Detailed Comparative Mapping of Cereal Chromosome Regions Corresponding to the *Ph1* Locus in Wheat

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ABSTRACT

Detailed physical mapping of markers from rice chromosome 9, and from syntenous (at the genetic level) regions of other cereal genomes, has resulted in rice yeast artificial chromosome (YAC) contigs spanning parts of rice 9. This physical mapping, together with comparative genetic mapping, has demonstrated that synteny has been largely maintained between the genomes of several cereals at the level of contiged YACs. Markers located in one region of rice chromosome 9 encompassed by the YAC contigs have exhibited restriction fragment length polymorphism (RFLP) using deletion lines for the *Ph1* locus. This has allowed demarcation of the region of rice chromosome 9 syntenous with the *ph1b* and *ph1c* deletions in wheat chromosome 5B. A group of probes located in wheat homoeologous group 5 and barley chromosome 5H, however, have synteny with rice chromosomes other than 9. This suggests that the usefulness of comparative trait analysis and of the rice genome as a tool to facilitate gene isolation will differ from one region to the next, and implies that the rice genome is more ancestral in structure than those of the Triticeae.

THE major cereals diverged from a common ancestor around 60 million years ago, and their chromosomes now differ in number, 25-fold in size and in the proportion of repetitive DNA within their genomes (MOORE 1995). The genome of hexaploid (bread) wheat (*Triticum aestivum* L. em Thell.), for example, consists of 1.7×10^{10} bp per 1C nucleus (BENNETT and SMITH 1976) and is composed of ~80% repetitive DNA (FLAVELL 1980). In contrast, the genome of rice (*Oryza sativa*) has only 4×10^8 bp per 1C nucleus (BENNETT and SMITH 1991) and consists of ~50% repetitive DNA (DESHPANDE and RANJEKAR 1980), making it more amenable to positional cloning techniques.

Genetic mapping of a particular plant species is conventionally carried out without reference to maps derived from related species. Recently, however, varying degrees of synteny at the genetic level have been reported between the genomes of a number of cereals including rice and wheat (KURATA *et al.* 1994a), rice and maize (*Zea mays* L.) (AHN and TANKSLEY 1993) and maize and sorghum [*Sorghum bicolor* (L.) Moench] (WHITKUS *et al.* 1992). The rice genetic map can be divided into sets of linked genes known as linkage blocks, and these blocks can be rearranged to form the maps of other cereals (MOORE *et al.* 1995a,b). This allows genetic information from different cereals to be combined, providing a large potential marker pool. The small size of the rice genome, and the isolation and partial sequencing of over 25,000 rice cDNA clones

(YAMAMOTO *et al.* 1995), will facilitate further the use of rice as a tool to isolate genes from larger and more complex genomes such as those of wheat and barley (MOORE *et al.* 1993).

The usefulness of rice as a tool for positional gene isolation relies on synteny being maintained at and above the megabase level. For a number of regions examined in rice and the Triticeae (DUNFORD *et al.* 1995), rice and barley (KILIAN *et al.* 1995) and rice, maize and sorghum (CHEN *et al.* 1997), synteny is maintained between genetically linked markers and markers physically linked by YAC clones carrying from several hundred kb to ~1 Mb of rice genomic DNA. This suggests that rice YAC contigs could be used to reveal the gene content of other cereal genomes, facilitating chromosome walking and jumping. However, to date little is known of the extent of synteny between cereal genomes below the genetic level but above the level of a single YAC. A recent study has identified regions in cereal genomes characterized by an extensive loss of synteny (MOORE *et al.* 1997) and it may be inappropriate to use rice as a tool to target genes in these areas. It is thus important to determine the extent of synteny between rice and target cereal genomes above the megabase level.

