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ORIGINAL PAPER

Microsatellite mapping of *Ae. speltoides* and map-based comparative analysis of the S, G, and B genomes of Triticeae species

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Abstract The first microsatellite linkage map of *Ae. speltoides* Tausch ($2n = 2x = 14$, SS), which is a wild species with a genome closely related to the B and G genomes of polyploid wheats, was developed based on two F_2 mapping populations using microsatellite (SSR) markers from *Ae. speltoides*, wheat genomic SSRs (g-SSRs) and EST-derived SSRs. A total of 144 different microsatellite loci were mapped in the *Ae. speltoides* genome. The transferability of the SSRs markers between the related S, B, and G genomes allowed possible integration of new markers into the *T. timopheevii* G genome chromosomal maps and map-based comparisons. Thirty-one new microsatellite loci assigned to the genetic framework of the *T. timopheevii* G genome maps were composed of wheat g-SSR (genomic SSR) markers. Most of the used *Ae. speltoides* SSRs were mapped onto chromosomes of the G genome supporting a close relationship between the G and S genomes. Comparative microsatellite mapping of the S, B, and G genomes demonstrated colinearity between the chromosomes within homoeologous groups, except for intergenomic T6A^{t}S.1G, T4AL.5AL.7BS translocations. A translocation between chromosomes 2 and 6 that is present in the *T. aestivum* B genome was found in neither *Ae. speltoides* nor in *T. timopheevii*. Although the marker order was generally conserved among the B, S, and G genomes, the total length of the *Ae. speltoides* chromosomal maps and the genetic distances between homoeologous loci located in the proximal regions of the S genome chromosomes were reduced compared with the B, and G genome chromosomes.

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Introduction

Ae. speltoides Tausch ($2n = 14$, genome formula SS) is a wild species assigned to the section Sitopsis of the genus *Aegilops*. Based on morphological characteristics (following Eig's (1929) classification), *Ae. speltoides* was further assigned to the monotypic subsection Truncata, whereas the other Sitopsis species, *Ae. searsii* ($S^{s}S^{s}$), *Ae. bicornis* ($S^{b}S^{b}$), *Ae. longissima* ($S^{l}S^{l}$), and *Ae. sharonensis* ($S^{sh}S^{sh}$), are considered to be members of the subsection Emarginata. *Ae. speltoides* was shown to be phylogenetically distinct from the other species of the section on the basis of C banding (Friebe and Gill 1996), variation in repeated nucleotide sequences (Dvorak and Zhang 1992), FISH with ribosomal RNA gene families (Badaeva et al. 1996), RFLP (Sasanuma et al. 1996), PAPD (Salina et al. 2006b), AFLP (Kilian et al. 2007) analysis, microsatellite analysis using wheat genomic SSRs (Adonina et al. 2005), and EST-derived SSRs (Zhang et al. 2006). *Ae. speltoides* is the only outbreeding Sitopsis species and shows the broadest genomic polymorphism among the species of Sitopsis section (Friebe and Gill 1996; Sasanuma et al. 1996; Giorgi et al. 2002; Kilian et al. 2007).

The genomes of all representatives of the Sitopsis section are related to the B and G genomes of polyploid wheats; however, the *Ae. speltoides* genome is considered

to be the most closely related one to these genomes and it is their most likely donor (Tsunewaki and Ogihara 1983; Dvorak and Zhang 1990; Feldman et al. 1995; Friebe and Gill 1996; Tsunewaki 1996). It has been suggested that similar parental forms of *Ae. speltoides* were involved in the origin of wheats of evolutionary lineages: emmer, including *T. dicoccum* (AABB) and *T. aestivum* (AABBDD), and timopheevii (*T. timopheevii* (A^tA^tGG), *T. militinae* (A^tA^tGG), *T. zhukovskyi* ($A^tA^tA^zA^zGG$)) (Peacock et al. 1981; Dvorak and Zhang 1990; Mori et al. 1995; Huang et al. 2002; Levy and Feldman 2002; Salina et al. 2006b). It should be noted that the differences between the S and B/G genomes are much greater than those between the A and D genomes and their donors, *T. urartu* and *Ae. tauschii*. This was inferred from the low percentage of pairing observed between the B and S genome chromosomes at a fully active *Ph1* locus; the majority of the A genome chromosomes formed bivalents with *T. urartu* chromosomes under the same circumstances (Kimber and Athwal 1972; Chapman et al. 1976; Dvorak 1976). The B–S pairing in ABDS, $ABDS^{l}$, and $ABDS^{sh}$ hybrids was found to be comparable (Fernandez-Calvin and Orellana 1994; Maestra and Naranjo 1998), indicating that the pairing of the B genome chromosomes with those of *Ae. speltoides* is not preferential. Thus, it remains unclear whether *Ae. speltoides* is truly the immediate B/G genome donor of polyploid wheats; if the currently existing polyploid wheats are most closely related to an extinct ancestor; or whether other species besides *Ae. speltoides* might have been involved in the origin of the B/G genomes. Whatever the possibilities, numerous studies on present-day wheats have demonstrated that it is the *Ae. speltoides* genome that is closest to the polyploid wheat B and G genomes.

Comparative genetic mapping has established that the content and linear order (colinearity) of markers has remained generally conserved during the millions of years of cereal evolution (reviewed in Devos and Gale 2000; Feuillet and Keller 2002). Comparative genomics at the genetic map level allows taking advantage of the genomic resources of one cereal species to accelerate gene discovery in related species and provides a basis for the investigation of cereal phylogeny. Molecular genetic mapping of the genomes of diploid ancestors of bread wheat (AABBDD) is used to supplement genomic analysis because their polymorphism level is higher and working with a single genome is easier; moreover, novel data regarding cereal phylogeny may be obtained. Molecular linkage maps of the A genome of diploid wheat have been developed using RFLP (Dubcovsky et al. 1996) and AFLP markers (Taenzler et al. 2002), and they have recently been saturated with SSRs (Singh et al. 2007). A high-density cytogenetic map comprising 732 loci (RFLPs, SSRs, ISSRs, defence-related genes, and retrotransposons) has been constructed for the *Ae. tauschii*, the D genome donor of the bread wheat (Boyko et al. 2002). The first linkage maps of the *Ae. speltoides* genome (SS) consisting of 137 RFLP loci were constructed by Luo et al. (2005). Comparison of the *Ae. speltoides* maps with those of *T. monococcum* showed that the order of markers is well conserved between the S and A^m genome chromosomes, except for 4/5 translocation, which is endemic for the A genome and the putative inversion of chromosome 2S (Luo et al. 2005). These *Ae. speltoides* linkage maps have enabled mapping of three *Ae. speltoides* genes and a QTL: the wheat *Ph1* suppressors, *Su1-Ph1* (3S), *Su2-Ph1* (7S), and *QPh.ucd-5S* (Dvorak et al. 2006), and a gene for spike morphology, *Lig* (3S) (Luo et al. 2005). Comparative mapping of the S genome with the related B and G genomes has not been performed thus far. Recently, linkage maps for *T. timopheevii* (A^tA^tGG) were constructed using SSRs markers (Salina et al. 2006a) and these could be used together with the *T. aestivum* B genome microsatellite maps (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/) for map-based comparison with the *Ae. speltoides* S genome maps. The development of the S genome microsatellite linkage maps represents an essential step in this comparative analysis. The construction of high-density linkage maps of *Ae. speltoides* using PCR-based markers that are amenable to high throughput and automatisation would provide a basis for further investigation in cereal phylogeny and use in studying the genetics and breeding of *Ae. speltoides* as a reservoir of useful genes in wheat improvement.

Microsatellites currently constitute one of the best-suited marker systems for the analysis of cereal genomes, including that of bread wheat. Using SSRs, numerous genes and a large set of QTLs were localised onto individual wheat chromosomes. They have been included into MAS (marker assisted selection) programs (reviewed in Ganal and Röder 2007). Wheat SSRs have been shown to be transferable to closely related species, including *Ae. speltoides* (Sourdille et al. 2001; Adonina et al. 2005), and can be useful in mapping their genomes. Linkage maps for *T. timopheevii* (A^tA^tGG) were constructed by applying SSRs derived from bread wheat (Salina et al. 2006a). Map-based comparison allowed the detection of chromosome translocations and rearrangements between *T. timopheevii* and *T. aestivum.* Nevertheless, in maps of the G genome, certain chromosomes are still poorly saturated with markers (Salina et al. 2006a), which complicates map-based comparison of the related B and G genomes as well as the monitoring of the introgression of the *T. timopheevii* material into bread wheat in the development of isogenic lines. In addition to genomic SSRs, EST-derived SSR markers are being widely applied in cereal genome analysis (Thiel et al. 2003; Yu et al. 2004; Zhang et al. 2005; Zhang

et al. 2006). The high transferability of these markers allowed their use in comparative mapping.

