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Comparative mapping of QTLs for agronomic traits of rice across environments using a doubled haploid population

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Abstract We report here the RFLP mapping of quantitative triat loci (QTLs) that affect some important agronomic traits in cultivated rice. An anther culture-derived doubled haploid (DH) population was established from a cross between an *indica* and a *japonica* rice variety. On the basis of this population a molecular linkage map comprising 137 markers was constructed that covered the rice genome at intervals of 14.8cM on average. Interval mapping of the linkage map was used to locate QTLs for such important agronomic traits as heading date, plant height, number of spikelets per panicle, number of grains per panicle, 1000-grain weight and percentage of seed set. Evidence of genotype-by-environment interaction was found by comparing QTL maps of the same population grown in three diverse environments. A total of 22 QTLs for six agronomic traits were detected that were significant in at least one environment, but only 7 were significant in all three environments, 7 were significant in two environments and 8 could only be detected in a single environment. However, QTL-by-environment interaction was trait-dependent. QTLs for spikelets and grains per panicle were common across environments, while traits like heading date and plant height were more sensitive to environment.

Key words Doubled haploid population · Quantitative trait loci (QTLs) · Molecular map · Rice · G × E interaction

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Introduction

Quantitative genetic studies have been facilitated by the development of molecular markers (Paterson et al. 1988; Stuber 1992). High-density molecular linkage maps permit one to locate quantitative trait loci (QTLs) by linkage analysis using segregating populations (Paterson et al. 1988; Lander and Bostein 1989). Most of the mapping studies have used F_2 or backcross populations, and these studies are difficult to replicate to obtain accurate phenotypic values for precise QTL mapping. The use of recombinant inbred lines (RILs) provides many advantages in QTL studies, but it will take a long time to develop such populations (Burr et al. 1988). Recently, many studies have employed doubled haploid (DH) populations to construct genetic maps and locate QTLs (Heun 1992; Barua et al. 1993; Backers et al. 1995; Lefebvre et al. 1995; Toroser et al. 1995; Uzunova et al. 1995). In contrast to RILs, DH lines derived from anther culture can reach homozygosity through a single generation. Because the lines are genetically homozygous, they can be propagated without further segregation. This characteristic allows for the precise measurement of quantitative traits by repeated trails and for a reduction in the environmental component of the total phenotypic variance.

Many studies of QTL mapping have been conducted in a fixed environment to evaluate the phenotype. These studies have thus ignored the genotype-by-environment (G × E) interaction, which is an important component influencing quantitative traits. A few exceptions are the studies conducted by Paterson et al. (1988) and Stuber et al. (1992). Paterson et al. (1991) investigated the predictive value of QTLs across environments in tomato by comparing QTL maps of F_2 populations and their F_3 families, which were grown in different environments. Their results showed that only 4 out of 29 QTLs could be detected in all of the environments tested. Stuber et al. (1992) studied the genotype-by-environment interaction for QTLs of maize by field evaluation of back-

Table 1 Means (top row) and variation range (bottom row) of six quantitative traits measured in three locations

Location[a]	Heading date	Plant height (cm)	1000-grain weight (g)	Spikelets per panicle	Grains per panicle	Seed set percentage (%)
BJ	100.8	82.3	23.6	136.7	106.9	76.8
	66.6–131.6	48.6–112.0	16.0–31.7	34.2–269.2	15.0–252.8	8.9–95.5
HZ	79.7	84.2	24.4	108.7	67.5	60.8
	67.3–97.5	44.2–114.8	15.3–34.3	34.3–197.3	2.2–150.7	4.6–86.6
HN	89.4	72.5	23.5	114.2	72.6	63.4
	67.5–106.2	50.8–96.6	16.7–30.9	43.0–252.0	2.0–195.7	1.1–95.0

[a] BJ, Beijing; HZ, Hangzhou; HN, Hainan

cross families in six diverse environments, but limited *evidence of G × E interaction was found. However, the populations they used were* F_2 and F_3 or backcross families, so the comparison across environments might be confounded by different generations. In the investigation presented here, we have used a permanent DH population to investigate the G × E interaction at individual QTLs by comparing QTL maps generated in three diverse environments.

