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Delimitation of the chromosomal region for a quantitative trait locus, *qUVR-10*, conferring resistance to ultraviolet-B radiation in rice (*Oryza sativa* L.)

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Abstract Wide variation in ultraviolet-B (UVB) resistance is observed among rice varieties. In a previous study, three quantitative trait loci (QTLs) controlling UVB resistance were detected by QTL analysis, using backcross inbred lines (BILs) derived from a cross between a *japonica* cultivar, 'Nipponbare', and an *indica* cultivar, 'Kasalath'. Among them, *qUVR-10*, a QTL for UVB resistance on chromosome 10, showed the largest effect. Plants homozygous for the Nipponbare allele at *qUVR-10* were resistant to UVB, unlike those homozygous for the Kasalath allele. To determine more precisely the chromosomal location of *qUVR-10*, we performed a linkage mapping of *qUVR-10* as a single Mendelian factor using advanced backcross progeny. Advanced progeny testing of F_4 families enabled us to determine the genotype classes of the *qUVR-10* locus with high reliability. As a result, *qUVR-10* was mapped between RFLP markers C60755S and C1757S, and co-segregated with C913A. In addition, a sequence showing high similarity to the *Arabidopsis* cyclobutane pyrimidine dimer (CPD) photolyase gene, which has been found to be involved in sensitivity to UV radiation in *Arabidopsis* and rice, was mapped in the candidate genomic region of *qUVR-10*. This result suggests that the CPD photolyase gene is a positional candidate for *qUVR-10*.

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Introduction

The absorption of harmful ultraviolet-B (UVB) radiation has adverse effects on plants, resulting in retarded growth and low yield (Teramura 1983). Every plant species has evolved defense mechanisms against UV radiation. There are two basic strategies. One is the accumulation of UV-absorbing compounds (Caldwell et al. 1983; Bharti and Khurana 1997), and the other is the development of an efficient DNA repair mechanism (Britt 1999).

In *Arabidopsis*, genetic and molecular analyses of several laboratory-induced mutants have contributed to our understanding of the mechanism of resistance to UV radiation (Bharti and Khurana 1997; Britt 1999). Several mutants that are hypersensitive to UV radiation have been isolated (Harlow et al. 1994; Jenkins et al. 1995; Jiang et al. 1997a, b). Among them, *UV resistance 2* and *3* (*uvr2* and *uvr3*) mutants are caused by mutations in cyclobutane pyrimidine (CPD)- and pyrimidine [6-4] pyrimidone dimer (6-4 product)-specific photolyase genes, respectively (Ahmad et al. 1997; Nakajima et al. 1998). *UV hypersensitive 1* and *3* (*uvh1* and *uvh3*) mutants carry mutations in the endonuclease genes for nucleotide excision repair, which have been isolated by a positional cloning strategy (Liu et al. 2000, 2001). A knockout mutant of *AtMYB4* that produces significantly higher than normal levels of sinapate esters, which are part of the UV-protecting sunscreen mechanism in the leaves, shows improved tolerance to UVB treatment (Jin et al. 2000).

No mutant for UVB response has been reported in rice. However, a wide variation in the level of UVB resistance has been observed among rice varieties (Sato and Kumagai 1993). Physiological approaches have been used to analyze the mechanism of protection against UVB radiation in rice (Hidema et al. 1997; Sato and Kumagai 1997). Recently, it was demonstrated that the UVB-sensitive rice cultivar 'Norin 1' contains defective CPD photolyase (Hidema et al. 2000). In addition, quantitative trait locus (QTL) analysis has been performed on UVB resistance, and three QTLs have been identified by using backcross inbred lines (BILs) derived from a cross

between an *indica* cultivar, 'Kasalath' (UVB-sensitive), and a *japonica* cultivar, 'Nipponbare' (resistant). Among them, *qUVR-10* (the *Q*TL for *u*ltrav*i*olet-B *r*esistance on chromosome *10*) showed the largest allelic difference, and plants homozygous for the Nipponbare allele at the QTL were more resistant to UVB than those homozygous for the Kasalath allele (Sato et al. 2003). However, the genes responsible for *qUVR-10* remain to be identified at the molecular level.

