Theor Appl Genet (1997) 95 : 799–808

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Analysis of QTL × environment interaction for yield components and plant height in rice

Received: 30 January 1997 / Accepted: 21 March 1997

Abstract An F_2 and two equivalent F_3 populations of an *indica-indica* cross of rice, Tesanai 2/CB, were constructed and grown in different environments. The identification of quantitative trait loci (QTL) for yield components and plant height and an analysis of QTL × environment interaction were conducted for three trials. Interval mapping of QTL for eight traits was employed with a threshold of LOD = 2 using the computer package MAPMAKER/QTL. A total of 44 QTL were detected in 18 intervals of nine chromosomes, including 3 for the number of panicles (NP), 5 for the number of filled grains (NFG), 6 for total number of spikelets (TNS), 3 for spikelet fertility (SF), 7 for 1000-grain weight (TGWT), 5 for grain weight per plant (GWT), 8 for plant height (PH) and 7 for panicle length (PL). The numbers of QTL detected in two or three trials were 1 for NP, 1 for NFG, 1 for TNS, none for SF, 4 for TGWT, 3 for GWT, 2 for PH and 5 for PL, making a total of 17. When a QTL was detected in more than one trial the direction and magnitude of its additive effect, the dominance effect and the degree of dominance were generally in good agreement. In all three trials, QTL were frequently detected for related traits in the same intervals. The directions of additive effect of QTL for related traits in a given interval were in agreement with few exceptions, no matter whether they were detected in the same trial or not. This result suggested that pleiotropism rather than close linkage of different QTL was the major reason why QTL for different traits were frequently detected in the same intervals. When gene pleiotropism was considered, 23 of the 29 QTL for yield and its components and 9 of the 15 QTL for plant stature were detected in more than one trial. This indicated that the detection of chromosomal segments harboring QTL was hardly affected by environmental factors.

Key words Rice · Yield components · Plant height · QTL × environment interaction · Pleiotropism

Introduction

Most agronomically important characteristics of crops are inherited quantitatively. The establishment of saturated molecular maps using restriction fragment length polymorphism (RFLP) techniques has made it possible to dissect Mendelian factors underlying complex traits. Systematic studies on mapping quantitative trait loci (QTL) have been conducted in a number of crop species (Paterson et al. 1988; Tanksley and Hewitt 1988; Keim et al. 1990; Stuber et al. 1992), while the effect of QTL × environment interaction has also been addressed in several studies in which QTL have been mapped in the same population in different environments (Paterson et al. 1991; Stuber et al. 1992; Hayes et al. 1993). It has been suggested that a substantial proportion of QTL affecting a trait are active across different environments (for a review see Tanksley 1993).

Recently, QTL mapping for yield components and other important traits under a single environment has also been reported in rice (Wang et al. 1994; Xu et al. 1994; Champoux et al. 1995; Courtois et al. 1995; Li et al. 1995; Xiao et al. 1996). In our previous studies, two F_2 populations were produced from two *indica-indica* crosses of rice and used for QTL mapping for yield and related characters (Lin et al. 1995, 1996). In the present experiment, equivalent F_3 lines of one of the populations, Tesanai 2/CB, were grown in both of two

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Communicated by K. Oono

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environments. QTL mapping was undertaken using data derived from the F_2 and the two F_3 populations. Results were explored to compare the number and location of QTL mapped across different generations and/or environments and to study the QTL × environment interactions.

Materials and methods

Plant materials and field experiments

An F_2 population of an *indica/indica* cross or rice, Tesanai 2/CB (TSA/CB), was constructed. A total of 48 plants of each parental line, 32 F_1 plants and 480 F_2 plants were grown with a spacing of 23 × 23 cm at the China National Rice Research Institute (CNRRI) Hangzhou, China in 1993 (hereafter referred to as F_2 trial). A single tiller was separated from each F_2 plant during the early tillering stage and transplanted individually, which provided the materials for the DNA extraction.

A randomly selected subset of 171 F_2 individuals was subjected to restriction fragment length polymorphism (RFLP) analysis, and the seeds from each F_2 individual were harvested. Each of the 171 F_3 lines was grown at both CNRRI (hereafter referred to as CNF_3 trial) in 1994 and the International Rice Research Institute (IRRI), Philippines (hereafter referred to as IRF_3 trial) in 1995. The experiments followed a randomized complete block design with three replications in the CNF_3 trial and two replications in the IRF_3 trial. The individual plot consisted of 12 plants in one row, with a spacing of 17 × 14 cm in the CNF_3 trial and 30 × 25 cm in the IRF_3 trial.

Eight traits (Table 1) were measured on individual F_2 plants. In the F_3 trials, the eight traits were measured on 10 plants in the center of the row, and average values were used for analysis.

