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A cytogenetic ladder-map of the wheat homoeologous group-4 chromosomes

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Abstract We report the results of chromosome maps of wheat homoeologous chromosomes 4A, 4B, and 4D using 40 RFLP markers and 39 homozygous deletion lines. Deletion breakpoints divide the chromosomes into 45 subarm intervals with 32 intervals distinguished by molecular markers. The chromosome maps confirm the homoeology of arms 4AS to 4BL and 4DL, and 4AL to 4BS and 4DS. The chromosome map of 4A reveals novel information concerning the 4AL-5AL-7BS cyclical translocation. The presence of homoeologous group-4 long-arm markers, *Xksu G10* and *Xpsr 1051*, intervening between the translocated 5AL and 7BS chromosome segments in 4AL suggests that the translocation events are more complex than was earlier believed. Chromosome maps confirm a pericentric inversion in Chinese Spring chromosome 4B. The consensus chromosome map is compared to the genetic map of wheat to construct a cytogenetic ladder-map (CLM). The CLM reveals an unequal distribution of recombination along the length of the chromosome arms. Recombination is highest in the distal half, and low in the proximal half, of the chromosome arms.

Key words Genetic linkage-map · Chromosome map · Cereal · Deletion mapping

Introduction

Cytologically based physical maps, or chromosome maps, are idiograms of wheat chromosomes depicting the positions of C-bands, deletion breakpoints, and the distribution of markers (Werner et al. 1992; Gill 1994). Chromosome maps are aligned to corresponding genetic maps by drawing lines between mutual loci, resulting in cytogenetic ladder-maps (CLMs) (Gill and Gill 1994). CLMs have been constructed for wheat chromosome 1B (Kota et al. 1993), as well as for homoeologous groups 2 and 3 (Delaney et al. 1994a, b), 6 (Gill et al. 1993), and 7 (Werner et al. 1992; Hohmann et al. 1994). The CLMs reveal a non-random distribution of RFLP loci and recombination along the length of the chromosome arms, with the distal region correlating with the highest densities of both molecular markers and recombination. Saturation mapping of specific gene-rich regions will expedite map-based cloning of genes in wheat. In this report we present the CLM of the group-4 chromosomes of wheat.

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Deletion stocks and RFLP markers

Thirty-nine homozygous deletion lines were used in the mapping of RFLP markers (Endo and Gill 1994). Breakpoints for each deletion are calculated from at least five C-banded chromosomes and are expressed as a fraction-length of the distance from the centromere. Because of their indirect calculation, fraction-lengths are not accurate and are regarded as only approximations of the deletion breakpoints. Forty low-copy probes were mapped and are listed in Table 1. The markers include seven barley cDNA probes (*Xbcd*, Cornell University, Ithaca, N.Y.), 12 oat cDNA probes (*Xcdo*, Cornell University, Ithaca, N.Y.), two *Triticum tauschii* (Coss) Schmal. genomic probes (*Xksu*, Kansas State University, Manhattan, Kan.), 13 wheat cDNA probes (*Xpsr*, Plant Science Research, Cambridge England), and six wheat genomic probes (*Xwg*, Cornell University, Ithaca, N.Y.). Of the 40 RFLP markers used, 17 are common among the A, B, and D genomes; three map only to the A and B genomes, one to the A and D genomes, seven to the B and D genomes, eight to the A genome, one to the B genome, and three to the D genome (Table 1, Fig. 1).

