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RFLP-based maps of the homoeologous group-6 chromosomes of wheat and their application in the tagging of *Pm12*, a powdery mildew resistance gene transferred from *Aegilops speltoides* to wheat

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Abstract Genetic maps of the homoeologous group-6 chromosomes of bread wheat, *Triticum aestivum*, have been constructed spanning 103 cM on 6A, 90 cM on 6B and 124 cM on 6D. These maps were transferred to a Chinese Spring (CS)×line #31 cross to locate a dominant powdery mildew resistance gene, *Pm12*, introgressed into line #31 from *Aegilops speltoides*. *Pm12* was shown to lie on the short arm of translocation chromosome 6BS-6SS.6SL in line #31, but could not be mapped more precisely due to the lack of recombination between the 6S *Ae. speltoides* segment and chromosome 6B. Possible strategies to reduce the size of the alien segment, which probably encompasses the complete long arm and more than 82% of the short arm of chromosome 6B, are discussed.

Key words *Ae. speltoides* · *T. aestivum* · RFLP · *Pm12* · Powdery mildew · Genetic maps

Introduction

Powdery mildew of wheat, caused by the fungus *Erysiphe graminis* f. sp. *tritici*, is one of the major diseases of wheat in Northern Europe as well as many other parts of the world, and can cause yield losses of up to 5% (Priestley and Bayes 1988). Several genes that confer resistance to different *E. graminis* pathogen isolates have been identified in wheat and its closely related species. A few of these have been incorporated into commercial wheat varieties but none has provided durable resistance (Bennett 1984). Strategies such as gene pyramiding, cultivar diversification and cultivar mixing may lead to increased resistance to powdery mildew. The effective use of such strategies depends greatly on the availability of a range of resistance genes that have previously not been widely used in breeding programmes. Extensive screening of bread-wheat varieties in many countries has yielded relatively few useful resistance genes; however, other members of the Triticeae family have the potential to provide a large pool of new resistance alleles and genes (Bennett 1984). Miller et al. (1988) identified several accessions of *Ae. speltoides* that carried resistance to powdery mildew, and introgressed one of the genes, *Pm12*, into bread wheat.

This paper describes the construction of a genetic map of the homoeologous group-6 chromosomes of wheat in a cross between the variety Chinese Spring (CS) and a synthetic hexaploid wheat, and the application of this map to locate the introgressed *Pm12* gene.

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Materials and methods

Plant material

Chinese Spring (CS) nullisomic-tetrasomic (NT) (Sears 1954) and ditelosomic (DT) (Sears and Sears 1979) lines were employed to determine the chromosome arm locations of RFLP loci and estimate their copy number. The group-6 genetic map was constructed using a population of 120 F_2 plants from the cross CS×'Synthetic' (the amphiploid *Triticum dicoccum*×*Aegilops tauschii*) (McFadden and Sears 1946; Sears 1976). *Pm12*, a dominant powdery mildew resistance gene from *Ae. speltoides* (JIC accesssion 2140008), was introgressed into the UK spring wheat variety Wembley to give line #31 (Miller et al. 1988). An F_2 population of 154 plants derived from the cross CS line #31 was used for mapping. RFLP loci were mapped either in the complete population or in a subset of plants.

Pm12 screening

The presence of the *Pm12* gene was assessed both in a glasshouse screen and a detached seedling leaf test as described in Miller et al. (1988).

