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Effects of genetic background and environment on QTLs and epistasis for rice (*Oryza sativa* L.) panicle number

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Abstract A double-haploid (DH) population and a recombinant inbred (RI) line population, derived from a cross between a tropical *japonica* variety, Azucena, as male parent and two *indica* varieties, IR64 and IR1552, as female parents respectively, were used in both field and pot experiments for detecting QTLs and epistasis for rice panicle number in different genetic backgrounds and different environments. Panicle number (PN) was measured at maturity. A molecular map with 192 RFLP markers for the DH population and a molecular map with 104 AFLP markers and 103 RFLP markers for the RI population were constructed, in which 70 RFLP markers were the same. Six QTLs were identified in the DH population, including two detected from field experiments and four from pot experiments. The two QTLs, mapped on chromosomes 1 and 12, were identical in both field and pot experiments. In the RI population, nine QTLs were detected, five QTLs from field conditions and four from the pot experiments. Three of these QTLs were identical in both experimental conditions. Only one QTL, linked to CDO344 on chromosome 12, was detected across the populations and experiments. Different epistasitic interaction loci on PN were found under different populations and in different experimental conditions. One locus, flanked by RG323 and RZ801 on chromosome 1, had an additive effect in the DH population, but epistatic effects in the RI population. These results indicate that the effect of genetic background on QTLs is greater than that of environments, and epistasis is more sensitive to genetic background and environments than main-effect QTLs. QTL and epistatic loci could be interchangeable depending on the genetic backgrounds and probably on the environments where they are identified.

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Introduction

The development of molecular maps in rice (McCouch et al. 1988; Causse et al. 1994; Kurata et al. 1994) has facilitated the identification of QTLs controlling important quantitative characters. Using molecular genetic linkage maps and QTL mapping, it is possible to estimate the number of loci controlling genetic variation and to characterize these loci with regard to their map positions, gene action and phenotypic effects, and to analyze their pleiotropic and epistatic interactions with other QTLs. Since the introduction of molecular markers, QTL mapping in numerous species and for various traits has been well-documented (Lin et al. 1996; Xiao et al. 1996).

Epistasis, or interactions between non-allelic genes, is an important factor that affects the phenotypic expression of genes and genetic variation in populations. Several reports have revealed evidence for epistatic interactions between QTLs (Paterson et al. 1988, 1991; Fatokun et al. 1992; Li et al. 1995a, b). Result from both classic evolutionary studies and recent QTL mapping experiments suggest the possible presence of three types of epistasis affecting complex traits: (1) interactions between QTLs, (2) interactions between QTLs and 'background' (modifying) loci, and interactions between 'complementary' loci. Genetic background effects on quantitative traits have also been well-documented in tomato (Tanksley and Hewitt 1988), rice (Li et al. 1997, 1998); soybean (Lark et al. 1995) and maize (Doebley et al. 1995; Cockerham and Zeng. 1996).

Panicle number (PN) plays an important role in the formation of yield in rice. Rao (1997) reported that PN has the highest direct positive effect on grain yield. PN is a quantitative trait. It is affected by various environmental factors including soil-fertilization, planting density and climatic factors such as light, temperature and water

supply. Many studies have identified QTLs for PN in rice (Xiao et al. 1996, 1998; Lin et al. 1996; Wu et al. 1996; Zhuang et al. 1997). These results indicated that PN is controlled by a series of QTLs with different expression in different genetic populations and in different environments. However, epistasitic loci for PN were not well documented and the relations among the genetic factors were not clear.

The present paper describes an analysis of QTLs and epistatic loci for PN, an important yield-component in rice, in different genetic backgrounds and environments based on greenhouse pot experiments and field experiments using two populations with one common male parent. The results were explored to compare the number and location of QTLs and epistatic loci mapped across different populations and/or environments, and to study the relationship between QTLs and environment and epistatic loci.

