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Mapping of QTLs for floating ability in rice

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Deepwater rice (floating rice) can survive under flooded conditions because of their floating ability. We conducted genetic analysis to elucidate the genetic control of floating ability by using an F₂ and BC₃F₂ populations derived from a cross between deepwater and non-deepwater rice varieties. Internode elongation is the most important trait responsible for this adaptation, and is characterized by two factors: timing of the initiation of elongation and the rate of elongation. The position of the lowest elongated internode (LEI) and the rate of internode elongation (RIE) were used to measure floating ability. Two QTLs for LEI were detected on chromosomes 3 (*qLEI3*) and 12 (*qLEI12*). For RIE, two QTLs were detected on chromosomes 1 (*qRIE1*) and 12 (*qRIE12*). We confirmed the genetic effects and map positions of *qLEI3*, *qLEI12* and *qRIE12* by using BC₃F₂ populations. Characterization of near-isogenic lines of *qLEI3*, *qLEI12* and *qRIE12* revealed that the LEI and RIE are at least partly controlled by different genetic pathways. Observation of near-isogenic lines suggested that the introgressed segment of *qLEI12* and *qRIE12* of chromosome 12 affected the deepwater-responsive elongation.

Key Words: deepwater rice, QTL, lowest elongated internode, rate of internode elongation.

Introduction

Deepwater rice (floating rice) is cultivated in flood-prone areas of South and Southeast Asia. In these areas, they are able to survive periods during the rainy season when the water level gradually rises to a depth of 1 m or more. By rapidly elongating their culms, the plants can avoid complete submergence and thereby survive the flooding. Plant length equals the sum of the lengths of the internodes, leaf sheaths and blades. In particular, changes in the internode length contribute most to the rapid elongation under rising water levels (Vergara *et al.* 1976). Deepwater rice is useful for the maintenance of plant diversity and of traditional ecosystems, and for stabilizing food production in flooded wetlands (Islam and Bennett 1998). In addition, the plant is a good material for studying stem elongation (Kende *et al.* 1998) and the genetic bases of phenotypic plasticity (Eiguchi *et al.* 1993).

Floating ability of rice, defined as survival ability under gradually increased rising water levels, involves two factors (Inouye 1987). One is the period when the plants start their internode elongation. Deepwater rice varieties initiate internode elongation early in the vegetative stage as compared with non-deepwater rice varieties. Even deepwater rice would die if it were submerged before it could begin internode elongation (Vergara *et al.* 1975). The position of the lowest elongated internode (LEI) is an appropriate indicator

for measuring this characteristic (Inouye and Mogami 1980). The second factor is the rate of internode elongation. If rice plants can elongate their internodes rapidly, this response is advantageous and favors survival during flooding. The rate of internode elongation (RIE) has been defined to evaluate this factor (Takahashi and Mochizuki 2000). Therefore, both LEI and RIE are critical for rice survival in flooded areas (Inouye 1987).

Quantitative trait loci (QTL) analysis and subsequent dissection of each QTL in uniform genetic backgrounds enable us to clearly characterize genetical and physiological evidences of complex traits. This genetical approach can be easily achieved by the use of abundant DNA markers in rice. Using the plant materials such as F₂, advanced backcross progeny and near-isogenic lines (NILs), we analyzed two important factors affecting floating ability, LEI and RIE, in the present study.

Materials and Methods

Plant materials

An F₂ population consisting of 116 plants derived from a cross between 'Taichung 65 (T65)' and 'Bhadua' (*Oryza sativa* L.) was used for the QTL analysis. Bhadua is an Indica variety that originated in Bangladesh, and is a typical deepwater rice cultivar. T65, a Japonica variety from Taiwan, is a non-deepwater rice.

To further map QTLs in the T65 background, BC₃F₂ populations were generated. Seventy-five BC₃F₁ plants were obtained by three backcrosses to the F₁ plants with T65.