DNA probes and marker analysis

cDNA and genomic clones were developed at the John Innes Centre (Chao et al. 1989; Devos et al. 1992; Harcourt 1992), or were obtained from the Japanese Rice Genome Project (RGC-clones, Kurata et al. 1994), B. Gill (KSU-clones, Gill et al. 1991), D. Grant (NPI-clones, personal communication), A. Breiman (TAV1929, personal communication), A. Kleinhofs (bNRp10, Cheng et al. 1986), D. Baulcombe (501, Lazarus et al. 1985; 2437, Baulcombe et al. 1987), R. Quatrano, (pGC19, Guiltinan et al. 1990), M. O'Dell (pTA71, Gerlach and Bedbrook 1979), J.G. Scandalios (pCat2.1c, Bethards et al. 1987), R. Thompson (pTag53, Bartels and Thompson 1983) and M. Gulli (ABA7; Gulli et al. 1995). A microsatellite sequence, PSR3200, isolated from a random *Sau*3A library and shown by NT analysis to be located on chromosome 6D (K. M. Devos, unpublished), was also mapped. RFLP analysis and classification of the DNA probes was carried out as described by Devos et al. (1992). Polymerase chain reaction (PCR) conditions were as described in Devos et al. (1995). Linkage analyses were performed using Mapmaker v.3.0, Whitehead Institute for Biomedical Research, Cambridge, Mass., USA.

Results

The homoeologous group-6 genetic map

In all, 62 DNA loci were mapped on the three group-6 homoeologues (Table 1 and Fig. 1). Of these, 38 were members of homoeologous sets of loci, i.e. were identified with RFLP probes which have previously been shown by aneuploid analysis and/or genetic mapping to detect homoeoloci on the A, B and D genomes of wheat and other Triticeae species. The remaining 24 loci were non-homoeologous, or chromosome-specific. These include supernumary gene 'copies' detected by cDNA probes, sequences detected by genomic probes, a microsatellite marker, and a nucleolar organising region. Map lengths spanned 103 cM on 6A, 90 cM on 6B and 124 cM on 6D. A con-

Table 1 Copy number, chromosome arm location and the locus detected by homoeologous group-6 probes

Probe	Locus	Type[b]	Copy number[c]	Location
PSR3200	*Xpsp3200*	MS	1	6DS
pTA71	*Nor*	G	H	1AS 1BS, 5AS 5DS, 6BS
bNRp10	*Xak466 (Nra)*	C	2	6AS 6BS 6DS, 7AS 4AL 7DS
2437	*Xpsr8 (Cxp3)*	C	L	6AS 6BS 6DS
pTag53	*Xpsr10 (Gli-2)*	C	M	6AS 6BS 6DS
pGC19	*Xrsq805 (Embp)*	C	L	3BL, 5AL 5BL 5DL, 6AL, 6BS, 7DL
pCat2.1c[a]	*Xpsr484 (Cat)*	C	2	5AL 4BL 4DL, 6AS 6BS 6DS
RGC69	*Xrgc69*	C	2	6AS 6BS 6DS, 7AL 7BL 7DL
pTtksuG8*	*XksuG8*	G	L	6BS
pTtksuG48*	*XksuG48*	G	L	6DS
ABA7	*Xpsr899*	C	1	6AS 2BS 6DS
PSR106	*Xpsr106*	C	2	6AS 6BS 6DS
PSR113	*Xpsr113*	C	1	6AS 6BS 6DS
PSR141*	*Xpsr141 (Pgk2)*	C	2	6AS 6BS 6DS
PSR167	*Xpsr167*	C	2	5B, 6AS 6BS 6DS
PSR301*	*Xpsr301*	G	L	6AS 6BS 6DS
PSR312	*Xpsr312*	G	1	6AS 6BS 6DS
PSR551[a]	*Xpsr551*	G	1	2BS, 6BS
PSR563	*Xpsr563*	G	L	4DL, 6AS, 7AS 7DS
PSR627	*Xpsr627*	G	1	6AS 6BS 6DS
PSR662	*Xpsr662*	G	L	1BS, 6AS, 7AS 7BS 7DS
PSR681[a]	*Xpsr681*	G	L	2AL 2BL 2DL, 6DS, 7BL
PSR831	*Xpsr831*	C	2	6AS 6BS 6DS
PSR904	*Xpsr904*	G	2	3AL 3DL, 6AS
PSR962	*Xpsr962*	G	L	6BS 6DS
PSR964	*Xpsr964*	G	L	6BS 6DS
PSR967*	*Xpsr967*	G	M	1A 1B, 4B, 5A, 6A
501	*Xpsr2 (a-Amy-1)*	C	L	6AL 6BL 6DL
RGC74*	*Xrgc74*	C	L	4D, 5A 5B 5D, 6BL
Npi253	*Xnpi253*	G	2	6AL 6BL 6DL, 7AS 7BS 7DS
pTtksuD12	*XksuD12*	G	1	6DL
PSR88[a]	*Xpsr88*	C	1	6AL 6BL 6DL
PSR142	*Xpsr142 (Prk)*	C	1	6AL 6BL 6DL
PSR149	*Xpsr149*	C	1	6AL 6BL 6DL
PSR154	*Xpsr154*	C	1	6AL 6BL 6DL
PSR371	*Xpsr371*	G	1	6AL 6BL 6DL
PSR546	*Xpsr546*	G	1	6BL 6DL
PSR605	*Xpsr605*	G	1	6AL 6BL 6DL
PSR908	*Xpsr908*	G	L	1BS, [2AS] 2DS, 6BL
PSR915	*Xpsr915*	G	L	6AL 6BL 6DL
PSR966*	*Xpsr966*	G	M	6AL 6BL 6DL
TAV1929*	*Xtav1929 (Cyp)*	C	2	6AS 6BS 6DS, 6AL