Construction of RFLP map and QTL mapping

A genetic map consisting of 89 RFLP markers was constructed as described by Lin et al. (1996) using the computer package MAPMAKER/EXP 3.0 (Lander et al. 1987; Lincoln et al. 1992a). QTL mapping was carried out for each of the three trials, respectively, using the approach of interval mapping in the computer package MAPMAKER/QTL 1.1 (Paterson et al. 1988; Lander and Botstein 1989; Lincoln et al. 1992b). A LOD threshold of 2.0 was used to declare the presence of putative QTL in a given genomic region. The percentages of variation explained by the QTL for the trait, the additive effect, the dominance effect and the degree of dominance were also estimated by MAPMAKER/QTL analysis.

Table 1 Traits measured in the F_2 and F_3 populations of Tesanai 2/CB

Trait abbreviation	Trait description
NP	Number of panicles/plant
NFG	Number of filled grains/panicle
TNS	Total number of spikelets/panicle
SF	Spikelet fertility (%)
TGWT	1000-grain weight (g)
GWT	Grain weight/plant (g)
PH	Plant height (cm)
PL	Panicle length (cm)

Results

Trait performances

Large segregation was observed for the eight traits in each of the three trials, and their phenotypic values were shown to be normally distributed (Table 2). For NP, NFG, TNS and GWT, the mean values in the F_2 trial and the IRF_3 trial were close to each other, but they were much higher than their counterparts in the CNF_3 trial. For the other four traits, SF, TGWT, PH and PL, there was little difference in mean values among the three trials.

Plant density was a major factor that differed among the three trials. As small spacing of 17 × 14 cm was used in the CNF_3 trial, plant density was much higher in this trial than in the other two trials. Higher plant density could result in decreased values of NP and TNS. The values of traits NFG and GWT were the product of the TNS and SF values, and of the NP, NFG and TGWT values, respectively. The lower mean values of these four traits in the CNF_3 trial were expected. On the other hand, the values of SF, TGWT, PH and PL were less affected by plant density. The similar mean values of these four traits were also not unexpected.

For all the traits, the standard deviations were larger in the F_2 population than in the two F_3 populations, whereas similar values were observed in the two F_3 populations. This might be due to different genetic characteristics of the two types of gene actions, additive effect and dominance effect. Only half of the dominance effect in the F_2 population can be expected in its F_3 population, while the same additive effect in the F_2 can be expected in the F_3.

The above results thus suggested that the data collected were feasible for QTL mapping.

QTL detection

A linkage map consisting of 89 marker loci had been constructed previously (Lin et al. 1996). It covered 1410.4 cM of the 12 rice chromosomes with an average interval of 18.3 cM between marker loci. This map was used as the framework for interval mapping of QTL for each of the eight traits.

Based on interval mapping using a LOD threshold of 2.0, the total numbers of QTL detected in the F_2, CNF_3 and IRF_3 trials were 28, 15 and 22, respectively, including 18, 9 and 14 for yield and its components, and 10, 6 and 8 for the two plant stature traits, respectively. Altogether, 29 different QTL were detected for yield and its components, and 15 were detected for plant stature (Fig. 1, Table 3).

Three QTL were detected for NP. The QTL *np4* on chromosome 4 was detected in both the F_2 and IRF_3

Table 2 Performances of the eight traits in the three trials

Trait[a]	Population[b]	Mean	SD	Kurtosis	Skewness
NP	F_2	9.32	4.09	−0.06	0.58
	CNF_3	5.90	1.81	3.19	1.54
	IRF_3	11.35	2.98	0.09	0.75
NFG	F_2	98.98	57.83	−0.47	0.24
	CNF_3	56.42	26.82	0.69	0.68
	IRF_3	104.78	31.47	0.88	−0.30
TNS	F_2	197.67	97.03	0.59	0.66
	CNF_3	118.36	36.63	0.44	−0.54
	IRF_3	163.16	38.57	0.96	0.46
SF	F_2	52.61	29.10	−1.22	−0.44
	CNF_3	43.52	16.06	−0.50	−0.34
	IRF_3	65.25	13.05	4.69	−1.45
TGWT	F_2	24.12	3.36	0.68	0.18
	CNF_3	22.68	2.33	0.68	−0.12
	IRF_3	21.48	2.32	−0.07	−0.05
GWT	F_2	23.92	19.01	0.70	1.05
	CNF_3	8.24	4.48	1.88	1.05
	IRF_3	17.90	5.24	2.16	0.58
PH	F_2	95.97	16.20	0.74	0.15
	CNF_3	89.92	13.48	1.22	0.16
	IRF_3	80.52	12.61	2.02	0.41
PL	F_2	24.37	3.27	−0.15	−0.22
	CNF_3	22.87	2.39	−0.41	−0.18
	IRF_3	21.34	2.27	−0.05	0.26

[a] See Table 1 for abbreviations

[b] F_2, F_2 population grown in CNRRI in 1993; CNF_3, F_3 population grown in CNRRI in 1994; IRF_3, F_3, population grown in IRRI in 1995

trials, whereas *np1* on chromosome 1 and *np2* on chromosome 2 were only detected in the IRF_3 trial and F_2 trial, respectively. The QTL *np4* was detected with LOD scores of 9.68 in the F_2 and 3.00 in the IRF_3. The LOD scores of 3.62 for *np2* in the F_2 and 2.43 for *np1* in the IRF_3 were obviously lower. No QTL for NP were detected in the CNF_3 trial.

