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Ming-Cheng Luo · Karin R. Deal · Zu-Li Yang
Jan Dvorak

Comparative genetic maps reveal extreme crossover localization in the *Aegilops speltoides* chromosomes

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Abstract A total of 137 loci were mapped in *Aegilops speltoides*, the closest extant relative of the wheat B genome, using two F_2 mapping populations and a set of wheat-*Ae. speltoides* disomic addition (DA) lines. Comparisons of *Ae. speltoides* genetic maps with those of *Triticum monococcum* indicated that *Ae. speltoides* conserved the gross chromosome structure observed across the tribe Triticeae. A putative inversion involving the short arm of chromosome 2 was detected in *Ae. speltoides*. A translocation between chromosomes 2 and 6, present in the wheat B genome, was absent. The ligustica/aucheri spike dimorphism behaved as allelic variation at a single locus, which was mapped in the centromeric region of chromosome 3. The genetic length of each chromosome arm was about 50 cM, irrespective of its physical length. Compared to *T. monococcum* genetic maps, recombination was virtually eliminated from the proximal 50–100 cM and was localized in short distal regions, which were often expanded compared to the *T. monococcum* maps. The wheat B genome and the genome of *Ae. longissima*, a close relative of *Ae. speltoides*, do not show the extreme localization of crossovers observed in *Ae. speltoides*.

Introduction

The chromosome complement of hexaploid wheat, *Triticum aestivum* L. ($2n = 6x = 42$), is composed of three genomes, A, B and D. The A and D genomes were contributed by *Triticum urartu* and *Aegilops tauschii*, respectively (Kihara 1944; McFadden and Sears 1946; Dvorak et al. 1993). Morphological comparisons of wheat with related diploid species and DNA variation studies pointed to *Aegilops speltoides* ($2n = 14$) as the most likely source of the B genome (Sarkar and Stebbins 1956; Dvorak and Appels 1982; Dvorak and Zhang 1990; Talbert et al. 1991; Wang et al. 1997).

Ae. speltoides (genome S) and its close relatives, *Ae. searsii* (genome S^s), *Ae. bicornis* (genome S^b), *Ae. longissima* (genome S^l), and *Ae. sharonensis* (genome S^{sh}), constitute the section Sitopsis of the genus *Aegilops*. The genomes of the five Sitopsis species are closely related. Hybrids between these species show a mode of seven bivalents at metaphase I (henceforth MI) or, as in those involving *Ae. longissima*, five bivalents plus one quadrivalent (Kihara 1954; Roy 1959). Classical taxonomy of Sitopsis placed *Ae. speltoides* into a monotypic subsection Truncata and the remaining four into subsection Emarginata (Eig 1929). This classification was upheld by molecular taxonomy; *Ae. searsii*, *Ae. bicornis*, *Ae. longissima*, and *Ae. sharonensis* formed one phylogenetic branch of the section whereas *Ae. speltoides* formed the other phylogenetic branch (Dvorak and Zhang 1992; Dvorak et al. 1998a, b). In nature, *Ae. speltoides* is a cross-pollinating species (although it readily self-pollinates in a greenhouse), whereas the four species of Emarginata are self-pollinating with a varying amount of cross-pollination.

Ae. speltoides is comprised of two morphological forms. In the form ligustica, spikes have a cylindrical shape, disarticulate below each spikelet, and the lateral spikelets are awned. In the form aucheri, spikes have a conical shape, disarticulate from stems at a single node at the bottom of the spike, and only the terminal spikelet is awned. The ligustica and aucheri forms segregate as two contrasting syndromes in natural populations. The ligustica syndrome is completely dominant over the aucheri syndrome. Although the two syndromes appear in varying frequencies in natural populations, the frequencies of homozygous ligustica, homozygous aucheri, and

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M.-C. Luo · K. R. Deal · Z.-L. Yang · J. Dvorak (✉)
Department of Plant Sciences, University of California,
Davis, CA 95616, USA
E-mail: jdvorak@ucdavis.edu
Fax: +1-530-7524361

heterozygous ligustica plants within populations leave little doubt that the two forms are part of single interbreeding taxon (Zohary and Imber 1963). Recombinant phenotypes occur in natural populations with frequencies lower than 0.1–0.2% (Zohary and Imber 1963). The chromosomal location of gene(s) controlling the ligustica/aucheri spike syndromes in the *Ae. speltoides* genome is reported here.

