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Quantitative Trait Loci Analysis for Plant Morphological Traits in Rice (*Oryza sativa* L.) Under Different Environments*

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Abstract: A Recombinant Inbred (RI) population derived from the cross of Asominori (*Japonica*)×IR24 (*Indica*), grown in Japan and China, were employed to detect Quantitative Trait Loci (QTLs) for seven morphological traits, viz., Flag-Leaf Length (FLL), width (FLW) and area (FLA), the Second Leaf Length (SLL), width (SLW) and area (SLA), Plant Height (PH), which mainly represent morphological characteristics of rice plants. Resultantly, approximately normal distributions and transgressive segregations of seven traits studied were observed, showing that all of these traits were quantitatively inherited and there existed positive correlations among them. Furthermore, a total of 29 QTLs associated with seven morphological traits were detected, which were mainly distributed on chromosome 1 (11 QTLs), 5 (5 QTLs) and 6 (5 QTLs). Among them, only 4 QTLs (*qSLL-1* for SLL, *qFLA-5* for FLA and both *qPH-1* and *qPH-2* for PH) were commonly expressed in two countries and QTL number varied with growth environment. Those results of this study will supply useful information for improving morphology of rice plants in Asian countries.

Key words: Quantitative Trait Locus (QTL), morphological traits, molecular marker, rice (*Oryza sativa* L.)

INTRODUCTION

Rice plays a remarkable role as food supplies in Asian countries including China and Japan. Morphological characteristics is one of the most important factors for rice breeders to select high-yielding rice with new ideal plant-type which was put forward by International Rice Research Institute in 1989 (IRRI, 1989). It was widely assumed that developing high-yielding rice can be on the foundation of improving the morphological characteristics (Wang *et al.*, 2005; Yue *et al.*, 2006). In rice, morphological characteristics, composed of the shape of flag-leaf, the second leaf and plant height, belongs to quantitatively inherited trait (Yan *et al.*, 1999; Mei *et al.*, 2005). The identification of Quantitative Trait Loci (QTLs) for rice morphological traits and the tightly linked molecular markers that flank those QTLs are necessary for breeding programs by the Marker-Assisted Selection (MAS). So far, few studies on mapping QTLs for plant morphological traits, such as plant height, leaf size and shape (Wu *et al.*, 1996; Yan *et al.*, 1999; Li *et al.*, 2001; Sheng *et al.*, 2004; Wang, 2004; Yue *et al.*, 2006), in rice have been conducted. However, previous QTL mappings for those morphological traits in rice were performed in a certain country or only involved in one or two traits. So the utilization of the resultant QTLs in previous studies is relatively limited, especially in all over the Asian countries.

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In this study, a Recombinant Inbred (RI) population derived from a *japonica* cultivar, Asominori and an *indica* cultivar, IR24, grown in Japan and China in two years, was used to explore QTLs for seven morphological traits, namely, Flag Leaf Length (FLL), width (FLW) and area (FLA), the Second Leaf Length (SLL), width (SLW) and area (SLA), Plant Height (PH), which mainly represent the morphological characteristics in rice and the results may provide more valuable information of QTLs for MAS to breed ideal morphological rice cultivars all over the Asian countries.

MATERIALS AND METHODS

Plant Materials

The RI lines used in this study, kindly provided by Professor A. Yoshimura of plant breeding laboratory, Agricultural Faculty of Kyushu University, Japan, were developed by single seed descent from the progeny of combination of a cross of *japonica* cultivar Asominori from Japan with *indica* cultivar IR24 developed by IRRRI. In past, one hundred sixty-five F₆ lines were obtained from 227 original F₂ individual plants. From these, 71 lines were randomly selected and used for mapping. The Restriction Fragment Length Polymorphism (RFLP) map covering 1275 cM in entire rice chromosomes was constructed with 375 markers from the F₆ and F₇ generations (Tsunematsu *et al.*, 1996). In the study, we used a subset of 289 RFLP markers without overlapping for all loci from the original genetic map (Tsunematsu *et al.*, 1996) to detect QTLs for morphological traits in rice, for which the average interval distance between pair of markers was 4.4 cM.

