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# RFLP-based genetic maps of the homoeologous group 5 chromosomes of bread wheat (*Triticum aestivum* L.)

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## Markers

Thirty-eight anonymous cDNA and gDNA clone sequences from the libraries described in Devos et al. (1992) were shown to be located on the homoeologous group 5 chromosomes of wheat by nullisomic-tetrasomic analysis, and 26 of these were mapped. Two further anonymous cDNA markers, *Xksu8* and *Xksu26* (Kam-Morgan et al. 1989) and the cDNA clones containing the coding regions for ADP-glucose-pyrophorylase (Olive et al. 1989), α-amylase-3 (Baulcombe et al. 1987), β-amylase-1 (Kreis et al. 1987), acyl carrier proteins I and III (Hansen 1987) and II (Hansen and Kauppinen 1991), a ubiquitin activating enzyme (Hatfield et al. 1990), a catalase (Bethards et al. 1987) and a bZIP protein (Guiltinan et al. 1990) also detected sequences on the wheat group 5 chromosomes. The genetic map position of the 18S.26S rDNA locus on the short arm of chromosome 5DS was determined using the clone pTa71 (Gerlach and Bedbrook 1979). The genetic location of a39 (PSR1201), a clone isolated using the *ph1b* mutant of Sears (1977) and mapping within the deletion on 5BL, was also determined. All DNA markers are presented with their chromosome arm location, copy number and relative hybridization strength in Table 1.

## Maps

The genetic maps were developed using a population of 120 individual $F_2$ plants from the wide cross 'Chinese Spring' × 'Synthetic' (Devos et al. 1992). Eight loci were mapped in one linkage group on the long arm of chromosome 5A, and 21 and 20 loci were mapped in linkage blocks spanning both arms on chromosomes 5B and 5D, respectively (Fig. 1 A). *Xpsr170-5A*, expected from the ditelosomic analysis to map on the short arm, was independent from all other 5A markers. Thus, the long arm linkage block could not be positioned relative to the centromere. The overall arrangement of the genetic maps of the homoeologous group 5 chromosomes, i.e. clustering of sequences around the centromere on 5D and conservation of gene order between the maps, was similar to that of the previously published wheat maps (Chao et al. 1989; Devos et al. 1992, 1993 b). The co-linearity of the three wheat maps (Fig. 1 A) and the rye maps (Devos et al. 1993 a; Plaschke et al. 1993) allowed the construction of a consensus map (Fig. 1 B) and the placement, by extrapolation, of a further 53 homoeoloci in addition to the 50 points mapped. Probes which detect homoeoloci on the wheat, rye and barley chromosomes are presented on the right-hand side of Fig. 1 B, while non-homoeologous markers are depicted on the left-hand side. The presence of a non-homoeologous translocation between the long arms of chromosomes 4A and 5A is well established (Naranjo and Fernández-Rueda 1991; Liu et al. 1992). With the development of the linkage map of chromosome 5A, however, the position of the 5AL.4AL breakpoint could be narrowed to the interval between *Xpsr370* and *Xpsr164*. Interestingly, there is no evidence to suggest that this translocation is different to the 5RL.4RL breakpoint in rye (Devos et al. 1993 a), which raises the possibility that they may represent the same evolutionary event prior to the divergence of the A and R genomes.

## The *XNor-3* locus

In bread wheat, nucleolus organizing regions (*Nor*) containing the 18S.26S ribosomal DNA multigene families

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**Table 1.** Chromosomal location in wheat, copy number in wheat (W), barley (B), and rye (R), and relative hybridization in rye and barley for group 5 probes