In spite of *Ae. speltoides* appearing as the most likely source of the wheat B genome, molecular criteria (Peacock et al. 1981; Dvorak et al. 1989; Dvorak and Zhang 1992; Huang et al. 2002) and meiotic chromosome pairing (Kimber and Athwal 1972) indicated an imperfect correspondence between the two genomes. In wheat, pairing between homoeologous chromosomes is prevented by the activity of the *Ph1* locus (Okamoto 1957; Riley and Chapman 1958). While there is essentially no pairing at MI between the A, B, and D genome chromosomes when this locus is expressed, the same chromosomes are extensively paired in the presence of a null allele of the locus or if it is genetically suppressed. The *Ph1* locus activity is completely or partially suppressed in *Ae. speltoides* × wheat hybrids by *Ae. speltoides Ph1* suppressors (Riley 1960; Dvorak 1972; Kimber and Athwal 1972; Chen and Dvorak 1984). The assessment of MI chromosome pairing in wheat × *Ae. speltoides* hybrids indicates that the A- and D-genome chromosomes pair preferentially and the B- and S-genome chromosomes pair preferentially if *Ph1* is suppressed (Maestra and Naranjo 1998); similar preferential pairing is, however, also observed in wheat hybrids involving *Ae. longissima* and *Ae. sharonensis* (Maestra and Naranjo 1997). However, when *Ph1* is fully active, there is very little pairing between *Ae. speltoides* chromosomes and those of the wheat B genome (Kimber and Athwal 1972). Under the same circumstances, most of the wheat A-genome chromosomes pair readily with *T. urartu* chromosomes (Chapman et al. 1976; Dvorak 1976) suggesting that the B and S genomes are more differentiated from each other than is the wheat A genome differentiated from the *T. urartu* genome.

Of the three diploid ancestors of polyploid wheat, only the *Ae. tauschii* genome has been subjected to comparative mapping (Gill et al. 1992). The *T. urartu* genome has not been mapped, but a detailed comparative genetic map was developed for its close relative, *Triticum monococcum* (2 n = 14, genomes A^m A^m) (Dubcovsky et al. 1996). Of the five Sitopsis species, only the *Ae. longissima* genome has been genetically mapped (Zhang et al. 2001); no attempt has been reported to map the genome of *Ae. speltoides*. Comparative maps of the *Ae. tauschii*, *T. monococcum*, and *Ae. longissima* genomes and the three wheat genomes show that with few exceptions their chromosomes are collinear. The A genome of wheat and the A^m genome of *T. monococcum* differ from the other genomes by a reciprocal translocation involving chromosome arms 4L and 5L (Devos et al. 1995). Wheat chromosome arm 4AL is also involved in a translocation with arm 7BS (Naranjo et al. 1987; Devos et al. 1995). This translocation is intergenomic and therefore had to originate during the evolution of polyploid wheat. The tips of wheat arms 2BS and 6BS are also involved in a translocation (Devos et al. 1993). This translocation is intragenomic and could therefore have originated either at the diploid or polyploid level. Because pairing studies in wheat × *Ae. speltoides* hybrids have revealed no major translocation differentiating the B and S genomes (Maestra and Naranjo 1998), the 2B/6B translocation should be present also in *Ae. speltoides*. Because the translocation is absent in *Ae. longissima* (Zhang et al. 2001) it should differentiate *Ae. speltoides* from *Ae. longissima*. The genome of *Ae. longissima* differs from other Sitopsis species by a $7S^l$ L/$4S^l$ L translocation (Naranjo 1995; Zhang et al. 2001).

Here, we report the construction of genetic maps of the *Ae. speltoides* genome using RFLP markers. RFLP markers facilitated comparisons of the maps with those of other Triticeae genomes. A logical genome for such comparisons is the wheat B genome. Most B-genome genetic maps are based on the ITMI mapping population consisting of recombinant inbred lines (RILs) (Van Deynze et al. 1995). Unfortunately, recombination frequencies derived from RIL populations cannot be compared with those derived from F_2 populations. The B-genome genetic map reported by Gale et al. (1993) is based on an F_2 population but it does not report actual distances along the B-genome chromosomes. Consequently, we elected to use the genome of *T. monococcum* as a reference for the comparative study of recombination in the *Ae. speltoides* genome. *T. monococcum* genetic maps share numerous markers with barley maps. Comparisons with barley showed that the *T. monococcum* genome is structurally similar to the barley genome and that recombination along *T. monococcum* chromosomes is similar to that along barley chromosomes, although greater incidence of recombination in distal regions of *T. monococcum* chromosomes was observed (Dubcovsky et al. 1996). A limited comparison of the *Ae. speltoides* genetic map could be made with the *Ae. longissima* map (Zhang et al. 2001) and with two maps of a single B-genome chromosome (Dubcovsky et al. 1997).

Materials and methods

Plants

Inbred *Ae. speltoides* lines 2-12-4-8-1-1-1 and PI36909-12-II were crossed. A single F_1 plant was grown in isolation in the greenhouse. A total of 86 F_2 plants grown in the greenhouse were used as a mapping population. This population will be designated as the (a) mapping population throughout. Eighteen additional F_2 plants from this cross were used to increase sample size in a study of the centromeric region of chromosome 3S. The (a) population was the primary mapping population of this study. An analogous population comprising of 88

F_2 plants was produced from the cross DV588-2-2 × PI369599-3. This population will be designated as the (b) mapping population. This population was used to verify some of the findings made with the (a) population and to map several strategically important loci that were not polymorphic in the (a) population.

