Myers, G.O., C.A. Fatokun, and N.D. Young. 1996. RFLP mapping of an aphid resistance gene in cowpea (Vigna unguiculata L. Walp). Euphytica 91:181–187.
Painter, R.H. 1951. Insect resistance in crop plants. Macmillan & Co., New York.
Rector, B.G., J.N. All, W.A. Parrott, and H.R. Boerma. 1998. Identification of molecular markers associated with quantitative trait loci for soybean resistance to corn earworm. Theor. Appl. Genet. 96:786–790.
Rowan, G.B., H.R. Boerma, J.N. All, and J. Todd. 1991. Soybean cultivar resistance to defoliating insects. Crop Sci. 31:678–682.
Rufener, G.K., S.K. St. Martin, R.L. Cooper, and R.B. Hammond. 1989. Genetics of antibiosis resistance to Mexican bean beetle in soybean. Crop Sci. 29:618–622.
SAS. 1988. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, NC.
Shoemaker, R.C. and J.E. Specht. 1995. Integration of the soybean molecular and classical genetic linkage maps. Crop Sci. 35:436–446.
Shoemaker, R.C., K. Polzin, J. Labate, J. Specht, E.C. Brummer, T. Olson, N. Young, V. Concibido , J. Wilcox, J.P. Tamulonis, G. Kochert, and H.R. Boerma. 1996. Genome duplication in soybean (*Glycine* subgenus *Soja*). Genetics 144:329–338.
Sisson, V.A., P.A. Miller, W.V. Campbell, and J.W. Van Duyn. 1976. Evidence of inheritance of resistance to the mexican bean beetle in soybeans. Crop Sci. 16:835–837.
Tamulonis, J.P., B.M. Luzzi, R.S. Hussey, W.A. Parrott, and H.R. Boerma. 1997a. RFLP mapping of resistance to southern root-knot nematode in soybean. Crop Sci. 37:1903–1909.
Tamulonis, J.P., B.M. Luzzi, R.S. Hussey, W.A. Parrott, and H.R. Boerma. 1997b. DNA markers associated with resistance to Javanese root-knot nematode in soybean. Crop Sci. 37:783–788.
USDA Germplasm Resources Information Network. 1997. Database Management Unit. National Germplasm Resources Laboratory. ARS Beltsville, MD. http://www.ars-grin.gov/.
Van Duyn, J.W., S.G. Turnipseed, and J.D. Maxwell. 1971. Resistance in soybean to the Mexican bean beetle. Crop Sci. 11:572–573.
Wiseman, B.R., F.M. Davis, and J.E. Campbell. 1980. Mechanical infestation device used in fall armyworm plant resistance programs. Fla. Entomol. 63:425–438.
Yencho, G.C., M.W. Bonierbale, W.M. Tingey, R.L. Plaisted, and S.D. Tanksley. 1996. Molecular markers locate genes for resistance to the Colorado potato beetle, *Leptinotarsa decemlineata*, in hybrid *Solanum tuberosum* × *S. berthaultii* potato progenies. Entomol. Exp. Appl. 81:141–154.
Young, N.D., and S.D. Tanksley. 1989. RFLP maps and the concept of graphical genotypes. Theor. Appl. Genet. 77:95–101.
Young, N.D., L. Kumar, D. Menancio-Hautea, D. Danesh, N.S. Talekar, S. Shanmugasundarum, and D.H. Kim. 1992. RFLP mapping of a major bruchid resistance gene in mungbean. Theor. Appl. Genet. 84:839–844.
Yu, Y.G., M.A. Saghai Maroof, G.R. Buss, P.J. Maughan, and S.A. Tolin. 1994. RFLP and microsatellite mapping of a gene for soybean mosaic-virus resistance. Phytopathology 84:60–64.
Yu, Y.G., G.R. Buss, and M.A. Saghai Maroof. 1996. Isolation of a superfamily of candidate disease-resistance genes in soybean based on a conserved nucleotide-binding site. Proc. Natl. Acad. Sci. (USA) 93:11751–11756.

Molecular Marker-Assisted Dissection of Genotype × Environment Interaction for Plant Type Traits in Rice (*Oryza sativa* L.)

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ABSTRACT

A doubled haploid (DH) population of 123 lines from IR64/Azucena was used to analyze the genotype × environment (GE) interaction for eight plant type traits in rice (*Oryza sativa* L.). The total genetic effects were partitioned into genetic main effects and GE interaction effects. These two kinds of predicted effects were used in mapping quantitative trait loci (QTLs). Four to nine QTLs affecting different plant type traits were detected. Results indicated that all common QTLs detected in both environments were controlled by genetic main effects and some also by GE interaction effects. Some genomic regions identified significant QTL in only one environment; some also showed genetic main effects. Those QTLs with genetic main effects could be used in marker-assisted selection across environments. For some other map regions, QTLs were controlled by only GE interaction effects without genetic main effects. Those QTLs could be included in marker-assisted selection only for specific environments. In most cases, the pairs of traits with a high genetic correlation shared more common QTL regions than those pairs of traits with a lower genetic correlation.

