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Mapping quantitative trait loci controlling seed longevity in rice (*Oryza sativa* L.)

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Abstract Quantitative trait loci (QTLs) controlling seed longevity in rice were identified using 98 backcross inbred lines (BILs) derived from a cross between a *japonica* variety Nipponbare and an *indica* variety Kasalath. Seeds of each BIL were kept for 12 months at 30 °C in dry conditions to promote loss of viability. To measure seed longevity, we performed an additional aging-processing treatment for 2 months at 30 °C maintaining seeds at 15% moisture content. We measured the germination percent of these treated seeds at 25 °C for 7 days as the degree of seed longevity. The germination of BILs ranged from 0 to 100% with continuous variation. Three putative QTLs for seed longevity, *qLG-2*, *qLG-4* and *qLG-9*, were detected on chromosome 2, 4 and 9, respectively. Kasalath alleles increased the seed longevity at these QTLs. The QTL with the largest effect, *qLG-9*, explained 59.5% of total phenotypic variation in BILs. The other two QTLs, *qLG-2* and *qLG-4*, explained 13.4 and 11.6% of the total phenotypic variation, respectively. We also verified the effect of the Kasalath allele of *qLG-9* using chromosome segment substitution lines. Furthermore, QTLs for seed dormancy were identified on chromosomes 1, 3, 5, 7 and 11. Based on the comparison of the chromosomal location of QTLs for seed longevity and seed dormancy, these traits seem to be controlled by different genetic factors.

Keywords *Oryza sativa* L. · Seed longevity · Seed dormancy · QTL analysis · Backcross inbred lines · Chromosome segment substitution lines

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Introduction

Seed longevity affects the regeneration cycle of accessions stored in genebanks. Rapid seed deterioration in humid tropical climates is a serious problem in rice production throughout monsoon Asia (Siddique et al. 1988). Genetic analyses of seed longevity in several crops have been performed (Piech et al. 1979; Singh and Har Ram 1986; Verma and Ram 1987). In rice, variation in seed longevity among cultivars originating from different ecogeographic regions has been reported (Oka and Tsai 1955; Ikehashi 1973; Siddique et al.1988; Chang 1991; Ellis et al. 1992). It was also reported that cultivars belong to the isozyme group II encompassing the aus and boro rice varieties of Bangladesh and India, survived longer than other groups of rice cultivars (Kameswara Rao and Jackson 1997). However, the inheritance of seed longevity has not been demonstrated in rice. Seed longevity may be influenced by the effect of temperature during seed development (Ellis et al. 1993).

In addition, the relationship between seed dormancy and seed longevity is not known. Many studies have been performed to answer this question but the results are not consistent (Roberts 1963; Ota and Takemura 1970; Ikehashi 1973; Siddique et al. 1988; Juliano et al. 1990).

DNA markers enable quantitative trait loci (QTLs) controlling complex traits to be identified (Tanksley 1993; Yano and Sasaki 1997). More comprehensive characterization of detected QTLs can be performed using near-isogenic lines of target QTLs (Lin et al. 2000; Monna et al. 2002). Recently, the molecular cloning of genes at QTLs has also been achieved using a map-based

strategy (Yano 2001). Thus, QTL analysis can provide a new strategy to understand the genetic control system of seed longevity. The objective of this study was to identify QTLs for seed longevity using backcross inbred lines (BILs) derived from a cross between *indica* and *japonica* varieties.

Materials and methods

Plant materials

Ninety eight BC_1F_9 lines (backcross inbred lines: BILs) derived from Nipponbare/Kasalath//Nipponbare (Lin et al. 1998) were used in the QTL analysis. The parental line, Nipponbare, is a *japonica* variety, and the other parental line, Kasalath, is an *indica* variety. Chromosome segment substitution lines (SLs) have been selected from advanced backcross progenies between Nipponbare as a recurrent parent and Kasalath as a donor parent by marker-assisted selection (M. Yano and S.Y. Lin, unpublished data). Four SLs were used to confirm the existence of the detected QTLs. In these SLs, the chromosome segments containing the QTLs detected were substituted with Kasalath chromosome segments in the genetic background of Nipponbare. All materials were cultivated in irrigated fields of the National Institute of Agrobiological Sciences, Tsukuba, Japan, in 1999.

