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Localization of the rice stripe disease resistance gene, *Stv-b^i*, by graphical genotyping and linkage analyses with molecular markers

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Abstract We used graphical genotyping and linkage analyses with molecular markers to determine the chromosomal location of the rice stripe disease resistance gene, *Stv-b*^{i}. The stripe resistance gene from the *indica* rice (*Oryza sativa*) cv 'Modan' was introgressed into several Japanese rice varieties. We found 4 RFLP markers in 'Modan', five susceptible parental rice varieties ('Norin No. 8', 'Sachihikari', 'Kanto No. 98', 'Hokuriku No.103' and 'Koganebare') and four resistant progeny varieties ('St. No. 1', 'Aichi No. 6', 'Aoisora' and 'Asanohikari'). Graphical genotyping of the resistant progeny revealed a chromosomal segment ascribable to 'Modan' and associated with stripe resistance. The chromosomal segment from 'Modan' was located at 35.85 cM on chromosome 11. Linkage analysis using 120 F_2 individuals from a cross between 'Koshihikari' (susceptible) and 'Asanohikari' (resistant) revealed another 8 RFLP markers in the same chromosome. We performed a bioassay for rice stripe resistance in F_3 lines of the F_2 individuals using infective small brown planthoppers and identified an 1.8-cM segment harboring the rice stripe disease resistance gene, *Stv-b*^{i}, between XNpb220 and XNpb257/XNpb254. Furthermore, *Stv-b*^{i} was linked by 0.0 cM to a RFLP marker, ST10, which was developed on the basis of the results of RAPD analysis. These DNA markers near the *Stv-b*^{i} locus may be useful in marker-assisted selection and map-based cloning of the *Stv-b*^{i} gene.

Key words *Oryza sativa* · Stripe resistance gene · Genetic map · Molecular markers

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Introduction

The rice stripe virus (RSV) is transmitted by the small brown planthopper *Laodelphax striatellus*. While *japonica* paddy rice varieties were susceptible to stripe disease until the 1960s, some *indica* and *javanica* varieties and *japonica* upland rice varieties were highly resistant (Washio et al. 1967). These upland varieties harbor two pairs of complementary dominant genes, *Stv-a* and *Stv-b* (Washio et al. 1968a). The *Stv-a* locus is linked with the glutinous endosperm (*wx*) and photosensitivity-1 (*Se-1*) loci on chromosome 6, but the location of *Stv-b* is unknown. *Stv-b* alone provided incomplete resistance in an upland rice variety (Washio et al. 1968c). Some *indica* paddy varieties have a different resistance gene, *Stv-b*^{i}, which is allelic with *Stv-b* and incompletely dominant (Washio et al. 1968b, c). Beginning in the 1960s, *Stv-b*^{i} was introduced by backcrossing from the *indica* paddy variety 'Modan' into the *japonica* paddy variety 'Norin No. 8'. The first resistant variety ('St. No. 1') was used for breeding stripe resistant varieties, and several resistant varieties having the *Stv-b*^{i} gene were subsequently bred in Japan. The *Stv-b*^{i} gene has provided stable resistance to rice stripe virus since it was first introgressed into *japonica* paddy rice varieties about 30 years ago. Hence, DNA markers for *Stv-b*^{i} would be very useful for marker-assisted selection in rice breeding. The location of this resistance gene locus was estimated by analysis of reciprocal translocations (Washio et al. 1968c).

Two independent intraspecific linkage maps have been constructed for rice using restriction fragment

length polymorphism (RFLP) techniques (McCouch et al. 1988; Saito et al. 1991). Recently, Causse et al. (1994) published a high-density interspecific map. However, *Stv-b*^{i} has not been linked to morphological or molecular markers, and its location in the rice genetic map is unknown. Random amplified DNA polymorphism (RAPD; Williams et al. 1990) has been used to generate many DNA markers that are tightly linked to the target genes. In the study described here, we used RFLP and RAPD techniques, along with graphical genotyping and linkage analyses, to define the location of *Stv-b*^{i} in rice genotypes resistant to rice stripe virus.

