Identification and High-Density Mapping of Gene-Rich Regions in Chromosome Group *1* of Wheat

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ABSTRACT

We studied the distribution of genes and recombination in wheat (*Triticum aestivum*) group *1* chromosomes by comparing high-density physical and genetic maps. Physical maps of chromosomes *1A*, *1B*, and *1D* were generated by mapping 50 DNA markers on 56 single-break deletion lines. A consensus physical map was compared with the *1D* genetic map of *Triticum tauschii* (68 markers) and a Triticeae group *1* consensus map (288 markers) to generate a cytogenetic ladder map (CLM). Most group *1* markers (86%) were present in five clusters that encompassed only 10% of the group *1* chromosome. This distribution may reflect that of genes because more than half of the probes were cDNA clones and 30% were *Pst*I genomic. All 14 agronomically important genes in group *1* chromosomes were present in these clusters. Most recombination occurred in gene-cluster regions. Markers fell at an average distance of 244 kb in these regions. The CLM involving the Triticeae consensus genetic map revealed that the above distribution of genes and recombination is the same in other Triticeae species. Because of a significant number of common markers, our CLM can be used for comparative mapping and to estimate physical distances among markers in many Poaceae species including rice and maize.

WHEAT (*Triticum aestivum* L. em. Thell), maize, and rice belong to the grass family Poaceae and probably originated from a common ancestor 50–60 mya (BENNETZEN and FREELING 1993 for review). Many recent reports have shown that the three crop plants have similar gene composition and colinearity (AHN and TANKSLEY 1993; AHN *et al.* 1993). The wheat genome (16,000 Mb) is about six times larger than that of maize and 35 times larger than the rice genome (BENNETT and SMITH 1976). The size of the genome containing genes is most likely to be similar for these species, implying that <3% of the wheat genome represent genes. If so, an understanding of the structural and functional organization of the gene containing regions is particularly important in wheat from both evolutionary perspectives and for molecular manipulations.

The cytogenetic ladder mapping (CLM) strategy (GILL and GILL 1994b, for review and description) in wheat is particularly powerful for studying the distribution of genes and recombination along the chromosomes. A "CLM" is a composite map generated by comparing one or more conventional genetic linkage maps with that of a physical map via common markers. The physical map is developed by dividing each chromosome into regions flanked by deletion breakpoints and marking them by C bands, protein and DNA markers. Individual physical maps of homoeologous chromosomes can be combined to generate a consensus physical map. The consensus physical map is compared with genetic linkage maps of wheat or of any of its wild or cultivated related species (*Triticum tauschii*, barley, oats, rye, or *T. monococcum*, for example).

The low-density CLMs have shown that both recombination and markers are distributed nonrandomly on the wheat chromosomes, and recombination was suppressed around the centromeres (WERNER *et al.* 1992; GILL *et al.* 1993; KOTA *et al.* 1993; DELANEY *et al.* 1995a,b; MICKELSON-YOUNG *et al.* 1995). Uneven distribution of recombination along chromosome length is a common phenomenon among eukaryotes (LICHTEN and GOLDMAN 1995 for review). Recombination hot spots and cold spots are observed in almost all well-studied eukaryotes. In humans and mice, recombination tends to localize more toward telomeres and less toward centromeres. Even the interstitial regions display considerable variation in recombination frequencies per unit distance. The correlation between the distribution of recombination and genes is still not clear although a general trend of higher recombination around genes has been observed. The high-density CLM of wheat homoeologous group *5* showed that wheat genes are arranged in clusters present mainly in the distal parts of the chromosomes (GILL *et al.* 1996). Most of the group *5* recombination was accounted for by the gene-clusters. In the present study, we show the distribution pattern of genes and recombination along homoeologous group *1* chromosomes of wheat and other Triticeae genomes.

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MATERIALS AND METHODS

Aneuploid stocks: Fifty-six deletion lines, generated using the gametocidal chromosome of *Aegilops cylindrica* (ENDO 1988; ENDO and GILL 1996) were used to generate the physical maps. Twenty-seven of these deletions were for the short arm and 29 were for the long arm. For the short arm, there were five deletions for chromosome *1A*, 18 for *1B*, and four for *1D*. The number of deletions for the long arm were five for *1A*, 16 for *1B*, and eight for *1D*. Nullisomic-tetrasomic (NT) lines (missing a pair of chromosomes, the deficiency of which is compensated for by a pair of homoeologous chromosomes) and ditelosomic lines (SEARS 1954) were used to assign DNA restriction fragments to their respective chromosome arms. All the deletion lines, genetic and aneuploid stocks are maintained at the Wheat Genetic Resource Center (WGRC), Throckmorton Hall, Kansas State University, Manhattan, KS.