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Because QTLs were detected on chromosomes 1, 3 and 12 in F_2 analysis, we conducted marker assisted selection in the BC_3F_1 by using simple sequence repeat (SSR) markers (Fig. 1) defining these QTL regions on chromosomes 1, 3 and 12. One plant heterozygous at the markers of chromosome 3 was selected. The result of whole genome survey using 125 SSR markers revealed that the BC_3F_1 plant still retained the retained two regions (RM3627-RM7075 and RM1003) on chromosome 1, one region (RM6997-RM8217) on chromosome 4 and one region (RM3155) on chromosome 8 (Fig. 1). The self-pollinated progeny of the BC_3F_1 plant was referred to as BC_3F_2 -A and used for QTL analysis. Similarly, another BC_3F_1 plant that was heterozygous for the markers of chromosome 12 was selected to obtain the BC_3F_2 -B population. The BC_3F_1 plant retained three regions on chromosomes 3 (RM3280), 4 (RM3524-RM8217) and 7 (RM8261-RM1306) (Fig. 1). No BC_3F_1

plant for individual that was heterozygous at the region between RM6703 and RM1067 (chromosome 1) could be obtained. The BC_3F_2 -A and BC_3F_2 -B populations consisted of 93 and 97 plants, respectively.

Two NILs, NIL3 and NIL12, were selected from BC_3F_2 -A and BC_3F_2 -B, respectively. NIL3 was fixed with Bhadua allele in the QTL region on chromosome 3. In NIL3, the other regions retained on chromosome 4 were eliminated but the two regions on chromosome 1 and one on chromosome 8 were still retained in heterozygous conditions. NIL12 was the NIL for the QTLs on chromosome 12 and still retained the other three regions on chromosomes 3, 4 and 7 in heterozygous conditions.

Evaluation of floating ability

In 2001, the T65 \times Bhadua F_2 seeds were germinated at 30°C in the dark for 48 h. Each germinated seed was sown in a 1.5 L plastic pot (11.3 cm diameter \times 13.0 cm depth) containing 1.7 kg paddy soil fertilized with 0.5 g N, 0.5 g P_2O_5 , and 0.5 g K_2O . For determining LEI, we monitored the leaf number on the main culm from the 5th leaf stage by marking leaves with oil-based colored ink. When the plants reached the 7th leaf stage, they were partly submerged to a depth of 10 cm above the soil surface in a 300 L plastic tank (80 cm diameter \times 60 cm depth). When internode elongation was observed, we recorded the LEI of each plant. The internode position corresponded to the leaf number, for instance, the internode whose upper node joining the 7th leaf was designated as the 7th internode.

Subsequently, plants that had begun internode elongation were subjected to rising water levels so that we could measure RIE. Each pot was suspended in water in a 2 m-deep concrete tank using a 2.5 m rope. The water depth was adjusted daily by lengthening the rope to lower each pot further beneath the water (i.e., each plant was lowered at a different rate). Positions of the plants were adjusted to ensure that half of the uppermost fully expanded leaf blade on the main culm in each plant remained above the water. Each individual was treated independently for 3 weeks. If a plant reached the bottom of the tank in less than 3 weeks, the treatment was ended. Immediately before and after the rising water treatment, we measured the lengths of all elongated internodes of the main culm. The lengths of the internodes that elongated during the treatment were given by subtraction, and RIE (cm d^{-1}) was calculated on the basis of this change in length. Any internode longer than 1 cm was designated as an elongated internode (Takahashi *et al.* 1988). The experiment was performed under a 16 h photoperiod, with natural light supplemented with light from sodium lamps to prevent the occurrence of internode elongation accompanying with the initiation of the flower buds. The experiments using the BC_3F_2 populations and NILs were conducted using the method basically the same as described above. BC_3F_2 -A was evaluated for LEI, but both LEI and RIE were measured in BC_3F_2 -B in 2003. In 2004, NILs were assayed for both traits.