Hexaploid wheat is made up of three related (homoeologous) genomes A, B and D with seven pairs of homologous chromosomes per genome (SEARS 1952). Tetraploid wheat has two homoeologous genomes A and B. There are genes present in polyploid wheat that maintain the stability of the A, B and D genomes by controlling meiotic pairing, allowing homologous, but not homoeologous, chromosomes to pair and recom-

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bine. The strongest effect on pairing is associated with the gene (or genes) of the *Ph1* (pairing homoeologous) locus on wheat chromosome 5B that suppresses homoeologous pairing within the polyploid wheat genome and is also responsible for the failure of polyploid wheat chromosomes to pair with homoeologues from related species and genera in hybrids (OKAMOTO 1957; RILEY and CHAPMAN 1958; SEARS 1977). There are deletions of this locus in both hexaploid (*ph1b*) (SEARS 1977) and tetraploid (*ph1c*) (GIORGI 1978) wheat that allow pairing of homoeologous chromosomes from the A, B and D genomes of wheat with one another, but, more importantly for breeding purposes, allow pairing with homoeologues from related species and genera. This study targets, for comparative mapping, the region containing the *Ph1* locus and demonstrates that synteny is conserved above the megabase level between this region on wheat chromosome 5B and a region of rice chromosome 9. It also discusses whether rice YAC contigs can be used to predict the gene content in this wheat chromosome region, thereby facilitating the cloning of the gene or genes of the *Ph1* locus.

MATERIALS AND METHODS

Rice YAC analysis: A collection of 148 YACs potentially derived from rice chromosome 9 (DUNFORD *et al.* 1995) was dotted onto nylon membranes to produce rice 9 YAC sets. YACs and probes from rice chromosome 9 were obtained from the Japanese Rice Genome Research Program. At the genetic level, rice chromosome 9 is syntenous with regions of wheat homoeologous group 5 (KURATA *et al.* 1994a), barley 5H (DUNFORD *et al.* 1995) and maize chromosomes 2 and 7 (AHN and TANKSLEY 1993). The rice 9YAC sets were screened with probes from these chromosomes; 43 probes from rice, 19 from wheat, 10 from barley, six from maize, and also with six oat sequences that map to areas of maize chromosomes syntenous with rice 9. Probes were purified using the Wizard PCR Preps DNA Purification System (Promega) and hybridized according to the methods of BEZANT *et al.* (1996). Blots were washed at low stringency (2× SSC, 0.5% SDS at 65°), and signal was detected using a PhosphorImaging system (Molecular Dynamics). Probes not detecting positive YACs on the rice 9YAC sets were used to screen a rice YAC library carrying 6934 clones representing all 12 rice chromosomes and estimated to contain the DNA equivalent of six haploid genomes (UMEHARA *et al.* 1995). The rice nine YAC sets were screened first because the colonies were better spaced and contained more DNA than the full library sets and were thus easier and quicker to score. Screening of the 6934 rice YAC clones on high density replica blots was used to confirm the order of markers suspected to lie within the *ph1b* and *ph1c* deletions. The presence of a particular sequence on a YAC was confirmed by the digestion of the YAC DNA from the positively hybridizing colony with various restriction enzymes, followed by electrophoresis and Southern blotting. These blots were then hybridized with the probe originally detecting the positive colony, and the size of the resulting band was compared with the size of band generated by the same probe on Southern blots of digested DNA from the rice cultivar, Nipponbare.

RFLP analysis and mapping in rice: Genomic DNA was extracted from the rice cultivars IR20 (Indica type) and 63-83 (Japonica type) using a modified CTAB method (MURRAY and THOMPSON 1980) and was digested with the restriction

enzymes *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV or *Hind*III (Northumbria Biologicals Ltd.). The resulting Southern blots were hybridized with 84 probes from rice, wheat, barley, maize and oats. Sixty-four probes showed restriction fragment length polymorphism (RFLP) between IR20 and 63-83, and of these, 44 were mapped. Five sets of rice mapping blots were prepared, each comprising genomic DNA from 123 F₂ plants and pooled F₃ families from the cross IR20 × 63-83. The DNA in each set was digested with a different restriction enzyme as for the parental DNA. Map locations were calculated using JOINMAP (STAM, 1993) with the Kosambi mapping function. The rice physical and genetic maps generated in this study were compared with the high resolution genetic map of rice produced by KURATA *et al.* (1994b).