Material and methods

Plant material and panicle-number measurement

A double-haploid (DH) population consisting of 134 lines (Guiderdoni et al. 1992) and a recombinant inbred (RI) population consisting of 150 lines **(**Wu et al. 2000**)**, derived from a cross between a tropical *japonica* male parent, Azucena, and *indica* female parents, IR64 and IR1552, respectively, were used in this study. The variation in PN among the two populations was evaluated in both field and pot experiments in HangZhou, China. In the field experiment, the 134 DH lines and the 150 RI lines and their parents, were evaluated in a randomized complete design with two replications. The germinated seeds were sown in a seedling bed on May 10, 1999, and seedlings were transferred to a paddy field 30 days later, with a single plant per hill spaced at 15 × 20 cm. Four-row plots were planted with eight plants per row, with parents being grown after every tenth plot as a control. The central eight plants in each plot were used for measuring panicle number. In the pot experiments, two seedlings of every line were potted with 15 kg of air-dried soil per pot and every line was planted in three pots. Panicle number was recorded after harvest. The temperature in the greenhouse ranged from 22°C to 39°C. The experiments were maintained under flooded conditions during the growing period. Fertility and cultivation practices were consistent with optimum rice production for these regions.

Molecular map construction

A molecular map with 104 AFLP markers and 103 RFLP markers was constructed for the RI population (IR1552 × Azucena). RFLP markers were tested for polymorphism by hybridizing radioactive DNA (Feinberg and Vogelstein 1984) from rice genomic clones (RG), rice cDNA (RZ) and oat cDNA (CDO) to fragments of plant DNA separated on agarose gels after digestion with the six restriction enzymes *Dra*I, *Eco*RI, *Eco*RV, *Hind*III, *Sca*I and *Xba*I, respectively. One hundred and three informative RFLP markers distributed throughout 12 chromosome were selected and scored on 150 RI lines, among which 70 RFLP markers were mapped on the molecular map based on the DH population.. AFLP analysis was conducted following the method of Vos et al. (1995), with minor modifications employed by Maheswaran et al. (1997). *Eco*RI/*Mse*I systems I (Life Technologies, 10544-013) were used to generate polymorphic AFLP markers, and a total of 16 primer-pair combinations were employed. One hundred and four AFLP markers were assigned to the 12 linkage groups at LOD >3 based on their linkage to the anchor RFLP markers using the Mapmaker/EXE 1.0 program (Lander 1993). The assigned markers were ordered using multi-point analysis at a LOD value of 3. The ripple command was used to verify the order of markers on each chromosome. The map distance (cM) was derived based on the Kosambi function.

A molecular map of the DH population comprising 175 molecular markers was provided by the International Rice Research Institute (Huang et al. 1994)**.** Eighteen new RFLP markers were added to the base map using the method described above.

Statistical analysis

One-way ANOVA (SAS/6.11, GLM) and interval-mapping analysis (Mapmaker/QTL) (Lander 1993) were performed for detecting molecular markers and QTLs associated with the variations in PN of the DH population in the field (PNF(DH)), PN of the DH population in the pots [PNP(DH)], the PN of the RI population in the field [PNF(RI)] and the PN of the RI population in the pots [PNP(RI)]. Epistasis for variations in the parameters was analyzed using the program QTLmapper (Wang et al. 1999). $P < 0.005$ for the Type-I error and a log-10 likelihood ratio (LOD) value of 2.4 were used as criteria to indicate putative QTL positions. The effects of a single allele substitution (assuming additivity between alleles) and R^2 values for each of the putative QTLs were estimated. Correlation analysis between the measurement parameters was performed using the correlation procedure of SAS.