Evaluation of seed dormancy and seed longevity

Bulked seeds from each BIL and seeds of individuals in each SL were harvested at 40 days after heading. Fifty seeds from each line were placed on two sheets of filter paper moistened with distilled water in a Petri-dish of 6-cm diameter. The seeds were germinated at 25 °C for 7 days. Germination was based on the emergence of some part of the embryo from the lemma. The germination percent was used to determine the degree of seed dormancy. The seeds were stored for 12 months at 30 °C in a drying machine (Yamato DK63, Tokyo) to promote loss of viability. Subsequently, seeds were germinated at 25 °C for 7 days and seed longevity was determined by the germination percent. The germination percents of Nipponbare and Kasalath were 92.0 and 99.1%, respectively, and the range of those for BILs was from 96 to 100%. Since the viability of the sample seeds still remained high and we could not determine differences in seed longevity among BILs, an additional aging treatment was performed according to Ikehashi (1973). The sample seeds were kept in air-tight containers over water and placed in an incubator at 30 °C until the seed moisture content attained 15~16%. Thereafter, we replaced water with a saturated potassium chromate (K_2CrO_4) solution to maintain the seed moisture content at a 15~16% equilibrium. After 2 months, we evaluated seed longevity. Seed moisture content and storage temperature are the most important factors affecting seed longevity during storage in rice (Roberts 1972; Justice and Bass 1978). The moisture content of the seeds was determined using a moisture tester (Kett Riceter-D, Tokyo).

RFLP analysis

RFLP analysis of BILs was performed according to the method described by Lin et al. (1998). Total DNA was extracted from leaf tissue of each selected plant according to the CTAB method (Murray and Thompson 1980). The DNA was digested with eight restriction enzymes, *Bam*H, *Bgl*, *Eco*RV, *Hind*III, *Apa*I, *Dra*I, *Eco*RI and *Kpn*I. Electrophoresis and Southern blotting were performed according to Kurata et al. (1994). Southern hybridization and signal detection were done with an ECL direct labeling and detection system (Amersham Pharmacia Biotech, UK). For the selection of SLs, a total of 127 markers covering the 12 rice chromosomes were used to estimate the substitution of chromosome segments in all selection processes.

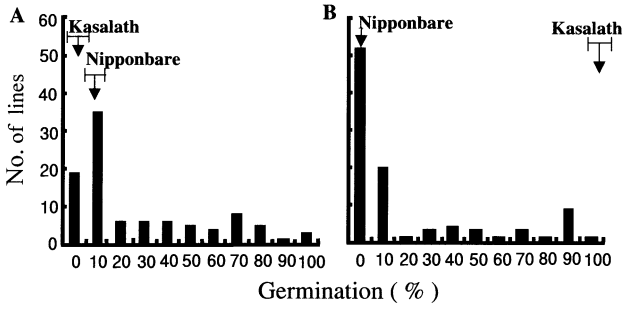

Fig. 1 Frequency distribution of seed dormancy (**A**) and seed longevity (**B**) in 98 backcross inbred lines derived from Nipponbare/Kasalath//Nipponbare. Parental values are indicated by the mean with a standard deviation

QTL analysis

Genotype data of 245 RFLP markers (http://rgp.dna.affrc.go.jp/publicdata/genotypedata BILs/genotypedata.html) were used for QTL analysis. To normalize the variance, the germination percent of each individual was transformed to the arc sine [=arc-sine $(\chi)^{1/2}$]. The chromosome locations of putative QTLs were determined by single-point analysis using the general linear model (GLM) procedure of SAS (SAS Institute 1989). One-way ANOVA was employed to test the significance of association at each locus between two genotype groups (homozygous for Nipponbare and Kasalath alleles). A probability level of 0.01 was used as a threshold to detect significant mean differences between the two genotype groups. MAPMAKER/QTL software (Lander and Botstein 1989; Lincoln et al. 1992) was also used to estimate the effects of the Kasalath alleles of detected QTLs with the 'F2 backcross' mode.

Results

Variations in seed dormancy and seed longevity in BILs

At harvesting time, the germination percents as the degree of seed dormancy of two parents, Nipponbare and Kasalath, were 2.3 and 7.4%, respectively. The germination percents of BILs ranged from 0 to 100% with continuous variation (Fig. 1A).

