Title
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Permalink
https://escholarship.org/uc/item/2sq2v9qr

Journal
Genetics, 168(2)

ISSN
0016-6731

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Publication Date
2004-10-01

DOI
10.1534/genetics.104.034850

Peer reviewed

A Chromosome Bin Map of 2148 Expressed Sequence Tag Loci of Wheat Homoeologous Group 7

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ABSTRACT

The objectives of this study were to develop a high-density chromosome bin map of homoeologous group 7 in hexaploid wheat (*Triticum aestivum* L.), to identify gene distribution in these chromosomes, and to perform comparative studies of wheat with rice and barley. We mapped 2148 loci from 919 EST clones onto group 7 chromosomes of wheat. In the majority of cases the numbers of loci were significantly lower in the centromeric regions and tended to increase in the distal regions. The level of duplicated loci in this group was 24% with most of these loci being localized toward the distal regions. One hundred nineteen EST probes that hybridized to three fragments and mapped to the three group 7 chromosomes were designated landmark probes and were used to construct a consensus homoeologous group 7 map. An additional 49 probes that mapped to 7AS, 7DS, and the ancestral translocated segment involving 7BS also were designated landmarks. Landmark probe orders and comparative maps of wheat, rice, and barley were produced on the basis of corresponding rice BAC/PAC and genetic markers that mapped on chromosomes 6 and 8 of rice. Identification of landmark ESTs and development of consensus maps may provide a framework of conserved coding regions predating the evolution of wheat genomes.

COMMON wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD) has a genome of ~16 million kilobases per haploid cell, which is 35 times larger than that of rice (*Oryza sativa* L.) and ~110 times that of Arabidopsis (Bennett and Smith 1976). It is composed of three genomes, contributed by *T. uratu* Tum. ex Gand. (A genome), *Aegilops speltoides* Tausch or an extinct close relative (B genome), and *Ae. tauschii* Coss. (D genome; McFadden and Sears 1946; Kihara 1954; Nishikawa 1983; Dvořák and Zhang 1990). The order of loci in these three genomes is thought to be colinear except for a 4A–5A–7B translocation, a putative 2B–6B translocation, and two inversions on chromosome 4A (Devos *et al.* 1995; Mickelson-Young *et al.* 1995).

A complete series of aneuploid wheat lines missing

an entire chromosome or an arm of a chromosome has been developed (SEARS 1954). More recently, a system of generating an unlimited number of deletion lines has become available; a chromosome with gametocidal properties from *Ae. cylindrica* host was used to generate frequent chromosome breaks in the wheat background (ENDO 1988). The deletions were isolated in a wheat background as the breaks were caused only in the gametes lacking the alien chromosome. Most of the deletions were from a single break followed by the loss of the chromosome region distal to the breakpoint (ENDO 1990). The systematic production of common wheat stocks containing terminal chromosomal deletions of various lengths has been reported and 430 deletion lines involving all 21 wheat chromosomes have been isolated (ENDO and GILL 1996). From this collection, deletion lines were selected for the present study that provided extensive coverage of the wheat genome, subdividing it into 159 chromosome bins (QI *et al.* 2003).

Physical maps of RFLPs produced using deletion stocks have been reported for the chromosomes of all seven homoeologous groups of hexaploid wheat (GILL *et al.* 1993; KOTA *et al.* 1993; HOHMANN *et al.* 1994, 1995; DELANEY *et al.* 1995a,b; MICKELSON-YOUNG *et al.* 1995; GILL *et al.* 1996a,b). Arm-specific physical maps and identification of gene-rich areas and genes controlling phenotypic traits have also been reported (ENDO and MUKAI 1988; ENDO *et al.* 1991; ENDO and GILL 1996; FARIS *et al.* 2000; SANDHU *et al.* 2001; WENG and LAZAR 2002). The physical maps of homoeologous group 6 and group 7 chromosomes and a comparative map of chromosomes 7 of wheat and barley (*Hordeum vulgare* L.) have been reported (WERNER *et al.* 1992; HOHMANN *et al.* 1995; WENG *et al.* 2000). Landmark loci, which represent cDNA clones and single- or low-copy genomic DNAs that correspond to highly conserved coding regions, are useful tools in locating orthologous loci across the Triticeae genomes. These regions are of significance in understanding genome evolution among the species of Triticeae. Conserved linkages with similar gene content and gene order have been reported among many related species (TANKSLEY *et al.* 1992; AHN and TANKSLEY 1993; SORRELLS *et al.* 2003). The high colinearity of molecular markers between wheat and barley genomes at the genetic-map level has been well documented, which will accelerate integrative mapping among species (DEVOS *et al.* 1995; VAN DEYNZE *et al.* 1995; DUBCOVSKY *et al.* 1996). Analyzing the degree of linkage conservation and synteny of chromosome segments between the homoeologous group 7 chromosomes of wheat and barley, HOHMANN *et al.* (1995) identified extensive homologies between these chromosomes.

Expressed sequence tags (ESTs) are partial sequences of cDNA clones that correspond to mRNA and facilitate the identification of many genes (ADAMS *et al.* 1991). These sequences have been used to develop new molecular markers to analyze genome structure and to dis-

cover genes in many organisms, such as human, mouse, rat, *Medicago trunculata*, maize (*Zea mays* L.), and rice (ADAMS *et al.* 1991, 1995; HILLIER *et al.* 1996; COVITZ *et al.* 1998; EWING *et al.* 1999; MARRA *et al.* 1999; SCHEETZ *et al.* 2001; FERNANDES *et al.* 2002). Previously, 238 genes with orthologous locations among the three genomes of wheat were identified. Thirty-nine (16.5%) of these genes were localized in the chromosomes of group 7 (MCINTOSH *et al.* 2003). Recently, a consortium of scientists (LAZO *et al.* 2004) identified ~117,000 ESTs developed from the sequences of cDNAs of different tissues and developmental stages primarily of hexaploid wheat (http://wheat.pw.usda.gov/project).

ESTs from this collection representing wheat unigenes were physically mapped to individual chromosomes/chromosomal intervals using wheat nullisomic and ditelosomic lines and deletion stocks (SEARS 1966; ENDO and GILL 1996). This study summarizes the mapping of >2000 EST loci to the three homoeologous group 7 chromosomes of wheat, an assessment of conserved loci, and the distribution of mapped EST loci to the chromosome bins defined by the deletion stocks. Patterns of distribution and duplication of loci within and among the group 7 chromosomes of wheat and comparisons with rice and barley genomes were investigated. This is the first report of the mapping of such a large number of ESTs to this homoeologous group, and location of these genes in the rice genome offers the possibility of positioning similar genes across grass genomes.

MATERIALS AND METHODS

Genetic stocks: In this study various cytogenetic stocks of the hexaploid wheat cultivar Chinese Spring (*T. aestivum*) were used. These were 24 nullisomic-tetrasomic (NT), 21 ditelosomic (DT), and 101 deletion lines (del) lines (SEARS 1954, 1966; SEARS and SEARS 1978; ENDO and GILL 1996). A detailed description of these stocks is provided in QI *et al.* (2003). The fraction length (FL) value of each deletion breakpoint identifies the position of the breakpoint from the centromere relative to the length of the complete arm. A bin is defined by two deletion breakpoints and is given a name followed by the arm fraction-length endpoints for which the deletion is diagnostic; *e.g.*, 7AL16-0.86-0.90 designates the region from a breakpoint at 86% of the 7AL arm to one at 90%. These aneuploid and deletion stocks provide a complete coverage of the wheat genome, subdividing it into 159 chromosome bins. All the genetic stocks selected for EST mapping were cytologically and/or molecularly verified by C-banding and Southern hybridization with >500 EST clones (QI *et al.* 2003).

EST singletons: The clones used in this study were developed from cDNA libraries of different tissues and developmental stages of wheat and other related species in the Triticeae tribe (LAZO *et al.* 2004; ZHANG *et al.* 2004). The cDNA clones were sequenced and clones with unique sequences (unigenes) were used in this study as probes for mapping all homoeologous chromosomes. The distribution of the mapped loci along the chromosomes of wheat genomes approximates mapped-EST distribution in wheat.

At the U.S. Department of Agriculture (USDA)-Agricultural

Research Service (ARS) Western Regional Research Center (Albany, CA), ~117,000 ESTs were produced from 43 cDNA libraries (primarily of wheat) representing a wide range of tissues, developmental stages, and environmental stresses (LAZO *et al.* 2004). Amplified PCR products for unigenes (inserts) were prepared and sent to 10 mapping laboratories (http://wheat.pw.usda.gov/NSF) for Southern hybridization.