PLANT TYPE is one of the most important traits to rice breeders. The component traits contributed to plant type are plant height (culm length), tiller number, culm angle (tiller angle), leaf dimensions and angles, and panicle characteristics (Chang and Li, 1991). Since the end of the 1950s, high-yielding rice varieties of reduced plant height with high lodging resistance, favorable plant type, and high harvest index have been released in almost all rice growing countries (Ming, 1987). These semidwarf, high-yielding varieties with improved plant type have played a vital role in the food sufficiency for countries where rice is a staple food. The yield potential of semidwarf indica rice is about 10 Mg/ha (IRRI, 1995). The further increase in yield potential is limited for semidwarf rice varieties because of (i) limited sink size, (ii) high percentage of unproductive tillers, (iii) short grain-filling duration, (iv) early senescence, and (v) susceptibility to lodging (IRRI, 1995). In recent years, tropical japonica varieties have been used for breeding new plant type lines (IRRI, 1995). Some elite breeding lines of new plant type with short stature, sturdy stems, larger panicles, reduced tillering, and with erect dark green and thick leaves, have been developed (IRRI, 1995). Most plant type traits in rice are quantitatively inherited and their performances are greatly affected by the envi-

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Abbreviations: GE, genotype × environment interaction; QTLs, Quantitative trait loci; DH, double haploid; RFLP, restriction fragment length polymorphism; LOD, likelihood ratio; RAPD, random amplified polymorphic DNA; SD, standard deviation; cM, centimorgan; PH, plant height; PN, panicle number; MTN, maximum tiller number; PPT, percentage of productive tillers; TA, tiller angle; FLL, flag leaf length; FLW, flag leaf width; FLA, flag leaf angle.

ronment, which has made it difficult to improve plant type traits by traditional breeding techniques (Chang and Li, 1991; Ming, 1987). Because DNA markers are not subject to environmental effects, marker-assisted selection of QTLs for plant type traits might greatly facilitate the further improvement of varieties with ideal plant type. QTLs for some plant type traits such as plant height and tiller number have been reported before (Wu et al., 1996; Lin et al., 1996; Zhuang et al., 1997; Li et al., 1995; Yan et al., 1998a,b), but no studies focusing on mapping QTLs for rice plant type traits have been reported yet.

Quantitative geneticists have long recognized the importance of genotype × environment interactions and have documented numerous cases of such interactions (Falconer, 1960; Westcott, 1986). Identification of QTLs which show consistency in expression across environments, even in diverse environments, would be desirable for marker-assisted selection programs (Veldboom and Lee, 1996a). Significant QTL × environment interactions have been reported in a number of cases (Mo, 1996; Xu, 1997). A total of 29 putative QTLs affecting mass per fruit, soluble solid concentrations, and fruit pH in a tomato (*Lycopersicon esculentum* Mill.) population grown in three different environments was identified (Paterson et al., 1991). Only four QTLs were identified in all three locations, 10 QTLs in two locations and 15 in a single location. In maize (*Zea mays* L.), only about 50% of the QTLs for morphological and yield traits were detected in both stressed and non-stressed environments (Veldboom and Lee, 1996a,b). QTLs for maize gray leaf spot disease resistance were also found to be inconsistent among environments (Bubeck et al., 1993). Lu et al. (1996) detected 22 QTLs for six agronomic traits in a rice DH population grown at three locations. Only seven were significant in all three environments, seven were significant in two environments and eight were significant in only one environment. A total of 44 QTLs was detected for yield components and plant height in three trials including F_2 and F_3 generations in rice, but only 17 were detected in more than one trial (Zhuang et al., 1997). In soybean [*Glycine max* (L.) Merr.], QTLs for plant height and lodging were inconsistent across environments, but were consistent for maturity indicating that genotype × environment interaction was trait dependent (Lee et al., 1996). In contrast, QTLs were relatively consistent across diverse environments for morphology, yield, and quality traits in maize (Stuber et al., 1992; Schon et al., 1994; Lübberstedt et al., 1997a,b). However, for all these reports, the QTL × environment interaction was predicted by comparing the QTLs detected separately in different environments.

In the present study, we used an indirect approach to analyze QTL × environment interaction (Zhu, 1998; Yan et al., 1998b). Since the genetic experiment was conducted in two replications in two different environments, the total genetic effects were first partitioned into genetic main effects and genotype × environment (GE) interaction effects. Then, these two kinds of predicted genetic effects were used in mapping QTLs. QTLs of genetic main effects and GE interaction effects for eight plant type traits including plant height (PH), maximum tiller number (MTN), panicle number (PN), tiller angle (TA), percentage of productive tiller (PPT), flag leaf length (FLL), flag leaf width (FLW), and flag leaf angle (FLA) in a DH population of indica and tropical japonica rice evaluated in two different environments were detected. Because the tropical japonica rice variety Azucena possessed some elite plant type characters such as sturdy stems, reduced tillering ability, and high percentage of productive tillers, our QTL mapping results may provide useful information for improvement of plant type traits by marker-assisted selection.

MATERIALS AND METHODS

Materials

A population of 123 DH lines derived from a cross between the irrigated indica variety IR64 and the upland japonica variety Azucena (Guiderdoni et al., 1992) was used in the experiment. Six restriction enzymes (*Dra*I, *Eco*RV, *Hin*dIII, *Sca*I, *Xba*I, *Eco*RI) were used for parental polymorphism survey. An RFLP map of the population was established by Huang et al. (1995) from the initial population of 135 DH lines with 135 RFLP markers coving the 12 chromosomes. This map was recently updated by adding 40 new isozyme and RAPD markers and presently contains 175 markers covering 2005 centimorgans (cM) with an average distance of 11.5 cM between pairs of markers (Huang et al., 1997). This new map was used for QTL analysis in the experiment.