With the progress that has been made in analysis of the genome, natural allelic variation has become a valuable resource for the functional analysis of plant genes (Alonso-Blanco and Koorneef 2000; Yano 2001). In particular, QTLs controlling tomato fruit size (Frary et al. 2000) and soluble solids content (Fridman et al. 2000), as well as flowering time in rice (Yano et al. 2000; Takahashi et al. 2001; Kojima et al. 2002) and in *Arabidopsis* (El-Din El-Assal et al. 2001), have been isolated by map-based strategies. Thus, natural allelic variation can be a resource to help us understand the molecular mechanism of biologically and agronomically interesting phenomena, such as UVB resistance in rice.

With the ultimate aim of map-based cloning of *qUVR-10*, we performed a fine-linkage mapping of *qUVR-10* using advanced backcross progeny. In the linkage mapping, we tested advanced progeny by using F_4 families in order to determine the genotype classes of *qUVR-10* with high reliability. As a result, we were able to map *qUVR-10* as a single Mendelian factor. In addition, a rice homolog of the CPD photolyase gene was found on the basis of the linkage mapping to be a positional candidate gene for *qUVR-10*.

Materials and methods

Plant materials

The plant materials used in this study are summarized in Fig. 1A. An F_1 plant, that was a cross between Nipponbare and Kasalath,