Results

Phenotypic performance

The parental performance and the segregation for PNF(DH), PNP(DH), PNF(RI) and PNP(RI) are shown in Fig. 1. The panicle numbers of IR64 and IR1552 in both field and pot experiments were significantly ($P < 0.01$) higher than those of Azucena. All the parameters were normally distributed. Transgressive segregants with a PN higher than those of IR64 and IR1552, or lower than that of Azucena, were observed in both populations and environments. PNF(DH) and PNF(RI) were highly significantly positively correlated with PNP(DH) and PNP(RI), respectively ($r = 0.44^{**}$ in the DH population, $r = 0.41^{**}$ in the RI population).

QTL analysis

QTL analysis was performed using both single-marker analysis and interval mapping. In the DH population, two QTLs were detected in the field experiment, located on chromosomes 1 and 12 and designated PNF(DH)1 and PNF(DH)12 (Table 1 and Fig. 2). These two QTLs explained about 14% and 8% of the total variation in PN, respectively. The positive alleles of the two QTLs were from IR64. In the pot experiments, four QTLs were detected. Two of them, on chromosome 1 and 12, in identical locations to those in the field experiment, were named PNP(DH)1 and PNP(DH)12 (Table 1 and Fig. 2). The contribution of PNP(DH)1 to the total variation in PN was similar to that of PNF(DH)1, but that of PNP(DH)12 was about 10% higher than that of PNF(DH)12 (Table 1). The other two QTLs were located on chromosomes 4 and 10

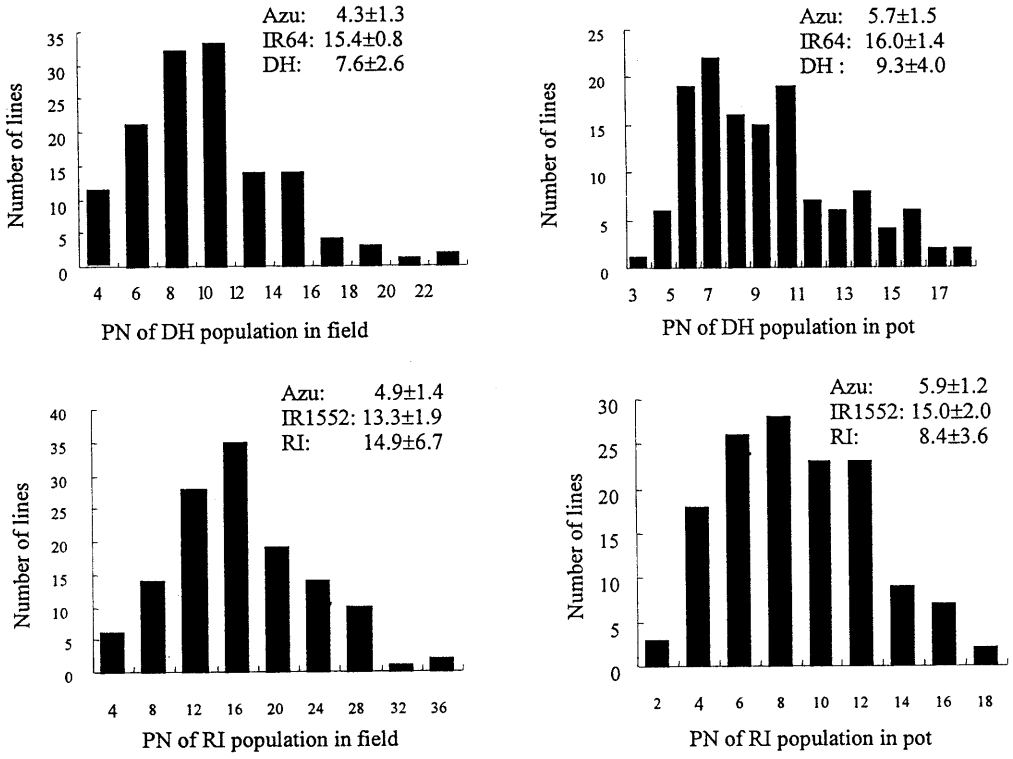

Fig. 1 Distribution of panicle number in a DH and a RI population in field and in pot experiments

