Genetic Map of Diploid Wheat, *Triticum monococcum* L., and Its Comparison With Maps of *Hordeum vulgare* L.

Jorge Dubcovsky,* Ming-Cheng Luo,* Gan-Yuan Zhong,* Ronda Bransteitter,* Amrita Desai,* Andrzej Kilian,† Andris Kleinhofs† and Jan Dvořák*

**Department of Agronomy and Range Science, University of California, Davis, California 95616 and †Department of Crop and Soil Science, Washington State University, Pullman, Washington 99164-6420*

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ABSTRACT

A genetic map of diploid wheat, *Triticum monococcum* L., involving 335 markers, including RFLP DNA markers, isozymes, seed storage proteins, rRNA, and morphological loci, is reported. *T. monococcum* and barley linkage groups are remarkably conserved. They differ by a reciprocal translocation involving the long arms of chromosomes *4* and *5*, and paracentric inversions in the long arm of chromosomes *1* and *4*; the latter is in a segment of chromosome arm *4L* translocated to *5L* in *T. monococcum*. The order of the markers in the inverted segments in the *T. monococcum* genome is the same as in the *B* and *D* genomes of *T. aestivum* L. The *T. monococcum* map differs from the barley maps in the distribution of recombination within chromosomes. The major 5S rRNA loci were mapped on the short arms of *T. monococcum* chromosomes *1* and *5* and the long arms of barley chromosomes *2* and *3*. Since these chromosome arms are colinear, the major 5S rRNA loci must be subjected to positional changes in the evolving Triticeae genome that do not perturb chromosome colinearity. The positional changes of the major 5S rRNA loci in Triticeae genomes are analogous to those of the 18S-5.8S-26S rRNA loci.

DIPLOID cultivated wheat, *Triticum monococcum* L. ssp. *monococcum* L. ($2n = 2x = 14$), is one of the most ancient crops domesticated in the Middle East (Harlan 1980). Populations of wild *T. monococcum* L. ssp. *aegilopoides* (Link) Thell. (syn. *T. baeoticum* Boiss., *T. thaoudar* Reut. ex Hausskn.) are distributed from Israel to Iran. *T. monococcum* is closely related to *T. urartu* Thum. ($2n = 2x = 14$). However, their hybrids are sterile (Johnson and Dhaliwal 1976). *T. monococcum* was assumed to be the ancestor of the *A* genome of polyploid wheats (Sax 1922; Kihara 1924), but recent evidence indicates that the source of the *A* genome of durum wheat (*T. turgidum L.*, $2n = 4x = 28$, genomes *AABB*), timopheevi wheat (*T. timopheevii* (Zhuk.) Zhuk., $2n = 4x = 28$, genomes *AAGG* = *AASS*) and bread wheat (*T. aestivum* L., $2n = 6x = 42$, genomes *AABBDD*) was *T. urartu* (Nishikawa 1983; Dvořák *et al.* 1988, 1993; Tsunewaki *et al.* 1991, 1993). Chromosome pairing and recombination between *T. monococcum* chromosomes individually substituted in wheat and the wheat chromosomes of the *A* genome is low if the wheat *Ph1* locus is active (Paull *et al.* 1994; Dubcovsky *et al.* 1995a), which indicates that some differentiation has occurred between these genomes. The existence of genome differentiation between *T. monococcum* and *T. urartu* is also evident from extensive differences in the restriction profiles of repeated nucleotide sequences and the promoter region of the 18S-5.8S-26S rRNA genes, which show very little intraspecific variation in the Triticum species (Dvořák *et al.* 1993). For these reasons, it was proposed to redesignate the genome of *T. monococcum* as A^m (Dvořák *et al.* 1993; Dubcovsky *et al.* 1995a).

In contrast to differentiation between the genomes of *T. monococcum* and *T. urartu*, there is no evidence for differentiation between the genome of *T. monococcum* ssp. *monococcum* and that of *T. monococcum* ssp. *aegilopoides*. No differences have been found in the restriction profiles of repeated nucleotide sequences between the two subspecies (Dvořák *et al.* 1988). Hybrids between the two subspecies show seven bivalents and no fixed translocation differences, and they are fully fertile (Kihara *et al.* 1929; Percival 1932). Partial genetic maps of chromosomes *1*A^m and *5*A^m based on crosses between winter (G1777) and spring (G2528) lines of ssp. *aegilopoides* and between ssp. *aegilopoides* and ssp. *monococcum* showed the same orders of markers and similar interval lengths (Dubcovsky and Dvořák 1995; Dubcovsky *et al.* 1995a).

A disadvantage of the cultivars of *T. aestivum* for genetic mapping is that they have low levels of polymorphism. Since cultivated and wild genotypes of *T. monococcum* show high levels of restriction fragment length polymorphism (RFLP) (Castagna *et al.* 1994; Le Corre and Bernard 1995), *T. monococcum* can be used to produce high-density RFLP maps that would complement the genetic maps of *T. aestivum*. A similar rationale was used for the construction of linkage maps of *T. tauschii* (Coss.) Schmalh. (Kam-Morgan *et al.* 1989; Gill *et al.*

Corresponding author: Jan Dvořák, Department of Agronomy and Range Science, University of California, Davis, CA 95616.
E-mail: jdvorak@ucdavis.edu

1991; LAGUDAH *et al.* 1991), the diploid donor of the *T. aestivum* D genome (KIHARA 1944; MCFADDEN and SEARS 1946). A detailed *T. tauschii* map has been reported by GILL *et al.* (1992). The fact that linkage groups in this map are longer than the linkage groups in the genetic maps of other species in the tribe Triticeae complicates comparisons. A map of chromosome *1A*^{m} of *T. monococcum* ssp. *aegilopoides* based on a G1777 × G2528 F_2 population has been reported and was of a similar genetic length as a map of chromosome *1A* of *T. aestivum* (DUBCOVSKY *et al.* 1995a) and a map of chromosome *1A* in a hybrid of a *T. aestivum* cultivar with a synthetic hexaploid wheat (VAN DEYNZE *et al.* 1995).

The tribe Triticeae comprises a number of genera in addition to the genus Triticum. Hordeum, which includes cultivated barley, is one of the most important. Hordeum and Triticum are classified into different subtribes of the tribe Triticeae, and their comparative genetic mapping may provide important information about chromosome evolution in the tribe and facilitate comparative genetic studies in wheat and barley.

Wheat-barley synteny comparisons revealed conservation of the synteny groups (HART *et al.* 1980; NIELSEN and HEJGAARD 1987; KAM-MORGAN *et al.* 1989; SHARP *et al.* 1989; LIAO and NICKS 1991; HART 1995). Some inconsistencies in the position of markers have been noted in several map comparisons (NAMUTH *et al.* 1994; DUBCOVSKY and DVOŘÁK 1995; VAN DEYNZE *et al.* 1995). However, too few common loci are on these maps to allow inferences on the structural relationships of the wheat and barley genomes. To gain insight into the structural relationships between the genome of *T. monococcum* and that of barley, and to investigate the patterns of recombination in the two genomes, markers previously mapped in barley by KLEINHOFS *et al.* (1993), KLEINHOFS (1994), and GRANER *et al.* (1993) were mapped in the *T. monococcum* genome in the present study.

MATERIALS AND METHODS

Mapping populations: The genetic map of *T. monococcum* was based on a population of 74 F_2 plants and from them derived F_3 families from the cross *T. monococcum* ssp. *monococcum* DV92 (female) × *T. monococcum* ssp. *aegilopoides* G3116 (male). The former is a cultivated einkorn wheat from an Italian collection grown at Titograd, Montenegro and was provided by P. E. MCGUIRE, the University of California, Davis. The latter is a wild population collected in Lebanon and was provided by L. B. JOHNSON, the University of California, Riverside. Additional loci were mapped on chromosome *1A*^{m} using a mapping population of 76 F_3 families from a cross between *T. m. aegilopoides* accessions G1777 and G2528, which were also provided by L. B. JOHNSON (DUBCOVSKY *et al.* 1995a). Meiosis was inspected in both F_1 hybrids and no abnormality in chromosome pairing was observed. Both hybrids were fully fertile. Maps of specific chromosome regions based on mapping populations in other species (Table 1) were employed in the investigation of the order of loci in regions with inversions between wheat and barley.

DNA hybridization: Nuclear DNAs were isolated from leaves of single F_2 plants or 10–20 pooled F_3 plants following the procedure of DVOŘÁK *et al.* (1988). DNAs from both parents were digested with *Apa*I, *Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Sst*I, *Xba*I, and *Hin*dIII to screen for polymorphism. Restriction endonuclease-digested DNAs were electrophoretically fractionated in 1% agarose gels and transferred to Hybond N+ nylon membrane (Amersham) by capillary transfer.

Clones used in this study are listed in Table 2. Prehybridization and hybridization were performed in a rotary hybridization chamber (National Labnet Company) at 65° as described earlier (DUBCOVSKY *et al.* 1994). 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. The membranes were washed in 2× SSC and 0.5% SDS for 30 min at 65°, 1× SSC and 0.5% SDS for 30 min at 65°, and 0.5 X SSC and 0.5% SDS for 15 min at 65°.

Isozymes and proteins: Bulks of F_4 seeds (for gliadins) or F_4 seedlings (for isozymes) of individual F_3 plants were used to map isozyme and *gliadin-2* loci. Isozymes Est-3, Pgd-3, and β-glucosidase were electrophoretically fractionated and stained as described by SUN and DVOŘÁK (1991) and CHELIAK and PITEL (1984). The electrophoretic separation and visualization of Est-1 was according to HART (1982). Gliadins were electrophoretically fractionated using acid polyacrylamide gel electrophoresis (A-PAGE) according to LAFIANDRA and KASARDA (1985).

Morphological markers: The color of seeds and the color of glumes were investigated by scoring these traits on 5 to 18 F_3 plants grown in the field.