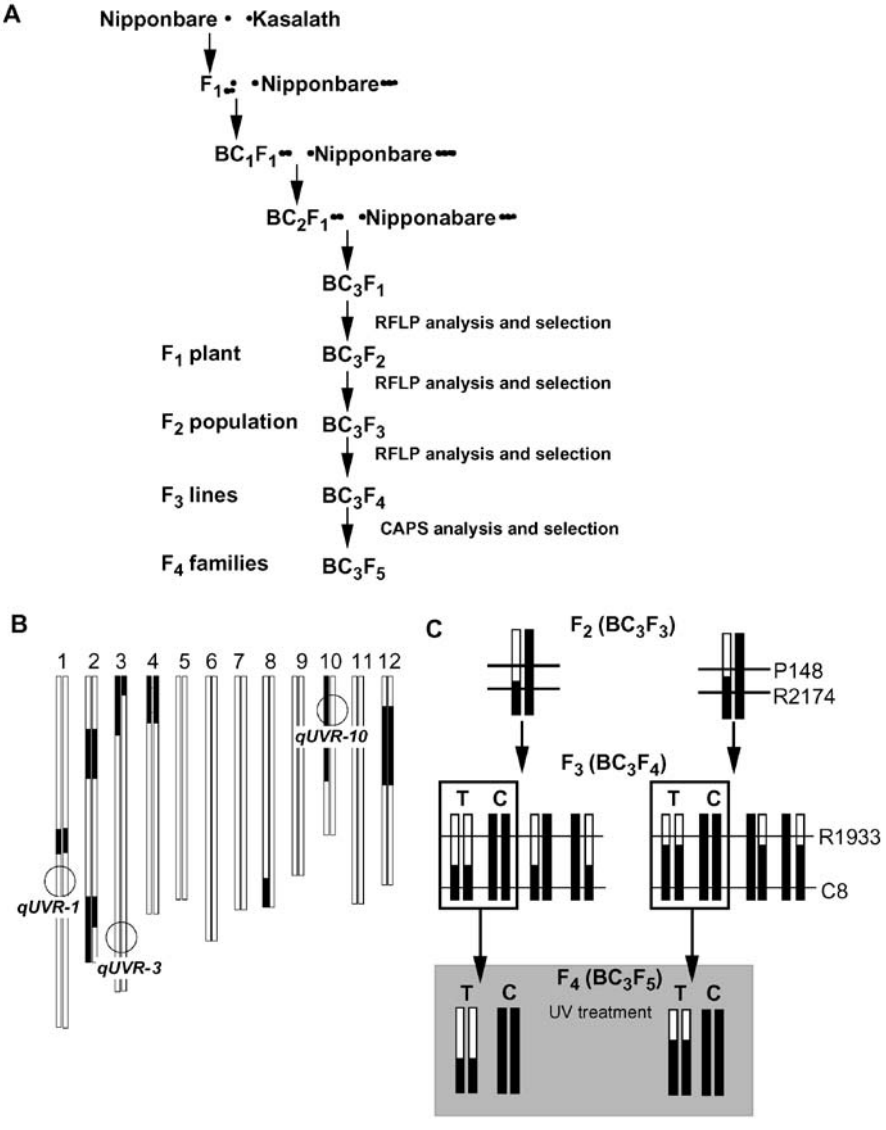

Fig. 1A–C Plant material used for fine mapping of *qUVR-10*. **A** Populations in this study were derived from a cross between Nipponbare (*japonica*, a UV-resistant cultivar) and Kasalath (*indica*, a UV-sensitive cultivar). **B** Graphical genotype of the BC_3F_2-12 plant, which was used as an F_1 plant for fine mapping of *qUVR-10*. *Black and white* regions represent the segments of the chromosomes derived from Kasalath and Nipponbare, respectively. The *circles* indicate QTLs detected in the QTL analysis using the BILs (Sato et al. 2003) **C** Plant materials of F_4 families for the Tester (T) and its Control (C), which were used for advanced progeny testing

was backcrossed with Nipponbare as a recurrent parent. Successive backcrossings were performed. By a whole-genome survey with restriction-fragment-length polymorphism (RFLP) markers, we selected a plant in the BC_3F_2 generation, BC_3F_2-12, which was suitable for the fine mapping of *qUVR-10*. In BC_3F_2-12, several chromosomal regions were homozygous for the Kasalath allele, but the *qUVR-10* region was heterozygous, and other putative QTL regions were homozygous for the Nipponbare allele (Fig. 1B). Self-pollinated progeny of BC_3F_2-12 (hereafter referred to as the F_2 population: 198 plants) and the following generations were used for the fine mapping of *qUVR-10*. BC_3F_4 lines (hereafter F_3 lines; 50 plants in each line) obtained from the selected F_2 plants were used for progeny testing to determine the genotype classes of *qUVR-10*. We also selected two F_3 plants homozygous for the recombinant chromosome (Tester; T) and the non-recombinant (Control; C) from each of the F_3 lines with the aid of two cleaved amplified polymorphic sequence (CAPS) markers (described below), R1933 and C8, flanking both sides of *qUVR-10*. Self-pollinated progeny (hereafter F_4 families) of each plant (T and C) were used for F_4 progeny testing (Fig. 1C).

Evaluation of UVB resistance

Evaluation of UVB resistance was performed according to the method of Sato and Kumagai (1997). In brief, 50 seeds of each BC_3F_4 line were sown and maintained at 25/18°C (day/night) with a 12-h photoperiod in a growth cabinet. Seedlings were allowed to grow for 3 weeks under visible light with or without additional UVB radiation, which was filtered through cellulose diacetate film to eliminate UV radiation with wavelengths below 290 nm. The distance between the UVB lamp and the leaf canopy was adjusted to give a UVB radiant flux per unit area of 1 W/m^2. The fresh weights of the aerial parts of the UVB-irradiated and unirradiated plants were measured 3 weeks after germination. UVB resistance was determined by the retardation of growth rate, and hence by the ratio (%) of fresh weight (RFW) of UVB-irradiated plants to that of unirradiated plants. In F_4 progeny testing, the method used for UVB irradiation was the same as that used in F_3 progeny testing. In addition, to determine the genotype of *qUVR-10* with high reliability, we observed differences between T and C in the occurrence of necrotic lesions on each leaf (50 plants in each line) after 3 weeks of UV irradiation. Nipponbare, Kasalath and a substitution line, SL-77, which was used to confirm the existence of the detected QTL in a previous study (Sato et al. 2003), were used as genotypic references of UVB-sensitive plants in the progeny testing.

