Complex genome rearrangements reveal evolutionary dynamics of pericentromeric regions in the Triticeae

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Abstract: Most pericentromeric regions of eukaryotic chromosomes are heterochromatic and are the most rapidly evolving regions of complex genomes. The closely related genomes within hexaploid wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD), as well as in the related Triticeae taxa, share large conserved chromosome segments and provide a good model for the study of the evolution of pericentromeric regions. Here we report on the comparative analysis of pericentric inversions in the Triticeae, including *Triticum aestivum*, *Aegilops speltoides*, *Ae. longissima, Ae. searsii, Hordeum vulgare*, *Secale cereale*, and *Agropyron elongatum*. Previously, 4 pericentric inversions were identified in the hexaploid wheat cultivar 'Chinese Spring' ('CS') involving chromosomes 2B, 4A, 4B, and 5A. In the present study, 2 additional pericentric inversions were detected in chromosomes 3B and 6B of 'CS' wheat. Only the 3B inversion pre-existed in chromosome 3S, $3S^l$, and $3S^s$ of *Aegilops* species of the *Sitopsis* section, the remaining inversions occurring after wheat polyploidization. The translocation T2BS/6BS previously reported in 'CS' was detected in the hexaploid variety 'Wichita' but not in other species of the Triticeae. It appears that the B genome is more prone to genome rearrangements than are the A and D genomes. Five different pericentric inversions were detected in rye chromosomes 3R and 4R, $4S^l$ of *Ae. longissima*, 4H of barley, and 6E of *Ag. elongatum*. This indicates that pericentric regions in the Triticeae, especially those of group 4 chromosomes, are undergoing rapid and recurrent rearrangements.

Key words: Triticeae, *Triticum aestivum*, pericentric inversions, translocation.

Résumé : La plupart des régions péricentromériques des chromosomes eucaryotes sont hétérochromatiques et constituent les régions qui évoluent le plus rapidement dans les génomes complexes. Les génomes très apparentés présents chez le blé hexaploïde (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD), de même que chez des hordées proches, partagent de grands segments chromosomiques conservés et s'avèrent un bon modèle pour l'étude de l'évolution des régions péricentromériques. Dans ce travail, les auteurs ont effectué une comparaison des inversions péricentromériques chez les hordées, incluant *Triticum aestivum*, *Aegilops speltoides*, *Ae. longissima*, *Ae. searsii*, *Hordeum vulgare*, *Secale cereale* et *Agropyron elongatum*. Antérieurement, quatre inversions péricentromériques avaient été identifiées chez le cultivar de blé hexaploïde 'Chinese Spring' (CS) impliquant les chromosomes 2B, 4A, 4B et 5A. Dans le présent travail, deux inversions péricentromériques additionnelles ont été détectées chez les chromosomes 3B et 6B du blé CS. Seule l'inversion 3B existait chez les chromosomes 3S, 3S1 et 3Ss chez les *Aegilops* de la section Sitopsis, les autres inversions étant survenues suite à la polyploïdisation du blé. La translocation T2BS/6BS rapportée précédemment chez CS a été détectée uniquement chez le blé 'Wichita', mais pas chez d'autres espèces d'hordées. Il semblerait que le génome B est davantage sujet à des réarrangements que ne le sont les génomes A et D. Cinq inversions péricentriques différentes ont été détectées chez les chromosomes 3R et 4R du seigle, 4S1 de l'*Ae. longissima*, 4H de l'orge et 6E de l'*Ae. elongatum*. Ceci indique que les régions péricentriques chez les hordées, surtout celles des chromosomes du groupe 4, sont l'objet de réarrangements rapides et récurrents.

Mots clés : hordées, *Triticum aestivum*, inversions péricentriques, translocation.

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Abbreviations: del, deletion; Dt, ditelosomic; DtA, ditelosomic addition; NT, nullisomic-tetrasomic (e.g., N2AT2D, nullisomic2A-tetrasomic2D); T, translocation.

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Introduction

In animals and plants, the pericentromeric regions have long been recognized as highly dynamic regions of chromosomes subjected to an unprecedented level of rearrangements, including duplications, inversions, and deletions (Eichler and Sankoff 2003). Comparison of the karyotypes of human and chimpanzee has revealed 9 pericentric inversions in chimpanzee chromosomes (Yunis and Prakash 1982), although human and chimpanzee show overall identity of 98.8% at the DNA-sequence level (Chen and Li 2001). Refinements of the pericentric inversion breakpoints at the molecular level carried out using bacterial artificial

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and P1-derived artificial chromosome clones derived from both human and chimpanzee are consistent with the previously characterized cytogenetic locations of the pericentric inversion breakpoints (Nickerson and Nelson 1998; Goidts et al. 2005; Kehrer-Sawatzki et al. 2005). The human pericentromeric regions are also hot spots for recent duplication events. Almost half of human chromosomes, including the Y chromosome, show duplicated DNA in the pericentromeric regions (Eichler 1998; Jackson 2003; Kirsch et al. 2005), and it has been suggested that pericentric inversions were important for the establishment of reproductive isolation and speciation of hominoids.

In grasses, the major cereal crops rice, maize, and wheat show conserved synteny except in the centromeric regions (Moore et al. 1997; Sorrells et al. 2003). In the Triticeae tribe, which includes hexaploid wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD), cytogenetic stocks and comparative mapping have been used to document chromosome rearrangements in the A, B, and D genomes of wheat and the related Triticeae genomes that encompass 12 million years of evolutionary history (Huang et al. 2002). Previous studies revealed a cyclic translocation involving chromosomes 4A, 5A, and 7B that is fixed in polyploid wheat (Naranjo et al. 1987; Anderson et al. 1992; Liu et al. 1992; Devos et al. 1995; Mickelson-Young et al. 1995; Nelson et al. 1995). In addition, a pericentric inversion in chromosome 4A resulted in arm homoeologies of 4AS = 4BL = 4DL, and 4AL = 4BS = 4DS. Another pericentric inversion has been documented in 4B (Dvorak et al. 1984; Endo and Gill 1984; Gill et al. 1991; Friebe and Gill 1994; Mickelson-Young et al. 1995). The wheat expressed sequence tag (EST) mapping project established further structural changes in 4A and confirmed the inversion in 4B, and additional pericentric inversions were reported for chromosomes 2B and 5A (Miftahudin et al. 2004; Conley et al.. 2004; Linkiewicz et al. 2004). In the present study, we report on a comparative analysis of pericentromeric regions of homoeologous group 2, 3, 4, 5, and 6 chromosomes. This was performed by centromere mapping of critical markers using a collection of telocentric chromosomes from diverse Triticeae species added to wheat as ditelosomic addition lines.

Materials and methods

Genetic stocks

Abbreviations used for wheat genetic stocks follow the nomenclature proposed by Raupp et al. (1995). The genetic stocks used in this study included 15 nullisomic-tetrasomic (NT) lines (1 chromosome pair is missing, and this loss is compensated by 4 copies of a homoeologous chromosome) and 26 ditelosomic (Dt) lines (1 chromosome pair is represented by 2 telosomes for either the short or long arm) developed in *Triticum aestivum* 'Chinese Spring' ('CS') involving homoeologous group 2, 3, 4, 5, and 6 chromosomes (Table 1; Sears 1954, 1966; Sears and Steinitz-Sears 1978). The N2AT2B and N4BT4D lines were selected from monosomic-2A – tetrasomic-2B and monosomic-4B – tetrasomic-4D stocks. The monotelosomic 5AS plants were obtained from the F_1 of the cross between ditelosomic 5AS-monotelosomic 5AL and N5AT5D plants. These genetic stocks were used to assign molecular markers to specific chromosomes and chromosome arms.

Wheat-alien ditelosomic addition lines, in which a pair of alien chromosome arms is added to the wheat complement, were used to assign molecular markers to specific alien chromosome arms. A total of 35 'CS'-alien ditelosomic addition (DtA) lines were used (Table 1). The first number designates the homoeologous group, followed by the genome symbol; the # sign is used to distinguish between chromosomes belonging to the same homoeologous group but derived from different accessions, and last is the arm location.

In addition, 27 deletion lines (del) homozygous for terminal deletions of various sizes involving homoeologous chromosomes of groups 2 and 6 were used (Table 2) (Endo and Gill 1996). The fraction length (FL) value of each deletion identifies the position of the breakpoint from the centromere relative to the length of the complete arm. The FL value involving satellite chromosome arms 1BS and 6BS was calculated independently for the region between the centromere and the secondary constriction, and for the satellite (Endo and Gill 1996). Thus, deletions with a breakpoint within the secondary constrictions have FL values greater than 1 (Table 2, del6BS-2). All genetic stocks are maintained at the Wheat Genetic and Genomic Resources Center (WGGRC) at Kansas State University, Manhattan, Kans.