Materials and methods

Plant materials

The rice varieties used in this study are shown in the pedigree in Fig 1a. This pedigree includes 'Modan', the original donor of *Stv-b*^{i}; four resistant varieties ('St. No. 1', 'Aichi No. 6', 'Aoisora' and 'Asanohikari'); and five *japonica* susceptible varieties ('Norin No. 8', 'Sachihikari', 'Kanto No. 98', 'Hokuriku No. 103' and 'Koganebare').

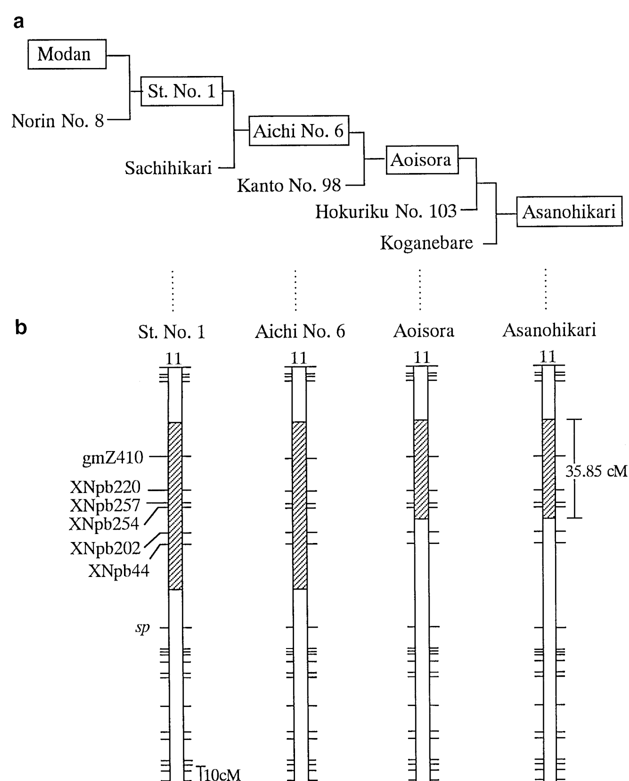

Fig. 1 a The pedigree of stripe resistant varieties derived from a resistant donor *indica* rice, 'Modan'. Varieties in *squares* are resistant. **b** Graphical genotypes of chromosome 11 in four resistant varieties. The *shaded portions* indicate the segment introgressed from 'Modan'. *Horizontal bars* represent RFLP markers developed by Saito et al. (1991). The morphological marker "short panicle" (*sp*) is shown for comparison with the classical rice map

We used 120 F_2 individuals obtained from a cross between 'Koshihikari' (susceptible) and 'Asanohikari' (resistant) for RFLP analysis. F_3 lines derived from each F_2 plant were used for the bioassay for stripe resistance. 'Nipponbare', a famous *japonica* paddy variety in Japan, and 'St. No. 1' ('Modan' × 'Norin No. 8^{6}') were used as its susceptible and resistant standard varieties, respectively.

Bioassay for stripe resistance

We performed the seedling test method to determine disease reaction (Washio et al. 1967). Twenty-five to thirty seedlings of each F_3 were planted in a small plastic dish and kept at 27°C. When the rice plants reached the 1.5–2.0 leaf stage, they were inoculated by exposure to infective small brown planthoppers for 2 days. After inoculation, the insects were removed, and the inoculated plants were transplanted into nursery boxes in a greenhouse. The F_3 lines were evaluated at 3–4 weeks after transplanting. F_2 individuals were classified as homozygous susceptible, heterozygous or homozygous resistant.

Molecular markers

In this study, 322 RFLP markers (prefix XNpb) cited by Saito et al. (1991) were used for graphical genotyping and linkage analyses. RFLP markers mapped on rice chromosome 11 in other RFLP linkage maps were also used for linkage analysis: 11 RFLP markers (prefix RG and CDO) provided by Cornell University (McCouch and Tanksley 1991) and 13 markers (prefix C, G, R and ST723) provided by the Rice Genome Research Program (RGP) of Japan (Kurata et al. 1994). Eight hundred 10-base random primers (Operon Technologies) were also used for RAPD analysis.