Field Experiments and Phenotypic Measures

The germinated seeds of RI lines, along with its parents, Asominori and IR24 were sown on 15, May, 2002 (Miyazaki, Japan) and 10, December, 2006 (Hainan, China), respectively. After 30 days (2002, Japan), 25 days (2006, China), all seedlings were transplanted to Experiment Farm of both Miyazaki University (Miyazaki, Japan) and Zhejiang Academy of Agricultural Sciences (Hainan, China) with single seedling per hill spaced at 10 by 15 cm, respectively. Each plot included 3-4 lines with 6 plants per line in both Japan and China. The other managements followed the local conventional methods. All experiments were conducted in randomized complete design with two replicates (Japan) and one replicate (China).

Five morphological traits (FLL, FLW, SLL, SLW and PH) were measured on the highest stem of each RI line. Then, two derived traits (FLA and SLA) were calculated according to the suggestions of Dong *et al.* (1996). Average values for each line were used for QTL analyses.

QTL Detection

We adopted Composite Interval Mapping (CIM) analysis (Zeng, 1994) performed by QTL Cartographer computer program software (Wang *et al.*, 2005) version 2.5 to identify significant marker locus-trait association. LOD of 2.6 was used for claiming the presence of putative QTLs in the current study. The additive effect and percentage of variation explained by an individual QTL were also estimated. The QTLs were named according to the suggestions of Couch *et al.* (1997).

RESULTS

Phenotypic Variation of RI Population and the Parents

In the RI population, continuous phenotypic variations and transgressive segregation for all seven traits studied were observed (Table 1). Both skewness and kurtosis for all traits were less than 1.0 and the values of median and mean were approximately equal for each trait, showing the segregations of all the traits fit approximately normal distributions in the RI population. Those results indicated that the seven morphological traits were quantitatively inherited and suitable for QTL analysis.

Table 1: Measurements and distribution analyses of seven morphological traits in RI population and the parents in Japan and China

RI population							
Trait ¹	Median	Mean	Skewness	Kurtosis	Range	Asominori	IR24
FLL	30.9/25.0 ²	30.8/25.6	0.47/0.29	0.00/-0.61	(18.5-47.5)/(18.7-35.3)	26.5/31.4	30.8/35.8
FLW	1.5/1.5	1.5/1.5	0.42/0.48	0.39/0.06	(1.1-2.1)/(1.1-2.1)	1.3/1.3	1.6/1.7
FLA	33.3/28.6	34.1/29.4	0.84/0.72	0.99/-0.19	(16.5-64.5)/(16.2-46.3)	25.4/31.4	37.9/45.6
SLW	1.2/1.3	1.2/1.3	0.22/0.07	1.565217	(1.0-1.5)/(1.0-1.6)	1.1/1.1	1.3/1.4
SLA	40.6/33.2	40.7/34.1	0.44/0.70	0.35/0.01	(22.6-64.1)/(21.1-55.1)	39.4/32.1	42.9/49.9
PH	96.0/78.0	97.7/75.6	0.26/0.13	0.919192	(75.0-131.0)/(51.7-103.3)	86.3/77.0	93.3/74.3

¹: FLL, FLW and FLA indicate flag-leaf length, width and its area, respectively; SLL, SLW and SLA indicate the second leaf length, width and its area, respectively; PH indicates the plant height; ²: The data on the left and right-side of slash in each cell were the results obtained in Japan (2002) and China (2006), respectively. All the data were measured in centimeter except SLA and FLA in square centimeter

Table 2: Correlation coefficients of seven morphological traits of RI population in Japan and China