Table 1 Clones, restriction enzymes used, number of bands, and number of bands scored

Clone[a]	Restriction enzyme and number of bands[b]		Number of bands scored			Clone[a]	Restriction enzyme and number of bands[b]		Number of bands scored		
			4A	4B	4D				4A	4B	4D
Xcdo 38	*Eco*RI	8	1	1	1	*Xksu G10*	*Hin*dIII	3	1	1	1
Xcdo 189	*Eco*RI	3	1	1	1	*Xpsr 104*	*Hin*dIII	3	1	1	1
Xcdo 484	*Eco*RI	3	1			*Xpsr 110*	*Hin*dIII	8	1	1	1
Xcdo 488	*Eco*RV	7	1			*Xpsr 115*	*Dra*I	4	1		
Xcdo 541	*Eco*RI	3	1	1	1	*Xpsr 119*	*Eco*RI	8	1		
Xcdo 1312	*Eco*RI	5		1	1	*Xpsr 139*	*Hin*dIII	7	1	1	1
Xcdo 1333	*Eco*RI	8		1	1	*Xpsr 144*	*Hin*dIII	7	1	1	1
Xcdo 1337	*Eco*RV	6	1	1		*Xpsr 157*	*Hin*dIII	7	1	1	1
Xcdo 1338	*Eco*RI	4	1		1	*Xpsr 160*	*Eco*RI	3	1		
Xcdo 1387	*Eco*RI	3			1	*Xpsr 163*	*Hin*dIII	3	1	1	1
Xcdo 1395	*Dra*I	5		1		*Xpsr 541*	*Hin*dIII	2			1
Xcdo 1400	*Eco*RV	5	1			*Xpsr 580*	*Eco*RV	4	1		
Xbcd 110	*Eco*RI	6	1	1	1	*Xpsr 584*	*Eco*RI	3	1	1	1
Xbcd 734	*Eco*RV	4	1	1		*Xpsr 1051*	*Hin*dIII	3	1	1	1
Xbcd 808	*Eco*RI	6	1			*Xwg 114*	*Eco*RI	4		1	1
Xbcd 1006	*Eco*RI	3	1	1	1	*Xwg 181*	*Eco*RI	3		1	1
Xbcd 1092	*Dra*I	4	1	1	1	*Xwg 184*	*Hin*dIII	8	1		1
Xbcd 1262	*Eco*RI	3		1	1	*Xwg 212*	*Eco*RI	3		1	1
Xbcd 1652	*Eco*RV	4	1	1		*Xwg 622*	*Eco*RI	12		1	1
Xksu C002	*Hin*dIII	6		1	1	*Xwg 876*	*Eco*RI	4	1	1	1

[a] *Xcdo*=Oat cDNA; Cornell University, Ithaca, N.Y.; *Xbcd*=Barley cDNA; Cornell University, Ithaca, N.Y.; *Xksu=Triticum tauschii* genomic DNA; Kansas State University, Manhattan, Kan.; *Xpsr*=Wheat genomic DNA; Plant Science Research Institute, Cambridge, England; *Xwg*=Wheat genomic DNA; Cornell University, Ithaca, N.Y.

