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Genomic regions affecting seed shattering and seed dormancy in rice

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Abstract Non-shattering of the seeds and reduced seed dormancy were selected consciously and unconsciously during the domestication of rice, as in other cereals. Both traits are quantitative and their genetic bases are not fully elucidated, though several genes with relatively large effects have been identified. In the present study, we attempted to detect genomic regions associated with shattering and dormancy using 125 recombinant inbred lines obtained from a cross between cultivated and wild rice strains. A total of 147 markers were mapped on 12 rice chromosomes, and QTL analysis was performed by simple interval mapping and composite interval mapping. For seed shattering, two methods revealed the same four QTLs. On the other hand, for seed dormancy a number of QTLs were estimated by the two methods. Based on the results obtained with the intact and de-hulled seeds, QTLs affecting hull-imposed dormancy and kernel dormancy, respectively, were estimated. Some QTLs detected by simple interval mapping were not significant by composite interval mapping, which reduces the effects of residual variation due to the genetic background. Several chromosomal regions where shattering QTLs and dormancy QTLs are linked with each other were found. This redundancy of QTL associations was explained by "multifactorial linkages" followed by natural selection favoring these two co-adapted traits.

Key words Wild and cultivated rice · Seed shattering · Seed dormancy · QTL analysis · Co-adapted gene block

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Introduction

An essential difference between wild and cultivated plants is whether or not they can propagate themselves without man's aid. Wild plants, particularly seed-propagating plants, disperse their seeds by shattering immediately after maturity, and the seeds then wait for the next season by dormancy in the form of soil-buried seeds. Seeds persisting on the plant are easily eaten by animals and, if seeds are not dormant, untimely germination under adverse conditions threatens the seedlings. Therefore seed shattering associated with dormancy is considered to be an adaptive strategy for wild plants. In contrast, non-shattering and non-dormant variants must have been selected during domestication, both consciously and unconsciously, by those who wanted efficient harvesting and seeding. It is true, however, that a certain degree of seed shattering is sometimes preferred by farmers for easy threshing, and weak dormancy is needed to prevent pre-harvest sprouting. Thus the genetic bases for those traits awoke the interest of both evolutionists and plant breeders.

The shattering habit in major cereals is considered to be under relatively simple genetic control as compared with other traits associated with domestication (Harlan 1975). In rice, four shattering genes, *sh1* (Nagao and Takahashi 1963, chr.11), *sh2* (Oba et al. 1990, chr.1), *Sh3* (Eiguchi and Sano 1990, chr.4) and *sh4* (Fukuta 1995, chr.3), have been so-far identified. To explain the segregation patterns of shattering in F_2 plants, a two-gene model has been proposed (Kadam 1936; Eiguchi and Sano 1990). While in several F_2s of crosses between non-shattering cultivars and shattering weedy rice strains, Tang and Morishima (1989) found various segregation patterns ranging, from monogenic to continuous, depending on the crosses.

Seed dormancy, in contrast, is a complex character influenced by many genetic and environmental factors, as reviewed by Li and Foley (1997). In addition to true embryo (kernel) dormancy, coat (hull)-imposed dormancy is involved. Recently a number of genetic studies on seed dormancy were carried out using molecular markers in various plant species such as barley (Oberthur et al. 1995;

Larson et al. 1996), wheat (Anderson et al. 1993), and *Arabidopsis* (van der Schaar et al. 1997). These studies conclusively demonstrated that seed dormancy is controlled by many QTLs widely distributed over the genome.

In rice, Seshu et al. (1986), as well as Takahashi (1997), proposed a two-gene model for seed dormancy based on conventional genetic analysis, although the chromosome locations of those genes could not be determined. Recently, marker-assisted studies detected many dormancy loci as mentioned below. Wild rice species are known to have more pronounced seed dormancy than cultivars and to differ in degree among species or ecotypes. But few genetic studies have been carried out with wild rice.

Our objective in the present study was to identify genomic regions affecting seed shattering and seed dormancy that differentiate wild and cultivated forms of rice, and to examine the association between those two traits. Recombinant inbred lines (RILs) derived from a cross between wild and cultivated rice strains were used as a mapping population.