Five QTL were detected for NFG. The QTL *nfg1* was detected in both the F_2 and IRF_3 trials, whereas *nfg2*, *nfg8* and *nfg12* were only detected in the F_2 trial and *nfg5* was only detected in the IRF_3 trial. When QTL detected in a same trial were compared, the LOD score was higher for *nfg1* than for other QTL . No QTL for NFG were detected in the CNF_3 trial.

Six QTL were detected for TNS. No QTL were detected in both generations. One QTL, *tns2*, was detected in adjacent intervals on chromosome 2 in the two F_3 trials. It was ambiguously considered as 1 QTL detected in different environments. All the other QTL, *tns1, tns3, tns4, tns8* and *tns*12, were only detected in either the F_2 trial or the IRF_3 trials. When QTL detected in a same trial were compared, the LOD score for *tns2* was higher than for other QTL.

Three QTL were detected for SF. None was detected in more than one trial, as QTL *sf1*, *sf2* and *sf5* were only detected in the F_2, CNF_3 and IRF_3 trials, respectively.

Seven QTL were detected for TGWT. One QTL, *tgwt4*, was detected in all three trials. Three QTL, *tgwt5a*, *tgwt5b* and *tgwt10*, were detected in two of the three trials. The number of QTL for TGWT detected across different environments was summed up to 4. Of the remaining 3 QTL, *tgwt1a* and *tgwt11* were only detected in the CNF_3 trials and *tgwt1b* was only detected in the F_2 trial. When QTL detected in the same F_3 trial were compared, the QTL detected in all three of the trials had the highest LOD score, followed by QTL detected in two trials and then QTL detected in a single trial. However, *tgwt1b*, detected in the F_2 trial only, had the highest LOD among the 3 QTL detected in the F_2 trial.

Five QTL were detected for GWT. One QTL, *gwt4*, was detected in all three trials. Two QTL, *gwt5* and *gwt8*, were detected in two of the three trials. The number of QTL for GWT detected across different environments was 3. The remaining 2 QTL, *gwt1* and *gwt2*, were the only ones detected in the F_2 trial. QTL for GWT detected in more than one trial did not have higher LOD scores than those detected in a single trial.

