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Gene actions of QTLs affecting several agronomic traits resolved in a recombinant inbred rice population and two testcross populations

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Abstract To understand the types of gene action controlling seven quantitative traits in rice, QTL mapping was performed to dissect the main effect (M-QTLs) and digenic epistatic (E-QTLs) QTLs responsible for the trait performance of 254 recombinant inbred lines (RILs) of "Lemont/Teqing", and two testcross (TC) F_1 populations derived from these RILs. The correlation analyses reveal a general pattern, i.e. trait heritability in the RILs was negatively correlated to trait heterosis in the TC hybrids. A large number of M-QTLs and E-QTLs affecting seven traits, including heading date (HD), plant height (PH), flag leaf length (FLL), flag leaf width (FLW), panicle length (PL), spikelet number per panicle (SN) and spikelet fertility (SF), were identified and could be classified into two predominant groups, additive QTLs detected primarily in the RILs, and overdominant QTLs identified exclusively in the TC populations. There is little overlap between QTLs identified in the RILs and in the TC populations. This result implied that additive gene action is largely independent from non-additive gene action in the genetic control of quantitative traits of rice. The detected E-QTLs collectively explained a much greater portion of the total phenotypic variation than the M-QTLs, supporting prior findings that epistasis has played an important role in the genetic control of quantitative traits in rice. The implications of these results to the development of inbred and hybrid cultivars were discussed.

Keywords Additivity · Overdominance · Heterosis · Epistasis · *Oryza sativa* L.

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Introduction

Rice is the staple food for more than half the world's population. Rice production has almost tripled since the 1960s, largely due to two major breakthroughs in genetic improvement, the use of the semidwarf gene leading to the Green Revolution since the 1960s and the successful exploitation of heterosis since the late 1970s (Yuan 1992; Khush 2001). However, contrary to this success in breeding, our understanding of the genetic basis of quantitative traits and heterosis remains incomplete. The relative importance of additive versus dominance gene effects is critical since the former is the key component for the genetic gain by selection and the latter largely determines the level of trait heterosis (Falconer 1981; Stuber 1994).

DNA markers have facilitated many QTL mapping studies in crop plants and QTLs affecting a wide range of traits in rice have been identified and mapped (Huang et al. 1996; Lin et al. 1996, 2000; Yano et al. 1997; Yu et al. 2002; Li 2001). However, information on the gene action of QTLs is particularly lacking, largely because most QTL mapping studies were based on individual recombinant inbred, double-haploid or BC populations, none of which allow dissection of the types of gene actions. Another limitation has been the inability to detect and

characterize multiple alleles associated with different phenotypic effects or with different types of gene action at QTLs, largely because of the exclusive use of bi-parental mapping populations. This lack of information on gene action and the number of multiple functional alleles at QTLs is one reason for the rare application of marker-assisted QTL manipulation to the genetic improvement of quantitative traits. In this paper, we further explore the gene action of QTLs responsible for trait performance and heterosis in a recombinant inbred and two testcross (TC) populations, towards a better understanding of the relative importance of additive and non-additive gene action in rice improvement.

Materials and methods

Plant materials and the phenotyping experiment

The mapping populations used in this study included a set of 254 F_{10} recombinant inbred lines (RILs) derived by single-seed decent from a cross between Lemont (*japonica*) and Teqing (*indica*). In addition, two TC populations were created. The first one consisted of 192 TC F_1 ($Z413F_1$s) hybrids from crosses between the RILs (used as females) and the tester, Zhong413 (Z413), which is a well-known indica restorer line from China. The second one comprised 187 TC F_1 ($IR64F_1$s) hybrids from crosses between the RILs and another tester, IR64, which is an *indica* inbred cultivar most widely grown in South and Southeast Asia developed by IRRI, as described previously (Li et al. 2001; Luo et al. 2001). The two testers were genetically unrelated. The parents of the RILs, Lemont and Teqing, F_1 hybrid (Lemont × Teqing), testers (Z413 and IR64) and a commercial hybrid, Shanyou63, were used as checks.