After aging treatments, the moisture contents of the seeds of BILs were checked and their germination percents were scored. The range of moisture contents in BILs was from 13.5 to 16.5%. The correlation between the moisture content and the germination percent was not significant ($r = 0.195$, $P > 0.05$) in BILs. Therefore, we decided to estimate seed longevity without taking the effect of moisture content into consideration in this study. Frequency distributions of the germination percent of BILs and their parental lines, Nipponbare and Kasalath, are shown in Fig. 1B. The averaged germination percent of Nipponbare was 0% and that of Kasalath was 96.7%. Thus the seed longevity of Kasalath was superior to that of Nipponbare. The germination percents of BILs ranged from 0 to 100% with continuous variation.

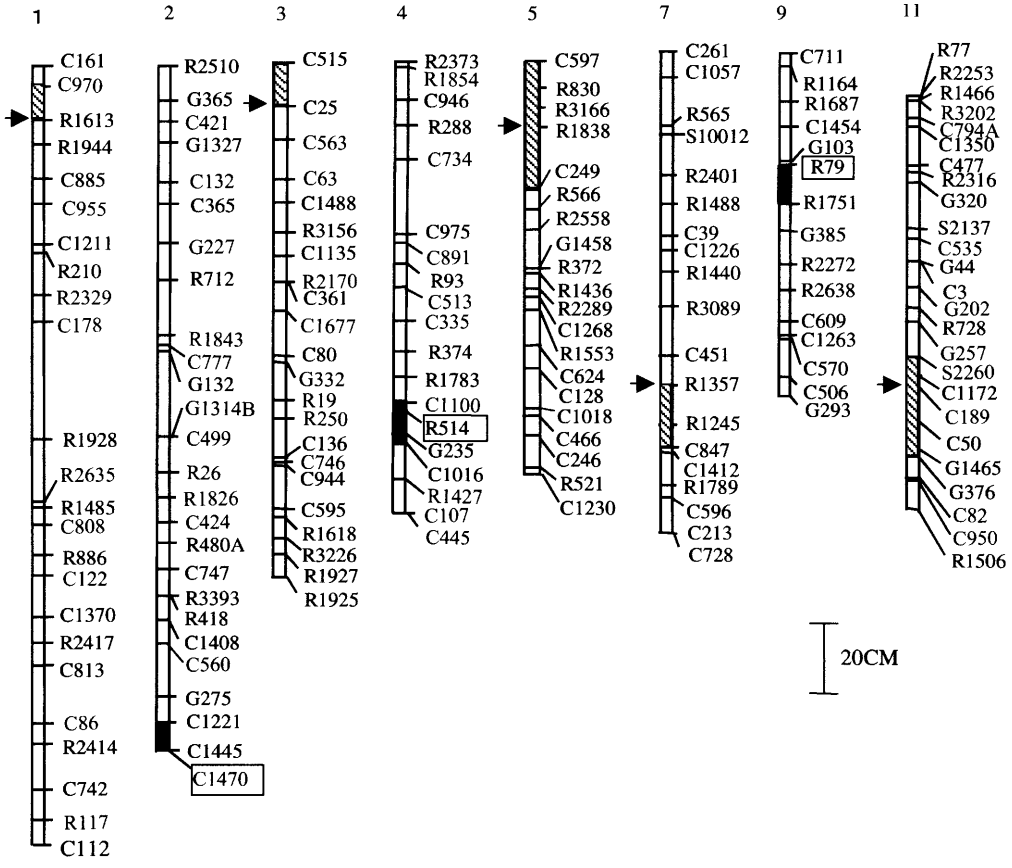

Fig. 2 Chromosomal locations of QTLs for seed dormancy and seed longevity in rice. *Striped and black bars* represent putative regions of QTLs for seed dormancy and seed longevity, respectively. A reduction of a 0.5 LOD value from the LOD peaks was used to define left and right borders of the confidence interval in MAPMAKER/QTL. *Arrows and box* indicate the nearest marker locus to the QTLs for seed dormancy and seed longevity, respectively, in markers which were significant at the 0.01 probability level based on ANOVA. Chromosomes with no QTLs are omitted from this figure

Table 1 Putative QTLs for seed dormancy and seed longevity in rice

Trait	QTL	NML[a]	Chr.	GLM/SAS Probability	MAPMAKER/QTL			
					LOD	% Variation[b]	AE[c]	DPE[d]
Seed dormancy	*qSD-1*	R1613	1	0.0006	2.63	11.6	14.5	K
	qSD-3	C25	3	0.0014	2.44	11.3	13.7	K
	qSD-5	R1838	5	0.0001	3.10	13.6	–13.6	N
	qSD-7	R1357	7	0.0076	1.49	6.8	–10.7	N
	qSD-11	C189	11	0.0018	2.12	9.7	13.3	K
					Total[e]	41.1		
Seed longevity	*qLG-2*	C1470	2	0.0007	2.809	13.4	14.4	K
	qLG-4	R514	4	0.0012	2.428	11.6	15.1	K
	qLG-9	R79	9	⟨0.0001	13.883	59.5	25.5	K
					Total[e]	68.2		

