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Comparative mapping of the wheat 5B short chromosome arm distal region with rice, relative to a crossability locus

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Abstract Colinearity between wheat and rice genomes is quite well established at the chromosome level, but less is known at a finer level. We tried to specify these relationships for the wheat 5BS chromosome-arm distal region, where a major locus for crossability was located. By developing AFLP markers, we succeeded to locate this major QTL more precisely. One cloned AFLP fragment mapped to rice chromosome 11, which was in agreement with a rice chromosome-11 linkage block reported in this region. However a second marker, a RFLP probe, showed a break in synteny because it mapped to rice long-arm chromosomes 1 and 5, while screening a rice BAC library with the same probe identified rice chromosomes 5 and 6. Therefore, we concluded that the syntenic relationships were more complex at the fine level. The observed results might indicate the presence of a linkage block carrying a crossability gene on wheat groups 1, 5 and 7, and also on rice chromosomes 5 and 6.

Keywords Synteny · QTL · BAC library · Kr genes · *Triticum aestivum*

Introduction

Although suggested before by many genetic and cytogenetic studies in cereals and other plant species, a conserved gene order between plant genomes has been described for more than a decade. The first studies reported colinearity between the tomato and potato genomes (Bonierbale et al. 1988) and between the three homoeologous genomes of hexaploid wheat (Chao et al. 1988). Since then, the significant development of molecular markers (RFLPs) led to numerous results, in particular in the Poaceae family (Ahn et al. 1993; Kilian et al. 1995; Van Deynze et al. 1995). Moore et al. (1995) have proposed a structure to align cereal genomes in a circle (revised in Gale and Devos 1998a), defining "rice linkage blocks" (Moore 1995) as this species has a small genome (Arumuganathan and Earle 1991) and the most-dense genetic map of the grasses (Causse et al. 1994; Harushima et al. 1998; URL: http://rgp.dna.affrc.go.jp/publicata/geneticmap2000). These reasons made rice a model species of choice in the Poaceae, because plant breeders hoped to clone genes in species of interest with large genomes, helped by the colinearity with the small genome of a model species (Gale and Devos 1998b). Actually, many comparative mapping studies involved rice and wheat, another economically important crop from the family (Kurata et al. 1994; Foote et al. 1997). Several approaches using colinearity at a fine level (i.e. microcolinearity) between wheat and rice to clone genes were attempted, obtaining various results. Sarma et al. (1998), looking for the wheat vernalization gene *Vrn-A1* in rice, found a QTL for flowering time at an orthologous location. Gallego et al. (1998) tried to isolate two wheat resistance genes *Lr1* and *Lr10* in rice, and showed a lack of synteny in one case as well as duplicated related genes in the other. Nevertheless, this study and the consecutive work led to the discovery of a new gene family (Feuillet and Keller 1999) and the evolutionary relationships between the duplicates (Feuillet et al. 2001).

In bread wheat, interspecific hybridization, especially with rye (*Secale cereale* L.), has been a tool for breeders for about a century, in order to improve this major cereal crop through alien gene introgression. Several recessive genes controlling wheat/rye crossability were described. *kr1*, the most effective (Lein 1943), was mapped to the long arm of chromosome 5B, whereas *kr2* was mapped to the long arm of chromosome 5A (Sitch et al. 1985). Consistent with the homoeologous location of *kr1* and *kr2*, a third gene named *kr3* was described on chromo-

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some 5D (Krolow 1970), but was reported to have an effect only in crosses of wheat with *Triticum tauschii* (Koba and Shimada 1993). Another gene named *kr4* was reported on chromosome 1A (Zheng et al. 1992) with an effect weaker than *kr1* but stronger than *kr2*. In all studies, homoeologous group 5 seems particularly involved in controlling crossability. Genetic maps for this group were obtained by Xie et al. (1993) and Nelson et al. (1995). Moreover, an intraspecific genetic map was constructed in our laboratory (Cadalen et al. 1997). A quantitative trait locus (QTL) analysis performed on this map confirmed the predominant role of chromosome 5B in promoting or repressing crossability with rye. Nevertheless, the major locus, named *Skr*, was surprisingly located distally on the short arm of chromosome 5B (Tixier et al. 1998). Two other minor QTLs were also detected on the long arm of chromosomes 7A and 5B.