DNA extraction and molecular techniques

Genomic DNA was isolated from young leaves of each variety or from leaves of each 8-week-old F_2 plant by the modified CTAB method (Murray and Thompson 1980). The purified DNA was digested with restriction endonucleases *Bam*HI, *Bgl*II, *Eco*RI, *Eco*RV or *Hin*dIII. After agarose gel electrophoresis (0.8% agarose gel and 1 × TAE buffer containing 0.5 μg/ml ethidium bromide), the digested DNA fragments of each variety were transferred to nylon membranes Hybond N^{+} (Amersham) by the capillary transfer method under the neutral conditions. After hybridization, the blots were washed at 42°C in washing buffer (6 *M* urea, 0.5 × SSC and 0.4% SDS), incubated in the detection reagent of the ECL system (Amersham) and then exposed to X-ray films for 1 h. RAPD analysis was performed as described by Williams et al. (1990). Amplified products were separated by 1.4% (w/w) agarose gel electrophoresis. Polymorphic amplified DNA fragments were isolated from agarose gel using the GENECLEAN kit (BIO101) and cloned using the TA cloning kit (Strategene).

Linkage analysis

Genetic distance was calculated using MAPL version 3.0 (Ukai et al. 1995). In this software, recombination values were calculated by the maximum likelihood method (Allard 1956) and then converted into genetic distance (cM) using the Kosambi function (Kosambi 1944). The putative order of the loci was estimated using the metric multidimensional scaling method.

Results

The chromosomal segment introgressed from 'Modan'

We performed RFLP analysis on ten varieties to identify the chromosomal segments introgressed from the *indica* rice 'Modan' into the resistant progeny (Fig. 1a). The genetic variation among the five *japonica* susceptible varieties used for this analysis was apparently very low; only 1 polymorphic RFLP marker was obtained from these varieties. Therefore, any additional polymorphic RFLP marker detected in the resistant progeny must be due to recombination with Modan's genetic contribution. The number of RFLP markers that hybridized with 'Modan'-specific bands decreased with each succeeding generation. There were 16 markers on chromosomes 2, 4, 5 and 11 in 'St. No. 1', 9 (on chromosomes 5 and 11) in 'Aichi No. 6', and 4 (on chromosome 11) in 'Aoisora' and 'Asanohikari'. These results suggest that the introgressed segment derived from 'Modan' is likely to be on chromosome 11. The graphical genotypes of chromosome 11 of the resistant progenies, 'St. No. 1', 'Aichi No. 6', 'Aoisora' and 'Asanohikari', are shown in Fig. 1b. The number of polymorphic RFLP markers on chromosome 11 also decreased from 6 in 'St. No. 1' to 4 in 'Asanohikari'. These 4 RFLP markers, gmZ410, XNpb220, XNpb254 and XNpb257, showed polymorphism between all of the susceptible and resistant varieties tested. These markers are mapped in a cluster on chromosome 11. The length of the introgressed segment in 'Asanohikari' was 35.85 cM according to the rice RFLP map developed by Saito et al. (1991).

Bioassay of stripe resistance

We performed six tests for each F_3 line. From the results of bioassays, the F_2 population was seen to have segregated into 26 : 56 : 38 for susceptible homozygous (S), heterozygous (H) and resistant homozygous (R). This segregation fit the expected 1(S) : 2(H) : 1(R) ratio (chi-square $=$ 2.93, $0.10 < P < 0.30$).

Screening of molecular markers for linkage analysis

RAPD and additional RFLP analyses were performed to isolate additional markers for linkage analysis. We used 800 random decamers to generate about 2,200 amplified DNA fragments from the genomic DNAs of the ten varieties used for genotyping analysis. Only 5 primers could be used to distinguish between the resistant and susceptible varieties. One primer amplified a DNA band only from susceptible varieties, while the other 4 primers generated diagnostic bands only from resistant varieties. There was no polymorphic band indicating an insertion/deletion. All 5 amplified DNA fragments were cloned and used as hybridization probes in RFLP analysis of the two varieties, 'Koshihikari' and 'Asanohikari'. One of five inserts, a 730-bp fragment amplified from a stripe resistant variety, showed polymorphism between the two varieties and was used as a RFLP marker ST10 for linkage analysis. In a subsequent survey of other RFLP markers on chromosome 11, we found 8 polymorphic RFLP markers which could distinguish between the resistant and susceptible varieties: CDO534, CDO365, CDO226 and RG103 (Cornell University); and C189, C1172, R3341 and ST723 (RGP).