Southern hybridization: Procedures used for genomic DNA isolation, restriction endonuclease digestion, gel electrophoresis, and DNA gel blot hybridization were as described in QI *et al.* (2003) and are available on-line at http://wheat.pw.usda. gov/NSF/project/mapping_data.html. For Southern analysis, genomic DNA was digested with *Eco*RI. Lambda DNA digested with *Hin*dIII and *Bst*EII was used as a size marker. Images of all autoradiographs are available on line at http://wheat.pw. usda.gov/cgi-bin/westsql/map_locus.cgi.

Localization of ESTs: EST loci were assigned to a specific chromosome, arm, and/or deletion bins on the basis of the presence or absence of the restriction fragments in a given set of DNA lanes of a Southern blot (SEARS 1954, 1966; ENDO and GILL 1996). Details of the mapping procedure can be found at http://wheat.pw.usda.gov/NSF/project/mapping.

Map construction: The group at North Dakota State University was responsible for analyzing the mapping data for homoeologous group 7 chromosomes (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi). On the basis of the physical size (in micrometers) of chromosomes and chromosome arms and on the relative length of chromosome intervals (bins), the expected number of EST loci for each was calculated (GILL *et al.* 1991; ENDO and GILL 1996). The χ^2-test was used to test for randomness of the distribution patterns of EST loci among the chromosomes, chromosome arms, and deletion bins of group 7 of wheat.

The EST probes that hybridized to only three RFLP fragments and mapped across the three genomes were identified. The homoeologous map positions of the loci produced by these probes and those associated with the ancestral translocation involving 7BS were identified on the basis of the overlapping FL values in the bins and were used in the construction of a consensus physical map of group 7.

Those ESTs that hybridized to more than three fragments, many of which mapped onto homoeologous group 7 chromosomes, identified duplicated loci. On the basis of the pattern of duplicated loci, different classes of duplicated regions were evident. Whenever duplicated fragments of a particular EST mapped in the same deletion bin it was considered as an intrabin duplication. Interchromosomal duplication was defined as those events where duplicated loci of a particular EST mapped to chromosome deletion bins other than those in group 7. The consensus duplication was defined for those ESTs whose loci mapped to consensus positions across the chromosomes of homoeologous group 7 as well as to consensus positions across the chromosomes of another homoeologous group. The intra- and interarm duplications were defined for those ESTs whose loci were duplicated into the same or another arm of chromosomes of homoeologous group 7.

EST density: The proportion of the chromosome for each deletion bin was calculated on the basis of GILL *et al.* (1991). The physical length, arm ratio data of a chromosome, and proportion of arm missing in chromosome bins were used in calculating the megabase values in deletion breakpoint-defined chromosome bins.

Chi-square statistics to test the homogeneity of EST content distribution along chromosome arms were used. The observed frequencies of ESTs in chromosome bins were tested against the null hypothesis of uniform EST distribution along the chromosome arms. Under the null hypothesis, the expected number of ESTs is proportional to the length of the bin. The distribution of EST loci along the physical length of each missing segment was analyzed by estimating the ratio of the percentage of mapped loci to the relative percentage of missing arm in the deletion breakpoint-defined regions (WENG and LAZAR 2002).

Ordering ESTs into chromosome bins and comparison of map positions: Deletion mapping provides a fast and efficient method of locating many loci within a chromosome bin; however, the order of loci within a bin cannot be determined. A putative order of ESTs can be inferred using *in silico* comparison to the rice genome sequence as reported by SORRELLS *et al.* (2003). Each mapped EST locus is a unique *Eco*RI restriction digest signature of known molecular weight, marking a specific expressed segment of an individual chromosome of wheat. We considered only ordering of the ESTs placed on the consensus map. Corresponding rice BAC/PACs were identified by searching the ESTs at http://www.gramene.org/perl/SeqTable and genetically mapped molecular markers corresponding to BAC/PACs were identified. On the basis of centimorgan distances of these markers in different rice chromosomes, the relative order of ESTs in the different chromosome bins was determined, and the map positions were compared. Considering the homoeologous relationship between chromosomes of group 7 of wheat and barley, map positions of barley chromosome 7 markers were compared to those of wheat group 7 markers (KLEINHOFS *et al.* 1993; HOHMANN *et al.* 1995). Corresponding rice BAC/PACs with markers were identified by searching the sequences of RFLP markers of chromosome 7 of barley at http://www.gramene.org/perl/SeqTable (KÜNZEL *et al.* 2000). Identified BAC/PACs were compared with the BAC/PACs and ESTs previously identified in the wheat consensus map.

RESULTS

Chromosome bin maps of 7A, 7B, and 7D: Nine hundred nineteen EST probes were mapped in homoeologous group 7 chromosomes of wheat, identifying 2148 loci. Among the ESTs, 528 mapped on 7A and identified 661 loci, 549 mapped on 7B and identified 719 loci, and 613 mapped on 7D and identified 768 loci. The distributions of ESTs without duplication and showing no ambiguous loci in 7A, 7B, and 7D are presented in Figure 1, A, B, and C, respectively. The χ^2 analysis indicated a significantly higher number of EST loci mapped into 7D even though it had the smallest physical size.

A total of 267 probes mapped to all three chromosomes of homoeologous group 7. Of these, 119 probes were unique, identifying only three loci. These probes were highly conserved among the genomes and could be considered as landmark probes. A consensus physical map of group 7 was developed with 117 (consensus position could not be resolved for two ESTs) of these probes, providing a framework map for chromosome 7 (Figure 2, A and B). An additional 49 probes could be added to this group if the ancestral translocation event involving 7BS was considered. These markers mapped to 7AS, 7DS, and the 5AL-4AL segment derived from 7B (Figure 2B).

Distribution of the loci and gene density: All of the 23 deletion breakpoints defined bins among the homo-

A

0.89

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BE426203  BE443129  BE443535  BF201979  BG313287  BG313770  BE495610  BE495610  BG607226  BF201146
BG604574  BE498320  BG262923  BF483968  BF484617  BF292439  BE590484  BE590763  BG274955  BG604834
BG604918  BF291727  BF200736  BE443549  BE494382  BE604043  BE604523  BM262681  BM138035  BE444421
BG262302  BG274908  BF490293  BE490728  BE489999  BF202488  BE606897  BE637490  BG274687  BM138536
BM134414  BE443381  BE442774  BF429350  BF202702  BE443120  BE497624  BE606678  BE490186  BE498428
BE443559  BE422466  BE490790  BE406897  BE586111  BE586077  BE585722  BE444470  BE444470  BE444421
BE443794  BE442648  BG398585  BF201333  BF201333  BE403972  BE403972  BE403972  BE403972  BE444280
BE498733  BE425147  BE422760  BE496124
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0.59

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BE500711  BF484705  BE403518  BE403518  BE426715  BE585543  BE404724  BE443401  BE490643  BE606973
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BE495393  BE493812  BE494001  BG607187  BE517844  BE494425  BG604855  BG313812  BF292144  BE606357
BE590476  BG274948  BG263193  BF473059  BF473739  BG262694           BF293121  BE406971  BE442812
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0.45

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BE606663  BE495005  BE490406  BE442939  BE498662  BE606193  BF478904  BE605201  BE497999  BE404111
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BE498338
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BE406976  BE442797  BF201628  BF474966  BF475129  BE443554  BM138650  BE493897  BE494078  BF293124
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BE471272
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0.0

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BG275086  BF482781  BF473119
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0.39

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0.71
0.74

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BE591002  BE591725  BF428786
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0.86
0.90