Field Experiment

The 123 DH lines and their parents, IR64 and Azucena, were evaluated in the field in a randomized complete design with two replications in the spring of 1996 in Hainan and in the summer of 1996 in Hangzhou. Hainan Island is located in the Southern China Sea with the east longitude of 110.1° and north latitude of 18.5°. The average temperature of the year is 25.5°C and the average temperatures in January and July are 20.9°C and 28.4°C, respectively. It has 2239.8 hours of sunshine and 1254.7 mm of raining per year. Hangzhou is located in the east of China with the east longitude of 120.1° and the north latitude of 30.1°. The average temperature of the year is 16.2°C and the average temperatures in January and July are 3.6°C and 28.7°C, respectively. It has 2014 hours of sunshine and a total of 1398.7 mm of raining per year.

The warm temperature in Hainan Island is suitable for rice to grow in the winter. Therefore, Hainan Island was used as a natural "greenhouse" to increase the segregation process for rice breeders in China. After the harvest of rice in autumn in the mainland of China, the rice breeders go to Hainan Island to plant the breeding materials. They will harvest rice there at the end of April and return to plant and select the breeding materials in their original locations during the normal seasons. Therefore, most rice varieties developed in China were alternately selected on both Hainan Island and the original locations on the mainland. As a result, most of these rice varieties are well adapted to Hainan Island. Hangzhou is the major rice production area in China. Therefore, we choose these two locations to carry out the experiment to study the GE interaction for rice plant type traits.

The germinated seeds were sown in a seedling bed and seedlings were transferred to the paddy field about 30 d later, with a single plant per hill spaced at 15 by 20 cm. Each plot included three to four lines with eight plants per line. Fertility

Table 1. Phenotypic data for the eight plant type traits of the rice DH population evaluated in two environments.

		Parent		DH population			
Location	Trait†	Azucena	IR64	Maximum	Minimum	Mean	SD‡
Hangzhou	PH	146.6	88.1	159.0	72.0	113.5	22.5
	PN	5.9	11.1	17.3	5.1	8.9	2.4
	MTN	6.7	15.3	21.2	6.7	11.7	3.1
	PPT	88.1	71.7	95.5	50.5	76.6	9.8
	TA	20.0	25.0	51.0	3.0	19.5	13.1
	FLL	34.7	29.3	54.3	19.0	33.4	7.5
	FLW	1.6	1.4	2.2	0.9	1.5	0.3
	FLA	95.0	5.0	130.0	3.0	49.3	33.4
Hainan	PH	140.1	73.7	159.9	58.6	104.3	23.7
	PN	3.5	6.1	11.6	3.5	6.8	1.5
	MTN	5.5	13.0	18.2	5.5	11.2	2.6
	PPT	64.0	47.0	81.0	34.0	61.0	8.7
	TA	12.5	24.7	56.3	5.7	20.8	11.3
	FLL	25.9	17.1	37.8	13.4	22.8	5.1
	FLW	1.5	1.2	2.0	1.0	1.5	0.2
	FLA	70.3	11.3	93.7	4.5	40.8	23.5

† Plant type traits: PH, plant height; PN, panicle number, MTN, maximum tiller number; PPT, percentage of productive tillers; TA, tiller angle; FLL, flag leaf length; FLW, flag leaf width; FLA, flag leaf angle.
‡ SD, standard deviation.

and cultivation regimes were consistent with the optimum rice production for the two regions.

Ten days after transplanting, tiller numbers were measured every 10 d in five central plants from each plot until all lines had reached their maximum tiller number. The greatest number of tillers was treated as maximum tiller number (MTN). The tiller angle (TA, the angle between main stem and its tillers) and flag leaf angle (FLA, the angle between flag leaf and the stem) were measured at the maximum tiller stage and heading stage, respectively. The panicle number (PN, also referred as to productive tiller number) were counted at maturity, and the percentage of productive tillers (PPT) was calculated as the productive tiller number divided by the maximum tillers. Plant type traits such as plant height (PH, from soil surface to the tip of the highest spike excluding awn), flag leaf length (FLL), and flag leaf width (FLW) were also measured at maturity. For all these traits, the middle five plants of each plot were measured.

Statistical Analysis Methods

Since the genetic experiments were conducted for 123 genotypes with two blocks within two locations (as different environments), an indirect approach was conducted to analyze QTL × environment interaction (Zhu, 1998; Yan et al., 1998b). The phenotypic performance of the *j*th genetic entry in the *k*th block within *h*th environment can be expressed by,

$$y_{hjk} = \mu + E_h + G_j + GE_{hj} + e_{hjk}$$

where μ is the population mean, fixed; E_h is the effect of the *h*th environment, $E_h \sim (0, \sigma^2_E)$; G_j is the genetic main effect, $G_j \sim (0, \sigma^2_G)$; GE_{hj} is the genotype × environment interaction effect, $GE_{hj} \sim (0, \sigma^2_{GE})$; e_{hjk} is residual effect, $e_{hjk} \sim (0, \sigma^2_e)$.

The MINQUE (1) method (Zhu, 1992; Zhu and Weir, 1996), which is a MINQUE method (Rao, 1971) with all prior values setting 1, was used to estimate variance components for each trait and for covariance components between two traits. Genetic and interaction correlation coefficients were then estimated. The genetic main effects (G) and interaction effects (GE) were predicted by the Adjusted Unbiased Prediction (AUP) method (Zhu 1993, Zhu and Weir, 1996). The Jackknife method was applied for obtaining estimates or predictors and their standard errors in a *t*-test for parameters (Miller, 1974).