Here, we report the construction of linkage maps of the *Ae. speltoides* S genome using (1) SSRs developed from the *Ae. speltoides* microsatellite enriched library; (2) wheat EST-SSRs, and (3) wheat genomic SSRs. We also report the integration of SSRs from *Ae. speltoides* and *T. aestivum*, including EST-SSRs, into the G genome chromosomal maps of *T. timopheevii*. The transferability of these SSRs markers between the related S, B, and G genomes made map-based comparison possible.

Materials and methods

Plants and mapping populations

The *Ae. speltoides* open-pollinated accessions 8, 25, and 37 were used to carry out two crosses, 8 × 37 and 25 × 37. The F_2 populations from the 8 × 37 and 25 × 37 crosses comprising 91 and 80 individuals, respectively, were obtained and will be designated throughout as the (a) mapping population and the (b) mapping population. Five disomic *T. aestivum–Ae. speltoides* addition lines (Friebe et al. 2000) were used to associate linkage groups with the *Ae. speltoides* 1S, 2S, 4S, 5S, and 7S chromosomes (lines for chromosomes 3S and 6S were unavailable). Using these lines, several non-polymorphic markers were located to particular *Ae. speltoides* chromosomes.

New markers were integrated into the *T. timopheevii* chromosomal maps using two F_2 mapping populations from the crosses *T. timopheevii* var. *timopheevii* × *T. timopheevii* var. *typica* (population I), and *T. timopheevii* K-38555 × *T. militinae* (population II) produced earlier (Salina et al. 2006a). The populations consisted of 74 individual plants each.

Four hexaploid wheat cultivars, Chinese Spring, Synthetic, Courtot, and Opata, were used to assess the transferability level of microsatellites from *Ae. speltoides* to *T. aestivum*. The Chinese Spring cultivar was used as a positive control while surveying the transferability of wheat genomic and EST-derived markers to the *Ae. speltoides* and *T. timopheevii* parental accessions.

DNA isolation, marker analysis, and map construction

DNA was extracted from fresh leaves using a CTAB protocol, as described by Tixier et al. (1998).

The following types of microsatellite markers were used for mapping of the *Ae. speltoides* genome and integration into the *T. timopheevii* chromosomal maps:

1. SSRs developed from the *Ae. speltoides* microsatellite-enriched library, *Xgpw* (Sourdille et al. 2004);
2. EST-derived wheat microsatellites, EST-*Xgpw* (Nicot et al. 2004; Sourdille et al., unpublished), *Xcfe* (Zhang et al. 2005), *Xksum*, and *Xcnl* (Yu et al. 2004);
3. *T. aestivum* genomic SSRs, *g-Xgpw* (Sourdille et al. 2004, unpublished), *Xgwm* (Röder et al. 1998), and *Xwmc* (Gupta et al. 2002), which were previously located to the B genome chromosomal maps. Information on the SSR markers used here is available at http://www.graingenes.org. The markers *Xgwm682*, *Xgwm779*, *Xgwm825*; *Xgwm856* were kindly provided by Dr. M.S. Röder, IPK, Gatersleben, Germany. Information on these markers is available upon request.

PCR reactions were carried out using M13 protocol as described by Nicot et al. (2004). Amplification products were detected using an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA). ABI GeneScan, version 2.1, and Genotyper, version 2.0, softwares (Applied Biosystems, Foster City, CA, USA) were used to determine the size of fragments based on an internal lane standard.

The parents of the mapping populations were open-pollinated *Ae. speltoides* plants. Therefore, the F_1 progeny were genotyped to establish their exact genotypes.

Genetic maps were constructed with the MAPMAKER/EXP ver. 3.0b computer program (Lander et al. 1987) using the Kosambi (1943) mapping function with an LOD threshold of 3.00. The *Ae. speltoides* chromosome orientation was determined using information on that of wheat homoeologous chromosomes.

The statistical significance of differences in the lengths of the compared intervals was assessed as described by Luo et al (2005). The map distances were converted to the recombination fraction using the Kosambi mapping function; maximum likelihood estimates of variance were calculated (Allard 1956). A z test was used to determine the significance of the differences between recombination fractions.

Ae. speltoides and wheat SSR markers were integrated into the *T. timopheevii* framework maps reported by Salina et al. (2006a).

Results

Transferability of SSR markers to the *Ae. speltoides* and *T. timopheevii* genomes

Ae. speltoides

Overall, 588 microsatellite markers were tested for polymorphism in three *Ae. speltoides* parental accessions, 8, 25,

Table 1 Transferability of SSR markers across the *Ae. speltoides*, *T. timopheevii*, and *T. aestivum* genomes

Marker type	Total markers tested	Markers giving amplification in		
		Ae. speltoides	*T. timopheevii*	*T. aestivum*
Ae. speltoides g-SSR	111	–	69 (62%)	73 (65.8%)
Wheat B genome g-SSR	191	122 (64%)	54%[b]	–
Wheat EST-SSR[a] (total)	116	93 (80.2%)	94 (81.0%)	–
Multiple bands in *T. aestivum*	58	49 (84.5%)	55 (94.2%)	
Single band in the genome	58	44 (75.9%)	39 (67.2%)	
A	16	12 (56.9%)	11 (68.7%)	
B	34	30 (75.0%)	25 (73.6%)	
D	80	2 (25.0%)	2 (25.0%)	

Transferability values were computed as the percentage of SSRs giving an amplification product on at least one of the parental accession

[a] GPWs, CNLs, and KSUMs; CFEs disregarded here, because CFEs known to amplify in *Ae. speltoides* (Zhang 2006) were used in the current work

[b] Salina et al. (2006a)

and 37. Specifically, these were the 111 *Ae. speltoides* genomic SSR markers, 191 wheat SSRs genomic (GWMs, g-GPWs, WMCs), and 286 wheat EST-derived SSRs (EST-GPWs, CFEs, CNLs and KSUMs). Of the EST-SSR pool, 170 markers (CFEs) were found to be amplified in the *Ae. speltoides* genome (Zhang 2006). Most of the used wheat genomic SSRs (91%) have been previously mapped on the B genome chromosomes of *T. aestivum* (Nicot et al. 2004; Röder et al. 1998; Ganal and Röder 2007), and the remaining wheat g-SSRs were mapped on the *T. timopheevii* G genome chromosomes (Salina et al. 2006a).

Of 286 EST-SSRs tested, 88.5% were amplified in the *Ae. speltoides* genome, and polymorphism was detected for 43.7% [(a) population] and 44.1% [(b) population]. Although only those CFEs for which amplification was observed in *Ae. speltoides* were chosen for mapping, 15 CFE markers were not amplified on the parental accessions. Of these, ten primer pairs amplified one locus in *T. aestivum* and the other primer pairs amplified two or more loci. The transferability values computed as the percentage of SSRs giving an amplification product on at least one of the parental accessions of the remaining 116 EST-SSRs (EST-GPWs, KSUMs, and CNLs) are given in Table 1.