Each linkage group was associated with a chromosome by hybridizing strategically selected clones with Southern blots of DNA of six DA lines of *Ae. speltoides* chromosomes added to the chromosome complement of *T. aestivum* cv "Chinese Spring." Seeds of the DA lines (Friebe et al. 2000) were provided by B. Friebe (Kansas State University). DA lines were available for only six chromosomes, a line for chromosome 3S was unavailable.

RFLP

Nuclear DNAs were isolated using a method described earlier (Dvorak et al. 1988a, b). Restriction endonuclease digested DNAs were electrophoretically fractionated in 1% agarose gels and transferred to Hybond N+ nylon membranes (Amersham) by capillary transfer in 0.4 N NaOH overnight (Luo et al. 1998). The membranes were then rinsed in 2× SSC for 5 min. DNA inserts were isolated from plasmids either by restriction enzyme digestion and electroelution or by PCR amplification using plasmid primers. Probes were ^{32}P-labeled by the random hexamer primer method (Feinberg and Vogelstein 1983). Prehybridization and hybridization were performed as described earlier (Dubcovsky et al. 1996). The membranes were washed in 2× SSC and 0.5% SDS for 30 min to 2 h at 65°, 1× SSC and 0.5% SDS for 30 min at 65°, and 0.5× SSC and 0.5% SDS for 12 min at 65°.

A total of 99 clones were used as hybridization probes. Except for wheat expressed sequence tags (ESTs), designated by their GenBank accession numbers, most of the clones were described and mapped on the *T. monococcum* genetic map (Dubcovsky et al. 1996). The ESTs were selected from the wheat EST database (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi).

Map construction

Genetic maps were constructed with the computer program MapMaker 3.0 (Lander et al. 1987; Lincoln et al. 1992) using the Kosambi (1943) mapping function. Multipoint analysis was used on individual linkage groups, using an initial LOD threshold of three and lowering the LOD threshold to two to map additional markers. *Ae. speltoides* maps were compared with maps of *T. monococcum* (Dubcovsky et al. 1996). To assess the statistical significance of differences in the lengths of compared intervals, intervals were converted from centimorgan into recombination fraction using the Kosambi function, and the maximum likelihood estimates of variance were computed (Allard 1956). The significance of differences between recombination fractions were determined by *z*-test.

Results

A total of 137 loci were mapped, 113 loci in the (a) mapping population and 24 in the (b) mapping population. The loci were allocated to 11 linkage groups. Each linkage group was assigned to a chromosome by hybridization of selected clones with the *Ae. speltoides* DA lines (Fig. 1). The association of a linkage group with chromosome 3S, for which a DA line was not available, was accomplished by default; if an *Ae. speltoides* restriction fragment was detected in the restriction profile of the Chinese Spring × *Ae. speltoides* amphiploid but not in the profiles of the six DA lines, it was assumed to be located on chromosome 3S. Linkage groups were allocated to arms on the basis of comparison of mapped markers with their location on the *T. monococcum* and wheat linkage maps and, for ESTs, wheat deletion maps.

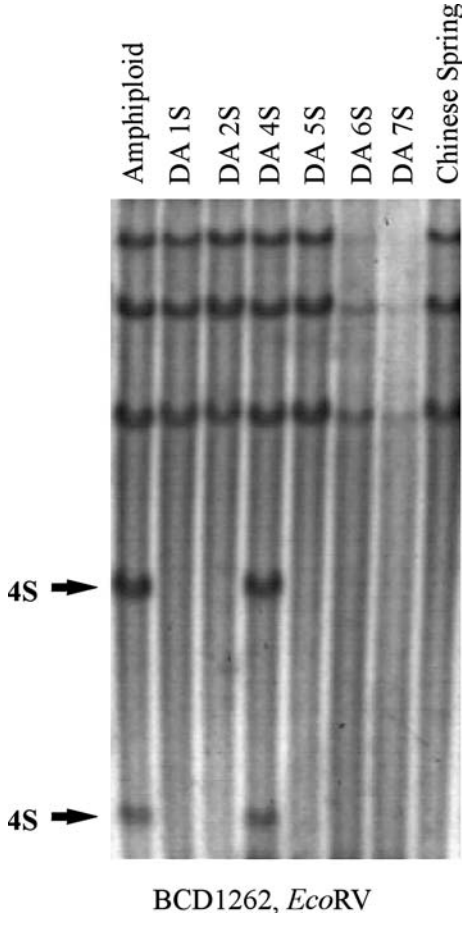

Fig. 1 Confirmation of the location of locus *Xbcd1262* on chromosome 4S. *Ae. speltoides* restriction fragments indicated by arrows are present in both the Chinese Spring × *Ae. speltoides* amphiploid and the disomic addition line 4S

Chromosome 1S

The total length of the (a) map of the 1S chromosome was 95.8 cM compared to the $1A^m$ map, which was 156.6 cM long. The shared region of the two maps was 92.2 cM long on the 1S map and 154.5 cM long on the $1A^m$ map. The difference was caused by a great contraction of the proximal regions in both arms on the 1S map (Fig. 2a). The 68.8 cM *XksuE18– XksuE8* interval spanning the centromere on the $1A^m$ map showed no recombination on the 1S (a) map and was a mere 4 cM long on the (b) map ($P < .01$) (Fig. 2a). In contrast, the distal interval *XksuG34–Xcdo393* in the long arm was comparable on the two maps and the short arm distal interval *XksuE18–XGlu3* was actually longer on the 1S map ($P < 0.01$). Interval *XksuE8–Xbcd161* was mapped on both the (a) and (b) maps. Its overall lengths, 12.1 cM on the (a) map and 14.5 cM on the (b) map, were similar and the order of markers was the same on both the (a) and (b) maps (Fig. 2a).