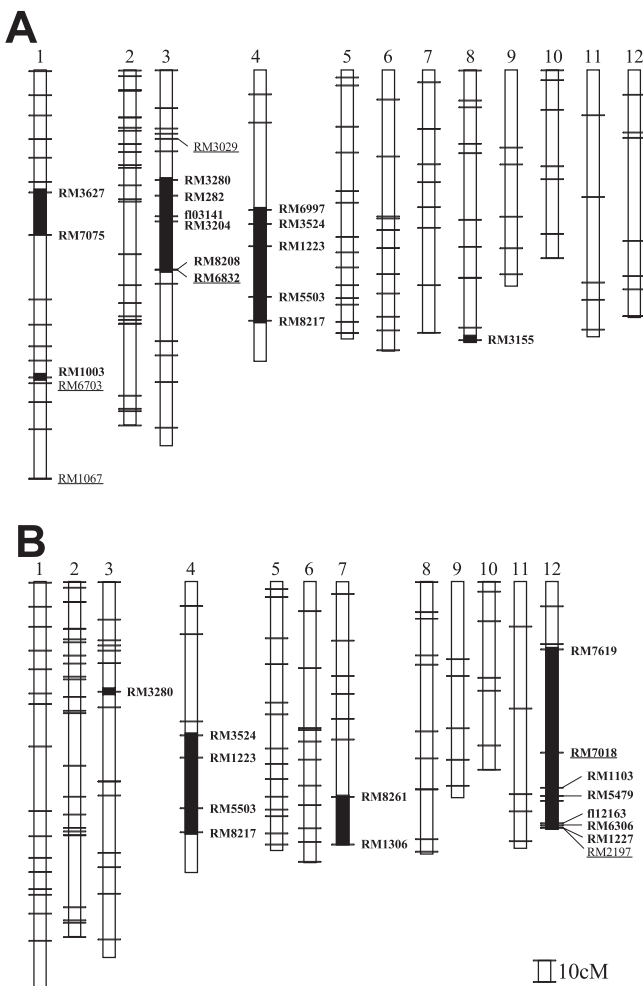


Fig. 1. Graphical genotypes of the selected BC_3F_1 plants for BC_3F_2 -A (A) and BC_3F_2 -B (B) used for QTL analysis in the BC_3F_2 and NIL development. Crossed lines show the position of SSR markers used for whole genome survey. The SSR markers used for the QTL analysis in BC_3F_2 are shown in gothic. The SSR markers on chromosomes 1, 3 and 12 used in the initial selection of BC_3F_1 plants are underlined.

Genotype identification using DNA markers

Ninety restriction fragment length polymorphism (RFLP) and 30 SSR markers (Fig. 3) were used for the whole genome genotype identification of the F_2 population derived from a cross T65/Bhadua. Total 125 SSR markers (Fig. 1) were used for marker assisted selection and QTL analysis in BC_3F_1 and BC_3F_2 . Probes for the RFLP markers included Nipponbare genomic clones (Npb; Saito *et al.* 1991), RFLP clones from Japan's Rice Genome Project (Harushima *et al.* 1998), and Ky11, a genomic clone of IR24, an Indica variety (Tsunematsu *et al.* 1996). The Npb clone was designated as XNpb on the linkage map. DNA extraction and Southern hybridization analysis were conducted following Kurata *et al.* (1994) for determination of the genotype of the RFLP loci. For the BC_3 materials, we performed DNA extraction according to the method of Dellaporta *et al.* (1983) with minor modifications. The information on the SSR markers (RM numbers) was obtained from McCouch *et al.* (2002). SSR markers with the prefix "fl" were developed by the authors. For the fl03141 marker, we used the forward primer 5'-GAGGAAGGAGACGCAGCA-3' and the reverse primer 5'-CACCGGGCTCCAGTTTTTC-3'. The primer set 5'-CGTCTGCATCGGAGTAGTAGC-3' and 5'-CACCACCCATAGCCATAGCC-3' was used for fl12163. These primers were designed from the genomic sequence of the rice (GenBank accessions AC137597 and AL713940). The PCR was conducted using the 15 μ l of PCR reaction mixture: 1 \times PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.15 μ l of 5 unit *Taq* DNA polymerase and 1 \times PCR dye (0.015% bromophenolblue and 3% glycerol) and 0.27 pmol primers, with 5 ng DNA templates. The conditions for amplification were 35 cycles of denaturation at 94°C, annealing at 55°C, and extension at 72°C for 30 s, respectively. For genotype identification, the PCR products were electrophoresed on 4% agarose gel.

