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A genome-specific repetitive DNA sequence from *Oryza eichingeri*: characterization, localization, and introgression to *O. sativa*

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Abstract In the course of transferring the brown planthopper resistance from a diploid, CC-genome wild rice species, *Oryza eichingeri* (IRGC acc. 105159 and 105163), to the cultivated rice variety 02428, we have isolated many alien addition and introgression lines. The *O. eichingeri* chromatin in some of these lines has previously been identified using genomic in situ hybridization and molecular-marker analysis. Here we cloned a tandemly repetitive DNA sequence from *O. eichingeri* IRGC acc105163, and detected it in 25 introgression lines. This repetitive DNA sequence showed high specificity to the rice CC genome, but was absent from all the four tetraploid species with BBCC or CCDD genomes. The monomer in this repetitive DNA sequence is 325–366-bp long, with a copy number of about 5,000 per 1 C of the *O. eichingeri* genome, showing 88% homology to a repetitive DNA sequence isolated from *Oryza officinalis* (2n=2*x*=24, CC). Fluorescent in situ hybridization revealed 11 signals distributed over eight *O. eichingeri* chromosomes, mostly in terminal or subterminal regions.

Keywords Repetitive DNA sequence · *Oryza eichingeri* · Fluorescent in situ hybridization · Introgression lines

Introduction

Moderately and highly repetitive DNA sequences may, in some cases, account for over 90% of a genome. Available evidence indicates that repetitive DNA sequences may influence chromosome structure and recombination events, and are likely to be active in the process of genome differentiation (Calderini et al. 1997; Uozu et al. 1997). For this reason, detailed knowledge of their abundance, sequence divergence, and genome distribution is critical to the full understanding of genome organization (Brown et al. 1998). Repetitive DNA sequences are either organized in tandem arrays or dispersed throughout the whole genome (Harrison and Heslop-Harrison 1995; Rokka et al. 1998). Tandemly repeated DNA sequences, including satellites, microsatellites, or gene units encoding ribosomal RNAs, represent a large proportion of the heterochromatin and often cluster predominantly at chromosome domains close to the telomeres and/or centromeres; whereas dispersed repetitive DNA sequences are found scattered on most or even all chromosomes, flanked by other repetitive or unique sequences (Schmidt and Heslop-Harrison 1996; Calderini et al. 1997; Rokka et al. 1998; Schmidt et al. 1998).

The DNA sequence of a repeat and its copy number at each chromosome site can all evolve rapidly, leading to its specificity to a certain genome/species, and even a chromosome (Galasso et al. 1995; Wang et al. 1995; Matyasek et al. 1997). Such changes have proved to be valuable in studies of species divergence and genome evolution, in order to determine the putative progenitor and to establish the evolutionary relationships among different species or genomes (Zhao et al. 1989; Tsujimoto and Gill 1991; Wu and Wu 1992; Kamm et al. 1995; Daud and Gustufson 1996; Matyasek et al. 1997; Thomas et al. 1997). In this respect, repetitive DNA probes are far superior to genomic DNA probes. For example, two closely related genomes, A and D, in hexaploid oat were clearly differentiated by a dual-FISH, using both A- and C-genome specific repeated DNA probes, which had been impossible by genomic in situ hybridization (Linares et al. 1998). Cordesse et al. (1991) could even differentiate the two subspecies of *Oryza sativa*, *indica* and *japonica*, according to their difference in the copy-number of a 352-bp, AA-specific tandem repeat.

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The species (genome)-specific repetitive DNA sequence is also a powerful molecular marker for analyzing the nuclear genome or chromosome composition in sexual or somatic hybrids and derivatives, as in the genera *Nicotiana*, *Brassica*, *Festulolium* and *Triticum* (Zhang and Dvorak 1990; Itoh et al. 1991; Perez-Vicente et al. 1992; Cabrera et al. 1995; Kapila et al. 1996; Calderini et al. 1997; Kamstra et al. 1997).