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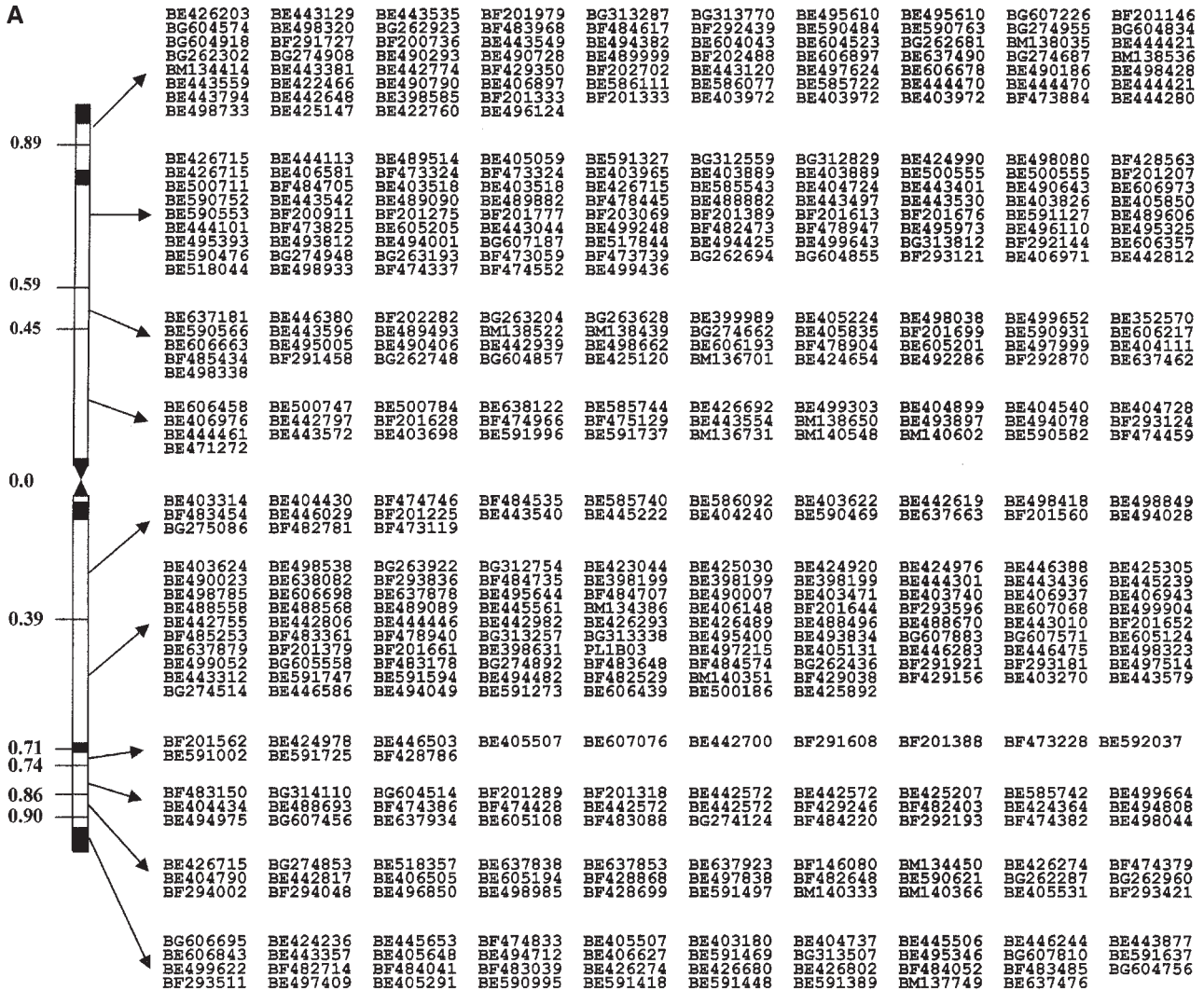
7A

FIGURE 1.—Physical EST maps of chromosomes of group 7 showing distribution of ESTs mapped in different deletion bins. The deletion bins for each chromosome are marked on the left. The intrabin duplicated loci are represented only once per bin. The number of loci per bin is that presented in Table 1 minus the duplications. Information on the exact locus designation and restriction fragment mapped to each bin can be found at http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi. The short arm of each chromosome is oriented toward the top while the long arm is toward the bottom. (A) physical map of chromosome 7A; (B) physical map of chromosome 7B; (C) physical map of chromosome 7D.

eologous group 7 chromosomes contained different numbers of EST loci (Table 1). A trend for increasing numbers of EST loci mapped from proximal to distal regions of all chromosome arms was observed. All of the centromeric bins except C-7BS1-0.27 contained a significantly lower number of EST loci than expected on the basis of the size of the bins (Table 1). Except for the distal bin of chromosome arm 7BS (7BS1-0.27-1.00), all other distal regions contained relatively higher numbers of EST loci. The relative density of ESTs was expressed as the percentage of mapped loci per unit of physical length for each deletion bin and chromosome arm. For example, bin 7AL1-0.39-0.71 distal to bin C-7AL1 is physically 32% of the arm length and 39% of the loci

on the long arm of chromosome 7A (7AL) were mapped to this bin (Table 1). Assuming the physical length of 7AL is 100 units then the ratio of mapped loci per unit arm length is ∼1.22. From Table 1, it is clear that in each arm the density of mapped loci per unit arm length increased from the centromeric region to the distal end, except for the short arm of chromosome 7B. The trend in 7BS can be explained by a double translocation event involving this arm (details presented later). The percentage of mapped loci per unit length among the distal chromosome deletion bins of all chromosome arms varied from 0.71 to 3.75.

The megabase content of DNA and gene densities for all deletion breakpoint-defined regions are summa-
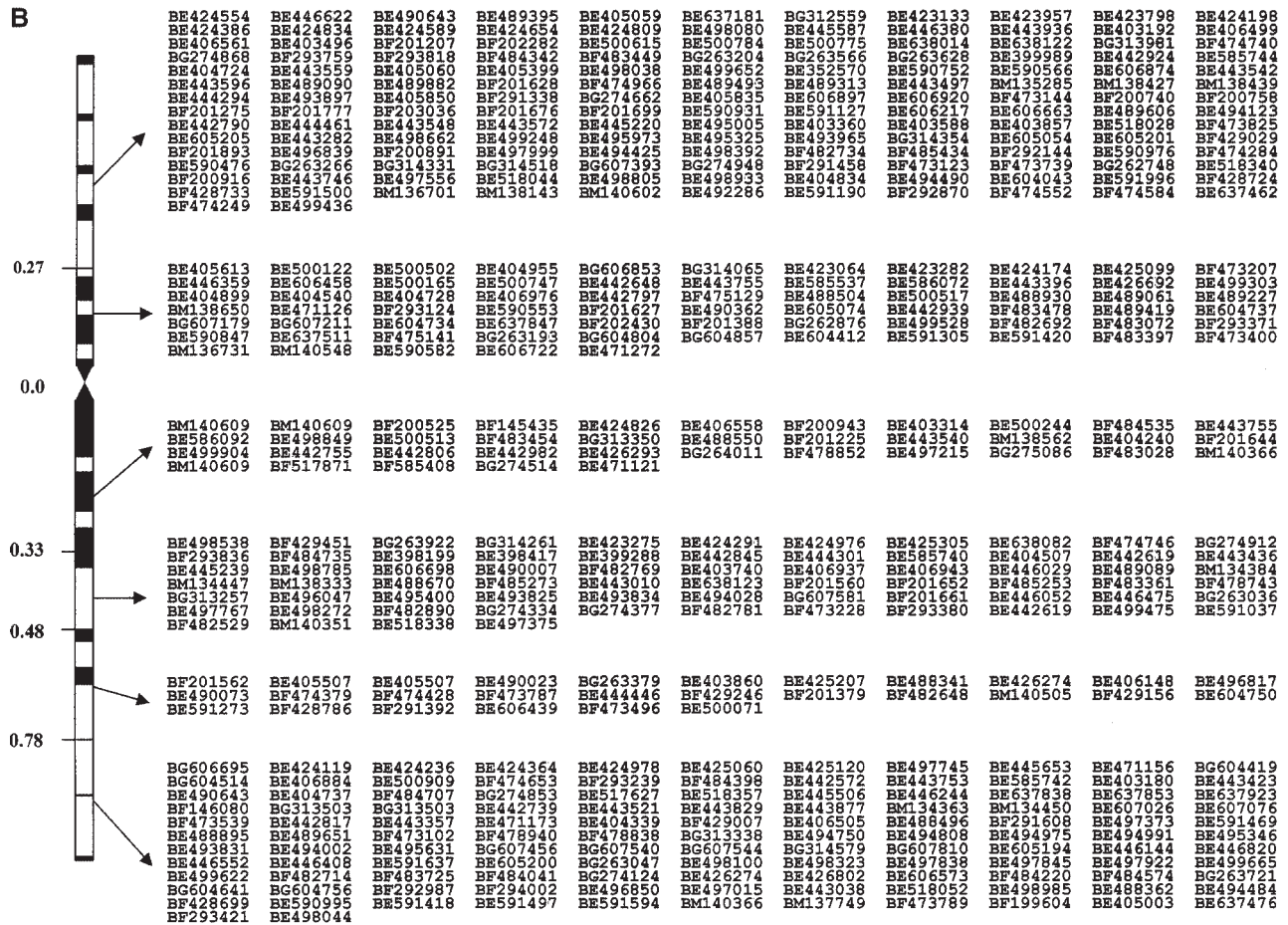
B

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BE406561  BE403496  BF201207  BF202282  BE500615  BE500784  BE500775  BE638014  BE638122  BG313981  BF474740
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BF474249  BE499436
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0.27

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BE405613  BE500122  BE500502  BE404955  BG606853  BG314065  BE423064  BE423282  BE424174  BE425099  BF473207
BE446359  BE606458  BE500165  BE442648  BE442648  BE443755  BE585537  BE586072  BE443396  BE426692  BE499303
BE404899  BE404540  BE404728  BE406976  BE442797  BF475129  BE488504  BE500517  BE488930  BE489061  BE489227
BM138650  BE471126  BF293124  BE590553  BF201627  BE490362  BG262876  BE442939  BE483478  BE489419  BE604737
BG607179  BG607211  BE604734  BE637847  BE202430  BF201388  BE604412  BE499528  BE482692  BF483072  BF293371
BE590847  BE637511  BF475141  BG263193  BG604804  BG604857          BE591305  BE591420  BF483397  BF473400
BM136731  BM140548  BE590582  BE606722  BE471272
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0.0