Locations	Japan (2002)							China (2006)						
	FLL	FLW	FLA	SLL	SLW	SLA	PH	FLL	FLW	FLA	SLL	SLW	SLA	
Japan	FLW	0.48**												
	FLA	0.92**	0.78**											
	SLL	0.75**	0.50**	0.76**										
	SLW	0.32*	0.83**	0.58**	0.27*									
	SLA	0.71**	0.81**	0.87**	0.85**	0.74**								
	PH	0.39**	0.21	0.39**	0.56**	0.10	0.54**							
China	FLL	0.64**	0.42**	0.64**	0.70**	0.31*	0.67**	0.54**						
	FLW	0.45**	0.81**	0.67**	0.37**	0.75**	0.67**	0.20	0.38**					
	FLA	0.66**	0.74**	0.80**	0.64**	0.63**	0.80**	0.46**	0.84**	0.82**				
	SLL	0.53**	0.45**	0.60**	0.72**	0.26*	0.65**	0.68**	0.80**	0.47**	0.77**			
	SLW	0.30*	0.67**	0.49**	0.18	0.66**	0.48**	0.06	0.20	0.86**	0.63**	0.24		
	SLA	0.55**	0.70**	0.71**	0.62**	0.55**	0.74**	0.53**	0.70**	0.80**	0.91**	0.86**	0.70**	
	PH	0.40**	0.28*	0.44**	0.62**	0.17	0.53**	0.88**	0.67**	0.33**	0.61**	0.83**	0.15	0.69**

* and ** represent significant at $p = 0.05$, $p = 0.01$ level, respectively, Trait abbreviations are as shown in Table 1

Correlations of Morphological Traits

Table 2 showed the correlations of the morphological traits in the two countries. In Japan (2002), in the case of leaf morphological traits, all leaf traits contributed positively to each other. For flag leaf, FLL had the largest correlation with FLA ($r = 0.92$, $p < 0.01$) and FLW correlated the most positively with SLW ($r = 0.83$, $p < 0.01$); for the second leaf, there was a strongly positive correlation between SLL and SLA ($r = 0.85$, $p < 0.01$). In China (2006), we found the similar results to those in Japan (2002). As for Plant Height (PH), in Japan, there were strong correlations each other except both FLW and SLW, which were similar to the results in China. Furthermore, significantly positive relationships ($r > 0.75$, $p < 0.01$) for pair traits between flag leaf and the second leaf were observed regardless of Japan and China, showing the high consistency of flag-leaf morphology with the second leaf. Moreover, it is not hard to find that all seven traits in Japan (2002) had significantly positive correlations ($r > 0.64$, $p < 0.01$) to its respective traits in China (2006). In detail, the maximal correlation coefficient was PH, up to 0.88, while the minimal one was down to 0.64 for FLL. The other coefficients for FLW, SLL, FLA, SLA and SLW are 0.81, 0.72, 0.80, 0.74 and 0.66, respectively. From these results mentioned above, overall the morphological characteristics of rice plants for the RI population were similar in the two Asian countries.

Mapping QTLs for Seven Morphological Traits

Fourteen QTLs for FLL, FLW and FLA, representing flag-leaf morphological characteristics, were identified (Table 3, Fig. 1). Among them, only QTL ($qFLA-5$) for FLA with the largest effect (LOD = 3.2) was commonly detected in both countries, which was located near XNpb81 on chromosomes 5 and explained 11.10% in Japan and 12.28% in China of phenotypic variation, respectively. However, the other 13 QTLs were distributed on chromosome 1(6QTLs), 2(1QTL),