Thus far, at least 20 repetitive DNA sequences, mostly in tandem array, have been isolated from various *Oryza* species, and some of them were highly specific to the AA, BB, CC, CCDD, EE or FF genomes (Zhao et al. 1989; Aswidinnoor et al. 1991; Cordesse et al. 1991; Wu and Wu 1992; Zhao and Kochert 1992; Reddy et al. 1993; Zhao and Kochert 1993; Wu and Wu 1994a, b; Kiefer-Meyer et al. 1995). Among them, seven repeats, i.e. TrsB from *Oryza brachyantha* (2n=2*x*=24, FF), RIRE1 from *Oryza australiensis* (2n=2*x*=24, EE), TrsA and G1034 from *O. sativa* (2n=2*x*=24, AA), Os48, OsG3–498 and OsG5–756 from *Oryza officinalis* (2n=2*x*=24, CC), have been physically localized to individual chromosomes using (fluorescent) in situ hybridization (Wu et al. 1991; Wang et al. 1995; Ohmido and Fukui 1997; Uozu et al. 1997). Nevertheless, none of them has been used to follow alien chromosome segment in wide rice hybrids.

Oryza eichingeri (2n=2*x*=24, CC) shows excellent resistance to brown planthopper, the most destructive pest in rice productivity. The resistant genes identified in IRGC acc105159 and 105163 have been transferred to *O. sativa* cv 02428 (Yan et al. 1997) and the gene from IRGC acc105159 has been localized to rice chromosome 2 using RFLP and SSR markers (Liu et al. 2001). In this investigation, we cloned a CC genome-specific, repetitive DNA sequence from *O. eichingeri* IRGC acc105163, and then used it as a probe to detect the *O. eichingeri* chromosome segment integrated into the *O. sativa* genome. This repeated DNA sequence, contained in four clones, was characterized in terms of DNA sequence, copy number, and physical distribution along *O. eichingeri* chromosomes.

Materials and methods

Plant materials

Thirteen entries from nine rice species plus some A-C intergenomic hybrids and derivatives were used in this study. The nine species are: (1) AA genome species: *O. sativa* cv 02428, which was developed in Jiangsu Academy of Agricultural Sci., P.R. China; (2) BBCC genome species: *Oryza minuta* IRGC acc. 101386, *Oryza punctata* IRGC acc. 100886 and 100937; (3) CC genome species: *O. officinalis* IRGC acc. 105088, *O. eichingeri* IRGC acc. 105159 and 105163; (4) CCDD genome species: *Oryza latifolia* IRGC acc. 100967, 100952 and 100170, and *Oryza grandiglumis* IRGC acc. 101405; (5) EE genome species: *O. australiensis* IRGC acc. 101397; and (6) HHJJ genome species: *Oryza ridleyi* IRGC acc. 100821. Seeds of the above 12 wild-species IRGC accessions were kindly provided by the International Rice Research Institute. The A–C intergenomic hybrids and their derivatives were produced in this laboratory, including (1): F_1 hybrid and 67 disomic plants from two crosses between *O. sativa* cv 02428 and *O. eichingeri* (IRGC acc. 105159 and 105163) (Yan et al. 1997, 2001); and (2) ten alien addition lines from cross between *O. sativa* cv 02428 and *O. officinalis* IRGC acc105088 (Yan et al. 1999; unpublished).

Cloning of repetitive DNA sequence

Genomic DNA of *O. eichingeri* IRGC acc. 105163 was partially digested with *Sau*3A, fractionated by electrophoresis through a 0.8% agarose gel, and stained with ethidium bromide. Fragments in the range of 0.5–2.0 kb were gel-purified using an Advantage PCR-Pure kit (Clontech Laboratories Inc.) and cloned into the *Bam*HI site of the pGEM-3Zf(+/–) vector. The ligation mixture was used to transform cells of *Escherichia coli* strain DH5α, and the cultures were plated on the ampicillin-containing LB medium freshly supplemented with X-Gal and IPTG, from which 1,716 white colonies were selected. A total of 19 positive clones, which gave strong signals with a [^{32}P]-labeled *O. eichingeri* DNA probe but faint or no signal with a [^{32}P]-labeled *O. sativa* DNA probe in the colony hybridization, were subjected to Southern-blot hybridization.

