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Chaofu Lu · Lishuuang Shen · Zhenbo Tan
Yunbi Xu · Ping He · Ying Chen · Lihuang Zhu

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

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Abstract We report here the RFLP mapping of quantitative trait loci (QTLs) which affect some important agronomic traits in cultivated rice. An anther culture-derived doubled-haploid (DH) population was established from a cross between indica and japonica rice varieties. A molecular linkage map comprising 137 markers was constructed based on this population which covered the rice genome at intervals of 14.8 cM on average. 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, 1 000-grain weight and the percentage of seed set, by interval mapping. 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 was detected which were significant in at least one environment, but only seven were significant in all three environments; seven were significant in two environments and eight could only be detected in a single environment. However, QTLs-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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C.-F. Lu · L.-S. Shen · P. He · Y. Chen · L.-H. Zhu (✉)
Plant Biotechnology Laboratory, Institute of Genetics, Chinese Academy of Sciences, Beijing 100101, China

Z.-B. Tan
The Rice Research Institute, Sichuan Agricultural University, Wenjiang, Sichuan 610013, China

Y.-B. Xu
Department of Agronomy, Zhejiang Agricultural University, Hangzhou 310029, China

Introduction

Quantitative genetic studies have been facilitated by the development of molecular markers (Peterson et al. 1988; Stuber 1992 a). High-density molecular linkage maps permit one to locate quantitative trait loci (QTLs) by linkage analysis using segragating populations (Paterson et al. 1988; Lander and Bostein 1989). 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 by using molecular markers (Ahn et al. 1993; Wang et al. 1994; Xiaco et al. 1994; Li et al. 1995a,b). Most of the mapping studies, however, have used F_2 or backcross populations, which are difficult to replicate in order to obtain accurate phenotypic values for precise QTL mapping. The use of recombinant inbred lines (RILs) has many advantages for 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; Backes 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 after a singly 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 trials and for a reduction of 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. Two notable exceptions are the studies conducted by Paterson et al. (1988) and Stuber et al. (1992b). 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 showed that only 4 out of 29 QTLs were detected in all testing environments. Stuber et al. (1992 b) studied the genotype-by-environment interaction for QTLs of maize by field evaluation of backcross 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 the use of different generations. Here, we have used a permanent DH population to identify chromosomal regions associated with some important argonomic characters and to investigate the G × E interaction at individual QTLs by comparing QTL maps generated in three diverse environments.

Materials and methods

Experimental population and phenotypic evaluation

A doubled-haploid (DH) population consisting of 132 DH lines was used in this study. The population was developed through anther culture of the F_1 hybrid between an indica rice variety Zhai-Ye-Qing 8 (Z) and a japonica variety Jing-Xi 17 (J).The agronomic performance of the DH population was evaluated in field experiments at three locations: Beijing, located at 39°N (degree of the north latitude); Hangzhou, which is at 32°N; and Hainan , which is at 18°N. The DH lines were grown in Bejing and Hangzhou between April and September of 1994, and in Hainan island between December 1994 and April 1995. All these locations had commonly been used for rice field experiments and thus had adequate insect, disease and weed control. In each of the three environments, the DH lines were orderly planted in doubled rows, the parents being grown every ten DH lines as a control. The days from sowing to heading (heading date), plant height, number of porductive 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 averaged values of ten individual plants from each line. Except for the number of productive tillers and panicle length, all six other 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 construction

Genomic DNA was extracted from young leaves, and then digested with the restriction enzymes *Bam*HI, *Bgl* II, *Dra*I,*Eco*RV, *Hin*dIII, *Sca*I and *Xba*I, and hybridized with RFLP markers as described by McCouch et al. (1988) markers were kindly provided by Drs. S. D. Tanksley and S. R. Mc Couch 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 version 3.0 (Lander et al. 1987; Lincoln et al. 1993 a). The genetical distances were calculated using the Kosambi function. The LOD threshold was fixed at 3.0 and the error detection item was used. The assignment of linkage groups or markers to their corresponding chromosomes was based on Causse et al. (1994) and Kurata et al. (1994). Based on the molecular map, the graphical genotypes of each line were established and the percentages of the parent genomes were estimated by the computer program HyperGene (Young and Tanksley 1989).