A model for the syntenic relationships of wheat homoeologous group-5 chromosomes with rice was proposed (Gale and Devos 1998a). Recently, a physical map of this group was established using deletion lines (Sarma et al. 2000). For the wheat chromosome 5B short arm it described a proximal zone where synteny was not determined, followed by a more-distal linkage block coming from rice chromosome 11, then a small undetermined region, and finally the distal part of the chromosome syntenic with rice chromosome 12.

As our long-term goal is the cloning of the *Skr* gene, the aim of the present work was to localize the *Skr* locus more precisely, and also to determine the relationships with rice in this particular region, in order to confirm the model already proposed.

Materials and methods

Plant material

The wheat mapping population consisting of 187 doubled-haploid (DH) lines from "Courtot" × "Chinese Spring" (CtCS) was previously described (Cadalen et al. 1997; Tixier et al. 1998). A set of nullisomic-tetrasomic lines (Sears 1966) was also used to assign loci to specific wheat chromosomes. A ditelosomic line for chromosome 5BL (i.e. lacking the short arm for chromosome 5B) (Sears and Sears 1978) was used to investigate the position of probes on the chromosome 5B.

The rice mapping population consisting of 107 DH lines obtained from anther culture of "IR64" × "Azucena" F_1-hybrids (Guiderdoni et al. 1992) was described by Huang et al. (1994).

Existing and new molecular data

The wheat data-set used as a basis was described by Cadalen et al. (1997). The rice mapping data-set was described by Huang et al. (1997). New molecular markers were added to the CtCS wheat map. AFLP markers were obtained according to the standard protocol (Vos et al. 1995) (primers, see Table 1) except that restriction enzyme *Tru*9I (Roche Diagnostics), an isoschizomer of *Mse*I, was used instead of the original enzyme, and that bands were revealed using a silver staining method (Bert et al. 1999), which allowed some specific bands to be cloned. We also added one microsatellite marker, gpw1072, coming from the "Génoplante" program. Several RFLP clones from rice maps (Grivet et al. 1996; Van Deynze et al. 1998) were tested on wheat using a non radioactive procedure (Lu et al. 1994). The probes tested for cross-hybridization, polymorphism and whenever possible mapping on the rice population were used with a standard radioactive protocol.

Table 1 AFLP primers and nomenclature

Code	Sequence
E32	5′GACTGCGTACCAATTCAAC 3′
E33	5′GACTGCGTACCAATTCAAG 3′
E35	5′GACTGCGTACCAATTCACA 3′
E36	5′GACTGCGTACCAATTCACC 3′
E37	5′GACTGCGTACCAATTCACG 3′
E41	5′GACTGCGTACCAATTCAGG 3′
M49	5′GATGAGTCCTGAGTAACAG 3′
M60	5′GATGAGTCCTGAGTAACTC 3′
M61	5′GATGAGTCCTGAGTAACTG 3′
M62	5′GATGAGTCCTGAGTAACTT 3′

BAC library, hybridization and subcloning

The rice bacterial artificial chromosome (BAC) library (cv Nipponbare, *japonica* subtype) employed was constructed based on restriction with *Hin*dIII at the Clemson University Genomics Institute (CUGI) and contained 36,864 clones with an average insert size of 128.5 kb (Budiman 1999).

Hybridization of probes onto BAC filters were conducted as described by CUGI (http://www.genome.clemson.edu/groups/bac/protocols/addressnew.html). BAC clones were subcloned as follows: after 16 h culture in LB medium with 12.5 µg/ml of chloramphenicol (Sigma), plasmid DNA was extracted according to Choi and Wing (1999). It was then subjected to *Hin*dIII restriction (Roche Diagnostics) for 3 h followed by heat-inactivation at 65 °C for 15 min. The mixture was used for ligation with T4 DNA ligase (Gibco BRL) into a commercially prepared pUC18 vector (Amersham), and transformed into JM109 *Escherichia coli* cells (Promega), according to the manufacturer's instructions.