RFLP and CAPS analysis

For RFLP analysis, all probes used in this study were selected from a high-density rice genetic linkage map including 3267 markers (http://rgp.dna.affrc.go.jp/publicdata/geneticmap2000/index.html). All procedures for DNA extraction, DNA digestion by restriction enzyme, electrophoresis and Southern blotting have been described previously (Kurata et al. 1994). Southern hybridization and detection were performed according to the protocols of the ECL Nucleic Acid Labeling and Detection System (Amersham Pharmacia Biotech, UK). Two CAPS markers, R1933 (5′ TAG ACC AGA GTG AAG AGA GAA G 3′ and 5′ TAA AGT GAA CCA ACT GCG TG 3′, and *Hae*III digestion) and C8 (5′ GTC TCT GGC GAG TCA TCT TC 3′ and 5′ CTT CAC ACG CGA CAT TAG C 3′, and *Apa*I digestion), which flanked *qUVR-10*, were chosen from 332 PCR-based genetic markers (http://rgp.dna.affrc.go.jp/publicdata/caps/index.html).

For mapping of contig 1,759, which contains a sequence with high similarity to that of the *Arabidopsis* CPD photolyase gene, a CAPS marker, C1 (5′ CTTTACCGTGAACTGGCTAG 3′ and 5′ ATTCTCAAGCTGTTCCCTCC 3′, and *Taq*I digestion) was developed in accordance with the sequence of contig 1,759 (http://btn.genomics.org.cn/rice/).

Linkage mapping and QTL analysis

Linkage analysis was performed by using Mapmaker/EXP 3.0 with the Kosambi function (Lander et al. 1987). QTL analysis was done by using Mapmaker/QTL ver 1.1 (Lander and Botstein 1989; Lincoln et al. 1992).

Results

Delimitation of *qUVR-10* by using BILs

In a previous study, 98 BILs derived from Nipponbare/Kasalath//Nipponbare (Lin et al. 1998), and genotype data of 245 RFLP markers (http://rgp.dna.affrc.go.jp/publicdata/genotypedataBILs/genotypedata.html) were used for the QTL analysis of UVB resistance (Sato et al. 2003). To more finely delimit the candidate chromosomal region of *qUVR-10*, we analyzed five additional RFLP markers (S2348, P148, C913A, C1757S and C148), which flanked *qUVR-10*, on the 98 BILs. A fine QTL mapping was performed by using these additional markers, in combination with the phenotype data for UVB resistance previously obtained by Sato et al. (2003). As a result, *qUVR-10* was mapped near RFLP marker C913A with a LOD score of 10.73. When we used the confidence interval of the QTLs as a 2.0 LOD value reduction from the peak LOD, *qUVR-10* was most likely localized between RFLP markers S2348 and C148 (Fig. 2A). We selected three informative lines (BIL-63, -85, -95), in which chromosomal recombination occurred in the flanking region of *qUVR-10*, as well as two lines, BIL-31 (homozygous for Nipponbare) and BIL-56 (homozy-

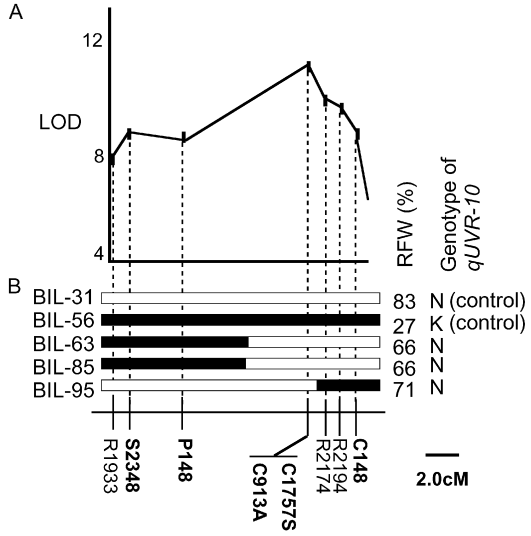

Fig. 2 **A** Interval mapping of *qUVR-10* using BILs, and **B** relationship between genotypes of eight RFLP markers on the short arm of chromosome 10 and phenotypic response of the selected BILs. Genotypes of *qUVR-10* were estimated from the RFW and are represented by *N* (homozygous for Nipponbare allele) and *K* (homozygous for Kasalath allele). *Boldfaced* RFLP markers represent the five additional markers used in this study (see Results)