[a] The fragments to which these probes hybridize have not been mapped
[b] MS indicates microsatellite, G=genomic DNA clone, C=cDNA clone
[c] Copy number estimation based on number of hybridizing fragments; L=low copy (3–5), M=moderately repeated, H=highly repeated
* Not all hybridizing fragments have been allocated to chromosomes

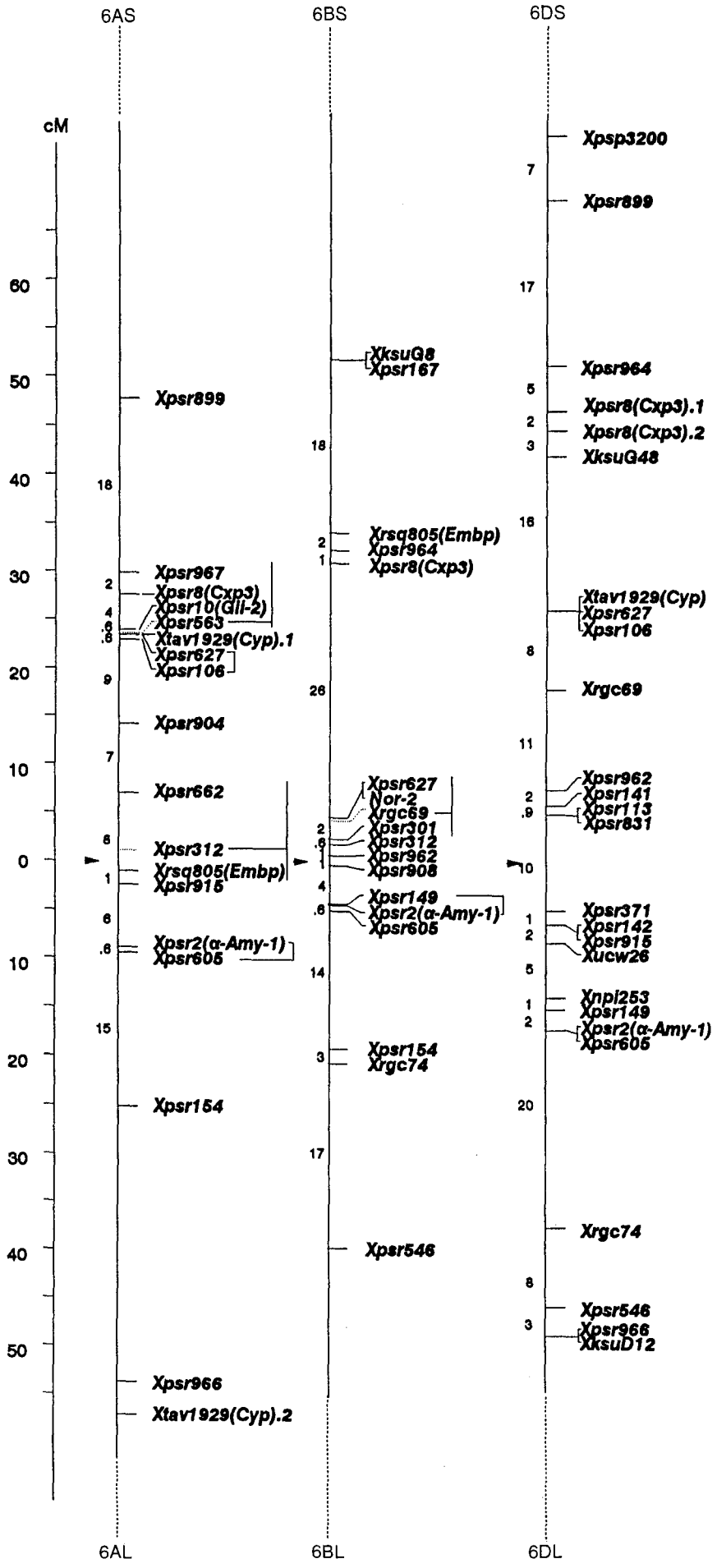
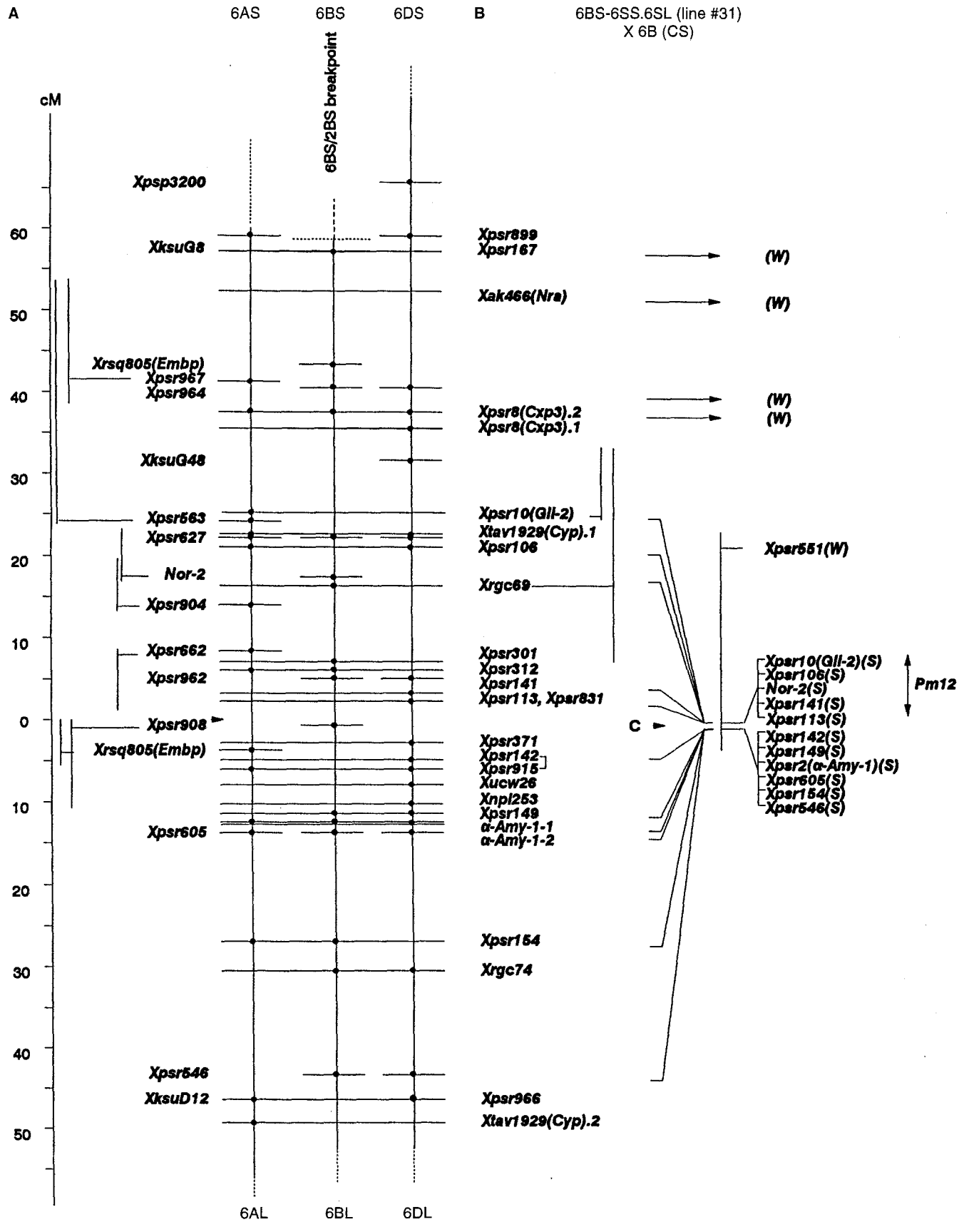