[a] Nearest marker locus of putative QTLs
[b] Phenotypic variation explained by each QTL
[c] Additive effects of Kasalath (1/2 weight) alleles by the arc-sine of germination percent
[d] Direction of phenotypic effect. N and K indicate that the Nipponbare and Kasalath allele increased the germination percent for seed dormancy and seed longevity, respectively
[e] Estimates obtained from a multiple-QTL model

QTLs for seed dormancy (*qSD*)

Five putative QTLs associated with seed dormancy were detected based on the ANOVA of RFLP results (Fig. 2, Table 1). These putative QTLs were mapped in the vicinity of R1613 on chromosome 1 (*qSD-1*), C25 on chromosome 3 (*qSD-3*), R1838 on chromosome 5 (*qSD-5*), R1357 on chromosome 7 (*qSD-7*) and C189 on chromosome 11 (*qSD-11*). Four putative QTLs, *qSD-1*, *qSD-3*, *qSD-5* and *qSD-11*, were also confirmed by MAPMAKER/QTL analysis using an empirical threshold of LOD = 2.0. However, *qSD-7* was not confirmed based on this threshold. Kasalath alleles increased the germination percent in the case of *qSD-1*, *qSD-3* and *qSD-11*, and the additive effects of Kasalath alleles in these QTLs were 14.5, 13.7 and 13.3% in the arc-sine transformation of germination percent, respectively. On the other hand, Kasalath alleles in the case of *qSD-5* and *qSD-7* decreased the germination percent and the additive effects were 13.6 and 10.7%, respectively. The percentage of