Linkage analysis and chromosomal location of stripe disease resistance gene

The 13 RFLP markers were used to investigate segregation in the F_2 population. Based on the segregation for these markers and for stripe resistance in F_2 populations, the genetic distance and best-fit gene orders were determined using the computer program MAPL. The stripe resistance gene, *Stv-b*^{i}, was mapped into the introgressed segment on chromosome 11 (Fig. 2). One polymorphic marker, RG103, was located within 4.2 cM from the *Stv-b*^{i} gene. RG103 marks the *Xa-21* locus that conditions resistance to rice bacterial blight disease (Ronald et al. 1992). The *Stv-b*^{i} gene was located in a 1.8-cM interval between XNpb220 and XNpb254/XNpb257. As shown in Fig. 3, XNpb220, XNpb257 and ST10 hybridized with different DNA fragments in the susceptible and resistant parents. Both mapping parents showed 2 XNpb254-hybridizing DNA fragments, 1 of which was polymorphic. No recombinants between ST10 and *Stv-b*^{i} were found out of 120 F_2 individuals. Stripe resistance is more closely associated with ST10 than any of the other markers, as shown by the graphical genotypes of several F_2 recombinants within the 1.8-cM interval (Fig. 4). The F_2 individuals which were

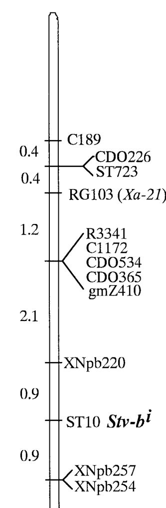

Fig. 2 RFLP map of the genomic region around the stripe resistance gene *Stv-b*^{i} on rice chromosome 11. The data for this map were obtained from the F_2 population derived from a cross between 'Koshihikari' and 'Asanohikari'. The RG103 marker is linked to the *Xa-21* locus (Ronald et al. 1992). The *rounded* and *flattened ends* represent the orientation toward the telomere and centromere, respectively

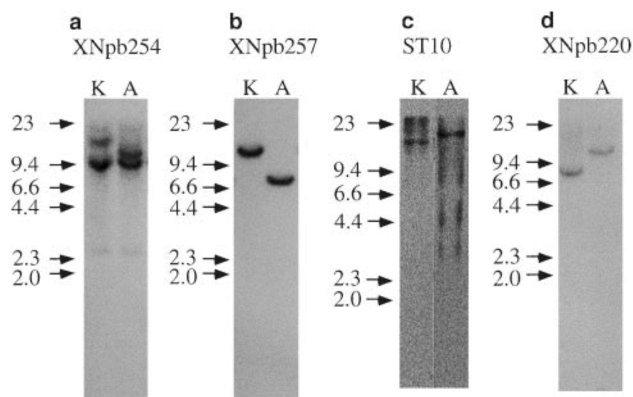

Fig. 3a–d Southern blots with the four markers linked to *Stv-b*^{i}. Panels: **a** *Eco*RV-digested genomic DNA hybridized with XNpb254, **b** *Eco*RV-digested genomic DNA hybridized with XNpb257, **c**, *Eco*RI-digested genomic DNA hybridized with ST10, **d** *Bam*HI-digested genomic DNA hybridized with XNpb220. *Lanes*: *K* stripe-susceptible parent, 'Koshihikari', *A* stripe-resistant parent, 'Asanohikari'. Fragment lengths according to lambda DNA size markers are shown to the *left* of each panel in kilobases (kb).