Restriction fragment length polymorphism (RFLP) analysis

Procedures used for genomic DNA isolation, restriction endonuclease digestion, gel electrophoresis, and DNA gel blot hybridization were as described in Qi et al. (2003). The genomic DNAs were digested with *Eco*RI, *Hin*dIII, *Dra*I, and *Bam*HI. Table 3 lists the EST markers used in this study, which were provided by Dr. O.D. Anderson, US Department of Agriculture (USDA), Agricultural Research Service, Western Regional Research Center, Albany, Calif.

Results

Characterization of pericentric inversions in the Triticeae

In hexaploid wheat, chromosome and arm homoeologies within sets of triplicated chromosomes are highly conserved, i.e., long arms are homoeologous to long arms, and short arms are homoeologous to short arms. However, a few exceptional cases of chromosomal rearrangements violating homoeology have been reported previously (Dvorak et al. 1984; Endo and Gill 1984; Naranjo et al. 1987; Gill et al. 1991; Anderson et al. 1992; Liu et al. 1992; Friebe and Gill 1994; Devos et al. 1995; Mickelson-Young et al. 1995; Nelson et al. 1995). The genomes of wheat and the related Triticeae also share large conserved chromosome segments and provide a good model for the study of the evolution of pericentromeric regions. Using wheat aneuploids and wheat-alien ditelosomic addition lines, EST loci can be assigned to individual chromosome arms in wheat and the Triticeae. Figure 1 gives an example of locating an EST to chromosome arms of wheat, *Ae. speltoides*, rye, and barley using the wheat and the wheat-alien aneuploid lines. Any change in arm location and marker order compared with ancestral karyotype allows the detection of structural chromosome aberrations, including pericentric inversions.

Table 1. List of genetic stocks used in the study.

TA No.*	Genetic stocks	Description	Reference
TA3263	M2AT2B†	Monosomic 2A-tetrasomic 2B	(Sears 1954)
TA3266	N2BT2D	Nullisomic 2B-tetrasomic 2D	(Sears 1954)
TA3267	N2DT2A	Nullisomic 2D-tetrasomic 2A	(Sears 1954)
TA3103	Dt2AS	Ditelosomic 2AS	(Sears and Steinitz-Sears 1978)
TA3114	Dt2BL	Ditelosomic 2BL	(Sears and Steinitz-Sears 1978)
TA3310	WI Dt 2BL	'Wichita' ditelosomic 2BL	(R. Morris, Dept. of Agronomy, University of Nebraska, Lincoln, 1991, personal communication)
TA3123	Dt2DS	Ditelosomic 2DS	(Sears and Steinitz-Sears 1978)
TA3124	Dt2DL	Ditelosomic 2DL	(Sears and Steinitz-Sears 1978)
TA7702	CS-AESP DtA2S#3S	CS-*Aegilops speltoides* ditelosomic addition 2S#3S	(Friebe et al. 2000)
TA7696	CS-AESP DtA2S#3L	CS-*Aegilops speltoides* ditelosomic addition 2S#3L	(Friebe et al. 2000)
TA3589	CS-HVUL DtA2HS	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 2HS	(Islam et al. 1981)
TA3590	CS-HVUL DtA2HL	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 2HL	(Islam et al. 1981)
TA3270	N3AT3D	Nullisomic 3A-tetrasomic 3D	(Sears 1954)
TA3272	N3BT3D	Nullisomic 3B-tetrasomic 3D	(Sears 1954)
TA3274	N3DT3B	Nullisomic 3D-tetrasomic 3B	(Sears 1954)
TA3104	Dt3AS	Ditelosomic 3AS	(Sears and Steinitz-Sears 1978)
TA3105	Dt3AL	Ditelosomic 3AL	(Sears and Steinitz-Sears 1978)
TA3115	Dt3BS	Ditelosomic 3BS	(Sears and Steinitz-Sears 1978)
TA3116	Dt3BL	Ditelosomic 3BL	(Sears and Steinitz-Sears 1978)
TA3193	Dt3DS	Ditelosomic 3DS	(Sears and Steinitz-Sears 1978)
TA3192	Dt3DL	Ditelosomic 3DL	(Sears and Steinitz-Sears 1978)
TA7533	CS-AESEA DtA3S^s#1S	CS-*Aegilops searsii* ditelosomic addition 3S^s#1S	(Friebe et al. 1995)
TA7534	CS-AESEA DtA3S^s#1L	CS-*Aegilops searsii* ditelosomic addition 3S^s#1L	(Friebe et al. 1995)
TA7519	CS-AELON DtA3S^l#2S	CS-*Aegilops longissima* ditelosomic addition 3S^l#2S	(Friebe et al. 1993)
TA7520	CS-AELON DtA3S^l#2L	CS-*Aegilops longissima* ditelosomic addition 3S^l#2L	(Friebe et al. 1993)
TA7739	CS-AESP DtA3S#3S	CS-*Aegilops speltoides* ditelosomic addition 3S#3S	(Friebe et al. 2000)
TA3566	CS-I DtA 3RS	CS-*Secale cereale* 'Imperial' ditelosomic addition 3RS	(Mukai et al. 1992)
TA3674	CS-AGEL DtA3EL	CS-*Agropyron elongatum* ditelosomic addition 3EL	(Dvorak and Knott 1974)
TA3591	CS-HVUL DtA3HS	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 3HS	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3592	CS-HVUL DtA3HL	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 3HL	(Islam et al. 1981, Islam and Shepherd 1988, 1992)
TA3278	N4AT4D	Nullisomic 4A-tetrasomic 4D	(Sears 1954)
TA3276	M4BT4D†	Monosomic 4B-tetrasomic 4D	(Sears 1954)
TA3279	N4DT4B	Nullisomic 4D-tetrasomic 4B	(Sears 1954)
TA3086	Dt4AS	Ditelosomic 4AS	(Sears and Steinitz-Sears 1978)
TA3117	Dt4AL	Ditelosomic 4AL	(Sears and Steinitz-Sears 1978)
TA3106	Dt4BS	Ditelosomic 4BS	(Sears and Steinitz-Sears 1978)
TA3125	Dt4DS	Ditelosomic 4DS	(Sears and Steinitz-Sears 1978)
TA3126	Dt4DL	Ditelosomic 4DL	(Sears and Steinitz-Sears 1978)
TA7535	CS-AESEA DtA4S^s#1S	CS-*Aegilops searsii* ditelosomic addition 4S^s#1S	(Friebe et al. 1995)
TA7536	CS-AESEA DtA4S^s#1L	CS-*Aegilops searsii* ditelosomic addition 4S^s#1L	(Friebe et al. 1995)
TA7521	CS-AELON DtA4S^l#2S	CS-*Aegilops longissima* ditelosomic addition 4S^l#2S	(Friebe et al. 1993)
TA7522	CS-AELON DtA4S^l#2L	CS-*Aegilops longissima* ditelosomic addition 4S^l#2L	(Friebe et al. 1993)
TA7703	CS-AESP DtA4S#3L	CS-*Aegilops speltoides* ditelosomic addition 4S#3L	(Friebe et al. 2000)
TA3567	CS-I DtA 4RS	CS-*Secale cereale* 'Imperial' ditelosomic addition 4RS	(Mukai et al. 1992)
TA3568	CS-I DtA 4RL	CS-*Secale cereale* 'Imperial' ditelosomic addition 4RL	(Mukai et al. 1992)
TA3593	CS-HVUL DtA4HS	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 4HS	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3594	CS-HVUL DtA4HL	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 4HL	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3063	N5AT5D	Nullisomic 5A-tetrasomic 5D	(Sears 1954)
TA3065	N5BT5D	Nullisomic 5B-tetrasomic 5D	(Sears 1954)
TA3067	N5DT5B	Nullisomic 5D-tetrasomic 5B	(Sears 1954)
	Mt5AS†	Monotelosomic 5AS	(L.L. Qi unpublished data)
TA3107	Dt5AL	Ditelosomic 5AL	(Sears and Steinitz-Sears 1978)

Table 1 (*concluded*).