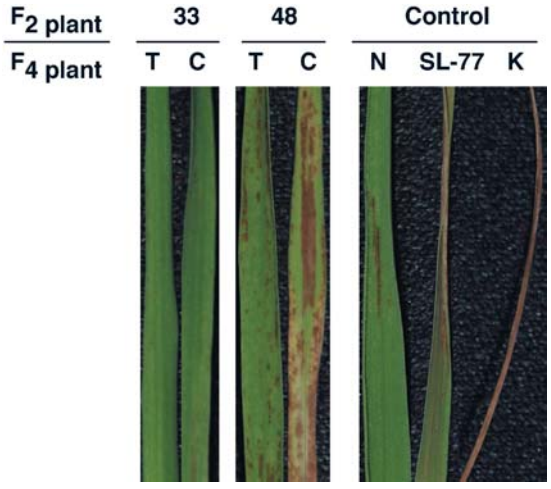

Fig. 3 Necrotic lesions of Tester (*T*) and its Control (*C*) derived from F_2 plants nos. 33 (homozygous for Nipponbare allele) and 48 (heterozygous), and from Nipponbare (*N*), Kasalath (*K*), and SL-44

gous for Kasalath), as genotype references. When the RFWs of the lines obtained by Sato et al (2003) were compared, three lines were homozygous for the Nipponbare allele at *qUVR-10*. Thus, *qUVR-10* is most likely located in the interval between RFLP markers P148 and R2174 (Fig. 2B).

Fine mapping of *qUVR-10* as a single Mendelian factor

To map *qUVR-10* as a single Mendelian factor, we determined the genotypes of ten RFLP markers, which were found to be located in the flanking region of *qUVR-10*, in 198 F_2 plants. We then selected seven informative plants in which recombination occurred between RFLP markers P148 and R2174, which flanked *qUVR-10*. The F_3 progeny of these seven plants were subjected to UVB irradiation, and the RFW was calculated. In the F_3 progeny testing, it was difficult to classify the seven F_3 plants into three genotype classes—homozygous for the Nipponbare or Kasalath alleles and heterozygous—on the basis of the RFWs, because the RFWs of the seven progeny showed continuous variation, and phenotypic classification was ambiguous (data not shown).

To determine the genotype class of F_2 plants at *qUVR-10* with high reliability, we selected recombinant homozygous plants (T and C) from each of the F_3 lines on the basis of marker-assisted selection (Fig. 1C), then analyzed the self-pollinated progeny (F_4 family) of those plants. The genotype classes of *qUVR-10* were determined from the RFW and from the level of occurrence of necrotic lesions on the leaves of F_4 families. Nipponbare, a resistant control, showed no, or a small number of, necrotic lesions on the leaves. In contrast, Kasalath and SL-77, a sensitive control, showed a large number of necrotic lesions on the leaves, resulting in shrinking of the leaves (Fig. 3). On the basis of this criterion, we could clearly classify the genotype classes of the F_3 plants. Hence, when both T and C were either UVB resistant or UVB sensitive, we presumed that the F_3 plant was homozygous for the Nipponbare or Kasalath allele, respectively, at *qUVR-10*. We could assume that the plants were heterozygous when both T and C showed different reactions to UVB (susceptibility and resistance, respectively). The genotype of the F_2 plants could be determined from that of the F_3 plants. As a result, F_2 plants nos. 32, 33, 37 and 47 were likely to be homozygous for the Nipponbare allele, and plants nos. 48, 52 and 53 were likely to be heterozygous (Fig. 4). These results clearly indicate that *qUVR-10* was mapped between the RFLP markers C60755S and C1757S, and co-segregated with RFLP marker C913A on the short arm of chromosome 10 (Fig. 5).