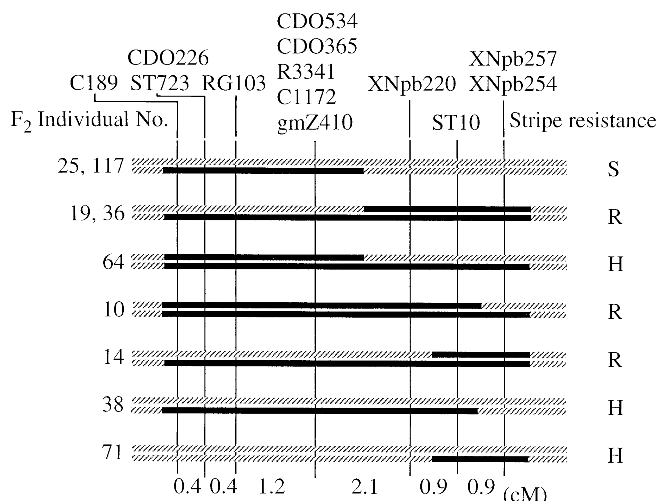

Fig. 4 The stripe-resistance phenotypes and the graphical genotypes of F_2 recombinants between gmZ410 and XNpb254/XNpb257 in the F_2 population. The *solid* and *hatched bars* represent chromosome regions derived from *indica* ('Modan') and *japonica*, respectively. The plants were classified as susceptible homozygous (*S*), heterozygous (*H*) and resistant homozygous (*R*) based on the results of the bioassay for stripe resistance

of the *indica*-homozygous genotype at the ST10 locus were resistant to stripe disease, the heterozygous individuals showed intermediate resistance and the plants that showed the *japonica* genotype at this locus were susceptible. From these results, it is clear that the *Stv-b*^{i} gene is located between XNpb220 and XNpb254/XNpb257 and is tightly linked to ST10.

Discussion

We identified an introgressed segment on chromosome 11 from stripe resistant variety 'Modan' that was associated with the resistance gene *Stv-b*^{i} in the four resistant progenies. The molecular markers on the introgressed segment were linked to stripe resistance, and the *Stv-b*^{i} gene is probably located in this chromosomal segment. Our findings are consistent with several other reports. It has been reported that two blast resistance genes derived from 'Modan', *Pi-k* and *Pi-f*, are located on chromosome 11 with 15% of recombination value (Shinoda et al. 1971). Linkage has been reported between the blast resistance gene *Pi-f* and stripe resistance derived from 'Modan' (Koumura et al. 1985). One of two stripe resistance genes in *japonica* upland rice has been significantly correlated with some RFLP markers on chromosome 11 (Ando et al. 1993). This resistance gene may be *Stv-b*, which is allelic with *Stv-b*^{i}. Therefore, it is highly probable that the *Stv-b*^{i} locus is on chromosome 11.

Only 4 out of 322 RFLP markers developed by Saito et al. (1991) showed polymorphism between the F_2 parents, 'Koshihikari' and 'Asanohikari'. We also used 24 RFLP markers found in two other rice RFLP maps. These markers were mapped in the chromosomal 11 region corresponding to the introgressed segment in 'Asanohikari'. Only one-third of these RFLP markers showed polymorphism. In the RAPD analysis, 5 polymorphic fragments were detected out of about 2,200 amplified products, but only 1 RFLP marker, ST10, was developed. The other 4 fragments were not useful because they showed no polymorphism in RFLP analysis of the mapping parents. Contrary to expectation, we identified a small number of polymorphic markers from the results of both analyses. We think that the length of the introgressed segment on chromosome 11 is shorter than 35.85 cM. The interval between C189 and XNpb254 or XNpb257 is 5.9 cM, as shown in Fig. 2.