Materials and methods

Plant materials

A Taiwanese Indica rice (*Oryza sativa* L.), Pei-kuh, was crossed as a female parent with a strain of Asian common wild rice (*O. rufipogon* Griff.), W1944, which is a perennial and partially outbreeding strain originally collected in China. *O. rufipogon* is widely distributed in the marshy areas in tropical and subtropical Asia and is considered to be the wild progenitor of cultivated rice, *O. sativa*. The F_1 plants of this cross showed partial seed sterility. F_2 seeds were obtained by selfing an F_1 plant.

One hundred and eighty-nine F_2 plants were grown in an experimental paddy field at the National Institute of Genetics, Mishima, in 1990. The progeny of 158 F_2 plants which flowered and set seed were used for further experiments. Using the single seed descent method, F_3 to F_7 generations were raised. Two to three panicles per plant were bagged after heading before flowering to avoid outcrossing and shattering, and seeds from bagged panicles were collected for raising the next generation. One hundred and twenty five RILs thus obtained were grown in 1995 (F_6), 1996 (F_7) and 1997 (again F_7), following a standard cultivation procedure, in the experimental paddy field in Mishima.

Polymorphism survey for map construction

DNA was extracted from fresh leaves of F_6 plants in 1995. DNA extraction, digestion, electrophoresis and Southern blotting were performed according to the methods described by McCouch et al. (1988). DNA hybridization was carried out using non-radioisotope ECL system (Amersham Int.). One hundred and forty seven markers, mostly RFLPs in addition to some isozyme and morphological markers, which proved to be polymorphic between parental lines, were surveyed in all RILs and used for map construction. Details of markers and map information will be given in our another paper (Cai and Morishima submitted). The DNA probes used were kindly provided by Dr. S. R. McCouch, Cornell University, USA, and by Dr. T. Sasaki, Rice Genome Research Program, NIAR, Japan.

Evaluation of seed shattering and seed dormancy

To examine the degree of shattering and dormancy at a given number of days after heading (DAH) for RILs with different heading dates, RILs were harvested 30 DAH according to their respective heading dates. The degree of seed shattering was evaluated in 1995 as well as in 1996 with two bagged panicles per plant. The proportion of seeds naturally shed (a), shed by hand gripping (b), and non-shed by hand gripping (c) were recorded. Giving the scores 2 (a), 1 (b) and 0 (c) to the respective groups, an averaged score was obtained for representing the degree of shattering of each line.

Seed dormancy for each RIL was evaluated by the germination percentage under the following six different conditions. In 1995, a germination test was done with intact seeds about 100 DAH. In 1996, the intact seeds were tested 30 DAH. In 1997 the seeds were air dried immediately after harvesting for 7 days in the greenhouse at about 30°C, and then intact (a) and de-hulled (b) seeds were tested. After 1 month, the germination test was conducted again using intact (c) and de-hulled (d) seeds. Ten seeds from each plant were placed in Petri dishes (1995 and 1997) or wrapped in moistened filter paper (1996) and germinated in the dark at 30°C. The number of germinated seeds after 7 days was counted.

Statistical Analysis

A linkage map was constructed using MAPMANAGER (Manly 1993) based on the segregation data of 147 markers in F_6 RILs. To determine primary linkage groups, known map information (Harushima et al. 1998; Causse et al. 1994) was taken into account.

The chromosomal locations of QTLs for shattering and dormancy were first determined by the simple interval mapping method (SIM) using QGENE program (Nelson 1997). Then, to reduce the effects of genetic background, data were also treated by MQTL software (Tinker and Mather 1995). MQTL provides the methods of composite interval mapping (CIM) in addition to simple interval mapping (SIM), and a permutation test to determine appropriate thresholds which can control the type-I error (false positive) in QTL mapping. We repeated 1000 simulations of marker analysis with each trait consisting of 125 psuedo-random numbers and established the *F*-ratio which was exceeded in 5% of these simulations. Based on the genome-wide 5% significance threshold thus obtained, QTLs were estimated initially by the SIM approach (MQTL). Then, significant QTLs were re-analyzed by CIM using non-significant markers selected for each chromosome as background loci. In this paper, the results obtained by SIM (QGENE) and CIM (MQTL) are presented. As CIM provides a multi-environment analysis, the shattering data for 2 years were jointly analyzed, but dormancy data obtained under different conditions were separately analyzed.