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BM140609  BM140609  BF200525  BF145435  BE424826  BE406558  BF200943  BE403314  BE500244  BF484535  BE443755
BE586092  BE498849  BE500513  BF483454  BG313350  BE488550  BE201225  BE443540  BM138562  BE404240  BF201644
BE499904  BE442755  BE442806  BE442982  BE426293  BG264011  BF478852  BE497215  BG275086  BF483028  BM140366
BM140609  BF517871  BF585408  BG274514  BE471121
```

0.33

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BE498538  BF429451  BG263922  BG314261  BE423275  BE424291  BE424976  BE425305  BE638082  BF474746  BG274912
BF293836  BF484735  BE398199  BE399288  BE399288  BE442845  BE444301  BE585740  BE404507  BE442619  BE443436
BE445239  BE498785  BE606698  BE490007  BF482769  BE403740  BE406937  BE406943  BE446029  BE489089  BM134384
BM134447  BM138333  BE488670  BF485273  BE443010  BE638123  BG607581  BF201662  BF485253  BF483361  BF478743
BG313257  BE496047  BE495400  BE493825  BE493834  BE494028  BF473228  BF201661  BE446052  BE446475  BG263036
BE497767  BE498272  BF482890  BG274334  BG274377  BF482781          BF293380  BE442619  BE499475  BE591037
BF482529  BM140351  BE518338  BE497375
```

0.48

```
BF201562  BE405507  BE405507  BE490023  BG263379  BE403860  BE425207  BE488341  BE426274  BE406148  BE496817
BE490073  BF474379  BF474428  BF473787  BE444446  BF429246  BF201379  BF482648  BM140505  BF429156  BE604750
BE591273  BF428786  BF291392  BE606439  BF473496  BE500071
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0.78

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BG606695  BE424119  BE424236  BE424364  BE424978  BE425060  BE425120  BE497745  BE445653  BE471156  BG604419
BG604514  BE406884  BE500909  BF474653  BF293239  BF484398  BE442572  BE443753  BE585742  BE403180  BE443423
BE490643  BE404737  BF484707  BG274853  BE517627  BE518357  BE445506  BE446244  BE637838  BE637853  BE637923
BF146080  BG313503  BG313503  BE442739  BE443521  BE443829  BE443877  BM134363  BM134450  BE607026  BE607076
BF473539  BE442817  BE443357  BE471173  BE404339  BF429007  BE406505  BE488496  BF291608  BE497373  BE591469
BE488895  BE489651  BF473102  BF478940  BF478838  BG313338  BE494750  BE494808  BE494975  BE494991  BE495346
BE493831  BE494002  BE495631  BG607456  BG607540  BG607544  BG314579  BG607810  BE605194  BE446144  BE446820
BE446552  BE446408  BE605200  BE605200  BG263047  BE498100  BE498323  BE497838  BE497845  BF497922  BE499665
BE499622  BF482714  BF483725  BF484041  BG274124  BE426274  BE426802  BE606573  BF484220  BF484574  BG263721
BG604641  BG604756  BF292987  BF294002  BE496850  BE497015  BE497845  BE518052  BE498985  BE488362  BE494484
BF428699  BE590995  BE591418  BE591497  BE591594  BM140366  BM137749  BF473789  BF199604  BE405003  BE637476
BF293421  BE498044
```

7B

FIGURE 1.—*Continued.*

rized in Table 1. For example, in the short arm of chromosome 7A, four deletion breakpoint-defined regions were examined, and 274 loci mapped to this arm. Eighty-four loci mapped to bin 7AS1-0.89-1.00, while 108 loci mapped to bin 7AS5-0.59-0.89, and 46 loci mapped to bin 7AS8-0.45-0.59. On average, 72% of all mapped loci in homoeologous group 7 chromosomes were located in the distal regions, and the number of loci mapped in these regions was about seven times higher than that in the centromeric chromosome bins. The highest density of EST loci was observed in bin 7AL16-0.86-0.90 followed by bin 7BL10-0.78-1.00. The megabase contents of these chromosome bins were 16.30 and 119.02, and 45 and 184 loci were mapped in these bins, respectively.

Duplication: Of the 267 probes mapped into the three genomes of homoeologous group 7 chromosomes, 63 (24%) identified duplicated loci either on the chromosomes of other homoeologous groups or on the same arm or different arms of chromosomes of group 7. Seven of these ESTs identified duplicated loci placed on the consensus regions across the three genomes of groups 3, 5, and 6. Eighty-five (31%) ESTs identified duplicated loci in the same deletion bin where they were placed. The distribution of ESTs producing duplicated loci along the length of the consensus chromosome 7 is presented in Figure 3 and the number of ESTs with each type of locus duplication pattern is presented in Table 2.

7BS > 4AL and 5AL > 7BS translocations: Of the 919 ESTs mapped to homoeologous group 7, 44 were mapped on the short arms of chromosomes 7A and 7D, but instead of mapping to the short arm of chromosome 7B they mapped to the long arm of chromosome 4A (Figure 2B). Out of these 44 probes 31 mapped to bin 7AS1-0.89-1.00 and 13 mapped to 7AS5-0.59-0.89. All of these 44 probes mapped to the distal bin of 7DS (7DS4-0.61-1.00). These probes also mapped to the distal 41% of the long arm of chromosome 4A. Twenty-nine mapped into bin 4AL4-0.80-1.00, 13 into bin 4AL5-0.66-0.80, and 2 mapped into bin 4AL13-0.59-0.66.

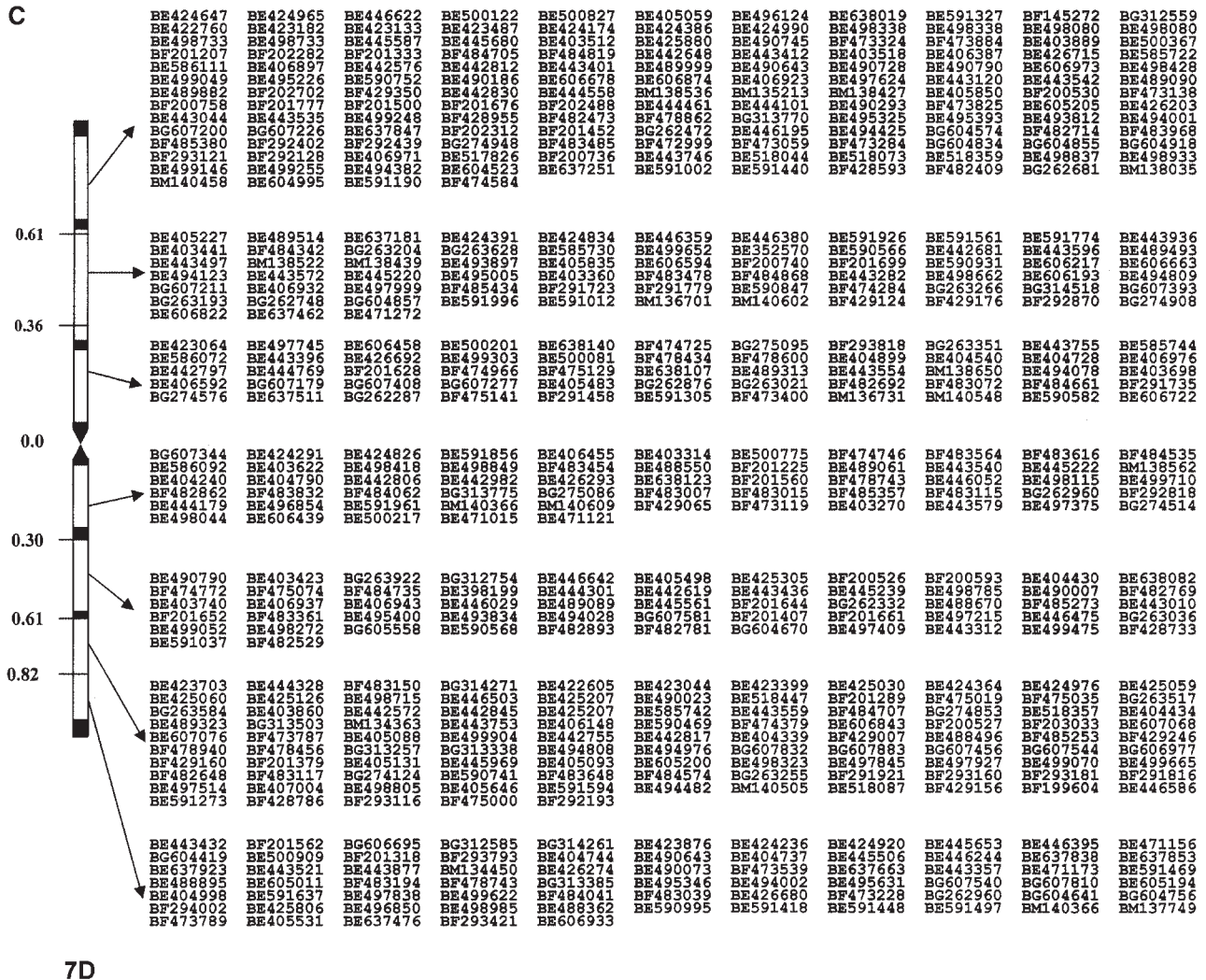Five of the probes mapped to the long arms of chro-

