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Identification of quantitative trait loci and epistatic interactions for plant height and heading date in rice

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Abstract Appropriate heading date and plant height are prerequisites for attaining the desired yield level in rice breeding programs. In this study, we analyzed the genetic bases of heading date and plant height at both single-locus and two-locus levels, using a population of 240 $F_{2:3}$ families derived from a cross between two elite rice lines. Measurements for the traits were obtained over 2 years in replicated field trials. A linkage map was constructed with 151 polymorphic marker loci, based on which interval mapping was performed using Mapmaker/QTL. The analyses detected six QTLs for plant height and six QTLs for heading date; collectively the QTLs for heading date accounted for a much greater amount of phenotypic variation than did the QTLs for plant height. Two-way analyses of variance, with all possible two-locus combinations, detected large numbers (from 101 to 257) of significant digenic interactions in the 2 years for both traits involving markers distributed in the entire genome; 22 and 39 were simultaneously detected in both years for plant height and heading date, respectively. Each of the interactions individually accounted for only a very small portion of the phenotypic variation. The majority of the significant interactions involved marker loci that did not detect significant effects by single-locus analyses, and many of the QTLs detected by single-locus analyses were involved in epistatic interactions. The results clearly demonstrated the importance of epistatic interactions in the genetic bases of heading date and plant height.

Keywords *Oryza sativa* L. · Molecular mapping · Heading date · Plant height · Quantitative trait loci · Digenic interaction

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Introduction

Heading date is a major determinant of the regional and seasonal adaptation of rice varieties, and plant height is one of the most important traits related to plant status and yield potential. Appropriate heading date and plant height are therefore pre-requisites for attaining the desired yielding level in rice breeding programs. Thus, understanding the genetic bases underlying the inheritance of the two traits has significant implications for rice improvement.

The recent advances in molecular marker technology and developments of high-density molecular marker linkage maps in rice (Causse et al. 1994; Harushima et al. 1998) have provided a powerful tool for elucidating the genetic bases of quantitatively inherited traits, including most of the agriculturally important traits. There have been many studies attempting to dissect the genetic bases of heading date and plant height using molecular marker-based genetic analyses. For heading date, at least nine chromosomal regions have been reported as showing significant effects in various rice populations (Li et al. 1995; Lin et al. 1996; Lu et al. 1996; Xiao et al. 1996; Yano et al. 1997; Xiong et al. 1999). Major QTLs detected with relatively large effects in most of the studies correspond well with the photoperiod-sensitivity genes identified previously. Yamamoto et al. (1998), using advanced backcross progeny, precisely mapped a major QTL on chromosome 6 (*Hd-1*), together with other two minor QTLs conditioning the trait. Additional analyses of F_2 populations from crosses between near-isogenic lines for the three QTLs revealed that the QTLs interacted with each other (Lin et al. 2000). Yano et al (2000) further defined a genomic region of 12 kb as a candidate for *Hd-1*, and functionally determined the gene of the *Hd-1* locus, which is allelic to *Sel* (photoperiod sensitive gene) and has high homology with CONSTANTS, a gene for flowering time in Arabidopsis.

There were also several reported molecular marker-based genetic analyses of plant height in rice, which detected a number of QTLs on nine of the 12 chromosomes

(Li et al. 1995; Lin et al. 1996; Lu et al. 1996; Xiao et al. 1996). The most comprehensive study is probably that of Huang et al. (1996) who analyzed QTLs for plant height in five populations, and found that 13 previously identified major dwarfing genes were located in close proximity to these QTLs. More recently, a gene for plant height mapped on chromosome 5 was cloned using a map-based cloning strategy (Ashikari et al.1999). This is a gene for the gibberellin-insensitive dwarf mutation in Dwarf 1 (*D1*) encoding the α-subunit of the GTP-binding protein (G protein).

However, all of the above-mentioned results were based on single-locus analyses, or interactions between QTLs detected by single-locus analyses. Recent genetic analyses using molecular markers in several plant species have clearly shown that, in addition to single-locus QTLs, epistatic interactions play an important role in the genetic basis of quantitative traits (Lark et al. 1995; Maughan et al. 1996; Li et al. 1997; Yu et al. 1997). A majority of the interactions involved loci that did not show significant effects by single-locus analyses, and many of the epistatic interactions also involved the QTLs that were detected by single-locus analyses. In such systems, the effect of genotypes at one locus would be dependent on the genotypes of other loci with which the locus interacted; interpretations and conclusions based on the single-locus analyses are therefore biased or inadequate in one way or another.