Consensus maps: The genetic and physical maps of rice chromosome 9 were compared with genetic consensus maps of regions of wheat, barley and maize syntenous with rice 9 at the genetic level (Figure 1). Using published data, a consensus map was produced for each of the following cereals: wheat (GALE *et al.* 1993; NELSON *et al.* 1995; GILL *et al.* 1996), barley (DUNFORD *et al.* 1995; BEZANT *et al.* 1996; LAURIE *et al.* 1996; QI *et al.* 1996) and maize (BURR *et al.* 1992; AHN and TANKSLEY 1993). Each consensus map was produced by manual alignment of markers common to each individual map and superimposition of markers unique to each map.

Screening for probes in the *ph1b* and *ph1c* deletions: Genomic DNAs extracted from hexaploid wheat cv. Chinese Spring, the Chinese Spring *ph1b* mutant (SEARS 1977), and three Chinese Spring nullisomic-tetrasomic lines (nulli-5A/tetra-5B, nulli-5B/tetra-5D and nulli-5D/tetra-5A) (SEARS 1966) were digested with each of five enzymes (as for rice, above) and used for Southern blotting. Fifty-two of the 84 cereal probes used for physical and genetic mapping were hybridized to these Southern blots, to select those probes detecting loci within the *ph1b* deletion. It was unnecessary to screen the remaining 32 probes as they were excluded from mapping within the *ph1b* deletion because of their map location. Similarly, genomic DNAs extracted from tetraploid wheat *Triticum durum* (L.) cv. Cappelli and the Cappelli *ph1c* mutant (GIORGI 1978) were used to define the distal end of the deletion regions, because the distal breakpoint of the *ph1b* deletion is further from the centromere than the distal breakpoint of the *ph1c* deletion (GILL *et al.* 1993). Of the original 84 probes, 24 were suspected to lie within the region defined by the *ph1b* deletion. Previous studies indicated that the *ph1b* deletion lines may carry additional deletions (CLARKE *et al.* 1992), so to confirm that these 24 probes were located within the *ph1b* deletion region itself (and not within a 5B deletion region at a different location), they were used to screen Southern blots containing digested genomic DNA from a doubled haploid population of 55 plants derived from a cross between the Chinese Spring *ph1b/ph1b* mutant line and a Chinese Spring (Cappelle-Desprez 5B) substitution line (SNAPE *et al.* 1995). These plants had been scored for the presence or absence of the *Ph1* gene(s) by crossing each line to an *Aegilops variabilis* accession and using cytological analysis to determine whether homoeologous chromosome pairing occurred. In the presence of *Ph1*, most meiotic cell chromosomes are univalent (low pairing), whereas in the absence of *Ph1*, multivalents (high pairing chromosomes) are common. RFLP loci cosegregating with a high chromosome pairing phenotype were deemed to lie within the *ph1b* deletion.

RESULTS

Rice YAC analysis: Of 84 probes hybridized to the rice 9YAC sets, 44 detected one or more YACs. Some