TA No.*	Genetic stocks	Description	Reference
TA3118	Dt5BL	Ditelosomic 5BL	(Sears and Steinitz-Sears 1978)
TA3127	Dt5DL	Ditelosomic 5DL	(Sears and Steinitz-Sears 1978)
TA7523	CS-AELON DtA5S^{l}#2S	CS-*Aegilops longissima* ditelosomic addition 5S^{l}#2S	(Friebe et al. 1993)
TA7704	CS-AESP DtA5S#3L	CS-*Aegilops speltoides* ditelosomic addition 5S#3L	(Friebe et al. 2000)
TA3569	CS-I DtA 5RS	CS-*Secale cereale* 'Imperial' ditelosomic addition 5RS	(Mukai et al. 1992)
TA3597	CS-HVUL DtA5HS	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 5HS	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3598	CS-HVUL DtA5HL	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 5HL	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3152	N6AT6B	Nullisomic6A-tetrasomic 6B	(Sears 1954)
TA3154	N6BT6A	Nullisomic 6B-tetrasomic 6A	(Sears 1954)
TA3157	N6DT6B	Nullisomic 6D-tetrasomic 6B	(Sears 1954)
TA3108	Dt6AS	Ditelosomic 6AS	(Sears and Steinitz-Sears 1978)
TA3109	Dt6AL	Ditelosomic 6AL	(Sears and Steinitz-Sears 1978)
TA3119	Dt6BS	Ditelosomic 6BS	(Sears and Steinitz-Sears 1978)
TA3120	Dt6BL	Ditelosomic 6BL	(Sears and Steinitz-Sears 1978)
TA3128	Dt6DS	Ditelosomic 6DS	(Sears and Steinitz-Sears, 1978)
TA3129	Dt6DL	Ditelosomic 6DL	(Sears and Steinitz-Sears 1978)
TA7525	CS-AELON DtA6S^{l}#2S	CS-*Aegilops longissima* ditelosomic addition 6S^{l}#2S	(Friebe et al. 1993)
TA3676	CS-AGEL DtA6ES	CS-*Agropyron elongatum* ditelosomic addition 6ES	(Dvorak and Knott 1974)
TA3705	CS-AGEL DtA6EL	CS-*Agropyron elongatum* ditelosomic addition 6EL	(Dvorak and Knott 1974)
TA3595	CS-HVUL DtA6HS	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 6HS	(Islam et al. 1981; Islam and Shepherd 1988, 1992)
TA3596	CS-HVUL DtA6HL	CS-*Hordeum vulgare* 'Betzes' ditelosomic addition 6HL	(Islam et al. 1981; Islam and Shepherd 1988, 1992)

Note: CS; *T. aestivum* 'Chinese Spring'; WI; *T. aestivum* 'Wichita'. All lines are in the 'Chinese Spring' background unless otherwise indicated.
*WGGRC collection accession number.
†N2AT2B and N4BT4D plants were selected from progenies of M2AT2B and M4BT4D; Mt5AS was selected from a cross between ditelosomic 5AS monotelosomic 5AL and N5AT5D.

Homoeologous group 2

The wheat group 2 ESTs BE500625 and BE404630 are diagnostic for detecting the inversion in chromosome 2B of 'CS' as reported by Conley et al (2004). BE500625 was mapped to short arms and BE404630 to long arms of chromosomes 2A and 2D but were mapped to opposite arms in 2B (Fig. 2). In 'Wichita', BE500625 was mapped to 2BL arm and BE404630 to 2BS arm, which is consistent with the locations of these ESTs on 'CS' chromosome 2B. BE500625 did not detect any polymorphic fragments on 2S and 2H present in the 'CS' - *Ae. speltoides* DtA2S#3S and DtA2S#3L or the 'CS'-barley DtA2HS and DtA2HL stocks and, thus, could not be mapped. EST BE404630 detected 1 polymorphic fragment each in the 'CS' - *Ae. speltoides* DtA2S#3L and 'CS'-barley DtA2HL stocks, indicating that its ancestral location is in the long arm (Fig. 2).

Homoeologous group 3

Chromosome 3B

ESTs BE637878, BE404508, and BG313557, which were mapped to 3AL and (or) 3DL, were all mapped to 3BS (Fig. 2). EST BF485348 was mapped to 3AS, 3DS, and 3BL. These results indicate that a pericentric inversion exists in chromosome 3B of 'CS'.

Chromosomes 3S, 3S^{l}, and 3S^{s}

A similar inversion was also observed in the group 3 chromosomes of *Ae. speltoides* (3S), *Ae. longissima* (3S^{l}), *and Ae. searsii* (3S^{s}). Three long-arm ESTs were mapped to the short arm of chromosome 3S, and this was consistent with their location in chromosome 3BS (Fig. 2). All polymorphic fragments of 3S detected by these ESTs were observed in the 'CS' *Ae. speltoides* Dt3S#3S stock. The short-arm EST BF485348 did not detect any polymorphism in the 'CS' *Ae. speltoides* Dt3S#3S stock. We were unable to check the presence of this EST in the 'CS' *Ae. speltoides* Dt3S#3L stock because this stock is not available. Two long-arm ESTs, BE404580 and BG313557, were mapped to the short arm of chromosome 3S^{l} (Fig. 2). One short-arm EST, BE585348, and 1 long-arm EST, BE404580, were mapped to the opposite arms of chromosome 3S^{s}, respectively (Fig. 2).

Chromosomes 3R, 3H, and 3E

EST BE404580, mapped to the long arms of 3A and 3D, detected a 3R polymorphic fragment in 'CS' rye DtA3RS, indicating the presence of a putative pericentric inversion in chromosome 3R, but the 'CS' rye DtA3RL line was not available for this study. Two long-arm ESTs, BE404580 and BG313557, were mapped to the long arm of 3H, and BG313557 was mapped to the long arm of 3E. The short-arm EST BF485348 detected a 3H polymorphic fragment only in the 'CS' barley DtA3HS stock and, therefore, was mapped to the short arm of 3H. The EST locations in barley are consistent with 3A and 3D and represent the ancestral linear order (Fig. 2).

Homoeologous group 4

Both chromosomes 4A and 4B have undergone pericentric

Table 2. List of deletion lines used in the study.

TA No.	Deletion line	Fraction length value
TA4516L5	2AS-5	0.78
TA4517L1	2AL-1	0.85
TA4518L4	2BS-4	0.75
TA4518L3	2BS-3	0.84
TA4518L1	2BS-1	0.53
TA4519L2	2BL-2	0.36
TA4519L6	2BL-6	0.89
TA4520L5	2DS-5	0.47
TA4520L1	2DS-1	0.33
TA4521L3	2DL-3	0.49
TA4521L9	2DL-9	0.76
TA4534L7	6AS-5	0.65
TA4540L1	6AS-1	0.35
TA4531L5	6AL-4	0.55
TA4541L8	6AL-8	0.90
TA4542L2	6BS-2	1.05
TA4542L5	6BS-5	0.76
TA4543L5	6BL-5	0.40
TA4510L4	6BL-3	0.36
TA4544L6	6DS-6	0.99
TA4544L4	6DS-4	0.79
TA4544L2	6DS-2	0.45
TA4545L6	6DL-6	0.29
TA4529L4	6DL-1	0.47
TA4542L3	6DL12	0.68
TA4534L10	6DL-11	0.74
TA4528L4	6DL-10	0.80

structural rearrangements, and the EST order in chromosome 4D serves as a standard for comparison.

Chromosome 4A

Chromosome 4A has a complex evolutionary history (Naranjo et al. 1987; Anderson et al. 1992; Liu et al. 1992; Devos et al. 1995; Mickelson-Young et al. 1995; Nelson et al. 1995). Two reciprocal translocations involving chromosome arms 4AL, 5AL, and 7BS and 2 inversions (1 pericentric and 1 paracentric) in chromosome 4A were previously identified. The EST mapping data revealed that an additional pericentric inversion occurred in the centromeric region of 4A marked by 4 ESTs: BF202969, BF202706, BE494281, and BE637507 (Miftahudin et al.. 2004, Fig. 2). The inversion moved a 4AL-native segment back to the 4AL arm, homoeologous to 4DL. We allocated an additional RFLP marker, BCD1262, to the inverted segment (Fig. 2). The pericentric inversion may also have relocated a 4AS-native segment back to the 4AS arm, homoeologous to 4DS. However, no markers were identified for this segment.

Chromosome 4B

Three ESTs, BF202969, BF202706, and BE497309, are diagnostic for detecting a pericentric inversion in 4B as reported previously (Miftahudin et al.). In the present study, 3 additional ESTs, BE494281, BE406512, and BE497635, were allocated to the inverted segment (Fig. 2).

Chromosomes 4S, 4S^l, and 4S^s

Five ESTs, mapped to the long arm of chromosome 4D, were all assigned to the long arm of chromosome 4S (Fig. 2). Two short-arm ESTs could not be mapped on chromosome 4S because the 'CS' *Ae. speltoides* DtA4S#3S stock is not available. Only 2 of the 8 ESTs tested, 1 short-arm and 1 long-arm EST, detected the 4S^s polymorphic fragments in 'CS' *Ae. searsii* DtA4S^s#1S and 'CS' *Ae. searsii* DtA4S^s#1L stocks, respectively, and were mapped to chromosome 4S^s. The gene order in chromosomes 4S and 4S^s was consistent with that of chromosome 4D and represents the ancestral linear order (Fig. 2). However, mapping of 6 ESTs to chromosome 4S^l indicated that this chromosome carries a putative pericentric inversion (Fig. 2). EST BF202706, a long-arm probe, detected the 4S^l polymorphic fragment in the 'CS' *Ae. longissima* DtA4S^l#2S and was mapped to the short arm of chromosome 4S^l.