Linkage map construction and QTL analysis

Linkage analysis was conducted with MAPMAKER/Exp v. 3.0 (Lander *et al.* 1987). The QTL analysis was performed with Windows QTL Cartographer Version 2.0 (Basten *et al.* 2004). Both simple interval mapping (SIM) and composite interval mapping (CIM) were used to detect QTLs. QTLs for LEI and RIE were declared significant at $P < 0.01$, with the LOD score given by 1000 permutations (Churchill and Doerge 1994, Doerge and Churchill 1996).

Results

QTL analysis in F_2 population

Bhadua, a typical deepwater rice variety, started internodal elongation at early vegetative stage, and the LEI value was 6.4 ± 0.5 . The non-deepwater rice variety parent, T65, showed 13.7 ± 0.5 of LEI. Average of the RIE of Bhadua and T65 were 8.1 cm d^{-1} and 1.5 cm d^{-1} , respectively. The two parameters, LEI and RIE, reflected the fact that Bhadua had higher floating ability than that of T65.

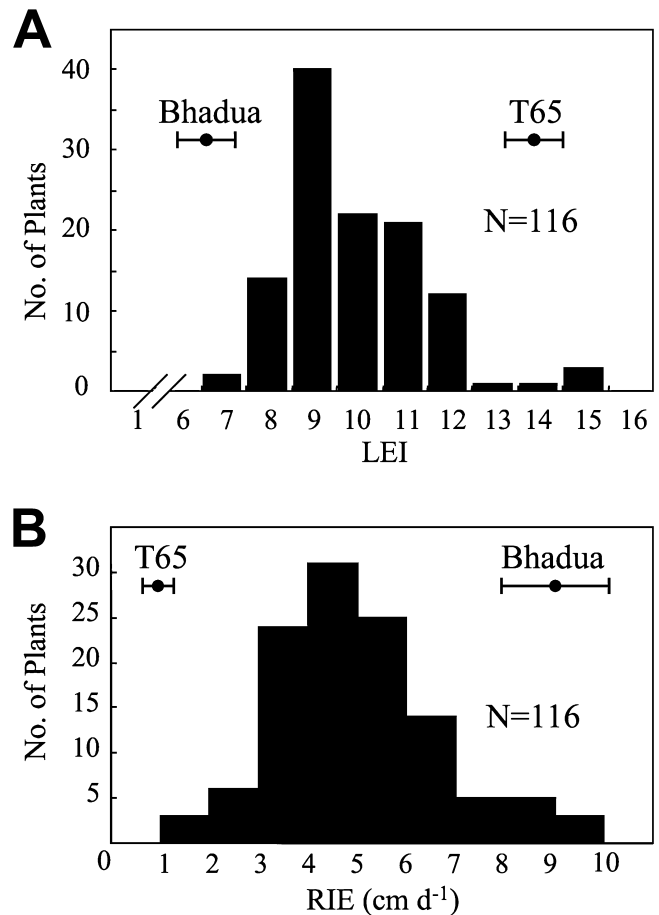


Fig. 2. Frequency distributions of (A) LEI and (B) RIE in the F_2 population (T65 \times Bhadua). Points and ranges indicate the average and standard deviation, respectively. LEI were 13.7 ± 0.5 for T65 and 6.4 ± 0.5 for Bhadua, respectively. RIE were 1.6 ± 0.2 and 8.1 ± 1.0 for T65 and Bhadua, respectively.

