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Comparative RFLP maps of the homoeologous group-2 chromosomes of wheat, rye and barley

K. M. Devos, T. Millan*, and M. D. Gale

Cambridge Laboratory, Colney Lane, Norwich, NR4 7UJ, United Kingdom

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Summary. Genetic maps of the homoeologous group-2 chromosomes were constructed, comprising 114 loci in wheat and 34 loci in rye. These include the genes coding for sucrose synthase, sedoheptulose-1,7-bisphosphatase, a bZIP protein (EmBP-1), a peroxidase and an abscisic acid-induced protein (#7). Overall, gene orders are highly conserved in the genomes of wheat, barley and rye, except for the distal ends of chromosome arms 2BS and 2RS, which are involved in interchromosomal, probably evolutionary, translocations. Clustering of loci in the centromeric regions of the maps, resulting from the concentration of recombination events in the distal chromosomal regions, is observed in wheat and rye, but not in barley. Furthermore, loci for which homoeoloci can be detected in rye and barley tend to lie in the centromeric regions of the maps, while non-homoeologous and wheat-specific loci tend to be more evenly distributed over the genetic maps. Mapping of the group-2 chromosomes in the intervarietal 'Timgalen' × 'RL4137' cross revealed that the *T. timopheevi* chromosome segment introgressed into chromosome 2B in 'Timgalen' is preferentially transmitted. Recombination is also greatly reduced in that segment.

Key words: Wheat – Rye – Barley – RFLP – Biochemical markers – Genetic maps

* *Present address:* Department of Genetics, ETSIA, Apdo 3048, 14080 Cordoba, Spain
Correspondence to: K. M. Devos

Introduction

In hexaploid bread wheat, *Triticum aestivum* (2n = 6x = 42), several traits, including resistance to several *Erysiphe graminis* D.C. (powdery mildew), *Puccinia graminis* Per. (stem rust), *Puccinia recondita* Rob.ex Desm (leaf rust), *Puccinia striiformis* Westend. (yellow rust) and *Tilletia carries* (D.C.) Tul. (bunt) strains, are controlled by genes on the homoeologous group-2 chromosomes (McIntosh 1988 and subsequent supplements). Other genes with agronomic importance are the semi-dwarfing genes, *Rht7* (Worland et al. 1980) and *Rht8* (Worland and Law 1986), located on chromosomes 2A and 2D, and the photoperiod response genes *Ppd1*, *Ppd2* and *Ppd3* also located on the group-2 chromosomes (Scarth and Law 1983).

The few morphological markers and disease resistance genes mapped to date on the homoeologous group-2 chromosomes of wheat include two linkage blocks, *Tg* (tenacious glumes) – *Lr22* (leaf rust resistance) – *W2* (glaucousness) reported by Dyck and Kerber (1970) and *Rht8* – *D4* (clump dwarf) – *Ppd1* – *Yr16* (yellow rust resistance) reported by Worland et al. (1986). Recently, genetic maps of the wheat genome, comprising mainly anonymous gDNA RFLP markers, have also been presented (Liu and Tsunewaki 1991).

In this paper we report the comparative mapping of 48 DNA probes, including 6 of known function, on the group-2 chromosomes of wheat, rye and barley. Two biochemical marker genes, subtilisin inhibitor and esterase-6, were also located. The DNA probes, most of which are wheat genomic or cDNA clones, have been characterized for their ability to reveal RFLP at each locus and their signal strength in rye and barley.

Table 1. Known function clones

Locus	Clone	Function	Source	Reference
XPer	POX375	Peroxidase	R. Dudler	Rebmann et al. (1991)
XSs2	pST3	Sucrose synthase	P. Carbonero	Maraña et al. (1988)
XSbp	S9.2	Sedoheptulose-1,7-bis-phosphatase	T. Dyer	Raines et al. (1992)
XEmbp	pGC19	bZIP protein	R. Quatrano	Guiltinan et al. (1990)
Xpsr899	#7	ABA-induced cDNA	M. Gulli	Personal communication

Materials and methods

Genetic stocks

DNA probes with homologous sequences in the group-2 chromosomes were identified by hybridization to DNA from nullisomic-tetrasomic (NT) and ditelosomic (DT) lines (Sears 1954) of the cv 'Chinese Spring' (CS) as described by Sharp et al. (1989). Their chromosomal locations in rye and barley were confirmed by analysis of the CS/*Secale cereale* cv 'Imperial' (Driscoll and Sears 1971) and CS/*Hordeum vulgare* cv 'Betzes' (Islam et al. 1981) single chromosome addition lines.