The phenotyping experiment was conducted at the experimental farm of the China National Rice Research Institute, Hangzhou, China. All materials were sown in the seedling nursery on May 25, 1996, and the 25-day old seedlings were transplanted into the three-row plots each consisting of a single row of a female RIL and the two tows of TC hybrids (one with Z413 and one with IR64) with 15 plants in each row. The spacing was 20 cm between plants within each row and 35 cm between rows. The plots were arranged in a complete randomized block design with three replications for each plot (RIL and TC F_1s) and the check plots of Lemont, Teqing, the Lemont × Teqing (F_1), Z413, IR64 and Shanyou 63. All materials were measured for the following traits: heading date (HD), which was recorded as days from sowing to the time when panicles emerged from the leaf sheath on 50% of the plants in a row plot; plant height (PH, in cm), which was measured of the height from the soil surface to the tips of the tallest panicles of five plants in a row plot; flag leaf length (FLL, in cm) and flag leaf width (FLW, in mm), which were measures as the length and width of the flag leaves of three main tillers on five plants in a row plot before reaching maturity; panicle length (PL), spikelet number per panicle (SN) and filled grain number per panicle (GN) were measured on five randomly selected plants in the middle of each plot after maturity. One derived trait, spikelet fertility (SF = 100*GN/SN), was calculated from two measured traits.

Genotyping experiment and data analyses

The genotyping of the RILs for 179 RFLP markers and three morphological markers, including *C* (apiculus color), *gl-1* (glabrous leaves) and *Ph* (grain reaction to phenol), were conducted at Texas A & M University; and the completed linkage map with 182 markers spanned 1,918.7 cM and covered 12 rice chromosomes with an average interval of 11.3 cM between adjacent markers as described previously (Li et al. 1999).

Square-root transformation was performed for SN to make the trait mean independent from trait variance. SAS Proc GML and CORR (SAS Institute 1996) were used to test the differences among the RILs and TC hybrids, and to obtain the basic statistics of the traits. The hybrid breakdown value (HB) is a component of inbreeding depression (Li et al. 1997b, 2001). It was calculated as follows: HB = RIL – MP, where MP = (Teqing + Lemont)/2 was the mid-parent value of two parents. Mid-parental heterosis (H_{MP}) of individual TC hybrids for each trait was calculated as follows: $H_{MP} = F_1 - MP$, where F_1 was the mean trait values of individual TC hybrids and MP = (RIL + tester)/2 was the mid-parental trait values of the corresponding female RIL and one of the testers.

QTL analyses were performed separately for the RI and two TC populations. For the RI population, the mean trait values from the three replications of individual RILs were used as input data. For each of the TC populations, the mean trait values and the mid-parental heterosis (H_{MP}) of individual TC hybrids were used as input data. Identification and mapping of the main-effect QTLs (M-QTLs) and digenic epistatic QTLs (E-QTLs) in each of the mapping populations were performed by interval mapping using the mixed linear approach and the computer software, QTLMapper (V1.0), as described previously (Wang et al. 1999; Li et al. 2001). The thresholds were $P \leq 0.005$ (an approximate LOD of 2.50) for M-QTLs and 0.001 (an approximate LOD of 3.0) for E-QTLs, respectively.

Results

Performance of the RILs and mid-parent heterosis of their TC hybrids

Table 1 shows the summary statistics of the seven measured traits of the parents, F_1 (Lemont × Teqing), RILs, two testers and two TC F_1 populations, as well as the mid-parental heterosis (H_{MP}) of the TC hybrids. Significant differences between the parents were observed for all traits. Lemont had greater trait values for HD, FLW and SF, while Teqing had greater values for the remaining four traits. The F_1 (Lemont × Teqing) plants showed significant levels of heterosis for all traits, including –7.5 days (–7.7%) for HD, 50.5 cm (54.1%) for PH, 3.5 cm (10.3%) for FLL, 1.5 mm (9.3%) for FLW, 3.5 cm (15.4%) for PL, 4.8 (41.2%) for SN and 4.3 percent (5.9%) for SF, respectively. Exhibiting continuous variation with transgressive segregation in both directions (Fig. 1), the mean values of the RILs were significantly lower from the mid-parental values for HD, PL, SN and SF, higher for PH and not different for FLL and FLW. The heritability estimated from the RILs, $Z413F_1$s and $IR64F_1$s was 0.942, 0.920 and 0.867 for HD, 0.936, 0.948 and 0.912 for PH, 0.898, 0.888 and 0.859 for FLL, 0.961, 0.958 and 0.918 for FLW, 0.855, 0.793 and 0.758 for PL, 0.545, 0.577 and 0.473 for SN, and 0.946, 0.923 and 0.894 for SF, respectively.