Fig. 1 Genetic maps of the homoeologous group-6 chromosomes of bread wheat. Centromeres are indicated by *arrows*. *Vertical bars* indicate the extent of the possible location of loci for which a unique map position could not be determined


A
6AS
6BS
6DS
6BS/2BS breakpoint
cM
Xpsp3200
XksuG8
Xrsq805(Embp)
Xpsr967
Xpsr964
XksuG48
Xpsr563
Xpsr627
Nor-2
Xpsr904
Xpsr662
Xpsr962
Xpsr908
Xrsq805(Embp)
Xpsr605
Xpsr546
XksuD12
6AL
6BL
6DL
B
6BS-6SS.6SL (line #31)
X 6B (CS)
Xpsr899
Xpsr167
(W)
Xak466(Nra)
(W)
(W)
Xpsr8(Cxp3).2
Xpsr8(Cxp3).1
(W)
Xpsr10(Gli-2)
Xtav1929(Cyp).1
Xpsr106
Xpsr551(W)
Xrgc69
Xpsr301
Xpsr312
Xpsr141
Xpsr113, Xpsr831
C
Xpsr371
Xpsr142
Xpsr915
Xucw26
Xnpi253
Xpsr149
α-Amy-1-1
α-Amy-1-2
Xpsr10(Gli-2)(S)
Xpsr106(S)
Nor-2(S)
Xpsr141(S)
Xpsr113(S)
Xpsr142(S)
Xpsr149(S)
Xpsr2(α-Amy-1)(S)
Xpsr605(S)
Xpsr154(S)
Xpsr546(S)
Pm12
Xpsr154
Xrgc74
Xpsr966
Xtav1929(Cyp).2

