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Identification of quantitative trait loci (QTLs) for heading date and plant height in cultivated rice (*Oryza sativa* L.)

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Abstract 'Lemont' and 'Teqing' are both semidwarf rice varieties that differ in heading date by only 6 days. However, when 'Lemont' and 'Teqing' are crossed there is transgressive segregation for both heading date (HD) and plant height (PH). By testing 2418 F_4 lines with 113 well-distributed RFLP markers, we identified and mapped chromosomal regions that were largely responsible for this transgressive segregation. *QHd3a*, a QTL from 'Lemont' that gives 8 days earlier heading, was identified on *chromosome 3* approximately 3 cM from the marker RG348. Another QTL with a large effect, *QHd8a*, which gives 7 days earlier heading, was identified on *chromosome 8* of 'Teqing' between RG20 and RG1034. Along with a QTL, *QHd9a* with a phenotypic effect of 3.5 days, these genomic regions collectively explain 76.5% of the observed phenotypic variance in heading date. Four QTLs which altered plant height from 4 to 7 cm were also mapped; these collectively explain 48.8% of the observed phenotypic variation in plant height. None of the QTLs for plant height mapped to *chromosome 1*, the location of the semidwarf gene *sd-1*. All three of the HD loci mapped to approximately the same genomic locations as PH QTLs, and in all cases, there was a reduction in height of approximately 1 cm for every day of earlier heading. The correspondence between the HD and some of the PH loci suggests that genes at these chromosome locations may have pleiotropic effects on both HD and PH. The observed heterosis in the F_1 plants for HD can be largely explained by the dominance for earliness of the identified HD loci and distribution of earlier heading alleles in the parents. However, overdominance observed at one of the PH QTL may, at least in part, be responsible for the observed heterosis in PH.

Key words RFLP · QTL · Rice · Heading date · Plant height · Pleiotropic effects

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Introduction

Rice can be grown under a variety of climatic conditions. However, when commercial rice varieties are being developed, it is important that their maturity be optimized for the particular environment in which they will be grown. The genes which control maturity in rice may be divided functionally into three categories: (1) genes for photoperiod sensitivity, (2) genes controlling the rate of vegetative (internode) development and (3) genes determining the total number of internodes on the plant's main stem.

Two genes controlling photoperiod sensitivity in rice, *Se-1* and *se-2*, have been mapped onto *chromosomes 6* and *7*, respectively (Kinoshita and Takahashi 1991; Mackill et al. 1993). Several other genes for photoperiod sensitivity have been identified in rice, including *Se-3, E-1, E-2, E-3* and *lf-1*, but their chromosomal locations remain unknown (Tsai 1986; Kinoshita and Takahashi 1991). The maturity gene *lf-2* does not appear to be photoperiod sensitive (Tsai 1986). Interestingly, the maturity gene *Ef-1*, which is located on *chromosome 7*, has multiple alleles that differ in their photoperiod sensitivity (Tsai 1986; Nakazaki et al. 1986). *Ef-1* also has pleiotropic effects on the number of leaves and elongated internodes on the main stem. Despite the efforts directed toward understanding the genetic basis of plant maturity, the genomic regions which are associated with maturity in non-photosensitive commercial rice varieties remain largely undefined.

Another important character associated with the productivity of rice is plant height. Extensive worldwide searches and work with mutagens have resulted in the dis-

covery and generation of more than 50 major genes for dwarfism or semidwarfism in rice (Kinoshita and Takahashi 1991). The semidwarf gene *sd-1* is the best characterized of these and has been extensively used to produce high-yielding semidwarf varieties (Hargrove et al. 1988; Rutger and Bollich 1989). The other dwarf or semidwarf genes have not been widely utilized in breeding programs because they are associated with poor agronomic performance (Rutger 1984; Kikuchi and Ikehashi 1984; Chang and Li 1984).

There must also be a number of other loci which affect the height of rice plants since quantitative variation in plant height has been frequently observed in rice breeding populations. This is also demonstrated by the development of rice varieties such as 'Maybelle' that are almost as short as semidwarf varieties, but which do not contain any of the known semidwarf genes (Bollich et al. 1991). Despite the effort that has been focused on manipulating plant height in rice breeding, genes or quantitative trait loci (QTLs) which control plant height in most commercial rice varieties remain largely uncharacterized, other than *sd-1*.

Since the efficiently manipulation of maturity and plant height is a critical component of rice improvement, the objective of the current study was to use molecular markers to further examine and characterize the genes and QTLs that control heading date and plant height in commercially important rice cultivars of divergent origin.

Materials and methods

Experimental procedures

The experimental materials were developed by crossing 'Lemont', a leading commercial semidwarf rice variety (tropical *japonica*, or *javanica*) in the southern US, with 'Teqing', a semidwarf *indica* rice variety from China that has an extremely high yield potential. From this cross, F_2 plants producing a minimum of 35 seed were randomly selected to produce 267 F_3 lines. Twelve F_3 lines did not provide enough plants for further study. From each of the remaining 255 F_3 lines, 7–11 plants were randomly selected to produce 2418 F_4 lines.