Classification of the probes and potential heterozygosity values for individual loci or sets of loci were assessed from hybridization patterns obtained with panels of 13 or 15 wheat varieties, 13 barley varieties and the two parents of the rye mapping population, as described in Devos et al. (1992a).

Mapping data were collected in populations of 120 F_2 or their F_3 families from two wheat crosses, CS × 'Synthetic' and 'Timgalen' × RL4137; a rye cross, Ds2 × RxL10; and a barley cross, *H. vulgare* cv 'Captain' × *H. spontaneum* (IPSR#2370).

Markers

DNA probes

Anonymous probes include 14 cDNA clones from the library described by Chao et al. (1989) (PSR100-PSR200), 4 gDNA clones from a wheat leaf *Pst*I library (Harcourt 1992). (PSR300-PSR460) and 22 gDNA clones from wheat *Pst*I and *Eag*I libraries (Devos et al. 1992a) (PSR540-PSR699; PSR900-PSR999). Known function clones are listed with their source in Table 1.

Protein loci

A subtilisin inhibitor, *Si-R1*, shown to be located on 2R, was analyzed as described by Koebner (1990). The grain esterase loci on the homoeologous group-2 chromosomes, *Est-6*, were characterized according to the method of Petchey et al. (1990).

RFLP mapping procedures

All techniques of DNA extraction, restriction enzyme digestion, gel electrophoresis, Southern transfer, probe labelling, filter hybridization and linkage analysis, using MAPMAKER 2.0, supplied by E. S. Lander, Whitehead Institute for Biomedical Research, Cambridge Mass, USA, were performed as described by Devos et al. (1992a).

Results

DNA probes were classified by their ability to detect homologous sequences in rye and barley and by whether the locations of hybridizing fragments could be defined as homoeologous sets, as described in Table 2 and Devos et al. (1992a). The chromosome arm locations of sequences with homology to these probes, their copy number per chromosome arm in wheat, barley and rye, and their relative signal strength in barley and rye are also given in Table 2.

Homoeologous group 2

The RFLP-based genetic maps of the homoeologous group-2 chromosomes constructed using the wheat cross CS × 'Synthetic', the rye cross Ds2 × RxL10, and the barley cross *H. vulgare* × *H. spontaneum* are presented in Fig. 1. Fifty-nine loci were mapped in CS × 'Synthetic', and 26 of the 33 polymorphic loci detected with the 39 probes that gave adequately strong signals in rye were mapped in Ds2 × RxL10. In the barley cross 6 loci were mapped to allow a comparison of gene order and recombination frequencies across the three Triticeae species.

A comparison of the level of polymorphism detected by the 37 homoeologous group-2 class *a*, *b*, *c*, and *d* probes revealed that 19 2A, 16 2B and 24 2D loci could be mapped in the wide cross CS × 'Synthetic', while only 4 2A and 6 2D, but 31 2B loci were polymorphic between 'Timgalen' and RL4137. 'Timgalen' carries an introgressed *T. timopheevi* segment in its 2B chromosome (R. A. McIntosh, personal communication), and the high level of polymorphism and the presence of rare alleles on chromosome 2B of 'Timgalen' indicates that most of this chromosome is of alien origin. Analysis of the segregation ratios in this cross revealed that all 16 2B loci examined showed distorted segregation ratios with preferential inheritance (72–82% instead of the expected 50%) of the *T. timopheevi* alleles, while both the 2A and 2D homoeoalleles were inherited in a Mendelian 1:2:1 or 3:1 fashion. Analysis of the segregation ratios of the same loci in the CS × 'Synthetic' population, essentially a wide cross involving a cultivated AB genotype × '*T. dicoccum*' and a cultivated D genotype × *Ae. squarrosa*, showed the expected ratios, $P > 0.05$, for 56 out of 59 loci.