The F_2 population showed a continuous frequency distribution of LEI (Fig. 2A). Three plants showed LEI of 15, which was higher than the average of T65, but no plant showing an LEI value lower than that of Bhadua. Considering the environmental errors, it was not regarded as transgressive segregation. The frequency distribution of RIE in the F_2 population was also continuous (Fig. 2B). RIE ranged from 1.0 to 9.2 cm d^{-1} , and transgressive segregation was not observed. The correlation between LEI and RIE was significant at $P < 0.01$ ($r = -0.61$).

The linkage map contained 120 DNA markers that covered the total genome, with an average interval of 16.5 cM between markers (Fig. 3). Threshold values of LOD score given by 1000 permutations were 4.6 for LEI and 4.2 for RIE ($P < 0.01$). Two QTLs for LEI were detected on chromosomes 3 (*qLEI3*) and 12 (*qLEI12*) (Fig. 3). For RIE, two QTLs were detected on chromosomes 1 and 12. On the regions of *qLEI3*, *qLEI12*, *qRIE1* and *qRIE12*, LOD scores peaked in the marker intervals XNpb144-RM8208, RM5479-fl12163, XNpb113-G54 and RM5479-fl12163, respectively (Fig. 3 and Table 1). The Bhadua allele lowered

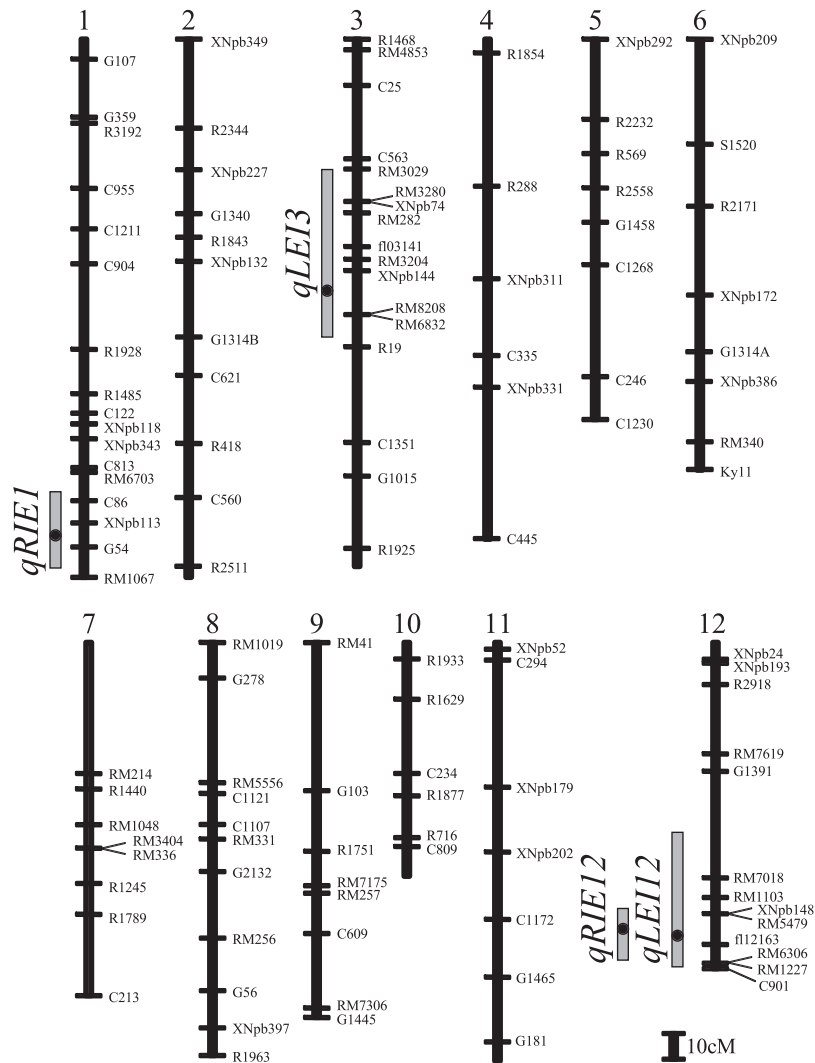


Fig. 3. A linkage map of the F₂ population (T65 × Bhadua). The vertical bars to the left of the maps indicate the regions in which the LOD scores are significant for the trait at 1% level. The filled circles on the bars indicate the position of the peak LOD score for each QTL.