The composite interval mapping (CIM) method (Zeng, 1993, 1994) was applied for detecting QTLs for the predicted genetic main effects:

$$\hat{y}_{j(G)} = \beta_{0(G)} + \beta^*_{(G)} X^*_j + \sum_i \beta_{i(G)} X_{ij} + \varepsilon_{j(G)}$$

and also for the predicted GE interaction effects:

$$\hat{y}_{hj(GE)} = \beta_{0(GE_h)} + \beta^*_{(GE_h)} X^*_{hj} + \sum_i \beta_{i(GE_h)} X_{hij} + \varepsilon_{hj(GE)}$$

where β_0 is the population mean for *G* or *GE*, β^* is the QTL effect for *G* or *GE*; X^*_j is the coefficient for QTL effect; β_i is the effect for the *i*th marker for *G* or *GE*; X_{ij} is the coefficient for the *i*th marker effect of the *j*th individual; and ε_j is the residual error of the *j*th individual for *G* or *GE*.

QTL Cartographer v. 1.1b (Basten et al., 1996) was used to detect QTLs and to estimate genetic effects of significant QTLs. The likelihood ratio value of 11.5, which in equal to a LOD score of 2.5 (Zeng and Weir, 1996), was used as the threshold to declare the detection of a QTL.

RESULTS AND DISCUSSION

Transgressive Segregation of Plant Type Traits

Transgressive segregation is the term used to describe the phenomenon in which some individuals in a segregating population out perform the parents (Xu, 1997). Significant transgressive segregation was observed for all plant type traits examined in the current study (Table 1). For all these traits, four or more significant QTLs were detected with opposite genetic effects (Table 2) Results indicated that alleles with positive and negative effects (increasing or decreasing trait values) were dispersed between the two parents. The occurrence of the transgression could be directly attributed to the association of all alleles of similar (positive or negative) effects at the multiple QTLs in the same individual. For example, among the nine genomic regions significantly affecting PH, Azucena alleles increased PH at four (ph1, ph3-2, ph4, and ph9) and IR64 alleles increased it at other four regions (ph2-1, ph2-2, ph8, and ph10). The association of these alleles with similar effects in progenies will result in the transgressive segregation of PH in the DH

Table 2. Map regions and estimated genetic effects of QTLs for plant type traits† across environments.

Trait	QTL‡	Chrom	Peak interval	Distance	Hangzhou	Hainan	G	GE§ in Hangzhou	GE§ in Hainan
				cM					
PH	ph1	1	RZ730-RZ801	33.1	−17.44¶	−18.98	−17.25	−4.55	−6.74
	ph2-1	2	AmylA/C-RG95	12.8	6.96	6.56	6.62		
	ph2-2	2	RG256-RZ213	10				2.57	
	ph3-1	3	RG348-RZ329	13.2				2.49	−2.57
	ph3-2	3	RG910-RG418A	17.9	−7.22	−7.93	−7.24	−1.55	−2.76
	ph4	4	RG163-RZ590	2.7	−9.38		−6.19	−4.93	
	ph8	8	Amy3D/E-RZ66	25.1					2.29
	ph9	9	RZ422-Amy3ABC	11.2		−5.23			
	ph10	10	RZ625-CDO93	7.4				2.61	
PN	pn1	1	RZ730-RZ801	33.1	1.22		0.79	0.95	
	pn2-1	2	Pall-RZ58	29.3		0.47			
	pn2-2	2	CDO686-Amy1A/C	8.8	−0.72	−0.72	−0.44		
	pn2-3	2	RG654-RG256	5.1					−0.67
	pn3	3	RZ448-RZ519	15	1.05	0.84	0.55		
	pn4	4	RZ675-RG163	21.4		0.68			
MTN	mtn1	1	RZ730-RZ801	33.1	1.63		0.78	1.19	
	mtn2-1	2	RG544-RG171	5.3	1.05				
	mtn2-2	2	CDO686-Amy1A/C	8.8			−0.91		
	mtn3	3	RZ448-RZ519	15	0.95	1.38	1.27		0.66
	mtn4	4	RG143-RG620	5.9				0.65	
	mtn5	5	RZ67-RZ70	12.8		−1.04			−0.58
	mtn6	6	RG172-CDO544	11.8			0.55		
PPT	ppt1	1	RZ801-RG810	2.6	2.7		1.1		
	ppt5	5	RZ70-RZ225	19.7		3.3	1.4		3.2
	ppt7	7	RG511-RG477	18.4	−3.3			−3.0	
	ppt8	8	RZ66-AC5	11.8		−3.4			−2.9
	ppt12	12	RG958-RG181	9.8	−3.3		−1.8		
TA	ta5	5	RG13-CDO105	4.2	3.78		2.87	2.20	
	ta7	7	CDO497-CDO418	15.1	−4.01		−2.35	−3.19	
	ta8	8	RG978-RG1	15.5	−3.83	−3.39	−2.85	−2.66	
	ta9	9	RZ228-RZ12	4.9	9.24	7.34	7.02	4.79	2.98
FLL	fll1	1	RZ730-RZ801	33.1	−2.92	−2.59	−2.19		
	fll2	2	RZ213-RG520	13.1	2.23		1.12		
	fll3	3	RZ394-pRD10A	18.5					−1.27
	fll4	4	RG163-RZ590	28.2	−3.58		−1.93	−2.12	
	fll6	6	Amy2A-RG433	4.4				3.45	
	fll9	9	RZ422-Amy3ABC	11.2			−1.25	−2.14	
	fll10	10	RZ625-CDO93	7.4		1.34			
FLW	flw1	1	RG173-Amy1B	15				−0.80	
	flw2	2	RZ318-Pall	6.3		−0.65			−0.42
	flw3-1	3	RG348-RZ329	13.2		−0.63			−0.43
	flw3-2	3	CDO87-RG910	9.2		−0.71			−0.39
	flw4	4	RG163-RZ590	28.2	−1.84	−1.24	−1.41	−1.03	
	flw7	7	PGMS0.7-CDO59	31.4				0.61	−0.56
	flw12	12	CDO344-RG958	15.9	−0.73				
FLA	fla1	1	RG810-RG331	9.2	−13.78	−10.04	−11.15	−6.47	
	fla4	4	RZ565-RZ675	16.8		−10.24			−5.62
	fla6	6	RG648-RG424	11		−7.79	−5.61		
	fla9	9	RZ422-Amy3ABC	11.2	−12.81		−6.12	−7.70	
	fla11-1	11	CDO127-RZ638	6	−10.94		−5.24		
	fal11-2	11	RZ536-Npb186	4.5	10.19		4.91		