Table 2. Chromosomal location in wheat, copy number in wheat (W), barley (B) and rye (R), and relative hybridization in rye and barley for different classes of group-2 probes

Probe	Chromosomal location in Chinese Spring			Copy number[f]			Signal strength[h]	
	A	B	D	W	B	R	B	R
cDNA class *a* Probes hybridizing within a homoeologous group, and showing strong signals in rye and barley								
pST3[a](*XSs2*), PSR107, PSR126, PSR135, PSR137, PSR146	2AS	2BS	2DS	1	1	1	+ + +	+ + +
POX375[a](*XPer*)	2AS	2BS	2DS	3	3	3	+ +	+ +
#7[a,b](*Xpsr899*)	–	2BS	–	1	1	1	+ + +	+ + +
	6AS	–	6DS	1				
PSR100	2AS	2BS	2DS	1	2	2	+ + +	+ + +
	5AL	5BL	5DL	1				
PSR102, PSR112	2AL	2BL	2DL	1	1	1	+ + +	+ + +
PSR108[c]	2AS	2BS	2DS	1	2	2	+ + +	+ + +
	7AS	7BS	7DS	1				
PSR109	2AS	2BS	2DS	4	5	5	+ + +	+ + +
	5AL	5BL	5DL	1				
PSR130	2AS	2BS	2DS	1	2	1	+ + +	+ + +
PSR131	2AS	2BS	2DS	1	1	2	+ + +	+ + +
PSR143	2AS	nd[d]	nd	1	1	1	+ + +	+ + +
PSR150	2AS	2BS	2DS	1				
	5AL	5BL	5DL	1	3	3	+ + +	+ + +
	7AS	7BS	7DS	1				
PSR151	2AL	2BL	2DL	2	1	1	+ + +	+ + +
cDNA class *b* Probes hybridizing within a homoeologous group, but with additional copies on other chromosomes, and showing strong signals in rye and barley								
pGC19[a] (*XEmbp*)	–	3BL	–	1				
	5AL	5BL	5DL	1	1	4	+ + +	+ + +
	6AL	6BS	–	1				
	–	–	7DL	1				
S9.2[a](*XSbp*)	–	2BS	–	1				
	–	2BL[e]	–	–	1	1	+ + +	+ + +
	3AL	3BL	3DL	1				
	–	7BL	–	1				
gDNA class *a* Probes hybridizing within a homoeologous group, and showing strong signals in rye and barley								
PSR304, PSR331, PSR901, PSR934	2AL	2BL	2DL	1	1	1	+ +	+ +
PSR380, PSR388, PSR630, PSR641, PSR919	2AL	2BL	2DL	1	1	1	+ + +	+ + +
PSR390	2AL	2BL	2DL	1	1	2	+ + +	+ + +
PSR571	2AL	2BL	2DL	1	2	1	+ +	+ +
PSR666	2AS	2BS	2DS	1	1	1	+ + +	+ + +
PSR687	2AL	2BL	2DL	1	2	4	+ +	+ +
	7AL	7BL	7DL	1				
PSR692	2AL	2BL	2DL	1	3	3	+ +	+ +
gDNA class *b* Probes hybridizing within a homoeologous group, but with additional copies on other chromosomes, and showing strong signals in rye and barley								
PSR540	2AL	2BL	2DL	1	3	1	+ + +	+ + +
	–	7BS	–	1				
PSR912	2AS	2BS	2DS	1	2	1	+ + +	+ + +
	5AL	–	5DL	1				
PSR946	–	–	2DS	1				
	7AL	–	7DL	1	1	1	+ +	+ + +
	–	–	7DS	2				

Table 2. (*Continued*)