Map construction: Maps were constructed with the aid of the computer program Mapmaker/EXP 3.0 (LANDER *et al.* 1987; LINCOLN *et al.* 1992) using the KOSAMBI function (KOSAMBI 1943). Multipoint analysis was used on individual linkage groups, using an initial LOD threshold of three and lowering LOD threshold to two to map additional markers. Preferred orders were checked by the "RIPPLE" command with a window-size of 5 and LOD threshold of 2. Markers with LOD < 2 were placed in the preferred locations and are indicated by nonitalicized parentheses on the maps. The goodness of fit of segregation for each pair of alleles was tested by the χ^2 test. The significance of the differences between recombination fractions in the same intervals in different maps was determined by the Z-test. Variances of the recombination fraction estimates were calculated according to ALLARD (1956).

The position of the centromere on the *1A*^{m} map was determined by telosomic mapping using *T. monococcum* telosomes in the genetic background of *T. aestivum.* The positions of the centromeres of the remaining chromosomes were inferred from *T. aestivum* and barley telosomic analyses.

Symbolism: Clones that hybridized to identical restriction fragments were assumed to be homologous. This is indicated by = signs on the maps in Figure 1. Different loci detected with the same clone were considered duplicated. Duplicated loci within a chromosome were designated according to the rules of nomenclature for molecular markers in wheat by attaching a decimal numeral. The nomenclature rules do not provide means to indicate that there is a duplicate locus on another chromosome. A chromosome on which a duplicate locus is located is indicated in brackets in Figure 1. In those cases in which duplicate loci have previously been designated by Arabic numerals, the earlier designations were used (*e.g.*, *Nor9* or *Est1*).

Map comparisons: The barley chromosomes were designated according to their homoeology with wheat chromosomes. To compare the patterns of recombination between

TABLE 1

Populations used for the construction of the *T. monococcum* genetic maps and comparison of the colinearity of *T. monococcum* and barley chromosomes

Species	Chromosome	Type of population	N	Parents	Reference
T. monococcum	All	F_2, F_3 families	74	DV92 × G3116	Present data
T. monococcum	$1A^m$	F_3 families	76	G2528 × G1777	Dubcovsky *et al.* (1995a)
T. aestivum/*T. monococcum*	$1A/1A^m$	RSLs[a]	96	CS × DS$1A^m$(CS*1A*)	Dubcovsky *et al.* (1995a)
T. turgidum	*1B*	RSLs	93	Langdon × DS *T. dicoccoides 1B*(Langdon *1B*)	Present data
T. aestivum	*1D*	RSLs	58	CS × DS Cheyenne*1D*(CS*1D*)	Present data
H. vulgare	All	DH[b]	150	Steptoe × Morex	Kleinhofs *et al.* (1993)
H. vulgare	All	DH	71	IGRI × Franka	Graner *et al.* (1991)
H. vulgare/*H. spontaneum*	All	F_2	135	Vada × *H. spontaneum*	Graner *et al.* (1991)
T. aestivum/*T. turgidum*	*4D*/*4B*	Recombinant inbread lines	129	*ph1c4B* × CS*4D*	Dubcovsky *et al.* (1996)

[a] Recombinant substitution lines.

[b] Doubled haploids.

the *T. monococcum* and barley homoeologous chromosomes, absolute and standardized map lengths were used. To standardize a map length, the distances between the most distal common markers on the maps of a homoeologous chromosomes were made equal, and the lengths of all intervals were proportionally adjusted. The distal regions of the maps of chromosomes $4A^m$ and $5A^m$ that are involved in a reciprocal translocation were excluded from this analysis. The recombination distribution in the *T. monococcum* and barley genomes was investigated by comparing the lengths of centromeric intervals and the lengths of the most distal common intervals on the maps of homoeologous chromosomes. For the comparisons of the centromeric intervals, an interval of 5 to 20 cM long was selected so that this interval was not zero or close to zero in either of the homoeologues.

Chromosome regions with potential differences in colinearity were investigated by mapping additional DNA markers in the critical regions of the *T. monococcum* or Steptoe × Morex barley maps (Table 1). When the position of a locus was not colinear but its neighbors were colinear in a homoeologous chromosome pair, the anomalous position of the locus was assumed to be caused by duplication and was not analyzed. When a pair of neighboring markers was in an inverted orientation, LOD scores for the alternative orders were calculated to establish the probability of the inverted order occurring by chance. A threshold of LOD = 3 was used (Risch 1992). Groups of three or more inverted markers, with LOD > 3 relative to the alternative order, and based on more than a single recombined chromosome in the investigated interval, were considered as real inversions.

RESULTS AND DISCUSSION

The cross between cultivated *T. monococcum* ssp. *monococcum* DV92 and population G3116 of wild ssp. *aegilopoides* was highly polymorphic. Approximately 85% of the clones revealed polymorphism for at least one of the nine restriction enzymes used for the screening of the parents. Three hundred thirty-five markers, including morphological markers determining blue aleurone (*Ba*) and black glume (*Bg*), isozyme markers β-glucosidase (β-*Gls*), esterase-1 (*Est1*), esterase-3 (*Est3*), and 6-phosphogluconate dehydrogenase-3 (*Pgd3*), 18S-5.8S-26S rRNA loci (*Nor9* and *Nor10*), 5S rRNA loci (*X5SDna-1A* and *-5A*), seed storage protein loci encoding gliadins (*Gli1, Gli2,* and *Gli3*), high-molecular-weight (H-M-W) glutenin subunits (*Glu1*), low-molecular-weight (L-M-W) glutenin subunits (*Glu3*), and triplet protein (*Tri*), and 25 environmental stress-related DNA markers (Dubcovsky *et al.* 1995b) were mapped in this population. The total genetic length of the seven linkage groups was 1067 cM (Figure 1). Twelve (3.6%) and 38 (11.3%) markers showed segregation distortion at the 1% and 5% probability levels, respectively. Marker orders were similar to those reported for *T. aestivum* linkage maps (Gale *et al.* 1995; Nelson *et al.* 1995a,b,c; Van Deynze *et al.* 1995) and deletion maps (Werner *et al.* 1992; Gill *et al.* 1993; Kota *et al.* 1993; Delaney *et al.* 1995a,b; Mickelson *et al.* 1995) with few exceptions (described below).

Duplicated loci: Of 328 mapped loci detected with DNA probes, 60 (30 × 2, 18.3%) were duplicated, 18 (6 × 3, 5.5%) were triplicated, 20 (5 × 4, 6.1%) were quadruplicated and five (1 × 5, 1.5%) were present five times; a total of 31.4% of the loci were present more than once in the genome (Figure 1). A total of 27.7% of the loci detected with cDNA clones, including the rRNA loci, were duplicated compared to 34.4% of the loci detected with genomic clones. This level is similar to 30% of locus duplication in the barley maps reported by Kleinhofs (1994) but is higher than 20% in the barley maps reported by Graner *et al.* (1993). The levels of locus duplication, calculated in the same way as for *T. monococcum* and barley, in species with small genomes, such as rice (*Oryza sativa* L.), which has a c-value

TABLE 2

DNA markers

Locus	Clone	Reference
Xabc	ABC (random barley cDNA clones)	Kleinhofs *et al.* (1993)
Xabg	ABG (random barley genomic clones)	Kleinhofs *et al.* (1993)
Xbg	BG (random barley genomic clones)	Kleinhofs *et al.* (1993)
Xbcd	BCD (random barley cDNA clones)	Anderson *et al.* (1992)
Xcdo	CDO (random oat cDNA clones)	Anderson *et al.* (1992)
Xwg	WG (random wheat genomic clones)	Anderson *et al.* (1992)
Xmwg	MWG (random barley cDNA or genomic clones)	Graner *et al.* (1991)
Xksu	KSU (random *T. tauschii* genomic clones)	Gill *et al.* (1991)
Xtam	TAM (random wheat genomic and cDNA clones)	Devey and Hart (1993)
XcsIH	CSIH (random *T. tauschii* genomic clones)	Lagudah *et al.* (1991)
Xglk	GLK (random wheat genomic clones)	Liu and Tsunewaki (1991)
Xpsr	PSR (wheat cDNA or genomic clones)	Gale *et al.* (1995)
X5SDna	pTa794	Gerlach and Dyer (1980)
XAga6	blpl	Kilian *et al.* (1994)
XAga7	WE:AGA7	Olive *et al.* (1989)
XAmy	—	Khursheed and Rogers (1988)
XβAmy1	pcbC51	Kreis *et al.* (1988)
Xbg1485(Ger)	—	Hurkman *et al.* (1994)
XBrz	pBz.Hv8-3	Wise *et al.* (1990)
XCab1	pKG1490	Barkardottir *et al.* (1987)
XChs	pcCHS11	Rohde *et al.* (1991)
XcsSR3(Gsp)	pGsp	Rahman *et al.* (1994)
Dhn2	pTZ19R-dhn2	Close and Chandler (1990)
Dhn3	pTZ19R-dhn3	Close and Chandler (1990)
Dhn6	pTZ19R-dhn6	Close and Chandler (1990)
XEm	p1015	Williamson *et al.* (1985)
XGli1 and *XGli3*	pcP387	Forde *et al.* (1985)
XGlu1	pDY10A/KS−	Anderson *et al.* (1989)
XGlu3	pTdUCD1	Cassidy and Dvořák (1991)
Xmsu433(Lec)	pNVR20	Reikhel and Wilkins (1987)
XNar7	—	Miyazaki *et al.* (1991)
XNor	pTa250.15	Appels and Dvořák (1982)
Xpsr8(Cxp3)	2473	Baulcombe *et al.* (1987)
Xpsr109(RbcS)	—	Barkardottir *et al.* (1987)
Xucd101(Esi2)	ESI2	Gulick and Dvořák (1990)
Xucd102(Esi3)	ESI3	Gulick and Dvořák (1990)
Xucd103(Esi4)	ESI4	Gulick and Dvořák (1990)
Xucd104(Esi14)	ESI14	Gulick and Dvořák (1990)
Xucd106(Esi18)	ESI18	Gulick and Dvořák (1990)
Xucd107(Esi28)	ESI28	Gulick and Dvořák (1990)
Xucd108(Esi32)	ESI32	Gulick and Dvořák (1990)
Xucd109(Esi35)	ESI35	Gulick and Dvořák (1990)
Xucd111(Esi48)	ESI48	Gulick and Dvořák (1990)
XTri	Tri25-11	Singh *et al.* (1993)
Xttu1934(Hsp16.9b)	pTtu1934(Hsp16b)	Weng *et al.* (1991a)
Xttu1935(Hsp17.3)	pTtu1935(Hsp17.3)	Weng *et al.* (1991b)
Xttu1936(Hsp26.6a)	pTtu(Hsp26.6a)	Weng *et al.* (1991a)
XVatp-A	pHTA	Dupont and Morrissey (1992)
XVAtp-B2	pHTB2	Berkelman *et al.* (1994)
XVAtp-B1	pHTB1	Berkelman *et al.* (1994)
Xwsu4(Dor4)	pMA1949	Morris *et al.* (1991)
Xwsu5(Dor5)	pMA1951	Morris *et al.* (1991)
Xwsu6(Dor2)	pMA1959	Morris *et al.* (1991)

of 0.45 pg/1c (Arumuganathan and Earle 1991), and common bean (*Phaseolus vulgaris* L.), which has a c-value of 0.66 pg/1c (Arumuganathan and Earle 1991), were 5.6% and 8.9% in maps reported by Saito *et al.* (1991) and Nodari *et al.* (1993), respectively. Although these levels of locus duplication are lower than that found here for *T. monococcum,* which has a large genome (c-value is 6.0 pg/1c, Arumuganathan and