| Probe | Wheat group 5 locations | | | Copy number[e] | | | Signal strength[g] | | Other wheat locations |
|---|---|---|---|---|---|---|---|---|---|
| | A | B | D | W | B | R | B | R | |
| Known function clones[a] | | | | | | | | | |
| pTA71 (*XNor*) | 5AS | – | 5DS | H | H | H | +++ | +++ | 1AS, 1BS, 6BS |
| pACP11[b] (*XAcl1*) | 5AS | 5BS | 5DS | 1 | 1 | 1 | +++ | +++ | |
| pcβC51 (*Xβ-Amy-1*) | 5AL | 4BL | 4DL | 2 | 2 | 2 | +++ | +++ | 2AS, 2BS, 2DS |
| pCat2.1c (*XCat*) | 5AL | 4BL | 4DL | 2 | 2 | 2 | +++ | ++ | |
| p33 (*Xα-Amy-3*) | 5AL | 5BL | 5DL | 1 | 1 | 2 | +++ | +++ | |
| WL:agal (*XAdpg1*) | 5AL | 5BL | 5DL | 1 | 2 | 1 | +++ | +++ | |
| pACPII (*XAcl2*), pUBA1 (*XUba*) | 5AL | 5BL | 5DL | 1 | 1 | 1 | +++ | +++ | |
| pGC19 (*XEmbp*) | 5AL | 5BL | 5DL | 5 | 1 | 4 | +++ | +++ | 3BL, 6AL, 6BS, 7DS |
| pACP1 (*XAcl3*) | – | 5BL | – | 2 | 1 | 1 | +++ | ++ | 7AS, 7BS, 7DS |
| Anonymous clones[c] | | | | | | | | | |
| PSR118, PSR1204 | 5AS | 5BS | 5DS | 1 | 1 | 1 | +++ | +++ | |
| PSR170 | 5AS | 5BS | 5DS | 3 | 2 | 2 | +++ | +++ | 3AL, 3BL, 3DL |
| PSR326 | 5AS | 5BS | 5DS | 2 | – | – | + | + | |
| PSR618 | – | 5BS | – | 4 | – | – | + | + | |
| PSR628 | 5AS | 5BS | 5DS | 1 | 1 | 1 | ++ | +++ | |
| PSR903 | – | – | 5DS | 3 | – | – | + | + | 2DS, 3AS, 3BS, 3DS |
| PSR929 | 5AS | 5BS | 5DS | 1 | M | 1 | ++ | +++ | |
| PSR940 | 5AS | 5BS | 5DS | 1 | 1 | nd[f] | ++ | nd | |
| PSR945 | 5AS | 5BS | 5DS | 1 | 1 | nd | +++ | nd | |
| PSR946 | – | – | 5DS[d] | 5 | 1 | 1 | ++ | +++ | 2DS, 7AL, 7DS, 7DL |
| PSR115 | 4AL | 5BL | 5DL | 1 | 1 | 1 | +++ | +++ | |
| PSR580 | 4AL | 5BL | 5DL | 1 | 1 | 1 | ++ | ++ | |
| PSR1206 | 4AL | 5BL | – | 2 | 2 | 2 | ++ | ++ | |
| PSR1316 | 4AL | 5BL | – | 2 | – | – | – | – | |
| PSR79, PSR128, PSR360 | 5AL | 5BL | 5DL | 1 | 1 | 1 | +++ | +++ | |
| PSR100 | 5AL | 5BL | 5DL | 2 | 2 | 2 | +++ | +++ | 2AS, 2BS, 2DS |
| PSR109 | 5AL | 5BL | 5DL | 5 | 5 | 5 | +++ | +++ | 2AS, 2BS, 2DS |
| PSR120, PSR145 | 5AL | 5BL | 5DL | 3 | 3 | 3 | +++ | +++ | |
| PSR150 | 5AL | 5BL | 5DL | 3 | 3 | 3 | +++ | +++ | 2AS, 2BS, 2DS, 7AS, 7BS, 7DS |
| PSR426, PSR370 | 5AL | 5BL | 5DL | 1 | 1 | 1 | ++ | +++ | |
| PSR574, PSR637, PSR906, PSR911, PSR1194 | 5AL | 5BL | 5DL | 1 | 1 | 1 | ++ | ++ | |
| PSR912 | 5AL | – | 5DL | 2 | 2 | 1 | +++ | +++ | 2AS, 2BS, 2DS |
| PSR918 | – | – | 5DL | 1 | – | – | – | + | |
| PSR1094 | 5AL | 5BL | 5DL | 1 | 1 | 1 | + | ++ | |
| PSR1101 | 5AL | 5BL | 5DL | 1 | – | 1 | – | ++ | |
| PSR1201 | 5AL | – | 4DL[d] | 3 | – | – | – | – | 1AS |
| | – | 5BL | – | | | | | | |
| PSR1202 | 5AL | – | – | M | – | – | – | – | |
| PSR164 | 5AL | 4BL | 4DL | 1 | 1 | 1 | +++ | +++ | |
| PSR567 | 7BS | 5BL | 5DL | 4 | 3 | 3 | ++ | ++ | 4BL, 4DL |

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

[a] Sources of the known function clones: pTA71, M. O'Dell; pACP1, pACP11, and pACPII, L. Hansen; pcβC51, M. Kreis; pCat2.1c, J.G. Scandelios; p33, D.C. Baulcombe; WL:aga1, W.W. Schuch; pGC19, R.S. Quatrano; pUBA1, P.M. Hatfield

[b] Anonymous clones are isolated from wheat cDNA (PSR50-PSR200) and gDNA (PSR numbers >300) libraries as described in Devos et al. (1992)