Chromosome 4R

Four of 6 ESTs mapped to 4DL detected the 4R polymorphic fragments on 'CS' rye DtA4RL and were assigned to 4RL (Fig. 2). One of the 2 short-arm ESTs was mapped to 4RS and 1 to 4RL, indicating a putative pericentric inversion in 4R.

Chromosome 4H

Five out of the 6 long-arm ESTs detected polymorphic fragments: 3 were mapped to 4HL and 2 to 4HS, suggesting the presence of a pericentric inversion in 4H (Fig. 2). This was also revealed by mapping of 2 short-arm ESTs to the long arm of chromosome 4H. ESTs BE497635 and BE497309 detected the 4H polymorphic fragments in both 'CS' barley DtA4HS and DtA4HL (Fig. 3). These data suggested that the 2 ESTs might map in the centromere of chromosome 4H, because 2 opposite telosomes of chromosome 4H share only a common centromere. After rechecking the DtA4HS and DtA4HL stocks we found that the telosome in DtA4HL appears to be a true telocentric, whereas the telosome in DtA4HS is actually an acrocentric chromosome with a very small 4HL segment present in the 4HS telosome. This explains why the polymorphic fragments of 2 ESTs were present in both stocks.

Homoeologous group 5

The presence of a pericentric inversion in chromosome 5A was described previously (Linkiewicz et al. 2004; also see Fig. 2). Five ESTs were mapped to 5AS, 5BL, and 5DL. The EST BE403618 was previously mapped to 5AL, 5BS, and 5DS (http://wheat.pw.usda.gov/NSF/project/mapping_data.html), further suggesting the presence of a pericentric inversion in chromosome 5A. In the present study, this EST detected a 5S^l polymorphic fragment on 'CS' *Ae. longissima* DtA5S^l#2S, indicating that the ancestral location of this EST is in the short arm of homoeologous group 5. No 5R or 5H polymorphic fragments were found on 'CS' rye DtA5RS, or 'CS' barley DtA5HS or DtA5HL.

Homoeologous group 6

Different pericentric inversions were detected in 6B of wheat and 6E of *Ag. elongatum*. The ancestral linear order

Table 3. EST clones used in the present study and their chromosome locations.

ESTs	Bin location	Other chromosome locations	EST	Bin location	Other chromosome locations
			BE406512	4AS1-0.20-0.63	
BE500625	C-2AS5-0.78			C-4BS4-0.37	
	C-2BL2-0.36	6BL, 6BS, 7BL		4DL9-0.31-0.53	
BE404630	C-2AL1-0.85		BE494281	C-4AL12-0.43	
	C-2BS1-0.53			C-4BL1-0.71	
	C-2DL3-0.49			C-4DL9-0.31	2BS, 1BL
BF485348	C-3AS4-0.45		BCD1262	C-4AL12-0.43	
	C-3BL2-0.22			C-4BL1-0.71	
	C-3DS3-0.24			C-4DL9-0.31	
			BE403618	C-5AL12-0.35	
BE637878	C-3BS1-0.33			5BS4-0.43-0.56	
	C-3DL2-0.27	1DL. 2DS, 2BS, 7AL		C-5DS1-0.63	
BG313557	C-3AL3-0.42		BE405809	C-6AS1-0.35	
	C-3BS1-0.33			C-6BL3-0.36	
	C-3DL2-0.27			C-6DS2-0.45	
BE404580	C-3AL3-0.42		BE405195	C-6AS1-0.35	
	C-3BS1-0.33			C-6BL3-0.36	
	C-3DL2-0.27			C-6DS2-0.45	
BE497635	C-4AL12-0.43		BE406602	C-6AS1-0.35	
	C-4BL1-0.71			C-6BL3-0.36	
	C-4DS1-0.53			C-6DS2-0.45	3DL, 4AL
BE497309	C-4AL12-0.43		BF428553	C-6AL4-0.55	
	C-4BL1-0.71			C-6BS5-0.76	
	C-4DS1-0.53			C-6DL6-0.29	
BF202706	C-4AL12-0.43		BE604879	6AS5-0.65-1.00	
	C-4BS4-0.37			6DS6-0.99-1.00	
	C-4DL9-0.31			2BS3-0.84-1.00	
BF202969	C-4AL12-0.43				
	C-4BS4-0.37				
	C-4DL9-0.31				

Fig. 1. An example of anomalous arm location revealed from mapping of a molecular marker to specific chromosome arms using wheat aneuploids. The genomic DNAs of NT, Dt, and DtA lines in homoeologous group 6 were digested with *Dra*I and hybridized with BE406602. The first fragment from the top was missing in N6AT6B and Dt6AL, and the third fragment was missing in N6DT6B and Dt6DL; thus, they were mapped to the short arms of 6A and 6D, respectively. The second fragment was absent in N6BT6A and Dt6BS and mapped to the long arm of 6B. Three additional fragments were observed in DtA6S#2S, DtA6RS, and DtA6HS and were mapped to the short arms of 6S, 6R, and 6H, respectively. Arrows point to the polymorphic fragments. The data revealed the ancestral location of BE406602 in group 6 short arms and anomalous location in the 6B long arm due to a pericentric inversion.

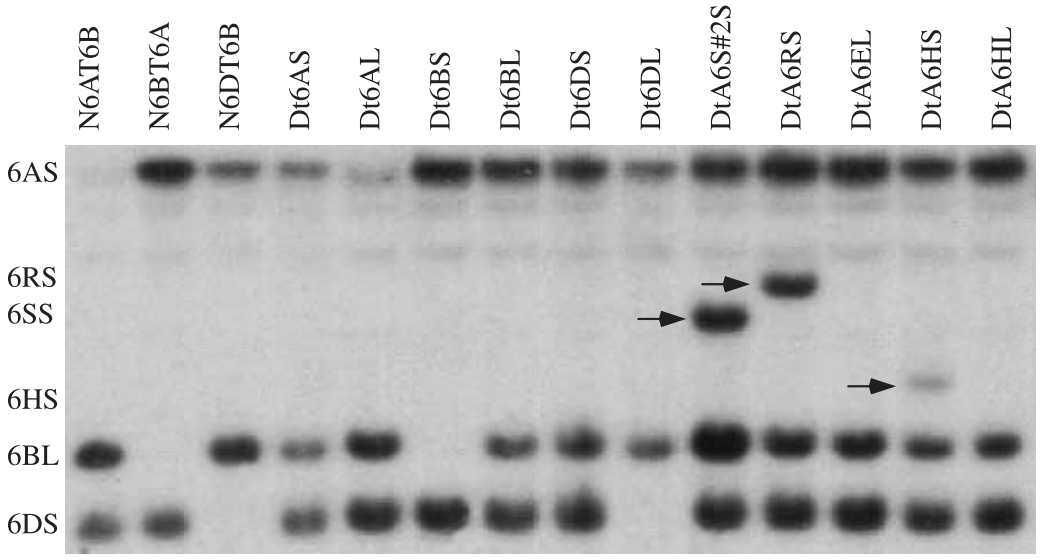


Fig. 2. Pericentric inversions in chromosomes of homoeologous groups 2, 3, 4, 5, and 6 of the Triticeae and a translocation involving 2BS and 6BS arms in 'CS' and 'Wichita' wheats. ESTs with blue color represent ancestral locations for the short arms and those with red color for the long arms.