Table 1. Characteristics of the QTLs that affect LEI and RIE detected in the T65/Bhadua F₂ population

Trait	QTL	Chromosome	Marker interval	Pos. ^a	Threshold ^b	LOD score	r ² (%) ^c	Additive effect ^d	Dominance effect ^e
LEI	<i>qLEI3</i>	3	XNpb144-RM8208	6.0	4.6	9.0	40.7	-1.5	-0.8
	<i>qLEI12</i>	12	RM5479-fl12163	10.0		11.7	38.5	-1.2	-0.6
RIE	<i>qRIE1</i>	1	XNpb113-G54	4.0	4.2	7.5	30.6	2.3	-0.5
	<i>qRIE12</i>	12	RM5479-fl12163	6.0		5.3	22.2	0.9	0.6

^a Genetic distance (cM) from the left marker of each interval where the peak LOD was scored.

^b Given by 1000 permutations at $P < 0.01$.

^c Phenotypic variation explained by a single QTL.

^d The values were calculated based on the following formula: ((trait values of Bhadua homozygotes) - (trait values of T65 homozygotes))/2.

^e The values were calculated based on the following formula: (trait values of heterozygotes) - (mid-point values).

LEI, and increased RIE. By CIM technique, the peak for *qLEI3* appeared on the interval RM282-fl03141. The interval was different from the result of SIM, but coincided with the results of the experiments using BC₃F₂-A described below. On the other QTLs, the intervals where the peak LOD appeared were the same in SIM and CIM. Any additional

QTLs by CIM were not detected for neither LEI nor RIE.

Mapping and characterization of QTLs in the nearly isogenic background of T65

Fig. 4 shows the frequency distributions of LEI and RIE in BC₃F₂-A and BC₃F₂-B. The LEI of both populations

