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RFLP mapping of QTLs for yield and related characters in rice (*Oryza sativa* L.)

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Abstract Quantitative triat loci (QTLs) for yield and related traits in rice were mapped based on RFLP maps from two indica/indica F_2 populations, Tesanai 2/CB and Waiyin 2/CB. In Tesanai 2/CB, 14 intervals carrying QTLs for eight traits were detected, including 3 for grain weight per plant (GWT), 2 for number of panicles per plant (NP), 2 for number of grains per panicle (NG), 1 for total number of spikelets per panicle (TNS), 1 for spikelet fertility (SF), 3 for 1000-grain weight (TGWT), 1 for spikelet density (SD), and 1 for number of first branches per main panicle. The 3 QTLs for GWT were located on chromosomes 1, 2, and 4, with 1 in each chromosome. The additive effect of the single locus ranged from 2.0 g to 9.1 g. A major gene (*np4*) for NP was detected on chromosome 4 within the interval of RG143-RG214, about 4 cM for RG143, and this locus explained 26.1% of the observed phenotypic variance for NP. The paternal allele of this locus was responsible for reduced panicles per plant (3 panicles per plant). In another population, Waiyin 2/CB, 12 intervals containing QTLs for six of the above-mentioned traits were detected, including 3 for GWT, 2 for each of NP, TNS, TGWT and SD, 1 for SF. Three QTLs for GWT were located on chromosome 1, 4, and 5, respectively. The additive effect of the single locus for GWT ranged from 6.7 g to 8.8 g, while the dominance effect was 1.7–11.5 g. QTL mapping in two populations with a common male parent is compared and discussed.

Key words *Oryza sativa* L. · RFLP · Yield traits · QTLs

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Introduction

The recent development of restriction fragment length polymorphism (RFLP) techniques makes it possible to investigate the inheritance of complex traits and to locate and manipulate individual genetic factors controlling these traits (Tanksley 1993). The techniques have been widely used to map quantitative trait loci (QTLs) in such crops as maize (Burr et al. 1988; Beavis et al. 1991; Stuber et al. 1987, 1992), tomato (Osborn et al. 1987; Nienhuis et al. 1987; Tanksley and Hewitt 1988; Paterson et al. 1988, 1990; Martin et al. 1989; de Vicente and Tanksley 1993), and soybean (Keim et al. 1990). In rice, QTLs mapping is very recent. Wang et al. (1994) located the genes conferring complete and partial resistance to blast in a durably resistant rice cultivar. QTLs for drought tolerance and root parameters for drought tolerance (Champoux et al. 1995) have also been mapped with the same population. Li et al. (1995) mapped the QTLs for heading data and plant height in rice and found 4 QTLs for heading date, including 2 major genes, 1 on chromosome 3 and the other on chromosome 8, and 7 QTLs for plant height. Rice yield is the final product of the manifestation of several components, such as number of panicles per plant, number of grains per panicle, fertility, and grain weight, and is supposed to be a very complex trait. The dissection of such a complex trait by means of the QTL mapping approach will be of great significance in helping breeders to enhance the yield potential of rice.

The present paper describes the genetic analysis of yield and related traits in rice, the localization of QTLs involved in controlling these traits on the molecular map of rice, and the estimation of the contribution of each QTL based on two F_2 populations derived from indica/indica combinations as well as the comparison of QTLs between the two populations with a common male parent.

Materials and methods

Plant materials

Two F_2 populations were established from two indica/indica combinations, Tesanai 2/CB (TSA/CB) and Waiyin 2/CB (WY/CB), which have a common male parent 'CB'. 'CB', a variety inclining to indica type is from California, USA, 'Tesanai 2' is from Guangdong, China, and is a high yielding variety notable for its large panicles, 'Waiyin 2' is from International Rice Research Institute (IRRI) and has comparatively larger grains.

Evaluation of the parents and of the F_1 and F_2 generations was carried out at the China National Rice Research Institute (CNRRI), Hangzhou, China, during 1993. A total of 48 plants for each parental line, 32 plants for each F_1, and 480 plants for each F_2 population were grown with a spacing of 23 × 23 cm. A single tiller was separated from each plant during the early tillering stage and was transplanted individually, which provided the materials for DNA extraction. At maturity, eight traits were measured on individual plants (Table 1).

Construction of RFLP map

Total DNA extraction, restriction endonuclease digestion, electrophoresis, Southern blotting, hybridization, and autoradiography were carried out as described by Zheng et al. (1990), and Lu and Zheng (1992). The restriction endonucleases *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV, and *Xba*I were used to digest total DNA. Altogether 167 probes were used, including rice genomic clones (RG), rice cDNA clones (RZ), and oat cDNA clones (CDO), all of which were a gift from Dr. S.D. Tanksley of Cornell University. The selected probes covered and the whole RFLP map of rice with an average interval between probes of about 12 cM. The majority of these clones represent single-copy sequences. Probes detecting polymorphism between the parents with at least one enzyme were used to detect the genotypes of each F_2 plant.