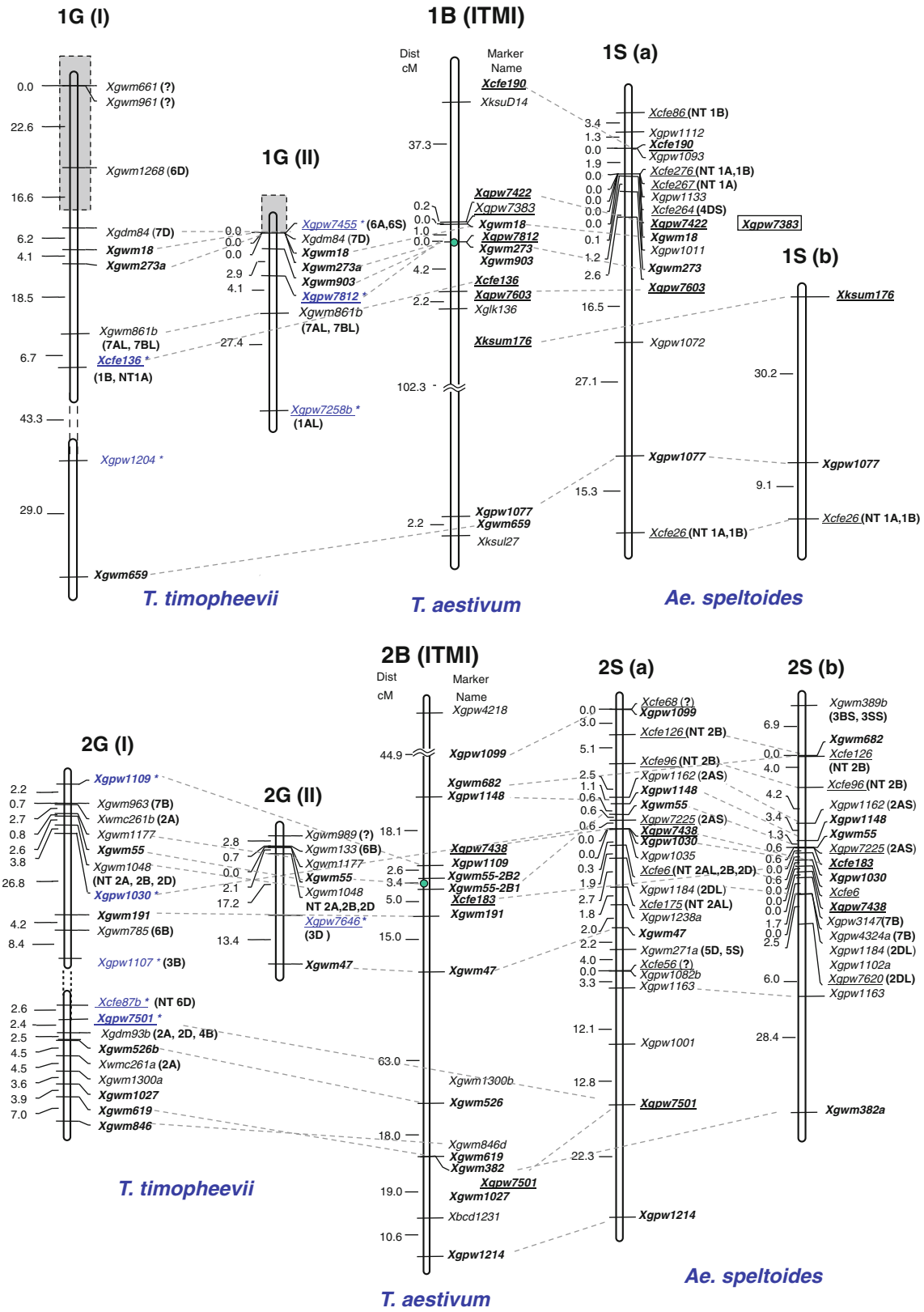
The transferability of wheat g-SSR was 64% (Table 1). Forty-seven percent of the g-SSRs detected polymorphism.

T. timopheevii

Of the 111 *Ae. speltoides* SSRs used, 69 (62%) resulted in amplification products in at least one of the *T. timopheevii* parental accessions, and 15 (13.4%) and 10 (9.0%) markers detected polymorphisms between the parents of the population I and population II, respectively.

The same pool of EST-derived SSRs, comprising 286 markers, that was used in the *Ae. speltoides* accessions, was applied for testing the four *T. timopheevii* parents. The transferability of the CFEs and the other EST-derived SSRs was estimated separately because we used only those CFEs that were shown to be amplified in *Ae. speltoides* (Zhang 2006), whereas the other EST-derived SSRs have not been previously tested for transferability to the related S genome. One hundred fifty-five (91.2%) of the 170 CFEs used were amplified in *T. timopheevii*. Of the 66 CFEs that gave a single amplification product in *T. aestivum*, 54 (81.8%) were amplified in *T. timopheevii* accessions, and of these, 13, 14, and 8 were assigned to the A, B, and D genome chromosomes (Zhang 2006), respectively; the remaining CFEs have not been mapped in *T. aestivum*.

Fig. 1 Comparative maps of the S genome of *Ae. speltoides*, the G ▶ genome of *T. timopheevii*, and the B genome of *T. aestivum*. The (a) and (b) *Ae. speltoides* population maps were constructed from the 25 × 37 and 8 × 37 F_2 mapping populations, respectively. The (I) and (II) *T. timopheevii* population maps were constructed from the *T. timopheevii* var. *timopheevii* × *T. timopheevii* var. *typica* and *T. timopheevii* K-38555 × *T. militinae* F_2 mapping populations, respectively. Markers mapped in the ITMI population (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/) are indicated by a *short horizontal bar*. Markers *without a bar* are from other wheat mapping populations (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/) or papers (Yu et al. 2004; Ganal and Röder 2007) and their positions are determined from common markers on the respective maps. EST-derived markers are *underlined*; loci mapped on the *T. timopheevii* genome in the course of the current work are indicated with an *asterisk*; loci, whose chromosomal location are determined using *T. aestivum–Ae. speltoides* addition lines (Friebe et al, 2000), are *boxed*. Loci in common between maps are connected in *dotted lines*. Loci in common between *Ae. speltoides*, *T. aestivum*, and *T. timopheevii* maps are shown in *bold* type. For the markers mapping to nonhomoeologous chromosomes, the mapping positions are indicated in *brackets* and also for the markers that allocated to chromosomes with nulli-tetrasomic stocks (NT) of Chinese Spring. Putative translocation is *boxed*. The approximate positions of centromeres on the *T. aestivum* chromosomes are indicated by *solid circles*



The transferability of CFEs located on the A, B, and D genome chromosomes was 81.8, 100 and 53.3%, respectively. Eighty-six (98%) of 89 CFEs that showed two or more bands in *T. aestivum*, amplified in *T. timopheevii*. The transferability values of the remaining 116 EST-SSRs (EST-GPWs, CNLs, and KSUMs) are given in Table 1.