In this study, we analyzed the genetic bases of heading date and plant height using a $F_{2:3}$ population derived from a cross between two rice lines by detecting single-locus QTLs and digenic epistatic interactions. The objective of the study was to characterize the genetic bases of heading date and plant height at both single-locus and two-locus levels.

Materials and methods

Materials and field planting

The genetic material involved 240 F_3 families, each derived from bagged seeds of a single F_2 plant from a cross between Zhenshan 97 and Minghui 63, the parents of Shanyou 63, the most-widely grown rice hybrid in China. The $F_{2:3}$ families together with two parents and the F_1 were transplanted into the field of the experimental farm of Huazhong Agricultural University in the 1994 and 1995 rice-growing seasons. The field planting followed a randomized complete block design with three replications. The plants were laid out at a distance of 17 cm between plants within a row and the rows were 27 cm apart. The field management followed essentially the normal agricultural practice. Only the 15 plants in the middle of each row were used for trait scoring. The height of each plant was measured at maturity as the length of the tallest tiller from the ground to the tip of the panicle. Heading date was recorded as the day of emergence of the first panicle for each plant in the number of days after July 1.

Molecular-marker assay

Approximately equal amounts of leaf tissues from 15 to 20 plants of each F_3 family were harvested and bulked for DNA extraction. Two classes of markers, RFLPs (restriction fragment length polymorphisms) and SSRs (simple sequence repeats), were used for surveying parental polymorphisms. RFLP analysis including digestion, Southern blotting, and hybridization followed the method described by Liu et al. (1997). SSR analysis followed the methods of Wu and Tanksley (1993). Polymorphic markers detected between the parents were used to assay the entire population of the 240 families, based on which the marker genotypes of F_2 individuals were deduced.

Data analysis

The estimates of mean and variance for each trait were based on the F_3 families. Genotype by year interaction was analyzed using a random model. Heritability for each year was estimated with the formula $h^2=\sigma_g^2/(\sigma_g^2+\sigma_r^2+\sigma_e^2/r)$, and was also estimated with the $h^2=\sigma_g^2/(\sigma_g^2+\sigma_{gl}^2/n+\sigma_e^2/nr)$ for the combined data analyses of 2 years, where σ_g^2 is the genotypic variance, σ_r^2 is the replications variance, σ_e^2 is the error variance, σ_{gl}^2 is the variance due to genotype by year interaction, r is the number of replications, and n is the number of years. The 90% confidence intervals for h^2 were calculated according to Knapp et al. (1985).

The molecular linkage map was constructed using Mapmaker 3.0 (Lincoln et al. 1992a). QTLs (quantitative trait loci) were detected using Mapmaker/QTL 1.1 (Lincoln et al. 1992b). The total phenotypic variation explained by all QTLs detected for each trait was estimated with the multiple-QTL model in Mapmaker/QTL 1.1.

The entire genome was searched for digenic interactions for each trait with two-way analysis of variance (ANOVA) using all possible two-locus combinations of marker genotypes on the basis of unweighted cell means. The sums of squares were multiplied by the harmonic means of the cell sizes to form the test criteria (Snedecor and Cochran 1980). The terms involved in each interaction (also referred to as epistasis), including additive by additive (AA), additive by dominance (AD) and dominance by dominance (DD), were partitioned as previously described in Yu et al. (1997). The statistical significance for each term was assessed using an orthogonal contrast test with the statistical package Statistica (StatSoft 1991).