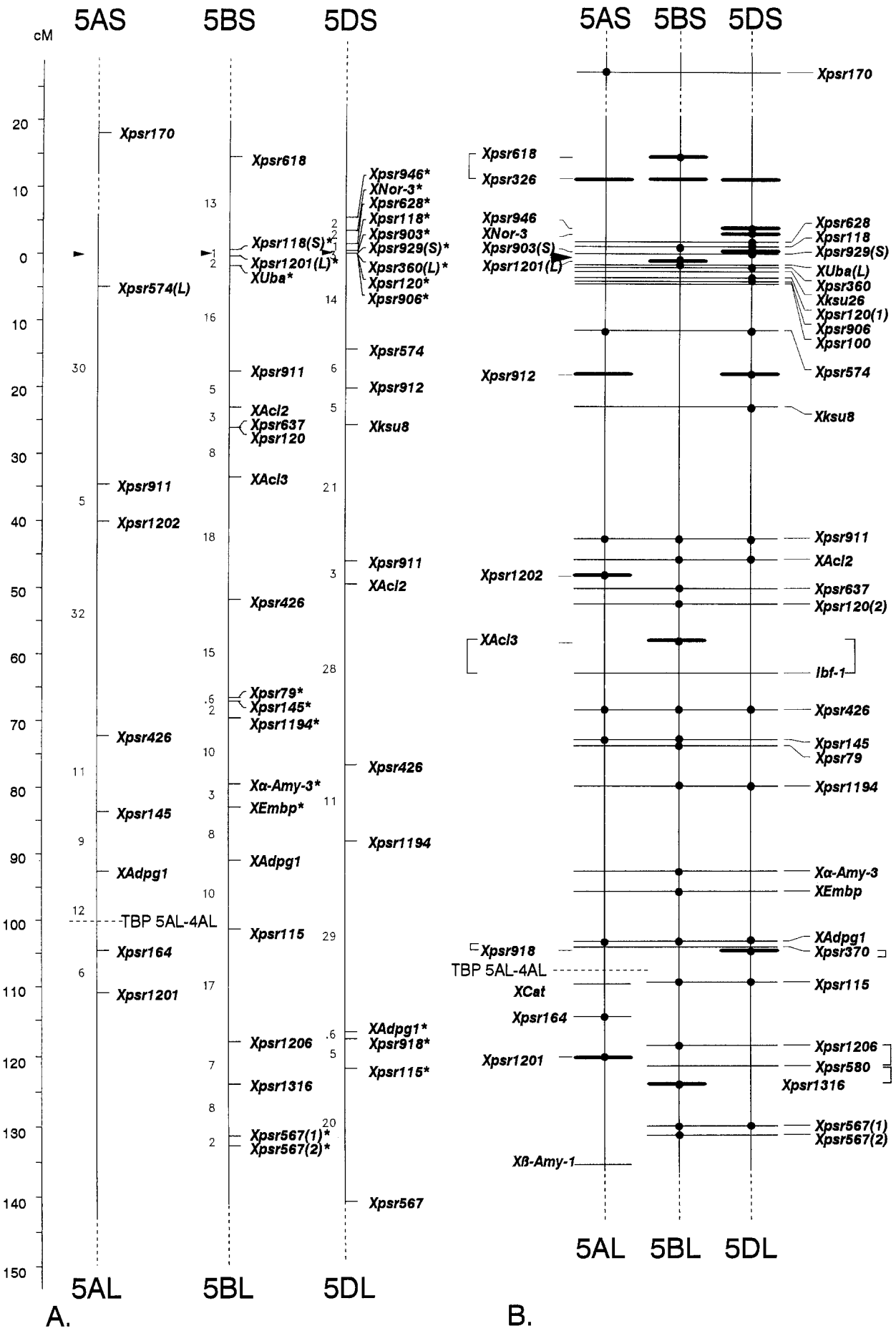
[c] Underlined probes have not been mapped

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

[e] The copy number is determined from the minimum number of hydridizing bands per genome over four restriction digests; M, Moderately repeated; H, highly repeated