TABLE 1
Rice YACs detected by two or more probes

Probe	YACs											
C711	Y2756											
C313	Y2756											
C1232	Y2756	Y6676										
R2807	Y2756	Y6676										
R1687	Y3152											
BCD351	Y3152											
BCD1087	Y2027	Y6035										
C1176	Y2027	Y6035										
Psr100	Y2027											
RZ206	Y3229	Y4076	Y4460									
R1016	Y3229	Y4076	Y4460									
CDO388	Y3804											
C2070	Y3804											
G1085	Y2591	Y3804										
R742A	Y2591											
G385	Y2591											
S10275	Y1275	Y3462										
umc5	Y1275	Y3462										
Psb52	Y273	Y1379	Y1396	Y3054	Y3960	Y5475						
R2272	Y273	Y1379	Y1396	Y1594	Y3054							
CDO412	Y1594											
Psr574	Y1594											
C1227	Y1594											
R2790	Y1228	Y2116	Y3158	Y4602	Y4884	Y5022	Y6008	Y7041				
R2638	Y1228	Y2116	Y3158	Y4602	Y4624	Y4650	Y4884	Y5022	Y6008	Y7041		
P88	Y4114	Y4624	Y4650	Y4884								
bnl15.40	Y4624											
Psr2B (α -Amy)	Y4114											
BCD926	Y2115	Y3530	Y4603	Y5213								
G1087A	Y2115	Y3530	Y4603	Y5213								
C846	Y2115	Y3530	Y4603	Y5213								
BCD157	Y142	Y2495	Y3371									
C1562 & R1562	Y142	Y1381	Y1675	Y2495	Y3371	Y4773	Y5213					
C985	Y142	Y1135	Y1381	Y1675	Y2207	Y2495	Y2842	Y3371	Y4219	Y4773	Y5213	
CDO57	Y142	Y1135	Y1381	Y1675	Y2207	Y2495	Y2842	Y3371	Y4219	Y4773	Y5213	
CDO786	Y142	Y1135	Y1381	Y1675	Y2207	Y2495	Y2842	Y3371	Y4219	Y4773	Y5213	
Psr150	Y142	Y1381	Y2495	Y3371	Y5213							
C670SA	Y142	Y1381	Y2495	Y3371	Y3960	Y5213	Y5475					
S1057	Y3960	Y5091	Y5475									
Psr601	Y142	Y647										
C609	Y5091											
R2840	Y3614	Y4470										
C662	Y4470											
C1263	Y647											
C570	Y3614											
C47	Y3614											
C506	Y1395	Y1457										
C632	Y1395	Y1457	Y6983									
R1683	Y6983											

Bold indicates YACs present in the set containing 6934 YAC clones representing the entire rice genome, but absent from the rice 9 YAC sets.

probes, particularly those corresponding to heat shock proteins (encoded by multigene families) detected multiple YACs. In five cases, YACs detected by a single probe formed parts of contigs mapping to two different regions of the chromosome, creating regions of duplication (Figure 1). Fifteen probes used to screen the sets

of 6934 YAC clones representing the entire rice genome detected one or more YACs. Results of hybridization of probes to the two sets of YAC filters allowed the formation of 14 YAC contigs covering part of rice chromosome 9. A list of YAC clones detected by two or more probes is provided in Table 1.

RFLP analysis and mapping in rice: Of the 84 probes analyzed for RFLP between rice IR20 and 63-83 cultivars, 64 were polymorphic. Of the polymorphic probes, 31 were effectively single copy, producing a single strong band, while the remainder were multicopy. Because washing stringency was low, some multicopy probes detected a strong single copy (major) band overlying less homologous (minor) copies. Forty-four of the polymorphic probes were mapped. Of these, 27 probes detected loci mapping to rice chromosome 9 and these were, without exception, major bands. Of the 27, four probes also detected minor bands, and these mapped to chromosomes other than 9. Wheat probes hybridized with the strongest intensity to rice sequences mapping in the homoeologous location, and with a weaker signal to DNA fragments mapping elsewhere. Six probes detected major bands mapping to chromosomes other than 9. For eight probes, the major band was nonpolymorphic, and so only the minor bands could be mapped. Bands mapping to rice chromosomes other than 9 were located on most of the other 11 chromosomes, but five probes, expected from comparative mapping to be tightly linked on rice chromosome 9, mapped to rice chromosome 11.