Probe	Chromosomal location in Chinese Spring			Copy number[f]			Signal strength[h]	
	A	B	D	W	B	R	B	R
gDNA class *c*	Probes hybridizing within a homoeologous group, and showing weak signals in rye and/or barley							
PSR379	2AS	2BS	2DS	2	–	1	+	+ +
PSR566	2AS	–	2DS	3	–	–	+	+
PSR609	2AL	2BL	2DL	2	–	M[g]	+	+ +
PSR649	2AS[e]	–	2DS	M	–	M	–	+ + +
PSR900	2AS	2BS	2DS	3^{A} $1^{B,D}$	–	3	+	+ +
PSR928	2AS	–	2DS	2	–	2	–	+ + +
PSR932	2AL	2BL	2DL	1	–	1	+	+ +
PSR933	2AS	–	2DS	3^{A} 1^{D}	4	–	+ +	–
gDNA class *d*	Probes hybridizing within a homoeologous group, but with additional copies on other chromosomes, and showing weak signals in rye and/or barley							
PSR681	2AL	2BL	2DL	1				
	–	–	6DS	1	–	3	+	+ + +
	–	7BL	–	1				
PSR903	–	–	2DS	1				
	3AS	3BS	3DS	1	–	–	+	+
	–	–	5DS	1				
gDNA class *e*	Probes hybridizing in a non-homoeologous fashion, and showing weak signals in rye and/or barley							
PSR549	1AL	–	–	4				
	–	2BS[e]	–	1	–	4	–	+ +
	3AL	–	–	1				
PSR593	–	2BS	–	1				
	–	4BS	–	1	–	–	–	+
	–	7BL	–	1				
PSR908	–	1BS	–	1				
	2AS[e]	–	2DS	1	–	–	–	–
		6BL	–	1				

Note: For PSR probes, more detailed descriptions of their characteristics, including charts of the CS fragment sizes in different restriction digests, are available

[a] Known function clones, see Table 1

[b] The sequences detected by #7 on chromosomes 6AS, 2BS and 6DS are probably homoeologous, since this probe is thought to be involved in a 2BS/6BS translocation

[c] Underlined probes have not been mapped

[d] nd, No data available

[e] Location obtained by linkage in varieties other than CS which is null at these loci

[f] The copy number is determined from the minimum number of hybridizing bands per genome over four restriction digests

[g] Moderately repeated probe (> 4 copies)

[h] The relative strength of the hybridization signal in comparison to wheat: + + +, signal comparable in strength to wheat; + +, weaker, but adequate signal; +, weak signal; –, no detectable hybridization

Knowledge of the chromosome arm location of unmapped loci and the evident conservation of gene order in the three wheat and the rye and the barley genomes (Fig. 1) allowed the placement, with some confidence, of a further 54 markers in wheat and 8 loci in rye, in addition to the mapped loci. The resulting consensus maps of wheat and rye and the level of polymorphism associated with each locus in wheat are shown in Fig. 2.

A deletion in DT 6BS

Hybridization of PSR108, PSR109, PSR666 and PSR899 to DNA from NT and DT lines of CS showed the absence of the 2BS band both in stocks lacking chromosome arm 2BS and in DT 6BS, indicating that the distal end of the short arm of chromosome 2B, where these probes subsequently were mapped, was deleted in the Cambridge Laboratory ditelosomic 6BS line.