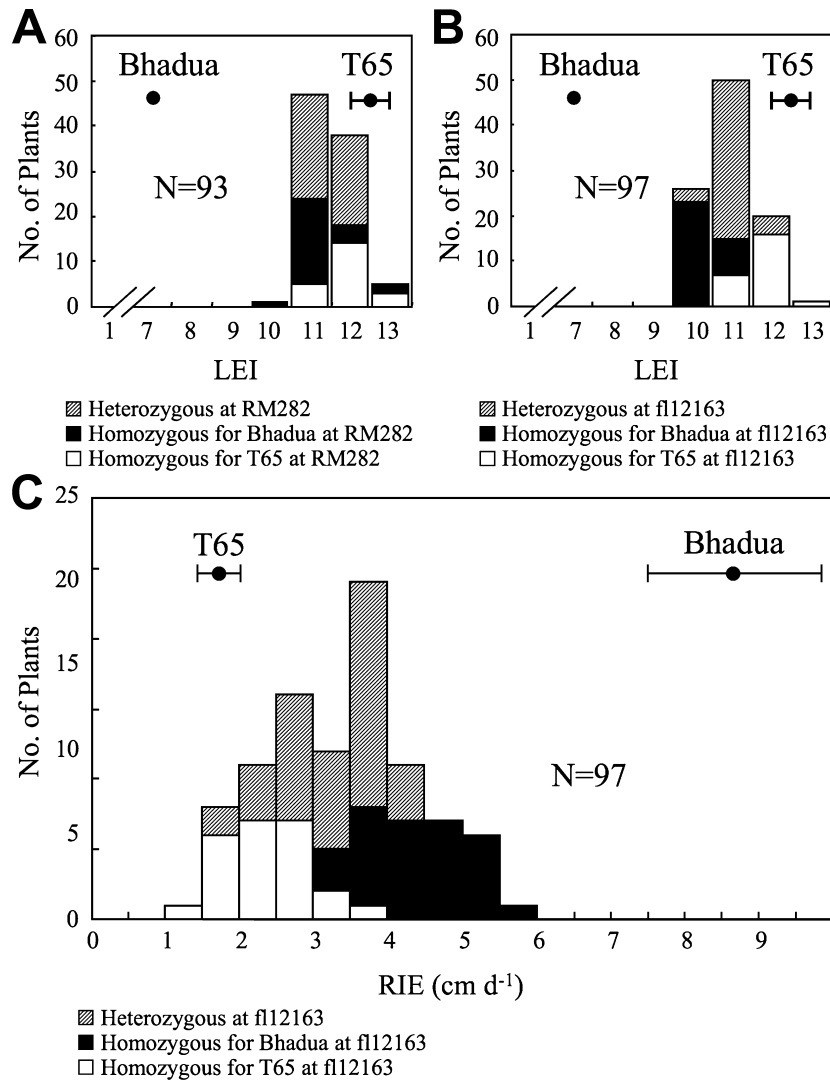


Fig. 4. Frequency distributions of LEI in BC₃F₂-A (A) and BC₃F₂-B (B), and that of RIE in BC₃F₂-B (C). Bars are filled differently according to the genotypes at the SSR markers nearest to the QTLs (A: RM282, B and C: fl12163).

fell within four LEI classes (10, 11, 12 and 13). However, no clear bimodal segregation was observed. It was also impossible to divide the segregation of RIE in BC₃F₂-B into distinct classes. In addition to the small variation on LEI from 10 to 13, it is considered that the fluctuation by environmental conditions caused continuous frequency distribution. In this experiment, performed in 2003, T65 showed an LEI value of 12.5 ± 0.7 , which was lower than the result in 2001 (LEI 13.7 ± 0.5). This difference was probably due to differences in experimental conditions, especially temperature. The temperature in 2003 was lower than that in 2001 (data not shown).

Because discrete segregation was not observed in the BC₃F₂ progeny, we conducted QTL analysis in these populations. In the interval between the markers RM282 and fl03141, peak LOD was scored for LEI in the BC₃F₂-A population (Table 2). No QTL was detected in the other retained regions on chromosomes 1, 4 and 8 (data not shown). In BC₃F₂-B, the LOD score peaked in the interval between

markers RM5479 and fl12163 for both LEI and RIE (Table 2). In the other segregation regions on chromosomes 3, 4 and 7, no QTL was detected (data not shown).

Two NILs, NIL3 and NIL12, were selected from the BC₃F₂-A and BC₃F₂-B, respectively. NIL3 and NIL12 were assayed for LEI and RIE and compared with T65 (Table 3). LEI of NIL3 and NIL12 were significantly lower than that of T65. RIE of NIL12 was significantly higher than that of T65. However, RIE of NIL3 was not significantly different from that of T65, indicating that *qLEI3* did not affect RIE. These results confirmed the QTL analysis in F₂ except that the effect of *qLEI12* to LEI was greater than that of *qLEI3* (Table 1, Table 2 and Table 3).

Discussion

This study is the first genetic analysis for both LEI and RIE as indicators of floating ability in rice. In addition, we obtained NILs for *qLEI3* and *qLEI12/qRIE12*. These lines

Table 2. Characteristics of the QTLs that affect LEI and RIE detected in the BC₃F₂-A and -B populations

Trait	QTL	Chromosome	Marker interval	Pos. ^a	Threshold ^b	LOD score	r ² (%) ^c	Additive effect ^d	Dominance effect ^e
LEI	<i>qLEI3</i>	3	RM282-fl03141	4.0	3.5	4.2	20.2	-0.4	-0.1
	<i>qLEI12</i>	12	RM5479-fl12163	10.0	3.3	20.4	65.7	-0.8	-0.0
RIE	<i>qRIE12</i>	12	RM5479-fl12163	5.0	3.5	20.5	64.7	1.0	0.1

^a Genetic distance (cM) from the left marker of each interval where the peak LOD was scored.

