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Quantitative Trait Loci (QTLs) Associated with Drought Tolerance in Vietnamese Local Rice (Oryza sativa L.)

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One hundred and thirty lines of F2 population derived from a cross between Khaunoongmo and Q5 were used to identify the quantitative trait loci (QTLs) related to drought tolerance in Vietnamese local rice in this study. The F₃ population was grown for phenotypic evaluation in the summer season of 2011 at the Center for Technology Development and Agricultural Extension, Hanoi, Vietnam under irrigated control. The standard evaluation system of International Rice Research Institution (IRRI) for drought sensitivity at vegetative stage was applied to evaluate the score of leaf rolling, leaf drying and plant recovery over the drought period. A number of SSR markers (765) were used for parental survey and of which 226 markers showed clear polymorphism (29.54%). These polymorphic markers were used to carry out genotyping F_2 population. Furthermore, three phenotypic traits under water deficit conditions were used for conducting a QTL analysis with Simple Interval Mapping (SIM) and Composite Interval Mapping (CIM) methods of QTL Cartographer 2.5 using 130 F_3 lines. Consequently, seven QTLs were detected on chromosome 4, 8, and 11: two QTLs for leaf rolling, three QTLs for leaf drying and two QTLs for plant recovery under water stress conditions. In addition, the logarithm of the odds (LOD) score of these QTLs ranged from 2.05 to 3.82, in which RM1359 linked to qLR—4 could explain 9.5% of leaf rolling variation, RM22654 linked to qLD–8-aexplained 12.6% of leaf drying variation and RM22806 linked to qPR-8 explained 3.58% of plant recovery variation under drought conditions. Therefore, these consistent QTLs for leaf traits under stress might be useful for marker–assisted selection for rainfed rice improvement.

Key words: drought tolerance, local rice, polymorphism, QTL, SSR

INTRODUCTION

Drought is the most widespread and damaging of all environmental stresses, affecting 23 million ha of rainfed rice in South and Southeast Asia (IRRI- Climate changereadyrice-http://irri.org/index.php?option=com_k2& view=item&id=9148&lang=en). Improving drought tolerance in rice is a goal of breeders targeting rainfed environments as well as other water-scarce regions. Molecular marker technology has now been found to facilitate better understanding of the genetic basis of the indices of tolerance, most of which are quantitatively inherited. Quantitative trait loci (QTLs) approach has assisted to identify QTLs for the stress tolerance related traits including root length, root weight, root thickness, plant height, leaf rolling and osmotic adjustment under hydroponics and other artificially created stress conditions.

In Vietnam, drought is natural disasters which caused the third severest damage after floods, storms and tends to occur severer, more difficult to control due

to climate change. The total of rice area in Vietnam is about 4.1 million ha, concentrated in the Red River Delta, North Central, South—central Coast, and Cuu Long River Delta. In the first half of 2011, drought has affected 62,000 ha of rice in North Central, representing over 24% of rice cultivated in this area, of which over 30,000 ha was severely damaged by drought.

Genetic improvement of adaptation to drought is addressed through the conventional approach by selecting for yield and its stability over locations and years. Although this approach has been successful to some degree in developing drought-tolerant varieties, such selection programs are expensive and slow in making progress (Ribaut et al., 1997; Zhang et al., 1999). The development of molecular marker technologies during the past ten years has revolutionized the genetic analysis of crops and made it possible to dissect complex quantitative traits (Zhang et al., 2001). The identification of QTLs is very important for studying of plants to grow and yield under unfavorable conditions solves problems of environmental stress. Drought tolerance is associated with many different morphological and physiological traits or responses including stomatal regulation, variation in leaf cuticle thickness, root morphology and depth, osmotic adjustment, antioxidant capacity, desiccation tolerance (membrane and protein stability), maintenance of photosynthesis and the timing of events during reproduction (Nguyen et al., 1997; Klueva et al., 1998). Since plant response to drought stress is quite complex, and is associated with a large number of phys-

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iological and biochemical changes, understanding of the nature of QTLs associated with drought stress is limited (Nguyen, 2000).