Results

Phenotypic variation

Phenotypic means and genotypic variances for plant height and heading date in parents and the $F_{2:3}$ population grown in 2 years are given in Table 1. Large differences between the two parents were revealed in both traits. The mean values of the traits in the F_1 were closer to the higher parent (Minghui 63) for both traits. Geno-

Table 1 Means, variance components and heritabilities estimated for plant height and heading date in parents, F_1 and the progenies across 2 years

Item	Plant height (cm)	Heading date (d)
Minghui 63	114.6	44.7
Zhenshan97	87.5	23.9
F_1	107.5	39.5
F_3 range	71.3–159.4	16.2–72.2
Variances		
σ^2_g	65.2±1.4	76.8±1.2
σ^2_{gl}	22.7±2.0	8.5±1.6
σ^2_e	12.1	8.1
Heritability (h^2)		
Estimate	0.83	0.93
Confidence interval (90%)	0.79–0.87	0.91–0.95

Table 2 Putative QTLs affecting plant height and heading date in 2 years detected with LOD 2.4 in the $F_{2:3}$ population from a cross between Zhenshan 97 and Minghui 63

Trait	QTL[a]	Flanking markers	LOD[b]	Var %[c]	Add.[d]	Dom.[e]
	1994					
Plant height	*ph1*	RG236-C547	3.0	14.6	4.16	3.59
	ph5b	RZ649-RM163	2.8	5.5	–0.16	4.24
	ph7	RG128-C1023	2.9	13.1	–3.71	4.34
	ph11	G44-C794	2.4	7.5	2.24	3.27
	Total		10.4	30.7		
Heading date	*hd3*	G144-RG393	2.0	5.3	–1.56	–3.65
	hd6	R1952-C226	8.7	17.1	4.99	–1.99
	hd7a	RM18-R1789	5.8	11.1	–3.77	1.72
	hd7b	MX2-RM18	3.7	19.2[f]	–4.87	–3.19
	hd7c	C1023-R1440	8.1	19.2	–5.21	–2.33
	Total		29.1	53.4		
	1995					
Plant height	*ph1*	RG236-C547	3.7	6.9	3.59	–0.22
	ph3	R1966-G144	2.6	6.1	2.81	–2.61
	ph5a	RM163-C624	3.7	7.0	–3.77	0.36
	ph5b	RZ649-RM163	3.1	5.8	–0.59	4.69
	ph7	C1023-R1440	5.2	9.7	–4.28	2.05
	Total		27.9	54.6		
Heading date	*hd3*	G144-RG393	2.2	5.3	–0.78	–4.44
	hd6	R1952-C226	13.9	25.3	6.57	–3.37
	hd7a	RM18-R1789	4.9	9.2	–3.67	2.24
	hd7b	MX2-RM18	4.8	32.0[f]	–6.88	–5.19
	hd7c	C1023-R1440	12.4	27.0	–7.09	–2.36
	hd11	C950-G389b	2.4	4.5	0.93	3.96
	Total		39.9	63.0		

[a] Numbers following the two letters represent the chromosome locations of the QTLs
[b] Log-likelihood value calculated by Mapmaker/QTL1.1
[c] Variation explained by each QTL
[d] Additive effect; positive values of the additive effect indicate that the Zhenshan 97 alleles are in the direction of increasing the traits
[e] Dominance effect; positive values of the dominance effect indicate that the heterozygotes have higher phenotypic values than the respective means of two homozygotes
[f] This QTL is located in an area with a large gap in the linkage map. The amount of variance is likely to be overestimated

typic variations of both traits among F_3 families were large and highly significant. Heritabilities were high for both traits (Table 1). Genotype by year interactions for the two traits, although statistically significant, were small compared with the main effects of genotypes.

Linkage map

The survey of 597 molecular markers, including 537 RFLPs and 54 SSRs, identified 151 polymorphic loci between the parents. A genetic map (data not shown) was constructed based on the data of 151 loci assayed on the 240 F_2 individuals by Mapmaker analysis. The map, covering a total 1841 cM with an average interval of 12.1 cM between adjacent loci, well-integrated the markers from two high-density RFLP linkage maps (Causse et al. 1994; Kurata et al. 1994).

QTLs for plant height

QTLs resolved by interval mapping with LOD 2.4 for both traits are presented in Table 2. Four QTLs (*ph1*, *ph5b*, *ph7* and *ph11* on chromosomes 1, 5, 7 and 11 respectively) were detected for plant height in 1994. These QTLs individually explained 5.5–14.6% of the total phenotypic variation, and collectively accounted for 31% of the total variation. Alleles from Minghui 63 at *ph5b* and *ph7* were in the direction of increasing plant height, while alleles from Zhenshan 97 of the remaining two QTLs increased plant height. In 1995, five QTLs, located on chromosomes 1, 3, 5 and 7 respectively, were identified for plant height. Each of the QTLs explained a relatively small amount of the phenotypic variance. Similarly, the Minghui 63 alleles at *ph5a*, *ph5b* and *ph7* increased plant height, and the Minghui 63 alleles at the other QTLs decreased the height. Three of the QTLs (*ph1*, *ph5b* and *ph7*) were resolved in both years.