The F_4 lines were drill planted into the field at the Texas A&M University System Agricultural Research and Extension Center in Beaumont, Texas, in the summer of 1990. Each F_4 line was planted in a single row plot 2.4 m long with a spacing of 28 cm between rows. The F_4 lines were planted in family groups separated by two-row check plots of 'Gulfmont', a sister line of the female parent 'Lemont' (Bollich et al. 1990). 'Gulfmont' was used to determine within plot variation and the F_4 data were adjusted accordingly. Eleven plots of 'Teqing' were also randomly located in the field. Twenty F_1 plants from the 'Lemont'×'Teqing' cross were transplanted into single row plots, 1.2 m×28 cm, with the parents in the summer of 1992. Heading date (HD) was defined as when 50% of the plants in a plot completely exerted at least one panicle. Plant height (PH) was determined by measuring 5 different plants in each F_4 row plot. Purple apiculus was determined visually, and glabrous leaves were determined by touching.

Restriction fragment length polymorphism (RFLP) survey and genotyping

Two hundred and forty loci at intervals of 5–10 cM were surveyed in the parents using RFLP probes obtained from Steven Tanksley's lab at Cornell University; approximately 80% of the probes detected RFLPs. A subset of 97 probes, which detected 113 RFLP marker loci, was selected that covered all 12 chromosomes with a spacing of approximately 19 cM. To reconstruct the marker genotypes of the original 255 F_2 plants, DNA was extracted from 10 grams of fresh leaf tissue mixed from approximately 15 F_3 seedlings per F_2 plant. The DNA extraction followed the procedure of Tai and Tanksley (1990) with minor modifications, and we used fresh leaf tissue instead of dehydrated tissue. Digestion of the DNA samples by *Eco*RV, *Hin*dIII, *Xba*I and *Sca*I; electrophoresis; Southern blotting; and hybridization followed standard procedures (McCouch et al. 1988; Yu et al. 1991).

Construction of linkage map

Linkage analyses were performed using the MAPMAKER program (Lincoln et al. 1990). A LOD score of 2.0 was used as a standard for all two-point analyses and a LOD score of 3.0 for all three-point and multipoint analyses, except in one case on *chromosome 8* where linkage between RG20 and RG1034 was in agreement with previously reported maps (McCouch and Tanksley 1991; Causse et al. 1994) and had a LOD of 1.9 using our data. The assignment of linkage groups or markers to their corresponding chromosomes was based on McCouch and Tanksley (1991).

Statistical analyses and interval mapping of QTLs

Chi-square tests were performed to examine if the observed allelic and genotypic frequencies of the marker loci deviated from the expected ratios so that the skewedness of the population could be determined. The mapping of QTLs was performed on the basis of the RFLP linkage map and breeding values of the 255 F_2 plants according to the method of interval mapping (Paterson et al. 1988; Lander and Botstein 1989) using MAPMAKER/QTL 1.1 (Lincoln et al. 1992). The breeding values of the F_2 plants were obtained by averaging data from their derived F_4 lines. On the basis of our estimated rice genome size of approximately 1800 cM, a LOD score of 2.4 was selected as the threshold for claiming presence of a QTL. With such a threshold, the probability that even a single false positive QTL would be detected anywhere in the rice genome is approximately 0.05. QTLs were designated with a *Q* to indicate they were detected through QTL mapping, followed by an abbreviation of the trait name and the chromosome number. A final letter was used to accommodate situations where more than one QTL affecting a trait might be identified on the same chromosome. When adjacent LOD peaks were noted, the possibility of two linked QTLs was tested. A single QTL was claimed unless a two-QTL model was determined to be 100 times more likely than a one-QTL model (2 LOD difference) (Lincoln et al. 1990).

The proportion of total genotypic variance explained collectively by all identified QTLs for each trait was obtained by fitting the model containing all QTLs for that trait in MAPMAKER/QTL. This was performed by specifying the genomic region containing the most significant QTL for the respective trait, sequentially including each lesser significant QTL in the model and then using MAPMAKER/QTL to estimate the *a* and *d* for all of the QTLs simultaneously.

When breeding values calculated from F_4 lines are used for phenotyping instead of data from F_2 plants, as was the case in our study, only a quarter of the dominance effect (*d*) of the F_2 plants would be expected to remain and contribute to the genotypic mean of their F_4 progenies. Therefore, the unconstrained model in MAPMAKER/QTL was used for all QTL mapping and the resulting estimates for *d* were multiplied by four. One-way ANOVA using SAS PROC GLM (SAS Institute 1987) was used to confirm the presence of each QTL. The two-factor model in SAS PROC GLM (SAS Institute Inc. 1987) was used to evaluate digenic interactions between identified QTLs as represented by their most closely linked markers. In each of these analyses, we used $pF_{\text{regression}}=p\text{MS}_{\text{regression}}/\text{MS}_{\text{residual}}$ (Haley and Knott 1992), which is an approximate likelihood ratio test that is