Table 1 QTLs associated with panicle number as indicated by single-marker analysis at the $P < 0.005$ threshold and interval-mapping analysis (LOD > 2.4)

QTLs	Marker interval	LOD[a]	Marker	Allele means		*P*	R^2
				IR64	Azucena		
PNF(DH)1	RG323/RZ801	5.42	RG323	11.11	9.10	0.0001	0.136
PNF(DH)12	CDO344/RG958	2.42	RG958	10.72	9.34	0.0031	0.075
PNP(DH)1	RG323/RZ801	4.13	RG323	9.96	8.17	0.0001	0.123
PNP(DH)4	RG163/RZ23	3.05	RZ23	9.44	8.05	0.0045	0.072
PNP(DH)10	G2155/RG134	3.26	G2155	7.94	9.75	0.0001	0.116
PNP(DH)12	CDO344/RG958	4.81	RG958	9.89	7.73	0.0001	0.173
QTLs	Marker interval	LOD[a]	Marker	IR1552	Azucena	*P*	R^2
PNF(RI)7	RG650/AGG-CAG8	3.67	RG650	16.93	11.61	< 0.0001	0.140
PNF(RI)9	RG667/RG141	3.13	RG667	16.21	11.49	0.0005	0.095
PNF(RI)11	AAG-CAT10/RZ797	2.42	RZ797	12.73	16.28	0.0003	0.070
PNF(RI)12	RG341/AGG-CTT4	2.61	RG341	16.17	11.04	0.0001	0.148
PNF(RI)12b	CDO344/RG543	2.64	CDO344	16.38	12.11	0.0005	0.095
PNP(RI)4	RZ69/AAC-CAG2	3.86	RZ69	6.95	9.59	< 0.0001	0.131
PNP(RI)7	RG650-AGG-CAG8	4.92	RG650	9.47	6.47	< 0.0001	0.159
PNP(RI)12	RG341/AGG-CTT4	3.28	RG341	9.03	6.47	< 0.0001	0.124
PNP(RI)12a	CDO344/RG543	3.95	RG543	9.16	6.58	< 0.0001	0.130

[a] Log_{10}-likelihood value

and designated PNP(DH)4 and PNP(DH)10 (Table 1, Fig. 2). PNP(DH)4 and PNP(DH)10 explained about 7% and 12% of the total phenotypic variation in PN. The positive alleles at PNP(DH)1, PNP(DH)4 and PNP(DH)12 were from IR64, but that at PNP(DH)10 was from Azucena.

In the RI population, five QTLs were detected from the field experiment, and four QTLs were detected from the pot experiment. The five QTLs for PNF(RI) were located on chromosomes 7, 9, 11 and 12, and designated PNF(RI)7, PNF(RI)9, PNF(RI)11, PNF(RI)12a and PNF(RI)12b (Table 1, Fig. 3). The contribution of the five QTLs to the total variation in PN was as high as 15% for PNF(RI)12a and as low as 7% for PNF(RI)11. Four QTLs for PNP(RI) were located on chromosomes 4, 7 and 12, and designated PNP(RI)4, PNP(RI)7, PNP(RI)12a and PNP(RI)12b. The contribution of the four QTLs to the to-