† Abbreviations for plant type traits are the same as in Table 1.
‡ The names of QTLs are based on the origins of chromosomes, for example, the QTL for plant height (PH) on chromosome 1 is named as ph1. ph2-1 and ph2-2 are the first and second QTL for plant height on chromosome 2, respectively.
§ G, genetic main effect. GE: genotype × environment interaction effect.
¶ Minus indicates the alleles from Azucena increase the phenotype of the trait.

lines. Similar results have been reported (Li et al., 1995; Xu, 1997).

QTL × Environment Interaction for Plant Type Traits

Significant GE interaction effects were observed for all eight traits of plant type investigated in the present study (Table 3). The percentage of the total genetic variance contributed by GE interaction effects ranged from 9% for PH to 70% for PPT. Therefore, besides phenotype data, the predicted genetic main effects and GE interaction effects were also used for QTL mapping. In most cases, the percentage of genetic main effect variance contributed to the total genetic variance corresponded well with the number and magnitude of common QTL regions in both environments (Tables 2 and 3). For example, about 90% of the total variance was contributed by genetic main effects for PH and three common QTLs with large magnitude were detected. But, only about 45 and 30% of the total variance was contributed by genetic main effects for PN and PPT, respectively. Only one or no common QTL was detected for these two traits in the two environments. Similarly, those traits that showed a high percentage of genetic main effects were associated with more QTLs or a larger magnitude of QTLs for genetic main effects (Tables 2 and 3).

Table 3. Estimated variances for the eight plant type traits† in two environments.

Component‡	PH	PN	MTN	PPT	TA	FLL	FLW	FLA
V_G	476.68**	1.71**	4.29**	30.48**	84.47**	17.54**	3.72**	374.29**
V_{GE}	47.17*	2.06**	3.49**	71.96**	61.60**	23.58**	2.76**	401.54**
V_e	22.25*	5.09**	7.80**	114.53**	3.98	1.06	0.14	54.36*
V_P	546.10	8.86	15.58	206.96	150.05	42.18	6.62	830.19

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Abbreviations for plant type traits are the same as in Table 1.
‡ V_G, V_{GE}, V_e, and V_P are genetic main effect, genotype × environment interaction effect, residual and phenotypic variances, respectively.

Common QTLs were found in 11 genomic regions for all plant type traits except PPT in both environments. They also showed significant QTLs for genetic main effects. Furthermore, seven of them showed GE interaction effects in at least one environment. The expression of gene or genes in those seven chromosomal regions was controlled by both genetic main effects and GE interaction effects. The other four genomic regions showed only significant QTLs for genetic main effects, which suggested that the gene expression was controlled by genetic main effects without significant interaction with the environment. Results indicated that common QTLs detected in different environments might also have significant GE interaction (Yan et al., 1998b).

We found some genomic regions, such as ph4 for PH, ta5 and ta7 for TA, that exhibited significant genetic main effects, but we only detected significant QTLs in one location. One possible explanation for this observation is that QTLs detected in one environment were biased because of the GE interaction. Therefore, sometimes, the QTL might be undetectable by phenotypic data in a single environment. Another explanation might be that the statistical method was not powerful enough to detect some minor QTLs. For many of these chromosomal regions, putative QTLs might be detected only if a lower threshold of LOD score was used. The third explanation might be due to the statistical artifact that may be caused by the indirect method used in the present study.

Although these QTLs were detected in only one environment, genetic main effects were still significant. Therefore, these QTLs could be used for marker-assisted selection across environment. But some QTLs such as ph9, pn2-1, and pn4 were only detected in one environment without significant genetic main effects, and others, for example, ph2-2, ph8, and pn2-3, were detected only with GE interaction effects. These results indicate that these QTLs are highly dependent on the environmental in which they were detected and should be considered for marker-assisted selection only for a specific environment. The traditional QTL mapping methods, such as interval mapping or composite interval mapping, can only compare the differences in QTLs detected in different environments. Our methods can provide more information about the nature of QTL × environment interaction, which could be useful for crop improvement by marker-assisted selection.