Recently, direct selection for grain yield under managed drought stress has been found to be effective in improving drought tolerance (Venuprasad et al., 2007; Kumar et al., 2008; Venuprasad et al., 2008), but the reliable application of managed stress is not possible for most upland rice breeding programs. This has led to the hypothesis that breeding for drought tolerance in rice could be facilitated by QTL mapping quantitative trait loci related to secondary component traits assumed to be related to drought tolerance (Price et al., 1999) for use in marker-assisted selection (MAS). Pursuing this approach, QTL for osmotic adjustment (Zhang et al., 2001), leaf rolling, leaf drying and relative water content (Courtois et al., 2000), root-related traits (Zhang et al., 2001; Courtois et al., 2003; Yue et al., 2006), stomatal conductance (Price et al., 1997) and several other traits potentially linked to drought tolerance have been mapped. Some attempts have been made to use such QTL in MAS schemes. Unfortunately, most QTL identified have not been repeatable over environments and/or populations (Bernier et al., 2008), or have not consistently affected either the target trait (Shen et al., 2001; Steele et al., 2006) or grain yield under stress (Steele et al., 2007) when introgressed into a susceptible cultivar.

Vietnam is a center of rice diversity with a thousand local rainfed lowland and upland varieties. The large local rice germplasms are providing rich gene sources for breeding of abiotic and biotic traits. However, the characterization and effective use of local germplasm is still limited because of lack of data on proper evaluations. In our previous studies, we conducted genotyping and phenotyping of a large collection of local Vietnamese upland rice varieties and identified a number of varieties expressing potential to drought tolerance. In this study, we aim to identify QTLs related to drought tolerance trait of local Vietnamese rice.

MATERIALS AND METHODS

Materials

Two lines, a traditional upland *Japonic*a cultivar from Vietnam, photosensitive, medium duration, showed stable yield under drought stress in upland conditions,

Khaunoongmo, and Q5, a rainfed lowland cultivar adapted in many regions, were used as parents to develop $\rm F_2$ population of 130 plants for genetic analysis. The 130 $\rm F_3$ lines harvested from each of the $\rm F_2$ plants were evaluated for drought tolerance under water deficit conditions.

Phenotypic Evaluation

A total of 130 F₃ families plus the two parental lines were pre-germinated and transplanted in the greenhouse for phenotypic evaluation. The experiment followed a complete randomized block design, with three replications (plots), five rows per plot $(0.6 \times 1.0 \,\mathrm{m}^2)$, 4 plants per row. The 390 plots, with a population density of 7,800 plants, were planted and 10 F₃ plants per plot were selected for evaluation. The experiment was carried out during the summer season of 2011 at the Center for Technology Development and Agricultural Extension, Hanoi, Vietnam under irrigated control. The plots were irrigated three times weekly. Starting at 45 days after sowing, water was withheld, and no rain fell during the stress period. Leaf rolling (after 14, 16, 18 and 22 days of drought), leaf drying (after 20, 22 and 23 days of drought), and plant recovery (after 10 days following watering) were assessed visually on a scale of 1–9 essentially according to the standard evaluation system of IRRI (SES, IRRI) (Table 1). These mean of leaf rolling, leaf drying and plant recovering score represented the respective F₂ individuals over the drought period.

Data of all the variables measured was subjected to Analysis of Variance (ANOVA) to estimate the level of variability among the F_2 population using IRRI–STAT ver. 4.0 software (IRRI). Broad sense heritability was computed from two–way analysis of variance (factors, genotype and replicate) of F_2 from the estimates of genetic (σ 2G) and residual (σ 2e) variance derived from the expected mean squares as %H²B = σ 2G/(σ 2G+ σ 2e/k) where k was the number of replications.