Genetic mapping and statistical analysis

Genetic maps were established with the computer software Mapmaker/exp v3.0b (Lander et al. 1987). The Kosambi centiMorgan (cM) function was used for all maps (Kosambi 1944). Markers were grouped and ordered at a LOD threshold of 3.

The locations and effects of putative QTLs were evaluated along chromosome 5B using the "marker regression" method described by Kearsey and Hyne (1994) for the one-QTL model and Hyne and Kearsey (1995) for a two-QTL model. These methods were slightly modified to use the reverse Kosambi mapping function (Kosambi 1944) for the prediction of QTL effects along the linkage group, in order to better fit the actual recombination frequency between markers. All computations were carried out using specialized programmes in the Splus language (Splus v3.4r1, MathSoft Inc.). Owing to the coding of the genotypic data, QTL additive values were positive when the favourable allele came from Chinese Spring and negative when it came from Courtot. Confidence intervals of QTL location and effect were estimated through 300 bootstrap re-samplings for the two-QTL model (Visscher et al. 1996).

Results

Wheat map development and QTL analysis

The QTL for the *Skr* locus was located distally on the 5BS chromosome arm, close to the loci *Xfba367-5B* and

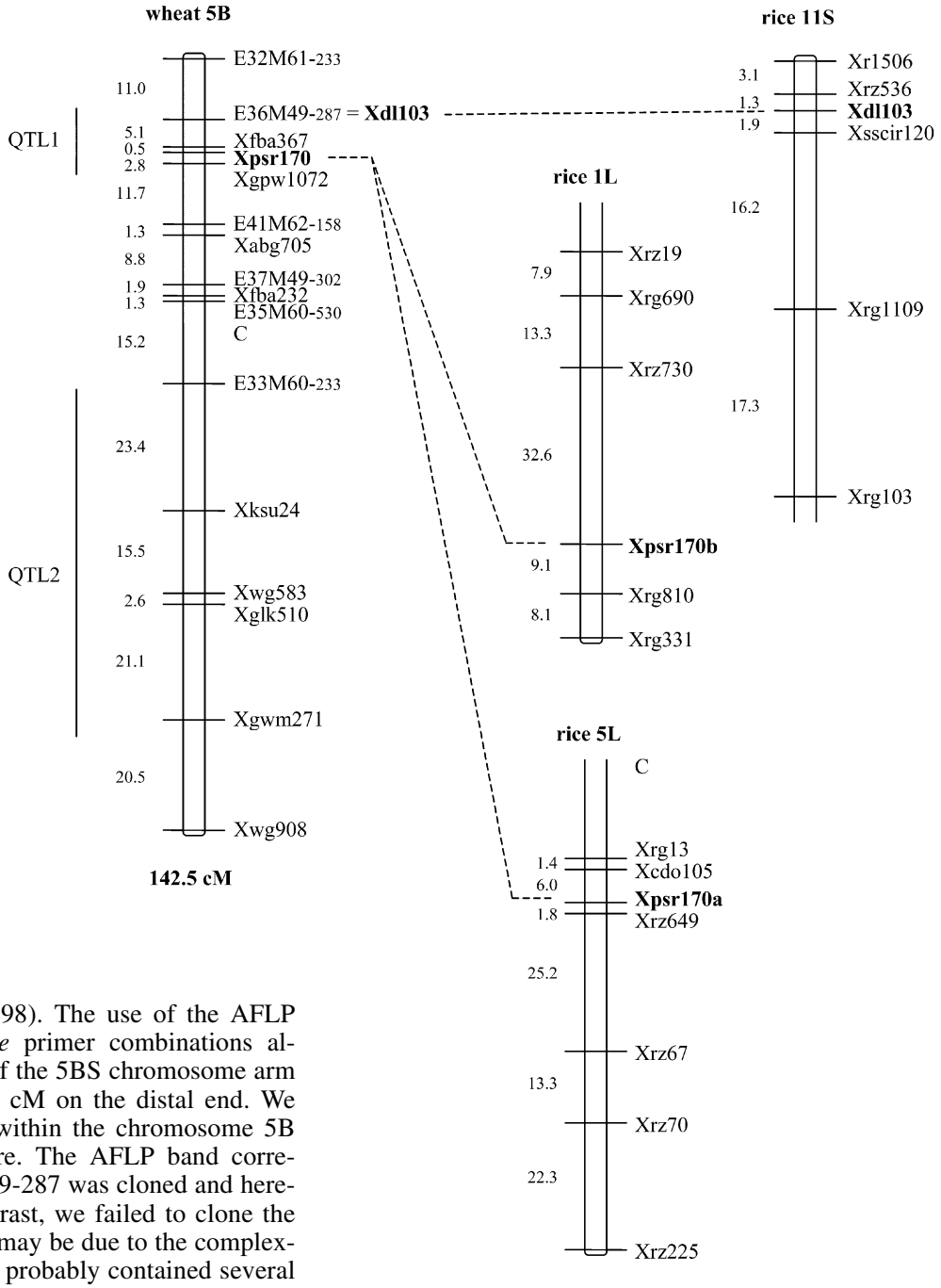

Fig. 1 Genetic map of wheat chromosome 5B and relationships with rice chromosome arms. *Distances shown on the left* of each chromosome are in centiMorgans. *C* indicates the approximate location of the centromere. *Vertical bars on the left* represent the confidence interval for each QTL

Xpsr170-5B (Tixier et al. 1998). The use of the AFLP technique with 144 *Eco/Mse* primer combinations allowed us to extend the map of the 5BS chromosome arm (Fig. 1), accounting for 16.1 cM on the distal end. We also added several markers within the chromosome 5B map closer to the centromere. The AFLP band corresponding to the locus E36M49-287 was cloned and hereafter named DL103. By contrast, we failed to clone the E32M61-233 fragment. This may be due to the complexity of the scored band, which probably contained several fragments of slightly different molecular weights; this confirmed that cloning of an AFLP band is not an easy process (Shan et al. 1999).