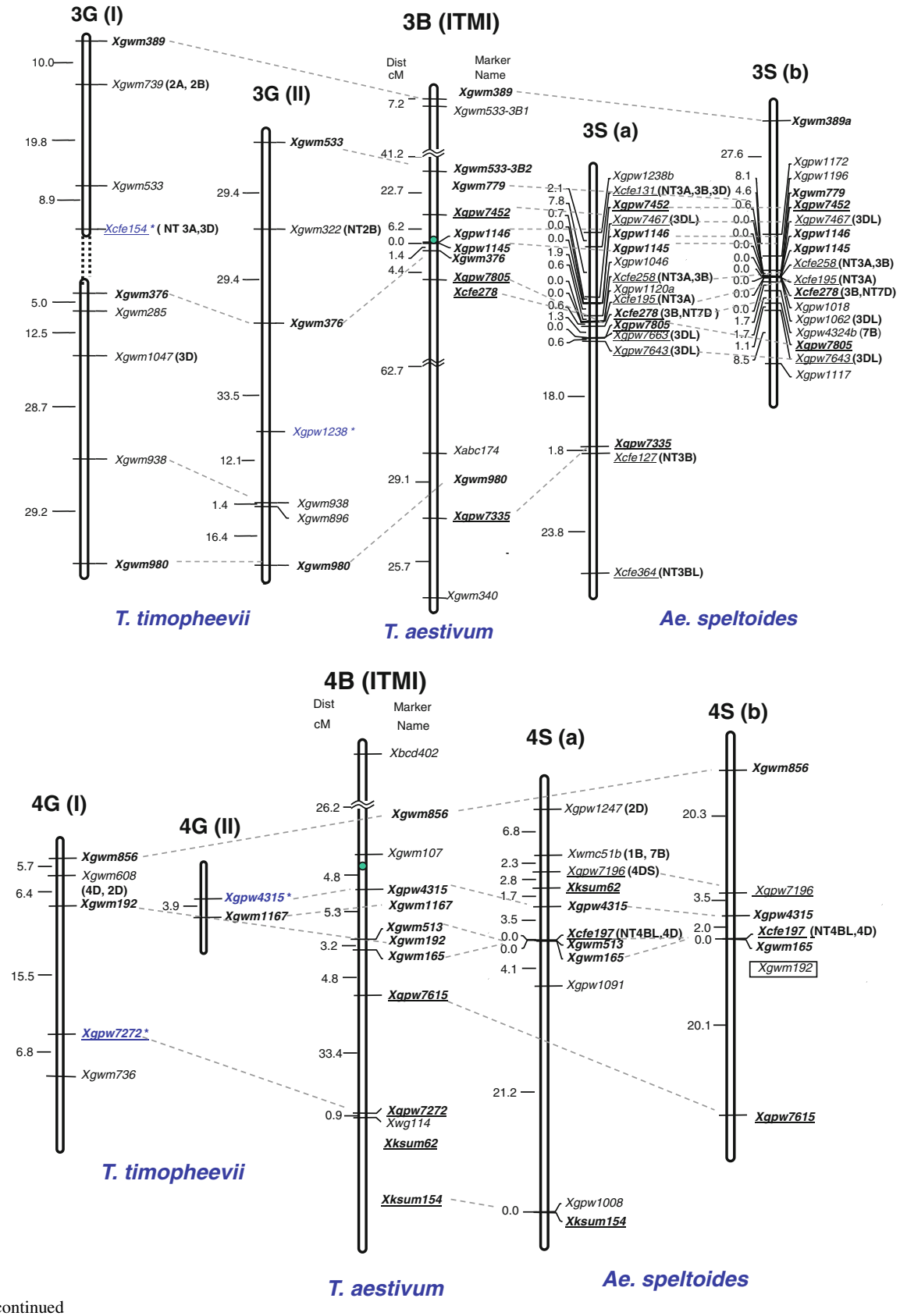


Fig. 1 continued

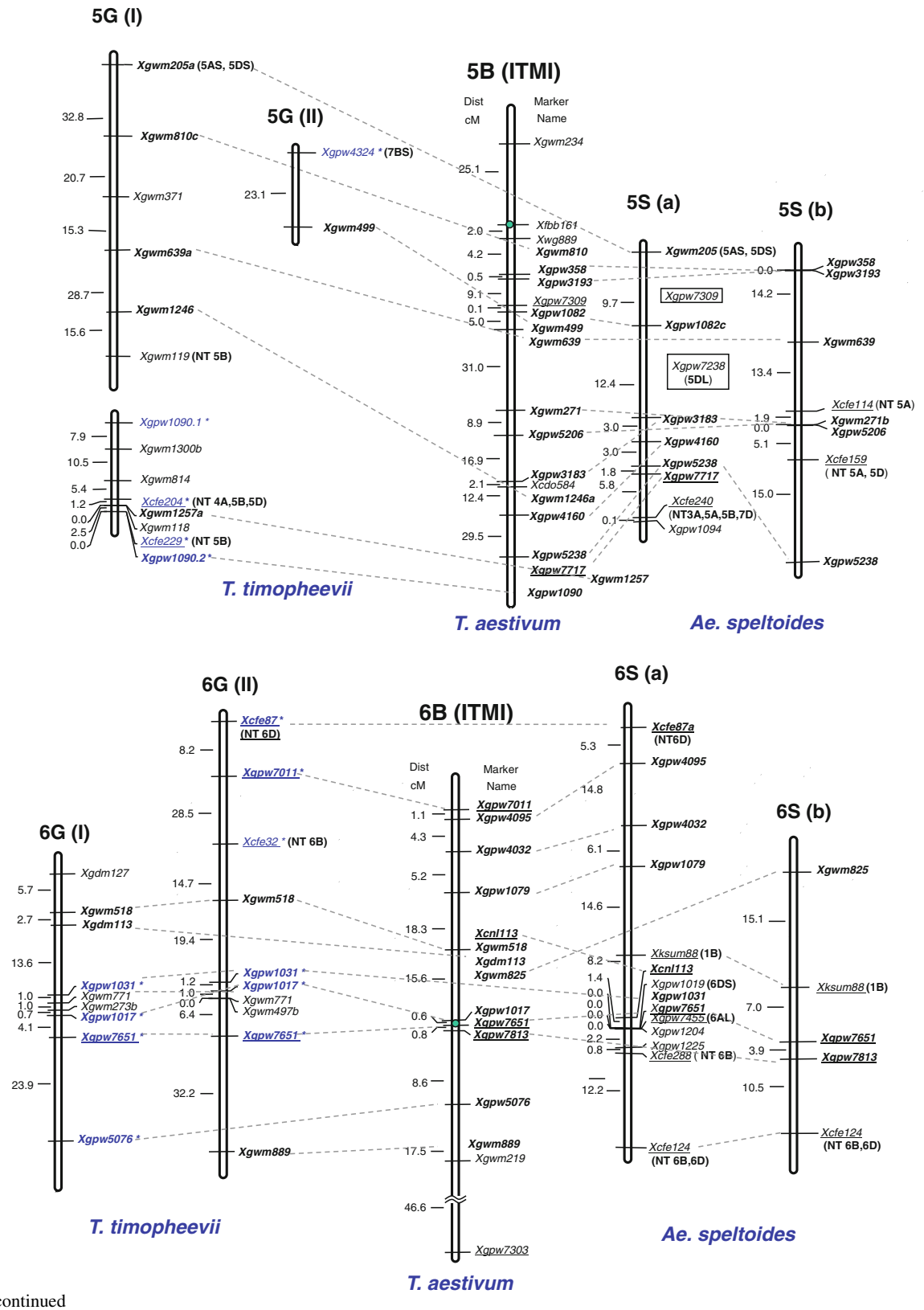


Fig. 1 continued

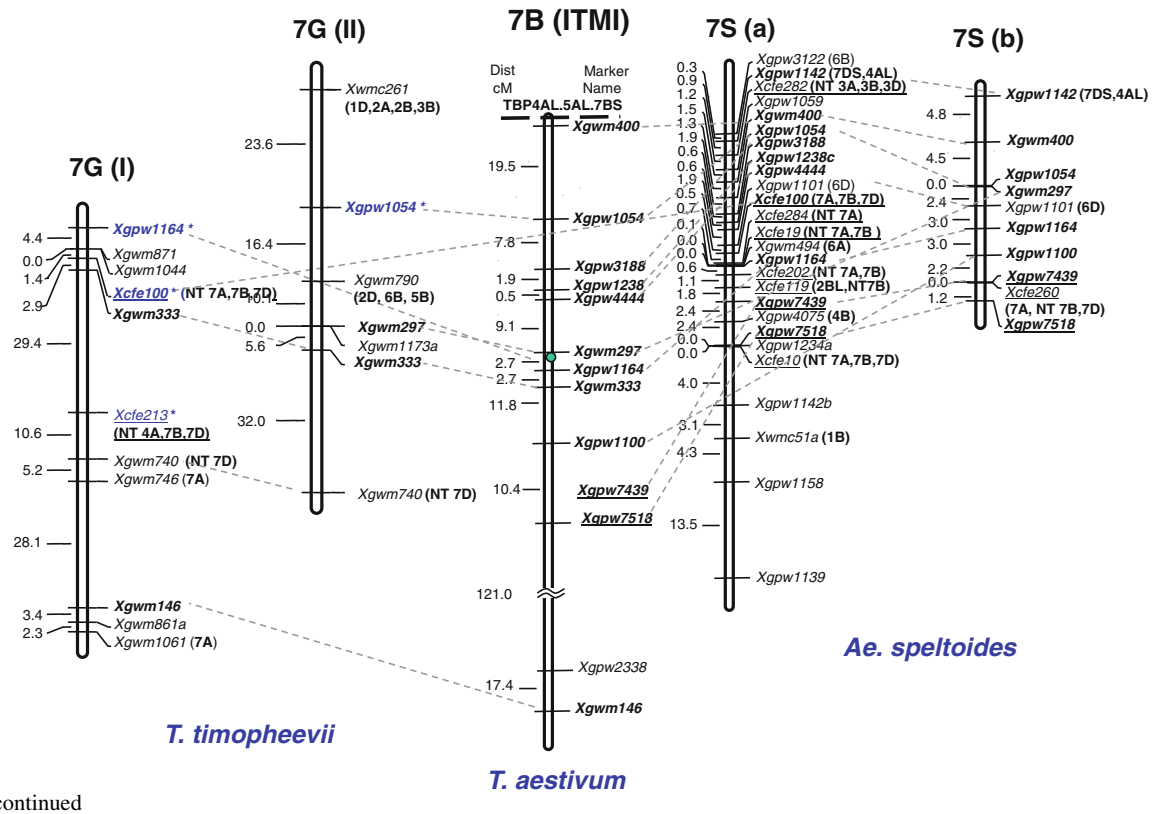


Fig. 1 continued

The total number of EST-SSRs, amplified in the *T. timopheevii* genome was 247 in the parents of the mapping population I and 249 on those of the mapping population II. Fifteen (6.1%) and 27 (10.8%) EST-SSRs detected polymorphisms between the parents of the mapping populations I and II, respectively.