DNA preparation and SSR analysis

Young leaves of each $\rm F_2$ and parental plants were sampled at the tillering stage. The genomic DNA was extracted by using the method of McCouch *et al.* (1988). SSR primer sequences were according to McCouch *et al.* (2002), IRGSP (2005), and Panel of 50 standard SSR markers (http://www.gramene.org/markers/microsat/50_ssr.html). PCR reactions were per-

Table 1. Standard evaluation system for drought sensitivity at vegetative stage (SES–IRRI)

Scale	Leaf rolling	Leaf drying	Plant recovery (%)
0	Leaves healthy	No symptoms	_
1	Leaves start to fold (shallow)	Slight tip drying	90-100
3	Leaves folding (deep V-shape)	Tip drying extended up to ¼	70-89
5	Leaves fully cupped (U-shape)	One–fourth to 1/2 of all leaves dried	40-69
7	Leaf margins touching (0-shape)	More than 2/3 of all leaves fully dried	20-39
9	Leaves tightly rolled (V–shape)	All plants apparently dead. Length in most leaves fully dried $% \left(1\right) =\left(1\right) \left(1\right$	0-19

formed in a volume of $15\,\mu l$ containing 30ng genomic DNA, $0.5\,\mu M$ of each primer, $200\,\mu M$ dNTPs, $1\times$ buffer, $1.5\,\mathrm{mM}$ MgCl₂, 1 U Taq DNA polymerase and H₂O. The PCR amplification was performed on a PCR system using the following program: $94^{\circ}\mathrm{C}$ for $5\,\mathrm{min}$, then $35\,\mathrm{cycles}$ at $94^{\circ}\mathrm{C}$ for $0.5\,\mathrm{min}$, $55^{\circ}\mathrm{C}$ for $0.5\,\mathrm{min}$, $72^{\circ}\mathrm{C}$ for $1\,\mathrm{min}$, with final extension step at $72^{\circ}\mathrm{C}$ for $7\,\mathrm{min}$. Amplified products were resolved on 3% agarose gels with ethidium bromide staining in $0.5\times$ TAE buffer. Gels were visualized under ultraviolet light using Herolab UV, Germany.

Genetic linkage map construction and QTL analysis

The genetic linkage map was constructed using MAPMAKER/EXP v.3.0 (Lander et al., 1987; Lincoln et al., 1993). Linkage groups were created with a LOD score of 2.0. QTLs analysis was identified using Simple Interval Mapping (SIM) and Composite Interval Mapping (CIM) methods of QTL Cartographer 2.5 (Wang et al., 2007). The significant threshold was estimated by performing 1000 permutations of each measurement (p<0.05) using QTL cartographer.

RESULTS

Phenotypic values of the F_3 families and parental lines

The analysis of leaf rolling, leaf drying and plant recovery of the 130 F_3 families and the parental lines were carried out in 2011 under water deficit conditions. The results showed that the Q5 had significantly higher values of leaf rolling and leaf drying, but lower plant recovery than that of the Khaunoongmo and the mean of leaf rolling, leaf drying and plant recovery of the F_3

Table 2. Distributions for leaf drying, leaf rolling, and plant recovery under stress derived from the cross Khaunoongmo $\times Q5$

Variety	Leaf drying	Leaf rolling	Plant recovery (%)	
Khaunoongmo	1.00 ± 0.87	1.22 ± 0.67	83.33 ± 10.00	
Q5	8.56 ± 0.88	8.33 ± 1.00	14.44 ± 8.82	
\mathbb{F}_2	5.29 ± 2.85	4.99 ± 2.57	40.06 ± 25.15	
CV%	30.5	33.5	27.3	
$\mathrm{H}^2\mathrm{B}$	0.96	0.94	0.98	

Mean (\pm standard deviation) and broad–sense heritability (H°B) of mapping population F₂, parental lines (Khaunoongmo and Q5) for leaf rolling (LR), leaf drying (LD) and plant recovery.

 $\textbf{Table 3.} \ \ \textbf{Phenotypic correlation between drought tolerance traits}$

	Leaf drying	Plant recovery		
Leaf rolling	0.30*	-0.23*		
Leaf drying		-0.78*		

^{*} Correlation is significant at 0.01 level of probability (2–tailed) (P<0.01)

were between Khaunoongmo and Q5 (Table 2).

The broad–sense heritability refers to the ratio of heritable variance to total variance. In this study, the broad sense heritabilities were high for all traits studied (94–98%). The phenotypic correlations between traits showed that leaf rolling was significantly positively correlated with leaf drying (r=0.3*) under stress (Table 3). Conversely, plant recovery was significantly negative correlated with leaf rolling (r=-0.23*) and leaf drying (r=-0.78*) under stress. These correlations indicated that leaf drying was more strongly associated with plant recovery compared with leaf rolling.