Southern blot hybridization

Genomic DNA from all the tested plants was extracted according to McCouch et al. (1988), digested with appropriate restriction endonuclease, electrophoresed on a 0.8% agarose gel, and transferred onto Hybond N^+ membranes (Amersham). The insert in each of the 19 positive clones was isolated by digestion with *Sma*I plus *Xba*I, and labeled with [^{32}P]. They were then hybridized to the filter containing DNA from *O. sativa* 02428 and two *O. eichingeri* IRGC accessions which were separately digested with five endonucleases (*Eco*RI, *Eco*RV, *Hin*dIII, *Bam*HI, and *Dra*I). The washing conditions were: 2×, 1× and 0.5×SSC/0.1% SDS, 20 min each at 65°C. All 19 plasmids were confirmed to contain repetitive DNA sequences specific to *O. eichingeri*, but only three clones, designated as I14, I23 and I33, were subcloned and characterized in detail. To understand their genome or species specificity, they were each hybridized against a similar amount of *Eco*RV-digested DNA from 13 rice species entries representing six rice genomes. In addition, they were hybridized to *Hin*dIII digests from ten *O. sativa–O. officinalis* addition lines and *Eco*RV digests from 67 *O. sativa–O. eichingeri* introgression lines in order to reveal their possible presence in those plants.

DNA sequencing and copy number estimation

Inserts in four subclones were sequenced from both directions on an Automatic DNA Sequencer (Model 373A, Applied Biosystems) using a sequencing kit (Amersham). The sequences were aligned with the Sequencher 3.1.1 software. The sequence of subclone I23–1 was searched at the National Center for Biotechnology Information (NCBI) database (http://www.ncbi.nlm.nih.gov/BLAST/) for sequence homologs using blastn. Genomic DNA of the parental species was diluted stepwise from 1 µg/10 µl to 2 ng/10 µl and that of the I23–1 insert from 225 ng/10 µl down to 0.012 ng/10 µl. The copy-number was then estimated by dot-blot hybridization.

Fluorescent in situ hybridization (FISH)

FISH was carried out as described (Yan et al. 2001). The insert from subclone I23–1 was labeled with digoxigenin-11-dUTP (Roche) and hybridized to root-tip metaphase cells prepared from a F_1 plant between *O. sativa–O. eichingeri* IRGC acc105163. Post-hybridization washings included: 2×SSC at 37°C for 2×5 min, 50% formamide-2×SSC at 45°C for 10 min, and 2×SSC

at 45°C for 2×10 min. Signals were developed by incubating with anti-digoxigenin-FITC (Roche) and amplified with rabbit anti-sheep-FITC (Roche). Images were captured on 400 ISO Kodak color film, scanned, and processed using Photoshop 5.0.

Results

Isolation of repeats and their genome specificity

A total of 1,716 genomic clones from *O. eichingeri* IRGC acc105163 were screened by colony hybridization; 19 clones were initially selected based on their strong hybridization to *O. eichingeri* total DNA and no or faint hybridization to *O. sativa* total DNA. They were further hybridized to the filter containing DNA from two IRGC accessions of *O. eichingeri* and *O. sativa* cv 02428 that were digested with five restriction endonucleases (*Eco*RI, *Eco*RV, *Hind*III, *Bam*HI and *Dra*I). Each clone produced a strong signal in all the lanes with *O. eichingeri* DNA, but weak or no signal in lanes with *O. sativa* DNA (data not shown), confirming the results of colony hybridization. Only three clones, namely, I14, I23 and I33, were chosen for detailed analysis because they could be easily detected in many disomic plants from a cross between *O. sativa* and *O. eichingeri* IRGC acc. 105163. They may belong to the same repeated DNA family, because (1) they produced almost identical profiles in the above Southern-blot hybridization, i.e. ladder-like bands in lanes of *Eco*RV digests and smears in lanes from the other four enzymes, and (2) they showed strong cross-hybridization.

In order to understand their genome specificity, the insert from each clone was hybridized to *Eco*RV digests of nine rice species representing AA, BBCC, CC, CCDD, EE or HHJJ genomes. The hybridization patterns were the same for all the three clones and that from clone I23 is shown in Fig. 1. The ladder-like hybridization pattern, indicating its tandem organization in the genome, was additionally observed only in the lane of another CC-genome species, *O. officinalis*. It seems that this repetitive DNA sequence is highly specific to the rice CC genome.