[b] Includes major and minor brands

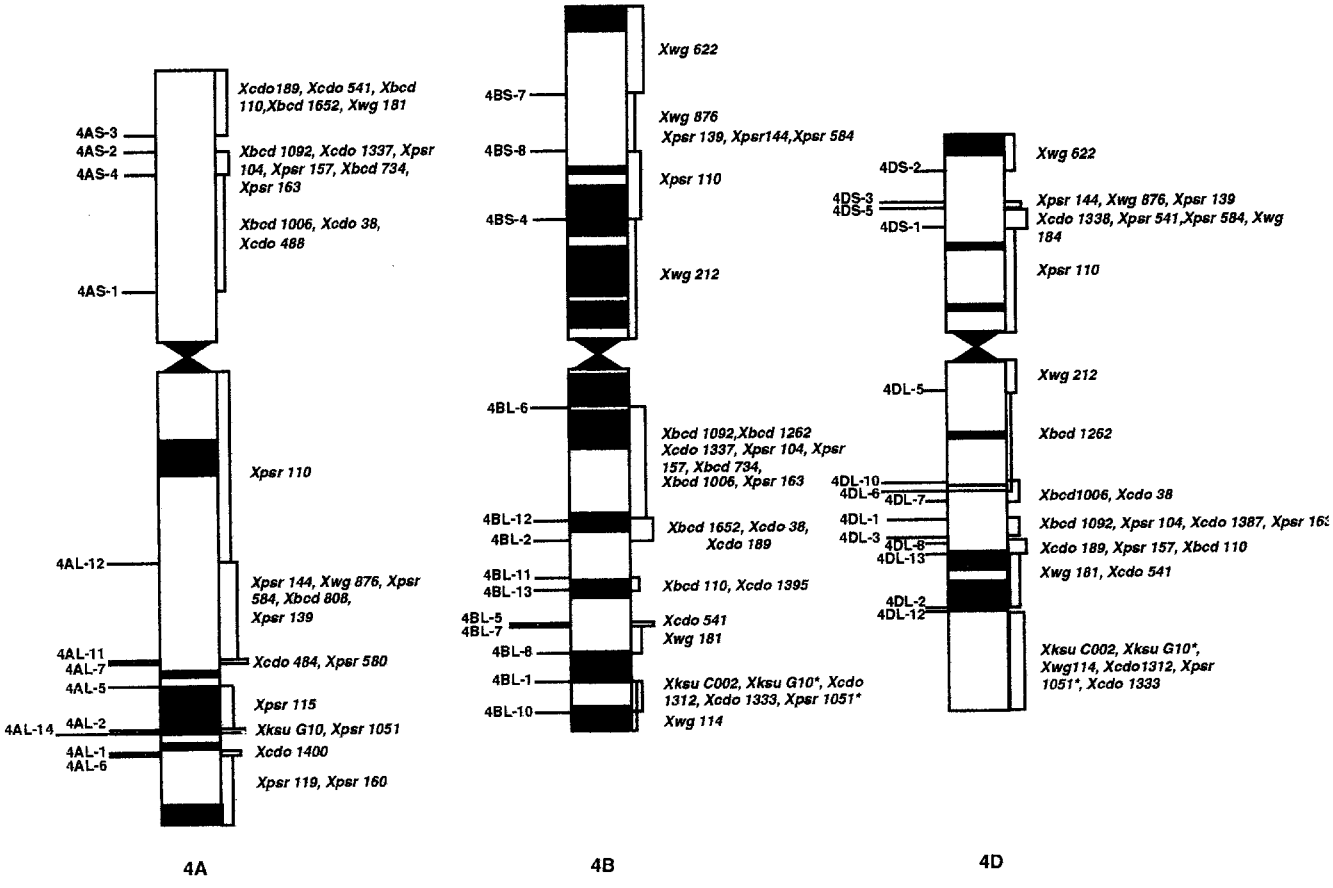

Fig. 1 Chromosome maps of wheat chromosomes 4A, 4B, and 4D. Deletions are shown at their approximate locations to the left of each chromosome and the distribution of RFLP loci is positioned on the right

Chromosome maps

Forty RFLP markers and 39 homozygous deletion lines were used to construct the homoeologous group-4 chromosome maps shown in Fig. 1. Deletion breakpoints divide the chromosomes into 45 sub-arm intervals with 32 tagged by molecular markers. The chromosome maps reveal sub-arm intervals with high densities of markers. For example, the sub-arm interval defined by deletions 4DL-1 and 4DL-13 on chromosome arm 4DL represents approximately 10% of the chromosome arm and contains 7 of the 19 probes mapped on the arm (Fig. 1).

The group-4 chromosome maps confirm previous results that chromosome arm 4AS is homoeologous to 4BL and 4DL, and 4AL is homoeologous to 4BS and 4DS (Hart and Langston 1977; Benito et al. 1984; Hart 1987; Naranjo et al. 1987; Anderson et al. 1992; Liu et al. 1992; Devos and Gale 1993). Co-linearity of the molecular markers that map to the A, B, and D genomes is maintained except for marker *Xcdo 38*. On chromosome arm 4BL *Xcdo 38* maps distal to *Xpsr 104*, *Xpsr 157*, and *Xbcd 1092*. However, on chromosome arm 4AS and 4DL, *Xcdo 38* maps proximal to the loci *Xpsr 104*, *Xpsr 157*, and *Xbcd 1092*. The reason for this discrepancy is not known.