QTL analysis was performed using the same phenotypic data as in Tixier et al. (1998). The analysis confirmed the presence of a major QTL on the short arm of chromosome 5B. The most-likely QTL location was within a 5.1-cM interval between *Xdl103-5B* and *Xfba367-5B* loci. However a two-QTL model, including a second QTL on the long arm of this chromosome, better fitted the distribution of phenotypic differences between marker classes, and allowed the residual mean squares to significantly drop from 68.9 to 3.0. This model could be accepted at a significance threshold of $\alpha = 0.01$. The first QTL was then located at 12.7 cM from the distal end of the chromosome short arm, within a confidence interval ranging from 8.7 to 20.9 cM (Figs. 1 and 2). Its additive value was –15.9, corresponding to a heritability value of 22.1%. The second QTL was located at 90.3 cM within a larger confidence interval ranging from 59.1 to 122.6 cM (Figs. 1 and 2). Its additive value was –7.9 and its heritability was 5.5%. The R^2 of the full model was raised to 23.1%. Although the linear model was not the best suited for such binomial data, we used it for convenience, after having checked that the residuals did not depart from Gaussian distribution.

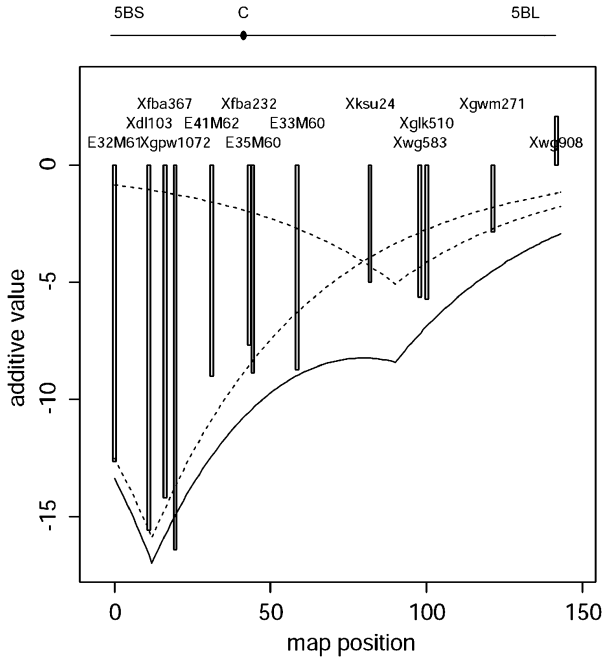

Fig. 2 The two-QTL model. Markers are represented along the abscissia, the short arm of the chromosome pointing to the left. The graph represents the phenotypic differences between classes for each marker locus (*vertical bars*). The *dotted line curves* correspond to the additive value predicted for each QTL. The *solid line curve* represents the same value for the two-QTL model, i.e. the sum of the dotted line curves