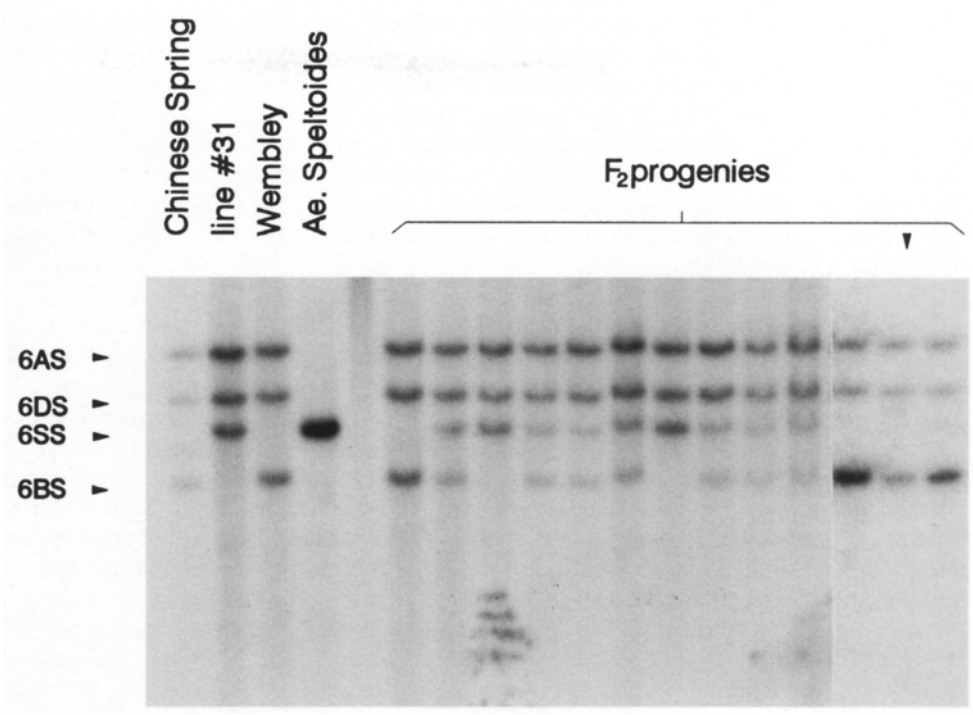


Fig. 3 Autoradiograph showing the hybridization pattern obtained with probe PSR113 to *Sst*I-digested DNA of CS, line #31, Wembley and *Ae. speltoides* (accession JIC2140008) and F_2 progenies from the cross CS line #31. The track indicated (▼) is the susceptible F_2 plant, hemizygous for the 6BS and 6SL loci, described in the text

sensus map of the homoeologous group-6 chromosomes is presented in Fig. 2. This consensus map includes both mapped points and the extrapolated locations of homoeoloci. Most points were located in the CS 'Synthetic' population, but a few were mapped only in rye or barley populations and shown by aneuploid analysis to be located on the wheat group-6 chromosomes.

Mapping of *Pm12*

Sixteen probes that detect loci on the homoeologous group-6 chromosomes (PSR546, PSR154, PSR605, 501, PSR149, PSR142, PSR113, PSR141, pTA71, PSR106, pTag53, 2437, PSR964, bNRp10, PSR167 and PSR551) (Table 1) were hybridized to *Eco*RI-, *Eco*RV-, *Dra*I-, *Hin*dIII- and *Sst*I-digested genomic DNA of CS, line #31, Wembley, and *Ae. speltoides* (Fig. 3). A comparison of the hybridization patterns with those of 21 CS NT lines showed that, within the resolution of our group-6 map, all of the long arm and a segment of the short arm, spanned by the centromere and *Xpsr10(Gli-2)*, of chromosome 6B of Wembley had been replaced by a chromosome segment of *Ae. speltoides* in line #31. Chromosomes 6A and 6D of line #31 carried wheat, i.e. Wembley, alleles at all loci examined. Eleven markers detected variation between chromosomes 6B of Wembley and line #31, and CS and line #31. One locus, *Xpsr551*, was polymorphic between chromosomes 6B of CS and line #31. The remaining four probes (2437, PSR964, bNRp10 and PSR167) gave identical hybridization patterns in CS, Wembley, and line #31. Markers showing polymorphism were mapped. *Pm12* co-segregated with the *Ae. speltoides* segment on chromosome 6B.