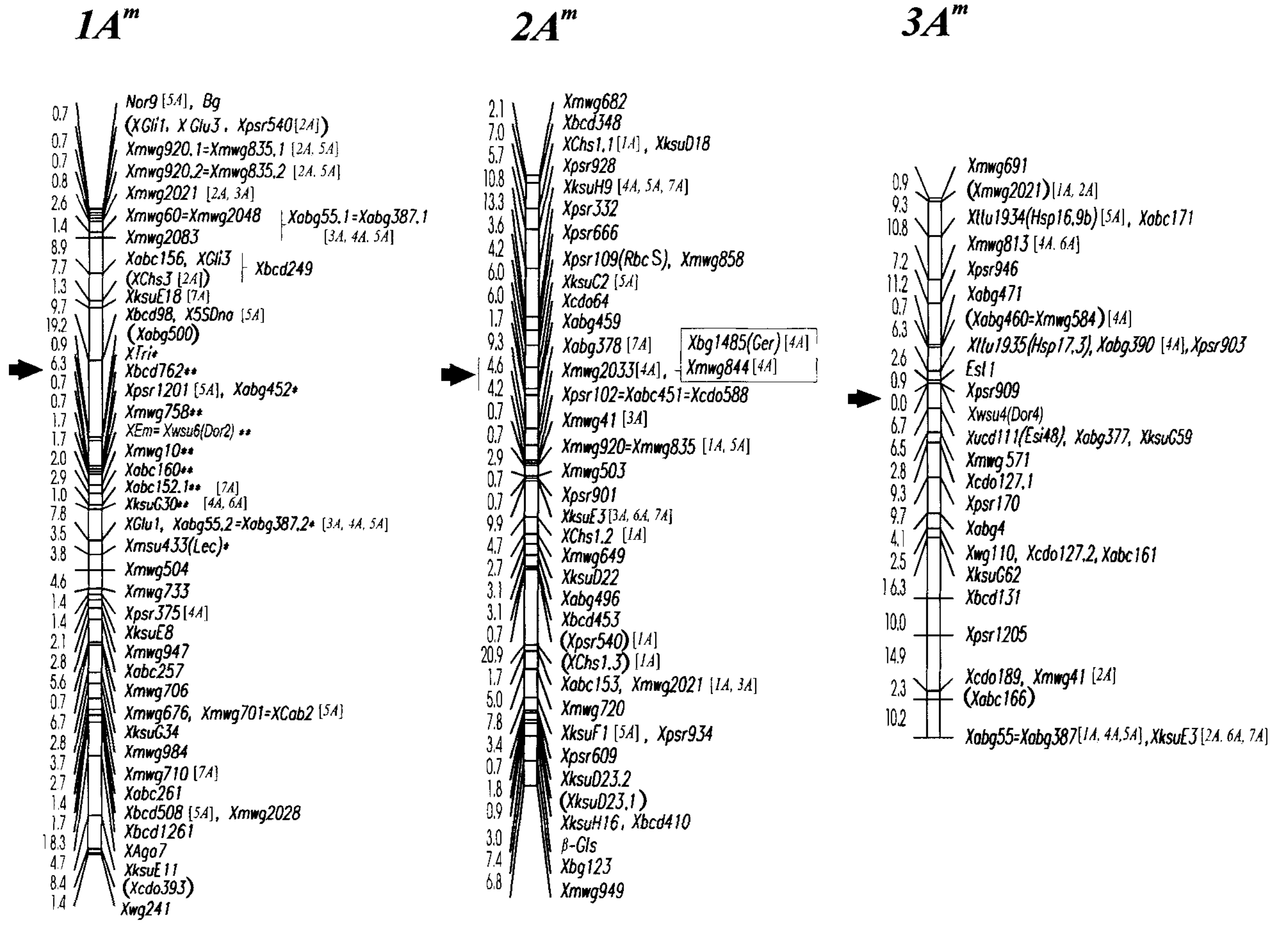

FIGURE 1.—Linkage maps of *T. monococcum* chromosomes *1*–*7*. Markers preceded by an X were mapped with DNA probes. The function of the markers not preceded by an X has been verified by other means. Markers to the right of vertical lines were mapped within the range indicated by the line. Asterisks indicate segregation distortions at $P < 0.05$ (*) and $P < 0.01$ (**). Approximate position of the centromeres based on telocentric analysis is indicated by arrows. Distances are given in cM. Duplicate loci within a chromosome are indicated by a decimal, and those among chromosomes are indicated by specifying chromosome location of duplicated loci between brackets. Markers with LOD < 2 are placed at preferred locations and are indicated by parentheses (not italicized).

EARLE 1991), the variation in locus duplication in the barley maps constructed by different workers illustrates the need for comparing maps constructed with probes subjected to the same selection criteria and using populations with similar levels of polymorphism to determine if the apparent relationship between the genome size and locus duplication is real.

Each chromosome may either have an equal probability to receive a duplicate locus during the process of a locus duplication (the null hypothesis) or the probability may differ; specifically, the chromosome on which the original locus resides may have a different probability to receive the duplicate locus than the remaining six chromosomes (the alternative hypothesis). Totals of 23 and 86 loci were duplicated intrachromosomally and interchromosomally (loci duplicated both intrachromosomally and interchromosomally were counted only as a single locus per chromosome in the calculation of the number of interchromosomal duplications), respectively. The probabilities of the intrachromosomal and interchromosomal duplications are different for the duplicated, triplicated, and quadruplicated loci. The expected numbers of the intrachromosomal and interchromosomal duplications were, therefore, calculated separately for the duplicated, triplicated, and quadruplicated loci using individual probabilities of interchromosomal and intrachromosomal duplications for duplicated, triplicated, and quadruplicated loci, and weighted averages were calculated from these values. The observed numbers of 23 intrachromosomal and 86 interchromosomal duplications did not statistically differ from a weighted average of expected 22 intrachromosomal duplications and 88 interchromosomal duplications ($P = 0.7$, χ^2 test), indicating that the null hypothesis was true. These results differ from those reported by GILL *et al.* (1991) for *T. tauschii* and O'DONOUGHUE *et al.* (1992) for oats who concluded that duplications are more frequent within chromosomes than between chromosomes. If the expected numbers of duplications are calculated as weighted averages of individ-