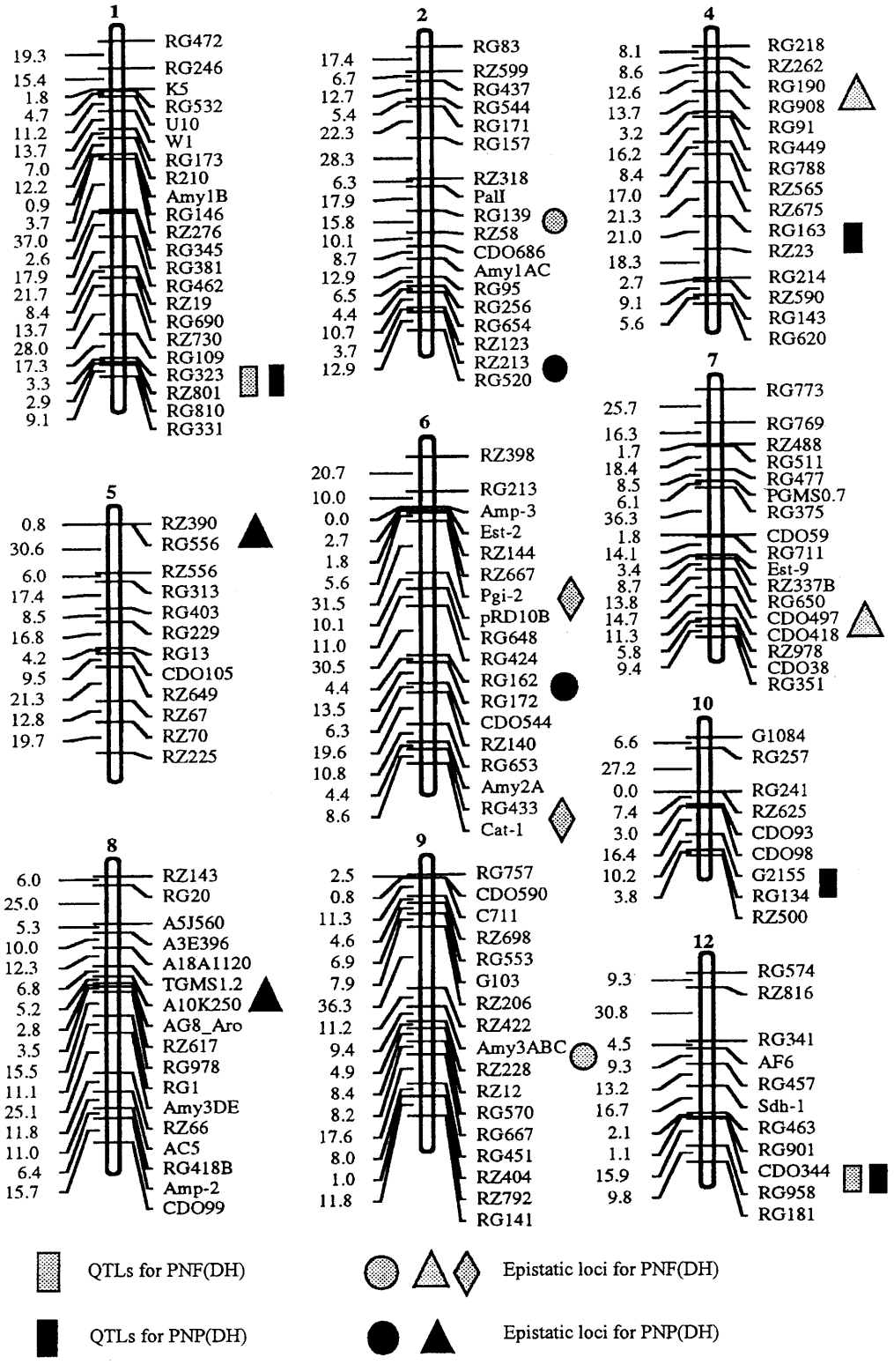

Fig. 2 The most likely location of QTLs and epistatic loci for PN in a DH population derived from a cross between IR64 and Azucena. The symbols for different parameters are shown above. The designation on the right is the marker name, and on the left is the map distance based on the Kosambi function

tal variation in PN ranged from 16% for PNP(RI)7 to 12% for PNF(RI)12a (Table 1). The positive alleles at PNP(RI)7, PNP(RI)12a and PNPRI(12)b were from IR1552, while that at PNP(RI)4 was from Azucena. The three QTLs on chromosome 7, flanked by RG650 and AGG-CAG8, and on chromosome 12, flanked by RG341 and AGG-CTT4, and by CDO344 and RG543, were identical in both the field and pot experiments. The contributions to the total variation in PN of the two QTLs flanked by RG650 and AGG-CAG8 on chromosome 7, and by RG341 and AGG-CTT4 on chromosome 12, were similar in both field and pot experiments.