C

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BE424647  BE424965  BE446622  BE500122  BE500827  BE405059  BE496124  BE638019  BE591327  BF145272  BG312559
BE422760  BE423192  BE423133  BE423487  BE424174  BE424386  BE424990  BE498338  BE498338  BE498080  BE498080
BE498733  BE498733  BE445587  BE445680  BE403512  BE425880  BE490745  BF473324  BF473884  BF403889  BE500367
BE201207  BE202282  BF201333  BF484705  BF484819  BE442648  BE443412  BE403518  BE406387  BE426715  BE585722
BE586111  BE406897  BE442576  BE442812  BE443401  BE489999  BE490643  BE490728  BE490790  BE606973  BE498428
BE499049  BE495226  BE590752  BE490186  BE606678  BE606874  BE406923  BE497624  BE443120  BE443542  BE489090
BE489882  BF202702  BF429350  BE442830  BE444558  BM138536  BM135213  BM138427  BE405850  BF200530  BF473138
BF200758  BF201777  BF201500  BF428955  BF482473  BE444461  BE404101  BE490293  BF473825  BE605205  BE462203
BE443044  BE443535  BE499248  BF428955  BF201452  BE478862  BG313770  BE495325  BE495393  BE493812  BE494001
BG607200  BG607226  BE637847  BF202312  BG262472  BG262472  BE446195  BE494425  BG604574  BF482714  BE483968
BF485380  BF292402  BF292439  BG274948  BF483485  BE472999  BF473059  BF473284  BG604834  BG604855  BG604918
BF293121  BF292128  BE406971  BE517826  BF200736  BE443746  BE518044  BE518073  BE518359  BE498837  BE498933
BE499146  BE499255  BE494382  BE604523  BE637251  BE591002  BE591440  BF428593  BF482409  BG262681  BM138035
BM140458  BE604995  BE591190  BF474584
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0.61

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BE405227  BE489514  BE637181  BE424391  BE424834  BE446359  BE446380  BE591926  BE591561  BE591774  BE443936
BE403441  BF484342  BG263204  BG263628  BE585730  BE499652  BE352570  BE590566  BE442681  BE443596  BE489493
BE443497  BM138522  BM138439  BE493897  BE405835  BE606594  BF200740  BF201699  BE590931  BE606217  BE606663
BE494123  BE443572  BE445220  BE495005  BE403360  BF483478  BF484868  BE443282  BE498662  BE606193  BE494809
BG607211  BE406932  BE497999  BF485434  BF291723  BF291779  BE590847  BF474284  BG263266  BG314518  BG607393
BG263193  BG262748  BG604857  BE591996  BE591012  BM136701  BM140602  BF429124  BF429176  BF292870  BG274908
BE606822  BE637462  BE471272
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0.36

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BE423064  BE497745  BE606458  BE500201  BE638140  BF474725  BG275095  BF293818  BG263351  BE443755  BE585744
BE586072  BE443396  BE426692  BE499303  BE500081  BE478660  BE478600  BE404899  BE404540  BE404728  BE406976
BE442797  BE444769  BF201628  BF474966  BF475129  BE638107  BE489313  BE443554  BM138650  BE494078  BE403698
BE406592  BG607179  BG607408  BG607277  BE405483  BG262876  BG263021  BF482692  BF483072  BF484661  BF291735
BG274576  BE637511  BG262287  BF475141  BF291458  BE591305  BF473400  BM136731  BM140548  BE590582  BE606722
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0.0

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BG607344  BE424291  BE424826  BE591856  BE406455  BE403314  BE500775  BF474746  BF483564  BF483616  BF484535
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BE404240  BE404790  BE442806  BE442982  BE426293  BE638123  BF201560  BF478743  BE446052  BE498115  BE499710
BF482862  BF483832  BF484062  BG313775  BG275086  BF483007  BF483015  BF485357  BF483115  BG262960  BF292818
BE444179  BE496854  BE591961  BM140366  BM140609  BF429065  BE473119  BE403270  BE443579  BE497375  BG274514
BE498044  BE606439  BE500217  BE471015  BE471121
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0.30

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BF474772  BF475074  BF484735  BE398199  BE444301  BE442619  BE443436  BE445239  BE498785  BE490007  BF482769
BE403740  BE406937  BE406943  BE446029  BE489089  BE445561  BF201644  BG262332  BE488670  BF485273  BE443010
BF201652  BF483351  BE495400  BE493834  BE494028  BG607581  BF201407  BF201661  BE497215  BE446475  BG263036
BE499052  BE498272  BG605558  BE590568  BF482893  BF482781  BG604670  BE497409  BE443312  BE499475  BF428733
BE591037  BF482529
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0.61