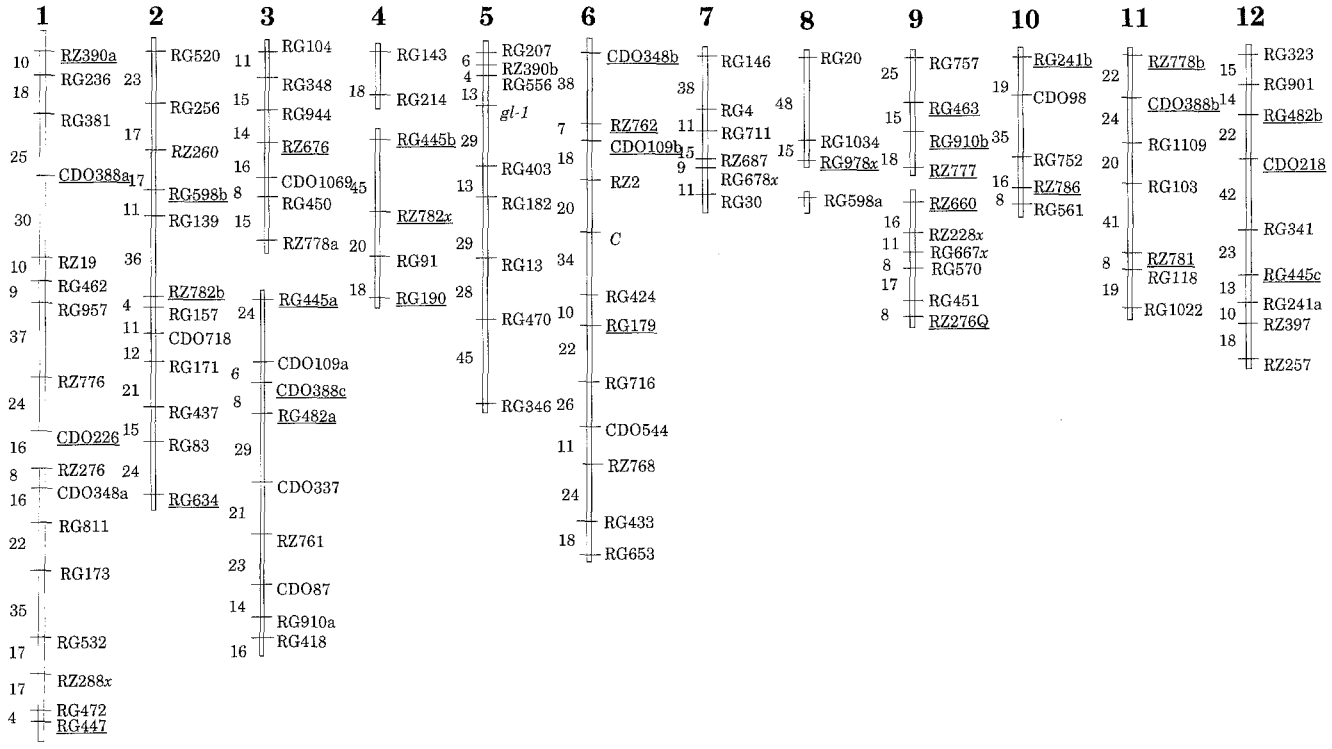

Fig. 1 A rice linkage map with 113 RFLP marker loci and two morphological markers constructed from 255 F_2 plants from the cross 'Lemont'×'Teqing'. The *numbers between* marker loci are Kosambi cM. The map locations of the *underlined* markers have not been described previously

more appropriate for unreplicated experiments than the traditional F test. pF has a χ^2 distribution with p (the number of parameters in the model) degrees of freedom. Since the mean of the F_4 lines was used in the analyses, 3/4 of the $(a \times d)$ and 11/16 of the $(d \times d)$ were confounded with the $(a \times a)$ effect in this experimental design. Thus, only highly significant interactions ($P<0.01$) between QTLs, due primarily to additive epistasis, were considered as evidence of epistasis.

Results

Construction of linkage map

The genotyping of the 255 F_2 progeny of 'Lemont'× 'Teqing' utilized 113 RFLP loci and two morphological markers. The resulting linkage map spanned 1840 cM and covered all 12 chromosomes with an average distance of 19.0 cM (Kosambi map units, Kosambi 1944) or 17.5±7.8% (recombination fraction) between markers (Fig. 1). There were gaps on *chromosomen 3, 4, 8* and *9*, but the genome coverage was estimated to be approximately 95%. The linear order of the markers matched that of Causse et al. (1994) except for RG190 and CDO109b, which mapped to different chromosomes, and five inversions: one on *chromosome 1* (RZ276 and CDO348a), one on *chromosome 5* (RG207 and RZ390b), two on *chromosome 6* (CDO544 and RZ768, RG433 and RG653) and one on *chromosome 12* (RG241a and RG341). We also report the location of 32 loci (detected by with 26 probes) that have not previously been mapped (Fig. 1 underlined).