QTL identification

Interval QTL mapping was carried out using the software MAPMAKER/QTL version 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 the at level of significance at $P = 0.05$ for the entire rice genome (Lander and Bostein 1989). In the present 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. The gene effect (additive effect, free of dominance) and the percent of phenotypic variation attributable to individual QTLs were both estimated at the peaks.

Results and discussions

RFLP map

A genetic map was constructed based on segragating RFLP data in 132 DH lines. This map had 137 well-distributed RFLP markers on 12 chromosomes with an average distance of 14.8 cM (Kosambi map units) between markers (Fig. 1). The linear order of the markers was 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 estimated to be approximately 95% according to the two above saturated maps.

Skewness of marker segregation in the DH population was observed. Forty-one (about 31%) out of 137 loci analyzed in the DH population 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

Table 1 Means and variation range 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 66.6–131.6	82.3 48.6–112.0	23.6 16.0–31.7	136.7 34.2–269.2	106.9 15.0–252.8	76.8 8.9–95.5
HZ	79.7 67.3–97.5	84.2 44.2–114.8	24.4 15.3–34.3	108.7 34.3–197.3	67.5 2.2–150.7	60.8 4.6–86.6
HN	89.4 67.5–106.2	72.5 50.8–96.6	23.5 16.7–30.9	114.2 43.0–252.0	72.6 2.0–195.7	63.4 1.1–95.0