0.82

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BE489323  BG313503  BM134363  BE443753  BE406148  BE590469  BF474379  BE606843  BF200527  BF203033  BE607068
BE607076  BF473787  BE405088  BE499904  BE442755  BE442817  BE404339  BF429007  BE488496  BF485253  BF429246
BF478940  BF478456  BG313257  BE445969  BE494808  BE494976  BG607832  BG607883  BG607456  BG607544  BG606977
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BF482648  BF483117  BG274124  BE590741  BF483648  BF484574  BG263255  BF291921  BF293160  BF293181  BF291816
BE497514  BE407004  BE498805  BE405646  BE591594  BE494482  BM140505  BE518087  BF429156  BF199604  BE446586
BE591273  BF428786  BF293116  BF475000  BF292193
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BG604419  BE500909  BF201318  BF293793  BE404744  BE490643  BE404737  BE445506  BE446244  BE637838  BE637853
BE637923  BE443521  BE443877  BM134450  BE426274  BE490073  BF473539  BE637663  BE443357  BE471173  BE591469
BE488895  BE605011  BF483194  BF478743  BG313385  BE495346  BE494002  BE495631  BG607540  BG607810  BE605194
BE404998  BE591637  BE497838  BE499622  BF484041  BF483039  BE426680  BF473228  BG262960  BG604641  BG604756
BF294002  BE425806  BE496850  BE498985  BE488362  BE590995  BE591418  BE591448  BE591497  BM140366  BM137749
BF473789  BE405531  BE637476  BF293421  BE606933
```

7D

FIGURE 1.—*Continued.*

mosomes 5B and 5D, and instead of mapping to a similar region on chromosome 5A, they mapped to the short arm of chromosome 7B (Figure 2B).

Ordering the EST loci among chromosome bins and comparison of map positions with rice and barley: Of the 117 probes (excluding those involved in the 7BS translocation) placed on the consensus map of homoeologous group 7, the possible order for 38 probes was determined on the basis of the molecular markers mapped to chromosomes 6 and 8 of rice (Figure 4), on the assumption of retained colinearity of loci among these species (SORRELLS *et al.* 2003). In general, the probes mapping to rice chromosome 6 all mapped distal to the centromere in the consensus wheat chromosome, while all those mapping to rice chromosome 8 mapped near the wheat centromere (Table 3, Figure 4). All the ESTs in interval 0.45–0.59 of the short arm corresponded to rice chromosome 6 except BE424174, which mapped to rice chromosome 8 (Table 3, Figure 4).

Eleven molecular markers mapped on chromosome 7 of barley identified corresponding EST probes mapped to consensus chromosome 7 of wheat, eight of which maintained the same relative order in both genomes. Three EST probes (BE500615, BE446380, and BE424174) mapped in reverse order into the 0.45–0.59 region on the short arm of wheat chromosome 7 (Figure 4).

DISCUSSION

Chromosome bin maps of 7A, 7B, and 7D: A total of 661, 719, and 768 loci were mapped to wheat chromosomes 7A, 7B, and 7D, respectively. On the basis of the relative sizes of these homoeologous chromosomes (7B > 7A > 7D), significantly higher numbers of EST loci were mapped to 7D followed by 7B and 7A (Figure 1, A, B, and C, respectively), which was in agreement with the findings of QI *et al.* (2003). The reduced number of loci on 7B might be explained by the reciprocal translocation, where unequal size fragments were exchanged between 4AL, 7BS, and 5AL. There are 44 7BS-specific ESTs on 4AL and 5 5AL-specific ESTs translocated to 7BS. Due to this uneven exchange, 7BS had
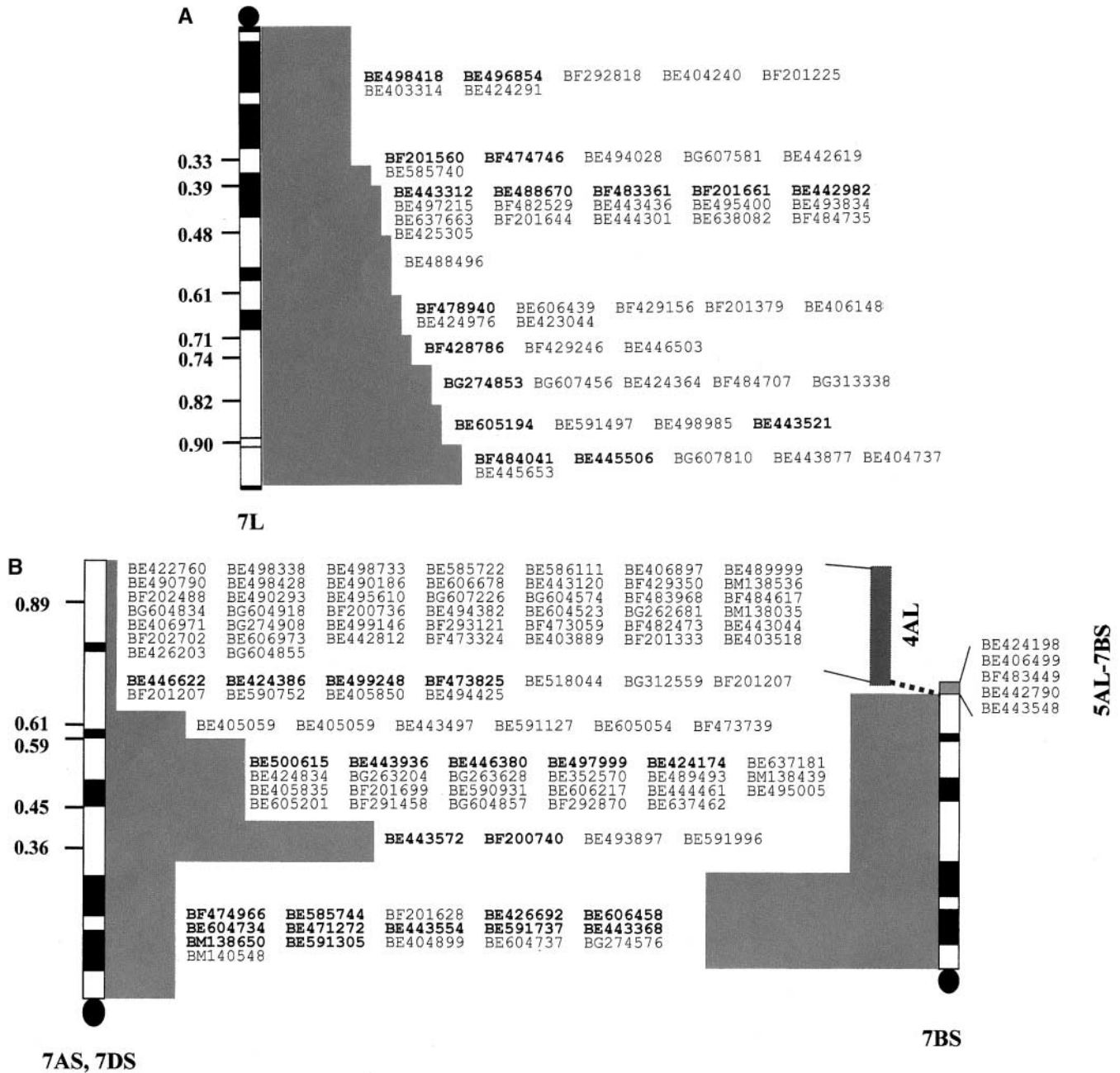
FIGURE 2.—Consensus map of homoeologous group 7 of wheat including the ancient translocation involving 7BS, 4AL, and 5AL. (A) consensus map of the long arm of group 7; (B) consensus map of 7AS and 7DS (on the left) with landmark probes shared with 7BS (0.00–0.59 interval). Forty-four EST detected loci mapped to 7AS and 7DS (0.59–1.00 interval) and translocated from 7BS to 4AL. A smaller segment of 5 EST detected loci representing an unequal translocation from 5AL to 7BS. Probes in boldface type were ordered on the basis of the corresponding markers mapped on the linkage maps of chromosomes 6 and 8 of rice.

the lowest number of EST loci as compared to other short arms of homoeologous group 7 chromosomes (Table 1).

Distribution of loci and gene density: Physical RFLP maps produced using deletion stocks have been reported for each of the seven homoeologous chromosome groups and for some chromosome arms (WERNER et al. 1992; KOTA et al. 1993; HOHMANN et al. 1994, 1995; DELANEY et al. 1995b; MICKELSON-YOUNG et al. 1995; ENDO and GILL 1996; GILL et al. 1996a,b; FARIS et al.

2000; SANDHU et al. 2001; WENG and LAZAR 2002). In most cases the numbers of markers analyzed were relatively low, and a majority of the markers were of unknown function or were genomic probes. The highest number of clones used in mapping the three homoeologous chromosome 7's was 111, and only 21 of these were cDNA probes (HOHMANN et al. 1995).

A higher marker density was generally observed in the distal regions as compared to the proximal regions of chromosome arms. AKHUNOV et al. (2003a) analyzed

TABLE 1

Chromosome bins with relative physical length, number of loci per bin, and ratio of mapped loci per unit arm length of group 7 of wheat

Chromosome arm and DNA content (Mb)[a]	Chromosome bin	% arm	Mb DNA	No. of loci[b]	χ^2 [c]	% loci	Loci/unit arm length
7AS = 407.53, χ^2 = 0.226	C-7AS8-0.45	45	183.40	36	61.81***	13	0.28
	7AS8-0.45-0.59	14	57.08	46	1.52	17	1.21
	7AS5-0.59-0.89	30	122.26	108	8.09**	39	1.30
	7AS1-0.89-1.00	11	44.83	84	96.24***	31	2.82
7AL = 407.53, χ^2 = 0.226	C-7AL1	39	158.94	31	59.95***	11	0.28
	7AL1-0.39-0.71	32	130.42	113	4.24*	39	1.22
	7AL17-0.71-0.74	3	12.33	16	6.05*	5	1.66
	7AL21-0.74-0.86	12	48.91	34	0.024	12	1.00
	7AL16-0.86-0.90	4	16.30	45	95.03***	15	3.75
	7AL18-0.90-1.00	10	40.75	52	18.02***	18	1.80
7BS = 360.65, χ^2 = 0.57	C-7BS1-0.27	27	97.38	84	2.26	32	1.18
	7BS1-0.27-1.00	73	263.28	180	0.83	68	0.93
7BL = 540.98, χ^2 = 0.38	C-7BL2-0.33	33	180.01	49	42.38***	14	0.39
	7BL2-0.33-0.63	30	162.29	92	2.79	25	0.83
	7BL7-0.63-0.78	15	81.15	40	3.97*	11	0.73
	7BL10-0.78-1.00	22	119.02	184	133.92***	50	2.37
7DS = 346.90, χ^2 = 0.620	C-7DS5-0.36	36	124.89	68	18.40***	21	0.61
	7DS5-0.36-0.61	25	86.73	75	0.21	24	0.96
	7DS4-0.61-1.00	39	135.29	173	20.09***	55	1.41
7DL = 381.59, χ^2 = 0.51	C-7DL5-0.30	30	114.48	72	13.18***	20	0.66
	7DL5-0.30-0.61	31	118.30	80	10.02***	21	0.71
	7DL2-0.61-0.82	21	80.14	120	23.91***	33	1.57
	7DL3-0.82-1.00	18	68.69	95	12.67***	26	1.44

[a] Relative distributions of loci mapped per chromosome were 7A = 815.06, χ^2 = 5.49, *P = 0.05; 7B = 901.63, χ^2 = 6.41, **P = 0.01; and 7D = 728.49, χ^2 = 22.33, ***P = 0.005.

[b] The loci presented here are those that were unambiguously assigned to each bin and not to the entire region, chromosome arm, or chromosome.

[c] Significance levels were *P = 0.05, **P = 0.01, and ***P = 0.005.

the distribution of EST loci in all chromosomes of the wheat genome using a subset of this project's mapped EST database and determined that in each arm the density of mapped loci increases from the centromeric region to the distal end. The distribution of mapped loci in our study along the arms of group 7 chromosomes supports that pattern.
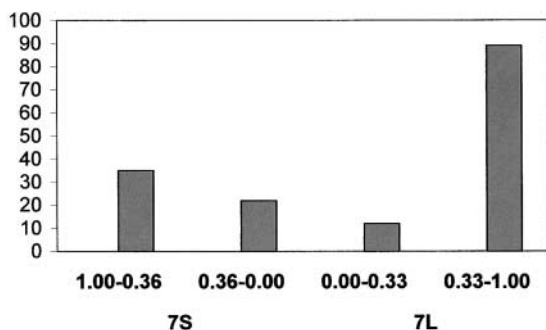