The chromosome map of 4A confirms the cyclical translocation involving 4AL, 5AL, and 7BS (Naranjo et al. 1987; Anderson et al. 1992; Liu et al. 1992). Clones *Xpsr 580*, *Xcdo 484*, and *Xpsr 115* map between deletions 4AL-11 and 4AL-2 and are donated by chromosome arm 5AL. Clones *Xcdo 1400*, *Xpsr 119*, and *Xpsr 160* map distal to deletion 4AL-1 and are donated by chromosome arm 7BS. A notable new finding is the detection of homoeologous 4L markers, *Xksu G10* and *Xpsr 1051*, in the distal 4AL arm between deletions 4AL-2 and 4AL-14. Notice that these markers intervene between the 5AL and 7BS translocated segments (Figs. 1, 2). The positions of *Xksu G10* and *Xpsr 1051* are exceptional because all other markers that map on the cytologically long arms of chromosomes 4B and 4D reside on the cytologically short arm of chromosome 4A (Fig. 1). The presence of markers *Xksu G10* and *Xpsr 1051* on the cytologically long arm of chromosome 4A suggests that the gross chromosomal rearrangements that chromosome 4A suffered are much more complex than was earlier believed. A diagrammatic representation of the genetic constitution of chromosome 4A is shown in Fig. 2.

Another notable finding is the detection of a pericentric inversion involving chromosome 4B. RFLP locus *Xwg 212* maps proximal to deletion 4BS-4 on the short arm of chromosome 4B and proximal to deletion 4DL-5 on the long arm of chromosome 4D (Fig. 1). This confirms earlier observations, based on C-banding and arm-ratio analysis, that Chinese Spring chromosome 4B contains a pericentric inversion (Gill et al. 1991).

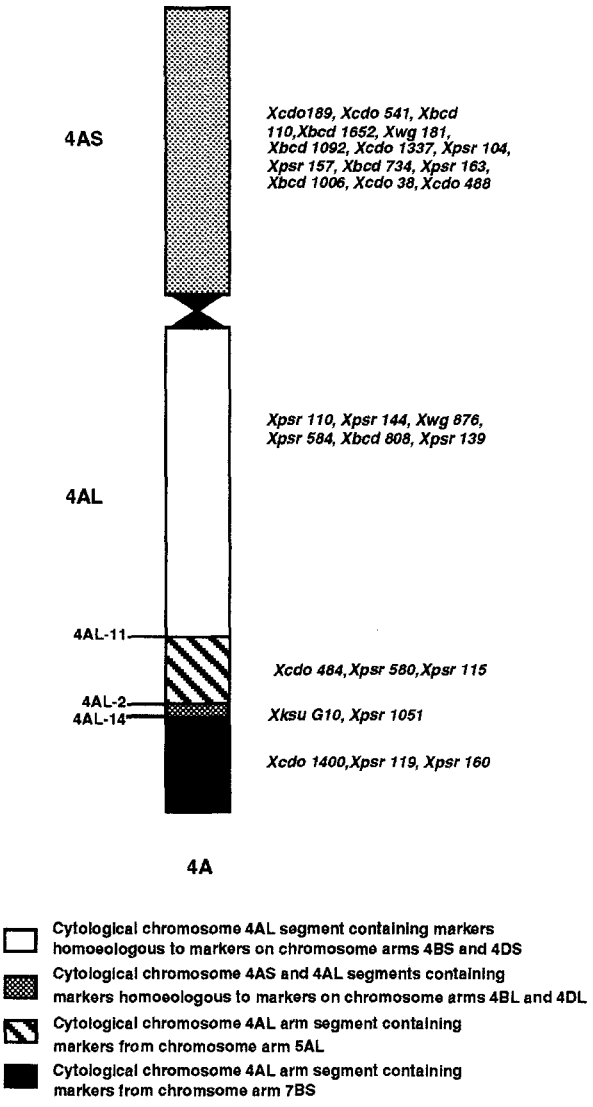

Fig. 2 Diagrammatic representation of the genetic constitution of chromosome 4A. The long-arm segment flanked by the deletions 4AL-2 and 4AL-14 is not drawn to scale