The program MAPMAKER (Lander et al. 1987; Stephen et al. 1990) was used to establish two RFLP maps based on the segregation data of the two F_2 populations, respectively. Distances between markers are presented in centiMorgans (cM) derived using the Kosambi function (Kosambi 1944) of the MAPMAKER program.

QTL mapping

Two analytical methods were used to identify QTLs. The PROC GLM procedure in the Statistical Analysis System (SAS) (SAS Institute 1988) was used to determine the associations between molecular markers and the QTLs for the studied traits. A per-chromosome significance level of $P = 0.0043$ (equivalent to an overall significant level of $P = 0.05$) was used for the significant levels of individual markers (Rebai et al. 1994; Wu and Li 1994). MAPMAKER/QTL (Lander and Botstein 1989) was also used to identify loci affecting quantitative traits on the basis of interval analysis. An LOD threshold of 2.5 was used to declare the presence of putative QTL in a given genomic region. The percentages of variation explained by the QTLs for the trait, the additive effect, the dominance effect, and the degree of dominance are estimated by MAPMAKER/QTL analysis.

Table 1 Traits analyzed in two F_2 populations ('Tesanai 2'/'CB' and 'Waiyin 2'/'CB')

Trait abbreviation	Trait description
GWT	Grain weight/plant (g)
NP	Number of panicles/plant
NG	Number of grains/panicle
TNS	Total number of spikelets/panicle
SF	Spikelet fertility (%)
TGWT	1000-grain weight (g)
SD	Spikelet density (number of spikelets per 10 cm of panicle)
NFB	Number of first branches/main panicle

Results and discussion

Phenotypes

In TSA/CB, the phenotypic values of the eight traits scored in the female parent TSA were all higher than those found in the male parent CB (Table 2); all were very significantly different ($P < 0.01$) except spikelet fertility (SF). The differences between the parents in WY/CB were similar to those in TSA/CB (Table 2). The fertilities of the F_1 plants of both crosses were $64.3 \pm 8.1\%$ and $74.2 \pm 7.8\%$, respectively, while the scores of the other seven traits of the F_1s in both crosses were more than mid-parent values or higher than the superior parents showing some degree of heterosis.

In the two F_2 populations, the segregations of 3 major components of yield were obvious, and the standard deviations in the F_2s were much larger than those, in the parents and F_1s. The skewness test showed that the phenotypic values of these traits were normally distributed (data not shown). For almost all of the traits there were some F_2 progenies showing extreme performance, with values either much larger or much smaller than those of the parents. This might be due to transgression or environmental effects, as the F_2 populations are much larger. The average number of panicles per plant (NP) was 9.3 ± 4.0 (range: 2–21) in TSA/CB and 8.1 ± 4.1 (range: 1–22) in WY/CB. The average number of grains per panicle (NG) in TSA/CB was 105 ± 58.0 (range: 4–248), while in WY/CB it was 98.6 ± 54.2 (range: 3–247). Average 1000-grain weight (TGWT) in TSA/CB was 24.1 ± 3.3 g (range: 13–34 g, while in WY/CB it was 29.5 ± 4.5 g (range: 19–42 g). The other five related traits studied similarly showed large segregation and normal distribution, indicating the feasibility of QTL mapping for all these traits in these two populations.

Construction of RFLP maps

Of the 167 RFLP markers tested, 73% revealed polymorphisms between the parents of the two crosses. For each F_2 population 171 plants were genotyped with 93 and 101 RFLP markers in TSA/CB and WY/CB, respectively.

Skewed segregations ($P < 0.05$) were observed for 20 out of the 93 markers tested in TSA/CB, but overall distributions of paternal alleles on all marker loci were symmetrical, the average of which was 0.478 ± 0.042. While in WY/CB 15 out of 101 markers tested skewed from the theoretical ratio 1:2:1 ($P < 0.05$), the frequency distributions of paternal alleles on all marker loci were also symmetrical, with an average of 0.489 ± 0.033. A

Table 2 Phenotypic values of yield components (*F* female · *M* male)

Cross	Trait[a]	Female (m ± SD)	Male (m ± SD)	*t*-value F-M	F_1 (m ± SD)	F_2 (m ± SD)
Tesanai 2/CB	GWT	40.5 ± 10.1	7.8 ± 2.6	12.22**	28.2 ± 7.7	23.9 ± 19.0
	NP	10.7 ± 2.5	5.1 ± 1.4	7.34**	7.7 ± 1.5	9.3 ± 4.0
	NG	150.7 ± 17.8	105.9 ± 17.9	6.85**	143.3 ± 23.4	105.5 ± 58.0
	TNS	178.9 ± 22.6	130.8 ± 20.2	7.85**	226.2 ± 31.6	197.0 ± 97.1
	SF	84.1 ± 4.2	81.1 ± 5.5	1.64	64.3 ± 8.1	53.2 ± 28.1
	TGWT	23.0 ± 2.1	14.9 ± 1.5	11.64**	25.0 ± 2.3	24.1 ± 3.3
	SD	82.5 ± 7.8	68.1 ± 6.6	5.41**	87.4 ± 9.5	79.6 ± 34.3
	NFB	12.3 ± 1.2	11.0 ± 1.3	2.73**	13.2 ± 1.9	12.8 ± 3.1
Waiyin 2/CB	GWT	32.3 ± 9.1	7.8 ± 2.6	9.93**	45.2 ± 10.7	24.0 ± 18.0
	NP	9.3 ± 2.3	5.1 ± 1.4	5.99**	8.4 ± 1.3	8.1 ± 4.1
	NG	139.3 ± 15.3	105.9 ± 17.9	5.48**	184.5 ± 40.9	98.6 ± 54.2
	TNS	169.1 ± 17.2	130.8 ± 20.2	5.59**	249.4 ± 45.1	174.8 ± 93.5
	SF	83.0 ± 3.3	81.1 ± 5.5	1.14	74.2 ± 7.8	56.0 ± 23.9
	TGWT	32.3 ± 2.1	14.9 ± 1.5	26.00**	31.1 ± 4.0	29.5 ± 4.5
	SD	52.1 ± 6.5	68.1 ± 6.6	−6.68**	83.2 ± 12.4	68.7 ± 31.9
	NFB	14.3 ± 1.8	11.0 ± 1.3	5.75**	19.4 ± 1.9	14.6 ± 4.6