Rice is one of the most important crops in the world. High-density restriction fragment length polymorphism (RFLP) maps have been recently constructed (Causse et al. 1994; Kurata et al. 1994), and some quantitative traits have also been studied using molecular markers (Ahn et al. 1988; Wang et al. 1994 Xiao et al. 1994; Li et al. 1995a,b). In this paperr, we describe a study using a DH population and an RFLP map to localize QTLs for a number of agronomic characters and to explore the possible G × E interaction.

Materials and methods

Experimental population and phenotypic evaluation

One doubled haploid (DH) population of consisting of 132 DH lines was utilized in this study. This population was developed through anther culture of the F_1 between *indica* rice var. 'Zhai-Ye-Qing 8'(Z) and *japonica* var 'Jing-Xi 17'(J). The agronomic performance of the DH population was evaluated in field experiments at three locations: Beijing, which is located at 39° N (degree of northern latitude); Hangzhou, which is at 32° N and Hainan, which is at 18° N. The DH lines were grown in Beijing and Hangzhou from April to September of 1994, and on Hainan Island from December 1994 to April 1995. All of these locations had previously been used for rice field experiments many times and thus there was adequate insect, disease and weed control. In each of the three environments, the DH lines were planted orderly in doubled rows, with the parents being grown between every tenth DH line as the control. The days from sowing to heading (heading date), plant height, number of productive tillers, panicle length, number of spikelets per panicle, number of grains per panicle, seed set percentage and 1000-grain weight were determined based on the average values of 10 individual plants from each line. Except number of productive tillers and panicle length, all other six traits were significantly different between the parents, and the means and variation range in each of the three environments are listed in Table 1.

RFLP assays and map contruction

Genomic DNA was extracted from young leaves, then digested with restriction enzymes *Bam*HI, *Bgl*II, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Sca*I and *Xba*I and hybridized with RFLP markers as described by McCouch et al. (1988). DNA markers were kindly provided by Drs. S.D. Tanksley and S.R. McCouch from Cornell University and RGP from Japan. Segregation data on RFLP markers were obtained from 132 DH lines. Chi-square tests were performed to examine if the observed allelic and genotypic frequencies of the marker loci deviated from the expected ratio (1:1) so that the skewedness of the population could be determined. An RFLP linkage map was then constructed using the software MAPMAKER/EXP ver.3.0 (Lander et al. 1987; Lincoln et al. 1993a). The genetical distances were calculated using the Kosambi function. The LOD threshold was fixed at 3.0, and the error detection was used. The assignment of the genetic maps of Causse et al. (1994) and Kurata et al. (1994) were used in assigning linkage groups or markers to their corresponding chromosomes. On the basis of the molecular map established, the graphical genotypes of each line were established and the percentages of the parent genomes were estimated by the computer program HypeGene (Young and Tanksley 1989).

QTL identification

Interval QTL mapping was carried out using the software MAPMAKER/QTL ver. 1.1 (Paterson et al. 1988; Lincoln et al. 1993b) on the SUN SPARC-10 workstation. The unconstrained model was used. A LOD score threshold of 2.4 would be needed to test at the $P = 0.05$ level of significance for the entire rice genome (Lander and Bostein 1989). In this investigation, we used a more stringent threshold of 3.0 for declaring the presence of a QTL, and we considered LOD scores between 2.0 and 3.0 as "suggestive". LOD peaks for each significant QTL were used to position the QTL on the linkage map. In case more than one peak was found on the same chromosome for the same trait, multiple-QTL models were used to determine whether the chromosome possessed single or multiple QTLs. Gene effect (additive effect, free of dominance) and percentage of phenotypic variation attributable to individual QTL were estimated at the peaks.