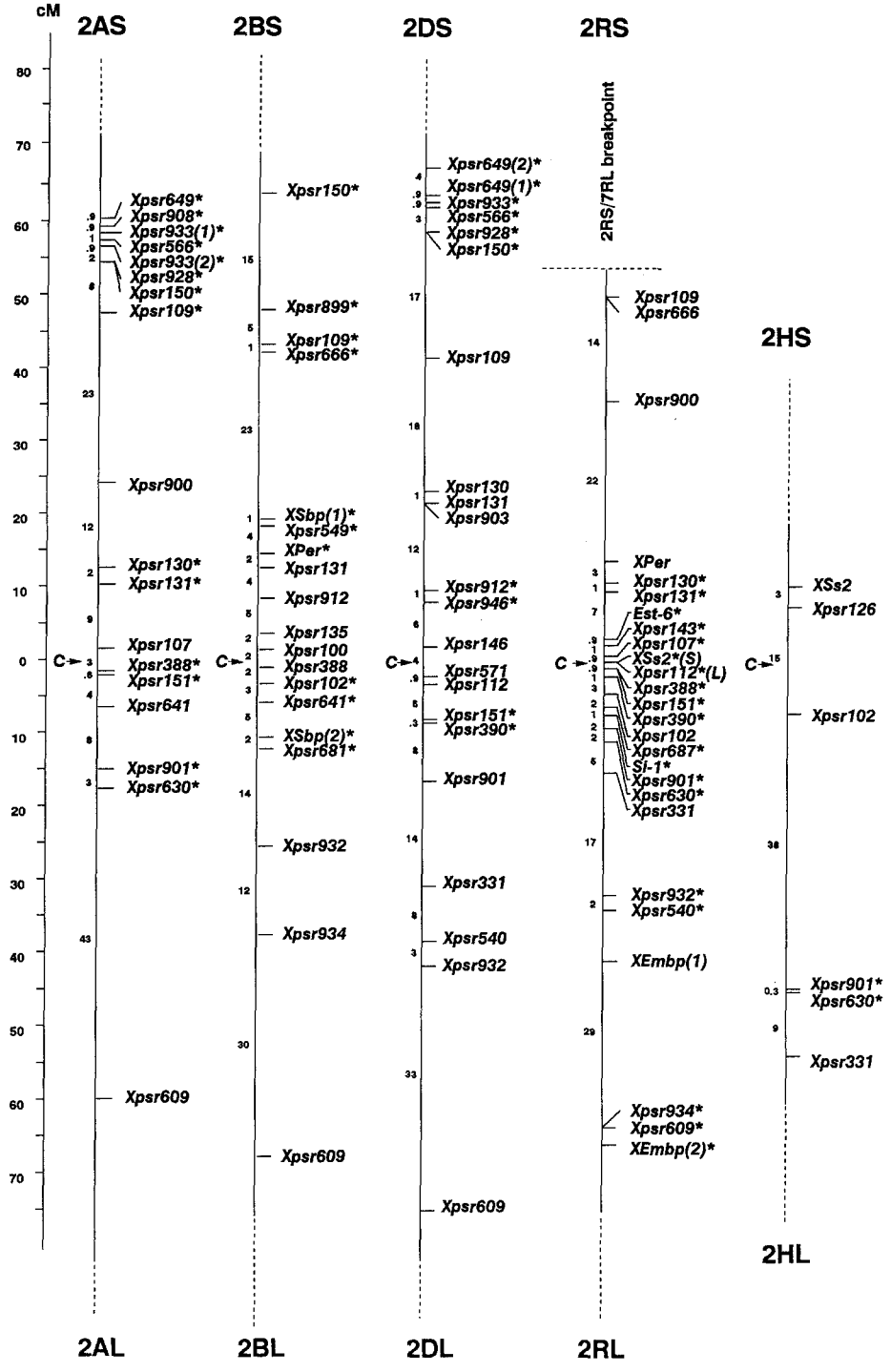

Fig. 1. RFLP maps of the homoeologous group-2 chromosomes of wheat, rye and barley. For many loci, the map position could be unequivocally determined (LOD > 2.5). For the marked (*) loci, which were detected by RFLP probes scored as 3:1 segregations, only a preferred location (LOD < 2.5) could be given

Discussion

Genetic maps

Homoeologous group-2 maps

The genetic maps of the wheat homoeologous group-2 chromosomes, shown in Fig. 1, comprise 59 RFLP loci, while 22 RFLP and two protein markers, *Si-1* and *Est-6*, were mapped on 2R. The markers along the wheat and rye chromosomes are clustered in the centromeric regions of the genetic maps, a feature that has also been observed in the homoeologous groups-1