Significant positive heterosis in the F_1 plants (Lemont × Teqing) was observed for all traits except HD, which show significant negative (early heading) heterosis. The average levels of trait heterosis of the TC populations were similar to those of the F_1 plants. The correlation was 0.98 ($P < 0.001$) between H_{MP} of the F_1 plants and the mean H_{MP} of the $IR64F_1$s, and 0.94 ($P < 0.001$) between the F_1 and the $Z413F_1$s, respectively. However, individual

Table 1 Summary statistics of heading date (HD) plant height (PH), flag leaf length (FLL) and width (FLW), panicle length (PL), spikelet number per panicle (SN, $\log_e$–transformed) and spikelet fertility (SF) of the 254 Lemont/Teqing recombinant inbred lines (RILs) and their two testcross F_1 populations (RILs × two testers, Z413 and IR64)

Item	HD Mean ± SD	PH Mean ± SD	FLL Mean ± SD	FLW Mean ± SD	PL Mean ± SD	SN Mean ± SD	SF Mean ± SD
Lemont (LT)	104 ± 1.7	79.3 ± 2.8	24.5 ± 1.6	17.9 ± 0.4	21.1 ± 1.1	10.8 ± 1.5	75.0 ± 3.0
Teqing (TQ)	91 ± 2.3	107.3 ± 3.9	33.5 ± 1.4	14.4 ± 0.4	23.5 ± 1.2	12.5 ± 1.3	70.1 ± 2.3
(LT × TQ) F_1	90 ± 2.0	143.8 ± 2.8	32.5 ± 1.7	17.6 ± 0.5	25.8 ± 0.9	16.4 ± 1.3	76.8 ± 3.2
(LT × TQ) H_{MP}	–7.5***	50.5***	3.5***	1.5**	3.5***	4.8***	4.3*
H_{MP}[a]							
Shanyou63	90 ± 1.7	118.9 ± 4.3	35.0 ± 3.6	18.9 ± 1.1	26.3 ± 0.9	13.3 ± 1.0	74.8 ± 2.3
RILs	94.9 ± 8.2	104.3 ± 12.3	29.5 ± 4.7	16.1 ± 2.2	21.1 ± 2.6	11.1 ± 1.5	68.3 ± 12.1
RIL – MP	–2.7**	11.2**	0.5	0.1	–1.8**	–0.7*	–1.8*
Z413	93.0 ± 1.6	112.8 ± 2.6	34.0 ± 1.3	15.5 ± 0.7	22.8 ± 1.6	13.3 ± 1.0	77.2 ± 2.3
IR64	97.3 ± 2.7	98.6 ± 3.6	28.5 ± 0.8	14.1 ± 0.4	23.5 ± 1.6	11.9 ± 1.7	83.2 ± 3.1
$Z413F_1$	89.9 ± 8.4	119.9 ± 13.9	33.2 ± 4.5	16.8 ± 2.1	23.7 ± 2.1	13.7 ± 1.6	74.3 ± 9.9
($Z413F_1$) H_{MP}	–3.9 ± 6.2	12.2 ± 13.0	4.0 ± 4.4	1.7 ± 1.7	1.7 ± 2.3	0.6 ± 1.7	–0.1 ± 10.0
$IR64F_1$	93.5 ± 5.2	122.3 ± 10.4	32.4 ± 3.9	16.3 ± 1.5	26.2 ± 1.9	13.2 ± 1.3	76.6 ± 8.3
($IR64F_1$) H_{MP}	–2.6 ± 5.3	18.8 ± 10.6	3.7 ± 4.2	1.8 ± 1.5	4.0 ± 2.3	2.4 ± 1.4	–0.1 ± 8.7

*, **, *** represent the significance levels of $P < 0.05$, 0.01, 0.001, respectively, based on t tests