Results

RFLP map

A genetic map was constructed based on segregating RFLP data in 132 DH lines. This map consists of 137 RFLP markers widely distributed over 12 chromosomes with an average distance of 14.8cM (Kosambi map units) between markers (Fig. 1). The linear order of the markers was found to be consistent with that of Causse et al. (1994) and Kurata et al. (1994) except for G39 and RZ337, which mapped to different chromosomes, and one inversion on chromosome 2 (RG654, RG322 and RG520). The genome coverage was es-

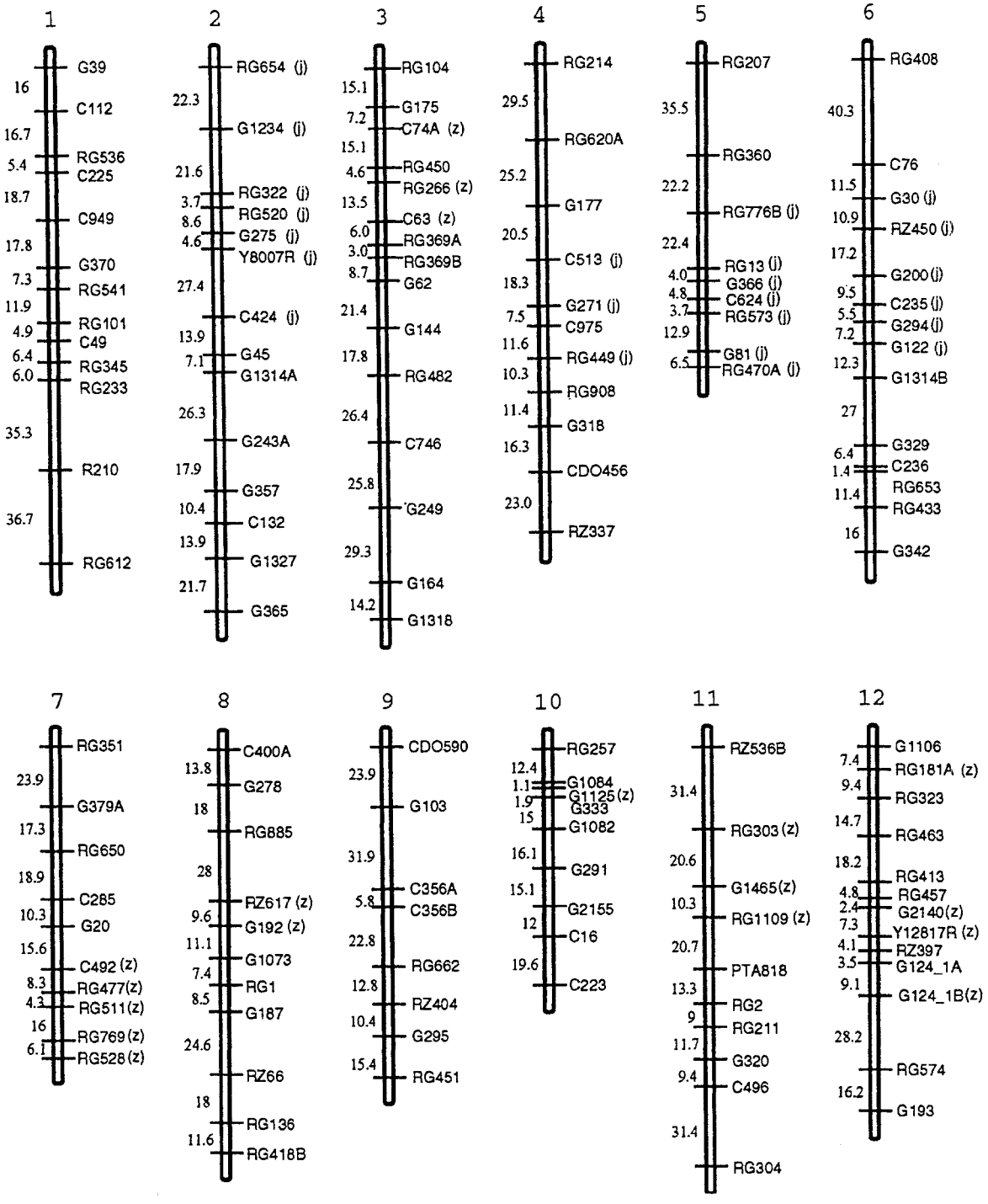

Fig. 1 A rice molecular linkage map with 137 RFLP markers constructed from 132 DH lines derived from the cross of 'Zhaiyeqing 8' × 'Jingxi 17'. Scale in Kosambi centiMorgans (cM) is shown on the *left* of each chromosome. The markers showing distorted segregation are marked with (*z*) or (*j*) indicating their favoring parent genotype *Z*/*Z* or *J*/*J*, respectively

timated to be approximately 95% on the basis of the two saturated maps mentioned above.