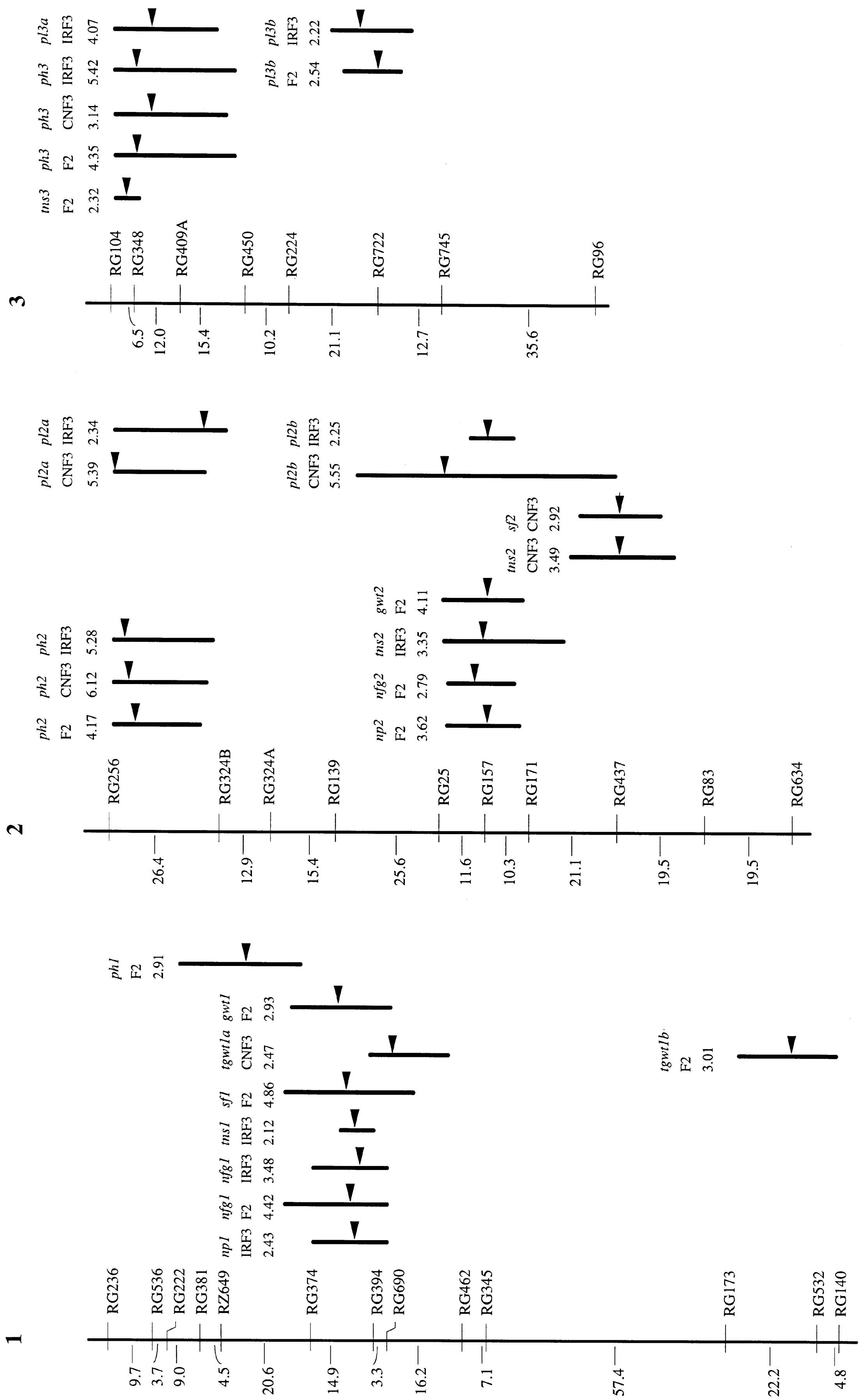
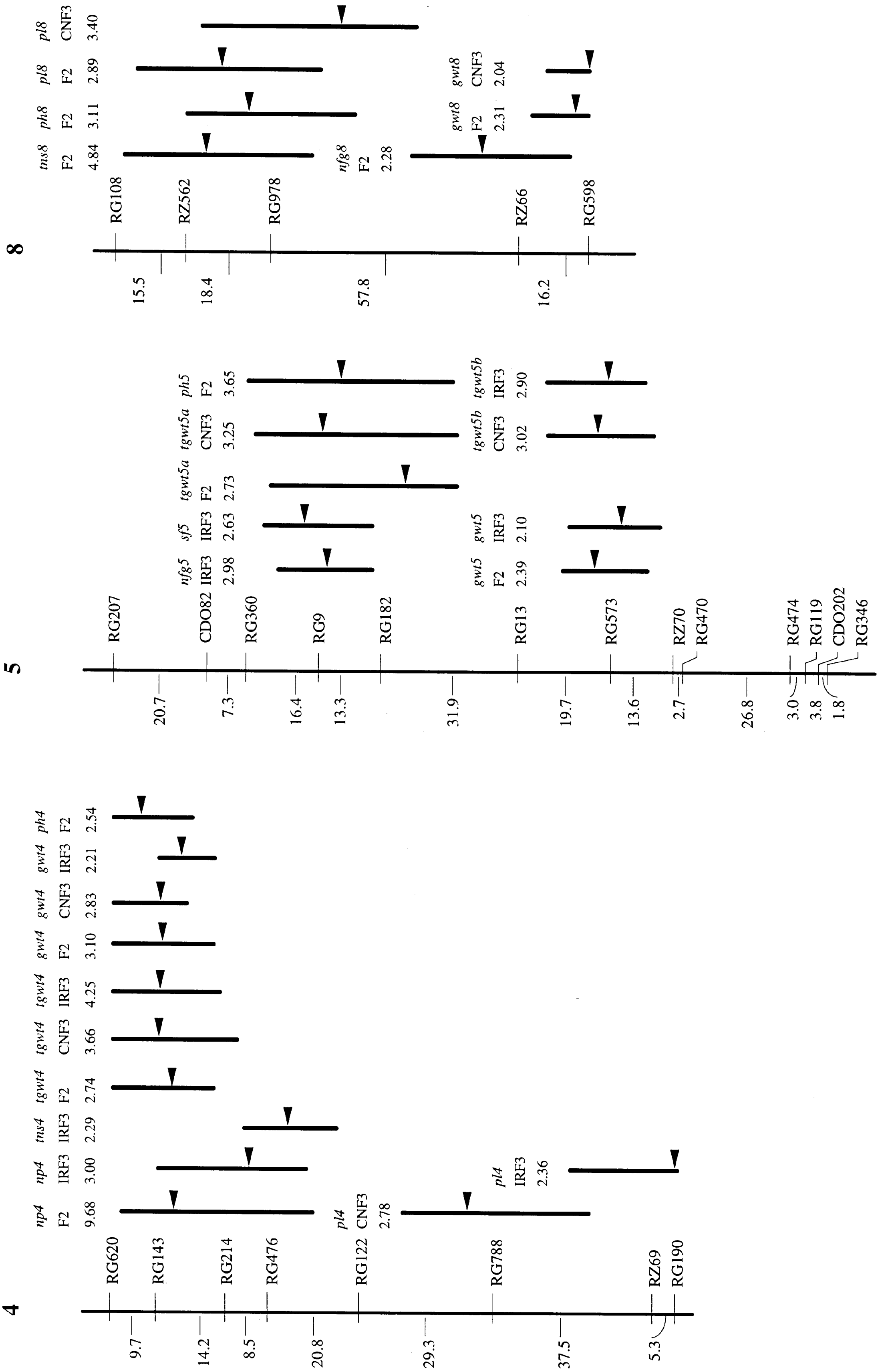