Additive gene effects of QTLs were estimated, but dominance effects could not be evaluated in RILs. Pairwise interaction between significant QTLs (epistasis) was tested using the QGENE program.

For the designation of QTLs, we followed the recommendation by McCouch et al. (1997).

Results

Seed shattering

The cultivated parent, Pei-kuh, is of the non-shattering type (0.25), whereas the wild parent, W1944, showed a high degree of shattering (2.00). The frequency distribution of phenotypes among RILs showed skewness in both years (clustering above the mean and below the tail). This is probably because the present evaluation method lumped all naturally shed seeds into a group scored as 2. For QTL analysis, the original data were

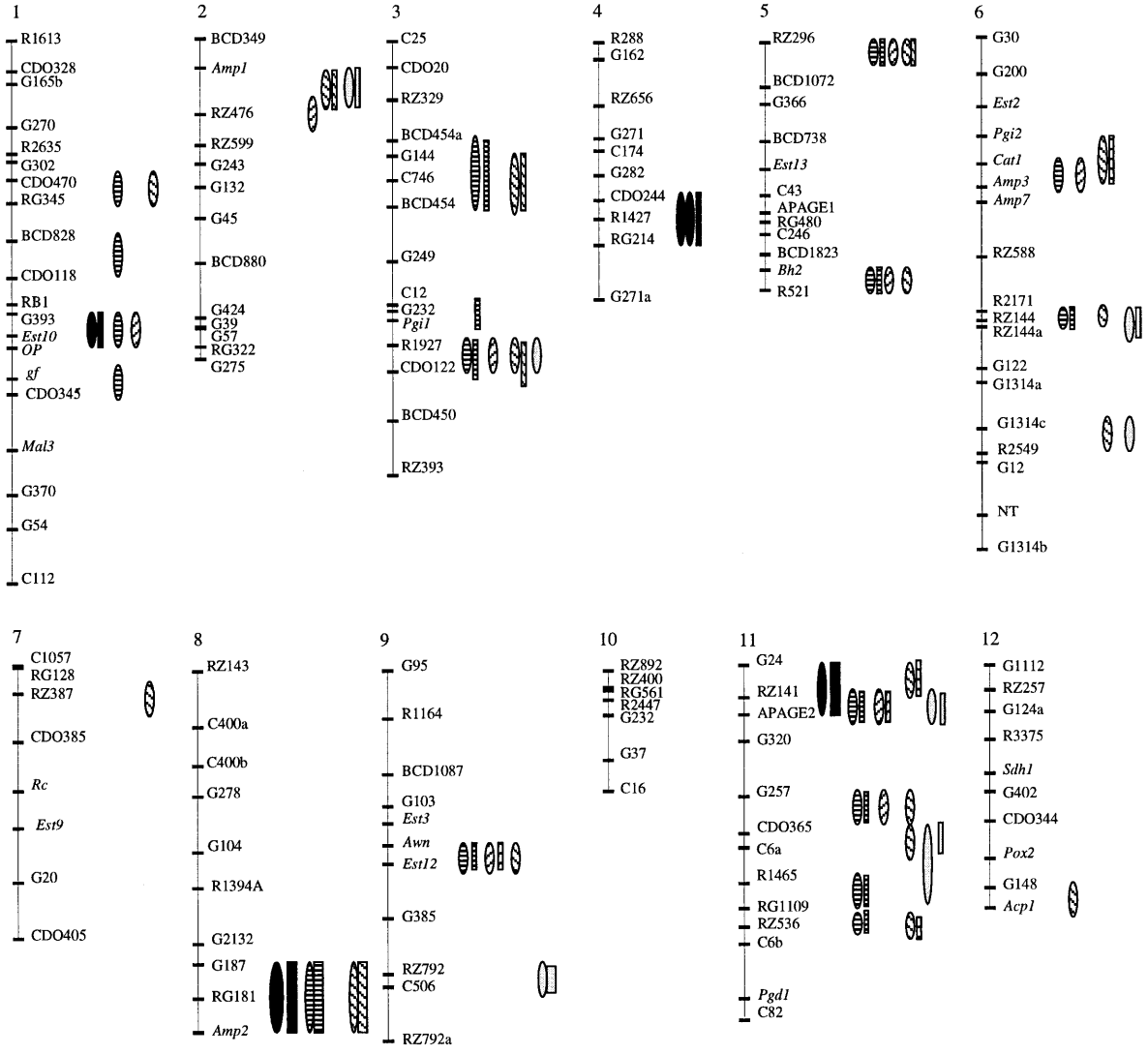

Fig. 1 Distribution for QTLs for seed shattering tested in 2 years and seed dormany tested under four different conditions (*a*, *b*, *c* and *d*). Details of the test conditions are given in the text. QTLs significant at the 5% level are presented. *Spindle and rectangular bars* represent regions detected by simple interval mapping and composite interval mapping, respectively. The linkage map was derived from the segregation data of Indica cultivar/wild rice recombinant inbred lines. | represents 20 cM. Shattering; Dormancy a; Dormancy, b; Dormancy, c; Dormancy, d