Arm ratio and fraction length (FL) measurements: The mean of 10 chromosomes was used for deletion lines measurements. Arm ratios were calculated by dividing the short arm measurements with that of the long arm. The breakpoint fraction length (FL) values of the short arm deletion lines were calculated by dividing the arm ratio of the deletion chromosome with that of its normal homologue. Fraction length values for the long arm deletions were calculated by dividing the arm ratio of the normal homologue with that of the deletion chromosome. The standard errors for the breakpoint FL values ranged from ±0.004 to ±0.022.

DNA probes and procedures: Fifty homoeologous group *1* probes from various Poaceae (Gramineae) species were used for deletion mapping. The chromosome location, number of DNA fragments detected, and the source of the probes are given in Table 1. Thirty (60%) probes were cDNA clones and 20 were genomic. Fourteen probes were barley cDNA (*bcd*), four were barley genomic (*abg* and *mwg*), 10 were cDNA clones from oats (*cdo*), nine were *Pst*I genomic clones from *T. tauschii* (*ksu*), six were wheat cDNA (*psr*), and seven were wheat genomic (*Tag* and *wg*). Thirty-five of the 50 probes were selected for physical mapping because of their location on the consensus genetic linkage map (VAN DEYNZE *et al.* 1995). An effort was made to select probes uniformly distributed over the entire map. The remaining 15 clones were identified to be wheat homoeologous group *1* probes either by mapping on nullisomic-tetrasomic lines (NT) or by their location on one or more genetic linkage maps of group *1*. The DNA gel blot hybridization techniques were as previously described (GILL *et al.* 1993).

Physical mapping: Forty-four of the 56 deletion lines were homozygous (each possesses a pair of deletion chromosome), one was hemizygous (only one deletion chromosome), and 11 were heterozygous (one deletion and one normal chromosome). Each group *1*-specific DNA band was mapped to a chromosome region flanked by breakpoints of the largest deletion possessing the band and the smallest deletion lacking it. For homozygous and hemizygous deletion lines, the DNA probes were scored for the presence or absence of the DNA fragment(s). For the heterozygous deletion lines, however, the DNA bands were scored for their intensities, as previously described (GILL *et al.* 1996). For the probes that detected more than one DNA band for a chromosome, the DNA fragments were scored to be nonallelic (different alleles shown by a letter at the end of probe name) if they map to different chromosome regions or if the probe detected more than two DNA fragments bigger than its own size.

Genetic mapping: The RFLP genetic linkage map of chromosome *1D* was developed using a F_2 population of 56 plants from a cross between two accessions of *T. tauschii* (TA1691 & TA1704) (GILL, K. S., *et al.* 1991, 1996). The consensus genetic linkage map of wheat homoeologous group *1* was constructed using the mapping information of 288 markers present on one or more of the 13 different linkage maps of wheat, *Triticum tauschii, T. monococcum,* barley, or oats (VAN DEYNZE *et al.* 1995). The consensus genetic linkage map is a hypothetical map constructed as follows: the wheat map with most number of markers was used as a base map. A locus was added to the consensus map only if its order agreed among various Triticeae maps and was present in at least two of the linkage maps. The consensus map revealed the relative genetic positions of 14 agronomically important genes, 17 known-function gene probes, 46 cDNA and 30 genomic clones. Although the consensus map consists of 108 markers, the relative genetic position of all 288 markers can be known by comparing the consensus map with the individual genetic maps. The 14 agronomically important genes include genes conferring resistance to diseases [leaf rust (*Lr, Lr21*), stem rust (*Sr33*), powdery mildew (*Pm3*)] preharvest sprouting (*Qphs.cnl*), fertility restoration gene (*Rf3*), and seed storage proteins.

RESULTS

Physical maps: The physical maps of chromosomes *1A, 1B,* and *1D* are shown in Figure 1. Genomic DNA of the deletion lines was cut with *Eco*RI for the mapping of 48 probes. Two probes were mapped using *Hin*dIII digested DNA (Table 1). The 50 probes detected 116 loci on the three group *1* chromosomes. Thirty-three probes detected 34 loci on chromosome *1A*, 42 probes detected 45 loci on *1B*, and 36 detected 37 loci on *1D*. Twenty-four probes detected loci on all three chromosomes and 13 detected on two of the three homoeologues. Thirteen probes detected loci on only one chromosome.

The markers were distributed nonrandomly on the chromosomes. Clusters of markers were observed that were interspersed by regions of low marker density. Specifically notice the regions bracketed by deletions 1AS-1 and 1AS-2, 1BS-11 and 1BS-4, 1BL-12 and 1BL-3, and 1DS-1 and 1DS-5 (Figure 1). Eleven markers mapped in the region that is 7% of the 1BS satellite (between 1BS-4 and 1BS-11). Large marker-poor regions were around the centromeres of 1A (1AS-1–1AL-1), 1B (1BS-21–1BL-11), and 1D (1DS-1–1DL-4). These encompass ~50% of the short arm and ~20% of the long arm. Some of the major marker-poor interstitial regions are: bracketed by the breakpoints of deletions 1AL-3 and 1AL-4, 1BL-9 and 1BL-5, and, 1DL-2 and 1DL-5.