Fig. 1 See page 804 for legend



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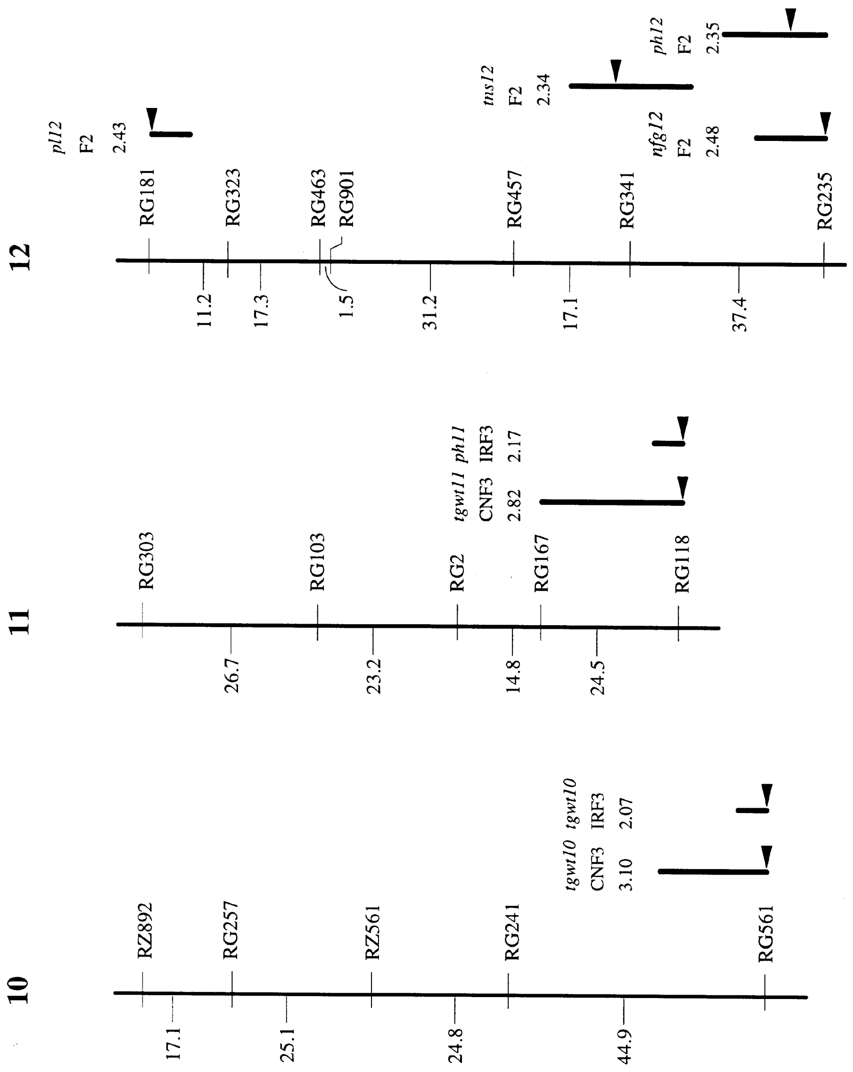

Fig. 1 RFLP linkage map showing locations of QTL for eight traits in the F_2, CNF_3 and IRF_3 trials. *Numbers at top* indicate chromosomes. Kosambi centiMorgans (cM) are to the *left* of chromosomes; *markers* are to the *right* of chromosomes. *Solid bar* to the right of the chromosomes represent intervals with LOD > 2, and *arrows* indicate the position of the peak LOD. QTL and the trial in which it was detected, and the peak LOD score are indicated *above the solid bar*

Table 3 The number of QTLs detected in the three trials

Trial	NP	NFG	TNS	SF	TGWT	GWT	PH	LP	Yield components	Plant stature	Total
F_2	2	4	3	1	3	5	7	3	18	10	28
CNF_3	0	0	1	1	5	2	2	4	9	6	15
IRF_3	2	2	3	1	4	2	3	5	14	8	22
One trial	2	4	5	3	3	2	6	2	19	8	27
Two trials	1	1	1	0	3	2	0	5	8	5	13
Three trials	0	0	0	0	1	1	2	0	2	2	4
Total	3	5	6	3	7	5	8	7	29	15	44