Intervals *XksuG34–centromere* and *Xcmwg706–centromere* were mapped on two different wheat 1B maps (Dubcovsky et al. 1997). Assuming that the centromere is between *XksuE8* and *XksuE18* (Fig. 2a), the two intervals were less than 5.4 and 3.6 cM long on the 1S (a) map (Fig. 2a). In contrast, on the 1B maps, the *XksuG34–centromere* interval was 41.0 cM and *Xmwg706–centromere* interval was 42.8 cM. The distal interval *Xmwg706–Xcdo393* was expanded on the 1S map compared to the 1B map, although the difference was not statistically significant. The interval was 48.1 cM on the 1S map and 35.7 cM on the 1B map ($P < 0.3$).

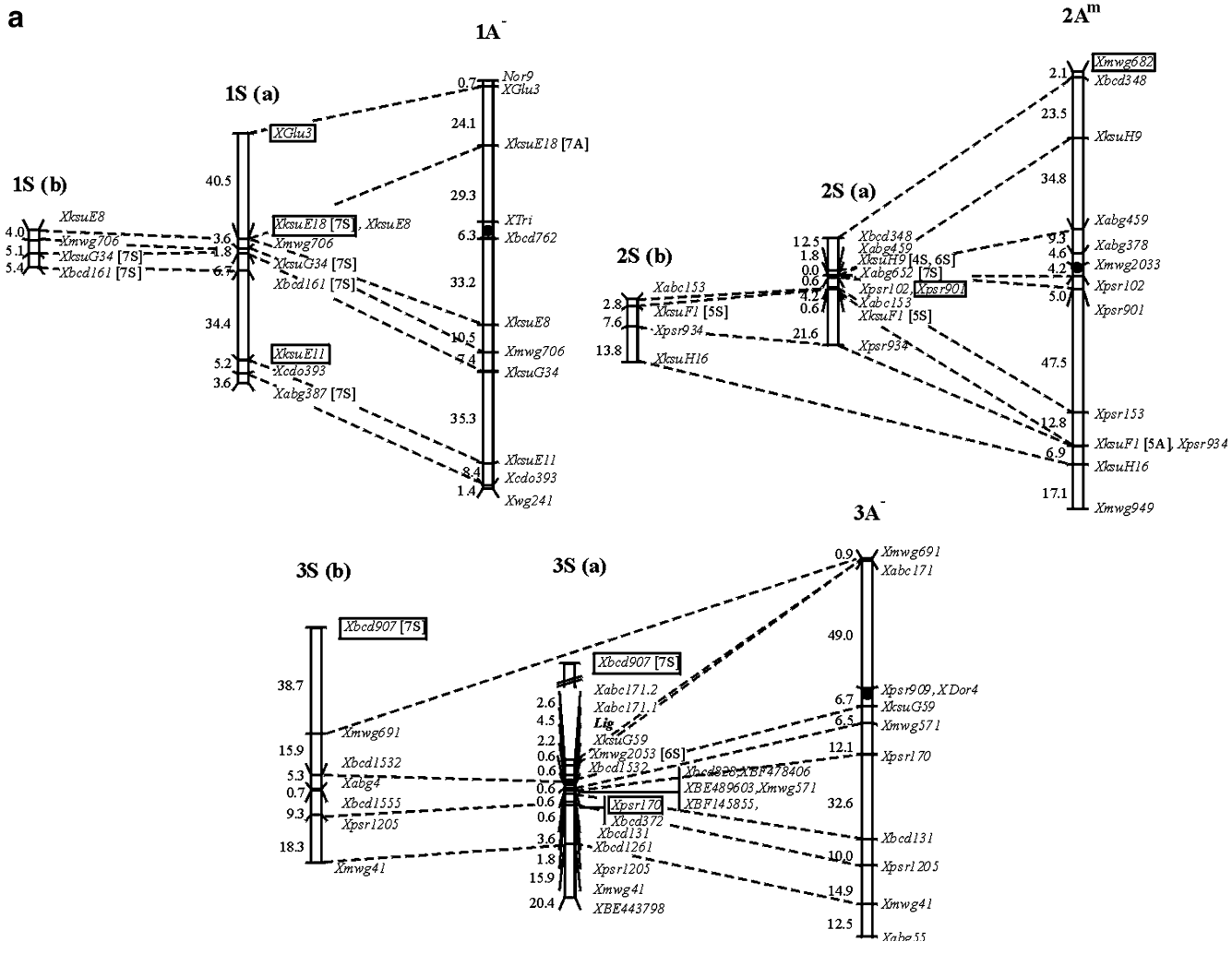

Fig. 2 Comparative maps of the S genome of *Ae. speltoides* and the A^m genome of *T. monococcum* (Dubcovsky et al. 1996). The **a** maps were