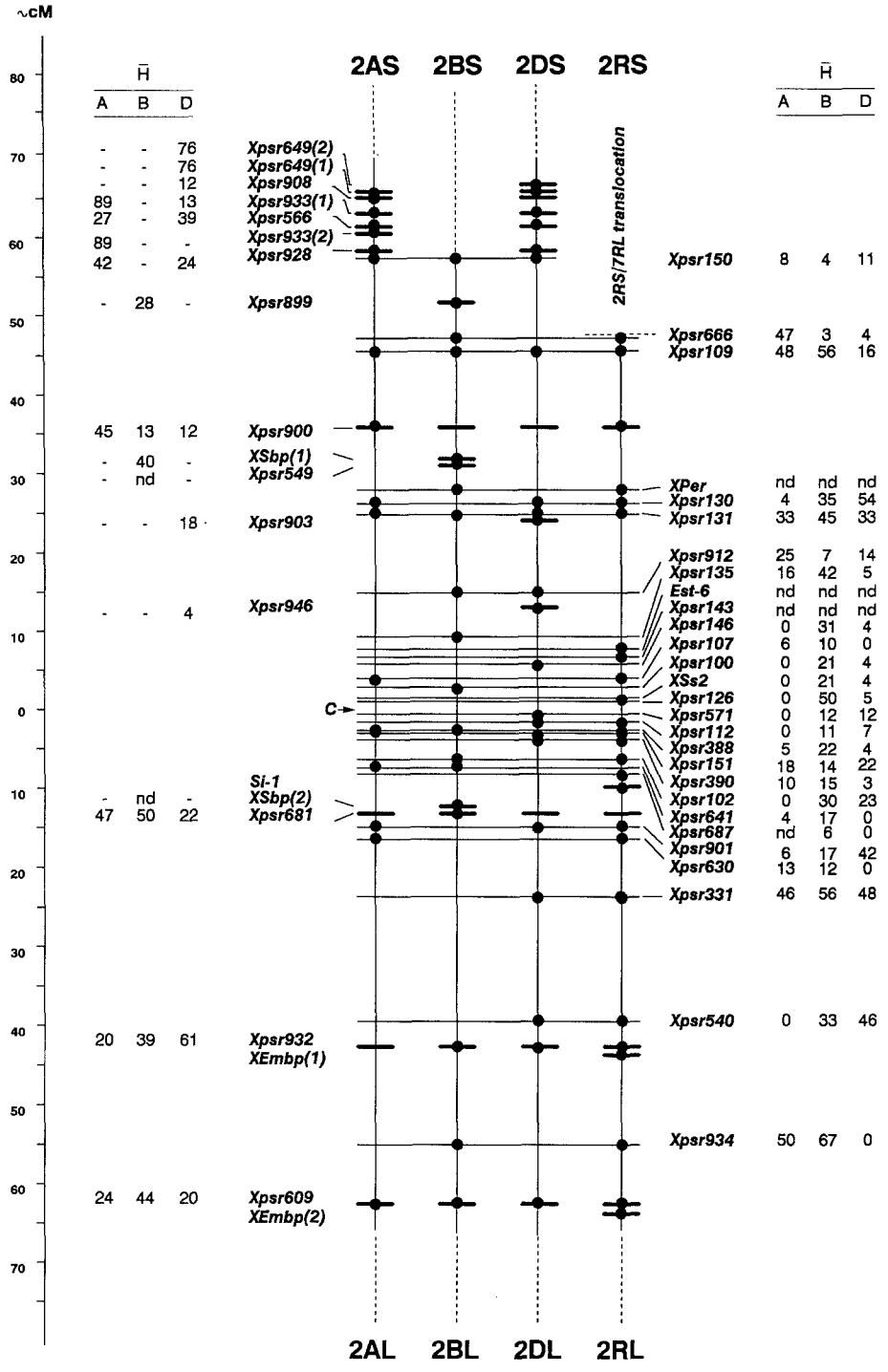

Fig. 2. Consensus maps of the homoeologous group-2 chromosomes of wheat and rye. ● Mapped loci, *full lines over the A, B, D and R chromosomes* indicate loci detected by class *-a* and *-b* probes (adequate hybridization signals in rye and barley), *bold line fragments* indicate map positions of non-conserved loci, *nd* no data available. $\bar{H} = 1 - \Sigma p_i^2$, were p_i is the frequency of each allele *i* in the sample of 15 wheat varieties, meaned over *Eco*RI, *Eco*RV, *Dra*I and *Hin*dIII digests. Potential heterozygosity values are calculated per chromosome rather than for individual gene copies, i.e. no account has been taken of copy number where this is > 1

(Wang et al. 1991), 3 (Devos et al. 1992a) and 7 (Chao et al. 1989) chromosomes. Overall, co-linearity between the chromosomes within a homoeologous group was conserved, except for the distal regions of the short arms of chromosomes 2B and 2R, which were likely to be involved in interchromosomal translocations. Few homoeoloci were mapped by Liu and Tsunewaki (1991), so that similar observations could not be made.