Chromosome consensus map

The similar order of RFLP markers among the A, B, and D genomes of the group-4 chromosomes indicated that homoeology was relatively conserved and a group-4 chromosome consensus map was constructed by ordering the deletion breakpoints of the homoeologous chromosomes. Deletion breakpoint orders are determined from fraction-length estimations and the results from RFLP analysis. However, since chromosome 4A has suffered several rearrangements, deletion breakpoints of the group-4 consensus map are ordered according to chromosomes 4B and 4D only. RFLP loci from chromosomes 4A, 4B, and 4D are allocated to the shortest chromosome interval while maintaining the linear order of markers.

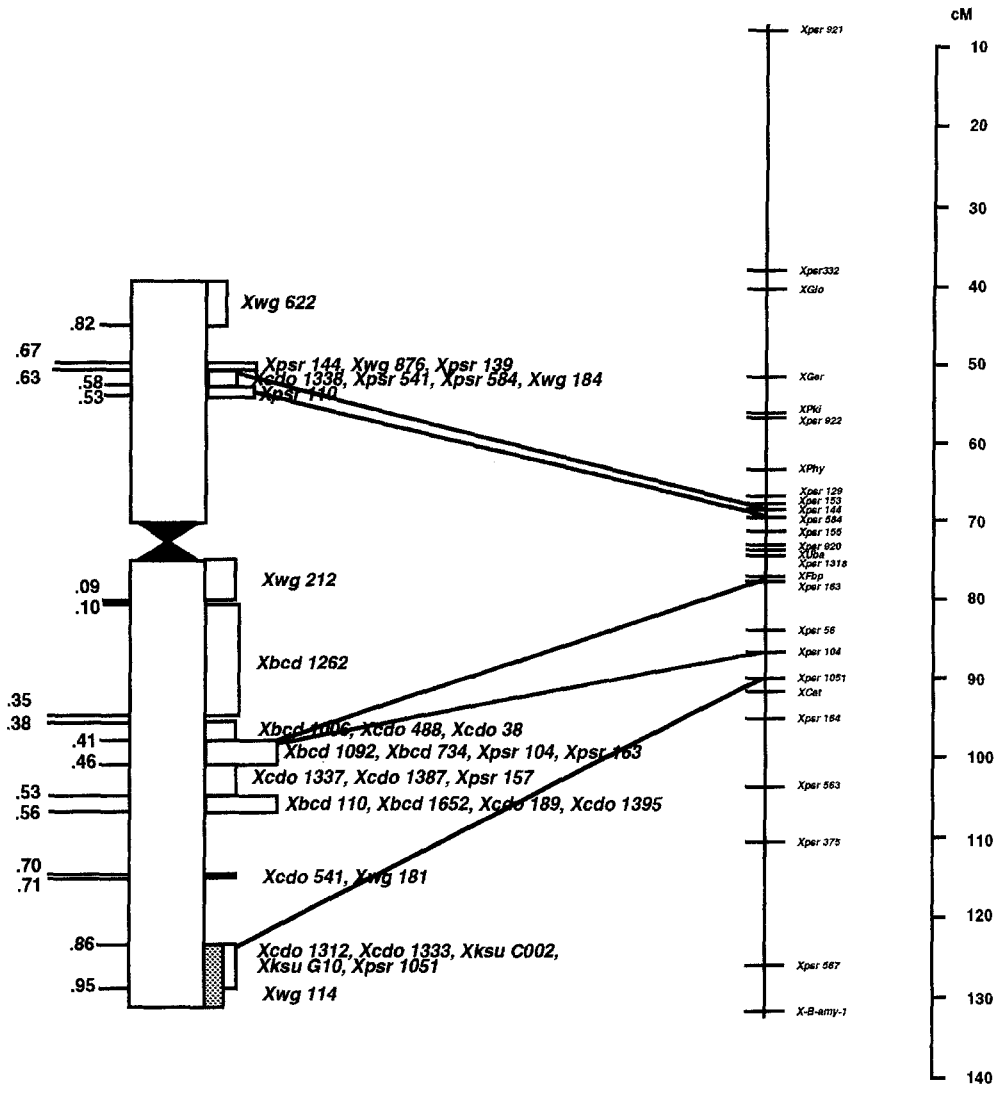

Fig. 3 Cytogenetic ladder-map (CLM) of the consensus group-4 chromosome map (left) and the consensus group-4 genetic map (right). Chromosomes are aligned at the approximate location of the centromere and mutual loci are connected by *lines*. Fraction-length estimates of deletion breakpoints are shown to the left of the chromosome map. The distribution of RFLP markers is shown to the right of both chromosome and genetic maps. The CLM shows the unequal distribution of recombination along the physical length of the chromosome. The genetic map was adapted from Devos and Gale (1993)

Notice the non-random distribution of molecular markers within three regions on the group-4 consensus map (Fig. 3). The short-arm region between deletion breakpoints 0.53 and 0.67 contains eight of the nine markers mapped. On the long arm, two marker-rich regions contain 20 of the 24 markers included on the consensus map. The long-arm region defined by deletion breakpoints 0.38 and 0.56 contains 14 markers and the long-arm region distal to deletion breakpoint 0.86 contains six markers (Fig. 3). The observed non-random distribution of markers on the wheat chromosomes indicates that the effective size of the wheat genome for molecular manipulation is smaller than the total size.

Cytogenetic ladder-map