The distribution of deletion breakpoints was also uneven on the chromosomes. It seems that deletions always occur in the marker-rich regions although the reverse may not be true. As a result, it was possible to localize the marker clusters to small chromosomal regions. All *1DS* deletions spanned only 13% of the arm and are in the marker-rich region (Figure 1). The corresponding regions in *1BS* and *1AS* were also preferred sites for breaks. Because of this, the markers mapping in or around the region were localized to small chromosomal regions in all three homoeologues. Fifteen of the 19 *1D* long arm markers mapped in the distal 30%. In chromosome *1B*, these markers were localized to smaller chromosomal regions because of the presence of nine deletions for the region. Six of the 15 markers

TABLE 1

The clones used for genetic and physical mapping of wheat homoeologous group *1* chromosomes

Clone[a]	cDNA(C)/ genomic(G)	Total no. of bands	Enzyme	No. of bands for			Chromosome location	
				1A	*1B*	*1D*	*T. tauschii*	Wheat
pHvabc160	C	4	*Eco*RI	1	1	1		*1L*
pHvabg387	G	4	*Eco*RI	1	1	1		*1L*
Adh	C	3	*Eco*RI	0	1	0	*1L*	*1L*
pTa71	C	8	*Eco*RI	0	1	0	*5D*	*1BS,5DS*
pHvcnlbcd22	C	3	*Eco*RI	1	0	0		*1L*
pHvcnlbcd98	C	5	*Eco*RI	1	1	1		*1S,7S*
pHvcnlbcd265	C	13	*Eco*RI	0	1	1		*1L*
pHvcnlbcd304	C	5	*Eco*RI	1	1	1		*1L*
pHvcnlbcd310	C	2	*Eco*RI	0	1	0		*1BL,1DL,7L*
pHvcnlbcd386	C	3	*Eco*RI	1	1	1		*1L*
pHvcnlbcd508	C	5	*Eco*RI	0	1	1	*1L,5L*	*1L,5L*
pHvcnlbcd738	C	1	*Eco*RI	0	1	0		*1L*
pHvcnlbcd762	C	4	*Eco*RI	1	1	0		*1S*
pHvcnlbcd921	C	3	*Eco*RI	1	0	1		*1L*
pHvcn1bcd1072	C	3	*Hin*dIII	1	0	0	*1S*	*1S*
pHvcn1bcd1434	C	3	*Eco*RI	1	1	1	*1S*	*1S*
pHvcnlbcd1562	C	3	*Eco*RI	0	1	1		*1L*
pAscnlcdo388	C	13	*Eco*RI	0	1	1	*1S,2L,3L,4S,5L,6*	1BS,1DS
pAscnlcdo393	C	4	*Eco*RI	2	0	0		*1L*
pAscnlcdo534	C	9	*Eco*RI	0	1	0		*1S,3L,6S,7S*
pAscnlcdo572	C	5	*Eco*RI	1	1	2		*1L*
pAscnlcdo580	C	5	*Eco*RI	1	2	1		*1S*
pAscnlcdo618	C	3	*Eco*RI	1	1	1		*1S*
pAscnlcdo658	C	3	*Eco*RI	1	1	1		*1S*
pAscnlcdo844	C	4	*Eco*RI	1	0	0		*1L*
pAscnlcdo1173	C	3	*Eco*RI	1	1	1		*1S*
pAscnlcdo1188	C	3	*Eco*RI	1	1	1		*1S*
pTtksud14	G	13	*Eco*RI	0	6	3	*1S*	*1S*
pTtksue8	G	3	*Hin*dII	0	1	1	*1L*	*1L*
pTtksue11	G	7	*Eco*RI	1	1	2	*1L*	*1L*
pTtksue18	G	6	*Eco*RI	1	2	2	*1S*	*1S,7B*
pTtksue19	G	7	*Eco*RI	1	2	2	*1S*	*1S*
pTtksuf43	G	5	*Eco*RI	1	1	1	*6S*	*1S,2DL,6DS*
pTtksug34	G	5	*Eco*RI	1	1	1	*1L*	*1L*
pTtksuh14	G	3	*Eco*RI	1	1	1		*1L*
pTtksui27	G	2	*Eco*RI	0	1	1	*1L*	*1L*
pTag136	G	1	*Eco*RI	0	1	0		*1B*
pTag163	G	5	*Eco*RI	0	1	0	*1L,2S,4L*	*1L,4L*
pTag558	G	3	*Eco*RI	1	0	0	*2L,3L,6S,7S*	*1L,2L,5D*
pTag710	G	3	*Eco*RI	0	0	1		*1L*
pTapsr161	C	4	*Eco*RI	1	1	1	*1S*	*1S*
pTapsr544	C	7	*Eco*RI	2	0	2	*1L*	*1L*
pTapsr569	C	4	*Eco*RI	1	1	1		*1S*
pTapsr601	C	5	*Eco*RI	1	1	0		*1S*
pTacnlwg241	G	5	*Eco*RI	0	1	1	*1L*	*1L*
pTacnlwg605	G	3	*Eco*RI	1	1	1		*1L*
pTacnlwg789	G	4	*Eco*RI	1	1	1	*1S,4L*	*1S,7D*
pTamwg36	G	3	*Eco*RI	1	1	1		*1S*
pTamwg710	G	5	*Eco*RI	1	1	1		*1L*
pTamwg938	G	4	*Eco*RI	0	1	1		*1S*