The overall proportion of *Z*/*Z* genotypes in the DH population was 49.6% as estimated by HyperGene (Young and Tanksley 1989). Out of 137 loci analyzed in the DH population 41(~31%) deviated significantly ($P \leqslant 0.05$) from the expected 1:1 monogenic ratio. Of these loci, 18 had an excess of *Z*/*Z* genotypes, and 23 had an excess of *J*/*J* genotypes. The chromosomal distribution of these distorted markers was not random. Most of them clustered at regions on chromosomes 2,3,4,5,6,7,11 and 12, and the markers showing distorted segregation in the same region had an excess of alleles from the same parent (Fig. 1).

Interval mapping of QTLs

Heading date

A total of 4 QTLs for heading date, *hd1*, *hd8*, *hd10a* and *hd10b*, were identified that were significant in at least one environment. The proportion of phenotypic variation explained by individual QTLs ranged from 9.3% to 35.4%. The QTL bordered by markers RG885 and RZ617 on chromosome 8, *hd8*, accounted for more than 30% of the phenotypic variation and had additive effects of 14 and 7 days in Beijing and Hangzhou, respectively (Table 2). But this QTL was not detected in Hainan. One QTL, *hd1*, could only be detected in Hainan. It had an additive effect of about 6 days, which promoted heading time earlier. Two QTLs, *hd10a* and *hd10b*, were identified on chromosome 10; *hd10a* could be detected in Beijing and Hangzhou, while *hd10b* was only significant in Hainan.

Plant height

A total of 5 QTLs for this trait, *ph3*, *ph4*, *ph7*, *ph8*, and *ph10*, were found to be significant in at least one environment (Table 2). They individually explained about 9.3–24.1% of the total phenotypic variation. The QTL on chromosome 8, *ph8*, which was significant in both

Table 2 Biometrical parameters of individual QTLs[a] for six agronomic traits in a three-environment trial of Z/J DH population

Trait	Locus	Marker internal	Trail[b]	LOD score	% Variation	Additive
Heading date	*hd-1*	C949-G370	HN	3.08	14.1	−5.87
	hd-8	RG885-RZ617	BJ	7.55	35.4	14.11
			HZ	5.98	33.0	7.75
	hd-10a	C16-C223	BJ	2.45	9.3	7.16
		G2155-C16	HZ	3.96	18.3	5.71
	hd-10b	RG257-G1084	HN	5.65	22.4	7.45
Plant height	*ph-3*	G62-G144	HN	3.62	19.0	−8.74
	ph-4	C513-G271	HN	3.61	16.2	8.37
		G177-C513	HZ	3.25	16.8	10.51
	ph-7	C285-G20	BJ	2.43	9.3	−7.93
		RG650-C285	HZ	2.52	12.7	−9.08
	ph-8	RG885-RZ617	BJ	4.23	24.1	13.08
		G1073-RG1	HZ	2.54	11.1	8.56
	ph-10	G1082-G291	HN	3.79	16.9	8.24
1000-grain weight	*gw-1*	C949-G370	BJ	3.49	13.2	2.06
			HN	2.88	19.0	0.50
			HZ	3.80	18.2	2.46
	gw-2	G1314A-G243A	BJ	4.17	18.6	2.46
			HN	3.38	16.4	0.47
			HZ	2.35	12.1	2.03
	gw-3	G164-G1318	HN	3.58	15.8	0.46
	gw-5	RG776B-RG13	BJ	2.88	13.3	−2.12
	gw-6	C235-G294	BJ	2.37	8.3	1.69
			HN	3.02	11.5	0.40
	gw-8	RG885-RZ617	BJ	3.08	16.1	2.32
		RZ617-G192	HZ	3.07	12.3	2.11
Spikelets per panicle	*spn-4*	RG214-RG620	BJ	4.12	19.4	40.61
		RG620A-G177	HN	4.46	18.8	30.94
			HZ	5.12	24.5	38.57
	spn-6	G122-G1314B	BJ	4.14	13.4	−34.93
			HN	2.81	13.8	−26.86
			HZ	5.83	25.1	−39.92
Grains per panicle	*gn-4*	RG214-RG620	BJ	2.63	12.9	35.86
		C513-G271	HN	6.53	26.5	39.29
		G177-C513	HZ	5.69	28.0	31.64
	gn-6	G294-G122	BJ	3.61	13.0	−37.63
		G122-G1314B	HN	4.56	19.4	−33.06
		G1314B-G329	HZ	4.53	25.9	−30.37
Seed set percentage	*ssp-4*	G271-C975	BJ	2.58	9.8	11.99
		RG449-RG908	HN	5.08	22.7	23.58
		C513-G271	HZ	3.32	17.4	13.44
	ssp-5	G366-C624	HN	3.84	13.9	19.35
	ssp-7	RG650-C285	HN	3.08	13.2	17.62