Rearrangements of 2BS

The group of tightly linked loci in the distal 2S chromosome region was composed of *Xpsr150*, a set of single-copy loci on the homoeologous group-2 chromosomes, and *Xpsr928, Xpsr933, Xpsr566, Xpsr908* and *Xpsr649*, which were detected by probes with homoeoloci on 2A and 2D, but not 2B (Fig. 3). The failure of all probes for loci distal to *Xpsr150* to detect sequences in the 2B genome indicated that this chromosome region had been deleted. Furthermore, the identification of clone #7 (PSR899) with homoeoloci on the short arms of chromosomes 2B, 6A, and 6D suggested the existence of a 2BS/6BS translocation. The distal map positions of *Xpsr899-6A* and *-6D* on the short arms of chromosomes 6A and 6D, obtained in preliminary linkage studies (unpublished results) was consistent with this hypothesis. The genetic location of *Xpsr150-2B* distal to *Xpsr899-2B* was unexpected, however, but can be explained if one postulates a translocation event in which part of the original 2BS became lost while the remaining distal segment became inverted. This result requires confirmation in other wheat varietal crosses.

Rearrangements of 2RS

Probes mapping distal to *Xpsr666* and *Xpsr109* which gave an acceptable signal in rye (PSR928, PSR649) could be shown to be located on 7R in the 'Imperial' rye addition lines. Linkage of these loci with other genes on 7RL has been confirmed (Rognli et al. 1992) in the Ds2 × RxL10 population. The identical location in these three independent rye genotypes indicates that the translocation is likely to be evolutionary, i.e., to have arisen during the speciation of *S. cereale*, and characterizes the rye genome.

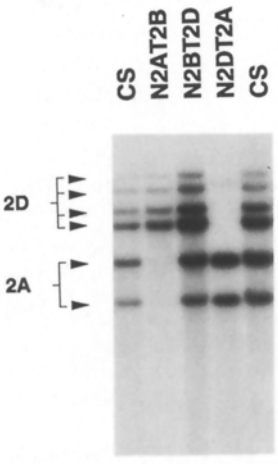

Fig. 3. Southern analysis of the homoeologous group-2 nullisomic-tetrasomics digested with *Hin*dIII and probed with PSR928

Map distances

Although the gene order was generally conserved between the three wheat genomes, and extended to the rye and barley genomes, the genetic distances between individual markers varied considerably. The observed recombination values between proximal loci were much higher in barley than in wheat and rye, while the more distal chromosome regions showed reduced recombination. Therefore, the characteristic clusters of sequences that span the centromeres on the genetic maps of wheat and rye chromosomes and presumably result from extreme localization of crossing-over were absent in barley (Fig. 1). This was also reported by Wang et al. (1992) in a study of chromosomes 1R and 1H. Examination of the barley RFLP maps constructed by Heun et al. (1991) and Graner et al. (1991) also reveals some clustering of sequences along the chromosomes. However, since the positions of the centromeres were not determined, no direct correlation could be made between the distribution of markers on these barley maps and the centromeric clustering observed in the wheat and rye maps.

A comparison of the map distances between the same loci on chromosomes 2A, 2B, and 2D suggests that chromosome 2D recombines more frequently than either 2A or 2B. This is demonstrated well on the short arm by the single-copy *Xpsr131* locus, which is located at a distance of 10 cM from the middle of the interval spanning the centromere on 2A, 12 cM on 2B and 22 cM on 2D. Similarly, *Xpsr932-2B* mapped 26 cM from the centromere on the long arm, while the genetic distance centromere – *Xpsr932-2D* amounts to 42 cM. A similar trend whereby D-genome chromosomes in the same CS × 'Synthetic' cross have higher recombination values than their homoeologous A and B chromosomes has also been observed for the group-3 chromosomes (Devos et al. 1992a). This would indicate that, in this cross, recombination occurs more readily between the *Ae. squarrosa* and the cultivated D genome than between the *T. dicoccum* AB and the cultivated AB genomes. Any extrapolation to cultivated wheat varieties is, of course, not possible at present. However, it is important to identify any such differences between genomes in order to predict the relative efficiency of gene 'tags' in the three genomes.

Duplicated loci

A number of probes, identified in Table 2, detect more than one locus per chromosome arm, and these probes should be employed with caution since there is growing evidence that some multigene families are dispersed over genetically large distances. The two copies of *XEmbp* on the long arm of chromosome 2R (Fig. 1) show this clearly. Others, however, such as the

chromosome-specific probe PSR454 on 3BL (Harcourt and Gale 1991) and PSR649 on 2DS identify multiple copies that are localized.