** Indicates 1% significant level
[a] See Table 1 for abbreviations

similar state of skewness was observed in other rice mapping populations (McCouch et al. 1988; Saito 1991). However, the availability of large number of RFLPs and their close linkage to each other may not pose problems in locating QTLs (Paterson et al. 1988).

A linkage map consisting of 89 marker loci from 12 linkage groups was constructed based on the TSA/CB population (Fig. 1). The map covers 1410.4 cM of the rice genome with an average interval of 18.3 cM between marker loci. Another genetic map comprised of 93 marker loci covering 12 linkage groups was also constructed based on the WY/CB population (Fig. 2). This map covers 1328.5 cM of the rice genome with an average interval of 16.4 cM between two markers. The average intervals are smaller than 20 cM in both maps so they are suitable for QTL mapping (Lander and Botstein 1989).

When the maps were compared to the map of Causse et al. (1994) it was found that most markers were located on the expected chromosome in the expected orders. In the two populations, 5 markers were located on different chromosomes – RZ649, RG634, RG348, RG190, and RG9. Close examination of the autoradiograms showed that multiple bands were generated with all of these markers except RG9. It is possible that the polymorphic bands scored in our populations are different from those of Causse et al. (1994). RG9 produced a null allele, which might also be a reason for its altered position.

RFLP maps with the same set of markers in two different populations (Figs. 1 and 2) provide an opportunity to compare the recombination frequencies between markers in different populations. On the basis of a two-point analysis, genetic distances (cM) for all of the common markers used in both populations were estimated. Regression analysis showed that the genetic distances of corresponding regions between the two populations are highly correlated (Fig. 3A). The correlation coefficiency is as high as 0.922, indicating that the overall recombination frequency between populations is comparable. On average, the distance between any 2 markers was found to be 2 cM smaller in WY/CB than in TSA/CB. In some regions of the rice chromosomes, the distances between markers can be very different in both populations (Fig. 3B). The differences can be larger than 15 cM and/or 1–2 times larger than the smaller values of recombination frequency in both populations. For example, the distance between RG690 and RG394 is 10.3 cM in WY/CB, which is 2 times larger than that in TSA/CB. This observation is similar to ones observed previously in F_2 and BC_1 populations (Abenes et al. 1994; Causse et al. 1994).

The consistency or variation in recombination frequency between loci from population to population has implications in practical marker-assisted breeding. For accurate identification of a target gene based on markers the kind of populations used need to be similar such that variation in the recombination frequency between populations is within a reasonable range.

QTL mapping for yield and yield-related characters

Each of eight characters were subjected to QTL mapping with both ANOVA and interval mapping procedures. In TSA/CB, 14 QTLs for the eight characters were detected by one-way ANOVA (Table 3); the same QTLs were also detected by interval analysis (Table 3). In WY/CB, 12 QTLs for six traits were detected by one-way ANOVA and again, all 12 QTLs were detected by interval analysis (Table 4). These results indicate that both statistical procedures produce very similar results.