Total no. of bands and No. of bands for *1A*, *1B*, and *1D* were counted from mapping on nulli-tetra lines of wheat cultivar Chinese Spring. The type of probe is indicated as C for the cDNA clones and G for genomic. The restriction enzyme used for genomic DNA digestion of the aneuploid lines is mentioned under Enzyme. The probes marked in bold are common to the consensus physical map, consensus genetic map and the linkage map of *T. tauschii;* the underlined probes were mapped only physically, and the rest of the probes are present on consensus physical and genetic linkage maps of wheat but not mapped in *T. tauschii.*

[a] *bcd, cdo,* and *wg* are barley cDNA, oats cDNA, and wheat genomic clones, respectively, from Dr. MARK SORRELLS (ANDERSON *et al.* 1992); mwg are barley genomic from Dr A. GRANER (GRANER *et al.* 1991); *psr* are wheat cDNA from Dr. MIKE GALE (DEVOS and GALE 1993); *Tag* are wheat genomic from Dr. KOICHIRO TSUNEWAKI (LIU and TSUNEWAKI 1991); and *Ttksu* are *T. tauschii PstI* genomic clones from our laboratory (GILL, K. S., *et al.* 1991).

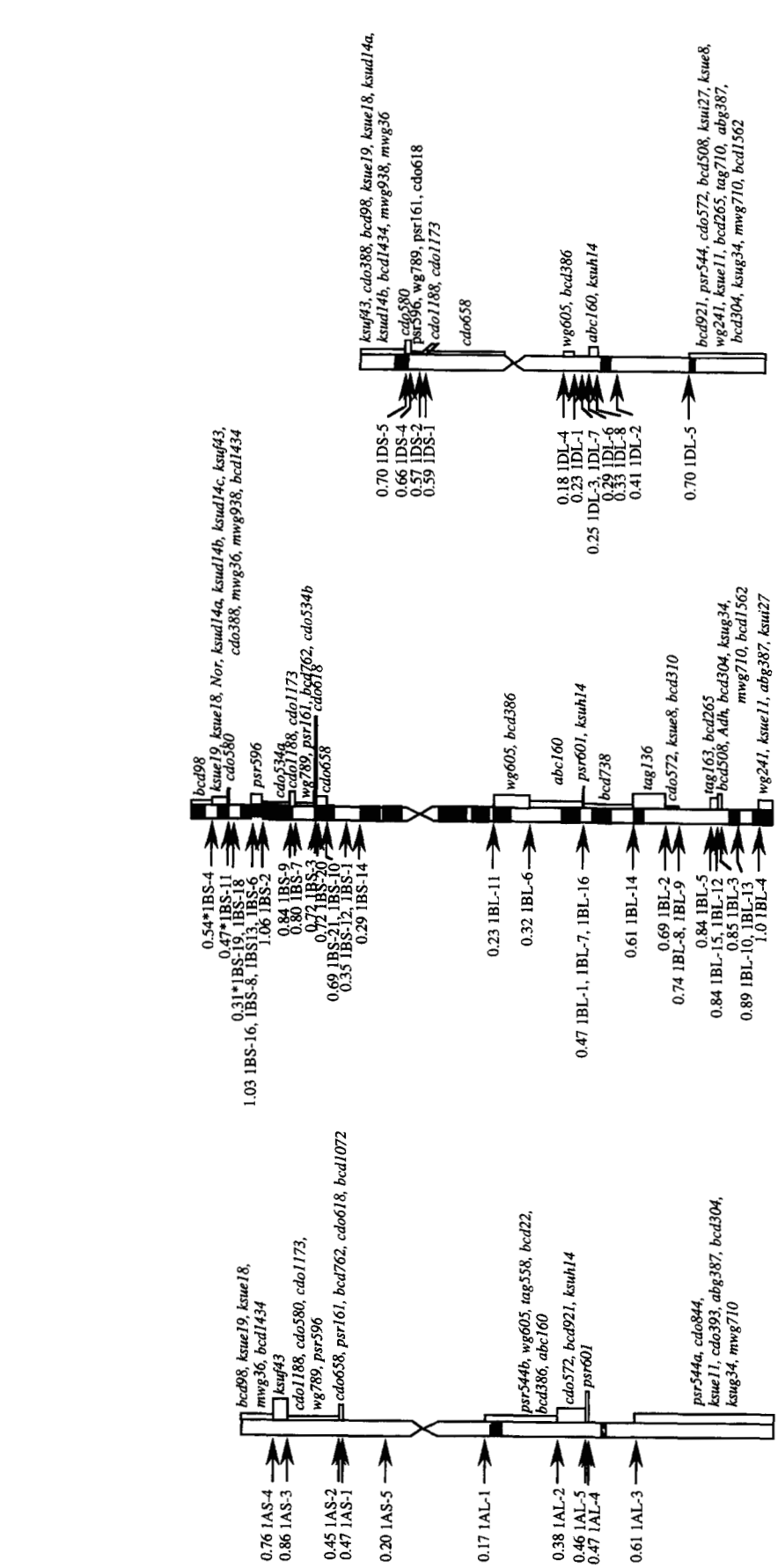

FIGURE 1.—Physical maps of chromosomes *1A*, *1B*, and *1D*. Relative chromosome length, arm ratios, and the C-banding patterns were drawn to the scale following the nomenclature for standard karyotype (GILL, B. S., *et al.* 1991). The deletion line breakpoints and the fraction length (FL) of the retained arm are marked by arrows on the left of the chromosome diagrams. The FL values with asterisks indicate the fraction length of the satellite retained in *1B*. The other FL values of *1BS* are for the short arm without the satellite. The probe loci and chromosome regions panelled by the deletion breakpoints are given on the right of the drawings.

mapped between FL 0.84 and 0.85 and four mapped in the telomeric region. Similarly, 10 markers mapping in the distal 30% of *1DS* were localized to smaller chromosome regions in *1BS* because of the presence of more deletions. The exception to this observation was for the distal 24–39% of both chromosomes *1A* and *1D* for which no deletion was observed. The corresponding regions of chromosome *1B* possessed 18 deletions. Both telomeric ends of chromosome *1B* possess diagnostic C bands that are not present on chromosome *1A* or *1D*. Without the telomeric C bands, it is difficult to detect small deletions, and thus all deletions for *1A* or *1D* were probably not recovered.

Except for a few probes, the location and the relative order of markers were similar among the three homoeologues (Figure 1). The probes *cdo572* and *bcd921* mapped in the distal 30% of chromosomes *1BL* and *1DL*, however, between FL 0.38 and 0.46 of chromosome *1AL*. Similarly, the markers *cdo1188* and *cdo1173* in chromosome *1DS* were present proximal to markers *psr161*, *wg789*, and *cdo618*, but were distal in chromosomes *1A* and *1B*.