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

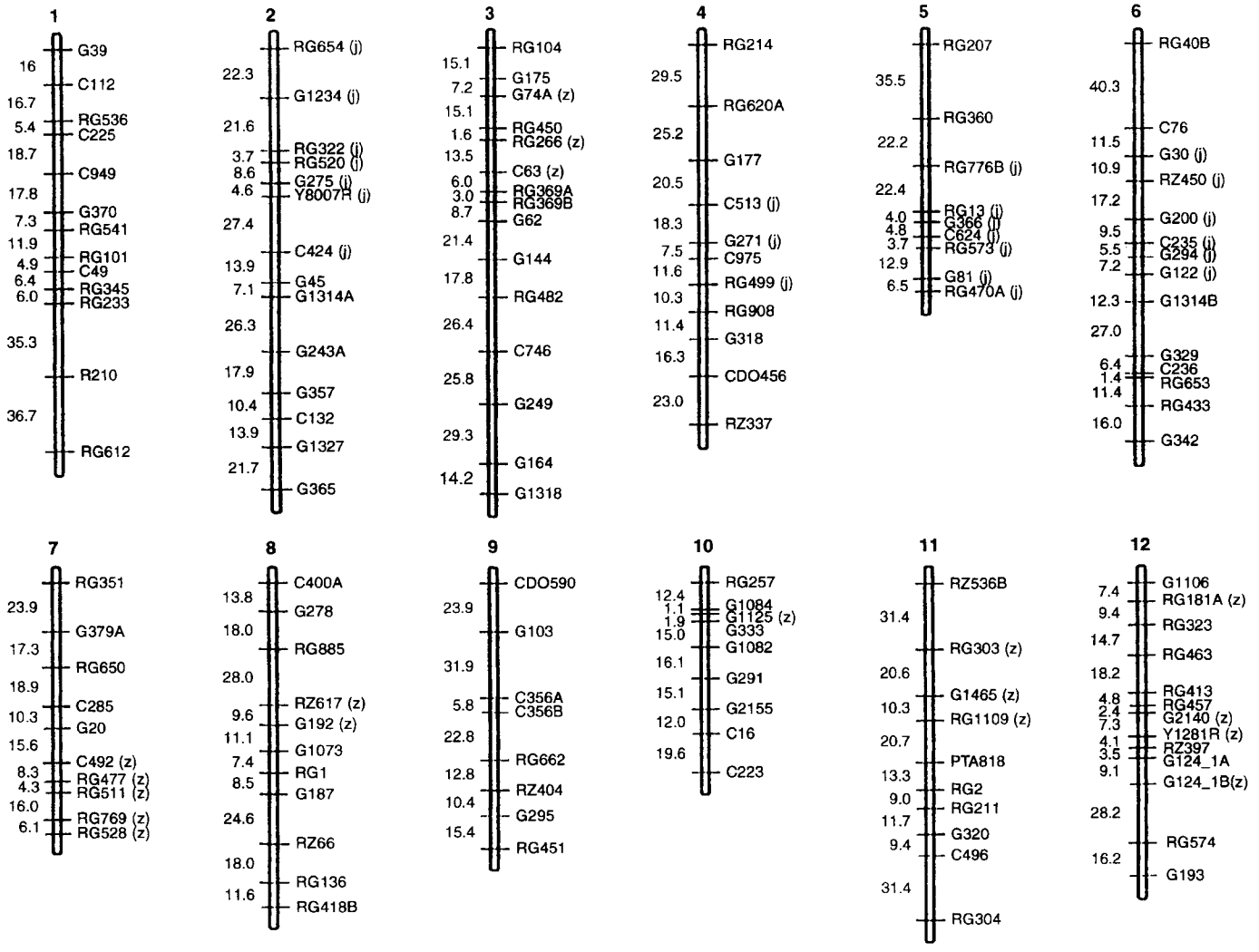

Fig. 1 A rice molecular linkage map with 137 RFLP markers constructed from 132 DH lines derived from the cross of "Zhaiyeqing 8" × "Jingxi 17". Scale in Kosambi cM is shown on the left of each chromosome. The markers showing distorted segregation are marked with (*z*) or (*j*) indicating their favoring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

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, 11 and 12, and the markers showing distorted segregation in the same region had an excess of alleles from the same parent (Fig. 1). The distorted segration, however, should not affect QTL mapping since the overall proportion of Z/Z genotypes in the DH population was 49.6% as estimated by HyperGene (Young and Tanksley 1989), which was very close to the expected 50%. Similar frequencies of distorted segregation were also observed in both the interspecific *O. sativa* × *O. longistaminata* (Causse et al. 1994) backcross and the inter-subspecific indica × javanica (McCouch et al. 1988) F_2 populations. In an F_2 population derived from the same cross which produced the DH population employed in the present study, 25.9% of the loci were skewed, and the indica genotype in the F_2 population was significantly greater than expected (Xu et al. 1995). A slightly higher proportion of skewed, segregating loci in the DH population favored the japonica alleles. One reason for this is likely to be the possible genotypic selection during anther culture. It is well known that japonica rice is more amenble to culture than indica rice, and thus the DH population consisted of more japonica-inclined regenerants.

Interval mapping of QTLs

By using the software MAPMAKER/QTL (version 3.0), QTLs for such agronomic characters as heading date, plant height, 1000-gain weight, spikelets per panicle, grains per panicle and seed-set percentage were identified, based on the above RFLP map. As mentioned in "Materials and methods", a conservation threshold of LOD $\geqslant$ 3.0 was used to identify the presence of a QTL and scores of 2.0–3.0 were regarded as "suggestive". Table 2 lists all QTLs with LOD $\geqslant$ 2.0, identified based on the phenotypic performance of the DH population in Beijing, Hangzhou and Hainan, respectively.

Table 2 Biometrical parameters of individual QTLs for six agronomic traits in a three-environment trial of a Z/J DH population. QTLs are named by trait abbreviations and chromosome number. In case where 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*). The environments in which a QTL was detected are indicated (BJ = Beijing in 1994, HN = Hainan in 1995, HZ = Hangzhou in 1994)

Trait	Locus	Marker interval	Trial	LOD score	% Var	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 wt.	*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

Heading date

A total of four QTLs for heading date, *hd1*, *hd8*, *hd10a* and *hd10b*, were identified which 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 (*hd8*) bordered by markers RG885 and RZ617 on chromosome 8 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, in which the LOD score was only 0.28. One QTL, *hd1*, could be detected in Hainan (LOD = 3.08). It had an additive effect of about 6 days which promoted an earlier heading time. However, it was not detected in Beijing and Hangzhou (LOD scored as 0.80 and 1.34, respectively). On chromosome 10 two QTLs, *hd10a* and *hd10b*, were identified; *hd10a* was detected in Beijing and Hangzhou whereas *hd10b* was only significant in Hainan.