[a] QTLs are named by trait abbreviations and chromosome number. In case more than one QTL affecting a trait was identified along the same chromosome, they are distinguished by letters indicating the temporal order in which the QTLs were identified (e.g. *hd-10a*, *hd-10b*)

[b] The environments in which a QTL was detected are indicated (BJ, Beijing in 1994; HN, Hainan in 1995; HZ, Hangzhou in 1994)

Table 3 Number of QTLs detected for six traits in three environments

Number of locations		Number of QTLs for traits						
		Heading date	Plant height	1000 grain weight	Spikelets per panicle	Grains per panicle	Seed set percentage	Total
One		2	2	2			2	8
Two	BJ, HZ	2	2	1				5
	BJ, HN			1				1
	HN, HZ		1					1
Three				2	2	2	1	7
Total		4	5	6	2	2	3	22

Beijing and Hangzhou, was at the same position as the QTL *hd8a* for heading date. Another QTL on chromosome 10, *ph10*, was located very near the position of *hd10a*. In addition, there was notable correspondence in both the directions and magnitudes of the additive effects between these QTLs for the two traits. An increased plant height of 1 cm from either *ph8* in Beijing and Hangzhou and *ph10* in Hainan was associated with about 1-day-later heading in the three respective locations. This finding is in agreement with the fact that the two traits are simply correlated ($r = 0.4168$).

1000-Grain weight

A total of 6 QTLs for this trait were identified as being significant in at least one environment (Tabel 2). Two QTLs, *gw1* and *gw2*, were significant in all three environments. Two other QTLs, *gw6* and *gw8* were significant in two environments. All of these QTLs had an additive effect for increased grain weight. With respect to the other 2 QTLs, *gw3* could only be detected in Hainan, while *gw-5* could only be detected in Beijing.

Spikelets per panicle and grains per panicle

These two traits are closely correlated ($r = 0.8529$) and just as expected, 2 QTLs each were detected for both traits, and the QTLs for the two traits located on the same chromosomal regions (Table 2). The loci *spn-4* and *gn-4* increased number of spikelets and grains per panicle while *spn-6* and *gn-6* had negative additive effects for spikelets and grains per panicle. All 4 QTLs could be detected in three environments.

Seed set percentage

Three QTLs were found for seed set percentage (Table 2). The QTL *ssp-4* was mapped to almost the same region on chromosome 4 in three environments. Two other QTLs, *ssp-5* and *ssp-7*, could only be detected in Hainan. All of the QTLs had a positive additive effect for increasing seed set percentage.

Evidence of genotype-by-environment interaction

A DH population is a kind of permanently segregating population. Its genetic structure is fixed, so it can be grown at different times and locations for detecting QTLs and evaluating the interactions between genotypes and environments, i.e. the phenotypic expression level of QTLs in different environments. In this study, we have identified 22 QTLs for six agronomic traits of rice in three different locations (environments), but only 7 of these were significant in all three of the environments tested, 7 QTLs were significant in two environments, and 8 QTLs could be detected only in a single environment (Table 3). Among the 7 QTLs found to be significant in all three environments, 2 were for grain weight, 2 for spikelets per panicle, 2 for grains per panicle and 1 for seed set percentage. No QTL significant in all environments was mapped for heading date and plant height. This result indicated that these latter two traits are more sensitive to environments.