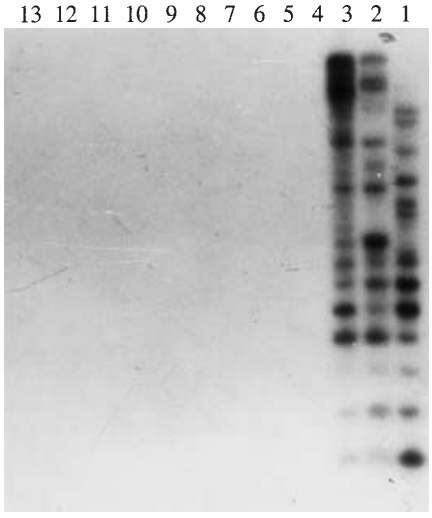

Fig. 1 Southern blot hybridization of clone I23 to *Eco*RV digests of genomic DNA from 13 materials in nine rice species. Materials from right to left are: *O. officinalis* IRGC acc. 105088 (2n=2*x*=24, CC), *O. eichingeri* IRGC acc. 105159 and 105163 (2n=2*x*=24, CC), *Oryza sativa* cv. 02428 (2n=2*x*=24, AA), *O. minuta* IRGC acc. 101386 (2n=4*x*=48, BBCC), *O. punctata* IRGC acc. 100886 and 100937 (2n=4*x*=48, BBCC), *O. latifolia* IRGC acc. 100967 and 100954 (2n=4*x*=48, CCDD), *O. grandiglumis* IRGC acc. 101405 (2n=4*x*=48, CCDD), *O. latifolia* IRGC acc. 100170, *O. australiensis* IRGC acc. 101397 (2n=2*x*=24, EE), and *O. ridleyi* IRGC acc. 100821 (2n=4*x*=48, HHJJ). Ladder-like signals were only detected in two *O. eichingeri* (lanes 2 and 3) accessions and one *O. officinalis* (*lane 1*) IRGC accession

DNA sequence and copy number

To determine the DNA sequences of the repeat units in the three clones, two *Sph*I fragments of clone I14 (I14–1 and I14–2), one *Sph*I fragment of I23 (I23–1) and one *Pst*I fragment of clone I33 (I33–1) were subcloned. They all showed the same hybridization profiles as the original clones and should contain the same repeat unit. The four subclones are 325-bp, 366-bp, 366-bp, and 364-bp long, respectively. As expected, they are highly homologous, with only minor divergence due to point mutations and deletion/insertion events (Fig. 2). A homology search at the NCBI database revealed 12 homologs for clone I23–1. For example, it shows 88% homology to an *O. officinalis* satellite DNA clone, PS027 (e-103, Reddy et al. 1993), and 84–94% homology to nine repetitive DNA sequences from six other rice species (e-34–e-97). Assuming that *O. eichingeri* has the same genome size as *O. sativa*, 4.3×0^8 bp, the copy number of this repeat was then estimated to be approximately 5,000 per 1C of the *O. eichingeri* genome.

Chromosomal localization

To clarify the chromosomal distribution of this repeated DNA family, the insert in clone I23–1 was labeled with digoxigenin-11-dUTP and hybridized to 24-chromosome somatic cells of an *O. sativa-O. eichingeri* F_1 hybrid. Eleven signals of various intensities, with nine residing close to or in the distal regions, could be detected on eight unidentified chromosomes which should all be from *O. eichingeri* (Fig. 3). No FISH signal was visible on the remaining four *O. eichingeri* chromosomes, presumably due to the absence of this repeat on those chromosomes or the insufficient resolution of this FISH technique.

Because this repetitive DNA also exists in *O. officinalis* (CC genome), we hybridized clone I23 to *Hin*dIII digests from ten *O. sativa–O. officinalis* addition lines. The added *O. officinalis* chromosomes in those lines have been identified using RFLP analysis, karyotype analysis and GISH technique (Yan et al. 1999; unpublished). Signals were detected on four addition lines, one