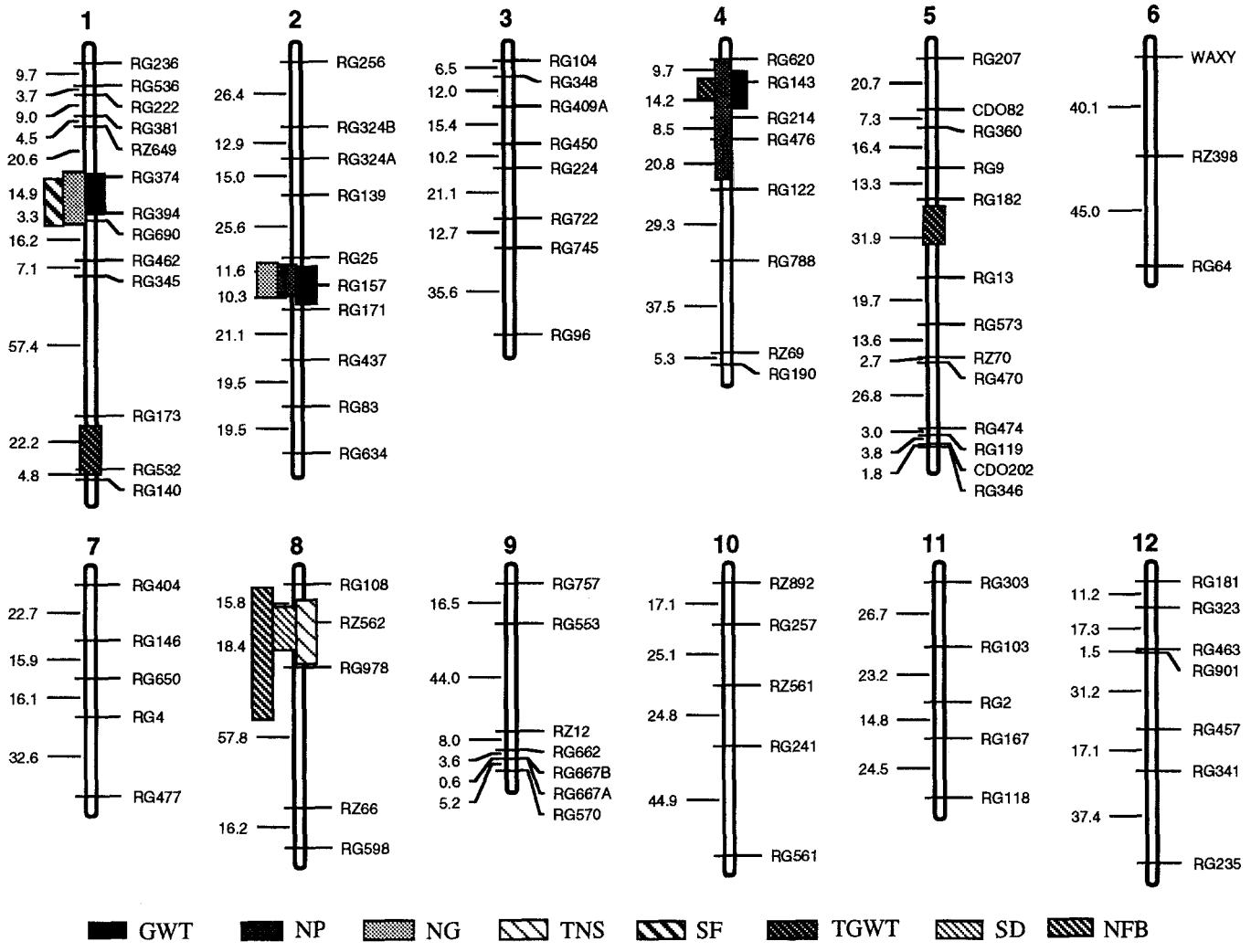

Fig. 1 RFLP linkage map showing location of QTLs for rice yield and yield components in the Tesanai 2/CB F_2 population. *Numbers at top* indicate chromosomes. Kosambi values (cM) are indicated *left* of the chromosomes, and markers are indicated *right* of the chromosomes. The *boxes* on the chromosomes represent intervals with a LOD > 2.5

The QTLs identified are named with a trait abbreviation followed by the chromosomal number.

On the basis of interval mapping, the QTLs controlling GWT, *gwt1*, *gwt2*, and *gwt4*, were located within 3 intervals, in TSA/CB; *gwt1* is located within RG374-RG394 on chromosome 1, *gwt2* within RG157-RG171 on chromosome 2, and *gwt4* within RG143-RG214 on chromosome 4 (Table 3; Fig. 1). QTLs *gwt1* and *-2* individually explained about 11% of the observed phenotypic variance (Table 3). The additive effect of a single locus ranged from 2.0 g to 9.1 g. The paternal alleles of all 3 QTLs represented reduced GWT, while the dominance effect of the 3 QTLs was indicated by increased GWT. Of these 3 QTLs the effect of *gwt1* was higher and reached 12.3 g. The degree of dominance of *gwt1* was also higher and overdominance was observed (Table 3). In WY/CB also, 3 intervals containing QTLs (*gwt1a*, *gwt4a*, and *gwt5*) controlling GWT were detected. QTL *gwt1a* was located within RG374-RG394 on chromosome 1, as in TSA/CB; *gwt4a* within RG788-RG190 on chromosome 4, and *gwt5* within CDO-RG360 on chromosome 5 (Table 4; Fig. 2). The percentages of the observed phenotypic variance explained by individual QTLs ranged from 10.1 to 22.3. The highest percentage of the observed phenotypic variance was explained by *gwt4a* having a higher level of gene effect. The additive effect of the CB allele reduced GWT by 8.85 g, and the dominance effect reduced it by 11.48 g. In both TSA/CB and WY/CB the total number of QTLs detected for yield was 3.