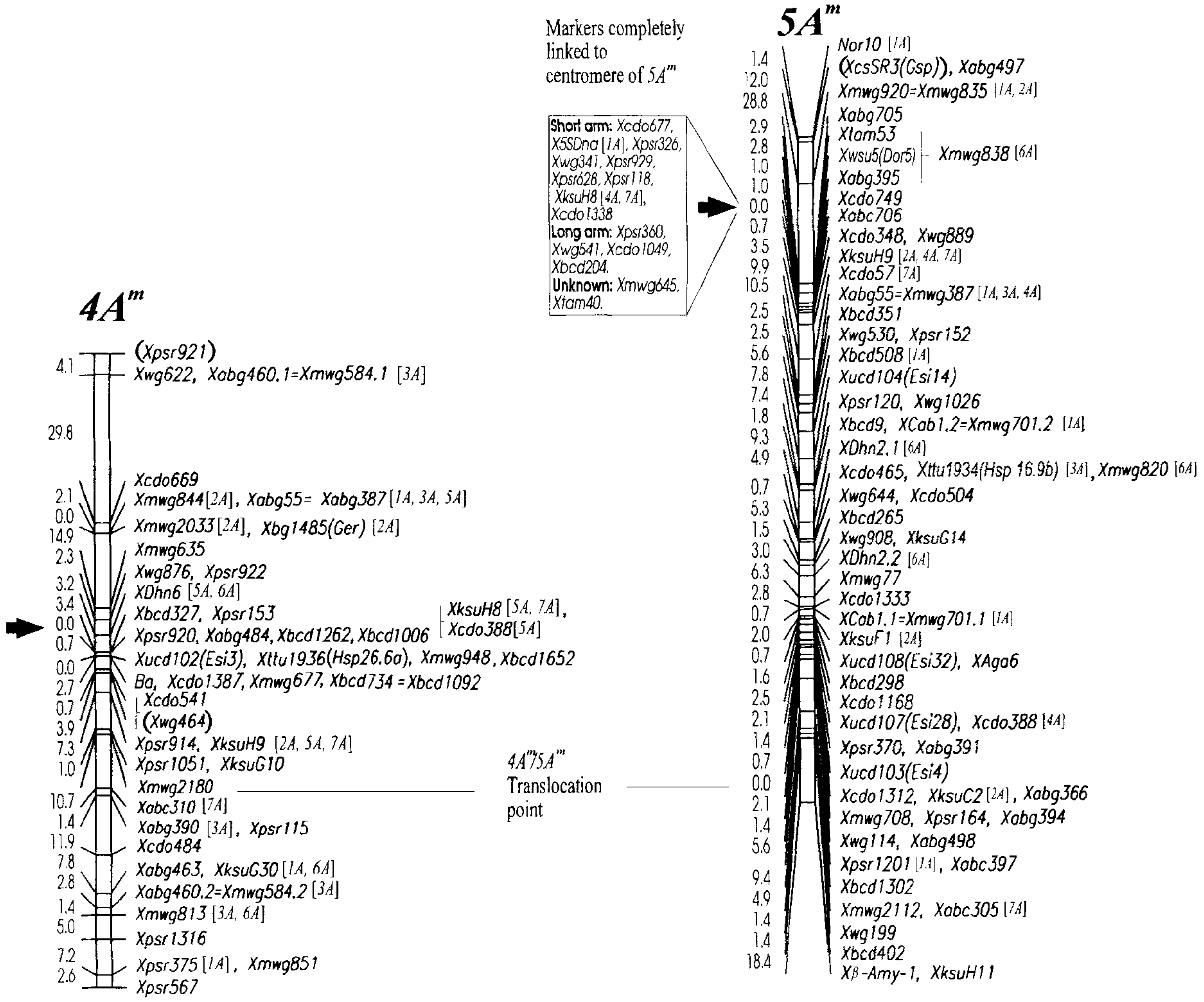

FIGURE 1.—*Continued*

ual classes of duplications, as done for the *T. monococcum* genome, the numbers of observed and expected intrachromosomal and interchromosomal duplications are not significantly different in the oat genome ($P = 0.20$) (indicating that the null hypothesis may also be true for oats) but are different ($P < 0.01$) for the *T. tauschii* genome. In the *T. tauschii* genome, intrachromosomal duplications are more abundant than interchromosomal duplication, as pointed out by GILL *et al.* (1991). A similar excess of intrachromosomal duplications ($P < 0.05$) was found on the Steptoe × Morex genetic map reported by KLEINHOFS (1994). The excess of intrachromosomal duplications was associated with frequent tandem duplications of loci on the *T. tauschii* and Steptoe × Morex maps. Tandemly duplicated loci accounted for 60% of the intrachromosomally duplicated loci on the *T. tauschii* map and 31% on the Steptoe × Morex map, but only 17% on the *T. monococcum* map. Whether these differences are real and reflect different evolutionary patterns in these species or are artifacts of mapping strategies and reflect differences among probes and mapping populations is not clear.

Chromosome *1*: A total of 51 molecular and one morphological marker (*Bg*) covering 157 cM were mapped on chromosome *1A^m* in mapping population DV92 × G3116 (Figure 1). Segregation distortion favoring G3116 alleles was observed around the centromere, between *XTri* and *Xmsu433(Lec)* on the DV92 × G3116 map (Figure 1). Nineteen additional molecular markers and one morphological marker, hairy glume (*Hg*), were mapped in mapping population G1777 × G2528 (DUBCOVSKY *et al.* 1995a). No segregation distortion was observed on that map. The lengths of 27 common intervals between these two *1A^m* maps were similar except for intervals *XGli3-XChs3* ($P < 0.05$), *XAga7-Xcdo393* ($P < 0.05$), *XEm-Xabc152.1* ($P < 0.05$), and *Xabc152.1-XGlu1* ($P < 0.05$), all of which were significantly longer on the DV92 × G3116 map than on the G1777 × G2528 map (DUBCOVSKY *et al.* 1995a). The lengths of 16 common intervals between DV92 × G3116 map and a *1A* map of *T. aestivum* (DUBCOVSKY *et al.* 1995a) did not significantly differ, except for the interval *XGlu3-Xmwg60*, which was significantly ($P < 0.01$) longer (18.4 cM) on the *T. aestivum* map than on the *T. monococcum* map (4.8 cM), and the intervals *Xbcd98-XTri* (9.0 cM) and *XksuE8-Xmwg676* (3.0 cM), which

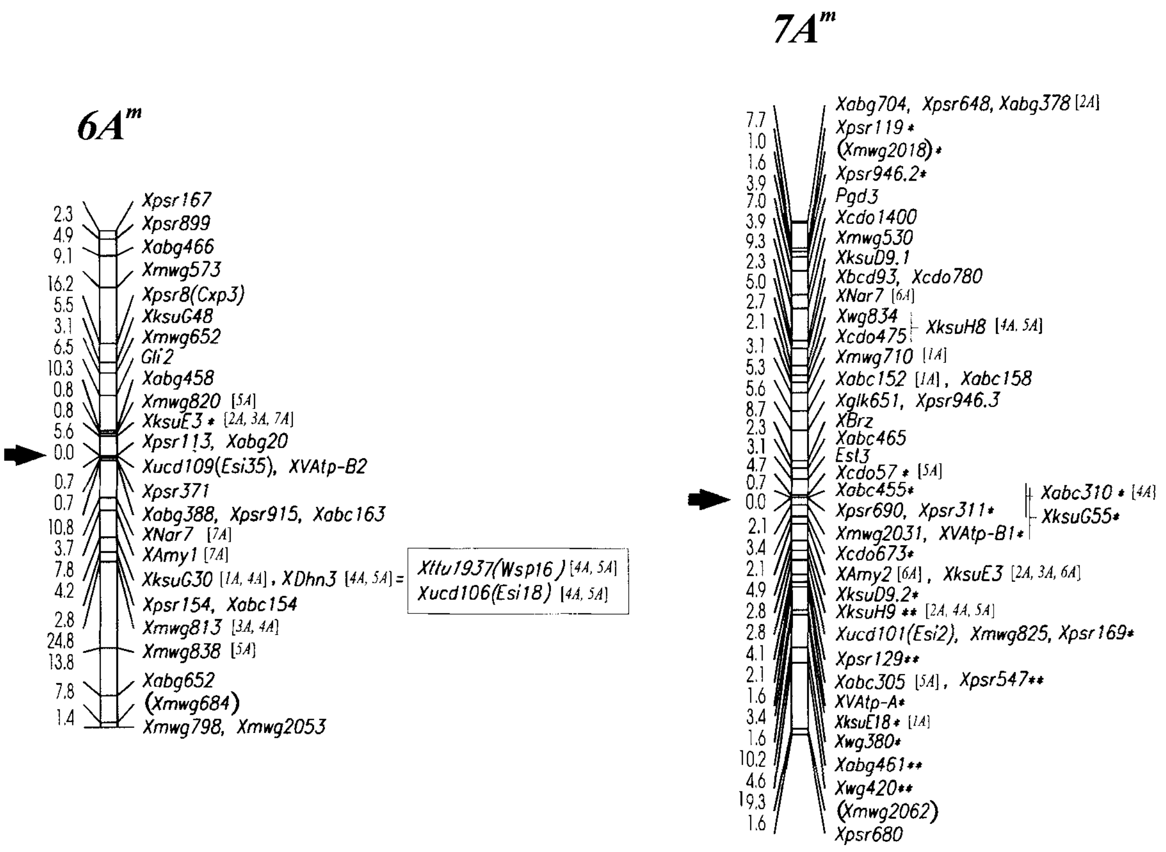

FIGURE 1.—*Continued*

were significantly ($P < 0.05$) shorter on the *T. aestivum* map than on the *T. monococcum* map (20.1 cM and 11.2 cM, respectively). The *T. aestivum 1A* map and the *T. monococcum $1A^m$* maps were colinear (present data and DUBCOVSKY *et al.* 1995a).

The morphological marker *Bg* was placed on both the DV92 × G3116 map and G1777 × G2528 map, and *Hg* was placed only on the G1777 × G2528 map. Glume pigmentation differed in G1777 and G3116. While G1777 had glumes solid black, G3116 had only a narrow black line at the glume margin. The other two parents had nonblack glumes. Since both black glume phenotypes mapped at the *Bg* locus, they are presumably controlled by different alleles of the *Bg* locus. We designate the recessive nonblack glume (DV92 and G2528) as *bg*, the solid black glume (G1777) allele as the *Bg(a)*, and the allele for the black line at the glume margin (G3116) as *Bg(b)*. Hairy glume was dominant over glabrous glume. No recombination was observed between *Bg* and *Hg* in the G1777 × G2528 mapping population.

Locus *Nor9* encoding the 18S-5.8S-26S rRNA (DUBCOVSKY and DVOŘÁK 1995) was mapped at the end of the linkage group of the short arm and was linked to *Bg* on the DV92 × G3116 map (Figures 1 and 2). On the G1777 × G2528 $1A^m$ map, *Nor9* was distal to *Bg* (DUBCOVSKY and DVOŘÁK 1995). Locus *X5SDna-1A* contains repeats with the short spacers among the *5S* RNA genes (DVOŘÁK *et al.* 1989). The locus is located in the middle of the short arm linkage map and is completely linked to *Xbcd 98*. No major *Nor* or *5SDna* loci were at similar positions on barley chromosome *1H* (Figure 2) (GRANER *et al.* 1993; KLEINHOFS 1994).

There are 14 loci in common between the DV92 × G3116 $1A^m$ map and the map of barley chromosome *1H* based on the Steptoe × Morex (S × M) mapping population. Markers are colinear for most of the length of the chromosome (Figure 2), except for the region *Xmwg733-Xmwg706* on the long arm, which is inverted (Figures 2 and 3).