FIGURE 3.—Pattern of distribution of EST loci duplicated along the length of the arms of consensus chromosome 7. The vertical axis is the number of loci. The horizontal axis divides the short and long arms into approximately a proximal one-third and distal two-thirds portions.

The highest density of EST loci, as revealed by χ^2 and ratio of percentage of mapped loci per unit arm length, was observed in bin 7AL16-0.86-0.90, which agrees with HOHMANN *et al.* (1995). The second-highest density of EST loci was observed in 7BL10-0.78-1.00. The estimated megabase content of bin 7AL16-0.86-0.90 is 16.30 and 45 loci were mapped in this bin; therefore, on average, 1 EST locus was mapped for every 362 kb in this region.

The difference in distribution of recombination along the chromosome length means that the amount of DNA per centimorgan varies depending on the location of the gene on a chromosome. A higher density of EST

TABLE 2

Number of ESTs in different duplication patterns

Duplication pattern	No. of ESTs
Intrabin	85
Interchromosomal	47
Unique (consensus) duplication	7
Intra-arm	5
Interarm	4
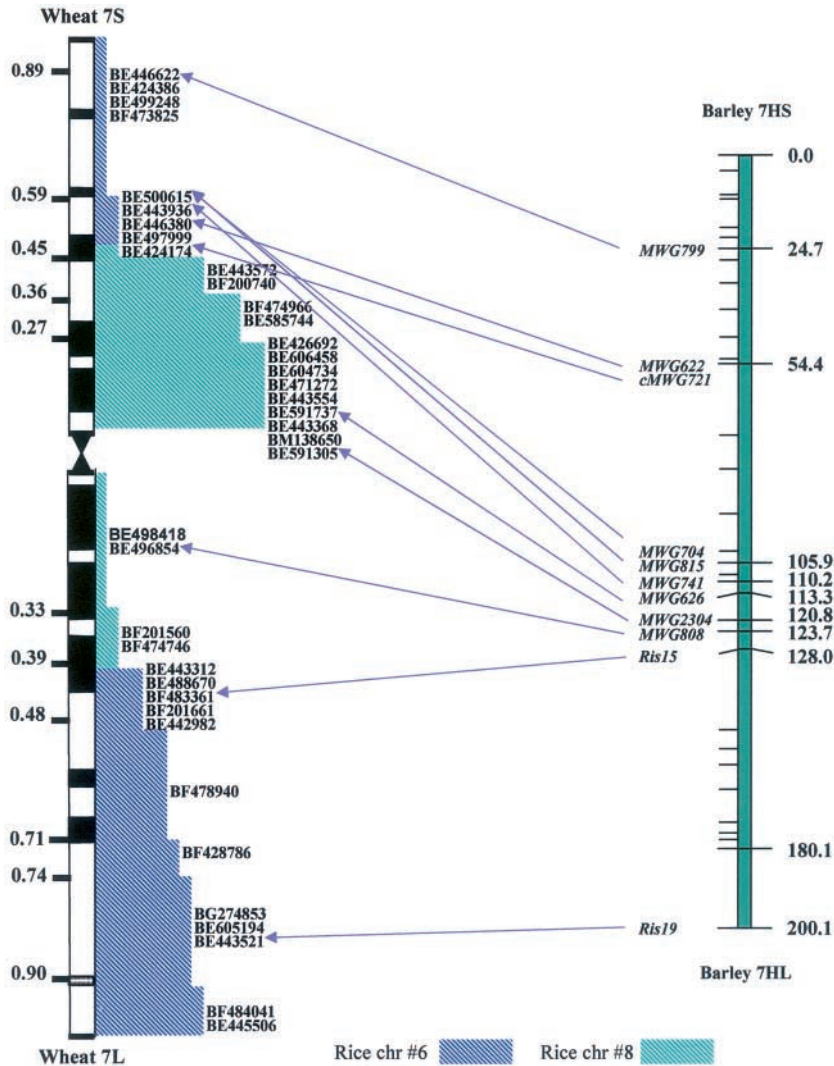
FIGURE 4.—Comparison of map positions of molecular markers of rice and barley with tentatively ordered EST loci on the consensus map of homoeologous group 7. The linkage map of barley chromosome 7, adapted from KÜNZEL *et al.* (2000), is depicted on the right. The stepwise increases in the height of the colored diagonal lines were used in wheat group 7 to differentiate among the regions.

loci in distal regions was correlated with a higher rate of recombination. Conversely, a lower density of EST loci in proximal regions was correlated with a lower rate of recombination (AKHUNOV *et al.* 2003a). Thus, the majority of genes in wheat appear to be located in the high-recombination areas, allowing for effective development and use of map-based cloning strategies to clone genes of interest.

Consensus map: Because many ESTs detected three orthologous loci among the three homoeologous group 7 chromosomes, and the loci appear to be colinear, it was possible to construct a consensus chromosome deletion bin map of homoeologous group 7. The consensus map provides a detailed resolution of the relative positions of mapped orthologous loci. Because of the colinearity of these loci across the chromosomes of group 7 and a lack of duplication anywhere else in the wheat genome, we identified these 166 loci as landmark markers for this homoeologous group.

Landmark loci, presented here as EST clones, could correspond to highly conserved regions and could be a helpful tool in the allocation of orthologous loci across

Triticeae genomes and will be useful in genetic mapping of orthologous genes. These regions may be of significance in understanding genome evolution among Triticeae species by analyzing chromosome structural rearrangements, recombination hot spots, suppression of recombination, and gene distribution, duplication, and elimination events in the genome. HOHMANN *et al.* (1995) designated 10 landmark RFLP loci, 5 each for the short and long arms of consensus chromosome 7. They suggested that these loci could be useful in targeting specific genes to specific regions of consensus chromosome 7. In our study 117 loci were colinear across the homoeologous group, and 68% (81/117) were mapped into the region close to the centromere. These loci mapped to the proximal region are possibly conserved over large evolutionary distances and could be linked to, or possibly represent, critical genes that necessitated their presence in the genomes during the establishment of polyploid species (AKHUNOV *et al.* 2003b). Because of their evolutionary importance we believe that these 117 loci should be present in closely related species.

TABLE 3

Putative order of wheat ESTs based on corresponding rice BAC/PAC and genetic markers

EST	Chromosomal interval[a]	Rice BAC/PAC	Genetic markers	Rice chromosome	Map position (cM) in rice
Short arm of wheat consensus chromosome 7					
BE426692	0.00–0.27	AP003892	RM308	8	104.8
BE606458	0.00–0.27	AP004163	R2027	8	108.9
BE604734	0.00–0.27	AP005439	R2027	8	108.9
BE471272	0.00–0.27	AP004464	R2027	8	108.9
BE443554	0.00–0.27	AP003914	R2662	8	110.3
BE591737	0.00–0.27	AP004163	RM3376	8	114.4
BE443368	0.00–0.27	AP003912	RZ572	8	117.0
BM138650	0.00–0.27	AP003928	S1570	8	117.0
BE591305	0.00–0.27	AP004044	R662	8	117.3
BF474966	0.27–0.36	AP004765	RZ926	8	100.4
BE585744	0.27–0.36	AP005509	R2118	8	103.6
BE443572	0.36–0.45	AP003892	RM149	8	103.7
BF200740	0.36–0.45	AP004761	S10655	8	102.4
BE500615	0.45–0.59	AP005619	R2171	6	50.4
BE443936	0.45–0.59	AP003524	P127	6	61.6
BE446380	0.45–0.59	AP004728	S2570	6	64.7
BE424174	0.45–0.59	AP003928	R662	8	117.3
BE497999	0.45–0.59	AP003626	R1559	6	88.9
BE446622	0.61–0.89	AP004806	R2291	6	10.2
BE424386	0.61–0.89	AP002069	R845	6	13.5
BE499248	0.61–0.89	AP002536	RZ2	6	25.6
BF473825	0.61–0.89	AP003458	L688	6	32.1
Long arm of wheat consensus chromosome 7					
BE498418	0.00–0.30	AP004591	C770	8	13.7
BE496854	0.00–0.30	AP004656	S1461	8	38.0
BF201560	0.30–0.39	AP005441	R2736	8	39.7
BF474746	0.30–0.39	AP005441	R2736	8	39.7
BE443312	0.39–0.48	AP003574	S20459S	6	65.8
BE488670	0.39–0.48	AP004745	R3188	6	66.7
BF483361	0.39–0.48	AP004729	S10555	6	78.8
BF201661	0.39–0.48	AP003941	RM1340	6	82.9
BE442982	0.39–0.48	AP005446	C30378S	6	87.5
BF478940	0.61–0.71	AP003771	S14023	6	114.3
BF428786	0.71–0.74	AP005192	L655	6	106.3
BG274853	0.74–0.90	AP003635	C556	6	105.6
BE443521	0.74–0.90	AP003568	C358	6	98.6
BE605194	0.74–0.90	AP004744	E4392S	6	105.6
BF484041	0.90–1.00	AP005750	S11239	6	123.1
BE445506	0.90–1.00	AP004685	C607	6	124.6

[a] The intervals of each consensus chromosome arm are presented from proximal to distal.

Duplication: There are duplicated loci (paralogous) on almost all of the RFLP linkage and physical maps of Triticeae species reported to date (ANDERSON *et al.* 1992; HOHMANN *et al.* 1994; NELSON *et al.* 1995; MARINO *et al.* 1996; WENG *et al.* 2000; WENG and LAZAR 2002). In a mapping study of the *T. monococcum* L. genome, DUBCOVSKY *et al.* (1996) identified >30% intra- or interchromosomal duplications. In our study, 24% of the ESTs mapping to group 7 identified duplicated loci either on the chromosomes of other homoeologous groups or on the same arm or different arms of chromosomes of group 7. Eighty-five (31%) ESTs identified duplicated

loci in the same deletion bin (intrabin) and these could have resulted from the internal cut site of *Eco*RI within a locus. The observed rate of duplication does not reflect the total duplicated loci of the wheat genome since we mapped only the chromosomes of homoeologous group 7. In an effort to map physically 6421 ESTs in the rice genome, WU *et al.* (1998) reported only 2.4% duplicated loci. Hence, there appears to be an order of magnitude more of duplicated loci per gene motif within the homoeologous group 7 chromosomes of wheat than in the small genome of rice. The growth or shrinkage of the plant genomes has been attributed