In addition to *Ae. speltoides* SSRs and wheat EST-SSRs, 55 wheat g-SSRs, specifically, g-GPWs and WMCs, located on the B genome chromosomes, 1B, 4B, 5B, 6B, and the distal parts of 7BS and 7BL, were used for integration into the *T. timopheevii* chromosomal map. The transferability of these markers was 53.3%. Five (6.6%) and seven (9.3%) wheat g-SSRs detected polymorphisms between the parental accessions of the population I and II, respectively.

Construction of chromosomal maps for two *Ae. speltoides* F_2 populations

Of the 111 *Ae. speltoides* genomic GPWs, 99 (89%) amplified fragments in the genome of 3 *Ae. speltoides* parental accessions, and 87 (78%) detected polymorphisms; however, 8 and 24 of these were not polymorphic among the F_1 plants from the (a) and (b) crosses, respectively. Finally, 50 and the 24 polymorphic *Ae. speltoides* GPW markers that gave strong distinct amplification products were used for genotyping the F_2 plants from the (a) and (b) crosses. After testing the polymorphic wheat EST-SSR and g-SSR markers in the F_1 plants from the both crosses, 30 g-SSRs and 55 EST-SSRs were used for genotyping of the F_2 plants of the (a) population, and 49 wheat genomic markers and 78 EST-derived SSRs were used for genotyping of the F_2 plants of the (b) population.

A total of 182 loci were mapped, 115 loci in the (a) and 67 in the (b) population. When the results of both populations were combined, 144 different loci were mapped; these included 48 *Ae. speltoides* SSRs, 56 wheat EST-derived SSRs, and 40 wheat genomic SSRs. Eight and three loci were found to be unlinked in the (a) and (b) populations, respectively. The mapped loci were assigned to seven linkage groups in each mapping population. These groups were associated with chromosomes 1S, 2S, 3S, 4S, 5S, 6S, and 7S, taking into account the chromosomal assignment of one or more markers of a group using *T. aestivum–Ae. speltoides* addition lines (Friebe et al. 2000) and marker location on the *T. aestivum* chromosomes.

Chromosome 1S: the chromosome 1S maps include 16 [(a) map] and 3 [(b) map] loci and span genetic distances of 69.4 cM (a) and 39.3 cM (b) (Fig. 1). The order of SSR loci on chromosome 1S corresponded to that on 1B. All of

the mapped CFEs were previously assigned to the group-1 chromosomes with the exception of *Xcfe264*, which was genetically mapped to chromosome 4DS (Zhang 2006). The *Xcfe190* locus (1SS) was genetically mapped to the terminal region of 1BS by Zhang (2006), and the *Xgpw1077* locus (1SL) has been located to the terminal part of the 1BL map (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/), which might indicate the colinearity of the entire 1S and 1B chromosomes. Clustering of the (a) map markers from the proximal part of the chromosome was prominent. The shared region of the 1B and 1S maps was 109.3 cM long on 1B (ITMI map) and 47.5 cM on 1S [(a) map].

Chromosome 2S: the maps of chromosome 2S consist of 23 loci in the (a) population and 19 loci in the (b) population, and they span genetic distances of 78.9 and 61.4 cM, respectively (Fig. 1). The order of loci on 2B and 2S was mostly the same. Clustering of the markers from the proximal part of the chromosome was observed in the maps of both mapping populations. The *Xgwm271a* (5D), *Xgwm389b* (3B), *Xgpw3147* (7B), and *Xgpw4324* (7B) loci have been mapped to non-homoeologous chromosomes in wheat. The primer pairs GWM271 amplified two loci in *Ae. speltoides*, which were mapped to chromosomes 5SL, at the syntenic position, and on 2SL, as well as three loci in *T. aestivum*, two of which were on chromosomes 5BL and 5DL, whereas the third locus was not located due to a lack of polymorphism. Thus, the cause of non-homoeologous *Xgwm271-2S* amplification could have been the presence of duplications of the locus. For GWM389, two loci, *Xgwm389-2S* and *Xgwm389-3S*, were mapped in *Ae. speltoides*, and one locus, *Xgwm389-3B*, was localised in *T. aestivum* (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical). The shared region between the *Xgpw1148* and *Xgwm382* loci was 125.1 cM long on 2B (ITMI map) and 41.7 cM on 2S (b) ($P < 0.05$). The 44.1 cM *Xgpw1148–Xgwm47* interval spanning the centromere on the 2B map was five times shorter on the 2S (a) map, being 8.8 cM, ($P < 0.001$). The distance between the *Xgwm55* and *Xgwm47* loci on 2G (population II) was 32.7 cM, and it was three times shorter, spanning 9.9 cM, on the 2S (b) map ($P < 0.001$) (Fig. 1).

Chromosome 3S: the maps of chromosome 3S contain 17 loci each and span genetic distances of 59.2 cM (a) and 52.8 cM (b) (Fig. 1). The order of the SSR loci mapped on chromosome 3S corresponded to that of 3B, with the exception of the wheat g-SSR, *Xgpw4324* (7B). All of the six mapped *Xcfe* loci have been previously assigned or mapped (*Xcfe278*) on the group 3 chromosomes. The shared short-arm region between *Xgwm389a* and *Xgpw1145* (centromere) was 77.3 cM in 3BS (ITMI map) and 40.9 cM in 3SS (b). The 12 cM *Xgpw7452–Xgwm7805* interval spanning the centromere on the 3B map was 12 cM on the 3B map and shorter on both 3S (a), were it spanned 5.1 cM ($P < 0.05$), and 3S (b), covering 4.0 cM ($P < 0.01$). The genetic distances between *Xgpw1145* and the long-arm locus *Xgpw7335* were 97.6 cM on 3BL (ITMI map) and 23 cM on 3SL (a) ($P < 0.001$). Four chromosome 3D loci, *Xgpw7467* [(a) and (b) maps], *Xgpw1062* (b), *Xgpw7663* (a), and *Xgpw7643* (a, b), had the same order on 3D and 3S.

Chromosome 4S: the maps of chromosome 4S consist of 11 loci in the (a) population and 6 loci in the (b) population, and they span genetic distances of 42.4 and 45.9 cM, respectively (Fig. 1). The order of loci on 4B and 4S was mostly the same, except for *Xksum62*, which was located in the terminal part of 4BL and in the proximal part of chromosome 4S, and two SSR loci, *Xgpw1247* (2D) and *Xwmc51b* (1B, 7B), located on non-homoeologous chromosomes in wheat. The interval *Xgwm165* (proximal part of 4BL)–*Xksum154* (distal part of 4BL) was 66.9 cM in 4B (ITMI map, Yu et al. 2004) and 25.8 cM in 4S ($P < 0.01$) (a).

Chromosome 5S: eight loci were mapped on chromosome 5S in each mapping population (Fig. 1). Markers were found in the same order on chromosomes 5S and 5B. The *Xgwm205* (5AS, 5DS) locus of the terminal part of the 5S map was previously mapped to the terminal part of the 5GS map by Salina et al. (2006a). The lengths of the chromosome 5S maps were 35.8 cM in the (a) population and 49.6 cM in the (b) population. The 115.5 cM interval *Xgpw358–Xgpw5238* on the long arm of 5B (ITMI map) was 49.6 cM long on the 5S (b) map. The 105.8 cM interval *Xgpw1082–Xgpw5238* on the 5BL ITMI map was 26.1 cM on the 5SL (a) map ($P < 0.001$). The short-arm SSR markers used in this study were found to be non-polymorphic either between the parents or in the F_1 plants. Thus, the short arm of 5S is currently presented by one locus, *Xgwm205*, and it is not yet available for a map-based comparison.

Chromosome 6S: the maps of chromosome 6S consist of 14 loci in the (a) population and 5 loci in the (b) population and span genetic distances of 65.6 and 36.5 cM, respectively (Fig. 1). The loci on 6S were ordered as on chromosome 6B, with the exception of *Xksum88*, which was shown to be located on 6SS (a, b) in *Ae. speltoides* and on the short arm of chromosome 1B in wheat (Yu et al. 2004). The shared region between the short-arm loci *Xcfe87* (terminal region) and *Xgpw7651* (centromeric region) was 45.1 cM in *Ae. speltoides* and 79.4 cM long in *T. timopheevii*. Most of the markers mapped to the long arm of 6S have not been mapped on 6BL, but they were either assigned to the chromosome-6 group, such as *Xcfe288* (NT 6B) and *Xcfe124* (NT 6B, 6D), or mapped to the homoeologous chromosome, such as *Xgpw7455* (6AL). The *Ae. speltoides* SSRs *Xgpw1204* and *Xgpw1225* have not

been mapped in wheat due to a lack of polymorphism (Boeuf, unpublished data).