Table 1 Location, significance level (*F*) and percent phenotypic variance explained (R^2) of QTLs affecting seed shattering. QTLs of *F*-ratio >8.9 (5% significance level) are presented

Locus	Chr.	Flanking markers	*F*	R^2
qSHT-1	1	G393-OP	16.0	12.0
qSHT-4	4	CDO244-RG214	20.0	14.8
qSHT-8	8	G187-*Amp2*	12.9	9.8
qSHT-11	11	G24-APAGE2	15.4	11.6

transformed to natural logarithms to obtain a more-normal distribution.

Simple interval mapping (SIM) detected four QTLs at the 5% significance level from the 1995 data; qSHT-1 (chr.1), qSHT-4 (chr.4), qSHT-8 (chr.8) and qSHT-11 (chr.11). Among these, qSHT-4 was also detected from the 1996 data at the same position. Composite interval mapping (CIM) based on the combined data of 2 years detected four QTLs significant at the 5% level at the same positions as SIM. The F-ratio and the percentage of variance explained by each QTL (R^2) are given in Table 1 together with their flanking markers. Their genomic regions are shown in Fig. 1 together with the dormancy QTLs. qSHT-4 gave the highest R^2 value (14.8%) and was consistently detected in 2 years by SIM and confirmed by CIM. Interaction between the detected QTLs and year was not significant at the 5% level.

The direction of additive gene effects was consistent with that expected from the phenotypic difference between the parents in all cases; wild rice-derived alleles increased the degree of shattering. Epistasis between the above four QTLs was not significant.