The phenotype of an individual is contributed not only by its genotype, but also by the interaction of the genotype with the environment. In recent years, QTL × environment interaction for different kinds of traits in various crops have been documented (Paterson et al., 1991; Bubeck et al., 1993; Veldboom and Lee, 1996a,b; Lu et al., 1996; Schon et al., 1994; Stuber et al., 1992; Lee et al., 1996; Zhuang et al., 1997). In these reports, QTL × environment interaction was inferred by comparing QTLs detected separately in different environments. It is argued that a QTL detected at a specific map region in one environment but not in another may indicate QTL × environment interaction. This is true only when GE interaction was not significant (Veldboom and Lee, 1996a,b; Jansen et al., 1995). If GE interaction is significant, QTLs detected in one environment could be biased. Furthermore, even in the absence of true QTL × environment interaction, a QTL can also be detected in one environment but not in another, because the chance of simultaneous detection in both environments is small (Jansen et al., 1995). On the other hand, common QTLs detected at different environments may not be conclusive in the absence of true QTL × environment interaction (Yan et al., 1998b). Therefore, it is impossible to exploit fully the GE interaction by comparing only QTLs detected in different environments. In the present study, DH lines were evaluated in two different environments with two replications in each. The total genetic effects were partitioned into genetic main effects and GE interaction effects. Therefore, the total QTL effect could also be partitioned into QTL main effect and QTL × environment interaction effect. The detection of significant QTLs for main effects indicates that the gene or genes at this genomic region are expressed in both environments and not subject to environment effects. The significant QTLs for interaction effects suggested that gene expressions at this region were environment dependent. Therefore, those QTLs with large genetic main effects will be more suitable for marker-assisted selection across environments.

Common QTLs for PH among Different Populations

In the present study, a total of nine genomic regions was detected to be associated with PH (Table 2). Among them, five QTLs were detected by phenotypic data in the two environments and three QTLs (ph1, ph2-1, and ph3-2) were common to both locations. Of these, two QTLs (ph1 and ph3-2) also showed significant genetic main effects and GE interaction effects. ph2-1 showed only significant genetic main effects and not GE interaction effects. ph4, detected only in Hangzhou by phenotypic data, showed genetic main effects as well as GE interaction effects in Hangzhou, but not in Hainan. ph9, which was detected only in Hangzhou, was not detected

Table 4. Comparing QTLs for plant height with other studies.

Present study			Common QTLs in other studies	
QTL†	Chrom	Linked marker	Populations	Reference
ph1	1	RZ730	CO39/Moroberekan; Palawan/IR64; Tesanai/C.B.	Zhuang et al., 1997; Huang et al., 1996
ph2-1	2	RG95	Waiyin/C.B.; Tesanai/C.B.	Huang et al., 1996
ph2-2	2	RZ213	Tesanai/C.B.; Lemont/Teqing	Li et al., 1995; Huang et al., 1996
ph3-1	3	RG348	CO39/Moroberekan; IR64/Azucena; Lemont/Teqing	Huang et al., 1996; Li et al., 1995
ph3-2	3	RG418A	IR64/Azucena	Huang et al., 1996
ph4	4	RZ590	Tesanai/C.B.; IR64/Azucena	Huang et al., 1996
ph8	8	RZ66	Zhaiyeqing 8/JingXi 17; Tesanai/C.B.	Lu et al., 1996; Huang et al., 1996
ph9	9	RZ422	IR64/Azucena	Huang et al., 1996
ph10	10	RZ625	CO39/Moroberekan	Huang et al., 1996

† The name of QTLs for plant height is the same as in Table 3.

by our method. Four QTLs (ph2, ph3-1, ph8, and ph10) were detected for GE interaction effects only, but not found with phenotypic data or genetic main effects. By comparing the QTLs for PH in the present study with those reported early, we found that significant QTLs for PH at all these nine genomic regions have been detected in other studies (Table 4) (Huang et al., 1996; Lu et al., 1996; Li et al., 1995; Zhuang et al., 1997). For example, ph1 which linked to RZ730 on chromosome 1, has been detected in at least three other populations including Co39/Moroberekan, Palawan/IR42 and Tesanai/C.B. (Huang et al., 1996; Zhuang et al., 1997). Similar result was also observed for panicle number. For example, common QTLs for pn1 and pn4 were also found in other populations (Wu et al., 1996; Lin et al., 1996).

Correlations between Plant Type Traits

The discovery of common chromosomal segments explains the genetic correlations obtained between traits. In the present study, it was found that the map region near RZ801 on chromosome 1 was associated with all of the investigated plant type traits except TA and FLW. In most cases, significant correlations were also observed between pairs of these traits. Results also showed that pairs of traits with a higher genetic correlation had more common QTL regions or QTLs with larger magnitude in common than those with a lower genetic correlation (Table 2; Table 5). Significant negative correlations were observed between PH and TN, as well as MTN. Five QTLs with opposite genetic effects were detected at similar chromosomal regions for both PH and PN. Three common QTLs with opposite genetic effects for PH and MTN were also found. Positive genetic main effect correlations among PH and FLL and FLA were also significant. There were three to four common QTLs for genetic main effects detected between these two pairs of traits. Genetic main effect correlations between PPT and MTN, FLL and TA, FLL and FLW, and FLL and FLA were all significant and common QTLs were detected. Significant correlations between TA and other traits were not observed, nor were common QTLs detected. It is interesting to note that some pairs of traits such as PH and FLL, PN and FLL, and PH and FLA showed significant correlations for genetic main effects but not GE interaction effects (Table 5). Although several common genomic regions affecting these pairs of traits were detected, no or only one QTL exhibited significant GE interaction effects in common. Results explain the genetic basis for the observation of significant correlations of genetic main effects and insignificant correlations for GE interaction effects among these pairs of traits.