Consensus physical map: The consensus physical map of wheat group *1* chromosomes was constructed by placing the markers to the shortest possible intervals, as previously described (GILL *et al.* 1996). Markers with discrepant location on the three chromosomes are marked by asterisks. The uneven distribution of markers was more pronounced from the consensus physical map compared to that from individual maps (Figures 2 and 3). Small regions of higher marker density (marked on the left of the consensus physical map and called marker clusters or marker-rich regions) were observed that were interspersed by large chromosomal regions that were essentially devoid of markers (marker-poor regions). Five major marker clusters were observed, two on the short arm and three on the long arm. Forty-three of the 50 (86%) loci were present in these clusters, which encompassed ~10% of the chromosomal area.

Genetic linkage mapping: The consensus genetic linkage map of Triticeae (VAN DEYNZE *et al.* 1995) consists of 108 markers. The order and approximate genetic distance among 288 group *1* markers can be deduced by comparing the consensus map with the individual linkage maps of various Triticeae species. The genetic linkage map of chromosome *1D* of *T. tauschii* is comprised of 68 loci. Of these, 51 were part of the 288 consensus map loci and 17 were unique. The *T. tauschii* map has the best resolution among all Triticeae maps because recombination in *T. tauschii* is about two to four times higher than the other Triticeae species. The *T. tauschii* map is colinear with the consensus linkage map and the relative distances are comparable (Figure 2). By comparing these two maps with each other and with other Triticeae maps, the relative genetic linkage relationship of 305 markers can be deduced.

Cytogenetic ladder map (CLM): The wheat homoeologous group *1* CLM was generated by comparing the consensus physical map with both the consensus genetic linkage map and the *1D* map of *T. tauschii* (Figure 2). There are 14 markers common to all three maps (marked in bold in Table 1), 17 between consensus physical map and the *1D* map, and 38 are common between the two consensus maps. From the genetic maps alone, it appeared that the markers are clustered around the centromeres. The CLM, however, clearly showed that the centromeric regions are devoid of markers. Figure 3 shows comparison of the distribution of recombination and markers. A good correlation is obvious between the distribution of the two. Little recombination was observed for ~40% of the chromosome region around the centromere (Figures 2 and 3). Recombination occurred predominantly in the marker-rich regions. Most of the short arm recombination occurred in the two marker clusters. The genetic distance of the short arm submicroscopic-marker cluster at FL 0.55 is ≥35 cM in *T. tauschii* (Figure 2). The genetic distance of a similar region at FL 0.85 of the long arm in wheat is ≥30 cM (the same distance in *T. tauschii* is expected to be >100 cM). The CLM constructed by comparing the consensus physical map with the *T. tauschii* linkage map is almost identical to the one constructed by comparing with the consensus linkage map of Triticeae (Figure 2).