[a] The mid-parental heterosis, $H_{MP} = F_1 - MP/2$, where MP was the mid-parental trait value (Lemont + Teqing)/2 for the LT/TQ F_1, (RIL + Z413)/2 for $Z413F_1$s, and (RIL + IR64)/2 for $IR64F_1$s, respectively

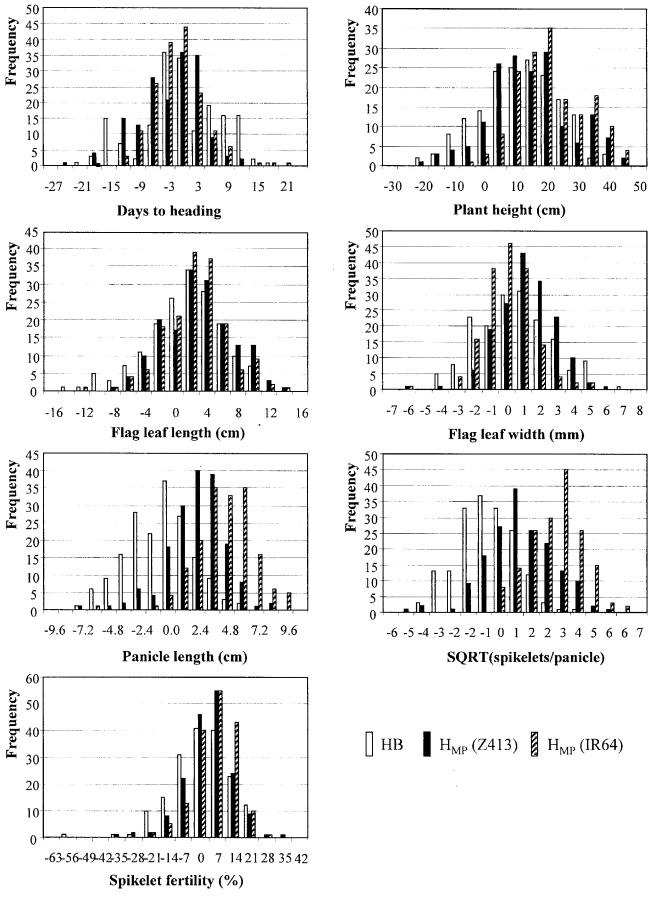

Fig. 1 Distribution of hybrid breakdown (HB) and mid-parent heterosis of Lemont/Teqing RILs and their testcross hybrids

hybrids within each of the TC populations showed different levels of heterosis distributed continuously around the mid-parental values from highly significant negative heterosis to highly significant positive heterosis (Fig. 1). The mean H_{MP} of $Z413F_1$s was –3.9 days for HD, ranging from –26.2 to 10.8 days; 12.2 cm for PH, ranging from –20.1 to 44.0 cm; 4.0 cm for FLL, ranging from –6.3 to 16.8 cm; 1.7 mm for FLW, ranging from –5.2 to 6.2 mm; 1.7 cm for PL, ranging from –7.5 to 7.7 cm; and 0.6 for SN, ranging from –4.9 to 4.9; and –0.1 percent for SF, ranging from –39.7 to 33.2 percent. The mean H_{MP} of $IR64F_1$s was –2.6 days for HD, ranging from –22.2 to 18.3 days; 18.8 cm for PH, ranging from –6.7 to 44.5 cm; 3.7cm for FLL, ranging from –10.2 to 20.4 cm; 1.8 mm for FLW, ranging from –3.9 to 7.3 mm; 4.0 cm for PL, ranging from –6.5 to 9.7 cm; 2.4 for SN, ranging from –0.7 to 6.4; and –0.1 percent for SF, ranging from –29.2 to 26.4 percent.