Chromosome 7S: the 7S maps consist of 26 loci in the (a) population and 10 loci in the (b) population. The total length of the (a) map was 44.7 cM and the (b) map was 21.1 cM long. The shared region between the *Xgwm400* and *Xgpw7518* loci was 66.4 cM on 7B (ITMI map), and it was four times shorter on 7S, spanning 15.9 cM in the (a) population ($P < 0.001$), and 16.3 cM in the (b) population ($P < 0.001$). By comparing the length of the '*Xgwm400*–centromere (*Xgpw7518* on *Ae. speltoides* maps)' interval on the *Ae. speltoides* maps and those of two *T. aestivum* maps constructed based on F_2 mapping populations (Dobrovolskaya et al. 2006, 2007), it was found that the intervals were 15.9 cM (a) and 16.3 cM (b) in *Ae. speltoides* and slightly longer, 22.3 and 22.6 cM, in *T. aestivum*. The order of markers within this region was the same on chromosomes 7B and 7S, except for a few markers, *Xgpw1101* (a, b), *Xgwm494* (a), and *Xgpw4075* (a), that have been mapped to non-homoeologous chromosomes in wheat (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical). The distal part of 7SL mainly contains *Ae. speltoides* genomic loci that have not been mapped in wheat due to a lack of polymorphism. The *Xgwm400* locus, which was mapped to the distal part of the 7BS (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/) was found to be linked to the *Xgpw1142* locus in both mapping populations. The GPW1142 primer pair amplified two loci in the terminal part of 7DS and 4AL, which may indicate that the short arm of chromosome 7S does not carry a translocation, in contrast to chromosome 7B, which was involved in the T4AL.5AL.7BS translocation. Apart from the *Xgpw1142* locus, the close linkage of *Xgwm400* to *Xgpw3122* (6B) and *Xcfe282* (NT 3A, 3B, 3D), which were located distally to *Xgwm400* in the (a) map, was observed, and this could be the consequences of duplications events.

Integration of new SSR markers into the *T. timopheevii* chromosomal maps

A portion of the polymorphic markers proved to be inappropriate for genotyping plants from the F_2 populations because of a complex amplification profile or weak amplification. Those markers that showed strong, distinct products were used for genotyping of the F_2 plants. A total of 55 loci were mapped, 31 loci in the mapping population I and 24 in the mapping population II. When the results for both populations were combined, 51 different loci were mapped, 31 on the G genome chromosomes (Fig. 1) and 20 on the A^t genome chromosomes (mapping data not shown). Most the *Ae. speltoides* SSR markers (84.6%) were located on the G genome chromosomes of *T. timopheevii*. The G genome chromosomal maps were enriched with new markers; five markers were mapped on chromosome 1G, 6 markers on 2G, 2 markers on 3G, 2 markers on 4G, 5 on 5G, 7 on 6G, and 4 markers on 7G, which extended the total length of the G genome chromosomal maps by 110.1 and 164.3 cM in population I and population II, respectively. Three primer pairs amplified loci on homoeologous chromosomes (*Xgpw7258-1G* and *Xgpw7258-1A*^{t}; *Xgpw4315-4G* and *Xgpw4315-4A*^{t}; *Xgpw7501-2A*^{t}, and *Xgpw7501-2G*), whereas CFE87 amplified two loci on the non-homoeologous chromosomes 2G and 6G. One primer pair amplified two different loci, *Xgpw1090.1* and *Xgpw1090.2*, on one chromosome, 5G. Most loci in the G genome of *T. timopheevii* were mapped to the homoeologous linkage groups corresponding to *T. aestivum* and/or *Ae. speltoides*. Four of the 31 G genome loci were mapped to the non-homoeologous chromosomes. The *Xgwm7455* locus, which mapped to the group 6 chromosomes in *T. aestivum* (6A) and *Ae. speltoides* (6S), was closely linked to the chromosome 1G loci in population II. This close linkage may confirm the presence of the T6A^{t}S.1GS translocation in *T. timopheevii* that was detected previously (Jiang and Gill 1994; Rodriguez et al. 2000; Salina et al. 2006a). The three remaining markers that amplified loci from non-homoeologous chromosomes, *Xgpw1107*, *Xgpw7646*, and *Xgpw4324*, produced multiple amplification fragments in *Ae. speltoides*, *T. aestivum,* and *T. timopheevii* and not all of these have been previously mapped.

The mapping results demonstrated that the order of the bread wheat and *Ae. speltoides* microsatellite markers involved in our analysis was retained in the majority of cases in the S, B, and G genome chromosomes. No synteny perturbation was shown for the homoeologous groups 2, 3, 4, 5, and 6, whereas chromosomes 1G and 7B were involved in the intergenomic T6A^{t}S.1GS and T4AL.7BS translocations. A comparison of the map distances between the same loci on the B, S and G genome maps revealed a reduction of these distances in *Ae. speltoides*, which was particularly prominent in the proximal region of S genome chromosomes.

Discussion

Map-based comparison of the S, G, and B genome chromosomes

Comparative maps of the B genome (*T. aestivum*), S genome (*Ae. speltoides*), and G genome (*T. timopheevii)* chromosomes showed that the order of the bread wheat and *Ae. speltoides* microsatellite markers involved in the analysis remained conserved in the majority of cases. Our results confirmed the occurrence of the previously

described T6A^{t}S.1GS translocation (Jiang and Gill 1994; Rodriguez et al. 2000; Salina et al. 2006a) and demonstrated that chromosome 7S was not involved in any translocation; in contrast, chromosome 7B was involved in the 4AL.7BS translocation (Naranjo 1990; Devos et al. 1995; Nelson et al. 1995; Hossain et al. 2004; Miftahudin et al. 2004), which appeared at the tetraploid stage (Naranjo 1990; Devos et al. 1995). Both translocations, T6A^{t}S.1GS and 4AL.7BS, are intergenomic and must have originated during the polyploidisation or the evolution of polyploid wheats. The T2BS.6BS translocation (Devos et al. 1993) present in polyploid wheats was not observed in the current study or in the earlier study (Luo et al. 2005) in *Ae. speltoides*. This translocation has also not been observed in *Ae. longissima*, which is another Sitopsis species (Zhang et al. 2001). The short arm of chromosome 2G is currently presented by SSRs located near the centromere, but 6GS, whose map is longer and has a greater number of markers, was shown to retain synteny with 6SS. This indicates an absence of the T2GS.6GS translocation in *T. timopheevii*. Taken together, these results may suggest that this translocation arose after polyploidisation only in the emmer lineage.

A comparison of map distances between the same loci on the B, S, and G genome maps revealed their reduction in *Ae. speltoides*, which was particularly conspicuous in the centromeric region of the S genome chromosomes. All of the shared regions of the B and S genome chromosomal maps were considerably shorter in *Ae. speltoides* than *T. aestivum*. The shared region of the 1B (ITMI) and 1S (a) maps was 109.3 cM long on 1B and 47.5 cM on 1S. Luo et al. (2005) compared the intervals between common markers on two 1S maps and two different 1B maps derived from F_2 mapping populations (Dubcovsky et al. 1997), and they found an eightfold reduction in proximal intervals of the *Ae. speltoides* maps as compared with *T. aestivum*. We found that the intervals spanning the centromere on chromosomes 2S and 3S were five and up to three times shorter compared with those on chromosomes 2B and 3B, respectively. In comparing the proximal intervals between common markers on the 7SS maps and 7BS maps, including the ITMI map and two maps derived from F_2 mapping populations (Dobrovolskaya et al. 2006, 2007), we detected a reduction in the *Ae. speltoides* interval length compared with all of the *T. aestivum* interval lengths, and there was a fourfold reduction when compared with the ITMI map. A considerable reduction was also found for the 2SL (twofold reduction), 3SS (1.89-fold reduction), and 5SL (2.3-fold reduction). The other maps of the *Ae. speltoides* chromosomal arms exhibited no common SSR markers with the most distal regions of the B genome maps. Based on our results and the previously reported data (Luo et al. 2005), it may be inferred that the reduction in the *Ae. speltoides* map length was not a consequence of the specificities of the particular *Ae. speltoides* or *T. aestivum* maps used for comparative analysis.