The order of markers in the interval *Xmwg733* to *Xmwg706* or *Xmwg676* on chromosome arm $1A^mL$ and chromosome arms *1AL*, *1BL*, and *1DL* of *T. aestivum* is the same (Figure 3). The order of seven common markers (*Xmwg733, Xbcd1930, Xbcd442, Xabc257, Xmwg706, Xmwg676,* and *Xmwg947*) within this region is inverted on the barley maps (Figure 3). Both the wheat and barley marker orders have high LOD scores (Table 3). At least five duplication events would be necessary to explain these two marker orders by gene duplication. A paracentric inversion is the most parsimonious explanation of the observed differences in the order of loci between the wheat and barley maps. Markers *Xmwg504* and *Xmwg984*, located on both sides of the inverted region, show the same orientation relative to the centromere in wheat and barley, indicating that they are outside of the inverted region. The length of the inversion

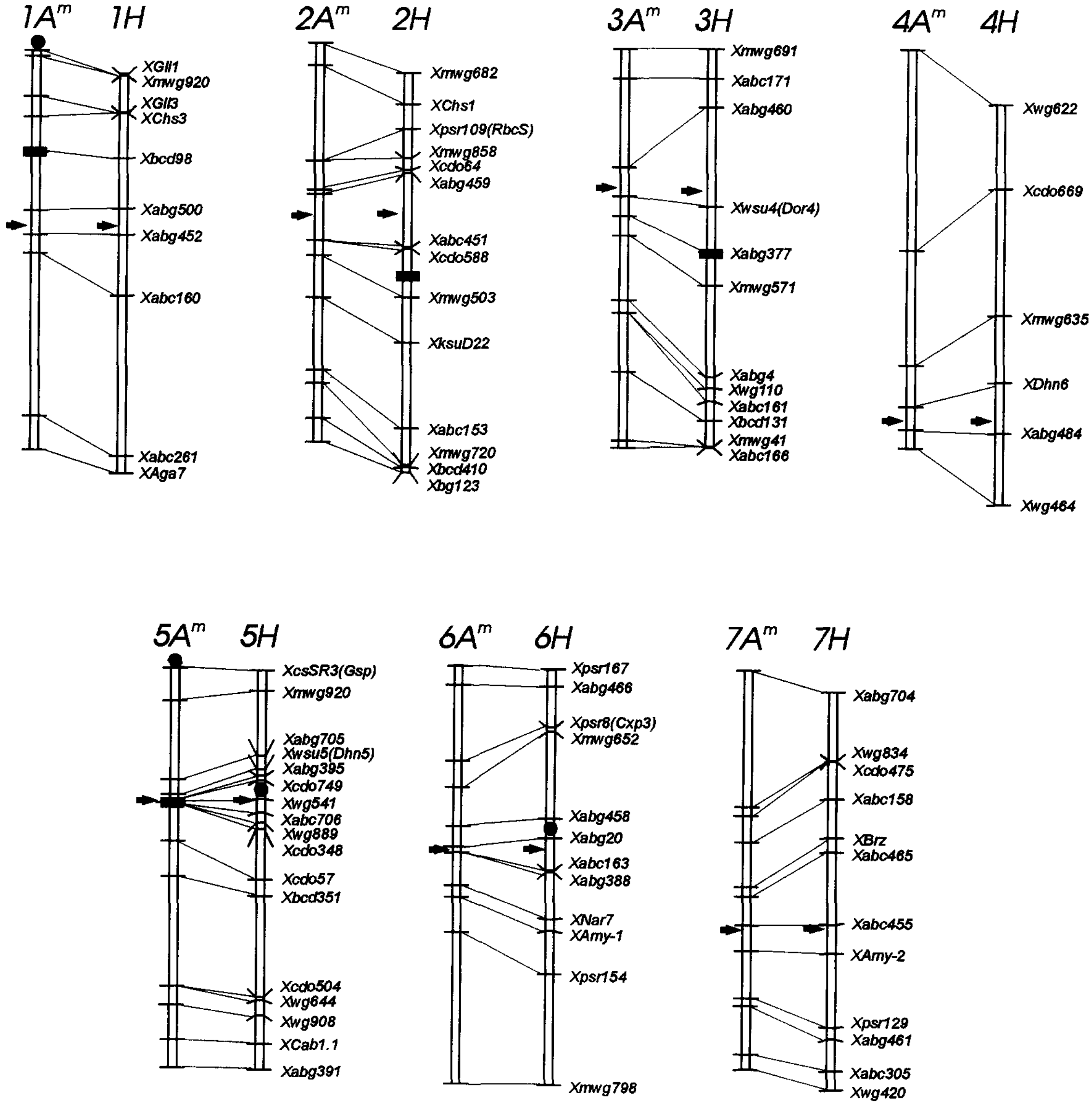

FIGURE 2.—Comparison of the patterns of recombination between standardized *T. monococcum* and Steptoe × Morex barley genetic maps. The approximate positions of the centromeres based on telocentric analyses are indicated by arrows. The positions of the *Nor* loci are indicated by ● and those of the *5SDna* loci by ■. The following noncolinear markers were excluded from the figure: *Xmwg733*, *Xabc257*, and *Xmwg706* from chromosome *1*; *Xabg471* from chromosome *3*; six markers in the translocated *5A*^{m}/*4A*^{m} segment of chromosome *4*; eight markers in the translocated *4A*^{m}/*5A*^{m} segment and *Xwg530*, *Xabg497*, and *Xbcd351* from chromosome *5*; *Xmwg820* from chromosome *6*; *Xwg380*, *Xabc310*, *XVAtp-B1*, and *Xcdo673* from chromosome *7*. Note the shorter centromeric regions and longer telomeric regions on the *T. monococcum* maps compared to the S × M barley maps.

is >10 cM (*Xmwg733-Xmwg706* interval) and <40 cM (*Xmwg504-Xmwg984* interval). Another marker that has a conflicting position between barley and *T. monococcum* is *Xmwg701*. Two duplicate *Xmwg701* loci, *Xmwg701.1* that is completely linked to *Xmwg706* and *Xmwg701.2* that is distal to *Xmwg710*, have been found on chromosome arm *1AL* of *T. turgidum* (J. DVOŘÁK unpublished data). Locus *Xmwg701.2* was also mapped in barley, and locus *Xmwg701.1* was also placed on the *1A/1A*^{m} map based on homoeologous recombination between *T. aestivum 1A* and *T. monococcum 1A*^{m} (DUBCOVSKY *et al.* 1995a). We assume, therefore, that this discrepancy between the barley and Triticum maps is caused by duplication of *Xmwg701*.

Chromosome *2*: Forty-two DNA markers covering 168 cM were mapped (Figure 1). In addition to the DNA markers, a structural gene locus encoding β-glucosidase was mapped on the long arm. G3116 had a null phenotype for this isozyme while DV92 showed two-bands, one staining more strongly than the other. The structure of the enzyme is unknown, and to our knowledge no β-glucosidase isozyme has been mapped in Triticeae. The locus was named *β-Gls*.

Loci *Xpsr540-2A*, *XChs1.3* (homologous to *XChs3*), and *Xmwg2021-2A*, spanning an interval of 22.6 cM are duplicated in a distal region of the map of the short arm of chromosome *1A*^{m} where they span an interval of 21.8 cM (Figure 1). It is unlikely, however, that this

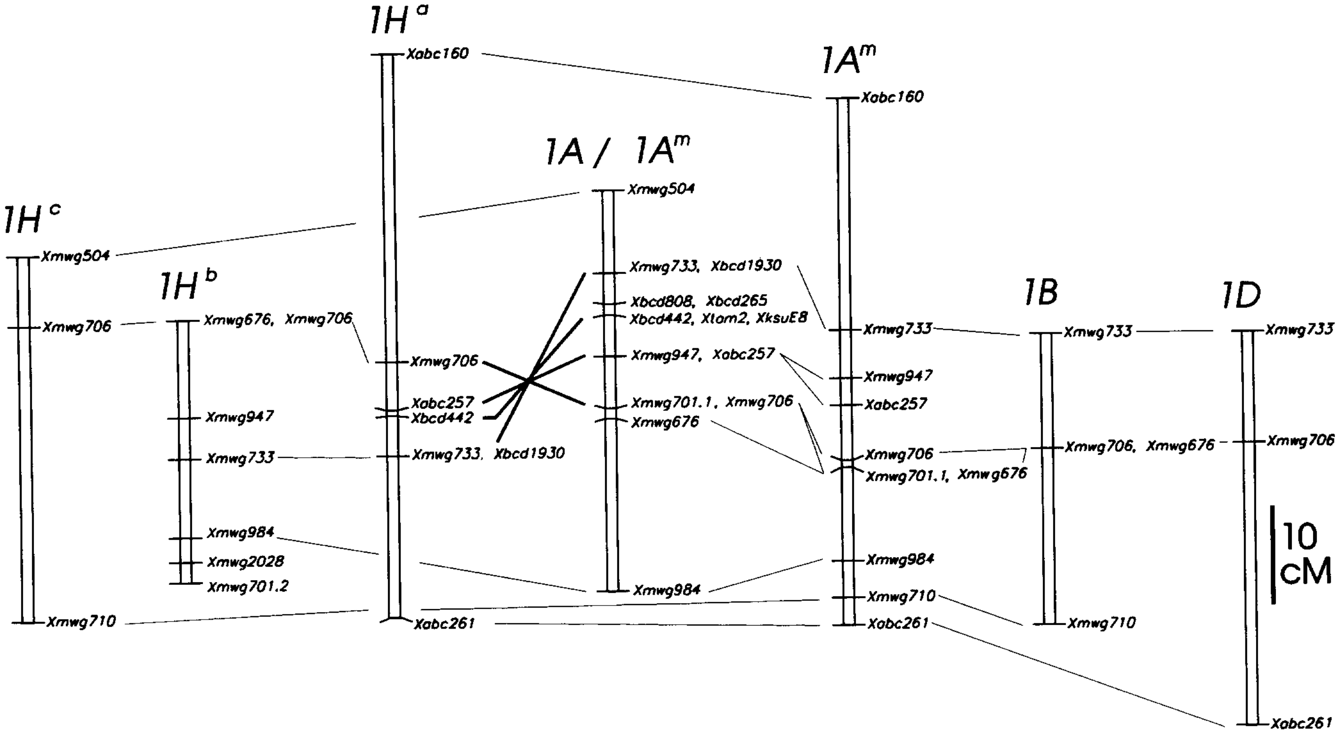

FIGURE 3.—Comparison of a chromosome region involving a paracentric inversion in the long arms of the chromosomes of homoeologous group *1* in Triticum and barley. The *1Ha*, *1Hb*, and *1Hc* maps are based on the Steptoe × Morex, IGRI × Franka, and Vada × *H. vulgare* ssp. *spontaneum* mapping populations, respectively (Table 1). The $1A^m$ map is based on the DV92 × G3116 population, those of *1B* and *1D* are based on populations described in Table 1, and the $1A/1A^m$ map is based on a population of RSLs produced by homoeologous recombination between *1A* of *T. aestivum* and $1A^m$ of *T. monococcum* (Table 1). Markers with LOD < 2 were placed at preferred locations and are indicated by parentheses (not italicized).

reflects a segmental chromosome duplication because the order of the loci is not the same and numerous loci that are within this region on chromosome $1A^m$ were not detected on chromosome $2A^m$ (Figure 1).