Eight QTL were detected for PH. Seven QTL for PH were detected in the F_2 trial, of which 2 QTL with the highest LOD scores (4.35 and 4.17 *vs.* 2.35 ~ 2.91), *ph2* and *ph3*, were also detected in both F_3 trials. The other 5 QTL, *ph1*, *ph4*, *ph5*, *ph8* and *ph12* were not detected in either F_3 trial. No additional QTL for PH were detected in the CNF_3 trial, while a new one with a LOD score of 2.17 was detected in the IRF_3 trial.

Seven QTL were detected for PL. Five QTL, *pl2a*, *pl2b*, *pl3b*, *pl4* and *pl8*, were detected in two of the three trials. Of the remaining 2 QTL, *pl3a* was only detected in the IRF_3 trial, and *pl12* was only detected in the

F_2 trial. When QTL detected in the same trial were compared, *pl3a* had the highest LOD score whereas *pl12* had the lowest LOD score.

A total of 10 QTL was detected in more than one trial for yield and its components and 7 for plant stature. It was obvious that a substantial proportion of QTL for TGWT, GWT and PL can be readily detected in different trials. For these three traits, QTL detected in more than one trial did not always have higher LOD scores than those detected in a single trial. On the other hand, only a small proportion of QTL for other traits could be detected across different trials, while QTL detected in more than one trial had higher LOD scores than those detected in a single trial.

Effects and actions of QTL readily detected in different traits

Theoretically, the additive effect will be equally expressed in both F_2 and F_3 populations, while only half of the dominance effect in the F_2 will be expressed in the F_3. QTL detected in more than one trial provided a chance to test the stability of the effects and action modes of QTL across different generations and environments.

In this study, QTL for the eight traits were located in 18 intervals on nine chromosomes. In 6 intervals, i.e. RZ649-RG374 and RG173-RG532 on chromosome 1, the only one on chromosome 11 and all 3 intervals on chromosome 12, no QTL for any given trait were detected in more than one trial (Fig. 1). In the other 12 intervals, at least 1 QTL was detected in more than one trial. The QTL located in these 12 intervals are listed in Table 4.

Altogether, 17 QTL, including 10 for yield components and 7 for plant stature, were detected in more than one trial. For 16 QTL, *nfg1, ph2, pl2a, pl2b, ph3, pl3b, np4, tgwt4, gwt4, pl4, twgt5a, twgt5b, gwt5, pl8, gwt8* and *tgwt*10, the direction of the additive effects of a given QTL was consistent among different trials (Table 4). In addition, the magnitude of the additive effect of a given QTL did not vary greatly among different trials, except that for *gwt4* and *gwt8* larger additive effects were shown in the F_2 trial than in the F_3 trials.

The only exception to the consistency of the directions of the additive effects was observed for the ambiguous QTL *tns2*. The additive effect of *tns2* was -21.5 in IRF_3 and 7.80 in the CNF_3.

Of the 17 QTL, 11 were detected in the F_2 trial and in either or both of the F_3 trials. Agreement to the expected action modes was shown for 8 QTL, including overdominance QTL *nfg1, ph3* and *gwt5*, dominance QTL *ph2* and *tgwt5a* and additive QTL *np4, tgwt4* and *gwt8*. For the remaining 3 QTL, *pl3b*, *gwt4* and *pl8*, the degree of dominance was higher in the F_3 than in the F_2. An additional 6 QTL were detected in both F_3 trials, but they were not detected in the F_2 trial. For 4 QTL, *pl2b*, *pl4*, *tgwt5b* and *tgwt10*, little difference was observed for their dominance effects and degrees of dominance between two trials. For *tns2*, agreement was observed for the dominance effect, while disagreement was observed for the degree of dominance due to conflicting results with respect to the additive effects. It can be seen that the gene action of a given QTL did not change greatly with a change in the environmental factors.

Clustering of QTL

It was shown that QTL for related traits were frequently detected in same intervals. In interval RG374-RG394 on chromosome 1, QTL were detected for all of the 6 yield traits. Moreover, all of the paternal alleles of these QTL reduced the trait value, whether or not they were detected in the same trial (Table 4). In other intervals in which QTL were detected across different trials, the directions of the additive effects of QTL were generally in agreement. These intervals included RG256-RG324B and RG25-RG437 on chromosome 2, RG104-RG409A on chromosome 3, RG143-RG214 on chromosome 4, RG9-RG182 on chromosome 5 and RZ562-RG978 and RZ66-RG598 on chromosome 8. It should be noted that in a majority of these intervals, QTL for yield components and plant stature were both involved.