constructed from the 2-12-4-8-1-1-1 × PI36909-12-II F_2 mapping population and **b** maps from DV588-2-2 × PI369599-3 F_2 mapping population. The lengths of intervals are in centimorgan. Loci for which chromosomal locations were confirmed by Southern hybridization with the DNAs of the disomic addition lines are boxed (*Xmwg682* was confirmed to be located on chromosome 2S, but could not be mapped in the two *Ae. speltoides* populations due to the lack of polymorphism, and therefore, the locus on chromosome $2A^m$ is *boxed*). Loci in common between maps are connected with *dotted lines*. The approximate position of the centromere is indicated with a solid circle on the *T. monococcum* maps. Chromosomal locations of duplicated loci are indicated in brackets

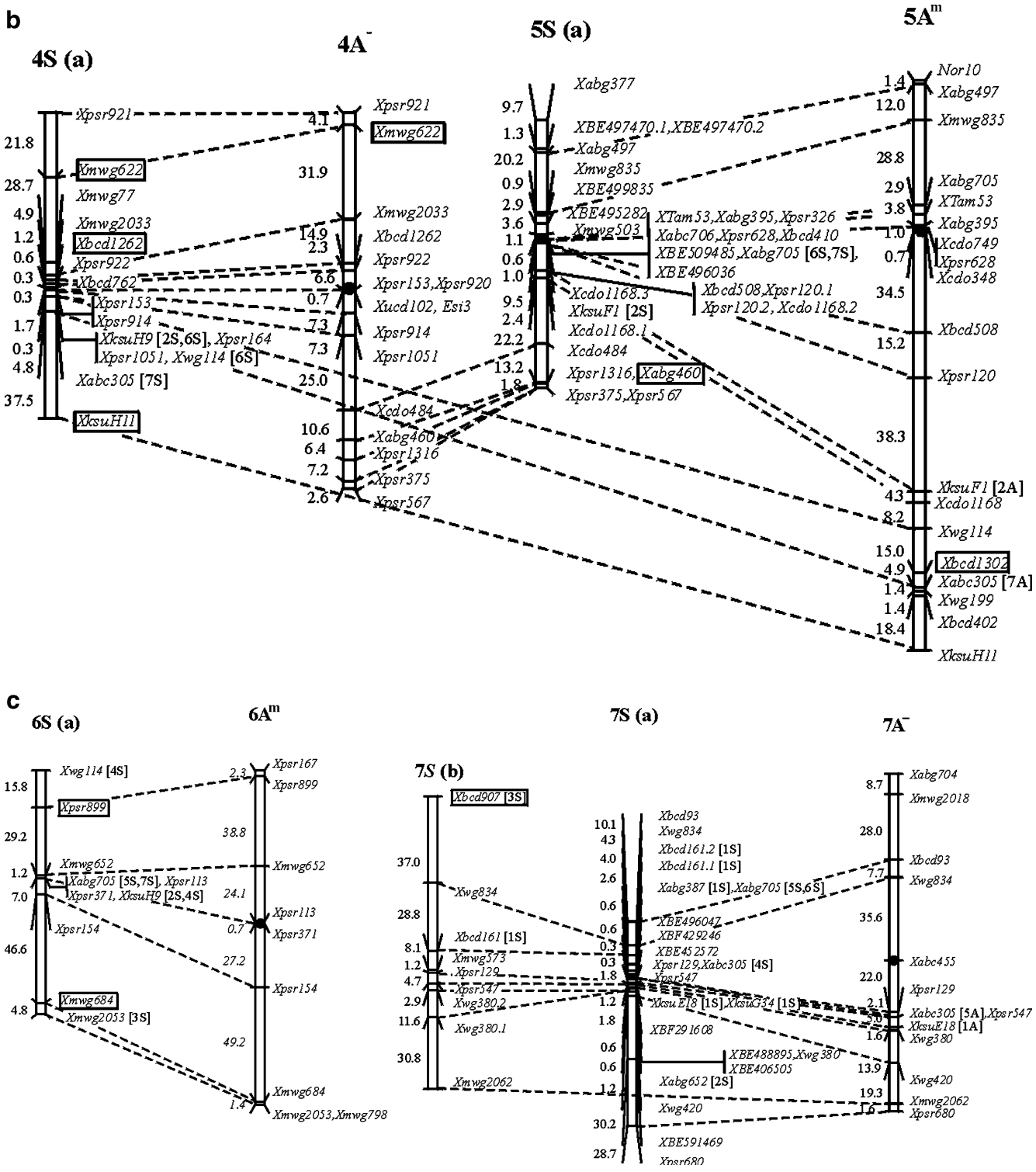

Fig. 2 (Contd.)

