}$
DS1S^{l}L(1D) × DS1S^{s}(1D)	106	14
DS2S^{l}S(2D) × DS2S^{s}(2D)	99	22
DS4S^{l}S(4D) × DS4S^{s}(4D)	101	0
DS5S^{l}L(5D) × DS5S^{s}(5D)	104	15
DS6S^{l}S(6B) × DS6S^{s}(6B)	More than 50	0
DS4S^{s}L(4D) × DS4S$^{l}_{sh}$(4D)	More than 100	1
DS4S^{l}S(4D) × DS4S$^{l}_{sh}$(4D)	26	6
DS4S^{l}L(4D) × DS4S$^{l}_{sh}$(4D)	More than 200	0
DS7S^{s}(7D) × DS7S^{l}L(7D)	172	36
DS7S^{l}S(7D) × DS4S$^{l}_{sh}$(4D)	More than 200	0

Table 3 Seeds per spikelet in 'Chinese Spring'-*T. searsii* disomic (DS) and ditelosomic substitution lines (*S* short arm, *L* long arm)

S^{s} chromosome	Missing wheat chromosome		
	A	B	D
1	2.6	2.5	2.3
1S	2.0	1.8	1.5
1L	2.2	2.2	1.6
2	2.6	2.0	2.8
2S	0.7[a]	–	–
2L	Sterile	–	0.9[a]
3	2.5	2.3	2.0
3S	0.6	Sterile[b]	Sterile[b]
3L	1.6	2.0*	1.0
4	1.6	2.1	2.4
4S	Sterile[a]	1.2	0.3
4L	Sterile	Sterile	2.0
5	2.0	2.8	2.1
5S	–	–	–
5L	1.1	1.5	2.2[a]
6	2.2	2.1	2.3
6S	1.3	1.9	2.0
6L	2.0	0.4	2.0
7	2.2	2.1	2.2
7S	2.7	2.2	–
7L	2.4	2.2	2.5

[a] Seed set based on two spikes only; all other data based on four or more spikes
[b] Will set an occasional seed under ideal conditions

Sporophytic and gametophytic compensation analysis

All of the 21 possible whole chromosome substitution lines, with the exception of DS4S^{s}(4A), set an average of two or more seeds per spikelet (Table 3). In general, the ditelosomic substitution lines, as expected, were less fertile than the whole chromosome substitutions, with several of the latter being sterile. The substitutions of the ditelosomics of chromosome 7S^{s} for the group 7 chromosomes of wheat appear to be an exception: 5 of the 6 possible ditelosomic substitutions were produced, and all of them appear to be as fertile as the whole chromosome substitutions.

The gametophytic compensation data showed that chromosome 2S^{s} is the only *T. searsii* chromosome that compensates well for all group 2 homoeologues of wheat (Table 4). Significant deviations from the expected 3:3:1 ratios were observed for 4A/4S^{s}, 5A/5S^{s}, and 7B/7S^{s} combinations, which involve structurally rearranged wheat chromosomes, but also for other combinations. Although the homoeologous chromosomes of *T. searsii* showed poor compensation for these three wheat chromosomes in male gametophytes, the whole chromosome substitutions 5S^{s}(5A) and 7S^{s}(7B) are as fertile and vigorous as the substitutions of these two *T. searsii* chromosomes for the other two members of groups 5 and 7. Although the substitution 4S^{s}(4A) is less fertile and vigorous than the substitution of this chromosome for 4B and 4D, gametic compensation appears to be a more sensitive test of relatedness than sporophytic compensation.

Phenotypic effects of the added *T. searsii* chromosomes and telosomes

Spike morphologies of the *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10 disomic chromosome addition and ditelosomic addition lines are shown in Fig. 4.

The spikes of the disomic addition line 1S^{s} are shorter than those of 'Chinese Spring' and exhibit partial sterility when grown under worse than normal conditions. Spikes of the ditelosomic addition line 1S^{s}S are shorter than those of 'Chinese Spring', while those of 1S^{s}L are morphologically similar to 'Chinese Spring' and are more fertile than those of the disomic addition line.

Spikes of the disomic addition line 2S^{s} have short awns and tenacious glumes. The ditelosomic addition line 2S^{s}L has short awns and is free-threshing, while the ditelosomic addition line 2S^{s}S is awnless and has tenacious glumes.