In all but one plant, the short arm loci *Xpsr10(Gli-2), Xpsr106, Nor-2, Xpsr141(Pgk2)* and *Xpsr113*, and the long arm loci *Xpsr142(Prk), Xpsr149, Xpsr2(a-Amy-1), Xpsr605, Xpsr154* and *Xpsr546*, were linked in the CS×line #31 population (Fig. 2), indicating a lack of recombination between the *Ae. speltoides* and wheat chromatin. In the single susceptible plant, the short arm carried Wembley alleles, while the long arm carried *Ae. speltoides* alleles. A comparison of the relative intensities of the hybridizing fragments indicated that this plant was hemizygous for the DNA probe sequences on chromosome arms 6BS and 6SL (Fig. 3). Therefore, we can conclude that *Pm12* is located in the short arm region of the translocated segment.

Fig. 2 Consensus map of the homoeologous group-6 chromosomes. **A** Centromeres are indicated by *arrows*. *Vertical bars* indicate the possible location of loci for which unique map positions could not be determined. (●) indicates mapped loci. *Intersections without dots* indicate likely map locations of loci identified by aneuploid analysis and extrapolated from the position(s) of mapped homoeoloci. **B** Genetic map of chromosome 6B (CS) 6BS-6SS.6SL (line #31) and its comparison to the consensus map. The origin of the alleles, detected with 16 probes in line #31, are indicated (W=Wembley, S=*Ae. speltoides*). The probes flanking the chromosome segment that carries the *Pm12* gene, are delineated by a *double-sided arrow*

Discussion

The CS×'Synthetic' map

Due to the low level of recombination in the centromeric region (Devos et al. 1992, 1993), genetic maps of bread

wheat typically show strong clustering of loci. Clustering, however, is much less pronounced in the genetic maps of the homoeologous group-6 chromosomes compared to those of other groups. This may, in part, be explained by the relatively small numbers of markers on the map. In addition, the low ratio (38/24) of homoeologous/non-homoeologous loci mapped may contribute to the lack of clustering, as the centromeric clusters of other wheat maps are comprised mainly of homoeologous loci (Devos et al. 1993).

Chromosome 6B carries the *Nor-B2* locus and a compression of the genetic map in the region of this locus is apparent when comparing the genetic maps of homoeologous chromosomes 6A, 6B and 6D. While the *centromere – Xpsr627* region spans approximately 23 cM on 6A and 26 cM on 6D, this distance is only about 4 cM on 6B. The distance *centromere – Xpsr8(Cxp3)*, on the other hand, amounts to 28 cM on 6A, 30 cM on 6B and 45 cM on 6D. Thus, it appears that, while recombination events are suppressed in the vicinity of the *Nor-B2* locus, they occur more frequently in the distal regions. The overall recombination frequency on chromosome 6B was not affected. The reduction of recombination in *Nor* regions was even more pronounced on the genetic map of chromosome 1B where the genetic length of the short arm, from centromere to the *Xpsr11(Glu-3)* locus, is 33 cM on 1A, 9 cM on 1B and 49 cM on 6D (K. M. Devos and M. D. Gale, unpublished results). No increase in recombination in the region distal to *Nor-B1* was observed. The physical location of the *Nor-B1* and *Nor-B2* loci is about 70% and 50–70% from the centromere on the short arms of chromosomes 1B and 6B respectively (Riley et al. 1958).