Comparison of rice 9 physical and genetic maps: A comparison of the genetic map produced by KURATA *et al.* (1994b) (not shown) with our genetic map of IR20 $\times$ 63-83 and our contig map (Figure 1) shows only slight differences in marker order. The major exception to this order was probe BCD351, which detects a multiple banding pattern on rice Southern blots and in barley has copies on at least three different chromosomes. A likely explanation for this discrepancy is the presence of a second copy on rice chromosome 9 that has not been mapped.

RFLP analysis of the *ph1b* and *ph1c* deletion regions: Of the 52 probes hybridized to the wheat deletion line blots, three detected bands in Chinese Spring that were absent from both deletion mutants, and one detected a band inside the *ph1b* deletion but outside the *ph1c* deletion. The quality of hybridization to the wheat deletion line blots was poor in most cases because of the use of heterologous probes. Confirmation that poorly hybridizing probes detect loci inside or outside the deletions may be possible using PCR-based assays (GILL and GILL 1996), which we are currently devel-

FIGURE 2.—Autoradiograph of a Southern blot of genomic DNA digested with *EcoRV* and hybridized with the wheat DNA probe Psr574. Figure shows, in lane order, λ HindIII DNA marker, Chinese spring euploid, parental lines (a Chinese Spring *ph1b/ph1b* mutant and a Chinese Spring (Cappelle-Desprez 5B) substitution) and 13 progeny lines derived from this cross, segregating for high (H) or low (L) chromosome pairing. The probe detects several bands. The arrow indicates the band missing in those lines showing a high pairing phenotype. For one wheat line high or low pairing status was undetermined (U).

oping. Of the 24 probes hybridized to Southern blots of the doubled haploid population, seven detected loci cosegregating with lines that exhibited a high chromosome pairing phenotype, and these were assigned to the *ph1b* deletion. An example of a probe detecting such loci is shown in Figure 2. The probe Wg564 detected several bands, one of which cosegregated with the high chromosome pairing phenotype lines, while another did not exhibit complete cosegregation. These two Wg564 bands (*wg564A* and *wg564B*) may represent different loci that are genetically closely linked and thereby define the proximal end of the *ph1b* deletion. The distal end of the *ph1c* deletion is defined by the markers *S1057* (outside the *ph1c* deletion and inside the *ph1b* deletion) and *Xpsr150* (inside both deletions). Since these markers map to the same YAC contig, it suggests that these YACs span the distal breakpoint of the *ph1c* deletion. For five markers, that they are located within the deletions was inferred from their position on

FIGURE 1.—A comparison of the physical and genetic maps of rice chromosome 9 with genetic consensus maps of wheat, barley and maize chromosomes. Marker names are color coded according to the species of origin and are designated as follows: C or Xrgc, cDNA clones derived from rice callus library; R or Xrgr, cDNA clones derived from rice root library; S, cDNA clones derived from rice shoot tissue; G, rz or Xrz, rice genomic DNA clones; wg or Xwg, wheat genomic DNA clones; psr or Xpsr, wheat DNA clones; umc or Xumc, maize DNA clones; bnl or Xbnl, maize genomic DNA clones; bcd, Xbcd, ksu or Xksu, barley cDNA clones; psb or Xpsb, barley genomic DNA clones; cdo or Xcdo, oat cDNA clones. The cM column shows the map distance of the locus from the top of the linkage group. The physical map shows only those markers hybridizing to overlapping YACs. Some of the probes detect more than one YAC mapping to different regions of the chromosome. Note the occurrence of duplicated loci (one set of duplicates indicated by brackets) and clusters of single copy probes. The region of overlap of the *ph1b* and *ph1c* deletions on wheat chromosome 5B and its equivalent regions on rice chromosome 9, barley 5H and maize 2 and 7 are indicated. Probes located on more than one map are connected by lines, revealing synteny. Where synteny has broken down, the rice chromosomes to which the probes map are indicated. Regions of synteny breakdown are indicated.

the genetic and YAC contig maps of rice chromosome 9 relative to markers known to lie within the deletions. The marker *Xksu8* maps inside the *ph1b* deletion but outside the *ph1c* deletion (GILL and GILL 1996). We confirmed this using the PCR-based assay of GILL and GILL (1996), but the three loci we mapped in this study were all assigned to rice chromosome 11 (Figure 1). Thus, the junctions of the *ph1b* and *ph1c* deletions have been defined on rice chromosome 9, but not in wheat, which may have insertions in this equivalent region.