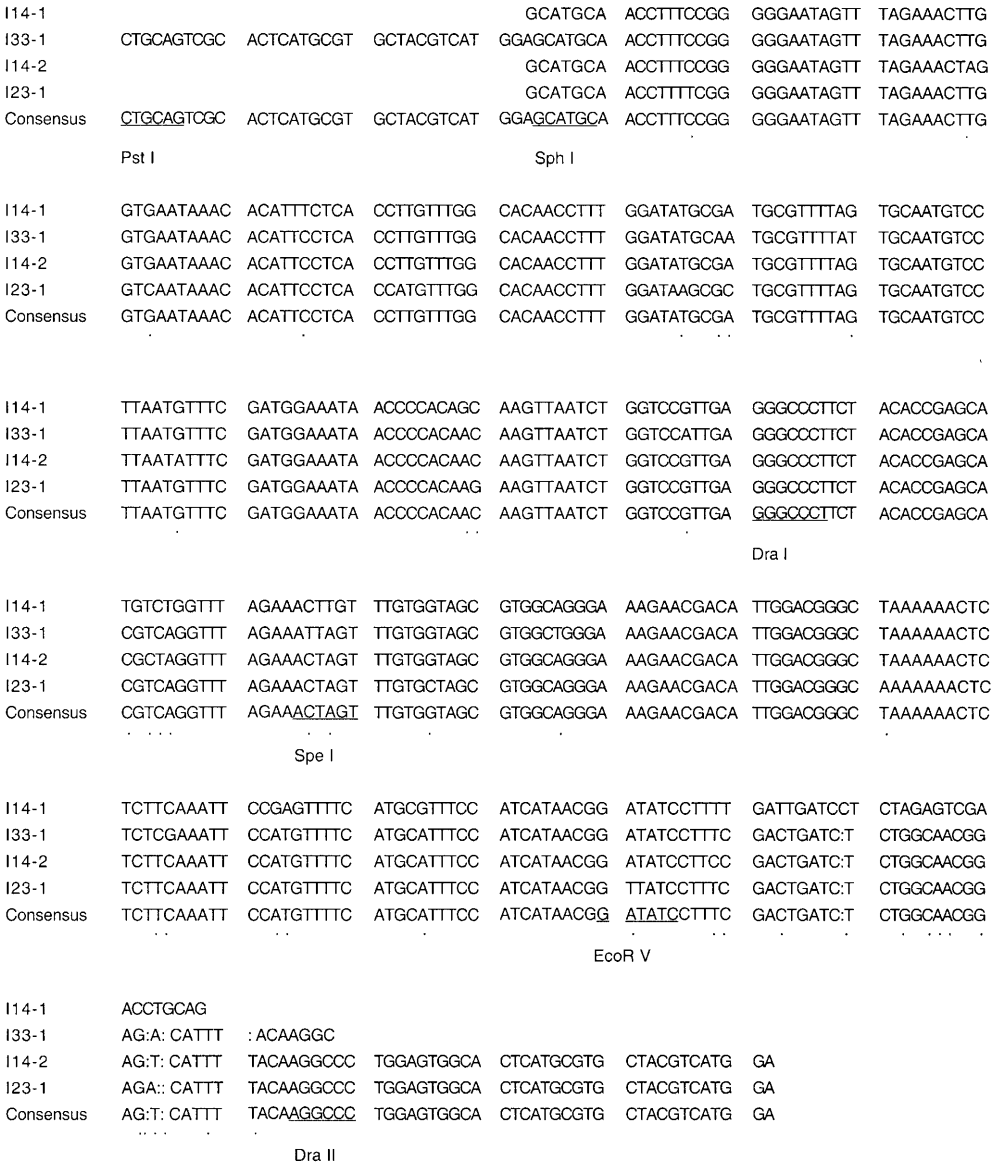

Fig. 2 Alignment of the nucleotide sequences of four cloned repeats from *O. eichingeri.* The length of clones I14–1, I14–2, I23–1and I33–1 was 325-bp, 366-bp, 366-bp, and 364-bp, respectively. Only a limited number of mutations and insertions/deletions was observed

with *O. officinalis* chromosome 9 (9C), two with chromosome 11 (11C), and one with chromosomes 10 and 11 (10C+11C), implying that the clone I23 related sequence may be located on the added chromosomes or may have been introgressed into the *O. sativa* chromosomes from those lines (Fig. 4).

The presence of cloned sequence in recombinant chromosomes

Clone I23 was hybridized to *Eco*RV-digested DNA of 67 disomic backcross plants from crosses between cultivated rice variety 02428 and the two IRGC accessions of *O. eichingeri*. Strong signals, also ladder-like, were detected in 25 out of the 45 plants from the cross involving IRGC acc. 105163, from which this repeat was isolated (Fig. 5), demonstrating that in those plants *O. eichingeri* chromatin containing this repeat has been transferred to *O. sativa*. In contrast, no signal was detected in any of the remaining 22 plants derived from the cross involving IRGC acc. 105159, although clone I23 could hybridize to the *Eco*RV-digested genomic DNA from this accession (Fig. 2).