The genetic map of CS×line #31

Line #31 is a BC_5F_3 product of a Wembley×*Ae. speltoides* cross with Wembley as the recurrent parent (Miller et al. 1988). The genomes of line #31 and Wembley are expected to be highly similar, except for the chromosome carrying the introgressed *Ae. speltoides* segment. Monosomic analysis of line #31 had previously indicated that *Pm12* was likely to be located on a group-6 chromosome (Miller et al. 1988). Therefore, a sample of DNA probes covering the homoeologous group-6 chromosomes was hybridized to Wembley, line #31, and *Ae. speltoides*. RFLP analyses clearly indicated that the *Ae. speltoides* segment carrying the *Pm12* gene had been introgressed into chromosome 6B and that line #31 carries a translocated chromosome 6BS-6SS.6SL with a breakpoint between *Xpsr8(Cxp3)* and *Xpsr10(Gli-2)*. These results are in agreement with pairing data of CS double ditelosomics for group 6 with chromosomes of line #31. In testcross F_1 progenies, both arms of chromosomes 6A and 6D paired fully with their homologues in line #31. The 6B telosomes, however, rarely paired. Interestingly, but possibly coincidentially, the 6BS-6SS.6SL translocation breakpoint is identical, within the limits of precision offered by the available marker loci, to the evolutionary translocation breakpoint from the segment of rye chromosome 6 transferred to rye chromosome 4 (Devos et al. 1993). The discrepancy between the results of the monosomic analysis, which indicated that *Pm12* had been introgressed into chromosome 6A (Miller et al. 1988), and the present RFLP analysis, which clearly shows that *Pm12* is carried by chromosome 6BS-6SS.6SL, may be due to the small number of F_2 plants (28) tested for powdery mildew resistance in the monosomic analysis.

As expected, nearly all of the observed recombination was localised distal to *Xpsr10(Gli-2)*, the most distal 6SS marker on chromosome 6BS-6SS.6SL (Fig. 2). The relative position of the *Xpsr551* locus with respect to *Xpsr8(Cxp3)*, *Xpsr964*, *Xak466(Nra)* and *Xpsr167* could not be determined as PSR551 did not detect polymorphism between the homoeologous group-6 chromosomes of CS and 'Synthetic', the parents of our main wheat mapping population. None of the other four probes revealed polymorphism between chromosomes 6B of CS and line #31. No recombination was observed between wheat chromosome 6B and the segment of 6S from *Ae. speltoides*. However, a single susceptible F_2 plant which carried Wembley alleles at all of the short arm loci and *Ae. speltoides* alleles at all of the long arm loci was identified. Since this plant was hemizygous for the 6BS and 6SL loci and the breakpoint was in the centromere region, it is likely that chromosome breakage took place following misdivision of unpaired 6B and 6BS-6SS.6SL chromosomes, giving rise to 6BS, 6BL, 6BS-6SS, and 6SL telocentrics, followed by the subsequent inclusion, and possible reunion, of chromosome arms 6BS and 6SL in one nucleus. The mildew-susceptible status of this F_2 plant allowed us to place the *Pm12* resistance gene on 6SS, in the segment spanned by *Xpsr10(Gli-2)* and the centromere.

Physical length of the *Ae. speltoides* segment

Genetic mapping indicated that the *Ae. speltoides* segment in line #31 spans the long arm and a segment of the short arm, including the locus *Xpsr10(Gli-2)*.Physically, the *Gli-2* locus has been determined to lie in the distal 18% of the short arm (Dvořák and Chen 1984), indicating that the 6BS segment in the 6BS-6SS.6SL chromosome is less than 18% of the short arm. The large amount of alien DNA in line #31 may account for the yield depression that appears to be correlated with the *Pm12* resistance gene (T. E. Miller and S. M. Reader, unpublished results). As line #31 was backcrossed five times during development, it is unlikely that further backcrossing will result in recombination between the wheat and *Ae. speltoides* segments. As more analyses of this type are undertaken on introgression lines carrying useful genes, more instances where the target genes are carried in a large segment of alien chromatin will be discovered. Probably the only recourse available to provide breeders with acceptable starting material will be to return to a relaxation of homoeologous pairing control, followed by re-selection for both the target gene and flanking markers. RFLPs are particularly effective for this breeding application because most probes that detect ho-

moeologous loci give signals in both cultivated wheat and wild relatives and reveal the required polymorphism.

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