Digenic interactions for plant height

One hundred and thirty one co-dominant markers, that formed 8,515 possible two-locus combinations, were used for testing digenic interactions in the rice genome with a two-way ANOVA. For plant height, interactions

Table 3 Digenic interactions for plant height that are simultaneously detected at $P<0.01$ in 2 years by two-way analysis of variance based on marker genotypes

Locus 1	Chrom.	Locus 2	Chrom.	1994			1995		
				Type[a]	*P*	Var%[b]	Type	*P*	Var%
R753	1	RZ404	9	AA	0.002	4.6	AA	0.000	6.6
R1468	1	C2807	4	DA	0.003	3.7	DA	0.010	2.4
R1468	1	R1440	7	DA	0.006	2.2	DA	0.003	2.4
RM5	1	RZ649[c]	5	AA	0.002	4.8	AA	0.005	3.3
C567	1	R1440	7	AA	0.007	3.4	AA	0.006	3.2
C567	1	RM12	12	DD	0.010	2.9	DD	0.000	4.1
RG236[c]	1	R1440	7	AD	0.000	6.2	AD	0.001	4.3
RG236[c]	1	C87	12	AA	0.000	5.9	AA	0.002	3.7
C112	1	C1087	3	AA	0.003	4.0	AA	0.005	3.2
C112	1	R1440	7	AD	0.001	5.7	AD	0.000	6.5
C112	1	RM4	11	AA	0.006	3.5	AA	0.010	2.7
C112	1	C87	12	AA	0.003	4.1	AA	0.006	3.1
R2510	2	RM17	12	DD	0.001	5.2	DD	0.010	1.9
C1087	3	RZ66	8	DA	0.006	3.5	DA	0.002	4.1
C1016	4	C2807	4	AA	0.001	4.9	AA	0.002	3.8
RG528	5	RG978	8	AA	0.010	2.4	AA	0.007	2.9
RG360	5	G342	6	AD	0.007	3.4	AD	0.002	3.8
R1674	5	RZ471[c]	7	AA	0.008	3.3	AA	0.004	3.3
R1014	6	RG424	6	AD	0.002	4.5	AD	0.005	3.3
RG424	6	RG128	7	AA	0.000	5.9	AA	0.001	4.5
RG653	6	R2272	8	DA	0.000	6.2	DA	0.001	4.3

[a] AA, additive by additive; AD, additive by dominance; DA, dominance by additive; DD, dominance by dominance. Some pairs of interacting loci are not listed, because these interacting loci are closely linked with the interacting loci have presented in the table

[b] Percentage of genotypic variation explained by the interactions

[c] Markers loci that detected significant effects on the trait by single-locus analysis

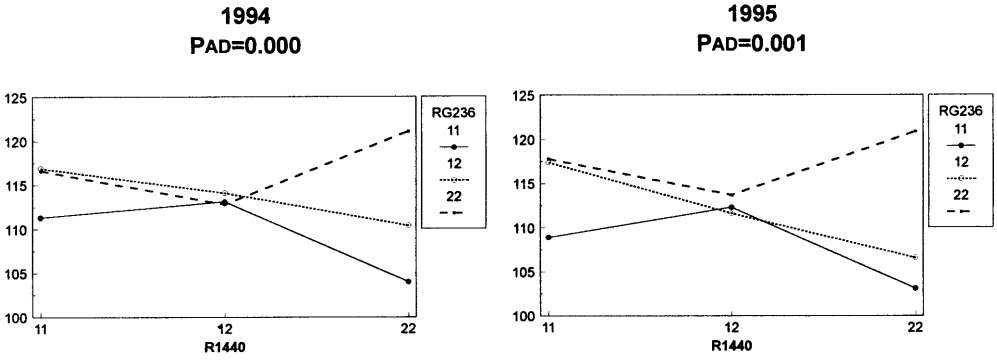

Fig. 1 The effect of interaction on plant height between the loci marked by RG236 and R1440 in 1994 and 1995. Pad is the probability for AD interaction. The vertical axis represents plant height (cm). 11, 12 and 22 represent the three genotypes of each locus: *11* homozygote for Minghui 63 allele; *22* homozygote for Zhenshan 97 allele; *12* heterozygote