Discussion

In the present study, a 325–366-bp, tandemly repetitive DNA sequence has been cloned from *O. eichingeri* IRGC acc. 105163 and has proved to be highly specific to the rice CC genome. By performing FISH on an *O. sativa–O. eichingeri* F_1 hybrid, this sequence was mapped to eight of the 12 *O. eichingeri* chromosomes.

This repetitive DNA sequence also was detected in another CC-genome species, *O. officinalis*, and it shows 88% homology to a repetitive DNA sequence in this spe-

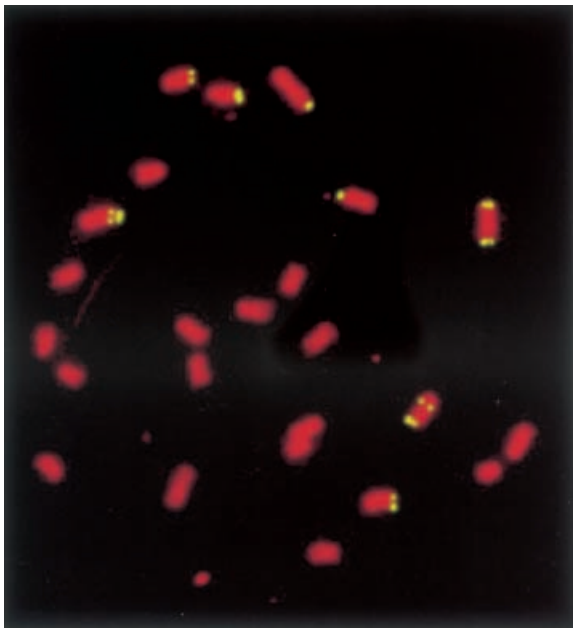

Fig. 3 FISH image of a metaphase chromosome cell from an *O. sativa–O. eichingeri* F_1 hybrid by using digoxigenin-labeled insert from clone I23 as a probe. Eleven signals, mostly in or near the terminal regions, were visible on eight *O. eichingeri* chromosomes (approximately 6,400×)

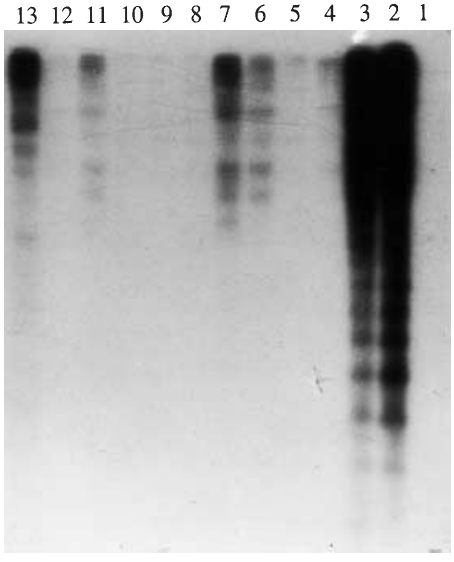

Fig. 4 Southern-blot hybridization of clone I23 to the *Hin*dIII-digested genomic DNA of *O. sativa* (*lane 1*), *O. officinalis* IRGC acc. 105088 (*lane 2*), F_1 hybrid (*lane 3*) and ten *O. sativa–O. officinalis* alien addition lines (*lanes 4–13*). Alien addition lines from the right on are: 48–1 (lane 4, *O. officinalis* chromosome no. was not identified), 48–4 (lane 5, 4C), 48–10 (*lane 6*, 11C), 48–13 (*lane 7*, 10C+11C), 48–16 (*lane 8*, 4C), 48–25 (*lane 9*, 4C), 48–34 (*lane 10*, 4C), 48–37 (*lane 11*, 11C), 48–39 (*lane 12*, 11C) and 48–41 (*lane 13*, 9C). 4C, 9C, 10C and 11C represented *O. officinalis* chromosomes 4, 9, 10 and 11, respectively. Signals were observed on plants 48–10 (*lane 6*), 48–13 (*lane 7*), 48–37 (*lane 11*) and 48–41 (*lane 13*)