Rice mapping of wheat probes

In a Southern-hybridization experiment the DL103 probe revealed four bands in rice (data not shown). Two of them were polymorphic, cosegregated in the mapping population and mapped 4.4 cM from the distal end of the rice 11S chromosome arm (Fig. 1). The FBA367 probe exhibited only a weak smear on rice and hence was not mapped. The PSR170 probe showed six clear bands on rice, four of them being polymorphic between "IR64" and "Azucena" (data not shown). These bands gave two distinct loci, *Xpsr170a* and *Xpsr170b*, mapped respectively to rice chromosome arms 5L and 1L (Fig. 1).

The three probes were tested against the rice BAC library. The DL103 probe gave a medium signal, but the ten unambiguously responding clones each belonged to a distinct contig. This may indicate hybridization to a moderately repeated rice sequence. The FBA367 probe showed a strong signal, as more than 300 clones were revealed (data not shown). This suggested FBA367 hybridizing to a repeated sequence in rice, which was consistent with the Southern-hybridization pattern. The PSR170 probe revealed 17 clones falling into two contigs containing respectively 74 and 31 clones in the complete CUGI set (*Hin*dIII and *Eco*RI BAC libraries). These contigs are to-date classified as #192 and #161, including 713 and 344 clones in the CUGI data where several BAC and PAC libraries were added, and were anchored to rice chromosomes 6L and 5L respectively (URL: http://www.genome.clemson.edu/projects/rice/fpc). We tried to anchor the rice contigs in wheat by subcloning some BACs and using the subclones as RFLP probes, but this was unsuccessful because of weak or no hybridization of the subcloned probes onto wheat (data not shown).

Discussion

In order to locate the QTL for the *Skr* locus with more accuracy, we developed AFLP markers. We successfully identified two markers mapped more distally than *Xfba367-5B*, and cloned one of them. However, we still need new molecular markers to achieve saturation mapping of the region. This may be done by developing more AFLP markers, since we only tried 144 primer combinations among the 4,096 theoretical combinations. It seems also feasible to more systematically exploit the previously published wheat and rice genetic maps, to look for RFLP probes that may map to the region. For example, the rice chromosome 11 map (URL: http://rgp.dna.affrc.go.jp/publicata/geneticmap2000) could provide 62 potentially new markers in this region.

The new QTL analysis actually allowed us to specify the location of the *Skr* locus, since the curve of the predicted additive value was now "peak-shaped" (Fig. 2). The newly computed confidence interval corresponded to a region between 8.7 and 20.9 cM from the distal end of the short chromosome arm. The effect of the second QTL on the long arm of chromosome 5B was much weaker than the first one, indeed its confidence interval was nearly 60-cM long. The variance part explained by our model was a little higher than the former model in which the locations of the QTLs were less accurate (Tixier et al. 1998): a 22.1% heritability value instead of 16.8% for the major QTL, and 5.5% instead of 3.3% for the second. This was also reflected in the additive values: 15.9 instead of 13.6 for the major QTL, and 7.9 instead of 6.1 for the second. Nevertheless, the significant map improvement on the distal end did not lead to a similar improvement in QTL detection. This may be explained by a large phenotypic variance due to environmental effects. We also noticed that the most-significant marker associated with the major QTL, *Xgpw1072*, showed a biased distribution from the expected 1:1 segregation ratio on our data, at a threshold of $\alpha = 0.025$. This slight distortion may have caused a mislocation of the locus on the map, thus disturbing the QTL computations. Therefore, a new genetic map on a large-sized population may eliminate the distortion and may lead to improved QTL results.