Segregation of marker loci in the F_2 population

The genomic composition of the F_2 plant population inferred from all marker loci had an approximately normal distribution with an average of 49.6% (±5.8%) of the genome coming from 'Lemont'. The chi-square tests of the frequencies of individual parental alleles in the 255 F_2 progeny indicated that alleles at 17 of the 115 mapped marker loci (14.8%) displayed significant deviation from the expected 1:1 ratio. The allelic frequency distortions did not generally favor alleles from either of the parents, but their chromosomal distribution was nonrandom and, in all cases, increased allelic frequencies were associated with alleles for increased fitness. For example, 'Lemont' alleles of 6 linked loci on *chromosome 5* (centered at RG403) and of 2 linked loci on *chromosome 3* (centered at CDO1069) were favored and associated with two QTLs affecting panicle fertility (data not shown). Alleles of 'Teqing' on *chromosome 6* (4 linked loci centered at RG433) and *chromosome 9* (2 linked loci centered at RG910b) were also favored and associated with two QTLs affecting panicle fertility and grain yield (data not shown). Selection against F_2 and F_3 genotypes with low fertility and/or low viability was likely since only those F_2 plants producing sufficient seeds to plant a F_3 row and only progeny from viable F_3 seeds were represented in the F_4 progeny observed in the study. However, the overall segregation distortion of alleles at marker loci was much less severe in the 'Lemont'×

'Teqing' cross than that observed in previous studies in rice involving a wide *indica*×*japonica* cross (Wang et al. 1993) and in interspecific crosses in tomatoes (Zamir and Tadmor 1987; Paterson et al. 1988).

The F_2 population was homozygous with an average of 21.8% and 22.5% (± 7.4%) of 'Lemont' and 'Teqing' marker alleles, respectively, and were heterozygous at 55.7% of the alleles. When individual marker loci were examined, 86 (76%) showed small, but significant deviation from the expected genotypic ratio of 1 homozygous 'Lemont': 2 heterozygotes: 1 homozygous 'Teqing'. Of these, 9 could be attributed to allele frequency distortion. Most of the loci with distorted segregation showed an excess of heterozygotes, while in only 5 cases (3.9%) were the homozygotes favored. Among the 72 loci exhibiting an excess of heterozygotes, the average degree of the deviation was small (11.4%), and it did not significantly affect identification of QTLs.

Genetic variation for heading date and plant height

The frequency distributions of the HD breeding values of the 255 F_2 plants and the phenotypic values of the 2418 F_4 lines were bimodal, thereby suggesting the involvement of genes with large effects (Fig. 2). In contrast, for PH the breeding value of the F_2 and that in the F_4 lines were approximately normally distributed, indicating polygenic segregation.

The HD of the parents differed by only 6 days, with 'Lemont' having a HD of 92.5±1.3 days and 'Teqing' having a HD of 98.4 ± 1.3 days. However, there was marked transgressive segregation for HD in the F_4 lines (ranging from 73 to 125 days) and for the calculated breeding values of the F_2 plants (78 to 115 days) (Fig. 2). PH showed a similar transgressive segregation. The height of 'Lemont' and 'Teqing' differed by approximately 10 cm, but the height of the F_4 lines varied from 63 to 144 cm and the calculated breeding values of the F_2 plants ranged from 75 to 132 cm. When F_1 plants were directly compared with parental plants in 1992, heterosis was observed for both HD and PH with F_1 plants being 14 days earlier than 'Lemont' and 24 cm taller than 'Teqing'.

Interval mapping of QTLs

Heading date

Two QTLs with large effects, *QHd3a* and *QHd8a*, were identified, each of which explained greater than 40% of the total genotypic variation in heading date (Fig. 3 and Table 1). *QHd3a* is located approximately 3 cM from the marker RG348, while *QHd8a* is located between RG20 and