The virtual elimination of recombination from the proximal 50–100 cM of *Ae. speltoides* genetic maps as compared with those of *T. monococcum* and its localisation in the short distal chromosome regions was originally observed by Luo et al. (2005). A comparing of the lengths of several intervals between common markers on the *Ae. speltoides* and *Ae. longissima* maps suggested that *Ae. longissima* is intermediate with respect to the crossover distribution between *Ae. speltoides* and *T. monococcum* (Luo et al. 2005). The characteristic clustering of loci in the centromeric regions of the maps, which results from the concentration of recombination events in the distal chromosomal regions has been observed in wheat (Devos et al. 1993; Gill et al. 1996; Akhunov et al. 2003), rye (Devos et al. 1993) and barley (Kunzel et al. 2000). This clustering was extremely prominent in *Ae. speltoides*. The mechanism underlying the elimination of recombination from the proximal regions of *Ae. speltoides* chromosomes and the localisation of crossovers in the short distal regions is unclear as yet. Maps of the chromosomes of the wheat B and G genomes did not show a crossover distribution of the kind observed in *Ae. speltoides*. Crossover localisation of this type might have arisen recently during *Ae. speltoides* evolution, or it might have been eliminated in the course of polyploidisation and the evolution of polyploid wheats of both emmer and timopheevii lineages.

Comparative microsatellite mapping of the S, B, and G genomes did not indicate a disturbance of the colinearity between the chromosomes within homoeologous groups. The translocations that differentiated these genomes, T6A^{t}S.1GS, T4AL.7BS, and T2BS.6BS, probably originated in the course of polyploidisation and the evolution of present-day polyploid wheats. No translocations were detected in the S genome. Despite this, inversions could escape detection because of specific recombination pattern (i.e., co-segregation of many loci in the proximal regions of the *Ae. speltoides* chromosomes). Comparative genetic mapping of another Sitopsis species, *Ae. longissima*, revealed that this species possesses the T4S^{l}L.7S^{l}L translocation along with the high degree of conserved colinearity with the basic wheat genome (Zhang et al. 2001). Genetic map comparisons of the other Sitopsis species have not been performed as yet because linkage maps for these species are still lacking.

In addition to their usefulness in phylogenetic research, the constructed microsatellite maps of *Ae. speltoides* and *T. timopheevii* indicate a high potential for the directed transfer of genes for biotic and abiotic stress resistance to the genome of *T. aestivum.* Both *Ae. speltoides* and *T. timopheevii* are rich sources of variability for resistance

to a number of diseases such as leaf, stem, and stripe rust (Dvorak 1977; Naik et al. 1998; Valkoun 2001; Brown-Guedira et al. 2003), and powdery mildew (Hsam et al. 2003; Perugini et al. 2007); for pest resistance (Friebe et al. 1996); and for high grain protein content (Goncharov 2002).

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References

Adonina IG, Salina EA, Pestsova EG, Röder MS (2005) Transferability of wheat microsatellite to diploid *Aegilops* species and determination of chromosomal localizations of microsatellites in the S genome. Genome 48:959–970

Akhunov ED, Goodyear JA, Geng S, Qi L-L, Echalier B et al (2003) The organization and rate of evolution of the wheat genomes are correlated with recombination rates along chromosome arms. Genome Res 13:753–763

Allard RW (1956) Formulas and tables to facilitate the calculation of recombination values in heredity. Hilgardia 24:235–278

Badaeva ED, Friebe B, Gill BS (1996) Genome differentiation in Aegilops. 1. Physical mapping of 5S and 18S–26S ribosomal RNA gene families in diploid species. Genome 39:1150–1158

Boyko E, Kalendar R, Korzun V, Fellers J, Korol A et al (2002) A high-density cytogenetic map of the *Aegilops tauschii* genome incorporating retrotransposons and defense-related genes: insights into cereal chromosome structure and function. Plant Mol Biol 48:767–790

Brown-Guedira GL, Singh S, Fritz AK (2003) Performance and mapping of leaf rust resistance transferred to wheat from *Triticum timopheevii* subsp. *Armeniacum*. Phytopathology 93:784–789

Chapman V, Miller TE, Riley R (1976) Equivalence of the A genome of bread wheat and that of *Triticum urartu*. Genet Res (Camb) 27:69–76

Devos KM, Gale MD (2000) Genome relationships: the grasses model in current research. Plant Cell 12:637–646

Devos KM, Millan T, Gale MD (1993) Comparative RFLP maps of the homoeologous group-2 chromosomes of wheat, rye and barley. Theor Appl Genet 85:784–792

Devos KM, Dubkovsky J, Dvorak J, Chinoy CN, Gale MD (1995) Structural evolution of wheat chromosome 4A, 5A, and 7B and its impact on recombination. Theor Appl Genet 91:282–288

Dobrovolskaya O, Arbuzova VS, Lohwasser U, Röder MS, Börner A (2006) Microsatellite mapping of complementary genes for purple grain colour in bread wheat (*Triticum aestivum* L.). Euphytica 150:355–364

Dobrovolskaya O, Pshenichnikova TA, Arbuzova VS, Lohwasser U, Röder MS, Börner A (2007) Molecular mapping of genes determining hairy leaf character in common wheat with respect to other species of the Triticeae. Euphytica 155:285–293

Dubcovsky J, Luo MC, Zhong GY, Brandsteitter R, Desai A, Kilian A, Kleinhofs A, Dvorak J (1996) Genetic map of diploid wheat, *Triticum monococcum* L. and its comparison with maps of *Hordeum vulgare* L. Genetics 143:983–999

Dvorak J (1976) The relationship between the genome of *Triticum urartu* and the A and B genomes of *Triticum aestivum*. Can J Genet Cytol 18:371–377

Dvorak J (1977) Transfer of leaf rust resistance from Aegilops speltoides to *Triticum aestivum*. Can J Genet Cytol 19:133–141

Dvorak J, Zhang HB (1990) Variation in repeated nucleotide sequences sheds light on the phylogeny of the wheat B and G genomes. Proc Natl Acad Sci USA 87:9640–9644

Dvorak J, Deal KR, Luo MC (2006) Discovery and mapping of wheat Ph1 suppressors. Genetics 174:17–27

Eig A (1929) Monographisch-Kritische Uebersicht der Gatung *Aegilops* Repertorium specierum novarum regni vegetabilis. F F Dahlem bei Berlin, Verlag des Repertoriums 55:1–228

Feldman M, Lupton FGH, Miller TE (1995) Wheats. In: Smartt J, Simmonds NW (eds) Evolution of crops. J Smartt and NW Simmonds Longman Group, London, pp 184–192

Fernandez-Calvin B, Orellana J (1994) Metaphase I bound arms frequency and genome analysis in wheat-*Aegilops* hybrids. 3. Similar relationships between the B genome of wheat and S or S^1 genomes of *Ae. speltoides*, *Ae. longissima* and *Ae. sharonensis*. Theor Appl Genet 88:1043–1049

Feuillet C, Keller B (2002) Comparative genomics in the grass family: molecular characterization of grass genome structure and evolution. Ann Bot 89:3–10

Friebe B, Gill BS (1996) Chromosome banding and genome analysis in dipoid and cultivated polyploid wheats. In: Jauhar PP (ed) Methods of genome analysis in plants. CRC Press, New York, pp 39–60

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91:248–254

Friebe B, Qi LL, Nasuda S, Zhang P, Tuleen NA, Gill BS (2000) Development of a complete set of *Triticum aestivum–Aegilops speltoides* chromosome addition lines. Theor Appl Genet 101:51–58

Ganal MW, Röder MS (2007) Microsatellite and SNP markers in wheat breeding. In: Varshney RK, Tuberosa R (eds) Genomics assisted crop improvement. Vol. 2: genomics applications in crops. Springer, Dordrecht, pp 1–24

Gill KS, Gill BS, Endo TR, Boyko EV (1996) Identification and high-density mapping of gene-rich regions in chromosome group 5 of wheat. Genetics 143:1001–1012

Giorgi D, D'ovidio R, Tanzarella OA, Porceddu E (2002) RFLP analysis of *Aegilpos* species belonging to the Sitopsis section. Genet Resour Crop Evol 49:145–151

Goncharov NP (2002) Comparative genetics of wheat and their related species. Siberian University Press, Novosibirsk, p 149

Gupta PK, Balyan HS, Edwards KJ, Isaac P, Korzun V, Röder M, Gautier MF, Joudrier P, Schlatter AR, Dubcovsky J, De la Pena RC, Khairallah M, Penner G, Hayden MJ, Sharp P, Keller B, Wang RCC, Hardouin JP, Jack P, Leroy P (2002) Genetic mapping of 66 new microsatellite (SSR) loci in bread wheat. Theor Appl Genet 105:413–422