Identification of QTLs associated with leaf rolling, leaf drying and plant recovering

A total of 765 SSR markers were surveyed and 226 (29.54%) of them showed polymorphism between the two parents (Table 4). A linkage map was constructed based on the data of 226 SSR markers assayed on 130 $\rm F_2$ plants using MAPMAKER/EXP v.3.0

Of 226 markers, 164 were clustered into 19 linkage groups corresponding to 12 chromosomes of rice. Chromosomes 5, 6, 7, 8 and 10 harbored one linkage group, while the remaining chromosomes (1, 2, 3, 4, 9, 11 and 12) each contained 2 linkage groups. The remaining 62 markers were not linked to any group. The linkage map covered 1,180.8 cM employing Kosambi mapping function, in which the average distance between two adjacent markers was 7.2 cM.

Single marker analysis and interval mapping procedures were used to detect the QTLs linked to physiomorphological traits under drought conditions. The identified QTLs were further confirmed using composite interval mapping (CIM) with a logarithm of the odds (LOD) threshold of 2.0. The results of CIM and the summary statistics for all significant QTLs are given in Figure 1 and Table 5.

A total of 7 QTLs were detected for three traits of

Table 4. Parental polymorphism survey using SSR markers

Chromosome No. of markers No. of polymorphism Ratio of polymorphism 1 105 37 35.24 2 74 20 27.03 3 83 25 30.12 4 63 10 15.87 5 69 18 26.09 6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33 12 54 21 38.89					
2 74 20 27.03 3 83 25 30.12 4 63 10 15.87 5 69 18 26.09 6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	omosome 1	ne No. of markers			
3 83 25 30.12 4 63 10 15.87 5 69 18 26.09 6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	1	105	37	35.24	
4 63 10 15.87 5 69 18 26.09 6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	2	74	20	27.03	
5 69 18 26.09 6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	3	83	25	30.12	
6 65 13 20.0 7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	4	63	10	15.87	
7 31 11 35.48 8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	5	69	18	26.09	
8 67 18 26.87 9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	6	65	13	20.0	
9 48 24 50.0 10 49 12 24.49 11 60 17 28.33	7	31	11	35.48	
10 49 12 24.49 11 60 17 28.33	8	67	18	26.87	
11 60 17 28.33	9	48	24	50.0	
	10	49	12	24.49	
12 54 21 38.89	11	60	17	28.33	
	12	54	21	38.89	
Total 765 226 29.54	Total	765	226	29.54	

Trait	QTL	Chr.	Marker	Position	LOD	Additive effect	Dominant	R ² (%)
Leaf rolling	qLR-4	4	RM1359	0.06	2.16	-0.966	0.1607	9.50
	qLR–8	8	RM23251	1.62	2.08	-0.564	-0.839	0.15
Leaf drying	qLD–8– a	8	RM22654	1.33	2.05	1.121	-0.7212	12.60
	qLD– 8 – b	8	RM23251	1.61	2.10	0.182	-1.3859	5.29
	qLD–8– c	8	RM23126	1.94	3.82	-1.330	-1.4556	1.78
Plant recovery	qPR-8	8	RM22806	0.43	2.10	-8.192	-3.456	3.58
	qPR-11	11	RM27027	0.84	2.06	-7.424	-6.7788	1.45

Table 5. QTLs detected for drought tolerance in Khaunoongmo × Q5 F₂ lines using composite interval mapping