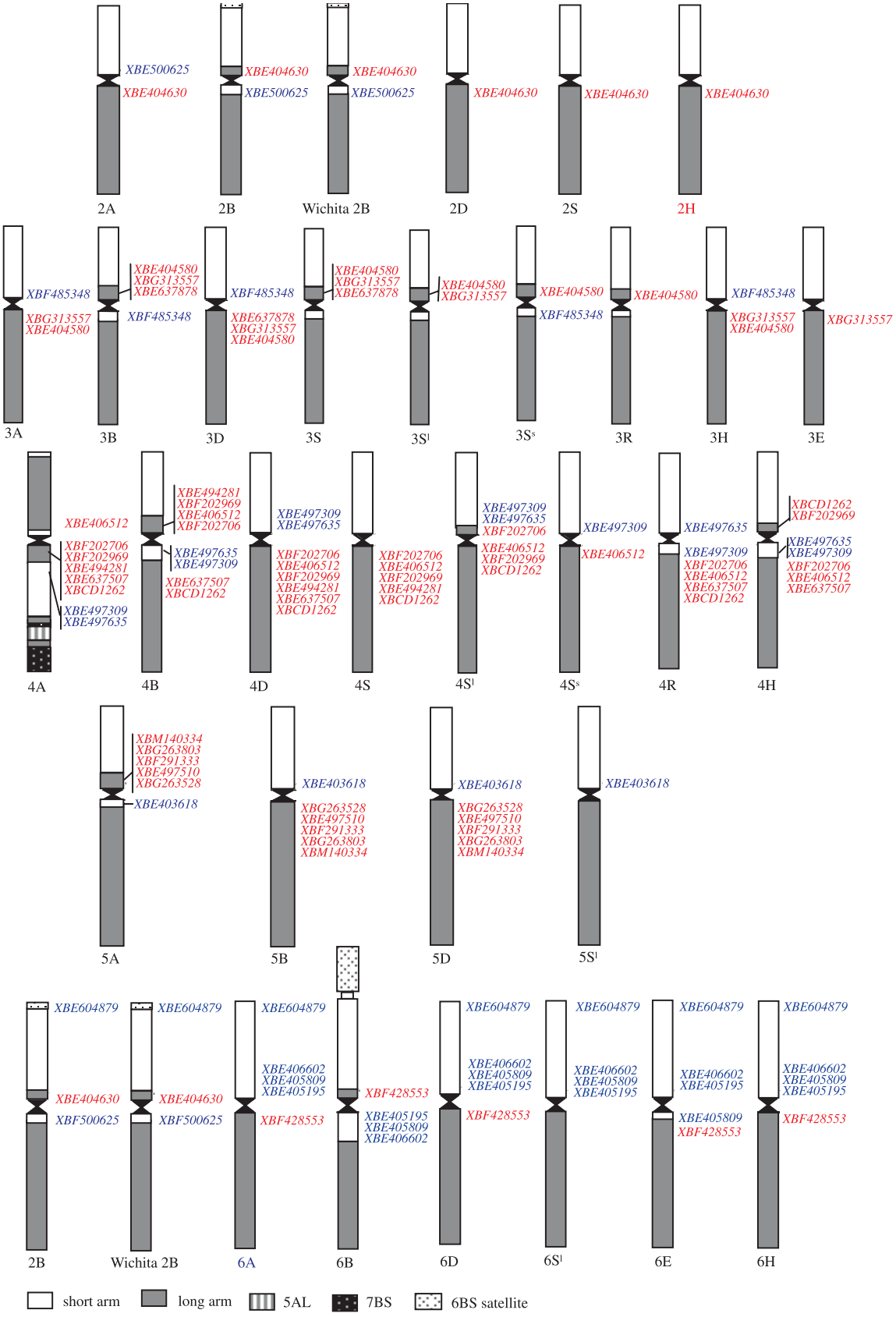
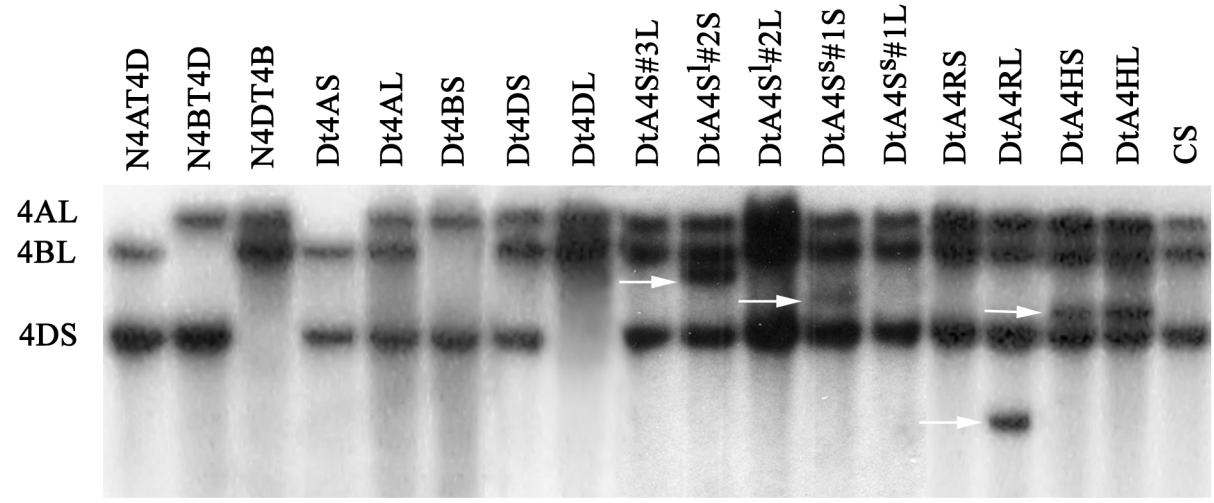


Fig. 3. An autoradiograph of a Southern hybridization of genomic DNAs from group 4 NT, Dt, DtA, and deletion lines. DNAs were digested with *Eco*RI and hybridized with BE497309. This EST was mapped to the proximal centromere of 4AL, 4BL, 4DS, $4S^{l}$#$4S^{s}$, $4S^{s}$#1S, and 4RL according to the hybridization patterns in NT, Dt, and DtA lines. A 4H polymorphic fragment is present in both DtA4HS and DtA4HL stocks (see explanation in the text). Arrows point to polymorphic fragments in the DtA stocks.



was maintained in chromosomes 6A, 6D, $6S^{l}$, and 6H (Fig. 2).

Translocation T2BS/6BS

A translocation involving the short arms of chromosomes 2B and 6B in hexaploid wheat has been proposed on the basis of genetic mapping data (Devos et al. 1993). The RFLP clone PSR899 has orthologous loci on 6AS, 6DS, and 2BS. This rearrangement of 2BS/6BS was also observed in tetraploid wheat by mapping the clones PSR899 on 6AS and 2BS (Blanco et al. 1998). However, the physical mapping data showed that PSR899 mapped to the chromosome bin 0.65–0.67 and not to a distal region in 6AS and 6DS (Weng and Lazar 2002). Recently, Conley et al. (2004) provided direct evidence for a 2B/6B translocation by mapping EST BE604879 to the distal bins of 2BS3-0.84-100, 6AS5-0.65-100, and 6DS6-0.99-100. In the present study, the same EST was used to test the locations on 2B of 'Wichita', $6S^{l}$ of *Ae. longissima*, 6E of *Ag. elongatum*, and 6H of barley. A restriction fragment that was missing in 'CS' N2BT2D and Dt2BL was also missing in 'Wichita' Dt2BL as compared with euploid 'Wichita', indicating that chromosome 2B in 'Wichita' also has a segment translocated from 6BS (Figs. 2 and 4). Polymorphic fragments were also detected by BE604879 in 'CS' *Ae. longissima* DtA6S#2S, 'CS' *Ag. elongatum* DtA6ES, and the 'CS' barley DtA6HS stock, but no polymorphic fragment was detected in alien ditelosomic addition lines involving homoeologous group 2. These data suggest that EST BE604879 was originally located on the short arms of homoeologous group 6 chromosomes. The 2BS-specific EST BE604879 fragments were missing in the genetic stocks of Dt6AL, Dt6BS, Dt6EL, del6BL-5, and del6DL-12, indicating that chromosome 2B in these stocks had undergone a deletion of the distal end harboring this marker (Fig. 4).