The growing period in Beijing and Hangzhou was between late April and September 1994, while in Hainan it was between early December 1994 and April 1995. Although the three locations were at different degrees of north latitude, the growing conditions in Beijing and Hangzhou were much similar. Among the 7 QTLs that were common between two environments, 5 were detected both in Beijing and Hangzhou, and among the 8 QTLs that were significant in one environment, 7 QTLs could only be detected in Hainan (Tables 2 and 3).

Discussion

Permanent segregating populations including recombinant inbreeds and doubled haploids have recently been employed to identify genes using molecular markers (Mohan et al. 1994; Heun 1992; Barua et al. 1993; Backes et al. 1995; Toroser et al. 1995; Uzunova et al. 1995). Such populations provide researchers with the characteristics of genetic homozygosity, and thus offer a particular advantage for QTL mapping. In this study, we used a DH population derived from a cross between an *indica* and *japonica* rice variety by anther culture. Skewed segregation was found for 31% of the markers in the DH population. However, this phenom-

enon is not unique to DH populations. Similar frequencies of distorted segregations have also been observed in both the interspecific *O. sativa* × *O. longistaminata* (Causse et al. 1994) and the intersubspecific *indica* × *javanica* (McCouch et al. 1988) populations. In a F_2 population derived from the same cross that produced the DH population in this study, 25.9% of the loci were skewed, and the *indica* genotype in the F_2 population was significantly more than expected (Xu et al. 1995). A slightly greater proportion of skewed segregating loci in the DH population favored the *japonica* alleles. One reason for this is likely to be possible genotypic selecion during anther culture. It is well-known that *japonica* rice is more amenable to culture than *indica* rice, and thus the DH population consisted of more *japonica*-inclined regenerants.

The effects of environments on QTLs could be extremely significant. Paterson et al. (1991) identified 29 QTLs for quantitative traits of tomato using F_2 amd F_3 populations in three evnironments, but only 4 QTLs were significant in all environments. Freyre and Douches (1994) used the clonally propagated potato to study the environmental effect of specific gravity on QTLs and found that only 2 of the 10 QTLs were significant in all of the three environments tested. In our present study in which one permanent DH population was used, evidence of QTL-by-environment interaction was also found. A total of 22 QTLs for six agronomic traits were identified as being significant in at least one environment, but only 7 QTLs were significant in all of the environments tested. However, the genotype-by-environment interaction was trait-dependent. For example, environments had little effect on QTLs for spikelets and filled grains per panicle. But for heading date and plant height, no QTLs were found to be common among the environments tested.

There are many environmental factors that may affect the phenotypic expression of quantitative traits. Finer dissection of these factors may result in a more precise mapping of QTLs and determination of the effects of each factor independently. The heading date of rice is influenced by a number of environmental factors including day lenght and temperature. Two genes for photoperiod sensitivity, *Se-1* and *Se-2*, on chromosome 6 and 7, respectively, have been identified to be related to heading date (Kinoshita and Takahashi 1991). In this study, we did not identity any QTLs associated with heading date that might correspond these genes on the two chromosomes, but our results with mapping different QTLs in different locations did imply that some QTLs were photosensitive. Beijing is located at 39° N while Hainan is found at about 18° N; therefore, Beijing has a longer day length than Hainan. No QTLs were found common to both environments. One QTL on chromosome 8 (*hd8*) bordered by RG885 and RZ617 was significant in Beijing. The LOD score was very high (7.55), and it explained over 30% of the total phenotypic variation and had an additive effect of 14 days. This QTL was also detected in Hangzhou, which is located at 32° N, with a lower LOD score (5.98) and a smaller additive effect (7 days). It could not be detected in Hainan. This QTL has also been detected in other mapping populations (Li et al. 1995; Xao et al. 1994) and thus merits further investigation.

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