Spikes of the disomic addition line 3S^{s} and ditelosomic addition line 3S^{s}S are shorter than those of 'Chinese Spring' and exhibit sterility in the upper one-third of their length. The rachis of DA3S^{s} and DA3S^{s}S is fragile and tends to break somewhere between the first and sixth spikelet. With respect to maturity, they head 10 days to 2 weeks

Table 4 Gametophytic compensation of *T. searsii* chromosomes for wheat chromosomes based on segregation of the progenies from the crosses ♀ 'Chinese Spring' × ♂ double monosomics ($20^{II}+2^{I}$)

Chromosome combination	Progeny from $21^{II} \times 20^{II} + 2^{I}$				χ^2 (3:3:1)
	21^{II}	$20^{II} + 2^{I}$	$21^{II} + 1^{I}$	$20^{II} + 1^{I}$	
1A/1S^s	8	3	–	2	4.49
1B/1S^s	16	3	3	1	8.97*
1D/1S^s	19	5	1	3	11.35**
2A/2S^s	10	7	4	2	0.88
2B/2S^s	13	10	4	1	0.40
2D/2S^s	14	12	4	1	0.18
3A/3S^s	13	12	–	3	4.22
3B/3S^s	18	6	–	1	11.00* *
3D/3S^s	15	7	1	1	5.10
4A/4S^s	24	2	3	1	19.83**
4B/4S^s	14	12	3	5	0.52
4D/4S^s	18	8	2	2	5.33
5A/5S^s	20	6	–	3	13.13**
5B/5S^s	12	13	3	1	0.33
5D/5S^s	16	15	–	–	5.20
6A/6S^s	15	8	1	4	4.39
6B/6S^s	17	3	6	1	10.44**
6D/6S^s	14	11	1	3	2.71
7A/7S^s	12	12	2	–	0.93
7B/7S^s	17	4	4	–	7.94*
7D/7S^s	14	15	–	1	4.87

* and **: significant at the 5% and 1% level, respectively

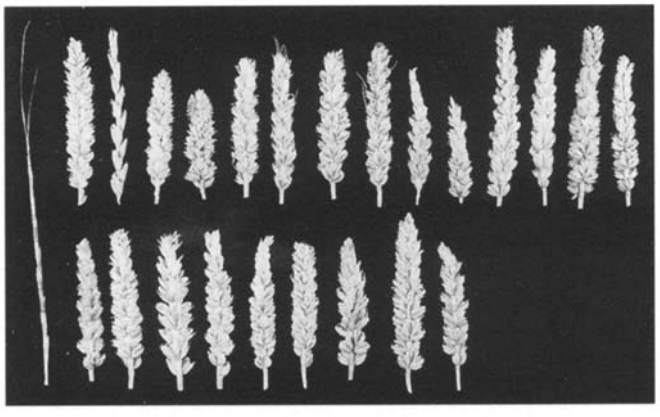

Fig. 4 Spike morphologies of *T. aestivum* cv 'Chinese Spring'-*T. searsii* no. TE10 disomic chromosome and ditelosomic addition lines (DA). *Left to right*: *T. searsii*; *upper row* 'Chinese Spring', 'Chinese Spring'-*T. searsii* no. TE10 amphiploid, DA1S^s, DA1S^{s}S, DA1S^{s}L, DA2S^s, DA2S^{s}S, DA2S^{s}L, DA3S^s, DA3S^{s}S, DA3S^{s}L, DA4S^s, DA4S^{s}S, DA4S^{s}L; *lower row* DA5S^s, DA5S^{s}S, DA5S^{s}L, DA6S^s, DA6S^{s}S, DA6S^{s}L, DA7S^s, DA7S^{s}S, DA7S^{s}L

later than 'Chinese Spring' under greenhouse conditions in Texas. Spikes of the ditelosomic addition line 3S^{s}L resemble those of 'Chinese Spring'.

Spikes of the disomic addition line 4S^s and the ditelosomic addition line 4S^{s}S are more lax at their base than those of 'Chinese Spring'. Spikes of the ditelosomic addition line 4S^{s}L are similar to those of 'Chinese Spring'.

Spikes of both the disomic addition line 5S^s and the ditelosomic addition line 5S^{s}L are lax at their base and often compact at their top. Variability in the latter character is a function of growing conditions with spikes of the same plant sometimes having both compact and non-compact tops. Spikes of the ditelosomic addition line 5S^{s}S are similar to those of 'Chinese Spring'.