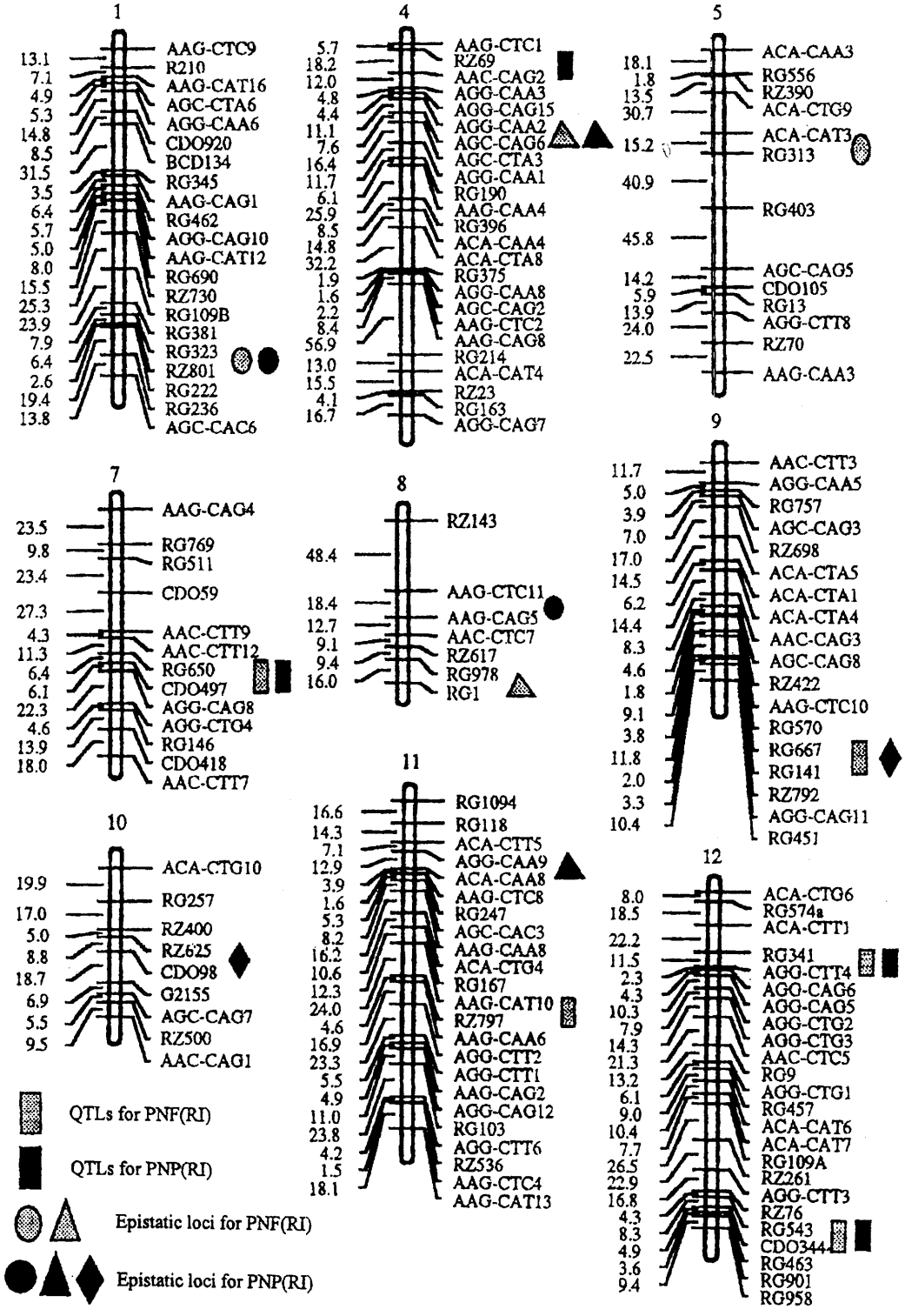

Fig. 3 The most likely location of QTLs and epistatic loci for PN in RI population derived from a cross between IR1552 and Azucena. The symbols for different parameters are shown. The designation on the right is the marker name, on the left is the map distance based on the Kosambi function