In these intervals, there were two exceptions to the general consistency. In the interval RG25-RG437, the direction of the additive effects of *tns2* and *sf2* was different from that of other QTL. However, the interval harboring *tns2* and *sf2* was only adjacent to that harboring other QTL. Therefore, it was likely that they in fact represented 2 different intervals for QTL. A similar situation was observed in the interval RG143-RG214, where the direction of the additive effect of *tns4* was different from that of other QTL (Fig. 1).

An only obvious exception to the general consistency was found in the vicinity of RG573 on chromosome 5. The paternal alleles of *tgwt5b* detected in the CNF_3 and IRF_3 trials reduced TGWT, while that of *gwt5* detected in the F_2 and IRF_3 trials increased GWT.

It was also interesting to see that all intervals harboring QTL for GWT also harbored QTL for 1 or more yield components, and all intervals harboring QTL for PL were correspondent or adjacent to that for PH.

Discussion

Genotype × environment interactions are very important to the expression of QTL. In the present study,

Table 4 Intervals in which at least one QTL was detected in more than one trial

Interval	QTL[a]	Trial	LOD[b]	% Variation explained	a[d]	d[e]	d/a[f]
RG374-RG394	*nfg1*	F$_2$	4.42	17.2	– 1.39	48.18	– 34.66
		IRF$_3$	3.49	13.4	– 1.36	23.41	– 17.21
	np1	IRF$_3$	2.43	10.7	– 1.20	– 0.89	0.74
	tns1	IRF$_3$	2.12	12.1	– 1.45	27.33	– 18.85
	sf1	F$_2$	4.86	18.2	– 4.60	25.00	– 5.43
	tgwt1	CNF$_3$	2.47	7.6	– 0.74	– 0.61	0.82
	gwt1	F$_2$	2.93	10.7	– 1.96	12.40	– 6.33
RG256-RG324B	*ph2*	F$_2$	4.17	15.1	– 8.18	5.76	– 0.70
		CNF$_3$	6.12	21.3	– 8.47	5.43	– 0.64
		IRF$_3$	5.28	19.1	– 7.71	4.18	– 0.54
	pl2a	CNF$_3$	5.39	15.4	– 1.34	0.39	– 0.29
		IRF$_3$	2.34	11.0	– 0.74	– 1.02	1.38
RG25-RG437	*pl2b*	CNF$_3$	5.55	17.6	– 1.38	– 0.43	0.31
		IRF$_3$	2.25	7.8	– 1.00	– 0.04	0.04
	np2	F$_2$	3.62	9.3	– 1.39	2.27	– 1.63
	nfg2	F$_2$	2.79	9.0	– 21.45	27.65	– 1.29
	tns2	CNF$_3$	3.49	9.4	7.80	18.6	2.38
	tns2	IRF$_3$	3.35	13.3	– 21.52	17.16	– 0.80
	sf2	CNF$_3$	2.92	8.1	5.10	4.83	0.95
	gwt2	F$_2$	4.11	11.4	– 9.14	7.10	– 0.78
RG104-409A	*ph3*	F$_2$	4.35	11.1	– 6.01	– 7.02	1.17
		CNF$_3$	3.14	10	– 5.32	– 4.06	0.76
		IRF$_3$	5.42	19.1	– 7.73	– 4.03	0.52
	pl3a	IRF$_3$	4.07	15.4	– 1.23	– 0.48	0.39
	tns3	F$_2$	2.32	6.6	– 16.73	– 44.54	2.66
-RG722-	*pl3b*	F$_2$	2.54	6.7	– 1.27	0.26	– 0.20
		IRF$_3$	2.22	11.8	– 0.80	– 0.89	1.11
RG143-RG214	*np4*	F$_2$	9.68	26.1	– 2.92	0.18	– 0.06
		IRF$_3$	3.00	10.9	– 1.41	– 0.08	0.06
	tgwt4	F$_2$	2.74	8.5	– 1.39	0.54	– 0.39
		CNF$_3$	3.66	11.0	– 1.08	– 0.14	0.13
		IRF$_3$	4.25	14.6	– 1.06	– 0.74	0.70
	gwt4	F$_2$	3.10	8.7	– 7.91	0.28	– 0.04
		CNF$_3$	2.83	8.5	– 1.76	1.21	– 0.69
		IRF$_3$	2.21	9.7	– 1.70	– 1.82	1.07
	tns4	IRF$_3$	2.29	11.5	16.76	7.06	0.42
	ph4	F$_2$	2.54	8.9	– 5.29	7.00	– 1.32
-RG788-	*pl4*	CNF$_3$	2.78	12.0	1.17	– 0.24	– 0.21
		IRF$_3$	2.34	8.4	0.92	0.10	0.11
RG9-RG182	*tgwt5a*	F$_2$	2.73	14.8	– 1.55	– 1.33	0.86
		CNF$_3$	3.25	11.5	– 1.06	– 0.18	0.17
	nfg5	IRF$_3$	2.98	12.6	– 8.35	18.53	– 2.22
	sf5	IRF$_3$	2.63	14.2	– 5.20	6.60	– 1.27
	ph5	F$_2$	3.65	10.5	– 7.45	1.89	– 0.25
-RG573-	*tgwt5b*	CNF$_3$	3.02	11.4	– 0.72	1.07	– 1.49
		IRF$_3$	2.90	10.9	– 0.64	1.08	– 1.69
	gwt5	F$_2$	2.39	11.0	1.27	12.71	10.01
		IRF$_3$	2.10	8.4	1.83	2.21	1.21
RZ562-RG978	*pl8*	F$_2$	2.89	9.7	1.23	0.93	0.76
		CNF$_3$	3.40	37.6	1.02	2.45	2.40
	tns8	F$_2$	4.84	15.7	35.76	54.21	1.52
	ph8	F$_2$	3.11	10.9	5.77	6.19	1.07
RZ66-RG598	*gwt8*	F$_2$	2.31	7.6	– 7.96	0.37	– 0.05
		CNF$_3$	2.04	6.4	– 1.53	– 0.69	0.45
	nfg8	F$_2$	2.28	14.1	– 30.86	9.45	– 0.31
RG241-RG561	*tgwt10*	CNF$_3$	3.10	10.1	– 1.00	0.41	– 0.41
		IRF$_3$	2.07	8.7	– 0.89	0.19	– 0.21