Plant height

A total of five QTLs for this trait, *ph3*, *ph4*, *ph7*, 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 Beijing (LOD = 4.23) and Hangzhou (LOD = 2.54), was located at the same position as the *hd8* QTL for heading date. This QTL was not significant in Hainan

(LOD = 1.25). Another QTL on chromosome 10, *ph10*, was 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. Increasing plant height by 1 cm due to either *ph8* in Beijing and Hangzhou or *ph10* in Hainan was associated with about a 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 six QTLs for this trait were identified which were significant in at least one environment (Table 2). Two QTLs, *gw1* and *gw2*, were significant in all three environments and two QTLs, *gw6* and *gw8*, were significant in two environments. All these QTLs had an additive effect for increased grain weight. For the other two QTLs, *gw3* could only be detected in Hainan while *gw5* could only be detected in Beijing.

Spikelets per panicle and grains per panicle

These two traits are closely correlated ($r = 0.8529$) and, as expected, for both traits two QTLs were detected respectively, and the QTLs for the two traits were located in the same chromosomal regions (Table 2). The loci *spn4* and *gn4* increased spikelets and grains per panicle, while *spn6* and *gn6* had a negative additive effects for spikelets and grains per panicle. The magnitude of their respective effects was also nearly the same. All four QTLs could be detected in all three environments.

Seed-set percentage

Three QTLs were found for seed-set percentage (Table 2). The QTL *ssp4* mapped nearly to the same region on chromosome 4 in the three environments. Two other QTLs, *ssp5* and *ssp7*, could be detected only in Hainan. All QTLs had a positive additive effect for increasing seed-set percentage.

Evidence of genotype-by-environment interaction

A DH population is one kind of permanent 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 the present study, we have identified a total of 22 QTLs for six agronomic traits of rice in three different locations (environments), but only seven QTLs were significant in all three testing environments; a further seven QTLs were significant in two environments, and eight QTLs could be detected only in a single environment (Table 3). However, the QTL-by-environment interaction is trait dependent. Among the seven QTLs significant in all environments, two were for grain weight, two for spikelets per panicle, two for grains per panicle, and one for seed-set percentage. No QTLs significant in all environments were mapped for heading date and plant height. This result indicated that these two traits are more sensitive to environment.

The growing period in Beijing and Hangzhou was between late April and September 1994 while that in Hainan was between early December 1994 and April 1995. Although the three locations were at different degrees of northern latitude, the growing conditions in Beijing and Hangzhou appeared to be more similar to one another than either was to the Hainan environment. Among the seven QTLs which were common between two environments, five were detected both in Beijing and Hangzhou; and among the eight QTLs which were significant in one environment, seven could be detected only in Hainan (Tables 2 and 3). This result suggested that these QTLs can be used with confidence for marker-assisted selection in similar environments.

There are many environmental factors which may affect the phenotypic expression of quantitative traits. By a finer dissection of these factors, more precise mapping of QTLs may be achieved and the effects of each factor be determined independently. The heading date of rice, for example, is influenced by a number of environmental factors including day length and temperature. Two genes for photoperiod sensitivity, *Se-1* and *Se-2*, on chromosomes 6 and 7 respectively had been identified which are related to heading date (Kinoshita

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

No. 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

and Takahashi 1991). In the present study, we have not identified QTLs for heading date which might correspond to these genes but different mapping results in different locations did indicate that some QTLs were photosensitive. Beijing is located at 39°N while Hainan is about 18°N, so that 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. It had a very high LOD score (7.55) and explained over 30% of the total phenotypic variation, with an additive effect of 14 days. This QTL was also detected in Hangzhou, which is located at 32°N, though with a lower LOD score (5.98) and a smaller additive effect (7 days). But it could not be detected in Hainan. This QTL was also identified in other mapping populations (Xiao et al. 1994; Li et al. 1995) and thus merits further investigation.

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