Chromosome 2S

The total length of map (a) of the 2S chromosome was only 41.3 cM compared to the 2A^m map, which was 167.8 cM long (Fig. 2a). The shared region of the two maps was 41.4 cM long on the 2S (a) map and 141.7 cM long on the 2A^m map ($P < 0.01$). Interval *Xbcd348–Xabc153* was 128.9 cM long on the 2A^m map but only 19.1 cM long on the 2S map. The map of the long arm was extended on the 2S (b) map by adding interval *Xpsr934–XksuH16*, which was 13.8 cM long (Fig. 2a), making the entire mapped region of the 2S chromosome 55.1 cM long. The pericentromeric interval *Xabg459–Xabc153*, which was 70.6 cM on the 2A^m map, was

contracted to mere 6.6 cM on the 2S map ($P < 0.01$). In contrast, the long arm distal interval *XksuF1–XksuH16*, which was 6.9 cM long on the $2A^m$ map was expanded to 35.4 cM on the (a) plus (b) combined 2S map ($P < 0.01$). Markers *Xabg459* and *XksuH9* showed a reversed order on the 2S map compared to the $2A^m$ map.

Chromosome 3S

The total length of map (a) of the 3S chromosome was 54.1 cM compared to the $3A^m$ map, which was 145.2 cM (Fig. 2a). The shared region of the two maps was 33.7 cM long on the 3S map and 131.8 cM long on the $3A^m$ map. The map of the short arm was extended by adding interval *Xbcd1532–Xmwg691* on the 3S (b) map, which was 15.9 cM long (Fig. 2a). On the 3S (b) map, the most distal interval in the short arm, *Xmwg691–Xbcd907*, was 38.7 cM long on the (b) map and was unlinked on the (a) map; it was associated with the arm by default using hybridization of the *Xbcd907* probe with DA lines. The combined (a) plus (b) map of 3S was 109.7 cM long.

The pericentromeric interval *Xabc171–Xbcd131*, which was 106.9 cM on the $3A^m$ map, was only 5.2 cM long on the *3S* map ($P < 0.01$). In contrast, the distal interval on the short arm, *Xabc171–Xmwg691*, which was 0.9 cM long on the $3A^m$ map, was expanded by an order of magnitude to 9.3 cM on the combined (a) plus (b) map of chromosome 3S ($P < 0.01$).

The (a) mapping population segregated for the ligustica and aucheri spike syndromes. No recombination within each syndrome was observed. Ligustica syndrome was dominant over the aucheri syndrome, 85 F_2 plants were ligustica and 19 were aucheri, which conforms to the expected 3:1 segregation ratio ($P = 0.77$). The syndromes were mapped as a single locus (*Lig*) in the centromeric region. The limited recombination in the centromeric block of markers (Fig. 2a) was caused by two two-strand double crossovers, which did not involve the syndromes.

Chromosome 4S

Only map (a) was constructed for the 4S chromosome (Fig. 2b). The map was 102.1 cM long. During the evolution of the A genome, chromosome $4A^m$ L arm was involved in a reciprocal translocation with the $5A^m$ L arm. Hence the distal portion (*Xwg114.1–XksuH11*) of the 4SL arm is on the $5A^m$ L arm. The portion that the 4S and $4A^m$ chromosomes shared was 59.3 cM long on the 4S map and 75.1 cM long on the $4A^m$ map. The pericentromeric interval *Xmwg2033–Xpsr1051* was 31.8 cM long on the $4A^m$ map but only 4.1 cM on the 4S map ($P < 0.01$). In contrast, the distal interval *Xmwg622–Xpsr921* in the short arm was greatly expanded on the 4S map, being 21.8 cM long on the 4S map compared to 4.1 cM on the $4A^m$ map ($P < 0.01$). Likewise, the distal interval in the long arm was expanded on the 4S map compared to its length on the $5A^m$ L arm. Interval *Xabc305–XksuH11* was 21.4 cM on the $5A^m$ L arm map but 37.5 cM on the 4S map ($P < 0.05$) (Fig. 2b).

Chromosome 5S

Only map (a) was constructed for chromosome 5S (Fig. 2b). The map was 90.4 cM long. In contrast, the map of $5A^m$ was 192.2 cM long. The 5S and $5A^m$ maps shared interval *Xabg497–Xcdo1168*. The interval was 42.2 cM long on the 5S map but 141.5 cM long on the $5A^m$ map ($P < 0.01$). This great difference in the length was caused by the contraction of the pericentromeric region on the 5S map. Pericentromeric interval *Xmwg835–Xpsr120* was 86.9 cM on the $5A^m$ map but was a mere 9.1 cM on the 5S map ($P < 0.01$). In contrast, the distal regions in both arms were expanded on the 5S map. In the short arm, interval *Xmwg835–Xabg497* was 12.0 cM long on the $5A^m$ map but 20.2 cM on the 5S map ($P < 0.1$). An 11.0 cM interval *Xabg497–Xabg377* was mapped at the tip of the short arm of 5S. Although none of the three markers distal to *Xabg497* were mapped in *T. monococcum*, they are very likely contained in the 1.4 cM interval *Xabg497–Nor10*, because the *Nor10* encoding 18S–26S ribosomal RNA is probably the terminal locus of the short arm of the $5A^m$ chromosome.