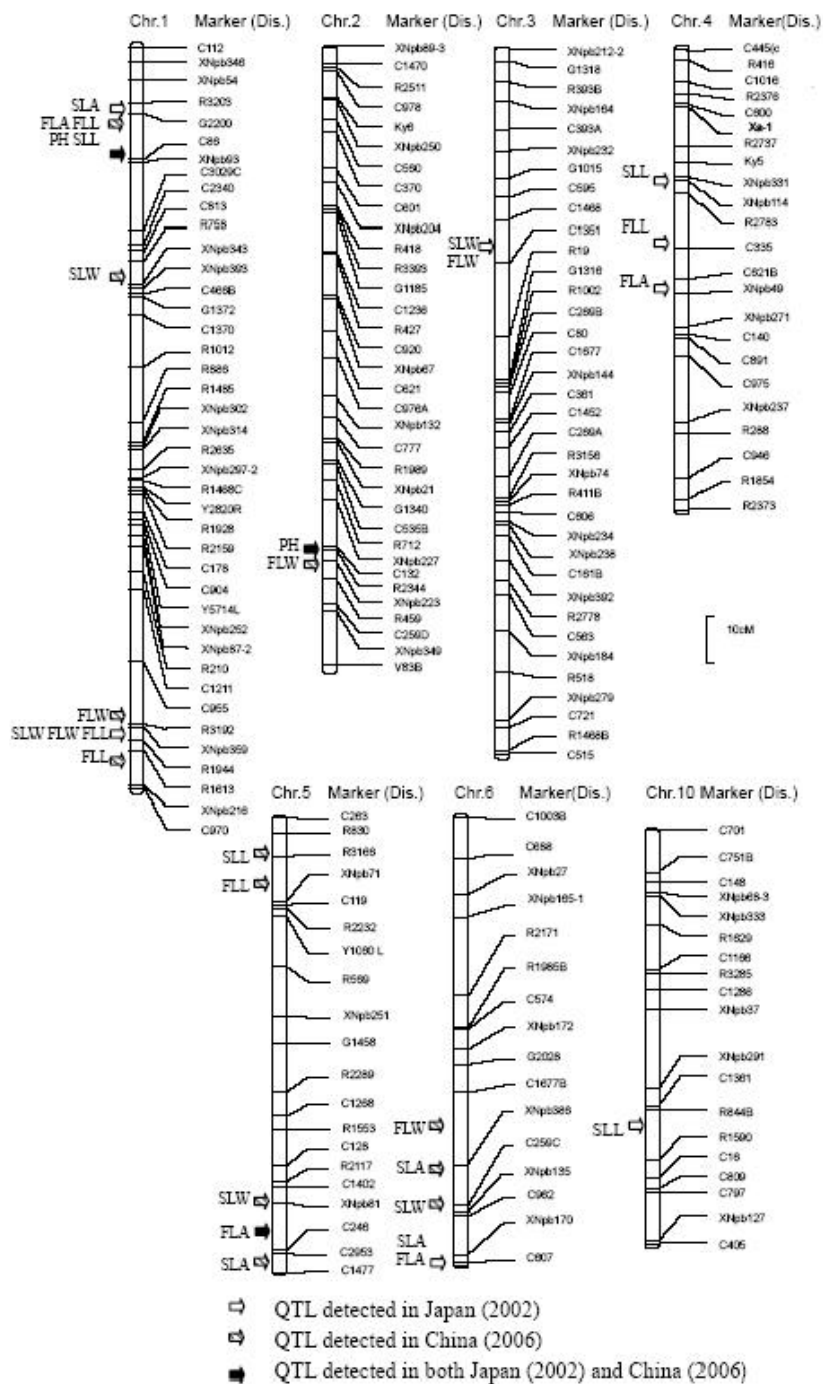


Fig. 1: Chromosomal locations of QTLs for seven morphological traits in RI population derived from a cross of Asominori/IR24. Arrowheads indicate the location of peak LOD. Trait abbreviations are as shown in Table 1

Table 3: QTLs associated with seven morphological traits using composite interval mapping (CIM) in RI population derived from Asominori/IR24