[f] nd, No data available

[g] 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


5AS
5BS
5DS
cM
Xpsr170
Xpsr574(L)
Xpsr911
Xpsr1202
Xpsr426
Xpsr145
XAdpg1
TBP 5AL-4AL
Xpsr164
Xpsr1201
Xpsr618
Xpsr118(S)*
Xpsr1201(L)*
XUba*
Xpsr911
XAcl2
Xpsr637
Xpsr120
XAcl3
Xpsr426
Xpsr79*
Xpsr145*
Xpsr1194*
Xα-Amy-3*
XEmbp*
XAdpg1
Xpsr115
Xpsr1206
Xpsr1316
Xpsr567(1)*
Xpsr567(2)*
Xpsr946*
XNor-3*
Xpsr628*
Xpsr118*
Xpsr903*
Xpsr929(S)*
Xpsr360(L)*
Xpsr120*
Xpsr906*
Xpsr574
Xpsr912
Xksu8
Xpsr911
XAcl2
Xpsr426
Xpsr1194
XAdpg1*
Xpsr918*
Xpsr115*
Xpsr567
5AL
5BL
5DL
A.
5AS
5BS
5DS
Xpsr170
Xpsr618
Xpsr326
Xpsr946
XNor-3
Xpsr903(S)
Xpsr1201(L)
Xpsr912
Xpsr1202
XAcl3
TBP 5AL-4AL
XCat
Xpsr164
Xpsr1201
Xpsr918
Xß-Amy-1
Xpsr628
Xpsr118
Xpsr929(S)
XUba(L)
Xpsr360
Xksu26
Xpsr120(1)
Xpsr906
Xpsr100
Xpsr574
Xksu8
Xpsr911
XAcl2
Xpsr637
Xpsr120(2)
Ibf-1
Xpsr426
Xpsr145
Xpsr79
Xpsr1194
Xα-Amy-3
XEmbp
XAdpg1
Xpsr370
Xpsr115
Xpsr1206
Xpsr580
Xpsr1316
Xpsr567(1)
Xpsr567(2)
5AL
5BL
5DL
B.

have been detected by *in situ* hybridization on chromosome arms 1AS, 1BS, 5DS, 6BS and 7DL (Mukai et al. 1991). The physical position of the *Nor-D3* locus, the 18S.26S rDNA site on chromosome 5DS, was at the distal end of that chromosome arm. Genetically, however, *XNor-D3* is no more than 3 cM from the centromere. Quantitatively similar results, where the relative genetic distance is shorter than the physical distance in centromeric regions, have been obtained for the *XNor-B1* and *XNor-B2* loci on chromosomes 1B (Snape et al. 1985) and 6B (Dvořák and Chen 1984) in wheat, and for the *XNor-R1* locus on rye (Wang et al. 1991)

## The *ph1b* deletion

Chromosome pairing in allohexaploid wheat is limited to homologues at metaphase I by the action of the *Ph1* gene on chromosome 5B. Two independent deletion lines are available, both of which lack the segment of 5BL carrying *Ph1* and in which homoeologous pairing occurs. These mutant lines are *ph1b* in the hexaploid wheat cv 'Chinese Spring' (Sears 1977) and *ph1c* in the tetraploid wheat cv 'Cappelli' (Giorgi 1978).

Recently, Clarke et al. (1992) described the isolation of a clone, a39 (PSR1201), from a library produced by PERT driven by *ph1b* genomic DNA. PSR1201 detects sequences on 5AL, 4DL, 5BL and 1AL, and the *Xpsr1201-5B* locus is deleted in both the *ph1b* and *ph1c* mutants. The probe has been mapped on both group 5 chromosomes (Fig. 1). *Xpsr1201-5A* is located in the distal region of 5AL within the segment translocated from 4A and is therefore likely to be homoeologous to the *Xpsr1201-4D* locus. *Xpsr1201-5B*, however, is located close to the centromere on 5BL. These locations, the presence of an additional copy on 1AL and the absence of a significant hybridization signal in rye or barley are consistent with the behaviour of PSR1201 as a 'non-homoeologous' clone. The location of *Xpsr1201-5B* indicates that, genetically, the *Ph1* locus lies close to the centromere on 5BL, which is consistent with the finding of Jampates and Dvořák (1986). The discrepancy between the genetic location of the deletion in the *ph1b* mutant near the centromere and its physical location near the middle of the long arm of 5BL (Dvořák et al. 1984) is again attributable to the distal localization of recombination.

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**Fig. 1A,B.** RFLP maps of the homoeologous group 5 chromosomes of wheat. **A** Linkage maps. For the marked loci (*) the map position could not be determined precisely (LOD <2.5) and only a preferred location could be given. *TBP*, Translocation breakpoint. **B** Consensus map. • Mapped loci, *full lines over the A, B and D genome chromosomes* indicate homoeoloci (conserved over the wheat, barley and rye genomes), *bold line fragments* indicate map positions of non-homoeologous loci, *Drackets linking markers* indicate adjacent loci for which the order could be based only on relative map distances in the A, B, D and R genomes

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