DISCUSSION

Figure 2 presents a comprehensive map of the wheat homoeologous group *1* chromosomes. The map reveals both physical and genetic distances among 305 markers, including 14 agronomically important genes. The 305 group *1* markers detected 716 loci on 15 Triticeae maps (VAN DEYNZE *et al.* 1995 and the present study). On an average, each probe is present on more than two maps providing ample common points for map comparisons. Because of the conserved gene synteny relationship among Triticeae and, to certain extent Poaceae species, the CLM can be used to enrich any homoeologous group *1* segment with more markers and to accurately estimate physical size per genetic map unit (base pairs/centimorgan). The markers *cdo580*, *cdo1173*, *cdo1072*, *cdo98*, *bcd386*, *bcd207*, *bcd738*, and *cdo393* are also mapped in rice (VAN DEYNZE *et al.* 1995). These markers cover the entire group *1* chromosome (Figure 2). A part of group *1* chromosome is homoeologous to rice chromosome *5* and the rest to chromosome *10*. With the availability of a few more common markers will make these CLMs useful in rice.

The advantage of using *T. tauschii 1D* linkage map in the CLM construction is that the *1D* map is of high density and of high resolution. The resolution of the *T. tauschii* map is greater than any other Triticeae map because of higher levels of recombination in *T. tauschii* (GILL K. S. *et al.* 1991; GILL and GILL 1994a). Therefore, mapping in *T. tauschii* may order markers that are com-