Trait	Japan (2002)						China (2006)					
	Chr	QTL ¹	Interval ²	LOD	Add ³	Var% ⁴	Chr	QTL ¹	Interval ²	LOD	Add ³	Var% ⁴
FLL	1	<i>qFLL-1a</i>	<i>XNpb359-R1944</i>	3.4	2.61	13.22	1	<i>qFLL-1b</i>	<i>G2200-C86</i>	6.9	2.14	26.46
	4	<i>qFLL-4</i>	<i>C335-C621B</i>	2.9	2.30	11.34	1	<i>qFLL-1c</i>	<i>R1613-XNpb216</i>	4.3	-1.74	14.45
FLW	1	<i>qFLW-1a</i>	<i>XNpb359-R1944</i>	3.2	-0.07	10.88	1	<i>qFLL-5</i>	<i>R3166-XNpb71</i>	6.2	2.14	22.64
	3	<i>qFLW-3</i>	<i>C1468-C1351</i>	3.3	-0.07	11.62	2	<i>qFLW-1b</i>	<i>R3192-XNpb359</i>	3.4	-0.08	11.09
SLL	1	<i>qSLL-1</i>	<i>G2200-C86</i>	9.3	4.17	33.87	1	<i>qSLL-1</i>	<i>G2200-C86</i>	6.0	3.15	30.26
	4	<i>qSLL-4</i>	<i>XNpb114-R2783</i>	5.1	2.84	15.99	5	<i>qSLL-5</i>	<i>R830-R3166</i>	3.1	1.94	10.25
SLW	10	<i>qSLL-10</i>	<i>R844B-R1590</i>	5.1	-3.01	18.53	6	<i>qFLW-2</i>	<i>XNpb223-R459</i>	5.0	-0.09	17.05
	1	<i>qSLW-1a</i>	<i>R3192-XNpb359</i>	3.8	-0.06	16.13	6	<i>qFLW-6</i>	<i>C1677B-XNpb386</i>	4.6	-0.10	18.41
FLA	3	<i>qSLW-3</i>	<i>C1468-C1351</i>	2.9	-0.05	12.77	5	<i>qSLW-5</i>	<i>C1402-XNpb81</i>	6.3	-0.07	23.30
	4	<i>qFLA-4</i>	<i>XNpb49-XNpb271</i>	3.0	3.46	10.30	6	<i>qSLW-6</i>	<i>XNpb386-C259C</i>	4.8	-0.06	16.07
SLA	5	<i>qFLA-5</i>	<i>XNpb81-C246</i>	3.2	-3.68	11.10	5	<i>qFLA-5</i>	<i>XNpb81-C246</i>	3.2	-2.70	12.28
	6	<i>qFLA-6</i>	<i>XNpb170-C607</i>	3.0	-3.52	10.46	1	<i>qFLA-1</i>	<i>G2200-C86</i>	12.5	9.81	48.46
PH	1	<i>qSLA-1</i>	<i>G2200-C86</i>	4.1	3.54	14.92	5	<i>qSLA-5</i>	<i>XNpb81-C246</i>	4.5	-3.06	17.57
	6	<i>qSLA-6a</i>	<i>XNpb170-C607</i>	2.6	-2.79	9.69	6	<i>qSLA-6b</i>	<i>XNpb386-C259C</i>	2.7	-2.42	8.71
PH	1	<i>qPH-1</i>	<i>G2200-C86</i>	13.3	10.44	49.25	1	<i>qPH-1</i>	<i>G2200-C86</i>	12.5	9.81	48.46
	2	<i>qPH-2</i>	<i>C132-R2344</i>	4.1	4.65	9.58	2	<i>qPH-2</i>	<i>C132-R2344</i>	2.9	3.34	5.91

¹: FLL, FLW and FLA indicate flag-leaf length, width and its area, respectively; SLL,SLW and SLA indicate the second leaf length, width and its area, respectively; PH indicates the plant height; ²: The data on the left and right-side of slash in each cell were the results obtained in Japan (2002) and China (2006), respectively. All the data were measured in centimeter except SLA and FLA in square centimeter. ³QTLs in bold format means the QTLs were commonly detected in Japan (2002) and China (2006). ⁴: Intervals markers in italic letters indicate the nearest marker linked to putative QTLs. ⁵: The positive values of additive effects indicate the alleles from Asominori with increasing effects. ⁶: Phenotype variation explained by detected QTLs