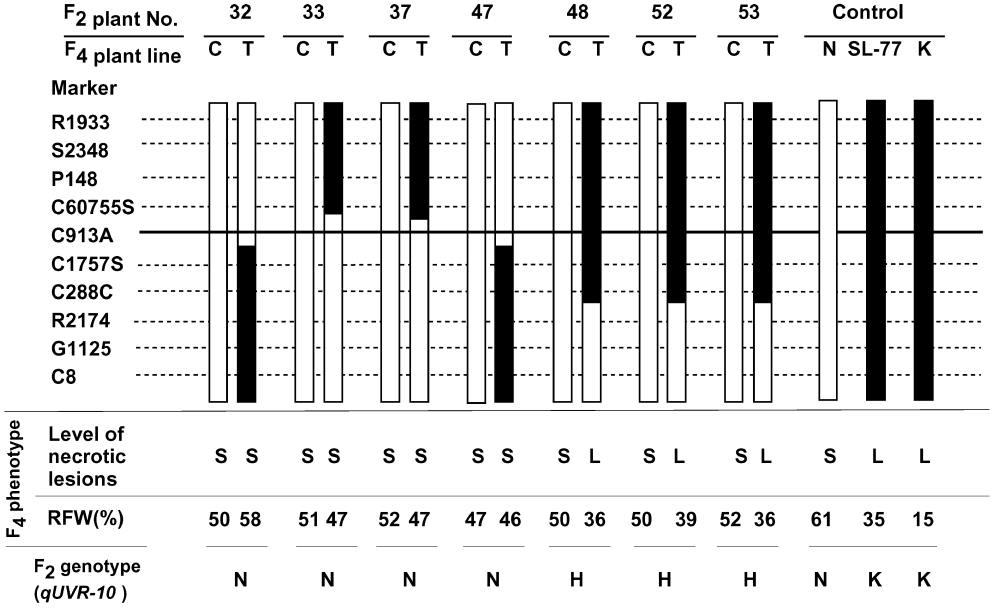

Fig. 4 Relationship between phenotype classes of the F_4 families and genotype classes of F_2 plants. Ten markers were used for genotyping. Nipponbare (*N*) was used as the resistant reference and Kasalath (*K*) and SL-77 were used as sensitive reference plants. The number of necrotic lesions is indicated by *S* (small number) and *L* (large number). The genotype of *qUVR-10* was determined from the level of necrotic lesions, and RFW is represented by *N* (homozygous for Nipponbare allele) and *H* (heterozygous). Plants homozygous for the Kasalath allele were not among the F_2 plants selected

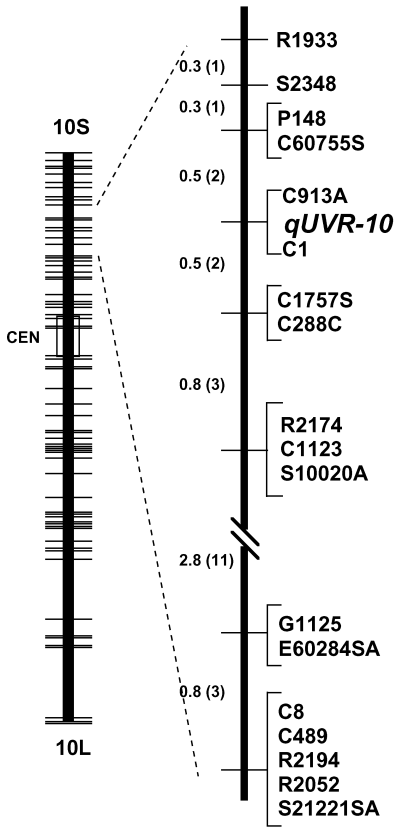

Fig. 5 Linkage map of chromosome 10, showing the location of *qUVR-10*. The *left vertical bar* indicates an RFLP linkage map constructed from the F_2 population of Nipponbare and Kasalath (Harushima et al.1998). The CAPS marker, *C1*, is located on contig 1,759 (http://btn.genomics.org.cn/rice/). The *right vertical bar* represents the linkage map constructed in this study. Map distances (cM) between adjacent RFLP markers are shown on the left. *Numerals in parentheses* indicate the numbers of recombinant F_2 plants. *Names* of DNA markers and QTLs are shown on the right