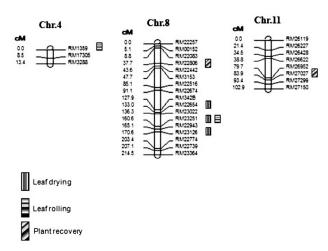


Fig. 1. Position of QTLs controlling drought avoidance parameters in Q5/Khaunoongmo population (LOD >2.0)

leaf rolling, leaf drying and plant recovery in which LOD score and phenotypic variation (R²) ranged from 2.05 to 3.82 and 0.15% to 12.60%, respectively. The number of QTLs per trait under stress were: 2 for leaf rolling (qLR-4, qLR-8), 3 for leaf drying (qLD-8-a, qLD-8-b, qLD-8-c) and 2 for plant recovery (qPR-8,qPR-11) (Table 5). The QTLs distributed unevenly among the chromosomes with 5 QTLs on chromosome 8, one on chromsome 4 and one on chromosome 11. The QTL qLR-4 for leaf rolling under water stress was identified near RM1359 on chromosome 4 with LOD score of 2.16 and R²=9.5%. For leaf drying, the closest marker linkage to qLD-8-a associated with leaf drying under the stress is RM22654, with LOD score of 2.05 and $R^2=12.6\%$. The QTL qPR-8 for plant recovery was identified near RM22806 on chromosome 8 with LOD score of 2.1 and R²=3.58%. Alleles from Khaunoongmo at 2 QTLs on chromosome 8 had positive effects on leaf drying while those from Q5 at the other QTLs contributed positively on leaf rolling, leaf drying and plant recovery. Therefore, there were obvious hotspots where QTLs for all three traits under drought stress conditions were detected including regions mostly on chromosome 8.

DISCUSSION

In this study, we have focused on three different traits (leaf rolling, leaf drying and plant recovery) involved in drought avoidance. Those are important traits highly correlated to yield under drought stress. Leaf drying scores were found to have negative correlation with rice yield and harvest index under drought stress while grain yield in control was not correlated with leaf rolling, leaf drying and leaf relative water content determined under water stress (Babu *et al.*, 2003). Leaf drying and leaf rolling negatively correlated with plant recovery indicated that these two traits were associated with plant water content and subsequently influencing the recovery rate (Courtois *et al.*, 2000).

The broad–sense heritability values of these drought tolerance traits were substantially high in this study. This suggested that there was predominance of additive gene action in the expression of these traits which can be improved through individual plant selection (Vange *et al.*, 1997; Makeen *et al.*, 2007; Rashwan, 2010). Moreover, the values obtained were even higher than those reported from other works on rice (Price *et al.*, 2002; Babu *et al.*, 2003).

The QTLs controlling three traits involved in drought tolerance were analyzed and shown that a common QTL for leaf rolling and leaf drying and other QTLs identified for all traits were located on chromosome 8. Consistently, other reports also showed that QTLs controlling leaf drying on chromosome 8. Using the CO39 and Moroberekan mapping population, QTL affecting leaf rolling, leaf drying, and relative water content were found, and these three traits were significant correlated (Price et al., 2002). A total of 11 QTLs (chromosomes 1, 2, 7, and 8) controlling leaf drying was identified (Price et al., 2002). One QTL lr8.1 (chromosome 8 near RM72) and one QTL lr4.1 (on chromosome 4 near RM518) were mapped for QTLs for leaf rolling (Lin et al., 2007). In addition, Babu et al. (2003) also identified two QTLs lr8.1 and ld8.1 mapped to the regions ME6_13-G187 and G2132-G1073, respectively, on chromosome 8. Yu et al. (2006) also reported that six QTLs were resolved for leaf-drying score and four QTLs for number of days to leaf rolling. The region RM502-RM264 on chromosome 8 showed a large effect on leaf drying (11.05%) while other region RM544-RM72 on chromosome 8 had effect on number of days to leaf rolling (6.55%). Also a QTL for number of days to leaf rolling on the region RM335-RM307 on chromosome 4 had effect on the trait (7.11%).

In recent years, many QTLs associated with quanti-

tative traits, such as root morphology, crop yields and stress tolerance, were mapped on different chromosomes and some progresses were made in molecular marker–assisted breeding (Kamoshita et al., 2002; Zhang et al., 2003; Wang et al., 2004; Shen et al., 2005; Neeraja et al., 2007). The promise of molecular marker–assisted selection in crop breeding still remains, but achieving practical benefits is taking longer than expected. The main reason for this delay is insufficient quality of markers, inadequate experimental design, high cost and complexity of the quantitative traits (Korzun, 2003). The QTLs, identified in this work might be useful for further study of QTL fine mapping and marker assisted–selection in breeding program of drought tolerance in rice.

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