Hossain KG, Kalavacharla V, Lazo GR, Hegstad J, Wentz MJ et al (2004) A chromosome bin map of 2148 expressed sequence tag loci of wheat homoeologous group 7. Genetics 168:687–699

Hsam SLK, Lapochkina IF, Zeller FJ (2003) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 8. Gene *Pm32* in a wheat-*Aegilops speltoides* translocation line. Euphytica 133:367–370

Huang S, Sirikhachornkit A, Su X, Faris J, Gill B, Haselkorn R, Gornicki P (2002) Genes encoding plastid acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the Triticum/Aegilops complex and the evolutionary history of polyploids wheat. Proc Natl Acad Sci USA 99:8133–8138

Jaccard P (1908) Nouvelles recherches sur la distribution florale. Bull Soc Vaud Sci Nat 4:223–270

Jiang J, Gill BS (1994) Different species-specific chromosome translocation in *Triticum timopheevii* and *T. turgidum* support diphyletic origin of polyploid wheats. Chromosom Res 2:59–64

Kilian B, Özkan H, Deusch O, Effgen S, Brandolini A, Kohl J, Martin W, Salamini F (2007) Independent wheat B and G genome origins in outcrossing *Aegilops* progenitor haplotypes. Mol Biol Evol 24:217–227

Kimber G, Athwal RS (1972) A reassessment of the course of evolution of wheat. Proc Natl Acad Sci USA 69:912–915

Kosambi DD (1943) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Kumar S, Tamura K, Nei M (2004) MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Brief Bioinforma 5:150–163

Kunzel G, Korzun L, Meister A (2000) Cytologically integrated physical restriction fragment length polymorphism maps for the barley genome based on translocation breakpoints. Genetics 154:397–412

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Levy AV, Feldman M (2002) The impact of polyploidy on grass genome evolution. Plant Physiol 130:1587–1593

Luo M, Deal KR, Yang Z, Dvorak J (2005) Comparative genetic maps reveal extreme crossover localization in the *Aegilops speltoides* chromosomes. Theor Appl Genet 111:1098–1106

Luo MC, Deal KR, Akhunov ED, Akhunova AR, Anderson OD, Anderson JA, Blake N, Clegg MT, Coleman-Derr D, Conley EJ et al (2009) Genome comparisons reveal a dominant mechanism of chromosome number reduction in grasses and accelerated genome evolution in *Triticeae*. Proc Natl Acad Sci USA 106:15780–15785

Maestra B, Naranjo T (1998) Homoeologous relationships of *Aegilops speltoides* chromosomes to bread wheat. Theor Appl Genet 97:181–186

Miftahudin KR, Ma X-F, Mahmoud AA, Layton J et al (2004) Analysis of expressed sequence tag loci on wheat chromosome group 4. Genetics 168:651–663

Mori N, Lui YG, Tsunewaki K (1995) Wheat phylogeny determined by RFLP analysis of nuclear DNA: II. Wild tetraploid wheats. Theor Appl Genet 90:129–134

Naik S, Gill KS, Prakasa Rao VS, Gupta VS, Tamhankar SA, Pujar S, Gill BS, Ranjekar PK (1998) Identification of a STS marker linked to the Aegilops speltoides-derived leaf rust resistance gene *Lr28* in wheat. Theor Appl Genet 97:535–540

Naranjo T (1990) Chromosome structure of durum wheat. Theor Appl Genet 79:397–400

Nelson JC, Sorrells ME, Van Deynze AE, Lu YH, Atkinson M, Bernard M et al (1995) Molecular mapping of wheat: major genes and rearrangements in homoeologous group 4, 5, and 7. Genetics 141:721–731

Nicot N, Chiquet V, Gandon B, Amilhat L, Legeai F, Leroy F, Bernard M, Sourdille P (2004) Study of simple sequence repeat (SSR) markers from wheat expressed sequence tags (ESTs). Theor Appl Genet 109:800–805

Peacock WJ, Gerlach WL, Dennis ES (1981) Molecular aspects of wheat evolution: repeated DNA sequences. In: Evans LT, Peacock WJ (eds) Wheat science—today and tomorrow. Cambridge University Press, Cambridge, pp 41–60

Perugini LD, Murphy JP, Marshall D, Brown-Guedira G (2007) *Pm37*, a new broadly effective powdery mildew resistance gene from *Triticum timopheevii*. Theor and Appl Genet 116:417–425

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier M-H, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Rodriguez S, Perera E, Maestra B, Diez M, Naranjo T (2000) Chromosome structure of *Triticum timopheevii* relative to *T. turgidum*. Genome 43:923–930

Salina EA, Leonova IN, Efremova TT, Röder MS (2006a) Wheat genome structure: translocations during the course of polyploidization. Funct Integr Genomics 6:71–80

Salina EA, Lim KY, Badaeva ED, Scherban AB, Adonina IG, Amosova AV, Samatadze TE, Vatolina TYu, Zoschuk SA, Leitch A (2006b) Phylogenetic reconstruction of Aegilops section Sitopsis and the evolution of tandem repeats in the diploid and derived wheat polyploids. Genome 49:1023–1035

Sasanuma T, Miyashita NT, Tsunewaki K (1996) Wheat phylogeny determined by RFLP analysis of nuclear DNA. 3. Intra- and interspecific variations of five *Aegilops* Sitopsis species. Theor Appl Genet 92:928–934

Singh K, Ghai M, Garg M, Chhuneja P, Kaur P, Schnurbusch T, Keller B, Dhaliwal HS (2007) An integrated molecular linkage map of diploid wheat based on a *Triticum boeoticum* × *T. monococcum* RIL population. Theor Appl Genet 115:301–312

Sourdille P, Tavaud M, Charmet G, Bernard M (2001) Transferability of wheat microsatellites to diploid triticeae species carrying the A, B and D genomes. Theor Appl Genet 103:346–352

Taenzler B, Esposti RF, Vaccino P, Brandolini A, Effgen S, Heun M, Schafer-pregl R, Borghi B, Salamini F (2002) Molecular linkage map of einkorn wheat: mapping of storage-protein and soft-glume genes and bread-making quality QTLs. Genet Res Camb 80:131–143

Thiel T, Michalek W, Varshney RK, Graner A (2003) Exploiting EST databases for the development and characterization of gene-derived SSR-markers in barley (*Hordeum vulgare* L.). Theor Appl Genet 106:411–422

Tixier MH, Sourdille P, Charmet G, Gay G, Jaby C, Cadalen T, Bernard S, Nicolas P, Bernard M (1998) Detection of QTLs for crossability in wheat using a doubled-haploid population. Theor Appl Genet 97:1076–1082

Tsunewaki K (1996) Plasmon analysis as the counterpart of genome analysis in plants. In: Jauhar PP (ed) Methods of genome analysis in plants. CRC Press, New York, pp 271–299

Tsunewaki K, Ogihara Y (1983) The molecular basis of genetic diversity among cytoplasms of Triticum and Aegilops species. II. On the origin of polyploidy wheat cytoplasms as suggested by chloroplast DNA restriction fragment patterns. Genetics 104:155–171

Valkoun JJ (2001) Wheat pre-breeding using wild progenitors. Euphytica 119:17–23

Yu J-K, Dake T, Singh S, Benscher D, Li W, Gill B, Sorrells M (2004) Development and mapping of EST-derived simple sequence repeat markers for hexaploid wheat. Genome 47:805–818

Zhang LY (2006) Study of the transferability of microsatellite markers derived from bread wheat (*T. aestivum*) or rice (*O. sativa*) ESTs (EST-SSRs) to their close and wild relatives and evaluation of their potential for the organization of genetic resources in the grass family. Doctoral Thesis, pp 45–101

Zhang H, Reader SM, Liu X, Jia JZ, Gale MD, Devos KM (2001) Comparative genetic analysis of the *Aegilops longissima* and *Ae. sharonensis* genomes with common wheat. Theor Appl Genet 103:518–525

Zhang LY, Bernard M, Leroy P, Feuillet C, Sourdille P (2005) High transferability of bread wheat EST-derived SSRs to other cereals. Theor Appl Genet 111:677–687

Zhang LY, Ravel C, Bernard M, Balfourier F, Leroy P, Feuillet C, Sourdille P (2006) Transferable bread wheat EST-SSRs can be useful for phylogenetic studies among the Triticeae species. Theor Appl Genet 113:407–418