A relatively small number of the QTLs detected seem not to fit to such a complex trait, and as it is generally believed that rice yield is controlled by many genes Many factors may have contributed to this phenomenon: (1) many genes are playing such very small roles that do not reach the threshold used; (2) each QTL detected may harbor many minor genes; (3) strong environmental effects and a single measurement in the F_2 plants result in a large non-genetic variation. However, as in the F_2 only 8 QTLs for yield were detected

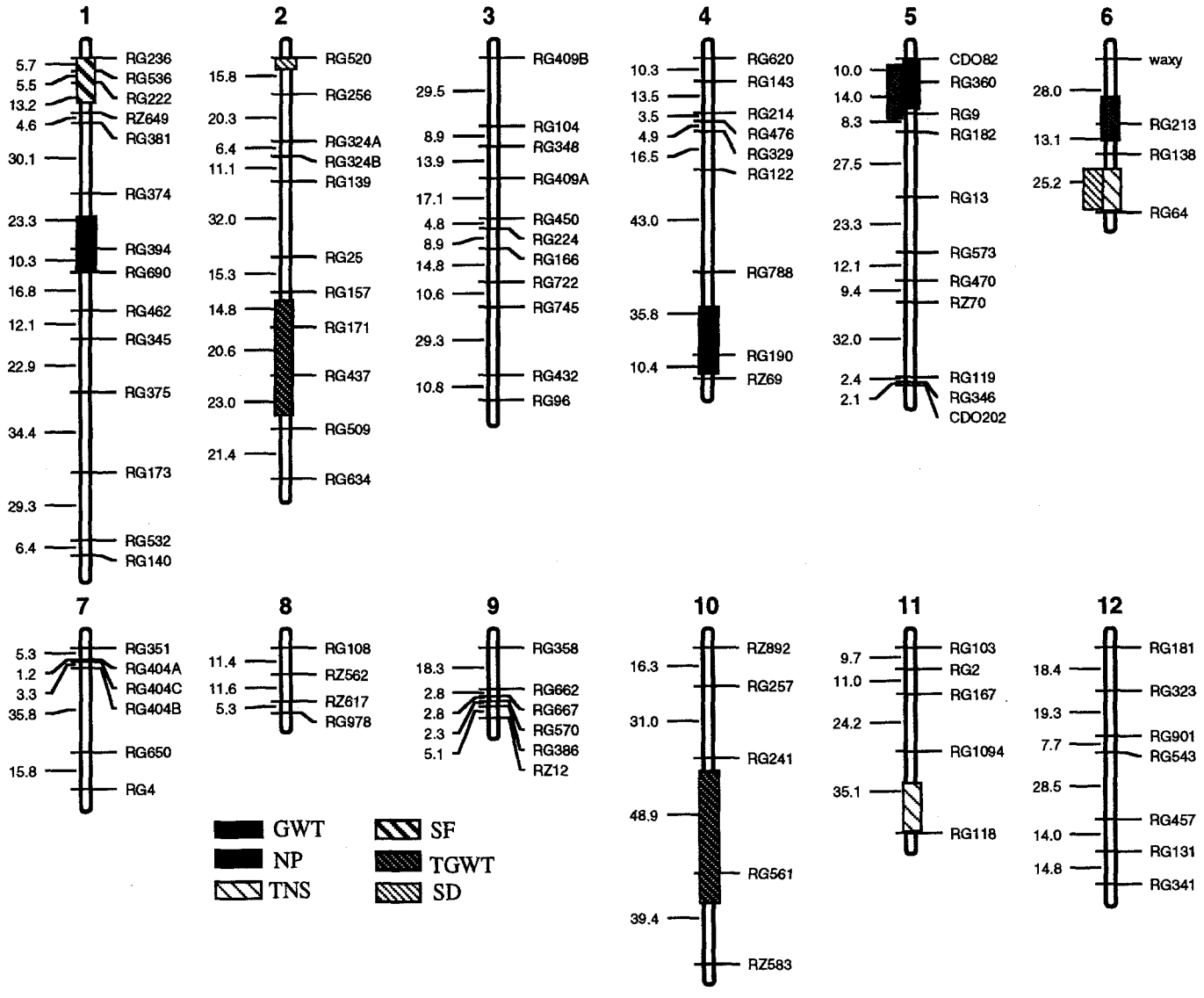

Fig. 2 RFLP linkage map showing location of QTLs for rice yield and yield components in the Waiyin 2/CB F_2 population. *Numbers at top* indicate chromosomes. Kosambi values (cM) are indicated *left* of the chromosomes, and markers are indicated *right* of the chromosomes. The *boxes* on the chromosomes represent intervals with a LOD > 2.5

with the replicated trial of a rice double-haploid lines (B. Courtois and N. Huang, unpublished data). As such the QTLs detected must possess a relatively large effect on yield.

QTLs and transgression

A total of 26 QTLs were detected in both populations. These QTLs were from both parents and can be seen from the sign of additive effect (Table 3 and 4). The additive effect is the measurement of the change in a population mean when an allele of a QTL is replaced/substituted by an allele from CB. A negative value indicates a reduction in performance and, therefore, the QTL from TSA or WY is the QTL-contributing parent. On the other hand, if the additive effect is positive, the contributing allele is from parent CB. Out of the 26 QTLs detected in both populations, 5 are derived from parent CB. When an individual receives positive alleles from both parents, it out performs the parents; when an individual receives negative alleles from both parents, its performance is inferior to either of its parents. As transgression is defined as the occurrence of individuals out-performing their parents, in a segregating population the recombination of positive QTLs would be the most likely genetic base of transgression.