There are 14 loci in common between the DV92 × G3116 map and the map of S × M chromosome *2H*. All are colinear (Figure 2).

Chromosome *3*: Thirty-one DNA markers were placed on the chromosome $3A^m$ map (145 cM). Additionally, a locus encoding esterase-1 (*Est-1;* JAASKA 1980) was mapped in the proximal region of the short arm (Figure 1).

There are 13 loci in common with S × M barley chromosome *3H* (Figure 2). These loci are colinear except for the interval *Xabg460-Xabg471*, which is in a reversed order on the barley map (Table 3). These two loci are separated by a single crossover in the *T. monococcum* map. The LOD score of the order, centromere-*Xabg460-Xabg471*, is only 1.73 times higher than the LOD score for the order, centromere-*Xabg471-Xabg460*

TABLE 3

Inverted groups of markers between *T. monococcum* and barley

Chromosome arms	Barley	LOD	*T. monococcum*	LOD
1HL, $1A^mL$	*Xmwg706-Xabc257-Xmwg733*	−24.2[a]	*Xmwg733-Xabc257-Xmwg706*	−35.3[c]
3HS, $3A^mS$	*Xabg471-Xabg460*	−10.3[a,b]	*Xabg460-Xabg471*	−1.7[c]
4HL, $5A^mL$	*Xwg114-Xabg394-Xabg366*	−8.4[a,b]	*Xabg366-Xabg394-Xwg114*	−12.3[c]
4HL, $5A^mL$	*Xβ-Amy1-XksuH11*	0.0[a,b]	*XksuH11-Xβ-Amy1*	−5.8[d]
7HL, $7A^mL$	*Xcdo673-XVAtp-B1*	−0.2[a]	*XVAtp-B1-Xcdo673*	−8.2[c]

LOD scores for the alternative orders were calculated using only markers present simultaneously in both genera within the inverted region. Completely linked markers were not considered in calculations. Orders of the markers are from the centromere to the telomere.

[a] KLEINHOFS (1994).

[b] KLEINHOFS *et al.* (1993).

[c] Present data.

[d] DUBCOVSKY *et al.* (1996).

(Table 3). Moreover, a similar order to that observed in barley was reported for wheat chromosomes of homoeologous group 3 (Nelson *et al.* 1996), indicating that the different order in *T. monococcum* is likely a chance deviation.

Chromosome *4*: The chromosome $4A^m$ map (127 cM) includes 46 DNA markers and the morphological marker *Ba* (Figure 1). Allele *Ba* (blue aleurone) present in G3116 is incompletely dominant over the nonblue aleurone allele present in DV92. The nonblue allele in DV92 is designated *ba*, and the incompletely dominant allele in G3116, which determines a half-blue seed phenotype, is designated *Ba(a)*. This allele differs from the solid blue allele that is located on the long arm of *Lophopyrum ponticum* chromosome *4* and that was introgressed into *T. aestivum* chromosome *4B* via Robertsonian fusion (Jan *et al.* 1981). We designate the *L. ponticum* incompletely dominant allele *Ba(b)*.

Markers *Xbg1485(Ger)-4A*, *Xmwg2033-4A* and *Xmwg844-4A* are completely linked in the middle of the map of the short arm. Duplicated loci *Xbg1485(Ger)-2A*, *Xmwg2033-2A* and *Xmwg844-2A* are completely linked in the centromeric region of the map of the long arm of chromosome $2A^m$ (Figure 1). This segment of chromosome $4A^m$ could possibly be duplicated in chromosome $2A^m$.

Duplicated *Xabg460.2-4A* and *Xmwg813-4A* loci are located in the proximal region of the map of the short arm of chromosome $3A^m$. However, the distances among the markers greatly differ. The interval *Xabg460.2-3A-Xmwg813-3A* is 19 cM long but the interval *Xabg460.2-4A-Xmwg813-4A* is only 1.4 cM long.

Six markers on the short arm and those in the proximal region of the map of the long arm (Figure 2) of the S × M chromosome *4H* are colinear with those on the map of chromosome $4A^m$. Colinearity is, however, interrupted in the distal 40 cM of the long arm map. In this region, six markers present on the S × M chromosome *5H* are on $4A^mL$, indicating that barley and *T. monococcum* differ by a reciprocal translocation (Devos *et al.* 1995). The translocation break point is between *Xmwg2180* and *Xabc310*. Detailed linkage comparisons of $4A^m$ with the hexaploid wheat chromosome *4A*, which was involved in numerous additional rearrangements, and the *T. aestivum* chromosomes *4B* and *4D*, which do not have the *4L/5L* translocation, have been reported (Devos *et al.* 1995).

Chromosome *5*: Eighty DNA markers were mapped. The map of chromosome $5A^m$ is the longest, 192 cM (Figure 1), among the seven maps. A large number of markers are concentrated in the centromeric region (Figure 1) that probably represents an extreme case of the suppression of recombination in the vicinity of the centromere that is apparent from the clustering of markers in the centromeric regions of all *T. monococcum* linkage maps. An alternative explanation of the absence of recombination in the centromeric region of the map of chromosome $5A^m$ is that DV92 and G3116 differ by a pericentric inversion. This alternative explanation seems, however, unlikely because similar genetic distances among markers in the vicinity of the centromere are observed on a map of chromosome $5A^m$ in the mapping population G2528 × G1777 (Dubcovsky and Dvořák 1995 and unpublished). Intervals *Xwsu5(Dor5)-Xpsr118-Xcdo1049-Xbcd351-Xbcd508* are 2.0, 0.0, 27.1, and 8.1 cM on the DV92 × G3116 map and 0.8, 0.0, 21.4, and 4.6 on the G2528 × G 1777 map. Marker *Xpsr118*, which is within the block of completely linked markers on the short arm, and *Xcdo1049*, which is within the block of completely linked markers on the long arm, did not recombine in either population. Additionally, the distances from the centromeric blocks of markers to the flanking markers, *Xwsu5(Dor5)* on the short arm and *Xbcd351* on the long arm, are similar on both maps. This agreement between the DV92 × G3116 map and G2528 × G1777 map would require to conclude that both pairs of parents were heterozygous for the same pericentric inversion if an inversion heterozygosity would be used as an explanation of the absence of recombination among the large number of centromeric markers on chromosome $5A^m$ in the mapping population DV92 × G3116. While this is not impossible, it is unlikely.

A large gap of 28 cM is in the middle of the map of the *5AS* arm. A similar gap is in this region on the *5HS* maps. The most distal marker on the map of the *5AS* arm is the *Nor10* locus encoding 18S-5.8S-26S rRNA. The *X5SDna-5A* locus containing the 5S rRNA gene repeats with the long spacers (Dvořák *et al.* 1989) is completely linked to the centromere (Figures 1 and 2).

The *Nor* locus and the *Xmwg920* locus, which are within a 12 cM terminal interval, are duplicated in a 2.1-cM terminal interval on the short arm of chromosome $1A^m$. However, other loci that are between these markers on chromosome $1A^m$ (*XGli1*, *XGlu3*, and *Xpsr540-1A*) are not between *Nor10* and *Xmwg920-5A* on chromosome $5A^m$. The absence of these markers on $5A^m$ makes it unlikely that the *Nor* and *Xmwg920* loci on $1A^mS$ originated by duplication of a terminal chromosome segment of $5A^mS$, as suggested by Gill and Appels (1988). There is no 5S rRNA locus on barley chromosome arm *5HS* (Kleinhofs *et al.* 1993) and the barley *Nor* locus *Rrn2* on the *5H* map is located in a position that is different from the position of *Nor10* on $5A^m$ (Figure 2) (Dubcovsky and Dvořák 1995).

In addition to the difference in the position of the *Nor* loci, the colinearity of 28 markers common between the S × M barley map and the $5A^m$ map is perturbed by five differences. The first one is the reciprocal translocation between $4A^m$ and $5A^m$, with a translocation break point between *Xucd103(Esi4)* and *Xcdo1312* in the $5A^mL$ arm (Figure 2) (for details see Devos *et al.* 1995).

The second difference is in the segment of chromosome *4* translocated to $5A^mL$. The order of five markers common between the *4HL* map and the segment of