3(1QTL), 4(2QTLs), 5(1QTL) and 6(2QTLs), respectively. In detail, for FLL, five QTLs (*qFLL-1a* and *qFLL-4* in Japan; *qFLL-1b*, *qFLL-1c* and *qFLL-5* in China) were detected with 11.34-26.46% of total phenotypic variation explained by individual QTL. For FLW, also five QTLs were detected and tentatively designated as *qFLW-1a* and *qFLW-3* in Japan and *qFLW-1b*, *qFLW-2* and *qFLW-6* in China, which explained 10.88-18.41% of total phenotypic variation. As for FLA, with the exception of the common QTL (*qFLA-5*), both *qFLA-4* and *qFLA-6* were found only in Japan, while *qFLA-1* only in China, which accounted for 10.30-12.14% of total phenotypic variation. More interestingly, the genomic regions of *qFLL-1a*, located near *XNpb359* and *qFLL-1b*, located near *G2200* on chromosome 1, corresponded to *qFLW-1a* and *qFLA-1*, respectively. In addition, the Asominori alleles at *qFLL-1b*, *qFLL-4*, *qFLL-5*, *qFLA-1* and *qFLA-4* increased the value of its respective traits, whereas the remaining nine QTLs decreased their values.

In the QTL mapping study (Table 3, Fig. 1) for SLL, SLW and SLA, representing the morphological characteristics of the second leaf in rice, thirteen QTLs were detected on chromosome 1 (4QTLs), 3 (1QTL), 4 (1QTL), 5 (3QTLs), 6(3QTLs) and 10(1QTL), respectively. Among them, the one common QTL for SLL was found across two different environments, tentatively named *qSLL-1*, located in interval markers between *G2200* and *C86* on chromosome 1, which could explain the highest variation for SLL (33.87% for Japan and 30.26% for China). For SLL, except for *qSLL-1* mentioned above, other 3QTLs (*qSLL-4*, *qSLL-5*, *qSLL-10*) were detected in a country, which explained 10.25-18.53% of total variations. For SLW, five QTLs (*qSLW-1a*, *qSLW-3*, *qSLW-1b*, *qSLW-5* and *qSLW-6*) with all positive effects from IR24 were identified. Individually, the largest effect QTL, *qSLW-5*, was located between *C1402* and *XNpb81*, which accounted for 23.30% of total variation. Additionally, four QTLs for SLA (*qSLA-1* and *qSLA-6a* for Japan, *qSLA-5* and *qSLA-6b* for China) with 8.71-17.57% of total variation explained by individual QTL were detected on chromosome 1, 5, 6 (2QTLs), respectively. Furthermore, Asominori alleles at *qSLL-1*, *qSLL-4*, *qSLL-5* and *qSLA-1* increased the value of its respective traits, whereas the remaining nine QTLs from Asominori decreased the values.

In the QTL mapping (Table 3, Fig. 1) of plant height (PH), two QTLs (tentatively designated as *qPH-1* and *qPH-2*) were detected, which were stably expressed QTLs across the two countries. Individually, *qPH-1* with the largest effect (LOD>12.5) was detected between the interval markers of G2200 and C86 on chromosome 1, which explained 49.25% for Japan and 48.46% for China of the total phenotypic variation, respectively. The other *qPH-2* was located between C312 and R2344, which accounted for 9.58% for Japan and 5.91% for China of the total phenotypic variation, respectively. In addition, both of the two alleles from Asominori increased the PH.

DISCUSSION

The comparative research of QTLs mapping for seven morphological traits, viz., flag leaf length (FLL), width (FLW) and area (FLA), the Second Leaf Length (SLL), width (SLW) and area (SLA), plant height (PH), representing plant morphological characteristics in rice under in two Asian countries (China and Japan) were conducted in the present study using RI lines derived from a cross of *japonica* Asominori and *indica* IR24 with 289 RFLP markers. Resultantly, among total 29 QTLs detected for the seven morphological traits, only four common QTLs (*qPH-1*, *qPH-2*, *qSLL-1* and *qFLA-5*) were effectively found under different growth environments (Japan and China). It is deduced that only few QTLs could be stably expressed without the influence of environmental factors and most of QTLs were sensitive to environments.