Chromosome 6S

Only map (a) was constructed for chromosome 6S (Fig. 2c). The total length of the map was 104.6 cM. The total length of the $6A^m$ map was 143.7 cM. The 6S map shared the 88.8 cM interval *Xmwg2053.2–Xpsr899* with the $6A^m$ map, on which it was 140.0 cM long. The great difference in the length of the shared interval was caused by the contraction of the pericentromeric interval *Xmwg652–Xpsr154*, which was 42.0 cM on the $6A^m$ map but only 8.2 cM on the 6S map ($P < 0.01$).

Chromosome 7S

Both (a) and (b) maps were constructed for chromosome 7S (Fig. 2c). The maps were 88.9 and 125.1 cM long, respectively. The pericentromeric interval *Xwg834–Xpsr547*, was 42.8 cM on the (b) map and 14.5 cM on the (a) map; the former was slightly shorter ($P < 0.22$) and the latter significantly shorter ($P < 0.01$) than in *T. monococcum*, where it was 59.7 cM. Of the distal intervals, only an interval in the long arm could be compared between 7S and $7A^m$. While interval *Xwg420– psr680* was 58.9 cM on the 7S (a) map, it was only 25.5 cM on the $7A^m$ map ($P < 0.01$).

Discussion

Crossover localization

Comparative maps of *T. monococcum* and *Ae. speltoides* chromosomes greatly differed in lengths and recombination distribution. Maps of *T. monococcum* ranged from about 150 to 200 cM but were only about 100 cM long in *Ae. speltoides*. This was not an artifact caused by inadequate marker coverage since markers that were most distal on *T. monococcum* maps were usually mapped on *Ae. speltoides* maps. When the lack of polymorphism in *Ae. speltoides* precluded the mapping of a most distal marker on a map of a *T. monococcum* arm, a closely linked marker or a marker that was even more distal on existing Triticeae maps but not mapped in *T. monococcum* was substituted. Nor was the recombination pattern exceptional to one *Ae. speltoides* mapping population. The (a) and (b) maps show similar recombination patterns in the intervals in which they could be compared, although some significant differences between the (a) and (b) maps were also detected.

The approximate length of 100 cM was evenly partitioned into the opposite arms of an *Ae. speltoides* chromosome; both arms were about 50 cM long. This observation suggested that only two crossovers occurred per chromosome in most meiocytes. Assuming correspondence between the chiasma and crossover, two chiasmata were expected per chromosome and 14 per meiocyte. In a large study of chiasma frequencies in *Ae. speltoides* natural populations, means of 13.4 and 13.3 chiasmata were observed at diakinesis and MI, respectively (Zarchi et al. 1972). The reported chiasma frequencies per cell closely agree with the genetic lengths of *Ae. speltoides* chromosomes reported here.

Great reductions in the overall lengths of the *Ae. speltoides* genetic maps in comparison to the *T. monococcum* maps were caused by the elimination of recombination from proximal regions and its localization to short distal chromosome regions. High levels of recombination in the distal regions of chromosomes and low in the proximal regions are also characteristic of wheat chromosomes (Dvorak and Chen 1984; Lukaszewski and Curtis 1993; Gill et al. 1996; Akhunov et al. 2003). Similar distribution of recombination occurs in barley (Kunzel et al. 2000) and is probably the norm in the tribe Triticeae. What makes the observations reported in this study unique is the extreme form of this distal crossover localization. We are not aware of any other intraspecific genetic map showing as an extreme distortion of recombination distribution as we observed in *Ae. speltoides*. In four arms, 2SS, 3SL, 4SL, and 6SL, the pericentromeric region showing no or greatly reduced recombination extended to the most distal bin on the deletion map of a homoeologous wheat chromosome arm (Delaney et al. 1995a, 1995b; Mickelson-Young et al. 1995; Weng et al. 2000). Although this did not permit the determination of the actual lengths of the regions in which crossovers were localized, it suggested that the upper limits of the lengths of those regions are about 40–50 Mb. Considering that the average *Ae. speltoides* chromosome is about 900 Mb long, the recombining regions must be less than 5% of the metaphase chromosome arm length in most chromosomes.

The localization of crossovers in physically short distal chromosome regions is consistent with the very low frequency of interstitial chiasmata in *Ae. speltoides*. Zarchi et al. (1972) reported a mean per cell of 0.5 interstitial chiasma at diakinesis and 0.3 at MI in natural populations of *Ae. speltoides*.

The elimination of crossovers from the proximal regions of the *Ae. speltoides* chromosomes was frequently compensated for by increased recombination rates in distal regions. The combined effects of these two tendencies were that each arm had approximately one crossover, i.e., it was 50 cM, irrespective of its actual length.