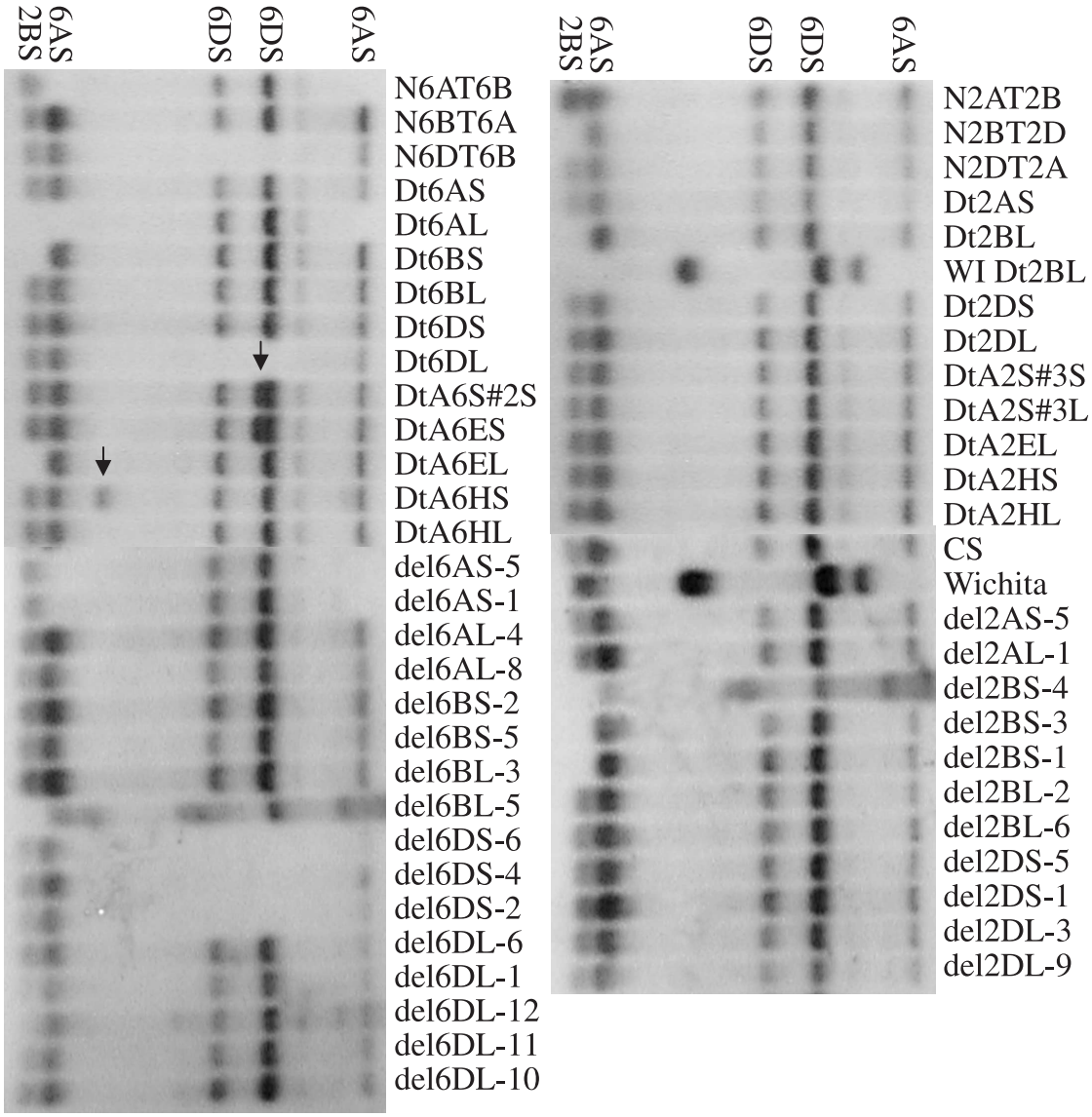
Discussion

Species-specific rearrangements vs. intraspecific chromosomal polymorphisms

Are the observed pericentromeric and other chromosomal rearrangements species specific or do they represent intraspecific polymorphisms? This distinction must be made to evaluate the relative role of a chromosomal polymorphism in the evolutionary history of a species. It is known that species belonging to the *Triticum–Aegilops* complex harbor extensive chromosomal polymorphisms in natural populations (Friebe et al. 1992; Badaeva et al. 1994, 2002, 2004; Kawahara 1988; Kawahara and Taketa 2000), and the polymorphisms probably play critical roles in adaptation of certain populations of a species to specific environmental conditions. As well, there are species-specific chromosomal rearrangements that are fixed in a species. The cyclic 4A, 5A, and 7B translocation has been observed in tetraploid wheat (*Triticum turgidum* L.) and hexaploid wheat, as well as in natural tetraploid wheat populations from diverse geographical areas (Gill and Chen 1987; Naranjo et al. 1987; Naranjo 1990). Similarly, the 6At-1G-4G translocation is fixed in *Triticum timopheevii* Zhuk., a sibling species of *T. turgidum* (Jiang and Gill 1994; Rodriguez et al. 2000). These translocations must have played an important role in the evolution of these polyploid wheat species (Gill 1991). It is also not unreasonable to suggest that species-specific translocations once represented local chromosomal polymorphisms and became fixed as the species went through an evolutionary bottleneck.

To distinguish between species-specific rearrangements and intraspecific chromosomal polymorphisms, we used 2 wheat cultivars with distinct evolutionary histories. The 'CS' genotype is an old landrace from Asia and represents a primitive chromosome arrangement. 'Wichita' wheat, for

Fig. 4. An autoradiograph of a Southern hybridization of genomic DNAs from NT, Dt, DtA, and deletion stocks of group 2 and 6 chromosomes of wheat. DNAs were digested with *Dra*I and hybridized with BE604879. The first and fourth fragments from the top are missing in N6AT6B, Dt6AL, del6AS-5, and del6AS-1 and were mapped to chromosome bin 6AS5-0.65-1.00. The second and third fragments are missing in N6DT6B, Dt 6DL, del6DS-2, del6DS-4, and del6DS-6 and were mapped to bin 6DS6-0.99-1.00. The fifth fragment is absent in N2BT2D and Dt2BL both in 'CS' and 'Wichita', in del2BS-4, del2BS-3, and del2BS-1 and was mapped to bin 2BS3-0.84-1.00. The 2BS fragment was also missing in Dt6AL, Dt6BS, DtA6EL, del6BL5, and del6DL12, indicating that 2B in these lines has a terminal deletion. Additional polymorphic fragments were observed in DtA6S#2S, DtA6ES, and DtA6HS, indicating an ancestral location of this EST in group 6. Arrows point to polymorphic fragments.



which certain cytogenetic stocks are also available, traces back to 'Turkey' wheat, which is an old landrace from Transcaucasia with winter-type plant habit. It was previously documented that 'Wichita' has the wild-type 4B chromosome, whereas 4B of 'Chinese Spring' had undergone a pericentric inversion (Endo and Gill 1984). Later analysis revealed additional 4B polymorphisms indicating recurrent origin of this inversion (Friebe and Gill 1994). The results of the present research together with those reported by Miftahudin et al. (2004) have led to the identification of several markers that further define the 4B inversion and may be useful in analyzing the hypothesis of recurrent origin of this inversion in different wheat cultivars.

The pericentric inversion of chromosome 2B in 'CS' was also observed in 'Wichita', indicating that this inversion is species specific. We also detected a 2B/6B translocation in 'Wichita' together with its occurrence in tetraploid wheat. The accumulating data indicate that this is also a species-specific chromosomal translocation. However, the 2B/6B translocation was polymorphic (present/absent) in various aneuploids in 'CS', indicating that the translocated segment is prone to breakage (Fig. 4).

Additional pericentromeric inversions were observed in 'CS' for chromosomes 3B, 5A, and 6B. We could not confirm their occurrence in 'Wichita' as suitable telosomic stocks were not available. However, we have available telosomic addition lines of *Ae. speltoides* in 'CS' and could test whether the observed rearrangements were present in the diploid donor species or arose following polyploidy.

Polyploidy and the origin of chromosomal rearrangements

There is accumulating evidence in the literature that the process of polyploidization is a trigger that induces chromosomal changes in the ancestral genomes that now share a nucleus. Of the 5 rearrangements observed in the B genome chromosomes of polyploid wheat, only the pericentric inversion in 3B pre-existed in *Ae. speltoides*, *Ae. longissima*, and *Ae. searsii*. The 2B/6B translocation present in polyploid wheat was not observed in *Ae. longissima* or in *Ae. speltoides* (Zhang et al. 2001; Luo et al. 2005). These data would seem to indicate that either these rearrangements arose after polyploidization, or *Ae. speltoides* is polymorphic for these rearrangements. It is also possible that *Ae. speltoides* is not the B genome donor of wheat (Huang et al. 2002).

Rapid and recurrent origin of pericentric inversions

The A, B, and D genomes diverged from a common ancestor about 3 million years ago (MYA), rye diverged from wheat about 6 MYA, and wheat and barley diverged from a common ancestor about 12 MYA (Huang et al. 2002). Except for the wheat chromosome 3B pericentric inversion that pre-existed in *Ae. speltoides, Ae. longissima,* and *Ae. searsii*, none of the wheat-specific inversions were detected in a collection of 14 informative chromosomes belonging to S, R, E, and H genomes of the Triticeae (Fig. 2). However, 5 independent pericentric inversions were detected in this small sample of 14 chromosomes, indicating a rapid, recurrent, and independent origin of pericentric inversions similar to those observed in hominids (Yunis and Prakash 1982). For group 2 and 5 chromosomes, only a small sample of chromosomes was available, and pericentric inversions were detected only in chromosome 2B for group 2 and 5A for group 5. Group 4 chromosomes had the highest rate of pericentric inversions, and 5 independent pericentric inversions (4A, 4B, $4S^l$, 4R, 4H) with different breakpoints were observed in a sample of 8 chromosomes. Why certain chromosomes are more prone to pericentric inversions is not clear. Group 4 chromosomes have the largest amount of pericentric heterochromtin known to be composed of tandem repeats, which may be more prone to chromosome rearrangements. Perhaps these regions also harbor large blocks of segmental duplications in the pericentromeres that are more prone to ectopic recombination inversion events, as has also been observed in hominids (Eichler 1998; Jackson 2003; Kirsch et al. 2005).