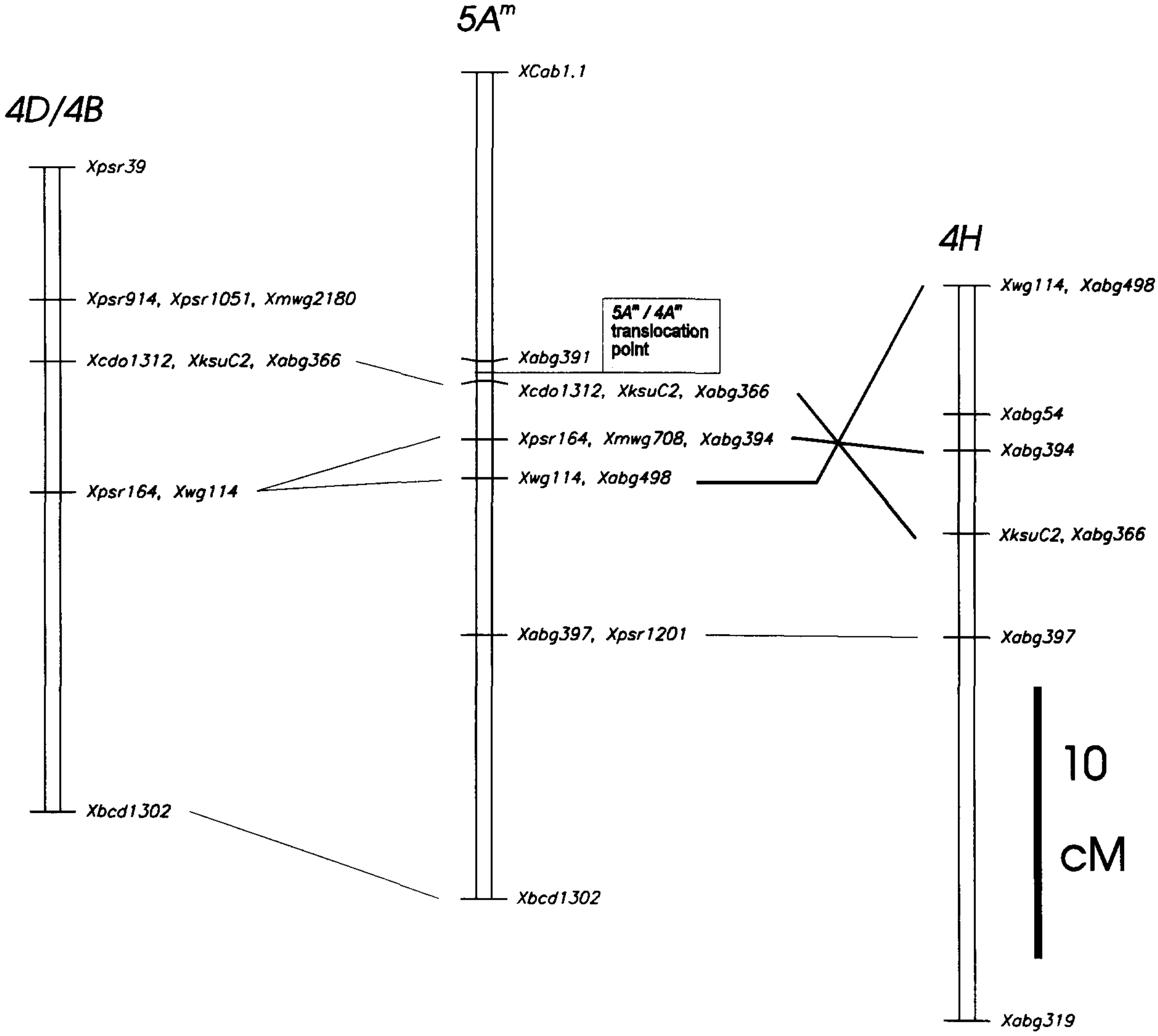

FIGURE 4.—Comparison of a chromosome region involving a paracentric inversion in the long arm of barley chromosome *4H* and the segment of the long arm of the *T. monococcum* chromosome arm *4L* translocated to the distal part of chromosome arm *5L*. The $5A^m$ and *4H* maps are based on the DV92 × G3116 and Steptoe × Morex populations, respectively, and that of *4D/4B* is based on a population produced by homoeologous recombination between chromosomes *4B* and *4D* (Table 1). Markers with LOD < 2 were placed at preferred locations and are indicated by parentheses (not italicized).

chromosome $4A^mL$ translocated to $5A^mL$ is inverted on the two maps (Figure 4). Both orders have high LOD scores compared to those of the alternative orders (Table 3). The order of loci present on $5A^mL$ is the same as on *4BL* and *4DL* (Figure 4). To explain the order of markers by gene duplication would require at least three independent duplication events. A paracentric inversion is the most parsimonious explanation of the inverted orientation of these markers on $5A^m$, *4B* and *4D*, on the one hand, and barley chromosome *4H*, on the other hand.

The third difference is in the order of two most terminal markers in the segment translocated from chromosome $4A^mL$. The two markers are oriented *β-Amy-1-XksuH11-telomere* on *4HL* but *XksuH11-β-Amy-1-telomere* on a map based on homoeologous recombination between 4B and 4D (DUBCOVSKY *et al.* 1996). On $5A^mL$, the markers are completely linked (Figure 1). While the 4B/4D order has a high confidence, the reported *4HL* order has the same probability as an inverted order (Table 3).

The fourth difference is in the location of *Xabg497*. This marker is located distally on the $5A^mS$ map (Figure 1) but proximally on the *5HS* map (KLEINHOFS *et al.* 1993). Since the intervening markers are colinear, we assume that this difference is due to a duplication of the *Xabg497* locus.

The fifth difference is in the position of *Xwg530*, which is distal to *Xbcd351* on the $5A^mL$ map but proximal to *Xbcd351* on the *5HL* map (KLEINHOFS *et al.* 1993). Since markers proximal to *Xbcd351* (*Xabc706, Xwg889, Xcdo348,* and *Xcdo57*) are not inverted and show the same orientation relative to the centromere on the $5A^mL$ and *5HL* maps (Figures 1 and 2), this difference is most likely also caused by a locus duplication.

Chromosome 6: Thirty DNA markers covering a region of 144 cM are on the chromosome *6A*^{m} map (Figure 1). Additionally, the *Gli2* locus was located on the short arm map by A-PAGE of seed proteins.

Segregation of alleles of the dominant marker *XksuE3* differed significantly from the expected 3:1 ratio ($P <$ 0.05) that likely is a sampling effect since no segregation distortion was observed for the flanking markers. A large gap of nearly 40 cM interrupted by a single marker, *Xmwg838*, is distally located on the long arm map. A similar lack of markers was observed in this region on the map of barley *6HL* in the S × M populations, possibly suggesting high recombination in this region.

Two markers, *XksuG30-6A* and *Xmwg813-6A*, which are 7 cM apart in the middle of the *6A*^{m}*L* map, are also closely linked (4.2 cM) in the distal quarter of the map of *4A*^{m}*L* arm (Figure 1). Since neither the intervening markers, *Xpsr154* and *Xabc154*, nor flanking markers in the region are duplicated on *4A*^{m}*L*, we conclude that these are not segmental duplications.

Of 13 markers common between *6A*^{m} and the S × M chromosome *6H*, only *Xmwg820* is at a different position. All other markers are colinear (Figure 2).

Chromosome 7: Forty-eight DNA markers were mapped on chromosome *7* (146 cM) in addition to loci for two isozymes, 6-phosphogluconate dehydrogenase-3 (*Pgd3;* SUN and DVOŘÁK 1991) and esterase-3 (*Est3,* JAASKA 1980) (Figure 1).

Two regions of distorted segregation were observed, a small one, with an excess of DV92 alleles on the short arm, and a large one, encompassing almost the entire map of the long arm, with an excess of G3116 alleles. A segregation distortion locus *SD-1* was mapped proximally on the long arm of chromosome *7* in *Lophopyrum ponticum* (ZHANG and DVOŘÁK 1990). It is not known whether *SD-1* is responsible for the segregation distortion observed here because no common marker exists between the two maps.

Of 16 *7A*^{m} duplicated loci, two tightly linked (5.3 cM) markers on *7A*^{m}*S*, *Xmwg710-7A* and *Xabc152-7A*, and one marker, *XksuE18*, on *7A*^{m}*L* are duplicated on chromosome *1A*^{m} (Figure 1). Markers *Xmwg710-1A* and *Xabc152-1A* are 47.9 cM apart and are separated by 15 loci of which none is duplicated on *7A*^{m}. Marker *XksuE18* is far from *Xmwg710* and *Xabc152* on both *1A*^{m} and *7A*^{m} maps (Figure 1). These observations provide no evidence for existence of a segmental duplication between chromosomes *1* and *7*, as suggested by VAN DEYNZE *et al.* (1995).

Twelve of 16 chromosome *7A*^{m} and S × M chromosome *7H* common markers are colinear. Differences were found in the positions of *XVAtp-B1, Xcdo673, Xwg380,* and *Xabc310.* The order centromere-*XVAtp-B1-Xcdo673* observed in *T. monococcum* is centromere-*Xcdo673-XVAtp-B1* in barley (KLEINHOFS 1994) (Figure 1). The *T. monococcum* order has a high confidence (Table 3), but the barley order had only a slightly better LOD score than the alternate order (Table 3). Additional evidence is needed to substantiate the order reported for barley before accepting this difference as a paracentric inversion. The difference in the position of *Xwg380* was most likely caused by locus duplication because three different *Xwg380* loci were mapped on the long arm of chromosome *7D* in *T. tauschii* (GILL *et al.* 1992). A locus detected by clone ABC310 in the centromeric region of the *7A*^{m} map was mapped in the middle of the *5HL* map in addition to the middle of the *7HL* map (KLEINHOFS *et al.* 1993). Since other markers on the long arm are colinear between *7A*^{m} and *7H*, this difference is almost certainly caused by locus duplication.

Two differences exist between chromosomes *7A*^{m} and *7D* (GALE *et al.* 1995). Probe PSR648 detects a locus on the short arm of chromosome *7A*^{m} but on the long arm of chromosome *7D*. Locus *Xpsr946.2* is present on both maps, but *Xpsr946.1* is located only on *7D* and *Xpsr946.3* only on *7A*^{m}. These differences are almost certainly caused by locus duplication.

Comparison of map lengths: The genetic lengths of the maps of the *T. monococcum* chromosomes were compared with the lengths of the maps of *T. aestivum* chromosomes *1A, 2A, 5A, 6A,* and *7A*. Chromosomes *3A*^{m} and *4A*^{m} were compared with chromosomes *3D* and *4D* because of insufficient numbers of markers in common with *3A* and *4A* (GALE *et al.* 1995). The total distance between the most distal common markers in all chromosomes was 714.2 cM in *T. monococcum* and 721.6 cM in *T. aestivum.* The average ratio of the genetic map lengths in hexaploid wheat relative to those in *T. monococcum* was 0.98 ± 0.07, suggesting a similar distribution of recombination among the chromosomes in the two species. Moreover, only eight out of 52 common intervals showed significant differences ($P < 0.05$) in genetic lengths.

The S × M barley genetic map is longer than the *T. monococcum* map. The genetic length of the S × M barley map, using the most distal markers common with the *T. monococcum* map (excluding the *4L/5L* translocated segments), is by 21% longer than the genetic length of the *T. monococcum* map between the same markers (1072 *vs.* 883 cM). The genetic map of each barley chromosome is longer than that of the homoeologous *T. monococcum* chromosome.