Stebbins (1971) suggested that outcrossing species in the tribe Triticeae have lower chiasma frequency compared to their self-pollinating relatives and have localized chiasmata. He speculated that the function of this mechanism is to lower the overall amount of recombination and preserve adapted gene combinations in outcrossing species. Similar differences between related self-pollinating and outcrossing species were observed in Collinsia, Polemonium and Crepis (Garber 1956; Stebbins 1971). The outcrossing *Ae. speltoides* and the largely self-pollinating *Ae. longissima* exemplify this contrast although they have similar chiasma frequencies. The frequency of interstitial chiasmata was triple in *Ae. longissima* of that in *Ae. speltoides* (Zarchi et al. 1972). The lack of common markers between the *Ae. speltoides* maps and those of *Ae. longissima* (Zhang et al. 2001) precluded an extensive comparison of recombination distribution in the proximal chromosome regions in the two species. Only two proximal intervals could be compared: *Xpsr934–centromere* and *Xpsr129–centromere*. The former interval was 17 cM on the *Ae. longissima* $2S^l$ map and 10.4 and 26.4 cM on the *Ae. speltoides* 2S (a) and (b) maps, respectively. The latter interval was 35 cM on the $7S^l$ map (Zhang et al. 2001) but only 1.2 and 2.4 cM on the *Ae. speltoides* 7S (a) and (b) maps, respectively. These comparisons and those facilitated by *T. monococcum* maps suggested that *Ae. longissima* is intermediate in crossover distribution between *Ae. speltoides* and *T. monococcum*.

Maps of the wheat B genome chromosomes do not show the crossover localization observed in *Ae. speltoides*, as illustrated here by the comparison of chromosomes 1S and 1B. Considering the recent divergence of the two genomes, the localization of crossovers either evolved recently in *Ae. speltoides* or was lost from the B genome during the evolution of polyploid wheat. A conspicuous feature of the *Ae. speltoides* chromosomes that is either absent or greatly reduced in most B-genome chromosomes are large telomeric and subtel-

omeric heterochromatic blocks (Dvorak and Knott 1990; Friebe et al. 2000). However, *Ae. longissima* chromosomes show similar amounts of telomeric and subtelomeric heterochromatin as do the *Ae. speltoides* chromosomes (Friebe et al. 1993). It is therefore hard to believe that heterochromatin alone is responsible for crossover localization in *Ae. speltoides*.

It may be tempting to speculate that the localization of crossovers in short regions of *Ae. speltoides* chromosomes is responsible for the low MI pairing between *Ae. speltoides* chromosomes and wheat chromosomes in wheat × *Ae. speltoides* hybrids with a fully active *Ph1* locus (Kimber and Athwal 1972). The lack of understanding of the genetic control of crossover localization in *Ae. speltoides* and its expression in wheat × *Ae. speltoides* hybrids calls for caution in drawing such a conclusion at this time.

Spike dimorphism

We observed no recombinant phenotypes between the ligustica and aucheri syndromes among 104 F_2 plants, which was not surprising considering that they occur with frequencies lower than 0.1–0.2% in natural populations (Zohary and Imber 1963). The principal components of the syndromes are the morphology of the awns and the type of rachis disarticulation. While no gene controlling awn development has been mapped on chromosome 3 in wheat, a gene controlling rachis disarticulation (*Br*) was previously mapped on the short arm of chromosome 3B (Watanabe et al. 2002). Since the syndromes completely co-segregated with other centromeric markers, we could not determine in which arm genes controlling the syndromes reside. It is therefore, possible that the *Br* locus is responsible for the rachis disarticulation component of the syndrome.

Genome structure

Except for the 4/5 translocation, which is endemic to the A genomes, no additional translocation differentiated the *Ae. speltoides* and *T. monococcum* genomes. Locus *Xpsr899* is on wheat chromosomes 6A, 2B and 6D, and it was suggested that the anomalous location of this locus on 2B was due to a 2B/6B translocation (Devos et al. 1993). *Xpsr899* was shown to be on $6S^l$ in *Ae. longissima* (Zhang et al. 2001). We showed here that the locus is also on 6S in *Ae. speltoides*. Since the location of *Xpsr899* on chromosome 6 is the ancestral state, and since no locus was detected on 2S, the 2B/6B translocation probably evolved during polyploid wheat evolution.

Only one inversion was detected in *Ae. speltoides* compared to *T. monococcum*. The order of loci *Xabg459* and *XksuH9* on 2S showed an inverted order compared to the $2A^m$ map. Because the relative positions of *Xabg459* and *XksuH9* were indicated by a single crossover on 2S, the existence of this inversion is tentative. The *T. monococcum* chromosomes were structurally closely related to those of distantly related barley (Dubcovsky et al. 1996). The structural similarity between the *Ae. speltoides* chromosomes and those of *T. monococcum* suggests that the *Ae. speltoides* genome conserved the gross chromosome structure observed across the tribe Triticeae.

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