detected for 101 and 257 two-locus combinations were found to be significant at the 0.01 probability level in 1994 and 1995, respectively. Clearly these numbers of significant interactions were much larger than the numbers based on chance events. Twenty two of the highly significant interactions were simultaneously detected in both years. The types of interactions (i.e. AA, AD and DD), determined by orthogonal contrast tests for the two-locus combinations, were also consistent in both years (Table 3). Each of the interaction terms individually accounted for 2–7% of the phenotypic variation. About half of the interactions involved dominant effects (e.g. AD, DA or DD). It should be noted that the majority of the significant interactions involved marker loci that did not detect significant effects by single-locus analysis. There were also digenic interactions that involved markers detecting QTLs (e.g. RG236 for *ph1* and RZ649 for *ph5b*) and marker loci that did not detect any effects on the trait by single-locus analysis (Table 3).

The locus pair, RG236 and R1440, showing a significant AD interaction effect on plant height (Table 3), was used as an example to illustrate the epistatic effect for this trait. As can be seen from Fig. 1, such AD interaction was featured such that the relative performance of the two homozygotes at the locus marked by RG236 was largely altered by the heterozygote of the locus marked by R1440. It should be noted that RG236 marked the QTL *ph1* that was detected by single locus analysis. However, the effect detected at the RG236 QTL was greatest when R1440 was homozygous for the Zhenshan 97 allele (22), much smaller when R1440 was homozygous for the Minghui 63 allele (11), and not detectable when R1440 was heterozygous.

Table 4 Digenic interactions for heading date that are simultaneously detected at $P<0.01$ in 2 years by two-way analysis of variance based on marker genotypes. See footnotes in the Table 3

Locus 1	Chrom.	Locus 2	Chrom	1994			1995		
				Type[a]	*P*	Var%[b]	Type	*P*	Var%
R753	1	C87	12	AA	0.003	4.3	AA	0.005	4.8
G359	1	R2174	10	AD	0.007	3.4	AD	0.007	2.9
C904	1	RZ66	8	AA	0.003	4.1	AA	0.003	3.5
C904	1	R2272	8	AA	0.001	5.1	AA	0.002	3.9
R1468	1	R514	4	AA	0.003	4.1	AA	0.003	3.5
R1468	1	C1023[c]	7	AA	0.002	4.4	AA	0.005	2.6
C112	1	R19	3	AA	0.007	3.4	AA	0.003	3.5
C112	1	C1087	3	AA	0.002	4.6	AA	0.003	3.6
RM148	3	R902[c]	6	DA	0.001	5.7	DA	0.001	4.1
RM168	3	RM18[c]	7	AD	0.000	6.2	AD	0.000	6.7
R321	3	C1447	5	AD	0.000	6.2	AD	0.009	2.8
C136	3	R1394	8	AD	0.006	3.5	AD	0.002	3.9
C1087	3	RM18[c]	7	AD	0.001	5.6	AD	0.000	5.3
RZ467	4	R543	11	AD	0.004	3.8	AD	0.001	4.4
RM163	5	R902[c]	6	AD	0.003	4.1	AD	0.001	3.9
G1458	5	RZ66	8	AA	0.002	4.6	AA	0.001	4.7
C734	5	C1121	8	AA	0.005	3.7	AA	0.002	3.9
C734	5	C794	11	DD	0.000	7.2	DD	0.000	6.4
RM122	5	R1440[c]	7	DA	0.004	3.8	DA	0.001	3.5
R902[c]	6	C962	6	DD	0.008	3.3	DD	0.001	3.9
C226[c]	6	C1023[c]	7	AA	0.002	4.7	AA	0.003	2.2
R1014[c]	6	RZ471[c]	7	AA	0.003	4.2	AA	0.000	4.0
R1014[c]	6	R1440[c]	7	AA	0.001	5.1	AA	0.000	4.1
R1014[c]	6	C1023[c]	7	AA	0.000	7.4	AA	0.000	5.0
G200[c]	6	C1023[c]	7	AA	0.000	5.6	AA	0.000	5.2
R2147	6	C1023[c]	7	AA	0.001	5.8	AA	0.000	5.4
C371	10	R2918	11	AA	0.005	3.7	AA	0.008	2.9