The difference between the S × M map and *T. monococcum* map reflects to a large extent a greater proportion of recombined chromosomes with single markers of one parent flanked on both sides by markers from the other parent (called "singletons" by SALL and NILSSON 1994) in the S × M data set than in the DV92 × G3116 *T. monococcum* data set. There were 103 singletons in the S × M data set (KLEINHOFS 1994) but only 31 in the *T. monococcum* data set. Singletons originate by two-strand double crossovers. Gene conversions and

TABLE 4

Comparisons of recombination frequencies in the proximal and distal regions of the DV92 × G3116 *T. monococcum* and S × M barley genetic maps

			Ratios between *T. monococcum*/S × M	
Chromosome	Region	Interval	Absolute distances	Standardized distances
1	Cent.	*Xabg500–Xabc160*	0.4	0.5
1	Term. S	*XGli1–Xmwg920*	2.0	2.2
1	Term. L	*Xabc261–XAga7*	1.8	2.0
2	Cent.	*Xabg459–Xabc451*	0.5	0.6
2	Term. S	*Xmwg682–XChs1.1*	0.6	0.7
2	Term. L	*Xbcd410–Xbg123*	3.5	4.0
3	Cent.	*Xabg460–Xwsu4(Dor4)*	0.2	0.3
3	Term. S	*Xmwg691–Xabc171*	0.8	1.1
3	Term. L	*Xmwg41–Xabc166*	3.1	4.3
4	Cent.	*XDhn6–Xwg464*	0.3	0.4
4	Term. S	*Xwg622–Xcdo669*	1.9	2.4
5	Cent.	*Xwsu5(Dor5)–Xcdo57*	0.3	0.4
5	Term. S	*XcsSR3(Gsp)–Xmwg920*	1.3	1.6
5	Term. L	—	—	—
6	Cent.	*Xabg458–XNar7*	0.5	0.6
6	Term. S	*Xabg466–Xpsr8(Cxp3)*	1.2	1.4
6	Term. L	*Xpsr154–Xmwg798*	1.2	1.4
7	Cent.	*Xabc455–XAmy-2*	0.4	0.5
7	Term. S	*Xabg704–Xwg834*	1.7	2.0
7	Term. L	*Xabg461–Xwg420*	0.6	0.8
Total	Cent.		0.40 ± 0.04**	0.50 ± 0.04**
	Term.		1.64 ± 0.26**	2.00 ± 0.33**

Cent., markers in the centromeric region; Ter. S, the most distal markers in the short arm; Ter. L, the most distal markers in the long arm. ** Indicates ratios statistically different from the ratio of 1.0 at the 0.01 probability level and standard errors of the means.

errors, however, produce similar results. Since each singleton adds ~1.5 cM to the S × M and *T. monococcum* maps, the differences in the total lengths between these two maps can be satisfactorily explained by the greater number of singletons in the S × M data set than in the DV92 × G3116 data set.

Rates of recombination in the centromeric and distal regions in the *T. monococcum* and barley genomes: The average ratio of the lengths of intervals delineated by markers on each side of the centromere on the *T. monococcum* maps to those delineated by the same markers on the S × M maps was 0.40 ± 0.04, which is significantly lower than the ratio of 1.0 ($P < 0.01$) that is expected if the intervals were of the same lengths (Table 4, Figure 2). A similar result (0.50 ± 0.04, Table 4) was obtained when chromosome maps were standardized to compensate for the difference in the absolute lengths of the *T. monococcum* and S × M barley maps (Table 4, Figure 2). The centromeric regions of the *T. monococcum* chromosomes appear to have lower crossover frequencies than the same regions in the S × M barley chromosomes. The opposite was found in the most distal regions, which show higher recombination in the *T. monococcum* chromosomes than in the S × M barley chromosomes (Table 4, Figure 2).

A second Steptoe × Morex-doubled haploid population (designated hereafter $S^2 \times M^2$) was recently produced by another culture (Devoux *et al.* 1995). The S × M population involved only female meioses, whereas the $S^2 \times M^2$ population involved only male meioses. The $S^2 \times M^2$ population showed 40% more ($P < 0.01$) recombination between the more distal markers than the S × M population (Devoux *et al.* 1995). Centromeric regions were not compared in that study. The expansion of the distal regions on the maps based on the male meioses relative to the maps based on the female meioses was also reported for Brassica (Lagercrantz and Lydiate 1995). The observed differences in the patterns of recombination between *T. monococcum* (male plus female meioses) and S × M barley (only female meioses) could, hence, be partially explained by sex-related differences in recombination. Additional differences may be superimposed on the sex-related differences in recombination since the centromeric regions of the *T. monococcum* maps showed reduced recombination when compared with common intervals on the IGRI × FRANKA barley map (Graner *et al.* 1993) that is based only on male meioses. Centromeric ratios between absolute distances in the seven centromeric regions of these maps were significantly different from 1 (*T. monococcum*/I × F = 0.67 ± 0.10, $P < 0.01$).

Structural differences between the *T. monococcum* and barley genomes: The chromosomes of *T. monococ-*

cum and those of barley show very few structural differences. The genomes of the two species differ by a *4L/5L* reciprocal translocation and paracentric inversions in *1L* and *4L* (*$5A^mL$* in *T. monococcum*) arms. Four additional inversion differences involving two loci each were observed, but because of insufficient numbers of common markers mapped in those regions or insufficient numbers of crossovers between those markers, it is not clear whether they are real. The *4L/5L* reciprocal translocation by which the genome of *T. monococcum* and the *A* genome of *T. aestivum* (Devos *et al.* 1995) differ from that of barley and the *B* and *D* genomes of *T. aestivum* may constitute structural variation that arose during the radiation of the genus Triticum (Devos *et al.* 1995). The marker order in the inverted regions is the same in the genome of *T. monococcum* and in the *B* and *D* genomes of *T. aestivum.* Because of basal divergence of the *A, B,* and *D* genome lineages during the Triticum phylogeny (Dvořák and Zhang 1992), the inversions originated either during the evolution of barley or in the evolutionary lineage leading to Triticum before the radiation of Triticum species. Inversions, such as those in *1L* and *4L,* can be used as evolutionary landmarks to study the phylogeny of taxa in the tribe Triticeae.

Although over 100 common markers were employed in the present study, it is likely that additional small inversions that differentiate the genome of *T. monococcum* from that of barley would be found if more common markers were employed. It was shown here that a minimum of 31.4% of loci are duplicated in the *T. monococcum* genome and 30% in the barley genome. Because of this extensive locus redundancy in the genomes of the tribe Triticeae and a high frequency of single noncolinear loci encountered in otherwise colinear chromosomes, a break in the colinearity due to an inversion can be easily concluded to be just another case of gene duplication if insufficient numbers of common markers are employed in comparative mapping. The inversion that differentiates chromosome arm *1L* in Triticum from *1L* in barley was not detected in the construction of consensus map of chromosome *1* in the tribe Triticeae (Van Deynze *et al.* 1995). The map was constructed by interpolation of different maps with limited number of common markers between any two maps. The failure to detect the inversion illustrates the fact that duplicated loci, particularly those within chromosomes, may obscure structural differences between linkage groups under those circumstances and that interpolations of maps with limited numbers of common markers do not ultimately substitute for mapping with common markers in the construction of high-density maps.

Triticum and Hordeum represent two basic lineages in the radiation of the tribe Triticeae. Although the age of Triticeae is not known, the fact that species of Triticeae are native to all continents testifies to an antiquity of the tribe. In that context, the finding of only a few structural differences between the genus Triticum and Hordeum is remarkable and raises a question as to the causes of this high conservation of gene order. One possibility is that maintenance of large-scale colinearity reflects functionality of a specific arrangement of loci on chromosomes.

Positional changes of 5S rRNA loci in genomes: It has been shown that the major *Nor* loci, which encode 18S-5.8S-26S rRNA, change position within the Triticeae genomes without perturbation of the colinearity of linkage groups (Dubcovsky and Dvořák 1995; see Figure 2). Evidence obtained here shows the existence of the same phenomenon for loci encoding 5S rRNA (Figure 2).

In *T. monococcum,* the 5S rRNA loci (*5SDna-1A* and *5SDna-5A*) were mapped on the short arms of chromosomes *$1A^m$* and *$5A^m$*. No 5S rRNA loci were detected on barley chromosome arms *1HS* and *5HS* either by RFLP mapping (Kleinhofs 1994) or by *in situ* hybridization (Leitch and Hesslop-Harrison 1993). Instead, loci encoding 5S rRNA (*5SrDNA-A* and *5SrDNA-B*) were mapped on the long arms of chromosomes *2H* and *3H,* respectively (Kanzin *et al.* 1993; Kleinhofs 1994). However, no major 5S rRNA loci were found by RFLP mapping on chromosomes *$2A^m$* and *$3A^m$*, or other homoeologues of groups *2* and *3* in Triticum by synteny mapping (Dvořák *et al.* 1989) or by *in situ* DNA hybridization (Mukai *et al.* 1990).

The order of six common markers on the short arms of chromosomes *$1A^m$* and *1H* is colinear, as is the order of six common markers, with the exception of *Xabg497,* on the short arms of *$5A^m$* and *5H* (Figure 2). Likewise, the order of eight common markers on the *T. monococcum* and barley chromosome arms *2L* is colinear and the order of nine common markers on the *T. monococcum* and barley chromosome arms *3L* is colinear (Figure 2). Locus *Xbcd98,* which is completely linked to *X5SDna-1A* on the short arm of the *$1A^m$* and *$1A^m$/1A* maps (Dubcovsky *et al.* 1995a), was also mapped on barley arm *1HS.* The locus is not duplicated in the vicinity of the barley 5S rRNA loci on the *2H* or *3H* maps (Kanazin *et al.* 1993). Locus *Xabg377,* which is tightly linked to the *5SrDNA-B* locus on *3H,* is not duplicated on *$1A^m$* or *$5A^m$* (Figure 1). Barley loci linked to *5SrDNA-A* and *5SrDNA-B, Xcdo588, Xmwg503, XksuD22,* on *2H,* and *Xwsu4(Dor4), Xmwg571,* on *3H,* have been mapped on *T. monococcum* chromosomes *$2A^m$* and *$3A^m$* and were not duplicated in the vicinity of *5SDna-1A* and *5SDna-5A* (Figure 1). These results show that the major 5S rRNA multigene loci, like the *Nor* loci (Dubcovsky and Dvořák 1995), change position in the genome without perturbation of the colinearity of chromosomes during evolution.

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