The group-4 consensus chromosome map was aligned to the consensus group-4 wheat genetic map (Devos and Gale 1993) and is presented as a CLM in Fig. 3. The CLM clearly reveals the unequal distribution of recombination along the length of the chromosome arms. The consensus CLM shows the high level of recombination in the distal portion of the chromosome arms. The distal half of the short arm represents over 70 cM of recombination and the distal half of the long arm represents over 50 cM. Recombination is suppressed in the proximal half of the short and long chromosome arms where less than 20 cM of recombination occurs. Unequal distribution of recombination along the physical length of chromosome arms is observed in barley (Linde-Laursen 1979), wheat (Dvorak and Chen 1984; Curtis and Lukaszewski 1991; Werner et al. 1992; Gill et al. 1993; Kota et al. 1993; Lukaszewski and Curtis 1993), rye and triticale (Lukaszewski 1992). Note the clustering of markers in the long arm between deletion breakpoints 0.38 and 0.46 (Fig. 3). This region represents 10 cM of recombination and appears recombinogenic compared to the proximal half of the short arm (53% of the length) and the long arm (41% of the length) which together represent less

than 10 cM of recombination. Because this region is rich in markers and appears to be recombinogenic, it would be an ideal region to begin saturation mapping.

Conclusion

The CLM of the group-4 chromosomes shows a non-random distribution of recombination along the length of the chromosome arms. Recombination is low in the proximal portion of the chromosome arms and is high in the distal portion. The distribution of markers, too, is non-random and often correlates with regions of high recombination. The chromosome maps confirm previous evidence that the cytologically short arm of chromosome 4A is homoeologous to the cytologically long arms of chromosomes 4B and 4D and that the cytologically long arm of chromosome 4A is homoeologous to the cytologically short arms of chromosomes 4B and 4D. However, the group-4 chromosome maps reveal novel information; namely, that markers *Xksu G10* and *Xpsr 1051* reside on the cytologically long arms of chromosomes 4A, 4B, and 4D and intervene between the translocated 5AL and 7BS chromosome segments. The chromosome maps also confirm a pericentric inversion in Chinese Spring chromosome 4B from the allocation of marker *Xwg 212*.

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