DISCUSSION

Synten between the genomes of several major cereal species has been shown by comparative mapping to occur both at the genetic level (MOORE *et al.* 1995a,b) and at the megabase level and below (DUNFORD *et al.* 1995; KILIAN *et al.* 1995). In this study, a detailed comparison has been made of the physical and genetic maps of rice chromosome 9 and the genetic maps of regions of wheat, barley and maize syntenous with rice 9 at the genetic level. The study reveals conservation of marker order between corresponding rice, wheat, barley and maize chromosomes above the megabase level, but also indicates a breakdown in synteny in one region of wheat homoeologous group 5 and barley chromosome 5H (Figure 1). Of the mapped markers, 73% showed synteny between rice and wheat, 80% between rice and barley and 71% between rice and maize. Probes from the nonsyntenous region of wheat homoeologous group 5 and barley 5H mapped to rice chromosomes 2, 8 or 11 rather than the expected rice chromosome 9. However, studies on the *Ph1* locus should not be affected by this region of synteny breakdown, which is distal to the distal end of the *ph1c* deletion.

MOORE *et al.* (1995b) demonstrated that wheat homoeologous group 5 is syntenous with rice chromosomes 3, 9, 11 and 12. Rice 9 was designated a single linkage block because rice probes located over the entire length of rice chromosome 9 hybridized to wheat homoeologous group 5 DNA (KURATA *et al.* 1994a). A recent report has demonstrated that the borders of rice linkage blocks correspond with centromeric and telomeric regions, and that these regions are characterized by an extensive loss of synteny between the cereal genomes, so one explanation of our results could be that some wheat, barley and maize chromosomes could have been created by the insertion of one rice linkage block into another, by the breakage and fusion of centromere sites (MOORE *et al.* 1997). The present study reveals that the synteny between rice 9, wheat 5 and barley 5H has been disrupted by insertions from rice chromosomes 2, 8 and 11, though the mechanism by which these smaller insertions have arisen is unknown. We have thus determined that probes on rice chromosome 9 may reveal the gene content of wheat homoeologous group 5 and barley 5H, but not visa versa, which also suggests that

the genome structure of rice is closer to that of the ancestral genome than are those of the Triticeae. The breakdown in synteny between the chromosomes of rice and other cereals implies that rice will be a useful tool for gene isolation in certain regions of the genome but not in others.

In this study, we have demonstrated conserved synteny above the megabase level between the region defined by the *ph1b* and *ph1c* deletions on wheat chromosome 5B and a region of rice chromosome 9, and have defined the extent of this region in rice. The equivalent region in rice to the *ph1b* deletion in wheat was defined at the proximal end by the probe Wg564, which detected two closely linked loci, *wg564A* and *wg564B*, one lying inside and one outside the deletion. The distal end of the *ph1c* deletion was defined by two probes hybridizing to the same YAC contig that spans the junction of the *ph1c* deletion. Our next goal will be the hybridization of probes to rice YAC and BAC (bacterial artificial chromosome) clone libraries to close the gaps between the contigs that span the rice 9 equivalent of the wheat *ph1b* and *ph1c* deletions. This will allow us to estimate more accurately the size of the region in rice corresponding to the deletions in wheat. In addition, we are currently developing wheat lines carrying smaller deletions around the *Ph1* locus that will enable us to target this locus more accurately.

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