Uneven rates of evolution of subgenomes in a polyploid nucleus

Seven pairs of chromosomes each from A, B, and D genomes constitute the hexaploid wheat nucleus. The A and B diploid species hybridized to form tetraploid (AABB) wheat less than 500 000 years ago (Huang et al. 2002). The AABB tetraploid wheat hybridized with a D genome diploid to form hexaploid wheat about 8000 years ago (Nesbitt and Samuel 1996; Dvorak and Akhunov 2005). Of the A, B, and D genome chromosomes, 2 from the A genome and 4 from the B genome were involved in pericentric inversions; only the 3B inversion pre-existed in the diploid donor. Clearly, the B genome is evolving at a faster rate than the A genome, as also indicated by RFLP polymorphism studies (Qi et al. 2004). The B genome also harbored more genes unique to wheat and not found in rice (See et al. 2006). Half of the genome- or chromosome-specific ESTs involved the B genome (Qi et al. 2004). The reasons why the B genome has evolved at a faster rate have been discussed previously (Akhunov et al. 2003; Qi et al. 2004) and may be related to its evolutionary history and the higher heterochromatic content of its chromosomes (Gill et al. 1991). The accumulating data support the notion that subgenomes in a polyploid nucleus evolve at different rates. The molecular mechanisms of differential evolution remain to be elucidated.

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References

Akhunov, E.D., Goodyear, A.W., Geng, S., Qi, L.L., Echalier, B., Gill, B.S., et al. 2003. The organization and rate of evolution of wheat genomes are correlated with recombination rates along chromosome arms. Genome Res. **13**: 753–763. doi:10.1101/gr.808603. PMID:12695326.

Anderson, J.A., Ogihara, Y., Sorrells, M.E., and Tanksley, S.D. 1992. Development of a chromosomal arm map for wheat based on RFLP markers. Theor. Appl. Genet. **83**: 1035–1043.

Badaeva, E.D., Badaeva, N.S., Gill, B.S., and Filatenko, A.A. 1994. Intraspecific karyotype divergence in *Triticum araraticum* (*Poaceae*). Plant Syst. Evol. **192**: 117–145. doi:10.1007/BF00985912.

Badaeva, E.D., Amosova, A.V., Muravenko, O.V., Samatadze, T.E., Chikida, N.N., Zelenin, A.V., et al. 2002. Genome differentiation in *Aegilops*. 3. Evolution of the D-genome cluster. Plant Syst. Evol. **231**: 163–190. doi:10.1007/s006060200018.

Badaeva, E.D., Amosova, A.V., Samatadze, T.E., Zoshchuk, S.A., Shostak, N.G., Chikida, N.N., et al. 2004. Genome differentiation in *Aegilops*. 4. Evolution of the U-genome cluster. Plant Syst. Evol. **246**: 45–76. doi:10.1007/s00606-003-0072-4.

Blanco, A., Bellomo, M.P., Cenci, A., De Giovanni, C., D'Ovidio, R., Iacono, E., et al. 1998. A genetic linkage map of durum wheat. Theor. Appl. Genet. **97**: 721–728. doi:10.1007/s001220050948.

Chen, F.C., and Li, W.H. 2001. Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of human and chimpanzees. Am. J. Hum. Genet. **68**: 444–456. doi:10.1086/318206. PMID:11170892.

Conley, E.J., Nduati, V., Gonzalez-Hernandez, J.L., Mesfin, A., Trudeau-Spanjers, M., Chao, S., et al. 2004. A 2600-locus chromosome bin map of wheat homoeologous group 2 reveals inter-

stitial gene-rich islands and colinearity with rice. Genetics, **168**: 625–637. doi:10.1534/genetics.104.034801. PMID:15514040.

Devos, K.M., Millan, T., and Gale, M.D. 1993. Comparative RFLP maps of homoeologous group 2 chromosomes of wheat, rye and barley. Theor. Appl. Genet. **85**: 784–792.

Devos, K.M., Dubcovsky, J., Dvorak, J., Chinoy, C.N., and Gale, M.D. 1995. Structural evolution of wheat chromosomes 4A, 5A, and 7B and its impact on recombination. Theor. Appl. Genet. **91**: 282–288.

Dvorak, J., and Akhunov, E.D. 2005. Tempos of deletions and duplications of gene loci in relation to recombination rate during diploid and polyploid evolution in the *Aegilops-Triticum* alliance. Genetics, **171**: 323–332. doi:10.1534/genetics.105.041632. PMID:15996988.

Dvorak, J., and Knott, D.R. 1974. Disomic and ditelosomic additions of diploid *Agropyron elongatum* chromosomes to *Triticum aestivum.* Can. J. Genet. Cytol. **16**: 399–417.

Dvorak, J., McGuire, P.E., and Mendlinger, S. 1984. Inferred chromosome morphology of the ancestral genome of *Triticum.* Plant Syst. Evol. **144**: 209–220.

Eichler, E.E. 1998. Masquerading repeats: paralogous pitfalls of the human genome. Genome Res. **8**: 758–762. PMID:9724321.

Eichler, E.E., and Sankoff, D. 2003. Structural dynamics of eukaryotic chromosome evolution. Science (Washington, D.C.), **301**: 793–797. doi:10.1126/science.1086132. PMID:12907789.

Endo, T.R., and Gill, B.S. 1984. Somatic karyotype, heterochromatin distribution, and nature of chromosome differentiation in common wheat, *Triticum aestivum* L. em. Thell. Chromosoma, **89**: 361–369. doi:10.1007/BF00331253.

Endo, T.R., and Gill, B.S. 1996. The deletion stocks of common wheat. J. Hered. **87**: 295–307.

Friebe, B., and Gill, B.S. 1994. C-band polymorphism and structural rearrangements detected in common wheat (*Triticum aestivum*). Euphytica, **78**: 1–5.

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

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

Friebe, B., Tuleen, N.A., and Gill, B.S. 1995. Standard karyotype of *Triticum searsii* and its relationship with other S genome species. Theor. Appl. Genet. **91**: 248–255.

Friebe, B., Qi, L.L., Nasuda, S., Zhang, P., Tuleen, N.A., and Gill, B.S. 2000. Development of a complete set of *Triticum aestivum-Aegilops speltoides* chromosome substitution lines. Theor. Appl. Genet. **101**: 51–58. doi:10.1007/s001220051448.

Gill, B.S. 1991. Nucleo-cytoplasmic interaction (NCI) hypothesis of genome evolution and speciation in polyploid plants. *In* Nuclear and organelle genomes of wheat species. Proc. Int. Symp. Cytoplasmic Engineering. *Edited by* T. Sasakuma and T. Kinoshita. Hokkaido, Japan. pp. 48–53.

Gill, B.S., and Chen, P.D. 1987. Role of cytoplasm-specific introgression in the evolution of the polyploid wheats. Proc. Natl. Acad. Sci. U.S.A. **84**: 6800–6804. doi:10.1073/pnas.84.19.6800. PMID:16578821.

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

Goidts, V., Szamalek, J.M., de Jong, P.J., Cooper, D.N., Chuzhanova, N., Hameister, H., and Kehrer-Sawatzki, H. 2005. Independent intrachromosomal recombination events underlie the pericentric inversions of chimpanzee and gorilla chromosomes homologous to human chromosome 16. Genome Res. **15**: 1232–1242. doi:10.1101/gr.3732505. PMID:16140991.

Huang, S., Sirikhachornkit, A., Su, X.J., Faris, J.D., Gill, B.S., Haselkorn, G., and Gornicki, P. 2002. Genes encoding plastid acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the *Triticum/Aegilops* complex and the evolutionary history of polyploid wheat. Proc. Natl. Acad. Sci. U.S.A. **99**: 8133–8138. doi:10.1073/pnas.072223799. PMID:12060759.

Islam, A.K.M.R., and Shepherd, K.W. 1988. Induced pairing between wheat and barley chromosomes. *In* Proceedings of the 7th International Wheat Genetics Symposium, Cambridge, England, 13–19 July 1988. *Edited by* T.E. Miller and R.M.D. Koebner. Institute of Plant Science Research, Cambridge Laboratory, Trumpington, Cambridge. Bath Press, Avon. pp. 309–314.