QTLs for heading date

Five QTLs (*hd3*, *hd6*, *hd7a*, *hd7b* and *hd7c*) located on chromosomes 3, 6 and 7 were detected for heading date in 1994, which jointly explained 53% of the total variance of this trait in this population. In 1995, six QTLs on chromosomes 3, 6, 7 and 11 were resolved for heading date, collectively accounting for 63% of the total phenotypic variation. Five of the QTLs were consistently identified in both years, and the one on chromosome 11 (*hd11*) was detected only in 1995. The QTL *hd3* on chromosome 3 was simultaneously detected in both years by interval mapping, with LOD scores slightly below the threshold 2.4. The Zhenshan 97 allele at *hd6* caused late heading, whereas alleles from Zhenshan 97 at other QTLs resulted in early heading. It should be noted that the QTL *hd7b* is located in an area with a large gap on chromosome 7, and it seemed likely that the amount of variance explained by this QTL (Table 2) was overestimated in the analysis.

Digenic interactions for heading date

Significant ($P<0.01$) interactions were detected by 126 and 131 two-locus combinations in 1994 and 1995, respectively; 39 of these highly significant interactions were simultaneously detected in both years. These numbers were also much larger than expected on the basis of chance events. The types of interactions as resolved by the orthogonal contrast tests were also highly consistent between the 2 years. The interactions involved a large number of marker loci, the majority of which were not detectable on the single-locus basis. Some interactions each involved a QTL (i.e. *hd7b* and *hd7c* on chromosome 7) and a locus that did not show an effect on heading date using single-locus analysis. There was also one case in which the interaction involved two QTLs, *hd7c* and *hd6*, each of which had significant effect on heading date, as indicated by the interactions involving several markers in the vicinity of *hd6* on chromosome 6 and markers surrounding *hd7c* on chromosome 7 (Table 4).

The locus pair, C226 (marking *hd6*) and C1023 (marking *hd7c*) detecting an AA interaction effect on heading date (Table 4), was used to illustrate the epistatic effect (Fig. 2). The feature of this AA interaction is such that no significant difference was detected at the C226 locus when C1023 was homozygous for the Zhenshan 97 allele (22); the difference became detectable as C1023 changed to heterozygous, and further increased when C1023 was homozygous for the Minghui 63 allele (11). Thus, clearly, the effect on phenotype of one QTL is largely dependent on the genotypes of the other QTLs.

Relationship between QTLs affecting plant height and heading date

Plant height in this population was highly correlated with heading date ($r=0.53$, $P<0.01$), such that taller

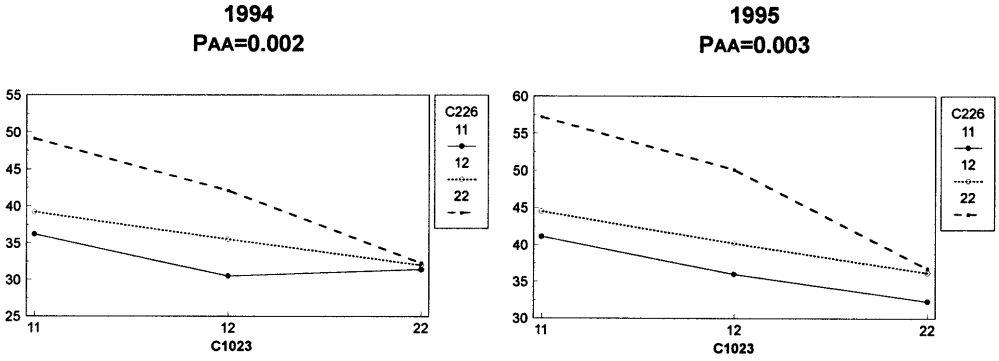

Fig. 2 The effect of interaction on heading date between the loci marked by C226 and C1023 in 1994 and 1995. Paa is the probability for AA interaction. The vertical axis represents heading date (number of days after July 1). 11, 12 and 22 represent the three genotypes of each locus: *11* homozygote for Minghui 63 allele; *22* homozygote for Zhenshan 97 allele; *12* heterozygote