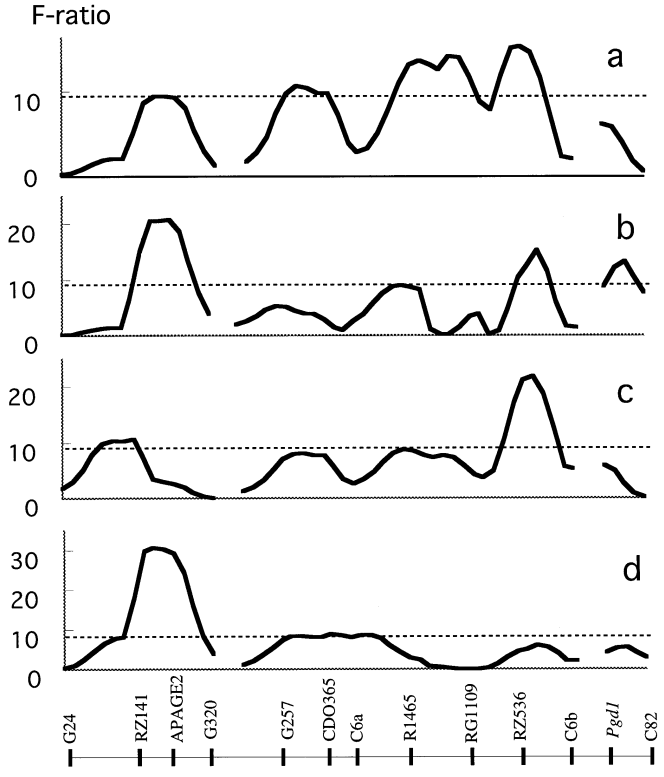

Fig. 2 a–d QTL-likelihood maps of the *F*-ratio for seed dormancy detected on chromosome 11 by composite interval mapping. Dormancy was evaluted under four different conditions, a, b, c and d (details are given in the text). The *dotted horizontal line* at *F*=8.9 indicates the threshold to detect a QTL at the 5% significance level. The linkage map is presented at the bottom. Two regions found in condition b at the distal end (right) of the chromosome were not analyzed by CIM because they were not significant in SIM

Seed dormancy

The cultivated parent, Pei-kuh, was non-dormant and gave a high germination rate (>90%) except in the 1996 test. The wild parent, W1944, showed varying degrees of dormancy depending on the test conditions. The phenotypic segregation pattern among RILs showed a high degree of skewness approaching the non-dormant cultivated parent, except in 1996. In the 1996 test, the phenotypic distribution markedly shifted toward the dormant type (low germination rate), probably because in that year we tested the seeds immediately after harvest without drying, and while the water content was still high. To obtain a more normal distribution of dormancy among the RILs, arcsine transformation was performed for the germination percentage.

The dormancy data of RILs evaluated under six conditions in 3 years were analyzed separately by SIM. For the 1995 and 1996 data, we detected two QTLs and one QTL by SIM. For the 1997 data tested under four conditions (a, b, c, d), 16, 9, 16, and 7 QTLs were identified, respectively, at a 5% significance level. To confirm this result, we conducted CIM to the data of 1997, and detected 12, 2, 8 and 5 QTLs for a, b, c and d conditions, respectively, at a 5% significance level as indicated in Table 2. Genomic regions estimated by SIM as well as by CIM are shown in Fig. 1. QTLs mapped at the same, or near, locations in different test conditions may be identical loci. CIM identified a total of 12 putative QTLs which might affect seed dormancy in various ways. It is obvious that chromosome 11 harbors important regions affecting seed dormancy. qDOR-11-2 showed the highest R^2 (21.8%) in test condition d. Evidence of QTLs obtained from CIM on chromosome 11 is shown in Fig. 2 in terms of the contours of *F*-ratio. Peaks of the *F*-ratio tended to appear in the same locations among the different test conditions, though they were not all significant.

From this experiment, it is not possible to distinguish clearly hull-imposed dormancy and kernel dormancy. However, the following inference may be possible. The loci which were significant only in intact seeds (a and c) and not significant in de-hulled seeds (b and d), qDOR-3-1, qDOR-3-3, qDOR-5-1, qDOR-8 and qDOR-11-6, might control hull-imposed dormancy. On the other

Table 2 Location, significance level (*F*) and percent phenotypic variance explained (R^2) of QTLs affecting seed dormancy evaluated under the four different conditions, a, b, c, and d. QTLs of *F*-ratio >8.9 (5% significance level) in composite interval mapping are presented. Test condition: a – intact seed, 30 DAH; b – de-hulled seed, 30 DAH; c – intact seed, 60 DAH; d – de-hulled seed, 60 DAH.
* Detected also by simple interval mapping

Locus	Chr.	Flanking markers	*F* (R^2)			
			a	b	c	d
qDOR-2*	2	*Amp1*-RZ476			10.9 (8.4)	14.8 (11.2)
qDOR-3-1*	3	G144-BCD454	17.8 (13.3)		22.8 (16.7)	
qDOR-3-2	3	C12-*Pgi1*	11.0 (8.4)			
qDOR-3-3*	3	R1927-CDO122	18.4 (13.7)		19.9 (14.7)	
qDOR-5-1*	5	RZ296-BCD1072	11.0 (8.4)		9.3 (7.2)	
qDOR-5-2*	5	*Bh2*-R521	9.5 (7.3)			
qDOR-6-1*	6	*Pgi2-Amp3*			21.1 (15.5)	
qDOR-6-2*	6	R2171-RZ144	16.8 (12.6)			10.9 (8.4)
qDOR-8*	8	RG181-*Amp2*	14.2 (10.7		15.5 (11.7)	
qDOR-9-1*	9	Awn-*Est12*	9.3 (7.2)	9.9(7.6)		
qDOR-9-2*	9	RZ792-C506				13.4 (10.2)
qDOR-11-1*	11	G24-RZ141			10.6 (8.1)	
qDOR-11-2*	11	RZ141-APAGE2	10.5 (8.1)	20.9 (15.4)		30.7 (21.8)
qDOR-11-3*	11	G257-CDO365	11.5 (8.8)			
qDOR-11-4	11	CDO365-C6a				8.9 (6.9)
qDOR-11-5*	11	R1465-RG1109	15.7 (11.8)			
qDOR-11-6*	11	RG1109-RZ536	16.9 (12.6)		21.9 (16.1)	