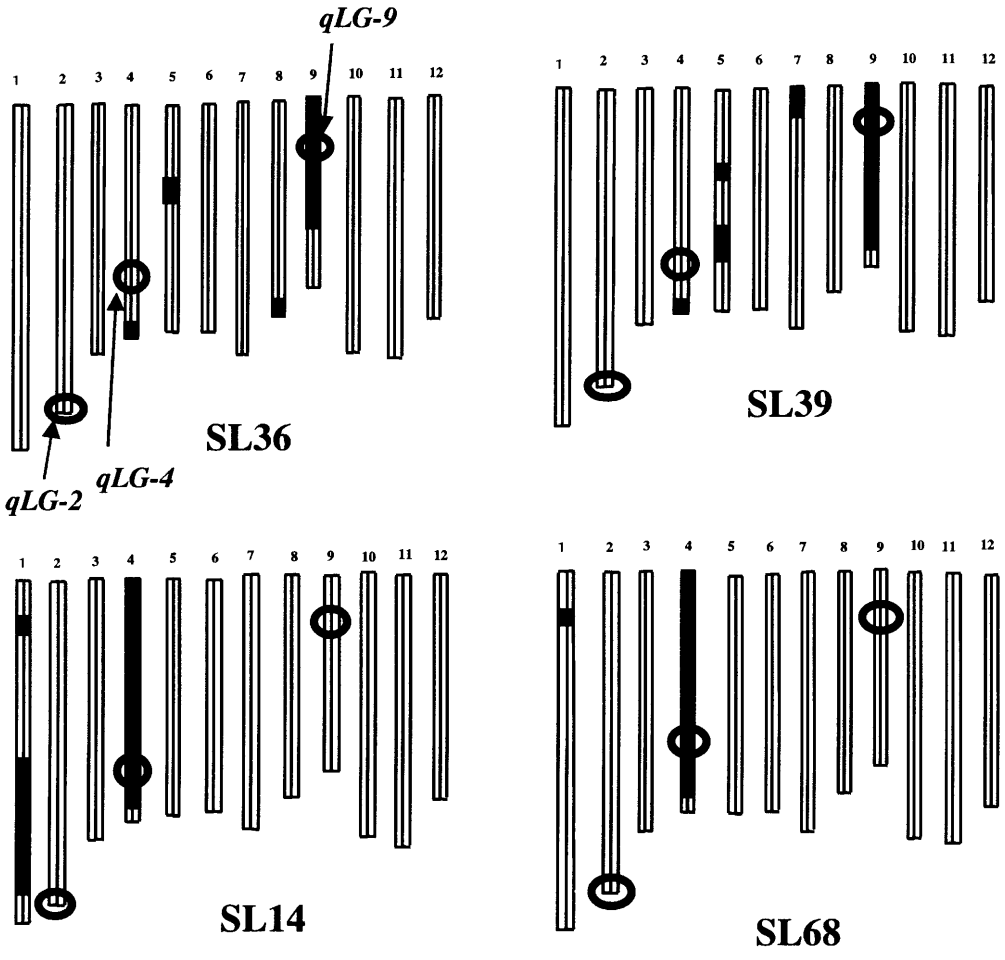

Fig. 3 Graphical genotypes of chromosome segment substitution lines (BC_4F_3) derived from a backcross between Kasalath and Nipponbare. Nipponbare was used as the recurrent parent. □: Nipponbare segment, ■: Kasalath segment

phenotypic variation explained by each QTL ranged from 6.8 to 13.6% based on MAPMAKER/QTL analysis. Total phenotypic variation explained by the five putative QTLs was 41.1% based on the multiple QTL model in MAPMAKER/QTL.

QTLs for seed longevity *(qLG)*

Three putative QTLs associated with seed longevity were detected based on ANOVA. These QTLs were mapped in the vicinity of C1470 on chromosome 2 (*qLG-2*), R514 on chromosome 4 (*qLG-4*) and R79 on chromosome 9 (*qLG-9*) (Fig. 2, Table 1). These QTLs were also confirmed by the analysis of MAPMAKER/QTL using LOD = 2.0 as a threshold. The additive effects of the Kasalath alleles in the case of *qLG-2*, *qLG-4* and *qLG-9* were14.4, 15.1 and 25.5% in the arc-sine transformation of germination percent, respectively, and Kasalath alleles resulted in increased germination. The percentage of phenotypic variation explained by each QTL ranged from 11.6 to 59.5% based on MAPMAKER/QTL analysis. *qLG-9* explained 59.5% of the total phenotypic variation in BILs. The total phenotypic variation explained by the three putative QTLs was 68.2% based on the multiple-QTL model in MAPMAKER/QTL.

Verification of the gene effect for *qLG-9*

In order to verify the existence of *qLG-4* and *qLG-9*, we selected four SLs from the advanced backcross progeny. Graphical representations of genotypes of the four SLs are shown (Fig. 3). In SL36 and SL39, segments of chromosome 9 including *qLG-9* were substituted with that of Kasalath in the background of Nipponbare and no other QTL for seed longevity was substituted. The segment of chromosome 4 including *qLG-4* was substituted in SL14 and SL68. Although some chromosome segments were also substituted with Kasalath in these SLs, these SLs were used to confirm the gene effect of *qLG-4* and *qLG-9*. Due to the non-availability of SL for *qLG-2*, we could not confirm the existence of the QTL in this study.

The moisture contents and the germination percents of these SLs and the parental lines are shown in Table 2. The difference of moisture contents among the lines were not significant ($P > 0.05$). The seed longevity of these SLs and the parental lines could be estimated without taking the effect of moisture content into consideration. The germination percents of SL36, SL39, Nipponbare and Kasalath were 77.3, 77.0, 0 and 96.7%, respectively. The seed viabilities of both SLs remained after Nipponbare had lost seed viability. We verified the effect of the Kasalath allele for *qLG-9* on seed longevity. The

Table 2 Seed longevity of the selected chromosome-segment substitution lines

Lines	QTL	Moisture content (%) (mean ± SD)	Germination percent (%) (mean ± SD)
SL36	*qLG-9*	15.0 ± 0.2	77.3 ± 6.7
SL39	*qLG-9*	14.8 ± 0.2	77.0 ± 9.7
SL14	*qLG-4*	15.7 ± 0.2	0
SL68	*qLG-4*	14.7 ± 0.2	0
Nipponbare		14.9 ± 0.3	0
Kasalath		14.5 ± 0.2	96.7 ± 4.8

germination percents of SL14 and SL68 were 0%, the same as Nipponbare; therefore the effect of *qLG-4* using SLs could not be detected.