The genetic correlations between pairs of traits could be contributed by either gene linkage or pleiotropy (Xu, 1997). In the current study, for most of the cases, the magnitude of genetic correlations corresponded well with the number of common QTL regions affecting both

Table 5. Correlations among plant type traits.

Trait	PH	PN	MTN	PPT	TA	FLL	FLW	FLA
PH	r_G‡	−0.64***	−0.52***	−0.18	−0.06	0.80***	0.29	0.77***
	r_{GE}	−0.28*	−0.10	−0.30	−0.06	0.30	0.37	−0.11
PN r_{G+GE}	−0.47***	r_G	0.95***	0.00	−0.01	−0.60***	−0.49***	−0.24***
r_P	−0.27***	r_{GE}	0.69	0.39*	0.18	−0.09	0.10	0.37
MTN r_{G+GE}	−0.39	0.81***	r_G	−0.34*	0.06	−0.45**	−0.43***	−0.02
r_P	−0.23***	0.81***	r_{GE}	−0.33	−0.03	0.08	−0.22	−0.02
PPT r_{G+GE}	−0.16	0.25	−0.31	r_G	−0.22	−0.29	0.17	−0.48
r_P	−0.11	0.33	−0.25	r_{GE}	0.35	−0.19	−0.48	0.40
TA r_{G+GE}	−0.06	0.08	0.02	0.12	r_G	−0.10	0.00	0.02
r_P	−0.05	0.03	0.01	0.04	r_{GE}	−0.13	−0.02	−0.06
FLL r_{G+GE}	0.57	−0.32	−0.18	−0.22	−0.11	r_G	0.36	0.72**
r_P	0.55*	−0.19*	−0.12	−0.13	−0.11	r_{GE}	0.49*	−0.02
FLW r_{G+GE}	0.28	−0.29***	−0.34	−0.22	−0.01	0.42***	r_G	0.21***
r_P	0.27	−0.30*	−0.24	−0.13	−0.01	0.42***	r_G	−0.05
FLA r_{G+GE}	0.49***	0.08	−0.02	0.10	−0.02	0.32***	0.09	
r_P	0.44***	0.07	−0.01	0.07	−0.03	0.30***	0.08	

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.
† Abbreviations for plant type traits are the same as in Table 1.
‡ The upper angle indicates genetic main effects (r_G) and GE interactions (r_{GE}) correlations and the low triangle indicates total genotype (r_{G+GE}) and phenotype (r_P) correlations, respectively.

traits; however, our genetic map only has 175 molecular markers, which is not dense enough to distinguish these two kinds of effects. But this information is still useful in marker-assisted selection for the improvement of plant type traits in rice. The genomic region near marker RZ801 on chromosome 1 detected common QTLs for PH, PN, MTN, PPT, and FFL and FLA, suggesting that this chromosome region plays an important role for the rice plant type traits. Therefore, by the selection of only one molecular marker, it is possible to improve several related traits simultaneously. It is possible to select individuals with shorter PH, higher PN and PPT, shorter FFL, and small FLA at the same time by the assisted selection of marker RZ801. This will make the molecular marker assisted selection for improvement of rice plant type traits more efficient.

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REFERENCES

Basten, C.J., B.S. Weir, and Z.-B. Zeng. 1996. QTL Cartographer. North Carolina State University.

Bubeck, D.M., M.M. Goodman, W.D. Beavis, and D. Grant. 1993. Quantitative trait loci controlling resistance to gray leaf spot in maize. Crop Sci. 33:838–847.

Chang, T.T., and C.C. Li. 1991. Genetics and breeding. p. 23–101. *In* B.S. Luh (ed) Rice production (vol. 1). Van Nostrand Reinhold, New York.

Falconer, R. 1960. Introduction to quantitative genetics. Ronald Press, New York.

Guiderdoni, E., E. Galinato, J. Luistro, and G. Vergara. 1992. Anther culture of tropical japonica/indica hybrids of rice (*Oryza sativa* L.). Euphytica 62:219–224.

Huang, N., B. Courtois, G.S. Khush, H.X. Lin, G.L. Wang, P. Wu, and K.L. Zheng. 1996. Association of quantitative trait loci for plant height with major dwarfing genes in rice. Heredity 77:130–137.

Huang, N., A. Parco, T. Mew, G. Magpantay, S. McCouch, E. Guiderdoni, J. Xu, P Subudhi, E.R. Angeles, and G.S. Khush. 1997. RFLP mapping of isozymes, RAPD and QTLs for grain shape, brown plant hopper resistance in a doubled haploid rice population. Mol. Breed. 3:105–113.

Huang, N., S.R. McCouch, T. Mew, A. Parco, and E. Guiderdoni. 1995. Development of an RFLP map from a doubled haploid population in rice. Rice Genetics Newslett. 11:134–137.

IRRI. 1995. Program report for 1994. International Rice Research Institute (IRRI), Los Baños, Philippines.

Jansen, R.C., J.W. Van Ooijen, P. Stam, C. Lister, and C. Dean. 1995. Genotype-by-environment interaction in genetic mapping of multiple quantitative trait loci. Theor. Appl. Genet. 91:33–37.