The spikes of the disomic addition line 6S^s are similar in appearance to those of 'Chinese Spring', but have reduced seed set in the upper one-quarter of their length. Spikes of the 6S^{s}S and 6S^{s}L ditelosomic addition lines are similar to those of 'Chinese Spring'.

Spikes of both the disomic addition line 7S^s and the ditelosomic addition line 7S^{s}S are more lax in their lower halves than those of 'Chinese Spring'. The ditelosomic addition line 7S^{s}L is similar to 'Chinese Spring'.

Discussion

The chromosome complement of *T. searsii* consists of seven meta- to submetacentric chromosomes with two pairs of satellited chromosomes, 5S^s and 6S^s, and is similar to that described by Teoh and Hutchinson (1983) and Teoh et al. (1983) for *Aegilop* species. One accession was homozygous for reciprocal whole arm translocations involving chromosomes 1S^s and 4S^s. Reciprocal whole arm translocations involving different chromosomes have been detected previously by C-banding analysis in *T. tauschii* (syn. *Ae. squarrosa*) (Friebe et al. 1992a), *T. sharonense* (Friebe and Gill 1995), and *T. araraticum* (Badaeva et al. 1994), but not in *T. dichasians* (syn. *Ae. caudata*, *Ae. markgrafii*) (Friebe et al. 1992b), *T. longissimum* (Friebe et al. 1993), *T. umbellulatum* (syn. *Ae. umbellulata*) (Friebe et al. 1995) and in *T. bicorne*, and *T. speltoides* (Friebe and Gill 1995).

T. searsii is morphologically very similar to *T. longissimum*, making it difficult to distinguish the two species. However, both species can be distinguished easily from each other by their distinct C-banding patterns. *T. searsii* has fewer and smaller C-bands than *T. longissimum*, and in this respect, is similar to *T. bicorne* (Friebe and Gill 1995). In the present study, several accessions that had been previously described as *T. searsii* were cytogenetically identified as *T. longissimum* (data not shown). Differences in C-banding patterns between closely related plant species have been observed earlier (Marks and Schweizer 1974; Bennett et al. 1977; Greilhuber et al. 1981; Greilhuber 1984). C-band positive regions generally correspond to constitutive heterochromatin that contain a large amount of repeated DNA sequences (Schweizer et al. 1990). Therefore, the observed differences in C-banding patterns reflect differences in the amount and chromosomal location of these sequences, which can undergo rapid changes, even between closely related species.

The homoeologous relationships of the *T. searsii* chromosomes present in the chromosome addition lines has been determined by isozyme analysis and morphological characters by Pietro et al. 1988. In their study it was shown that chromosome $4S^s$ carries the *T. searsii* genes *Acph-S^s1* (acid phosphatase-1) and *Aco-S^s2* (aconitase-2), both markers for group 4 long arm, and that chromosome $7S^s$ possesses the gene *Ep-S^s1* (endopeptidase-1), which is a group 7 long arm marker. Since a ditelosomic addition line derived from the whole $4S^s$ chromosome addition line carried neither the genes *Acph-S^s1* nor *Aco-S^s2*, both should be located on the $4S^s$L arm (Pietro et al. 1988).

In contrast, chromosome $4S^l$ from *T. longissimum* carries the gene for *Adh-S^l1* (alcohol dehydrogenase-1, a group 4 short arm marker) as well as the group 7 long arm gene *Ep-S^l1* (Hart and Tuleen 1983). Furthermore, in *T. searsii* the telosome $7S^sS$ has a gene for purple coleoptiles that is a group 7 short arm marker, whereas in *T. longissimum* this trait is encoded by a gene located on the longer arm of $7S^l$ (Friebe et al. 1993).These results suggest that *T. searsii* differs from *T. longissimum* with respect to a translocation involving $4S^l$ and $7S^l$. It has been suggested that in *T. longissimum* a longer segment from a group 7 long arm (having the *Ep-S^l1* gene) was replaced by a shorter segment from a group 4 long arm, resulting in the arm relocation of the gene for red colepotiles (Friebe et al. 1993).