Discussion

An association between seed dormancy and seed longevity has been reported (Ota and Takemura 1970; Siddique et al. 1988). However, Roberts (1963) based on experiments using three *indica* and two *japonica* varieties and one *Oryza glaberrima*, reported there was no association. Ikehashi (1973) observed that some *indica* varieties had long seed longevity in spite of having weak seed-dormancy. For seed dormancy, we detected five putative QTLs located on chromosomes 1, 3, 5, 7 and 11. Lin et al. (1998) also detected five putative QTLs for seed dormancy located on chromosomes 3, 5, 7 (two QTLs) and 8. For seed longevity, three putative QTLs were located on chromosomes 2, 4 and 9 in the present study. Based on the results of these studies, the putative QTLs for seed longevity were different from the QTLs for seed dormancy. These results suggest that seed dormancy and seed longevity are controlled by different genetic factors in Kasalath, supporting no association between the seed dormancy and longevity reported in several earlier studies (Roberts 1963; Ikehashi 1973; Juliano et al. 1990).

Lin et al. (1998) reported that the QTLs for seed dormancy using the same BILs (BC_1F_5) derived from Nipponbare/Kasalath//Nipponbare were cultivated in the same field as this study in 1995. The locations of *qSD-5* and *qSD-7* are likely to correspond to the two QTLs detected by Lin et al. (1998). However, QTLs linked to C1488 on chromosome 3, R1440 on chromosome 7 and C390 on chromosome 8 that were identified by Lin et al. (1998), were not detected in our study. The locations of *qSD-1*, *qSD-3* and *qSD-11* were also not detected by Lin et al. (1998). The seeds of Nipponbare in our study showed a higher level of seed dormancy compared with that in the study by Lin et al. (1998). Seed dormancy is affected by environmental factors, such as temperature during ripening, degree of maturity and drying condition after harvest (Roberts 1962; Ikehashi 1973; Seshu and Sorrells 1986). In particular, average temperatures during the ripening period of BILs in 1995 and 1999 were 21.9 and 25.1 °C, respectively, and the difference was large. Ikehashi (1973) reported that seed dormancy was affected by temperature during the ripening period and various types of response to temperature were observed among different rice germplasm accessions. The differences between the results of the two studies might be due to genotype-environmental interaction in consideration of the difference of temperature during the ripening period between 1995 and 1999.

In this study, we could not detect the effect of *qLG-4* using SLs. The reason for this result might be specific interaction between *qLG-4* and other loci. However, using small populations such as the 98 BILs in this study, it may be difficult to detect QTLs with specific interaction (Yano and Sasaki 1997). It was also difficult to explain the reason why the existence of *qLG-4* was not confirmed using SLs in this study. Further studies are necessary to confirm the effects of *qLG-4* and *qLG-2*.

Recently, Japanese rice breeders have been breeding rice varieties for direct seeding culture to reduce rice production costs. Seeds for direct seeding culture will need to have uniform quality for the stable establishment of seedlings under various stresses; for example, cool temperatures and anaerobic conditions. Yamauchi and Winn (1996) reported that aging seeds reduced seedling establishment in anaerobic soil and suggested that varieties tolerant to aging would be useful for breeding rice varieties for direct seeding. Thus the improvement of seed longevity will be an objective of rice breeding programs in Japan. In this study, *qLG-9*, with a large effect on seed longevity was detected, and explained 59.5% of the total phenotypic variation in BILs. We confirmed that the Kasalath allele in the case of *qLG-9* increased seed longevity remarkably by using SLs. The Kasalath allele in the case of *qLG-9* will be useful for improving seed longevity. Marker-assisted selection (MAS) will be a helpful method to select plants with *qLG-9* because the phenotyping for seed longevity is not easy due to environmental conditions during seed development, seed processing and in storage, and the long time it takes to loose seed viability. The results of this study may be used in backcross breeding with MAS for the improvement of seed longevity. Yamamoto et al. (1998) reported the successful fine mapping of three QTLs for heading date using selected advanced backcross progeny. For the establishment of MAS for seed longevity in rice breeding programs, it will be necessary to find additional DNA markers that are tightly linked with *qLG-9* by fine mapping.

Recently, genes at QTLs have been isolated for fruit size and a yield-related trait in tomato (Frary et al. 2001), and heading date in rice (Yano et al. 2000) by the map-based strategy. *qLG-9*, the QTL with the largest effect, will be an appropriate target for map-based cloning. The isolation of the genes at QTLs for seed longevity will be necessary to understand genetic mechanisms of this trait and help to establish a new genetic diagnosis of seed longevity to predict the regeneration interval of rice accessions stored in genebanks.

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