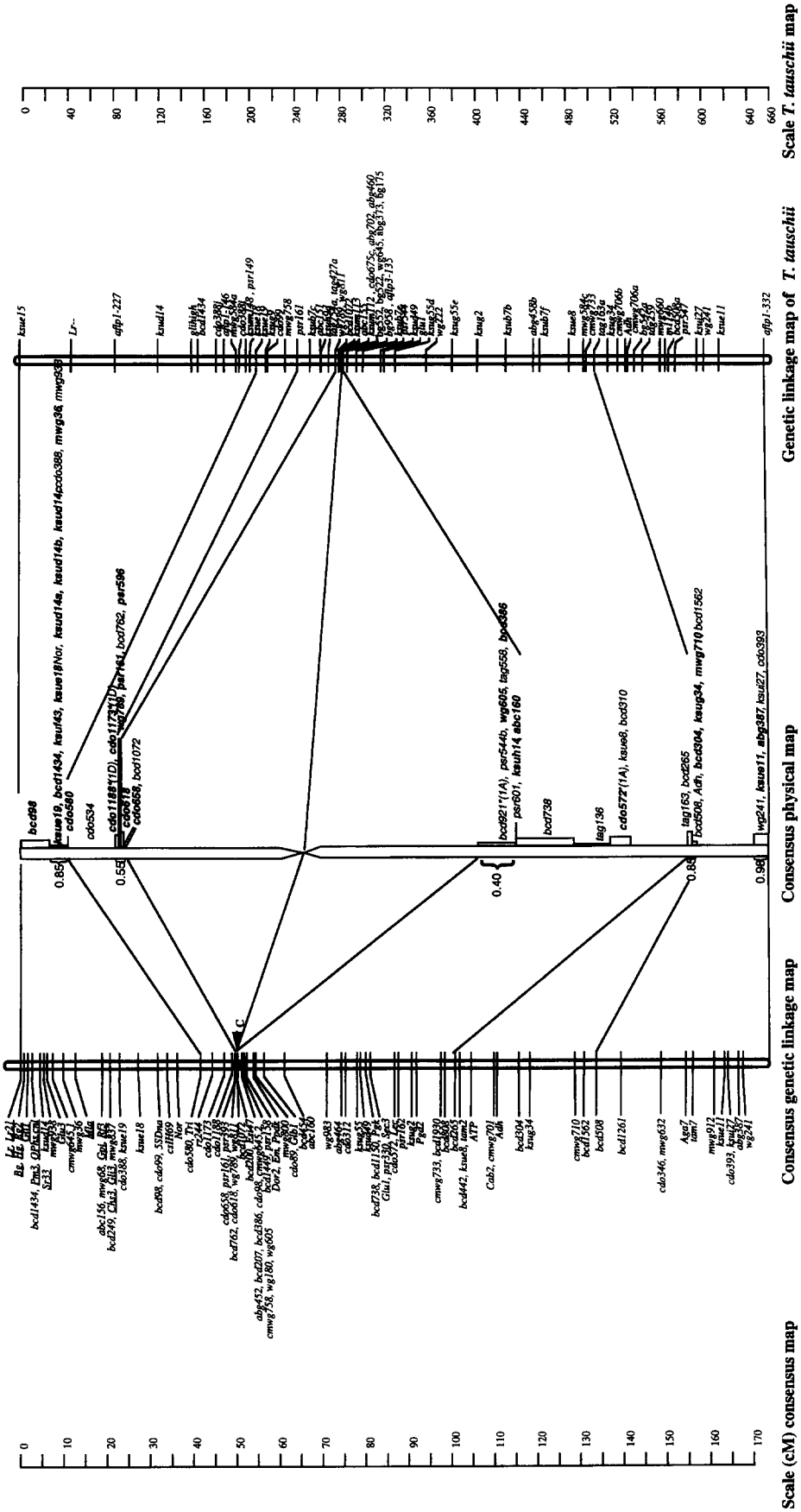

FIGURE 2.—A cytogenetic ladder map (CLM) of wheat homoeologous group *1*. Consensus physical map of wheat group *1* (center) was compared with the genetic linkage maps of *1D* of *T. tauschii* (right) and the consensus genetic linkage map of wheat homoeologous group *1* (left). The average of the three group *1* chromosomes were taken for the arm ratio of the consensus physical map. Some of the common markers across maps are joined by lines. The marker loci in bold lettering on the consensus physical map were present on all three chromosomes of group *1*. The markers with asterisks have a different physical location in the chromosome shown in parenthesis next to the asterisk, compared to the other two homoeologues. The gene clusters are marked on the left of the consensus physical map along with their approximate FL value.

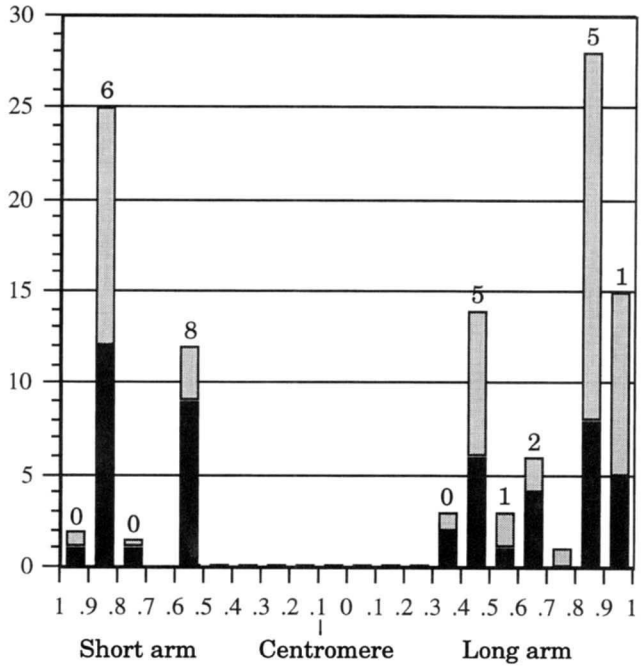

FIGURE 3.—The distribution pattern of markers and recombination on wheat homoeologous group *1* chromosomes. Homoeologous group *1* chromosome was divided into 20 regions each equivalent to FL 0.1. The number of markers for each region were counted from the consensus physical map. The recombination for each region was estimated from the consensus genetic linkage map. The recombination between markers mapping in adjoining regions was divided equally between the two regions. ▨, recombination 3 × cM, ■, number of markers. The numbers on top of the bars represent the number of cDNA clones mapping in the region.

pletely linked in other species. As observed for other chromosomes, the relative order of group *1* markers is the same between wheat and *T. tauschii*. The *T. tauschii* map will become an important tool for fine genetic mapping prior to map-based cloning. Gene synteny conservation between *T. tauschii* and wheat for a region of interest can be confirmed by comparing the *T. tauschii* map with consensus physical and genetic linkage maps. The relative recombination between wheat and *T. tauschii* can also be found by comparing the consensus genetic linkage map with the *T. tauschii* map.

The gametocidal gene(s) preferentially break marker-rich regions of the chromosomes (GILL *et al.* 1993, 1996). In the present study also, the marker-rich regions always seem to have deletion breakpoints in their vicinity (Figure 1). As a result, it was possible to identify and allocate the marker-clusters to small regions. Most of the group *1* markers (86%) were present in five major clusters that were spaced by large marker-poor chromosomal regions. The five clusters encompassed ~10% of the chromosomal region. The actual size of the cluster regions is probably even smaller. The accuracy of determining the actual size of a marker cluster depends upon the number of deletion breakpoints in the region. It may be possible to localize these clusters to even smaller regions with the availability of more deletions.