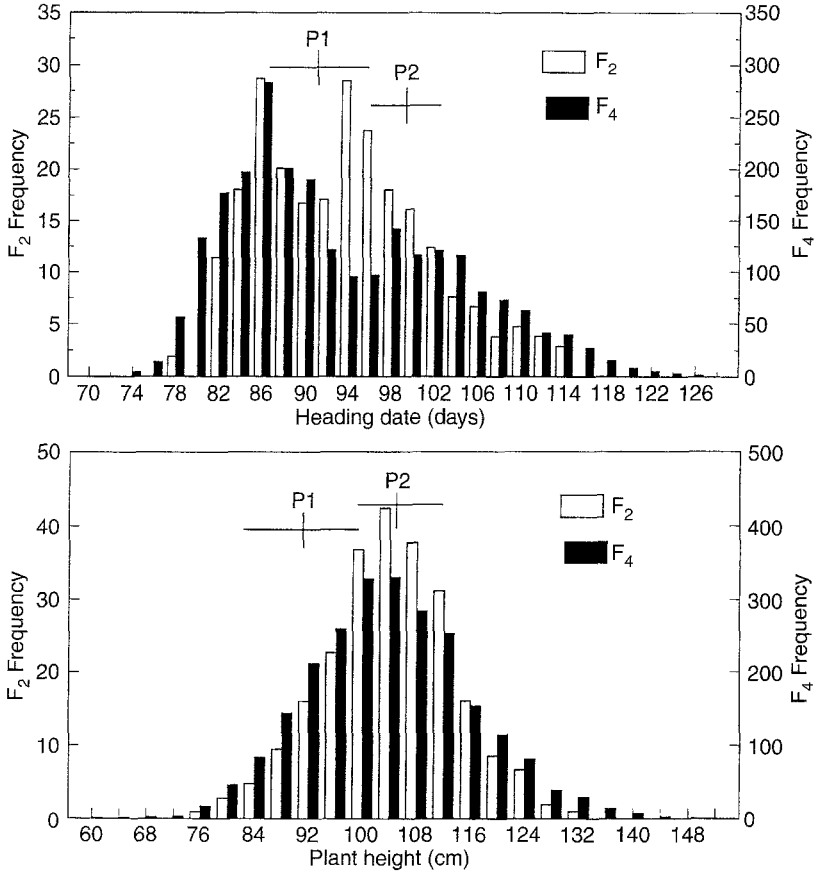

Fig. 2 Frequency distributions of the breeding value for heading date and plant height of 255 F_2 plants from the cross 'Lemont'×'Teqing'. *P1* is 'Lemont' and *P2* is 'Teqing'. Also shown are the frequency distributions of the 2418 derived F_4 lines from which these breeding values were calculated

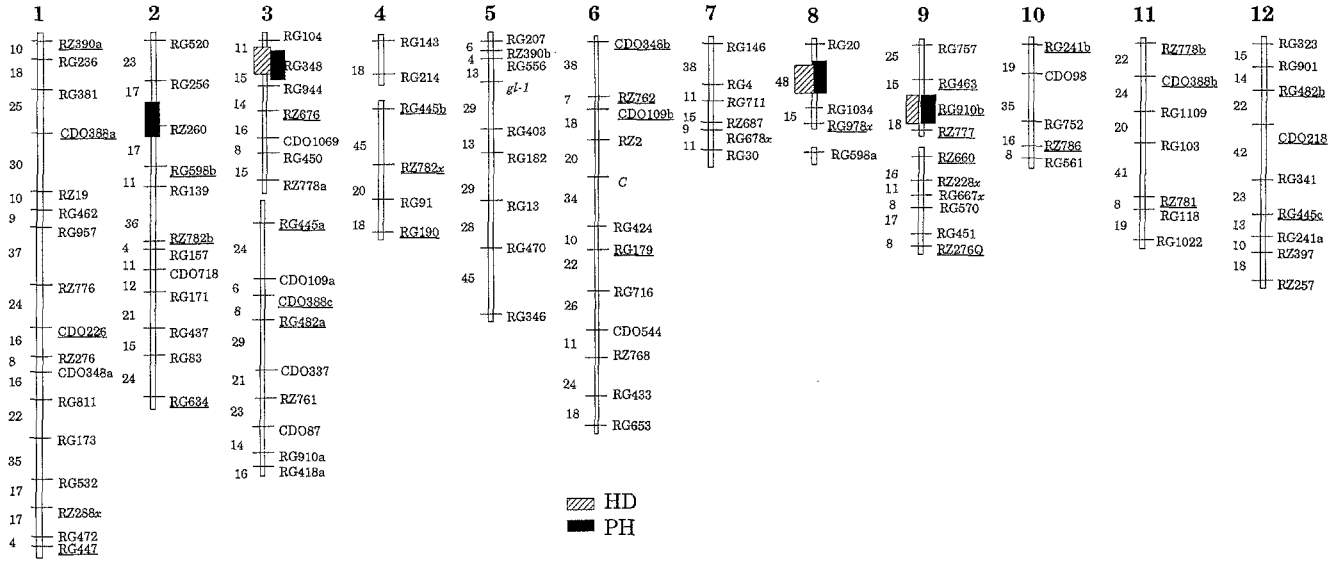

Fig. 3 Chromosomal regions associated with the control of heading date and plant height in the cross 'Lemont'×'Teqing'. The *shaded boxes* cover the region where the QTLs are most likely located based on where the likelihood score was within tenfold (1 LOD) of its maximal value (90% likelihood interval as per Paterson et al. 1988). *Underlined* markers as in Fig. 1

RG1034. These genes had additive effects of 8 and 7 days, respectively. Earlier heading was promoted by the 'Lemont' allele of *QHd3a* and by the 'Teqing' allele of *QHd8a* . In addition, we identified *QHd9a*, which had an additive effect of 3.5 days. Both *QHd3a* and *QHd8a* appeared overdominant for earliness with *d/a* ratios of 1.66 and 2.06, respectively. *QHd9a* exhibited partial dominance (*d/a*=0.53) toward lateness. Multiple QTL model analysis indicated that these three QTLs collectively explained 78.8% of the observed genotypic variation and 76.5% of the phenotypic variation of HD in the 'Lemont'×'Teqing' cross. Results from ANOVA confirmed the three HD QTLs (Table 1) and indicated the presence (*P*=0.004) of a QTL at a region between RZ2 and CDO109b on *chromosome 6* that had a subthreshold LOD peak score of 2.11.