The C-banding patterns of *T. searsii*, *T. bicorne*, and *T. speltoides* chromosomes are very different from that of *T. longissimum*, making it impossible to detect the translocation difference (Friebe and Gill 1995). However, the C-banding pattern of *T. longissimum* is similar to that of *T. sharonense* (Friebe and Gill 1995). The overall C-banding pattern of the short arm of the *T. sharonense* chromosome $7S^l_{sh}$ is similar to that of $7S^l$L, and the distal region of $7S^l_{sh}$L has similarities to $4S^l$L, confirming the 4/7 translocation in *T. longissimum*.

The presence of reciprocal translocation differences between *T. searsii* and *T. longissimum* was detected earlier by meiotic pairing analysis, where the F_1 hybrids between both species frequently formed five bivalents plus one quadrivalent at meiotic metaphase (Feldman et al. 1979). Because $5^{II}+1^{IV}$ configurations were only observed in testcrosses between *T. longissimum* and other S-genome species, but not in intercross hybrids between *T. sharonense*, *T. bicorne*, and *T. speltoides* (data summarized by Feldman et al. 1979), this indicates that *T. longissimum* is cytogenetically distinct from all other S-genome species and suggests further that the S^l genome is relatively younger than the S, S^l_{sh}, S^b, and S^s genomes.. Meiotic pairing analyses in triploid hybrids of *T. searsii* with *T. longissimum* (4x), *T. speltoides* (4x), and *T. bicorne* (4x) indicated that the S^s genome is equally distant to the S, S^l, and S^b genomes (Yen and Kimber 1990).

The present study shows that only $2S^s$ compensates well for all group 2 homoeologous chromosomes of wheat. Poor gametophytic compensation was observed in chromosome combinations $1B/1S^s$, $1D/1S^s$, $3B/3S^s$, $4A/4S^s$, $5A/5S^s$, $6B/6S^s$, and $7B/7S^s$. Although *T. searsii* is closely related to *T. longissimum*, S^s genome chromosomes in general do not compensate well for their wheat homoeologues, whereas S^l genome chromosomes, except for the rearranged translocation chromosomes $4S^l$ and $7S^l$, show good sporophytic and gametophytic compensation ability. This suggests that the compensation ability may be determined by several major genes that are present in *T. longissimum* and absent in *T. searsii*. This further implies that the S^l genome of *T. longissimum* is more similar to the A, B, and D genome of cultivated bread wheat than the S^s genome of *T. searsii*.

The meiotic pairing data suggest that the *T. searsii* chromosomes $1S^s$, $2S^s$, $5S^s$, and $7S^s$ have homoeology to the corresponding *T. longissimum* chromosomes. However, no pairing was observed between $4S^s$ and $6S^s$ and the corresponding short arm telosomes of *T. longissimum*, indicating that these arms are not fully homoeologous. Homoeology is further indicated between $4S^s$L, $4S^l$S, and $4S^l_{sh}$ of *T. sharonense*. No pairing was observed between $4S^l$L and $4S^l_{sh}$, supporting the rearranged structure of the $4S^l$L arm.

Meiotic pairing analysis (Naranjo et al. 1987, 1988; Gill and Chen 1987; Naranjo 1990) as well as RFLP data (Liu et al. 1992; Devos et al. 1993) have revealed the presence of a large pericentric inversion in chromosome 4A and a cyclical translocation involving chromosome arms 4AL, 5AL and 7BS in *T. turgidum* and *T. aestivum*. A 4AL/5AL translocation is also present in *T. monococcum* (Naranjo et al. 1988; Jiang and Gill 1994b). Furthermore, it has been shown that *Secale cereale* has a 4RL/5RL translocation with the breakpoints in similar regions as the 4AL/5AL translocation in wheat, and it was suggested that this translocation is an ancient one and must have occurred very early (Devos et al. 1993). However, neither chromosomes 4B and 5B of *T. aestivum* nor chromosomes $4S^s$, $4S^l_{sh}$, $4S^b$, and 4S of *T. searsii*, *T. sharonense*, *T. bicorne*, and *T. speltoides* are structurally rearranged. C-banding analysis showed that the S and S^l/S^l_{sh} genomes of *T. speltoides*, *T. longissimum*, and *T. sharonense* are more similar to the B genome of wheat than those of the S^s, and S^b genomes of *T. searsii* and *T. bicorne*. It is likely that the original pro-

genitor of the B genome was an ancient S-genome species that is now extinct and that the present S genomes have undergone several modifications.

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