plants headed later. Inspection of the map locations of the QTLs for these two traits showed that QTLs *ph7*and *hd7c* with larger effects on plant height and heading date respectively, coincided around C1023 on chromosome 7. As can be seen from Table 2, the allele of *ph7* from Zhenshan 97 reduced the height, and the allele from the same parent at *hd7c* reduced the number of days to heading. The effect detected for this region that might be caused by the same QTL influencing both traits, may provide an explanation for this correlation. Moreover, one locus pair (C112 on chromosome 1 and C1087 on chromosome 3) also appeared to affect the two traits simultaneously with the same AA interaction (Tables 3 and 4). Thus, both single-locus QTLs and epistatic interactions were involved as the genetic basis of the high correlation of plant height and heading date in this population.

Discussion

The overall feature of the genetic basis for plant height and heading date as revealed by this study is that each trait is controlled by several QTLs plus a large number of epistatic interactions. For plant height, Huang et al. (1996) conducted QTL mapping using five populations, which detected a total of 23 QTLs. Eight of the QTLs were observed in at least two populations, the remaining 15 in only one population, but none of the QTLs was detected in all five populations. Four (*ph1, ph3, ph5b* and *ph7*) of the six QTLs detected in the present study, including three simultaneously detected in both years, corresponded well with those detected by Huang et al. (1996), and the other two have not been reported in previous studies. One of the QTLs on chromosome 5 (*ph5b*) may correspond with the *sdg* locus identified by Liang et al. (1994).

A number of QTLs for heading date have also been reported previously. Of the QTLs that detected relatively large genetic effects in this study, *hd6* may well correspond with the locus *En-Se-1* for photoperiod response (marked by C226) on chromosome 6, which was designated as *Hd-3* in a previous study (Yamamato et al. 1998). There was epistatic interaction between *Hd-3* and *Hd-1* (*Se-1*) (Lin et al. 2000). However, the cloned QTL (*Hd-1*) was not detected in the present study. The QTL *hd7b* is located in approximately the same region as a QTL (*Hd-2*) for flowering time reported previously. Additionally, the QTL *hd7c* may also correspond with the E1 locus (*Hd-4*) suggested previously by Yano et al. (1997). And *hd3*, a QTL detected with a minor effect in both years in this study, also corresponded with a locus on chromosome 3 for flowering time identified previously (Li et al. 1995; Xiao et al. 1996). The QTL *hd11* is located closely to the interval with a QTL on chromosome 11 found previously (Xiong et al. 1999).

It would be interesting to estimate the amount of genetic variation in the population that can be accounted for by single-locus QTLs and two-locus interactions, respectively. Although presently there has not been a computer program that is able to conduct a combined analysis of single-locus QTLs and two-locus epistatic interaction for such F_2 data set, some ideas can be gained by comparing the total amount of the variance accounted for by the QTLs of the trait with the estimate of heritability. As can be seen from Table 2, the single-locus QTLs in combination explained 30.7% and 54.6% of the phenotypic variation for plant height in the 2 years, and accounted for 53.4% and 63.0% of the phenotypic variation for heading date. Whereas, the calculated heritabilities for plant height were 94.1% and 95.8% in 1994 and 1995, respectively, the heritabilities estimated for heading date were 96.4% and 97.3% in 1994 and 1995, respectively. The magnitudes of the gaps between the total amounts of variation explained by the single-locus QTLs and the estimated heritabilities may be regarded as indications of the amounts of variations due to epistatic effects. Thus, for plant height, epistatic effects may account for 40% to 60% of the phenotypic variation, and for heading date epistatic interactions may explain 30% to 40% of the phenotypic variation. However, the possibility should be recognized that the overall effects of single-locus QTLs may be underestimated because of QTLs with smaller effects that failed to reach the LOD 2.4 threshold. It should also be noted that several of the single-locus QTLs were involved in the two-locus interactions in both years for both traits. Thus, clearly, epistasis plays a major role as the genetic basis of plant height and heading date in this population, although major genes for both traits have been identified in the literature.

The results have clear implications for rice breeding programs. Even for traits that are traditionally considered to have a relatively simple genetic basis, the actual genetic constitutions are still complex. Thus, breeders have to take into account such complexity and test the effects of individual loci in the targeted genetic background in order to obtain the expected phenotypes for the genes of interest.

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