Lee, S.H., M.A. Bailey, M.A. Mian, T.E. Carter, Jr., D.A. Ashley, R.S. Hussy, W.A. Parrott, and H.R. Boerma. 1996. Molecular markers associated with soybean plant height, loging, and maturity across locations. Crop Sci. 36:728–735.

Li, Z.K., S.R.M. Pinson, J.W. Stansel, and W.D. Park. 1995. Identification of quantitative trait loci (QTLs) for heading date and plant height in cultivated rice (*Oryza sativa* L.). Theor Appl Gent 91: 374–381.

Lin, H.X., J.Y. Zhuang, H.R. Qian, J. Lu, S.K. Ming, Z.M. Xiong, N. Huang, and K.L. Zheng. 1996. Mapping QTL for plant height and its components by molecular markers in rice (*Oryza sativa* L.). Acta Agronomica Sinica 22:257–263 (in Chinese).

Lu, C., L. Shen, Z. Tan, Y. Xu, P. He, Y. Chen, and L. Zhu. 1996. Comparative mapping of QTLs for agronomy traits of rice across environments using a doubled haploid population. Theor. Appl. Genet. 93:1211–1217.

Lübberstedt, T., A.E. Melchinger, D. Klein, H. Zegenhardt and C. Paul. 1997a. QTL mapping in testcrosses of European flint lines of maize: I. Comparison of different testers for forage yield traits. Crop Sci. 37:921–931.

Lübberstedt, T., A.E. Melchinger, D. Klein, H. Zegenhardt and C. Paul. 1997b. QTL mapping in testcrosses of European flint lines of maize: II. Comparison of different testers for forage quality traits. Crop Sci. 37:1913–1922.

Miller, R.G. 1974. The jackknife — a review. Biometrika 61:1–15.

Ming, S.K. 1987. Breeding of semi-dwarf rice. p. 66–67. *In* S.R. Yuang (ed.) Rice. China Agriculture Press, Beijing (in Chinese).

Mo, H.D. 1996. Advances in quantitative genetics — QTL mapping and its application. Scientia Agricultura Sinica 29(2):8–16 (in Chinese).

Paterson, A.H., S. Damon, J.D. Hewitt, D. Zamir, H.D. Rabinowitch, S.E. Lincoln, E.S. Lander, and S.D. Tanksley. 1991. Mendelian factors underlying quantitative traits in tomato: Comparison across species, generations, and environments. Genetics 127:181–197.

Rao, C.R. 1971. Estimation of variance and covariance components MINQUE theory. J. Multivar Anal 1:257–275.

Schon, C.C., A.E. Melchinger, J. Boppenmaier, E., Brunklaus-Jung, R.G. Herrmann, and J.F. Seitzer. 1994. RFLP mapping in maize: Quantitative trait loci affecting testcross performance of elite European flint lines. Crop Sci. 34:378–389.

Stuber, C.W., S.E. Lincoln, D.W. Wolff, T. Helentjaris, and E.S. Lander. 1992. Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 132: 823–839.

Veldboom, L.R., and M. Lee. 1996a. Genetic mapping of quantitative trait loci in maize in stress and non-stress environments: I. Grain yield and yield components. Crop Sci. 36:1310–1319.

Veldboom, L.R., and M. Lee. 1996b. Genetic mapping of quantitative trait loci in maize in stress and non-stress environments: II. Plant height and flowering. Crop Sci. 36:1320–1327.

Westcott, B. 1986. Some methods of analyzing genotype-environment interaction. Heredity 56:243–253.

Wu, P., G. Zhang, and N. Huang. 1996. Identification of QTLs controlling quantitative characters in rice using RFLP markers. Euphytica 89:349–354.

Xu, Y.B. 1997. Quantitative trait loci: Separating, pyramiding, and cloning, Plant Breed Reviews 15:85–139.

Yan, J.Q., J. Zhu, C.X. He, M. Benmoussa, and P. Wu. 1998a. Quantitative trait loci analysis for developmental behavior of tiller number in rice (*Oryza sativa* L.). Theor. Appl. Genet. 97:267−274.

Yan J.Q., J. Zhu, C.X. He, M. Benmoussa, and P. Wu. 1998b. Molecular marker assisted dissection of developmental behavior of plant height in rice (*Oryza sativa* L.) Genetics 150:1257–1265.

Zeng, Z.B. 1993. Theoretical basis for separation of multiple linked gene effects in mapping quantitative trait loci. Proc. Natl. Acad. Sci. (USA) 90:10972–10976.

Zeng, Z.B. 1994. Precision mapping of quantitative trait loci. Genetics 136:1457–1468.

Zeng, Z.B., and B.S. Weir. 1996. Statistical methods for mapping quantitative trait loci. Acta Agronomica Sinica. 22:535–549.

Zhu, J. 1992. Mixed model approaches for estimating genetic variances and covariances. J. Biomath. 7:1–11.

Zhu, J. 1993. Methods of predicting genotype value and heterosis for offspring of hybrids. J. Biomath. 8:32–44.

Zhu, J. 1998. Mixed model approaches for mapping quantitative trait loci. Hereditas (Bejing) 20(Sup):137–138.

Zhu, J., and B.S. Weir. 1996. Diallel analysis for sex-linked and maternal effects. Theor. Appl. Genet. 92:1–9.

Zhuang, J.Y., H.X. Lin, J. Lu, H.R. Qian, S. Hittalmani, N. Huang, and K.L. Zheng. 1997. Analysis of QTL × environment interaction for yield components and plant height in rice. Theor. Appl. Genet. 95:799–808.