^b Given by 1000 permutations at $P < 0.01$.

^c Phenotypic variation explained by a single QTL.

^d The values were calculated based on the following formula: ((trait values of Bhadua homozygotes) - (trait values of T65 homozygotes))/2.

^e The values were calculated based on the following formula: (trait values of heterozygotes) - (mid-point values).

Table 3. LEI and RIE of NIL3, NIL12 and T65 (The values indicate the average \pm standard deviation)

Line	LEI	RIE
NIL3	12.4 \pm 0.7 b ^a	1.6 \pm 0.2 a
NIL12	10.5 \pm 0.5 a	3.1 \pm 0.6 b
T65	13.3 \pm 0.6 c	1.4 \pm 0.2 a

^a Different letters indicate significant difference at 5% level by Tukey-Kramer multiple comparison.

will be used in physiological bioassays to further characterize each QTL. This genetic methodology should always be used to dissect complex traits to simple Mendelian factors (Yano *et al.* 2001).

Our method for measuring RIE is capable of measuring the full potential elongation rate (Takahashi and Mochizuki 2000). By evaluating both LEI and RIE, we found that LEI and RIE are under different control to some extent, although a QTL region on chromosome 12 (*qLEI12* and *qRIE12*) is shared by both traits. This linkage between *qLEI12* and *qRIE12* is the cause of the observed correlation between LEI and RIE. To characterize the QTLs, we subjected two NILs, NIL3 and NIL12, to the assays for LEI and RIE. As we expected from the QTL analysis in the F₂ population, *qLEI3* did not affect the RIE (Table 3). This evidence clearly indicated that LEI and RIE should be treated as different traits.

We observed that NIL12 elongate its plant length up to near 2 m at the end of the rising water level treatment. In the paddy field, however, plant length of NIL12 was about 1 m (data not shown). These results indicated that NIL12 has ability to change its plant length depending on the water level conditions. It is suggested that *qLEI12/qRIE12* are involved in the deepwater-responsive elongation. Hence, *qLEI12/qRIE12* might explain a major portion of the phenotypic plasticity generally observed in deepwater rice varieties.

Nemoto *et al.* (2004) reported the results of their QTL analysis of early elongation ability in deepwater rice variety 'Goai' by using LEI as the indicator. They identified QTLs for LEI on chromosomes 3 and 12, which were located at almost the same positions as in our results. On the same region of chromosome 12, they also detected QTL affecting LEI from different deepwater variety 'Habiganj AmanVIII' (Tang *et al.* 2005). These QTLs for LEI are probably widely

distributed among deepwater rice varieties. One of the deepwater tolerance genes, *dw3*, was identified by Eiguchi *et al.* (1993). Plants with *dw3* in the background of T65 had an LEI value of 10. Moreover, in their study, the rice plants survived a water level increase of 10 cm every other day. From these results, we hypothesize that these plants they assessed have RIE comparable to that of the NIL12. Hence, it is possible to consider that *dw3* is one of the alleles at *qLEI12* and/or *qRIE12*. In the almost the same region of *qRIE1*, Sripongpangkul *et al.* (2000) detected the QTL controlling internode elongation in gradual water level rising conditions.

We are now developing the NIL of *qRIE1* to comprehensively understand the floating ability in rice. An immediate follow-up experiment to the current study would logically focus on elucidating whether *qLEI12* and *qRIE12* were the same gene or not. A high-resolution linkage analysis of these loci is currently underway to address this question.

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