QTLs present in both populations

In general, 1–3 QTLs were detected for each trait in both populations (Table 3 and 4). Comparisons of QTLs for individual traits showed that the majority of the QTLs were present in only one of the two populations. For

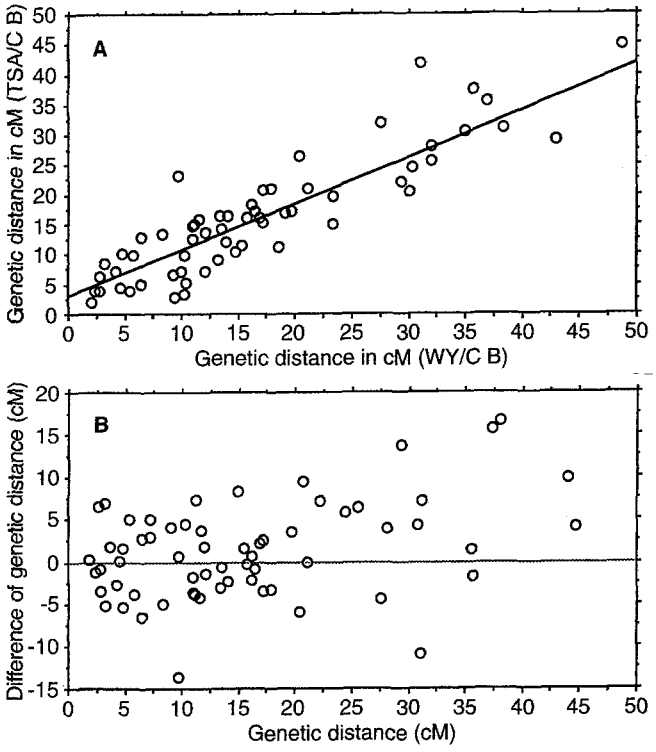

Fig. 3A–B The correlation and variation of genetic distance (in cM) between two populations. *Panel A* shows the scatter diagram of 64 pairs of genetic distances between the same markers in two different populations. **Panel B** shows the scatter diagram of the differences in genetic distances between corresponding regions in both populations versus the smaller value of genetic distances in either one of the two populations

example, 3 QTLs were detected for trait GWT, but only 1 (*gwt1*) was detected in both populations. The performance of each of the female parents is very different and likely to be controlled by a different set of operating genes. All together, we found only 1 QTL (*gwt1*) that was shared by both populations. The presence of different QTLs in different populations provide an opportunity to combine them to produce new breeding lines with a higher yield potential. As DNA markers are not subject to environmental effects, marker-aided selection of the QTLs can be conducted in the early generations of a breeding program.

Effect of QTLs

Among the 26 QTLs for various traits detected in both populations, 20 QTLs explained phenotypic variances larger than 10%. Some of the QTLs, such as *np4*, *gwt4a*, *tgwt10*, and *nfb8*, explained more than 20% of the variance. If a QTL can explain a larger variation than, and is significantly different from, other QTLs (e.g., has a much larger LOD score), one would assume that it would be a major gene rather than a QTL. QTL *np4* (Table 3) from TSA seems to have such characteristics (Fig. 1). Number of panicles (NP) is generally considered to be under the control of both major and minor genes. The *np4* might be a major gene which is linked to other QTLs such as *np2* having a lesser effect to control development of the panicle.

QTLs with dominance and trait heterosis

Many QTLs in both populations showed significant levels of dominance effect (Table 3 and 4). The majority of the dominance effects were positive and there were a few cases of over-dominance. For most traits, these high levels of dominance effect can be related to the heterosis observed in the F_1 hybrids (Table 2). For example, all 3 QTLs of TNS in the two populations showed a very

Table 3 QTLs detected for yield components based on interval analysis (MAPMAKER/QTL) in the Tesanai 2/CB F_2 population

Trait[a]	QTL[b]	Interval	*P*-value[c]	LOD[d]	% Variation[e] explained	a[f]	d[g]	d/[a][h]
GWT	*gwt1*	RG374–RG394	0.0030	2.93	10.7	−1.96	12.36	6.32
	gwt2	RG157–RG171	0.0001	4.11	11.4	−9.14	7.10	0.78
	gwt4	RG143–RG214	0.0005	3.10	8.7	−7.91	0.28	0.04
NP	*np2*	RG157–RG171	0.0003	3.62	9.3	−1.39	2.27	1.64
	np4	RG143–RG214	<0.0001	9.68	26.1	−2.92	0.18	0.06
NG	*ng1*	RG374–RG394	0.0003	4.41	17.2	−1.39	48.18	34.57
	ng2	RG25–RG157	0.0021	2.79	9.0	−21.46	27.65	1.29
TNS	*tns8*	RZ562–RG978	<0.0001	4.84	15.5	35.70	53.64	1.50
SF	*sf1*	RG374–RG394	0.0001	3.86	12.2	−5.10	25.00	4.92
TGWT	*tgwt1*	RG173–RG532	0.0033	3.01	12.6	1.63	−1.50	−0.92
	tgwt4	RG143–RG214	0.0027	2.74	8.5	−1.39	0.55	0.39
	tgwt5	RG182–RG13	0.0042	2.73	14.8	−1.55	−1.33	−0.86
SD	*sd8*	RZ562–RG978	0.0001	3.73	10.9	11.79	14.69	1.25
NFB	*nfb8*	RG108–RZ562	<0.0001	6.49	20.9	1.91	−0.49	−0.25