A study of interchromosomal duplications, shown by the multichromosomal locations in Table 2, indicates a tendency for group-2 clones to hybridize preferentially with sequences on group-5 and 7 chromosomes. At present, the data is too fragmentary to postulate an evolutionary relationship between these chromosomes, but the hypothesis should be considered as evidence accumulates.

Mapping of known function clones and isozymes

Four known function clones, *XPer*, *XSs2*, *XSbp* and *XEmbp*, were mapped on the homoeologous group-2 chromosomes of wheat, rye and barley. *XPer*, one of the three loci detected by the pathogen-induced clone POX375 (Rebmann et al. 1991), is located on the short arm of the homoeologous group-2 chromosomes and is likely to correspond with the isozyme marker *Per-2* (Bosch et al. 1986). However, as yet, no isozyme studies have been carried out to confirm the co-segregation of both peroxidase markers. *XSs2*, a single locus detected by a cDNA probe coding for a sucrose synthase enzyme (Maraña et al. 1988), also mapped on the short arm of the group-2 chromosomes. The *XSs2* locus, for which a group-2 location has been confirmed by P. Carbonero (personal communication), showed tight linkage with the centromere. The chromosomal locations and variability in wheat, barley and rye of the *XSbp* loci, detected by the S9.2 (Raines et al. 1992) probe, and the *XEmbp* loci, detected by pGC19 (Guiltinan et al. 1990), have been described elsewhere in detail (Devos et al. 1991, 1992b). A subtilisin inhibitor, *Si-1*, previously located on chromosome arm 2RS by analysis of the CS/*S. cereale* 2RS ditelocentric chromosome addition lines (Koebner 1990), mapped on the long arm, but close to the centromere (Fig. 1).

Chromosome 2B of 'Timgalen'

The relatively high level of allelic variation detected on chromosome 2B in the 'Timgalen' × RL4137 cross probably derives from the fact that 'Timgalen' has a *T. timopheevi* (AAGG) chromosome segment carrying stem rust (*Sr36*) and powdery mildew (*Pm6*) resistance genes (R. A. McIntosh, personal communication). Segregation patterns at the 16 2B RFLP loci mapped in this cross showed distortions with preferential inheritance (~ 80%) of the alien alleles. In a study of the inheritance of stem rust resistance transferred from *T. timopheevi* to a common wheat variety, Nyquist (1962) reported that pollen carrying the alien chromosome segment on 2B was greatly favored over pollen lacking this segment. Indeed, preferentially transmitted alien chromosomes are commonly observed in cytogenetic studies of Triticeae genomes (Endo 1990). A 2B genetic map based entirely on aberrant segregation ratios was constructed in the 'Timgalen' × RL4137 cross. This linkage map showed reduced recombination in the chromosome region analyzed (*Xpsr131* – *Xpsr934*) and was only partially co-linear with the other wheat maps and the rye and barley maps. This latter observation is probably the result of an effect of distorted segregation ratios on the MAPMAKER linkage analysis and is not necessarily a reflection of chromosomal rearrangements in the *T. timopheevi* segment.

Conservation of sequences and levels of polymorphism

The co-linearity between the wheat, rye and barley maps allowed the interpolation of additional markers on the four linkage maps (Fig. 2). An analysis of the distribution of sequences along the chromosomes showed that the centromeric clusters mainly comprised loci which were detected by probes that provided strong signals in wheat, barley and rye (probe classes *a* and *b*), while class *c*, *d*, *e* and *f* probes tended to be more evenly distributed over the genetic maps. If this is indeed a general situation, then a corollary is that if total map coverage is required, mapping should be carried out, at least in part, by probes derived from the target species. Indeed, mapping with cDNAs, which tend to hybridize well across genera and species, would have provided a very limited group-2 map, since only seven of the 18 cDNAs mapped more than 20 cM from the centromeres. Consequently, the points on the consensus map for the homoeologous group 2 presented here will find different applications. The homoeologous loci, shown on the right-hand side of Fig. 2, will be of value in further comparative mapping and particularly in the manipulation of alien chromosomes or segments introgressed to wheat. The non-homoeologous loci, shown on the left-hand side of the figure, will be of more value in intervarietol wheat genetic studies and breeding, particularly so because the levels of polymorphism are often reasonably high.

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