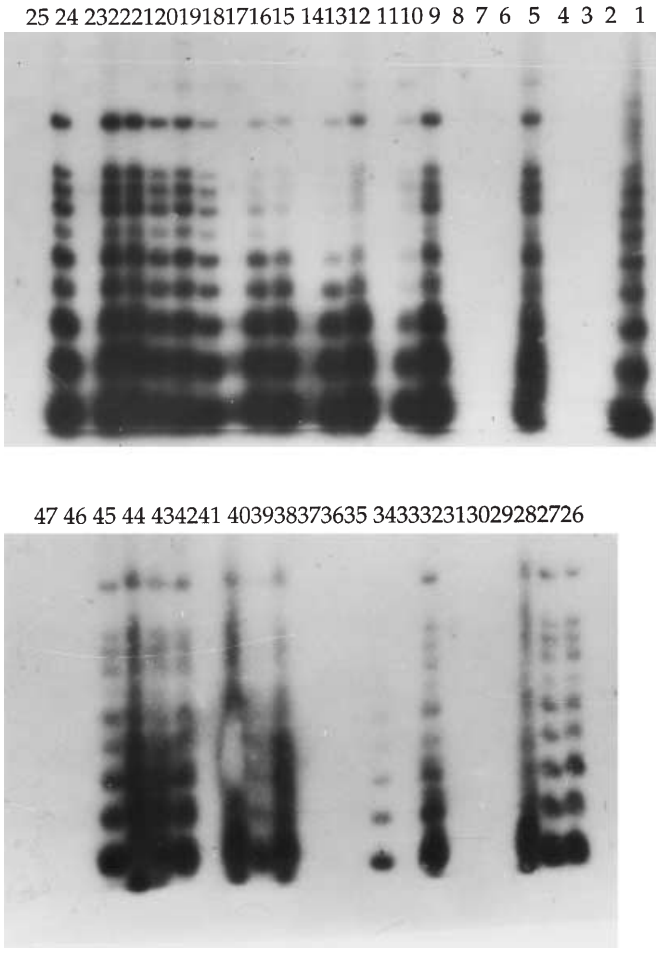

Fig. 5 Southern-blot hybridization of clone I23 to the *Eco*RV-digested genomic DNA of *O. sativa* (*lane 2*), *O. eichingeri* IRGC acc. 105163 (*lane 1*), and 45 disomic plants (*lanes 3–47*) from *O. sativa*×*O. eichingeri* IRGC acc. 105163. Strong signals were detected in 25 disomic plants

cies (Reddy et al. 1993). In this study, this repetitive sequence was detected in the alien addition lines with *O. officinalis* chromosome 9 (9C), chromosomes 10 and 11 (10C+11C), and chromosome 11 (11C). In a similar study, Reddy et al. (1993) mapped its homolog to *O. officinalis* chromosomes 6 (6C) and 8 (8C) by using eight alien addition lines. As shown in Fig. 2, however, this repetitive sequence was not detected in any of the following four tetraploid rice species: *O. minuta* (BBCC), *O. punctata* (BBCC), *O. latifolia* (CCDD) and *O. grandiglumis* (CCDD), raising one of several possibilities. (1) extensive genome rearrangements, probably deletions, have occurred in those BBCC- or CCDD-genome species following the polyploidization, which has led to the loss of this repetitive DNA; (2) it represents a fast-evolving sequence, therefore its homolog is no longer recognizable by the hybridization method; or (3) the CC-genome ancestor of those species did not contain this repetitive DNA sequence. In fact, great variations within the same species, from highly abundant to entirely absent, have been reported for some rice repeti-

tive DNA sequences (Wu and Wu 1992; Kiefer-Meyer et al. 1995; Thomas et al. 1997). For example, the repetitive DNA sequence pS027 from *O. officinalis,* which showed strong similarity to this repetitive DNA, could only be detected in some *O. officinalis* accessions (Reddy et al. 1993). Cordesse et al. (1991) and Kiefer-Mayer et al. (1995) also observed that none of the five CC-genome specific repeats from *O. officinalis* could be detected in CCDD-genome accessions.

Some genome-specific, repetitive DNA sequences have been effectively used to monitor alien chromatin introgression in wheat (Zhang and Dvorak 1990). In our effort to transfer useful genes from distantly related wild species to cultivated rice, we have obtained many disomic backcross plants from the cross *O. sativa*×*O. eichingeri*. Most of them have been confirmed as introgression lines using morphological traits, molecular markers, and genomic in situ hybridization (Yan et al. 1997, 2001). By using this repetitive DNA as a probe, we have identified the introgressed *O. eichingeri* segment in 25 disomic plants.

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