[a] See Table 1 for abbreviations
[b] QTLs are named by trait abbreviations plus chromosomal number
[c] *P* value refers to the probability of the association between QTL and the marker having the larger effect
[d] Log_{10} likelihood
[e] Percent phenotypic variance explained
[f] Additive gene effect at the putative QTL
[g] Dominance effect at the putative QTL
[h] Degree of dominance

Table 4 QTLs detected for yield components based on interval analysis (MAPMAKER/QTL) in the Waiyin 2/CB F_2 population. See footnotes to Table 2 for definitions of column headings

Trait	QTL	Interval	*P* value	LOD	% Variation explained	a	d	d/[a]
GWT	*gwt1a*	RG374–RG394	0.0037	3.13	11.5	−6.70	−6.56	−0.98
	gwt4a	RG788–RG190	0.0001	4.67	22.3	−8.85	−11.48	−1.30
	gwt5	CDO82–RG360	0.0022	3.14	10.1	−8.59	−1.66	−0.19
NP	*np5*	RG360–RG9	0.0017	2.86	9.9	−1.99	−0.24	−0.12
	np6	waxy-RG213	0.0023	2.86	12.1	−1.51	−1.16	−0.76
TNS	*tns6*	RG138–RG64	<0.0001	5.01	13.1	−38.04	28.14	0.74
	tns11	RG1094–RG118	0.0013	4.38	12.5	−54.71	−43.41	−0.79
SF	*sf1a*	RG536–RG222	0.0010	3.25	9.4	−8.27	−6.80	−0.82
TGWT	*tgwt2*	RG171–RG437	0.0003	4.23	14.8	−2.42	0.57	0.24
	tgwt10	RG241–RG561	0.0021	3.52	22.8	−2.89	1.32	0.46
SD	*sd2*	RG520–RG256	0.0003	3.13	12.3	3.92	−21.09	−5.38
	sd6	RG138–RG64	<0.0001	5.15	13.3	−14.62	6.30	0.43

significant dominance effect, which matched the significant heterosis for this trait in both populations (Tables 2–4). While this observation was expected, we also observed a different phenomenon. For TGWT, we observed heterosis on this trait in TSA/CB (Table 2), but we found little dominance on 3 detected QTLs. This observation is similar to that observed by de Vicente and Tanksley (1993).

Trait correlations and chromosome regions with multiple QTLs

Classical quantitative genetics assumes that character correlation is attributable to the effect of pleiotropy or the very close linkage of genes. This assumption remains largely untested because of the lack of appropriate tools. If this assumption is correct, we would expect that QTLs for correlated characters would be mapped to the same regions of rice chromosomes. We know that SD is closely correlated to TNS and that the correlation coefficient is as high as 0.9680. As expected, we found that QTLs controlling SD (*sd8*) in TSA/CB also controlled TNS (*tns8*). Chromosomal regions with multiple QTLs were also observed for other correlated characters (Figs. 1 and 2). Thus our mapping of QTLs on rice chromosome provides evidence that genetic correlation is due to pleiotropy or linkage.

Relationship between parental differences and QTL mapping

Both of the female parents used are high-yielding varieties. 'Tesanai 2' is characterized by a larger number of panicles, the so-called "panicle type", while 'Waiyin 2' is characterized by its larger grain weight, the so-called "grain type" (Table 2). It is generally believed that a large difference between parents would facilitate the mapping of QTLs: one would expect to map more QTLs or QTLs with larger effects for those characters that vary greatly between the parents. Certainly for NP, NG, and TNS, a total of 5 QTLs were mapped for the "panicle type" population (Table 3), while only 4 were mapped in the "grain type" population (Table 4). Furthermore, we observed larger effects of the QTLs in the "panicle type" population. For TGWT, 5 QTLs were found in two populations, but the effects of QTLs in "grain type" were larger as measured by the total percent variation explained by the QTLs. While these traits were found to correspond to our expectation, others did not. For SD and NFB, the results were just the opposite. More QTLs and QTLs with a larger effect for SD were detected in WY/CB although the difference between parents was smaller in WY/CB than in TAS/CB. On the other hand, no QTLs for NFB were uncovered in WY/CB despite the fact that the difference was larger in WY/CB than in TSA/CB. It is suggested that populations of parents with greater genotypic differences favor the mapping of QTLs but sometimes mapping efficiency is trait-dependent.