[a] QTLs are named by trait abbreviations plus chromosomal number

[b] Log_{10} likelihood

[c] Percentage phenotypic variance explained

[d] Additive gene effect at putative QTL

[e] Dominance effect at the putative QTL; the value of d estimated using F$_3$ data is expected to be half of the actual value

[f] Degree of dominance

QTL mapping was undertaken using F_2 and F_3 populations of an *indica/indica* cross TSA/CB. The comparison across the three trials was confounded by three factors, the generation, the plant density and the trial site.

In the present study, only 17 QTL of the total 44 QTL were detected in more than one trial, indicating that individual QTL seem to be sensitive to the environment. This was in agreement with the results reported by Paterson et al. (1991). However, QTL for different traits showed different stabilities. A substantial proportion of QTL for GWT, TGWT and PL was active across generations and/or environments, although the QTL for NP, NFG, TNS, SF and PH changed greatly across different trials. In addition, QTL with higher LOD scores for NP, NFG, TNS and PH could be more readily detected than those with lower LOD scores. Therefore, the present study tends to support the general conclusion made by Tanksley (1993), i.e. a substantial proportion of QTL affecting a trait can be identified under different environments, especially QTL having major effects.

It is interesting that the most complicated trait, GWT, was more readily detected than its components, NP and NFG. The pleiotropism of genes may provide an answer. Classical quantitative genetics assumes that trait correlation can be attributed to the effect of pleiotropy or to the tight linkage of genes. If pleiotropism was the major reason, the coincidence of both the locations of QTL for related traits and the directions of their genetic effects can be expected. If the close linkage of genes was the major reason, the directions of the genetic effect of QTL for different traits may be different although the coincidence of the locations of QTL can still be expected. A general coincidence of the locations and the directions of the genetic effects of QTL for related traits was observed in the present study, and all intervals harboring QTL for GWT also harbored QTL for one or more yield components. This suggested that pleiotropism rather than the close linkage of different QTL might be the major reason for the correlation of related traits.

When gene pleiotropism was considered, 23 of the 29 QTL for yield and its components and 9 of the 15 QTL for plant stature were detected in more than one trial. Only *tgwt1b, tns3, tns8, tgwt11, nfg12* and *tns12* for yield components and *ph1, ph4, ph5, ph11, pl12* and *ph12* for plant height were each detected in a single trial. In addition, multiple QTL in a same interval generally acted in the same direction. It therefore appeared that the detection of chromosomal segments harboring QTL and the directions of the effects of these intervals were hardly affected by environmental factors.

In the present study, while the plant density employed in the CNF_3 trial was much higher than that employed in the other two trials, it was a normal plant density used in commercial rice production in China. Consequently, fewer QTL were detected in the CNF_3 trials. If the conclusion of gene pleiotropism is proven to be true, every effort, including the employment of a low degree of plant density, should be made to detect as many intervals harboring QTL as possible under a single environment. Normal plant density may then be employed for a confirmation of the putative QTL and for an analysis of the QTL × environment interactions, which will facilitate marker-assisted selection in rice breeding.

Acknowledgements We greatly acknowledge the financial support provided by the Chinese Rice Genome Program, the Rockefeller Foundation's Rice Biotechnology Program and the Asian Rice Biotechnology Network.

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