hand, the loci significant in de-hulled seeds (b and/or d), qDOR-9-2, qDOR-11-2 and qDOR-11-4, are probably responsible for kernel dormancy.

All significant QTLs showed the same direction of additive gene effect as that expected from the phenotypic difference between the parents; namely, wild-rice alleles increased the degree of seed dormancy. Epistasis between detected QTLs never approached a significance level.

Linkages between QTLs for shattering and dormancy

As shown in Fig. 1, QTLs for shattering and dormancy were widely scattered over the genome, though the number of QTLs was much less in shattering than in dormancy. Further it was noticed that three out of four shattering QTLs were accompanied by dormancy QTLs. Those regions harbor the non-recombinant gene sets exhibiting shattering associated with dormancy, or non-shattering associated with non-dormancy. The shattering locus with the largest effect, qSHT-4, was not linked with any dormancy QTL. This locus might belong to a different category from other shattering QTLs.

Discussion

The methods currently used for QTL mapping still involve various problems to obtain reliable results, as reviewed by Jansen (1996) and Kearsey and Farquhar (1998). To reduce the genetic variation due to QTLs outside the region of interest, we applied the multiple-QTL method (CIM) in addition to the single-QTL method (SIM). For shattering QTLs distributed on the four different chromosomes, both methods yielded the same results. For dormancy QTLs with a larger number, however, some QTLs were significant in SIM, but not in CIM. This was particularly evident in the chromosomes on which multiple QTLs were present, suggesting that the effects of background markers are critical.

Distorted segregation in the mapping population is another factor affecting the detection of QTLs. In our RILs, about 50% of markers showed a significant excess of cultivar-derived allele, and most RILs carry about 60% cultivar-alleles and 40% wild-alleles on average. Yet, this degree of distortion is much less than that usually observed in RILs derived from an Indica/Japonica cross of cultivars. The effect of distorted segregation in the present study, if any, may not be so large, though its possibility can not be ruled out. In this paper, marker-trait association of a 5% significance level was referred to for convenience as a QTL. A deeper analysis using near isogenic lines on a fine map is necessary to confirm the existence of real QTLs and the association of shattering and dormancy.

Among four QTLs for shattering detected in the present study, qSHT-1 and qSHT-4 are probably identical to the already known genes *sh2* and *Sh3*, respectively, judging from their chromosomal locations, though further examination is needed for confirmation. Eiguchi and Sano (1990) found that *Sh3* on chromosome 4 (most probably qSHT-4) is closely linked with *Spr3*, a gene for spreading panicle which is an important trait of wild rice for effective dispersal of seeds, and they argued for its adaptive significance as a gene complex. Similarly, we found that qSHT-1 detected on chromosome 1 is linked with a newly found locus "OP" (open panicle), probably another locus for spreading-panicle. qSHT-1 was linked with an isozyme locus *Est10* which is known to be diagnostic for distinguishing truly wild rice by its specific allele *Est10-4* (Wang et al. 1992). Thus, qSHT-1 and qSHT-4 seemed to be important genes conferring seed shattering in wild rice.