Comparing results from all four cases, it was shown that the negative allele in Azucena at the locus linked with CDO344 on chromosome 12 was expressed in both the genetic backgrounds of IR64 and IR1552 under both pot and field conditions.

Epistatic effect analysis

Different epistatic effects were identified under different experimental conditions in the DH population. Three pairs of epistatic loci for PNF(DH) were detected under field conditions (Table 2). Each pair of epistatic loci explained about 10% of the total variation in PNF(DH).

Table 2 Epistatic loci associated with panicle number as indicated by the QTLmapper program

Trait	Chrom.	Marker interval	Chrom.	Marker interval	LOD value[a]	AAij[b]	R^2
PNF(DH)	2	RG139/RZ58	9	Amy3ABC/RZ228	3.5	–0.79	0.10
	4	RG190/RG908	7	CD=497/CDO418	2.9	–0.81	0.10
	6	Pgi-2/pRD10B	6	RG433/Cat-1	3.1	–0.86	0.11
PNP(DH)	2	RZ13/RG520	6	RG162/RG172	4.1	0.97	0.12
	5	RZ390/RG556	8	TGMS1.2/A10K250	3.4	–1.26	0.20
PNF(RI)	1	RG323/RZ901	5	ACA-CAT3/RG313	5.9	2.00	0.07
	4	AGC-CAA2/AGC-CAG6	8	RG978/RG1	7.8	2.81	0.11
PNP(RI)	1	RG323/RZ801	8	AAG-CTC11/AAG-CAG5	4.7	1.11	0.07
	4	AGC-CAA2/AGC-CAG6	11	AGG-CAA9/ACA-CAA8	4.2	1.06	0.06
	9	RG667/RG141	10	RZ625/CDO98	5.9	1.35	0.10

[a] Log_{10}-likelihood value
[b] AAij is the additive × additive epistatic effect

From the pot experiment, only two pairs of epistatic loci were detected, on chromosomes 2/6 and 5/8**,** but the pairs located on chromosomes 5 and 8 explained about 20% of the total phenotypic variation (Table 2).

In the RI population, two pairs of epistatic loci for PNF(RI) were identified (Table 2). One epistatic pair located on chromosomes 1 and 5 explained about 7% of the total variation in PNF(RI). From the pot experiment, three epistatic loci were identified (Table 2). One epistatic pair located on chromosomes 1 and 8 explained about 7% of the total phenotypic variation. It was noted that the locus on chromosome 1 flanked by RG323/RZ801 which was detected as a QTL in the DH population showed a strong interaction locus with two loci on chromosomes 5 and 8, respectively, in this case.

Discussion

The two female parents, IR64 and IR1552, have similar panicle number under both pot and field conditions, and were about three times than that of Azucena (Fig. 1); but the QTLs detected for PN in the DH population (IR64 × Azucena) was different from those identified in the RI population (IR1552 × Azucena). In the pot experiment, the number of QTLs detected was the same in the two populations. In the field conditions, however, five QTLs in the RI population were detected, while only two QTLs were found in the DH population. In the greenhouse, the environmental conditions were relatively uniform compared with those in field; therefore, the difference in QTL numbers detected in the two populations under field conditions may reflect the difference in response to environments in the two female parents.

Based on our results, only one QTL, located on chromosome 12 and linked to CDO344, was detected in both populations under pot and field conditions, indicating that this QTL would be a candidate for use in marker-aid selection for higher panicle number. One QTL on chromosome 4 was identified in both populations under field conditions, but it may not be the same locus due to its different allelic effects (Table 1).