Plant height

Four QTLs for PH were mapped to 4 of the 12 rice chromosomes (Fig. 3 and Table 1). The two QTLs with the largest effects, *QPh3a* and *QPh8a,* individually explained 21% and 25% of the genotypic variation, respectively, and each had an additive effect of approximately 7 cm for increased height. The other two QTLs, *QPh2a* and *QPh9a,* explained 7.9% and 8.4% of the genotypic variation, respectively, and each had an additive effect of approximately 4 cm for increased PH. For all of the PH QTLs except *QPh8a*, the alleles for increased height were from the taller parent, 'Teqing'. Three of these QTLs (*QPh2a*, *QPh3a* and *QPh8a*) had partial dominance effects toward shortness

Table 1 Genetic parameters as estimated by interval mapping and ANOVA of the QTLs affecting heading date (HD) and plant height (PH) identified in the cross 'Lemont' × 'Teqing'

QTL locus[a]	Flanking markers	Interval mapping				ANOVA				
		a[b]	d	R^2_G	LOD	*a*[b]	d	R^2_G	*pF*	*P*
QHd3a	RG348-RG944	8.14	–13.48	0.447	24.46	6.60	–9.90	0.307	163.54	<0.0001
QHd8a	RG20-RG1034	–7.05	–14.52	0.425	8.16	–3.63	–6.44	0.091	37.60	<0.0001
QHd9a	RG910b-RZ777	3.46	1.84	0.075	3.01	2.47	2.25	0.040	13.11	0.0044
	Total[c]	15.87	–17.29	0.788	38.33					
QPh2a	RG654-RZ260	4.13	–0.88	0.079	3.18	3.17	0.39	0.046	17.69	0.0005
QPh3a	RG348-RG944	6.76	–0.89	0.211	10.50	5.98	–0.85	0.168	74.00	<0.0001
QPh8a	RG20-RG1034	–7.03	–4.32	0.251	5.22	–3.86	–0.44	0.074	27.51	<0.0001
QPh9a	RG910b-RZ777	4.19	17.80	0.084	3.12	2.68	8.40	0.032	10.70	0.0135
	Total[c]	18.90	5.58	0.534	22.02					

[a] Individual QTLs are designated with "Q" indicating QTLs with LOD≥2.4, the abbreviation of the trait name and chromosome number followed by a letter is to accommodate situations where more than one QTL affecting a trait is identified on the same chromosome
[b] The additive effect (*a*) is the effect associated with substitution of a 'Lemont' allele by the corresponding 'Teqing' allele
[c] Estimates are obtained from a multi-QTL model fitting all QTLs (LOD≥2.4) simultaneously

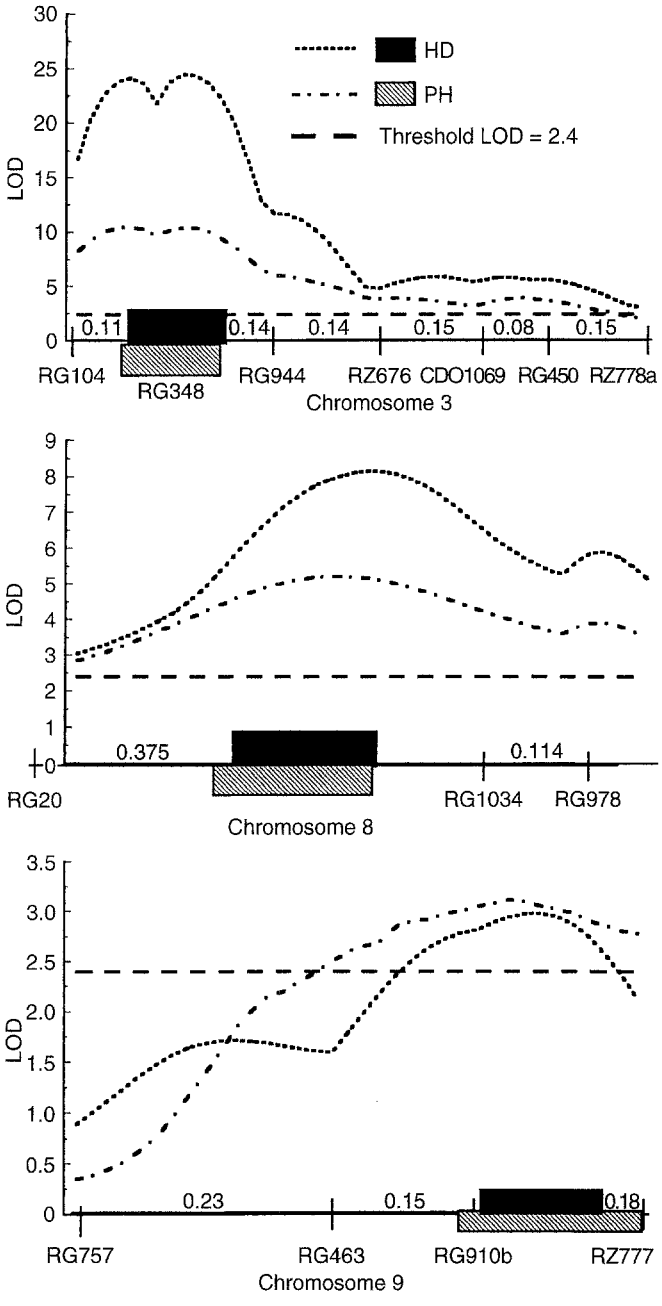

Fig. 4 QTL likelihood maps of LOD scores for heading date and plant height on *chromosomes 3*, *8* and *9*. The corresponding chromosomal region is shown below the LOD score graphs with the positions of the RFLP marker loci and the approximate recombination fraction between them indicated. The *shaded boxes* are as in Fig. 3. It should be noted that even though the LOD scores on *chromosome 3* had a double peak, a two-QTL model did not give a significantly better fit of the data