With the advent of high-density RFLP maps and transposon tagging techniques, more than 10 resistance genes have been cloned from plants. In rice, one bacterial leaf blight resistance gene was isolated by map-based cloning (*Xa-21*; Song et al. 1994). For map-based cloning, it is important to identify molecular markers tightly linked to a target gene and to map the gene within a short interval of molecular markers. In this study, we mapped the *Stv-b*^{i} gene within a 1.8-cM interval and identified four *Stv-b*^{i}-linked DNA markers, XNpb220, XNpb254, XNpb257 and ST10. An F_2 population consisting 120 plants may be sufficient for fine mapping. There is a possibility that the existence of 1 recombinant between two loci in the population can cause a change of map distance of at least 0.4 cM. However, as shown in Fig. 4, it is obvious that the *Stv-b*^{i} gene is closely linked to ST10 and that the *Stv-b*^{i} gene is located in the interval between XNpb220 and XNpb254/XNpb257. These markers can be used to isolate the *Stv-b*^{i} gene.

Eleven resistance genes to different kinds of diseases have been located in two regions on chromosome 11;

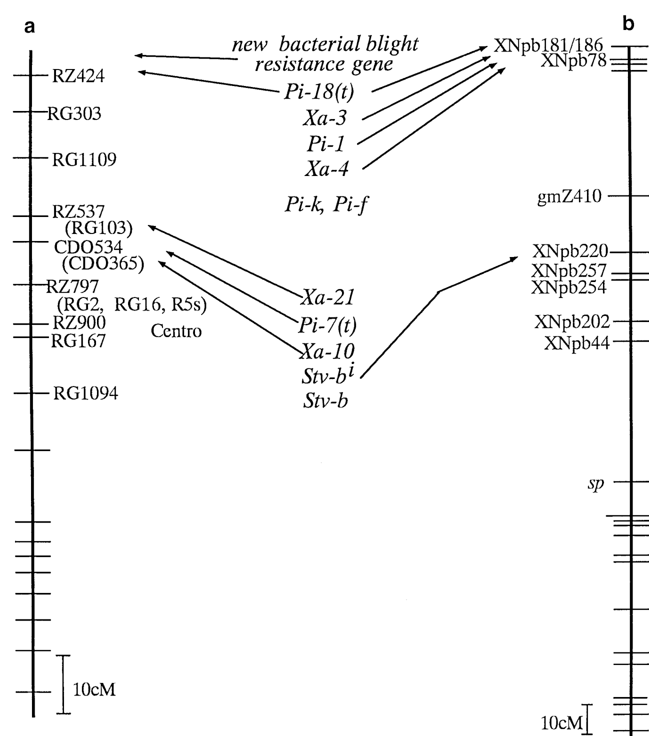

Fig. 5a, b Rice resistance genes located on chromosome 11 based on the molecular map of Causse et al. (1994a) and Saito et al. (1991b). Arrows connect resistance genes with their linked molecular markers. *Horizontal bars* represent the RFLP marker loci

one region is near the telomere and the other is near the centromere (Fig. 5). In addition to *Xa-21*, *Pi-k*, *Pi-f* and *Stv-b*, there are four bacterial blight resistance genes and three blast resistance genes mapped on chromosome 11 (Yoshimura et al. 1993; Lin et al. 1995; Mew et al. 1994; Wang et al. 1994; Ahn et al. 1996). These resistance genes may be on the short arm of chromosome 11 based on the location of the centromere (Van Deynze et al. 1995) and presence of 5S ribosomal DNA gene on the short arm (Kamisugi et al. 1994). The reason for the clustering of many resistance genes on chromosome 11 is unknown. Song et al. (1994) pointed out that sequence comparison of these resistance genes on rice chromosome 11 may lead to clues regarding the evolution of plant disease resistance. In this study, we determined that the *Stv-b^i* gene is also located near these resistance genes on chromosome 11. We are now isolating the *Stv-b^i* gene for characterization and sequencing.

In Japan, many studies now in progress are aimed at developing molecular markers linked to genes associated with various agricultural traits, including disease resistance. The development of molecular markers in combination with polymerase chain reaction (PCR) techniques has enabled marker-assisted selection as a new breeding method. Heterozygous B_nF_1 plants, which are difficult to identify by bioassay, can be easily identified using the molecular marker ST10, which is tightly linked to *Stv-b^i*. A set of primers based on the sequence of ST10 can be used for PCR-assisted selection for stripe disease resistance in addition to the standard biological assay in rice breeding programs.

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