Table 2 shows the correlation between the performance of individual female RILs and the F_1 performance or the mid-parent heterosis of their TC hybrids in two TC populations, which revealed four general aspects of the gene actions that determined the trait performance in the TC hybrids. First, the performance of the TC hybrids was largely determined by the dominance gene action for all traits, as indicated by the high positive correlation between the F_1 values and H_{MP} values. The average R^2 (determination coefficient) between the F_1 values and H_{MP} values was 75.0% (ranging from 66.6% for SF to 81.4% for SN) in the $Z413F_1$ population, and 60.4% (ranging from 49.6% for HD to 68.4% for PH) in the $IR64F_1$ population, respectively. Second, the additive gene action, however, contributed only a small portion to the F_1 performance of the TC hybrids. The average R^2 between the female RILs and their TC F_1s was 18.1% (ranging from 0.4% for SN to 51.4% for HD) in the

Table 2 Phenotypic correlation for seven traits between the performance of the Lemont/Teqing recombinant inbred lines (RILs) and the performance or mid-parental heterosis (H_{MP}) in their testcross F_1 hybrids with two testers, Z413 and IR64

Trait	Z413 testcross F_1s						IR64 testcross F_1s					
	RIL vs F_1	R^2	RIL vs H	R^2	F_1 vs H	R^2	RIL vs F_1	R^2	RIL vs H	R^2	F_1 vs H	R^2
HD	0.717	0.514	0.325	0.106	0.892	0.796	0.364	0.133	–0.405	0.164	0.704	0.496
PH	0.385	0.148	–0.056	0.003	0.900	0.810	0.253	0.064	–0.335	0.112	0.827	0.684
FLL	0.276	0.076	–0.258	0.067	0.857	0.735	0.188	0.035	–0.418	0.175	0.813	0.662
FLW	0.627	0.394	0.135	0.018	0.856	0.733	0.366	0.134	–0.373	0.139	0.727	0.529
PL	0.207	0.043	–0.365	0.133	0.835	0.698	0.076	0.006	–0.538	0.289	0.800	0.640
SN	0.059	0.004	–0.377	0.142	0.902	0.814	0.144	0.021	–0.446	0.199	0.821	0.675
SF	0.296	0.087	–0.311	0.096	0.816	0.666	0.299	0.089	–0.429	0.184	0.734	0.539
Mean	0.367	0.181	–0.130	0.081	0.865	0.750	0.241	0.069	–0.421	0.180	0.775	0.604

$Z413F_1$ population, and only 6.9% (ranging from 0.6% for PL to 13.4% for FLW) in the $IR64F_1$ population, respectively. Third, there was a general negative correlation (R^2 = 18.0%) between the additive and the dominance gene actions for all traits in the $IR64F_1$ population, respectively. But in the $Z413F_1$ population, this was not the case for HD and FLW, suggesting the presence of partial dominance QTLs for the two traits segregating in this population. Fourth, the $IR64F_1$ population tended to show a greater level of non-additive gene action for all traits than the $Z413F_1$ population. This was not surprising since Z413 is more closely related to Teqing than IR64. These results clearly implicated that the performance of the TC hybrids for all measured traits was largely determined by dominance gene action, and additive and dominance gene actions for most traits appeared in opposite directions in the TC populations.

Main-effect QTLs (M-QTLs) detected in the RILs, TC F_1s and mid-parent heterosis

Table 3 shows a total of 32 M-QTLs affecting the seven traits in the RILs and TC populations. These M-QTLs were mapped to all 12 rice chromosomes except chromosome 9 (Fig. 2). Six M-QTLs were identified for HD, explaining 15.4%, 50.7% (30.0% for H_{MP}) and 8.3% (7.7% for H_{MP}) of the total trait variances in the RILs, $Z413F_1$s and $IR64F_1$s, respectively. Of these M-QTLs, *QHd3* was a dominant M-QTL with a dominance effect of 2.1 days for early heading. Interestingly, *QHd8* was also a dominant M-QTL but with a dominance effect causing delayed heading by 2.4 days. *QHd7*, *QHd11* and *QHd12* appeared to be additive M-QTLs as they were detectable only by the F_1 trait values but not by the H_{MP} values. *QHd4* appeared to be overdominant since its effect estimated from the H_{MP} values was greater than that from the F_1 trait values.