The genetic region we focused on being the distal part of the 5BS chromosome arm, we initially expected this region to be colinear to the rice chromosome 12, as proposed by Sarma et al. (2000, Fig. 1 in this reference). The mapping of the DL103 probe to rice chromosome arm 11S proved that our hypothesis had to be reconsidered. Nevertheless, our results could still fit the model

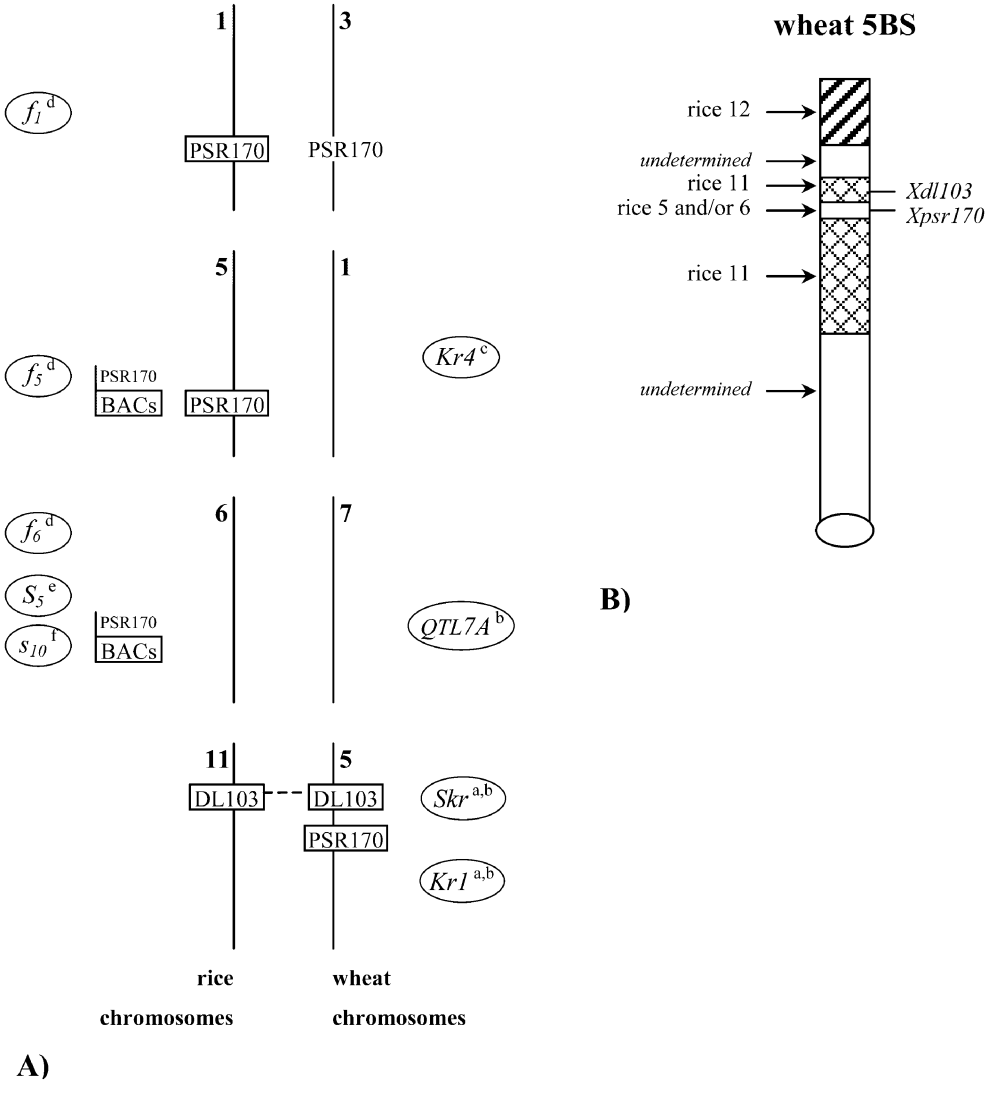

Fig. 3 **A**) Schematic relationships between rice chromosomes and wheat homoeologous groups. Probes and BAC contigs from this study are in *boxes*. QTLs of crossability (in wheat) and wide compatibility (in rice) are in *circles*. Data taken from: [a] this study; [b] Tixier et al. (1998); [c] Zheng et al. (1992); [d] Wang et al. (1998); [e] Liu et al. (1997); [f] Lorieux et al. (2000). **B**) Proposed relationships between wheat chromosome arm 5BS and rice chromosomes