The discovery of genetic linkage and the same genomic locations for QTLs/gene can explain the inter-relationships among traits studied. In the present study, a total of 29 QTLs detected were distributed on chromosome 1 (11QTLs), 2(2QTLs), 3 (2QTLs),4(3QTLs), (5QTLs), 6 (5QTLs) and 10 (1QTL), respectively, moreover, most of them were located on those genomic regions linked to G2200 (5QTLs) and XNpb359 (5QTLs) on chromosome 1, C132 on chromosome 2 (2QTLs), C335 on chromosome 4 (3QTLs), XNpb81 on chromosome 5 (3QTLs) and XNpb135 on chromosome 6 (5QTLs), respectively (Table 3 and Fig. 1). More interestingly, it was found that *qFLA-1* and *qFLL-1a* (chromosome 1), *qSLW-1*, *qFLW-1b* and *qFLL-1b* (chromosome 1), *qSLW-3* and *qFLW-3* on chromosome 3, *qSLA-6* and *qFLA-6* on chromosome 6 shared the same genomic locations, respectively, showing they maybe have pleiotropy effects. Those results can explain the inter-relationships among morphological traits studied (Table 2).

In addition, IR24 is a semi-dwarf variety carrying a recessive *sd-1* gene on chromosome 1 (IRRI, 1975), which was reported to locate near C86 (Kinoshita *et al.*, 1995; Yoshimura *et al.*, 1997). Therefore, it can be concluded that the *qPH-1* in this study is the same location of *sd-1* gene. This is consistent with previous observations (Cho *et al.*, 1994; Huang *et al.*, 1996; Wu *et al.*, 1996; Hittalmani *et al.*, 2003). Interestingly, also we found that there were obviously different variations for PH in the same RI population in the two countries (Table 1) and plant heights, ranging from 75.0 to 131.0 cm, with the mean of 97.7 cm in Japan (2002) were much higher than those in China (2006), ranging from 51.7 to 103.3 cm, with the mean of 75.6 cm in China by about 20 cm (Table 1). From those results, it may be deduced that *qPH-1* and *qPH-2* in Japan are much easier to express their functions for PH than in China. This hypothesis partly might be supported by the results of QTL analysis (Table 3) that additive effects of *qPH-1*(10.44 cm) and *qPH-2* (4.65 cm) in Japan are stronger than in China (9.81 cm for *qPH-1* and 3.34 cm for *qPH-2*).

It was reported that the photosynthesis of carbohydrate produced by functional leaves, especially flag leaf and the second leaf, can supply 80% capacity in cereals (Yue *et al.*, 2006). Thus, improving the leaf area is one effective way to add photosynthesis of carbohydrate in rice. In view of higher correlations between leaf length and leaf area than leaf width and the high consistency of flag-leaf morphology with the second leaf (Table 2), it might be efficient to enlarge leaf area by improving the FLL to increase the production of photosynthesis of carbohydrate, which coincided with the previous results (Peng *et al.*, 2007).

One of the major objectives of QTL mapping is to identify QTLs for agriculturally important traits and then put the QTL into application in breed programs by MAS. Generally, the feasibility of using MAS in breeding programs is dependent on the reproducibility of marker-QTL associations across generations, population and environments (Dudley, 1993). Considering the geographic distinctiveness of the locations, the commonality of loci detected indicates the environment independent expression of the gene(s) in question (Hittalmani *et al.*, 2003). Thus, loci with less consistent expression can only be used for selection at specific locations, such as *qFLL-1b*, which only was detected in China, accounting for 26.46% of total variation for FLL. In contrast, QTL such as *qPH-1*, which consistently expressed its function over two counties, are preferred for molecular breeding.

From the results of the study, it is concluded that there exist high correlations among morphological traits studied in rice, QTLs associated with morphology of rice vary with growth environment. In addition, the tightly linked molecular markers that flank the QTLs detected in this study may be useful for the improvement of morphology of rice.

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