Five M-QTLs were detected for PH, accounting for 27.8%, 30.2% (25.2% for H_{MP}) and 8.6% (10.3% for H_{MP}) of the total trait variances in the RILs, $Z413F_1$s and $IR64F_1$s, respectively. *QPh3a* and *QPh6* were detected only in the RILs. *QPh8* appeared to be a dominant M-QTL detected in both RILs and $Z413F_1$s. *QPh4* was overdominant with a large dominance effect for increased height and was detected in both $Z413F_1$s and $IR64F_1$s. Identified in the $Z413F_1$s, *QPh3b* was an underdominant M-QTL with a dominance effect for reduced height.

Only two additive M-QTLs (*QFll2* and *QFll3*) were identified for FLL, which explained 18.7%, 11.5% and 13.2% of the total trait variances in the RILs, $Z413F_1$s and $IR64F_1$s, respectively.

Five M-QTLs affecting FLW were identified, which explained 46.3%, 30.8% (15.5% for H_{MP}) and 5.8% (10.0% for H_{MP}) of the total trait variances in the RILs, $Z413F_1$s and $IR64F_1$s, respectively. Four of the M-QTLs (*QFlw1*, *QFlw6*, *QFlw8* and *QFlw12*) appeared to be additive. *QFlw4*, detected in all three populations with large LOD scores, was a very interesting one. It appeared to be a dominant M-QTL in the $Z413F_1$s with a dominance effect of 0.58 mm for increased FLW, but it had a very large dominance effect of 0.55 mm for reduced FLW in the $IR64F_1$s, suggesting the presence of multiple alleles at this locus.

Three M-QTLs affecting PL were detected, which explained 11.3% (15.6% for H_{MP}) and 8.5% of the total trait variances in the $Z413F_1$s and $IR64F_1$s, respectively. Two of the M-QTLs (*QPl2* and *QPl8*) appeared to be additive and *QPl10* was overdominant.

Four M-QTLs affecting SN were identified, which explained 28.0% and 7.2% (6.9% for H_{MP}) of the total trait variances in the RILs and $Z413F_1$s, respectively. Two of these M-QTLs (*QSn1* and *QSn6*) appeared to be additive. *QSn3* appeared to be a completely dominant one and *QSn11* appeared to be overdominant.

Seven M-QTLs affecting SF were identified, which explained 6.6% and 35.0% (33.9% for H_{MP}) of the total trait variances in the $Z413F_1$s and $IR64F_1$s, respectively. Of these, four (*QSf5*, *QSf6*, *QSf8* and *QSf10*) appeared to be additive. Of the three remaining M-QTLs, *QSf7* and *QSf11* appeared to be underdominant with dominance effects of 3.2% and 3.1% for reduced fertility in the $IR64F_1$ hybrids, while *QSf10* appeared to be an overdominant one with a dominance effect of 2.6% for increased fertility in the TC F_1s.

Table 3 Main-effect QTLs affecting heading date (HD), plant height (PH), flag leaf length and width (FLL, FLW), panicle length (PL), spikelet number per panicle (SN) and spikelet fertility (SF) detected in the Lemont/Teqing RILs and their testcross hybrids with testers, Z413 and IR64