Conclusion

QTL mapping of rice yield and related characters is the first step in applying marker technology to breeding programs for the improvement of yield potential. We used two F_2 mapping populations to identify QTLs controlling rice yield and its components. In TSA/CB, 14 QTLs for eight different traits were detected, among which 1 (*np4*) was found to be a major gene. In WY/CB, 12 QTLs for six traits were detected but no major gene was found. Among the QTLs identified from both populations, a few were shared in both populations and were from the same male parent (CB). This could be due to the fact that the two female parents were very different from each other in both overall performance and origin. It is possible that there are two different sets of positive QTLs for yield and yield components in the two parents, reflecting a very complex genetic control system for these traits. It also offers an opportunity that we can

now to combine positive QTLs from both parents to examine the effect of QTLs.

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References

Abenes MLP, Tabien RE, McCouch SR, Ikeda R, Ronald P. Khush GS, Huang N (1994) Orientation and integration of the classical and molecular genetic maps of chromosome 11 in rice. Euphytica 76:81–87

Beavis WD, Grant D, Albertsen M, Fincher R (1991) Quantitative trait loci for plant height in four maize populations and their associations with qualitative genetic loci. Theor Appl Genet 83: 141–145

Burr B, Evola SV, Burr RA, Beekman JS (1988) Gene mapping with recombinant inbreds in maize. Genetics 118:519–526

Causse MA, Fulton TM, Cho YG, Ahn SN, Chunwongse J, Wu K, Xiao J, Yu Z, Ronald PC, Harrington SE, Second G, McCouch SR, Tanksley SD (1994) Saturated molecular map of the rice genome based on an interspecific backcross population. Genetics 138:1251–1274

Champoux MC, Wang G, Sarkarung S, Mackill DJ, O'Toole JC, Huang N, McCouch SR (1995) Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. Theor Appl Genet 90:969–981

Keim P, Diers BW, Olson TC, Shoemaker RC (1990) RFLP mapping in soybean: association between marker loci and variation in quantitative traits. Genetics 126:735–742

Kosambi DD (1994) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121: 185–199

Lander ES, Green P, Abbrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Li ZK, Pinson SRM, Stansel JW, Park WD (1995) Identification of two major genes and quantitative trait loci (QTLs) for heading date and plant height in cultivated rice (*Oryza sativa* L.). Theor Appl Genet 91:374–381

Lu YJ, Zheng KL (1992) A simple method for extraction of DNA in rice. Chin J Rice Sci 6:47–48

Martin B, Nienhuis J, King Gm Schaefer A (1989) Restriction fragment length polymorphisms associated with water use efficiency in tomato. Science 243:1725–1728

McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffman WR (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829

Nienhuis J, Helentjaris T, Slocum M, Rugger B, Schaefer A (1987) Restriction fragment length polymorphism analysis of loci associated with insect resistance in tomato. Crop Sci 27:797–803

Osborn TC, Alexander DC, Fobes JF (1987) Identification of restriction fragment length polymorphisms linked to genes controlling soluble solids content in tomato fruit. Theor Appl Genet 73: 350–356

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete RFLP linkage map. Nature 335:721–726

Paterson AH, Deverna JW, Lanini B, Tanksley SD (1990) Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes in an interspecies cross of tomato. Genetics 124:735–742

Rebai A, Goffinet B, Mangin B (1994) Approximate thresholds of interval mapping tests for QTL detection. Genetics 138:235–244

Saito A, Yano M, Kishimoto N, Nakagahra M, Yoshimura A, Saito K, Kuhara S, Ukai Y, Kawase M, Nagamine T, Yoshimura S, Ideta O, Ohsawa R, Hayano Y, Iwata N, Sugiura M (1991) Linkage map of restriction fragment length polymorphism loci in rice. Jpn J Breed 41:665–670

SAS Institute (1988) SAS users guide: statistics. SAS Institute, Gary, NC.

Stephen EL, Lincoln SE, Lander ES (1990) Constructing genetic maps with MAPMAKER: a tutorial and reference manual. A Whitehead Institute for Biomedical research, Cambridge, USA

Stuber CW, Edwards MD, Wendel JF (1987) Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors infuencing yield and its component traits. Crop Sci 27: 639–648

Stuber CW, Stephen EL, Wolff DW, Helentjaris T, Lander ES (1992) Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 116:823–839

Tanksley SD (1993) Mapping polygenes. Annu Rev Genet 27: 205–233

Tanksley SD, Hewitt J (1988) Use of molecular markers in breeding for soluble solids content in tomato – a re-examination. Theor Appl Genet 75:811–823

Vicente MCD de, Tanksley SD (1993) QTL analysis of transgression in an interspecific tomato cross. Genetics 134:585–596

Wang GL, Mackill DJ, Bonman M, McCouch SR, Champoux MC, Nelson RJ (1994) RFLP mapping of genes conferring complete and partial resistance to blast in a durably resistant rice cultivar. Genetics 136:1421–1434

Wu WR, Li WM (1994) A new approach for mapping quantitative trait loci using complete genetic marker linkage maps. Theor Appl Genet 89:535–539

Zheng KL, Shen B, Yu F, Zhao CZ, Qi XF, Xu XM (1990) Restriction fragment length polymorphisms in rice. Chin J Rice Sci 4: 145–149