and the remaining QTL, *QPh9a,* exhibited overdominance toward increased height (*d/a* ratio=4.25). Collectively, these four PH QTLs explained 53.4% of the genotypic variation and 48.8% of the phenotypic variation in the F_2 plants, respectively. Results from ANOVA confirmed these four PH QTLs and also suggested ($P<0.01$) QTLs at three regions that had LOD scores between 2.0 and 2.23 when analyzed using MAPMAKER/QTL. These regions had an R^2 of approximately 4% and additive effects of 2–3 cm. They were located near RG418a on chromosome *3* and on chromosome *12* between RG323 and RG901 and between RG241a and RZ397. At LOD=2.0, there is only a 10% probability of identifying a single false positive, so it is unlikely that all three of these regions with 2.0<LOD<2.4 are not PH QTLs.

Epistasis between QTLs for morphological traits

The two-factor models using SAS PROC GLM (SAS Institute 1987) indicated that there was no evidence (all $P>0.01$) for the presence of digenic epistasis between the QTLs and the genomic regions associated with HD and PH. Such a lack of significant epistasis between QTLs was similar to that observed in most of the preceding gene mapping studies (Stuber et al. 1987, 1992; Paterson et al. 1988, 1991).

Evidence of pleiotropic effects

Since heading date and plant height are physiologically related, it is of interest to examine the genetic relationship between the two traits. As expected, the simple correlation between HD and PH was highly significant ($r=0.514$, $P<0.0001$). Also, maps of LOD scores for HD and PH showed similar patterns (Fig. 4). The two PH QTLs with the largest phenotypic effects, *QPh3a* and *QPh8a*, mapped to approximately the same chromosome locations as the HD QTLs *QHd3a* and *QHd8a*.*QPh9a* also mapped to approximately the same location as *QHd9a*. In addition, there was notable correspondence in both the directions and magnitudes of the additive effects between these HD and PH loci. Reduction in PH by 7 cm due to either *QPh3a* and *QPh8a* was associated with 7–8 days earlier heading and reduction in PH by 4 cm due to *QPh9a* was associated with 3.5 days earlier heading (Table 1). The dominance effects of the HD and PH loci were in the same direction, although their apparent magnitudes differed substantially (Table 1).

Discussion

The bimodal phenotypic distribution of heading date in the F_2 plants and the F_4 lines suggests that genes with large effects are involved in its inheritance. In agreement with this prediction, we mapped two QTLs with additive effects of 8 and 7 days, *QHd3a* and *QHd8a*, each of which explains over 40% of the observed genotypic variation. We were also able to identify *QHd9a*, which would have gone undetected using traditional methods. *QHd9a* explains only 7.5% of the observed genotypic variation but has an additive effect of 3.5 days and may be useful in breeding. Collectively, the three HD QTLs account for 79% of the genetic variation (Table 1).

The chromosomal locations of *QHd3a*, *QHd8a* and *QHd9a* identified in the 'Lemont' × 'Teqing' cross did not correspond to those reported for the mapped maturity genes *Ef-1, Se-1,* and *se-2* (Kinoshita and Takahashi 1991). Unlike *E-1*, *E-2*, *E-3*, *se-2*, *Se-3*, and *lf-1*, HD loci identified in this cross would be predicted to be non-photosensitive since heading date in neither parent is significantly affected by photoperiod. However, the effect of photoperiod on *QHd3a*, *QHd8a* and *QHd9a* remains to be directly tested. It is also possible that some of these loci have multiple alleles that differ in their photoperiod sensitivity as does the earliness gene *Ef-1* (Tsai 1986; Nakazaki et al. 1986). Whether *QHd3a*, *QHd8a* and *QHd9a* are related to *lf-2*, the only unmapped gene for early flowering reported not to be photosensitive (Tsai 1986), also remains unknown. Interestingly, the region on *chromosome 6* which had a subthreshold LOD score of 2.11 for HD is approximately the same chromosomal region in which *Se-1*, a gene previously reported to be responsible for photosensitivity in rice, is located (Kinoshita and Takahashi 1991; Mackill et al. 1993).

From pedigree analysis, the semidwarf gene *sd-1* is known to be present in 'Lemont' (Bollich et al. 1985). Incorporation of this gene into traditional (tall) *japonica* backgrounds reduced plant height by 15–20 cm through approximately proportional reductions in the length of the top five internodes (Foster and Rutger 1978). However, the segregation for plant height in the 'Lemont'×'Teqing' cross was not due to segregation of *sd-1*. None of the plant height QTLs were on *chromosome 1* where *sd-1* is known to reside (Khush and Kinoshita 1991). The lack of segregation of a PH QTL in this region suggests that the semidwarf gene in 'Teqing' is allelic to *sd-1*. It also suggests that the PH QTLs identified in this study may be used in conjunction with *sd-1* to adjust plant height in 3- to 7-cm increments to fit specific requirements. The effect of these QTLs in the absence of *sd-1* cannot be determined from our present data.