to the growth and shrinkage of repeated nucleotide sequences (BENNETZEN 2002; SANMIGUEL *et al.* 2002); however, the growth of the wheat genomes also appears to have been accompanied by the concomitant accumulation of dispersed gene duplications. The similar proportions of duplicated loci to overall genome size of wheat and rice suggest that the accumulation or deletion of repeated sequences and genes could have been coupled and controlled by a common mechanism.

The duplicated loci tend to be located in the distal regions of chromosome arms (Figure 3), whereas the landmark loci were mostly proximal (Figure 2). The distribution of duplicated loci across the wheat genomes was highly correlated with the recombination rates along hexaploid wheat chromosome arms and along chromosome arms in diploid species of the Triticum-Aegilops alliance (DVOŘÁK *et al.* 1998; AKHUNOV *et al.* 2003a). This relationship has been attributed to either hitchhiking of neutral loci with genes selected by natural selection or linkage of neutral loci to mildly deleterious genes not favored by natural selection (CHARLESWORTH 1994). In both scenarios, there is a greater chance for a neutral locus and, by extension, for polymorphism for a duplicated locus, to be eliminated if it is in a low-recombination region than if it is in a high-recombination region. Therefore, it could be suggested that polymorphisms for neutral locus duplications are expected to survive and become fixed preferentially in high-recombination regions. Identification of duplicated regions between homoeologous group 7 and homoeologous groups 3, 5, and 6 of wheat implied that these duplications existed prior to polyploidization (QI *et al.* 2003).

7BS > 4AL and 5AL > 7BS translocation: On the basis of the location of structural genes on chromosomes 4BL, 4DL, and 5AL (AINSWORTH *et al.* 1983), and of endosperm peroxidase on 4AL, 7AS, and 7DS (KOBRECHEL and FILLET 1975), NARANJO *et al.* (1987) proposed a double translocation, 4AL to 5AL, 5AL to 7BS, and 7BS to 4AL, in the genome of Chinese Spring wheat. ANDERSON *et al.* (1992) analyzed these translocations by RFLP analysis using genomic probes and supported the translocations proposed by NARANJO *et al.* (1987). WERNER *et al.* (1992) reported a segment of the short arm of chromosome 7B had been translocated to the long arm of chromosome 4A and suggested that ∼20% of the distal region of the 4AL chromosome was derived from a translocation of 7BS. In the present study, we identified loci corresponding to 44 probes mapped to bins 7AS1-0.89-1.00, 7AS5-0.59-0.89, 7DS4-0.61-1.00, 4AL4-0.80-1.00, 4AL5-0.66-0.80, and 4AL13-0.59-0.66 (Figure 2B). Even if we consider that a portion of the chromosomal region between 4AL5-0.66-0.80 and 4AL13-0.59-0.66 was mapped by the loci of these probes, at least 34% of the 4AL chromosome arm at the distal region was derived from a distal translocation event involving 7BS.

ANDERSON *et al.* (1992) supported the proposed translocation between 5AL and 7BS by assigning a 5AL-specific fragment of the probe BCD87 to chromosome 7BS. We examined the probes mapped to 7BS and identified loci corresponding to five probes (Figure 2B) that mapped distal on 7BS, 5BL, and 5DL. We could not identify the position of the translocated segment on 7BS because the linear orders of these probes are not known. Our analysis supported the proposed translocation between 5AL and 7BS although the chromosomal segment involved in this translocation appears much smaller than the translocation between 7BS and 4AL, which is in agreement with JIANG and GILL (1994).

Ordering EST loci and comparison of map position with rice and barley: Homoeology between wheat and rice genomes was first studied by AHN *et al.* (1993) followed by KURATA *et al.* (1994) and VAN DEYNZE *et al.* (1995) at the macro level. SORRELLS *et al.* (2003) compared rice and wheat genomes at the micro/DNA sequence level. All those studies indicated that rice chromosomes 6 and 8 are homoeologous with Triticeae group 7 chromosomes. Of the 117 ESTs located on the group 7 consensus map, 38 were located to rice BAC/PACs with corresponding genetic markers, and 11 of the BAC/PACs correspond with the sequence of RFLP markers mapped to chromosome 7 of barley (Table 3 and Figure 4). The terminal regions (100.4–118.9 cM) of the long arm of rice chromosome 8 corresponded with the centromeric region (0.0–0.59) of the long arm of consensus chromosome 7 of wheat (Figure 4). The short arm region (13.7–39.7 cM) of rice chromosome 8 corresponded with the centromeric region of the long arm (0.0–0.39) of consensus chromosome 7 of wheat. About 39% of the distal region of the long arm of consensus chromosome 7 corresponded with a 26-cM region of the long arm of chromosome 6 of rice, indicating a putative homoeologous relationship of genes involved in these regions of wheat and rice. The present study identified putative regions of gene content conservation between the wheat group 7 consensus chromosome and rice chromosomes 6 and 8. Orthology of these loci with rice suggests a possible ancestral origin of these loci and that their presence precedes the divergence of the wheat and rice lineages. Hence the proximal low-recombination region of wheat chromosomes could be a region of evolutionary conservation, which is in agreement with the findings of AKHUNOV *et al.* (2003a) and SORRELLS *et al.* (2003). Using the rice genome as a template one can predict colinearity with the wheat genomes; however, microsynteny studies have suggested that, in most cases, colinearity will need to be verified at the DNA sequence level (HAN *et al.* 1999; BENNETZEN and RAMAKRISHNA 2002). The ordering of mapped ESTs within chromosome bins would be an important enhancement for the wheat/rice comparative analysis.

Although the wheat homoeologous group 7 map is based on consensus physical maps that combine dele-

tions from 7A, 7B, and 7D chromosomes that differ in size and in amount of heterochromatin, the results obtained by comparing them to the barley chromosome 7 linkage map are in good agreement with those reported by WERNER *et al.* (1992), HOHMANN *et al.* (1995), and KÜNZEL *et al.* (2000). Except for the reverse order of four ESTs mapped into the 0.45–0.59 regions on the group 7 consensus map of wheat, the relative positions of all markers and ESTs were maintained between wheat chromosome 7 and barley chromosome 7 (Figure 4). The reverse order of these ESTs corresponding to the molecular markers mapped on rice chromosome 6 identified a minor inversion of the similar region of group 7 chromosomes that has been reported by HOHMANN *et al.* (1995). Thus, these results suggest the ordering of EST probes and map position in comparison of wheat chromosomes of homoeologous group 7 with chromosomes of rice and barley.

The localization and distribution of EST loci into bins along the homoeologous group 7 chromosomes directly reflects the distribution of genes and gene-rich regions of this group in wheat. Identification of landmark probes and putative map positions in rice and barley genomes suggested a detailed analysis of ESTs mapped in the wheat genome could provide valuable information in mapping and identification of genes across grass genomes.

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Communicating editor: J. P. Gustafson