M-QTL	Ch	Marker interval	RILs[a]			Testcross F_1(Z413)[a]			Testcross H_{MP} (Z413)			Testcross F_1 (IR64)[a]			Testcross H_{MP}(IR64)		
			LOD	Effect	R^2	LOD	Effect	R^2	LOD	Effect	R^2	LOD	Effect	R^2	LOD	Effect	R^2
QHd3	3	C515–RG348a	3.36	–1.9	5.8	9.47	–3.6	16.0	6.86	–2.1	12.9						
QHd4	4	RZ590b–RG214										2.99	–1.3	8.3	3.53	–1.5	7.7
QHd7	7	C586–CDO405				2.85	–2.1	4.8									
QHd8	8	G104–G1314a	5.88	2.3	9.6	10.21	3.5	16.5	7.57	2.4	17.1						
QHd11	11	RZ537b–RG16				4.04	2.2	5.9									
QHd12	12	RG901a–G402				4.14	–2.4	7.5									
QPh3a	3	RG104–C515	5.05	–3.3	7.8												
QPh3b	3	RZ284–RZ403b				1.77	–3.2	5.5	2.43	–3.0	5.6						
QPh4	4	*Ph*–G379				5.26	4.4	8.8	4.61	4.0	8.0	5.25	3.1	8.6	5.98	3.8	10.3
QPh6	6	HHU37–RZ682	7.73	–4.8	12.3												
QPh8	8	CSU754–G104	4.60	3.2	7.7	7.50	5.5	15.9	5.53	4.6	11.6						
QFll2	2	RG520–RZ446b										4.57	–1.23	13.2			
QFll3	3	G249–RG418	11.51	–2.63	18.7	3.43	–1.37	11.5									
QFlw1	1	C131–RG472				2.24	–0.39	6.1									
QFlw4	4	*Ph*–G379	10.34	1.09	16.1	16.32	1.14	24.7	7.97	0.58	15.5	2.36	0.32	5.8	5.77	–0.55	10.0
QFlw6	6	RZ682–C236	8.98	–0.74	12.5												
QFlw8	8	G56a–R662a	7.09	–0.61	9.5												
QFlw12	12	RG341a–RG869	4.88	0.57	8.2												
QPl2	2	RG520–RZ446b										2.52	0.47	8.5			
QPl8	8	CSU754–G104				4.83	0.76	11.3									
QPl10	10	CDO98–RG752							3.41	0.96	15.6						
QSn1	1	RG236–RZ801	3.48	–0.37	5.1												
QSn3	3	G249–RG418	11.50	–0.75	15.7				3.76	0.41	6.9						
QSn6	6	RG653–RZ508	4.34	–0.50	7.2												
QSn11	11	RZ900–G44				4.34	0.50	7.2	3.03	0.42	7.7						
QSf3	3	RG348a–C636x													4.18	2.6	7.9
QSf5	5	Y1049–R569a										4.30	2.8	10.8			
QSf6	6	RZ2–*C*										3.30	–2.2	6.9			
QSf7	7	RG30–RG29													4.21	–3.1	12.8
QSf8	8	G2140–RZ323a										4.05	–2.6	8.5			
QSf10	10	RG561–C223				2.32	2.10	6.6									
QSf11	11	RZ797b–RG1094d										4.97	–2.6	8.8	4.32	–3.2	13.2

[a] In the RILs, QTL effects were associated with the Lemont allele (due to replacement of the Teqing alleles by the Lemont allele). In the testcross F_1s populations, QTL effects were estimated by the heterozygote (Lemont/tester) – the heterozygote (Teqing/tester), where the tester was either Z413 or IR64