Positional candidate of *qUVR-10*

The UVB-sensitive rice cultivar Norin 1 contains defective photolyase (Hidema et al. 2000). A BLAST search of the *Arabidopsis* CPD photolyase cDNA sequence (AF053365) on the rice genome database (Yu et al. 2002; http://btn.genomics.org.cn/rice/) revealed that contig 1,759 contained a sequence with high similarity to *Arabidopsis* CPD photolyase. To clarify the chromosomal location of contig 1,759, we developed a CAPS marker, C1, based on the photolyase-like sequence of contig 1,759. As a result of linkage mapping, C1 was mapped between RFLP markers C60755S and C1757S, and cosegregated with RFLP marker C913A and *qUVR-10* (Fig. 5). The rice CPD photolyase gene is therefore a positional candidate gene for *qUVR-10*.

Discussion

By using advanced backcross progeny we were able to map the QTL, *qUVR-10*, for UVB resistance as a single Mendelian factor. Recently, several QTLs for heading date and field resistance to blast disease have been mapped as single Mendelian factors (Fukuoka and Okuno 2001; Lin et al. 2002, 2003; Monna et al. 2002). These studies clearly demonstrate that the use of advanced progeny enables us to minimize the phenotypic variation derived from non-target QTLs (chromosomal regions) and, hence, to map QTLs precisely. This study verifies that the strategy can be applied to stress tolerance features such as UVB resistance. In general, the phenotype of the level of UVB resistance can be affected by environmental conditions. This makes it difficult to determine genotype classes with high reliability on the basis of phenotype classes. In fact, the phenotypic variation in the F_3 progeny did not allow us to determine the genotype classes of F_2 plants in this study. However, further-advanced progeny, such as the F_4 lines, could be used to determine the genotype classes. Our ultimate goal is to clone *qUVR-10*. In this study, we established a basis for the map-based cloning of *qUVR-10*. We now need to perform linkage analysis of a larger population to further delimit candidate regions for *qUVR-10*.

In *Arabidopsis*, the genes responsible for the DNA repair mechanism have been cloned by analyzing UV-hypersensitive mutants (Ahmad et al. 1997; Nakajima et al. 1998; Liu et al. 2000, 2001). Comparison between the chromosomal location of the rice homologues of these genes and that of *qUVR-10* is an alternative approach to the identification of *qUVR-10*. In this study, it was revealed that one of the functional candidates for *qUVR-10*, the CPD photolyase gene, was located in the candidate genomic region by linkage mapping. Therefore, CPD photolyase can be a strong functional and positional candidate of *qUVR-10*. Furthermore, the increasing amount of genomic sequence data derived from the International Rice Genome Sequencing Project (IRGSP) enabled us to find such functional and positional candidate genes (http://rgp.dna.affrc.go.jp/IRGSP/). We found four putative chalcone syntase (CHS) genes in the candidate genomic region of the *qUVR-10* (data not shown). The CHS is the key enzyme for the biosynthesis of flavonoids, which is a UV-absorbing compound (Bharti and Khurana 1997). These genes are also positional and functional candidates for *qUVR-10*. Further analysis, such as a high-resolution mapping and sequence comparison of those candidate genes, will be required to determine the most probable candidate for *qUVR-10*. Our next step will be to perform a genetic complementation analysis by transformation of these positional candidate genes. Biological approaches will also be used, for example, by comparing CPD photoreactivation and accumulation of UV-absorbing pigments between Nipponbare and a nearly isogenic line of *qUVR-10*.

The depletion of the stratospheric ozone layer by chlorofluoromethanes and other gasses has resulted in

increases in solar UVB radiation. Sato and Kumagai (1993) indicated that UVB resistance of rice varieties is not related to the geographical origin of the varieties. The rice varieties cultivated in tropical areas, where the amount of solar UVB is greater, are not always UVB resistant, as observed in this study. Future, the increases of harmful UVB radiation might therefore affect the growth and yield of UVB-sensitive rice cultivars, especially in the tropics. We considered that *qUVR-10*, as a QTL with a relatively large effect on the phenotypic variation in the UVB resistance, will be useful for the development of improved cultivars. Therefore, the map location and flanking DNA markers are useful tools for the introduction of the *qUVR-10* into UVB sensitive rice varieties by marker-assisted selection.

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