The fact that the 3 HD loci mapped to similar genomic locations as PH QTLs suggests that genes at these loci may have pleiotropic effects on both HD and PH. The predicted direction and magnitude of additive gene effects at these QTLs are consistent with a pleiotropic effect in which a 1-cm reduction in PH is associated with an each day earlier HD. However, the correlation between HD and PH was not absolute in that one PH QTL, *QPh2a*, was not associated with HD (LOD = 0.33). Furthermore, although the dominance effects of the HD and PH loci were in the same direction, but their apparent magnitudes differed substantially (Table 1). *QHd3a* and *QHd8a* showed overdominance of approximately 10 and 13 days, respectively, toward earliness, while *QPh3a* and *QPh8a* exhibited partial dominance toward decreased PH by 1 and 4 cm, respectively. In contrast, *QHd9a* showed dominance of 2 days toward lateness while *QPh9a* showed overdominance of 18 cm toward increased PH. It should be pointed out that defining HD as when there is complete exertion of one or more panicles by 50% of the plants in a F_4 line biased data toward earliness for F_4 lines segregating for HD. Thus, dominance effects for earliness (i.e. *QHd3a and QHd8a*) were likely overestimated, while dominance for lateness (i.e. *QHd9a*) may have been underestimated. All our dominance data must be also interpreted with caution due to the excess of heterozygosity detected throughout the genome in this population.

Genes that determine which node of the rice stem develops into the panicle and those which control the rate of internode elongation would be expected to alter both heading date and plant height. In studies conducted at Beaumont, it was found that 'Teqing' has three to four more internodes on the main stem and faster internode development rate than 'Lemont' (L. T. Wilson, personal communication). Thus, genes affecting the rate of vegetative development and the internode at which the panicle develops would be expected to be segregating in our population, and may have been responsible for the HD and PH QTLs. This remains to be directly tested, but similar pleiotropic effects of genes controlling maturity and plant height have been reported in rice (Nakazaki et al. 1986) and other crop species (Wallace et al. 1993).

The results of this study demonstrate that large phenotypic differences between the parents for quantitative traits of interest are not always required for successful gene mapping. 'Lemont' and 'Teqing' differ in heading date by only 6 days, but we were able to map two QTLs with large phenotypic effects of 7–8 days and one QTL with a phenotypic effect of 3.5 days. Similarly, even though the parents differed in height by only 10 cm, we were able to map four PH QTLs with phenotypic effects of 4–7 cm.

The small difference in heading date between the parents but marked transgressive segregation in the progeny can readily be explained by the fact that both 'Lemont' and 'Teqing' contained alleles for early heading at different QTLs. The observation that the F_1 plants were 14 days earlier than the earlier parent, 'Lemont', can also be explained by dominance and/or partial dominance of the early alleles. Although two of our HD QTLs exhibited $d/a>1$, this data does not provide irrefutable evidence of true overdominance since they were likely biased toward earliness and the use of F_4 data provided inflated estimates of d for these loci.

The situation with plant height is more complex. The sum of the additive effects at the PH QTLs exceeded the small difference in PH between the parents, but this does not appear to be adequate to explain the marked transgressive segregation observed in the progeny. Also, a simple additive-dominance theory does not adequately explain the observation that the F_1 plants were 24 cm taller than the taller parent, 'Teqing'. Three of the four PH QTLs, *QPh2a, QPh3a* and *QPh8a*, showed partial dominance toward shorter stature. Even if the remaining identified QTL, *QPh9a*, showed complete dominance toward increased height, the F_1 plants would still not be expected to be taller than 'Teqing'. Thus, the fact that the d/a ratio determined for *QPh9a* was greater than 1 may be indicative of true overdominance. Two of the regions which were associated with sub-threshold LOD scores for PH also exhibited overdominance for increased height. Overdominance for PH

QTLs is consistent with the striking heterosis observed in the F_1. However, one must be careful when interpreting our dominance estimates since F4 plants were used and the general excessive heterozygosity likely caused an overestimation of dominance effects.

The availability of genetic loci which alter heading date in 4-, 7- or 8-day increments and which alter plant height in 3- to 7-cm increments make it feasible to "fine-tune" genotypes to meet specific requirements of local conditions. Having molecular markers will allow these loci to be used more precisely to manipulate heading date or plant height than would be possible on the basis of phenotypic selection. However, it should be noted that we estimated the effects of these genes within a single population with data collected from a single year. The general utility of these loci will depend on their expression in other genetic backgrounds and environments and on whether they are associated with undesirable traits, either because of pleiotropic effects or tight linkage. Many known dwarf or semidwarf genes other than *sd-1* have not been widely utilized in breeding programs because they are associated with poor agronomic performance (Rutger 1984; Kikuchi and Ikehashi 1984; Chang and Li 1984). In preliminary studies, we have not detected association between the HD and PH QTLs described here and undesirable agronomic performance, but we did detect an association between alleles for decreased height at *QPh2a*, *QPh3a*, *QPh8a* and *QPh9a* with increased sheath blight susceptibility which is discussed in the accompanying paper (Li et al. 1995).

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