The effects of environments on QTLs have been recognized by others. Paterson et al. (1991) identified 29 QTLs for quantitative traits of tomato using F_2 and F_3 populations in three environments, but only four QTLs were significant in all environments. Freyer and Douches (1994) found in potato that only two of the ten QTLs were identical in all of the three environments tested. Lu et al. (1996) identified 22 QTLs for six agronomic traits of rice using a DH population in three diverse environments, but only seven were detected in all three environments. In the present study, different QTLs were also detected in pot and field experiments in the same population, and the different effects of the same QTL were also found in the pot and field experiments. The QTLs with larger genetic effects could be more readily detected than those with smaller effects. This supported the conclusion that a substantial proportion of QTLs affecting a trait can be identified under different environments, especially QTLs having major effects.

Twelve QTLs for panicle number in rice have been identified, distributed on six chromosomes (Lin et al. 1996; Wu et al. 1996; Xiao et al. 1996, 1998; Zhuang et al. 1997). Only two QTLs within RG25-RG437 on chromosome 2 and within RG143-RG214 on chromosome 4 were found in more than one experiment. These results indicated that panicle number is controlled by a series of QTLs with different expression in different genetic populations. In the present study, the detection of QTLs for panicle number were identified in two populations, which were derived from the same male parent, Azucean. Among the QTLs identified from both populations, only one QTL, located on chromosome 12 and linked to CDO344, was detected in both populations. This could be due to the major genetic diversity between the female parents. The level of polymorphism between IR64 and IR1552 was 42.3%, which supported the above conclusion (data not shown). The QTLs identified in this study were not coincident with the previously reported QTLs. The detection of QTLs was based on the difference of alleles between the parents. It means that the QTLs detected in different populations may not be coincident due to the different genetic diversity between the parents.

A considerable body of classical evidence has strongly suggested the prevalence of epistatic effects on quantitative traits in genetic populations (Spickett and Thoday 1966; Allard 1988). Interaction analysis of rice yield and it's components revealed evidence for the presence of epistasis between QTLs (Li et al. 1997; Li et al. 1998; Xiao et al. 1998). Different epistatic effects were detected in the two populations and under the two experimental conditions, which indicates that the effects of genetic background and environments are greater on epistatic loci than on QTLs. Li et al. (1998) suggested the possible presence of three types of epistasis affecting complex traits. In this study, all of the epistatic loci did not interact with the identified QTLs in same population or the same environment, which means that only the third type of epistasis, involving interactions between 'complementary' genes, was observed. Although this type of epistasis is perhaps the most important one, it has been less often reported. This might be due to the weak ability of the previous method for detecting epistasis. Using QTLmapper 1.0 based on mixed linear models, many epistatic interactions between 'complementary' genes were detected and these belonged to the major type of epistasis, indicating the importance of this type of epistasis. It is noted that in the DH population the locus (RG323/RZ801) was detected as a QTL, while in the RI population the locus was an allele-site involved in an epistatic interaction. In other words, QTL and epistatic loci could be interchangeable in the two populations. In addition, some epistatic loci detected in this study were identical to the previously reported QTLs. For example, the epistatic loci within Pgi2-pRD10B on chromosome 6 and within RZ625-CDO98 on chromosome 10 were identical to the QTLs reported by Lin (1996) and Courtois (1995), respectively. These results supported the hypothesis that QTLa and their epistatic loci are interchangeable, depending on the genetic background and probably on the environment in which they were identified (Li et al. 1997). It is reasonable to assume that an epistatic locus can be detected as a QTL when alleles at another locus with which it interacts is the same between the parents. In other words, QTLs and epistatic loci are interchangeable depending on their genetic backgrounds. Thus, more epistatic loci were detected in the populations of parents with greater genotypic differences.

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