since a second region, more proximal on the chromosome arm 5BS, was reported to be colinear to rice chromosome 11. Unfortunately, we were not able to extend synteny in the vicinity of the *Xdl103* locus: the sugarcane SSCIR120 probe, which mapped close to DL103 on the rice map (Fig. 1), gave an unclear hybridization pattern on wheat (data not shown). Moreover, the CDO344 probe which was located distally within the last wheat chromosome 5B deletion (FL 0.81), thus corresponding to rice chromosome 12 (Huang et al. 1997; Sarma et al. 2000), was not polymorphic between Courtot and Chinese Spring.

We mapped the wheat PSR170 probe to rice chromosomes 1 and 5. However, two additional monomorphic bands on the hybridization pattern may reveal up to two other loci in rice. With the same probe, we were able to identify 17 rice BAC clones included in two contigs located on chromosomes 5 and 6. To our knowledge, such a result was not reported previously in these species. The anchoring of the contig on chromosome 5 was consistent with the locus detected on the same chromosome. Regarding the other contig, it may correspond to the monomorphic bands, which may presumably be located to rice chromosome 6. PSR170 revealed several loci in wheat, hybridizing to as many as nine bands with some of them assigned to homoeologous groups 3 and 5 (GrainGenes database, URL: http://wheat.pw.usda.gov). The wheat loci on group 3 probably corresponded to the locus found on rice chromosome 1 (Fig. 3A) since the relationships between these chromosomes were already described (Kurata et al. 1994). The wheat loci on group 5 did not find correspondence with the expected rice chromosomes 12 or 11. This suggested that the model proposed by Sarma et al. (2000) should be more complex at a fine level, including at least a break in synteny around the *Xpsr170* locus (Fig. 3B). This is not surprising as the homoeologous group 5 was described to have one of the most-complex syntenic relationships with rice among the wheat groups (Saghai Maroof et al. 1996).

Regarding the character of interest, i.e. wheat crossability, we revealed some original results. Starting from the *Skr* QTL on the wheat chromosome 5B, we used two wheat probes that mapped to three rice loci and recog-

nized two rice BAC contigs; we thus identified four rice regions (Fig. 3A). The rice chromosome-11 region was consistent with the model proposed, although to our knowledge no QTL for a similar trait was reported in this region. The locus on rice chromosome 1 was consistent with the loci previously reported on wheat homoeologous group 3. We noticed that on rice chromosome 1 a QTL for wide compatibility was described (Wang et al. 1998); this result seemed original as no crossability locus was ever reported on the syntenic wheat group 3. The locus on rice chromosome 5, confirmed by screening a rice BAC library, may correspond to f_5, a major QTL for F_1-hybrid fertility in rice *indica* × *japonica* crosses (Wang et al. 1998). It is interesting to note that among the wheat group-1 chromosomes, syntenic to rice chromosome 5, chromosome 1A is carrying the *Kr4* gene (Zheng et al. 1992). The rice chromosome 6, identified with BACs, is known to carry two QTLs for the same wide-compatibility trait, S_5 (Liu et al. 1997) and f_6 (Wang et al. 1998), but also s_{10}, a locus controlling male sterility in F_1 hybrids from an *Oryza sativa* × *Oryza glaberrima* cross, also inducing a strong segregation distortion (Lorieux et al. 2000). The syntenic wheat group is homoeologous group 7 (Gale and Devos 1998a), among which chromosome 7A was reported to carry a QTL for crossability (Tixier et al. 1998).

Finally, the existing QTL data (Tixier et al. and this study) suggest that PSR170 is not directly involved in the *Skr* locus. Our hypothesis is that it may be present in a block along with a crossability gene, which block may be duplicated on wheat groups 5, 1, 7 and possibly 3 (Fig. 3A). This block might correspond to a rice block controlling hybrid sterility, which phenomenon might be part of the same family as the crossability mechanisms. Further data are obviously needed to address this issue.

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