The present study suggests that the shattering habit of wild rice is controlled by at least four genes. This situation in rice seems to differ from sorghum, where there is evidence for a single major gene (Paterson et al. 1995a), and barley, having two major loci whose alleles are geographically differentiated (Takahashi 1955). Paterson et al. (1995b) presented a comparative map of QTLs for shattering and other traits in maize, sorghum and rice. Comparing their map with ours, putative regions for some shattering QTLs detected in the present study seemed to correspond to the regions of maize chromosomes harboring shattering QTLs; rice chr. 1 (qSHT-1)/maize chr. 3 and chr. 8, and rice chr. 4 (qSHT-4)/maize chr. 2, though a precise comparison is not possible because of insufficient common markers.

Our study demonstrated that seed dormancy in rice is controlled by a large number of genes as pointed out in many other species. All chromosomes except for chromosome 4 and 10 harbor seed-dormancy genes. Chromosomes 3, 5, 6, 9 and 11 seemed to carry more than two independent dormancy loci (Fig. 1). Most studies done by conventional genic analysis with cultivated rice supported a two-gene model for seed dormancy (Takahashi 1997; Seshu and Sorrells 1986). Recent marker-assisted studies revealed a number of QTLs for dormancy. Wan et al. (1997) reported that isozyme loci *Pgi1* (chr3), *Amp3* and *C* (chr.6), *Est9* (chr.7) and *Acp2* (chr.12) are linked with dormancy genes, respectively. Lin et al. (1998) found five regions on the RFLP map of chromosomes 3, 5, 7 and 8 which are supposed to harbor seed-dormancy genes. Dormancy QTLs detected in our study seemed to coincide with at least three found by Wan et al. (1997) and four by Lin et al. (1998), though further confirmation is needed.

As already pointed out, seed dormancy in rice is partly influenced by the seed coat. Breakdown of seed dormancy by de-hulling (Seshu and Sorrell 1986) suggests that the seed coat is related to permeability or O_2 diffusion. On the other hand, Miyoshi et al. (1995) found that dormancy was increased by removing the hull in some Japonica rice varieties. Their result indicates that the effect of moisture conditions on seed dormancy might differ by genotypes. Further, various environmental factors such as temperature and humidity at the seed maturing

stage are also important (Takahashi 1997). In our study, the percentage of germination in 1996 was markedly lower than that found in other years, suggesting that seed dormancy was retained owing to a high water content in the seeds. This indicates that post-harvest drying is effective in breaking seed dormancy.

Our preliminary experiment with the same RILs showed that the locations of five out of six QTLs controlling mesocotyl elongation, as well as its response to ABA and GA, were coincident with those of dormancy QTLs (Katsuta-Seki et al. 1999). These plant hormones are known to be responsible for germination behavior or the degree of dormancy, and also for the elongation of the rice mesocotyl (Takahashi 1973). This coincidence might reflect an aspect of the pleiotropic effects of QTLs controlling the endogenous hormone level.

At the phenotypic level, seed shattering associated with seed dormancy characterizes wild rice, and non-shattering associated with non-dormancy characterizes cultivated rice. In the F_2 generation of a cross between wild and cultivated rice, however, it is generally known that the association almost disappears. This suggests that the major factor causing the trait association is not a developmental or pleiotropic effect of a single key gene, nor the close linkage of two major genes, but rather natural selection for these two co-adapted traits. Among our RILs, the correlation coefficients between the two traits were weak (0.18 for the 1995 data and 0.29 for the 1996 data). Regions carrying both shattering QTLs and dormancy QTLs detected in the present study are distributed over the different chromosomes. Therefore, those regions could be recombined resulting in a weak correlation between the two traits in the segregating population.

Chromosomal regions carrying shattering and dormancy QTLs were found to harbor additional QTLs affecting other traits which distinguish between wild and cultivated rice, such as awn length, anther length and seed fertility, etc. (Cai and Morishima submitted). Those traits responsible for the domestication processes are controlled by numerous QTLs. One possible explanation for the clustering phenomenon found in our study may be “multifactorial linkages” which are inevitably caused by the random distribution of multiple factors determining two or more characters over the limited number of chromosomes (Grant 1981). It can not be ruled out, however, that pleiotropic effects, as yet unknown, are at least partly involved in the association of QTLs for different traits. Further, natural selection favoring a co-adapted character set might have contributed to the maintenance of such gene blocks.

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