The marker distribution in the present study may reflect the distribution of genes on the chromosomes. Thirty of the 50 physically mapped markers are from expressed genes. Similarly, 61 of the 108 loci on the consensus genetic linkage map and 19 of the 68 loci on the genetic linkage map of *T. tauschii* represent expressed sequences. No obvious difference was observed in the distribution pattern of the genomic *vs.* expressed sequence (cDNA) markers. The consensus genetic map consists of predominantly cDNA clones and *1D* map is that of genomic clones. However, the physical distribution pattern of markers of the two maps were similar (Figure 2). Since almost all markers present on the group *1* CLM (Figure 2) were mapped genetically, thus selected for their ability to detect polymorphism, one may argue that the marker distribution in the present study reflects that of less conserved genes. It has been postulated that highly conserved genes (housekeeping genes) may be present in recombination-poor regions of chromosomes and less-conserved genes map in recombination-rich regions (MOUCHIROUD *et al.* 1991). This correlation between the extent of polymorphism in the gene sequence with its location on chromosome was not observed in wheat (GILL *et al.* 1996). Both polymorphic and nonpolymorphic probes can be physically mapped using deletion lines because the DNA fragment bands are scored for their presence or absence (see MATERIALS AND METHODS). No differences were observed in the distribution pattern of polymorphic *vs.* nonpolymorphic cDNA probes for group *5* chromosomes.

It is well established in wheat and many other organisms that recombination is unevenly distributed on the chromosomes (RICK 1971; DVORAK and CHEN 1984a; STEINMETZ *et al.* 1987; BOLLAG *et al.* 1989; GANAL *et al.* 1989; WERNER *et al.* 1992; GILL *et al.* 1993; LICHTEN and GOLDMAN 1995). Recombination in the centromeric region is suppressed irrespective of the amount of heterochromatin present in the region (GILL *et al.* 1993, 1996). Based on high-density CLMs, it is apparent that most of the observed recombination occurs in the gene-clusters. Based on our results, it is difficult to determine if recombination occurs only in gene-rich regions or it occurs in gene-poor regions also but is not fully detected because of the lack of markers. Previously undetected recombination events were revealed in maize, barley (NILSSON *et al.* 1993), rice, and wheat by mapping more markers. In rice, a RFLP genetic linkage map with 1383 markers (KURATA *et al.* 1994) is 30% longer than the map with 600 markers (TANKSLEY *et al.* 1993). Based on the data on two to four polymorphic C bands, average about two crossovers per arm were observed for chromosome *5BL* of wheat (DVORAK and CHEN 1984B; CURTIS and LUKASZEWSKI 1991). However, when 36 markers were mapped on the arm, the average number of crossovers increased to about four (GILL and GILL 1994a).

The marker densities in the gene-rich regions are

very high. Eighty-six percent of the markers were present in the gene-rich regions encompassing ~10% of the chromosome. By comparison of the physical and the genetic maps, it appears that the distribution of the rest of the 258 group *1* markers also follows a similar pattern. Twenty-five of the 108 consensus linkage map markers (between marker *bcd1434* and *cdo580*) map in the gene cluster region at FL 0.85 (Figure 2). Nine of these markers are agronomically important genes (underlined on the consensus genetic map). Six agronomically important genes map in the chromosome region immediately distal to this region and are probably part of the same gene cluster. If the distribution of all group *1* markers follows the same pattern, 262 of the 305 markers map in the five gene clusters spanning 10% of the group *1* chromosome. The haploid wheat chromosome complement is 235 μ in length (GILL, B. S., *et al.* 1991), containing 16 million kb of DNA (BENNETT and SMITH 1976). The average size of a wheat homoeologous group *1* chromosome is 10.4 μ (GILL, B.S., *et al.* 1991). Therefore, the chromosome length of the five gene-clusters is ~1 μ which translates to ~68 Mb of DNA. The region is marked by 262 probed and flanked by 16 deletion breakpoints (total markers 278). Therefore, the average distance between the markers is 244 kb, which is within the range of long-range mapping, contiguous mapping, and map-based cloning. The order of the gene cluster region markers can be resolved because recombination is high in these regions.

In conclusion, the cytogenetic ladder mapping strategy is proving to be very powerful in revealing the structural and functional domains of wheat chromosomes. The genes in wheat are present in clusters, four to six per chromosome, usually located toward the telomeric ends. The clusters are probably spaced by nontranscribing repetitive DNA blocks, which comprise >80% of the genome. Most of recombination occurs in these gene clusters.

The base pair/centimorgan estimates for the gene-cluster regions of wheat were comparable with similar regions in rice and tomato (GILL *et al.* 1996). These estimates ranged from 118 kb/cM for the gene-cluster region to 22 Mb/cM for the gene-poor regions (GILL *et al.* 1996). The base pair/centimorgan estimates in rice range from 120 kb to 1 Mb (UMEHARA *et al.* 1995). It would be interesting to find if the lower estimates in rice are for the gene-rich regions. These comparisons suggest that the gene-cluster regions among plants of varying genome sizes are similar in gene-density and recombination, therefore, should be equally accessible to molecular manipulations. The main difference in the genome structure between a large and a small genome plant is in the size of gene-poor blocks separating the gene-rich blocks. Since the observed recombination mainly occurred in the gene-rich regions, the base pair/centimorgan estimates for the gene-poor regions should correspond to their size. These estimates for wheat are 22 Mb/cM and for rice are 1 Mb/cM. The 22-fold difference in the size of gene-poor regions compares well with the 35-fold difference in the genome size of the two species.

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