Islam, A.K.M.R., and Shepherd, K.W. 1992. Production of wheat-barley recombinant chromosomes through induced homoeogous pairing 1. Isolation of recombinants involving barley arms 3HL and 6HL. Theor. Appl. Genet. **83**: 489–494.

Islam, A.K.M.R., Shepherd, K.W., and Sparrow, D.H.B. 1981. Isolation and characterization of euplasmic wheat-barley chromosome addition lines. Heredity, **46**: 161–174.

Jackson, M. 2003. Duplicate, decouple, disperse: the evolutionary transience of human centromeric regions. Curr. Opin. Genet. Dev. **13**: 629–635. doi:10.1016/j.gde.2003.10.011. PMID:14638326.

Jiang, J., and Gill, B.S. 1994. Different species-specific chromosome translocations in*Triticum timopheevii* and *T. turgidum* support the diphyletic origin of polyploid wheats. Chromosome Res. **2**: 59–64. doi:10.1007/BF01539455. PMID:8162322.

Kawahara, T. 1988. Confirmation of primitive chromosome structure in the hexaploid wheats. Theor. Appl. Genet. **75**: 717–719.

Kawahara, T., and Taketa, S. 2000. Fixation of translocation 2A–4B infers the monophyletic origin of Ethiopian tetraploid wheat. Theor. Appl. Genet. **101**: 705–710. doi:10.1007/s001220051534.

Kehrer-Sawatzki, H., Sandig, C., Chuzhanova, N., Goidts, V., Szamalek, J.M., Tanzer, S., et al. 2005. Breakpoint analysis of the pericentric inversion distinguishing human chromosome 4 from the homologous chromosome in the chimpanzee (*Pan troglodytes*). Hum. Mutat. **25**: 45–55. doi:10.1002/humu.20116. PMID:15580561.

Kirsch, S., Weiß, B., Miner, T.L., Waterston, R.H., Clark, R.A., Eichler, E.E., et al. 2005. Interchromosomal segmental duplications of the pericentromeric region on the human Y chromosome. Genome Res. **15**: 195–204. doi:10.1101/gr.3302705. PMID:15653831.

Linkiewicz, A.M., Qi, L.L., Gill, B.S., Ratnasiri, A., Echalier, B., Chao, S., et al. 2004. A 2500-locus bin map of wheat homoeologous group 5 provides insights on gene distribution and colinearity with rice. Genetics, **168**: 665–676. doi:10.1534/genetics.104.034835. PMID:15514043.

Liu, C.J., Devos, K.M., Chinoy, C.N., Atkinson, M.D., and Gale, M.D. 1992. Homoeologous translocations between group 4, 5 and 7 chromosomes in wheat and rye. Theor. Appl. Genet. **83**: 305–312.

Luo, M.C., Deal, K.R., Young, Z.L., and Dvorak, J. 2005. Comparative genetic maps reveal extreme crossover localization in the *Aegilops speltoides* chromosomes. Theor. Appl. Genet. **111**: 1098–1106. doi:10.1007/s00122-005-0035-y. PMID:16088396.

Mickelson-Young, L., Endo, T.R., and Gill, B.S. 1995. A cytogenetic ladder-map of the wheat homoeologous group-4 chromosomes. Theor. Appl. Genet. **90**: 1007–1011.

Miftahudin, Ross, K., Ma, X.-F., Mahmoud, A.A., Layton, J., Rodriguez Milla, M.A., et al. 2004. Analysis of expressed sequence tag loci on wheat chromosome group 4. Genetics, **168**: 651–663. doi:10.1534/genetics.104.034827. PMID:15514042.

Moore, G., Roberts, M., Aragon-Alcaide, L., and Foote, T. 1997. Centromeric sites and cereal chromosome evolution. Chromosoma, **105**: 321–323. doi:10.1007/s004120050190. PMID:9087373.

Mukai, Y., Friebe, B., Gill, B.S. 1992. Comparison of C-banding patterns and in situ hybridization sites using highly repetitive and total genomic rye DNA probes of 'Imperial' rye chromosomes added to 'Chinese Spring' wheat. Jpn. J. Genet. **67**: 71–83.

Naranjo, T. 1990. Chromosome structure of durum wheat. Theor. Appl. Genet. **79**: 397–400. doi:10.1007/BF01186085.

Naranjo, T., Roca, A., Goicoechea, P.G., and Giraldez, R. 1987. Arm homoeology of wheat and rye chromosomes. Genome, **29**: 873–882.

Nelson, J.C., Sorrells, M.E., Van Deynze, A.E., Lu, Y.H., Atkinson, M., Bernard, M., et al. 1995. Molecular mapping of wheat: major genes and rearrangements in homoeologous groups 4, 5, and 7. Genetics, **141**: 721–731. PMID:8647405.

Nesbitt, M., and Samuel, D. 1996. From staple crop to extinction? The archaeology and history of hulled wheats. *In* Hulled wheats. Promoting the conservation and use of underutilized and neglected crops. Proceedings of the 1st International Workshop on Hulled Wheats, 21–22 July 1995, Castelvecchio Pascoli, Tuscany, Italy. *Edited by* S. Padulosi, K. Hammer, and J. Heller. International Plant Genetics Research Institute, Rome, Italy. pp. 41–100.

Nickerson, E., and Nelson, D.L. 1998. Molecular definition of pericentric inversion breakpoints occurring during the evolution of humans and chimpanzees. Genomics, **50**: 368–372. doi:10.1006/geno.1998.5332. PMID:9676431.

Qi, L.L., Echalier, B., Friebe, B., and Gill, B.S. 2003. Molecular characterization of a set of wheat deletion stocks for using in chromosome bin mapping of ESTs. Funct. Integr. Genomics, **3**: 39–55. PMID:12590342.

Qi, L.L., Echalier, B., Chao, S., Lazo, R.G., Butler, G.E., Anderson, O.D., et al. 2004. A chromosome bin map of 16,000 expressed sequence tag loci and distribution of genes among the three genomes of polyploid wheat. Genetics, **168**: 702–712.

Raupp, W.J., Friebe, B., and Gill, B.S. 1995. Suggested guidelines for the nomenclature and abbreviations of the genetic stocks of wheat, *Triticum aestivum* L. em Thell, and its relatives. Wheat Inf. Serv. **81**: 50–55.

Rodriguez, S., Perera, E., Maestra, B., and Naranjo, T. 2000. Chromosome structure of *Triticum timopheevii* relative to *T. turgidum.* Genome, **43**: 923–930. doi:10.1139/gen-43-6-923. PMID:11195344.

Sears, E.R. 1954. The aneuploids of common wheat. Univ. Mo. Agric. Exp. Stn. Res. Bull. **572**: 1–58.

Sears, E.R. 1966. Nullisomic-tetrasomic combinations in hexaploid wheat. *In* Chromosome manipulations and plant genetics. *Edited by* R. Riley and K.R. Lewis. Oliver and Boyd, Edinburgh, Scotland. pp. 29–45.

Sears, E.R., and Steinitz-Sears, L.M. 1978. The telocentric chromosomes of common wheat. Proceeding of the 5th International Wheat Genetics Symposium, New Delhi, 23–28 February 1988. *Edited by* S. Ramanujam. Indian Society of Genentics and Plant Breeding, New Delhi, India. pp. 389–407.

See, D.R., Brooks, S., Nelson, J.C., Brown-Guedira, G., Friebe, B., and Gill, B.S. 2006. Gene evolution at the ends of wheat chromosomes. Proc. Natl. Acad. Sci. U.S.A. **103**: 4162–4167. doi:10.1073/pnas.0508942102. PMID:16537502.

Sorrells, M.E., La Rota, C.M., Bermudez, C.E., Greene, R.A., Kantety, R., Munkvold, J.D., et al. 2003. Comparative DNA sequence analysis of wheat and rice genomes. Genome Res. **13**: 1818–1827. PMID:12902377.

Weng, Y., and Lazar, M.D. 2002. Comparison of homoeologous group-6 short arm physical maps of wheat and barley reveals a similar distribution of recombinogenic and gene-rich regions. Theor. Appl. Genet. **104**: 1078–1085. PMID:12582615.

Yunis, J.J., and Prakash, O. 1982. The origin of man: a chromosomal pictorial legacy. Science (Washington, D.C.), **215**: 1525–1530. PMID:7063861.

Zhang, H., Reader, S.M., Liu, X., Jia, J.Z., Gale, M.D., and Devos, K.M. 2001. Comparative genetic analysis of the *Aegilops longissima* and *Ae. sharonensis* genomes with common wheat. Theor. Appl. Genet. **103**: 518–525. doi:10.1007/s001220100656.