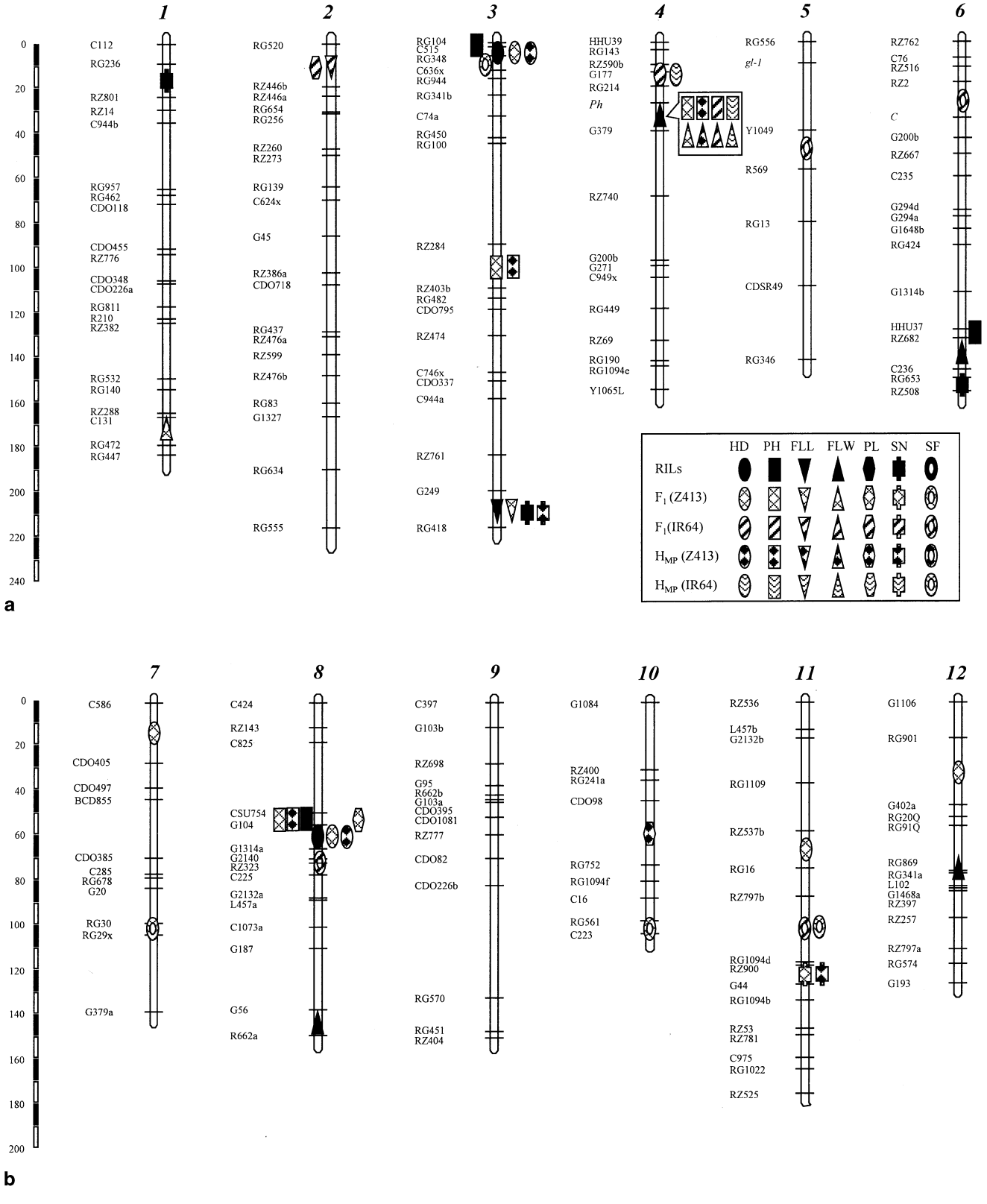

Fig. 2 Main-effect QTLs mapped in Lemont/Teqing RI and two relative testcross populations using RILs, F1s and mid-parental heterosis values as input data

Table 4 Digenic epistatic QTL pairs affecting heading date (HD), plant height (PH), flag leaf length (FLL) and width (FLW), panicle length (PL), spikelet number per panicle (SN) and spikelet fertility (SF) identified in 254 Lemont/Teqing RILs

Trait	Ch.	Marker interval *i*	Ch.	Marker interval *j*	LOD	A^a_i	A^a_j	AA^a_{ij}	R^{a2} (%)
HD	1	CDO348–CDO226a	3	C636x–RG944	3.21			1.7	6.6
HD	8	**CSU754–G104**	11	**RZ53–RZ781**	11.10	2.3***	1.1*	–2.3	11.1
HD	11	RZ536a–L457b	12	**RG20q–RG91q**	3.01	0.9*		1.3	3.8
PH	2	C624x–G45	9	RZ777–CDO82	3.78			–2.9	6.2
PH	2	RZ476a–RZ599	11	RZ537b–RG16	4.24			–3.0	7.0
PH	2	RG634–RG555	7	C285–RG678	4.65			3.5	9.0
PH	3	RZ474–C746	6	RZ2–*C*	3.08			3.1	7.1
PH	3	G249–RG418	8	**G2140–RZ323a**	2.91			2.5	4.6
FLL	1	**RG532–RG140**	1	RG472–RG447	4.47	–0.6*		1.1	6.7
FLL	1	CDO226a–RG811	9	RZ777–CDO82	5.86	–0.6*		1.2	7.7
FLL	3	C74a–RG450	3	C944a–RZ761	4.86			1.3	8.4
FLL	4	RG143–G177	8	L457a–C1073a	4.30			–1.1	5.9
FLW	1	CDO118–CDO455	11	G2132b–RG1109	3.93			0.35	5.4
FLW	1	**C131–RG472**	9	RZ777–CDO82	4.28		–0.28*	–0.45	7.3
FLW	3	G249–RG418	11	RZ797b–RG1094d	3.40			0.45	7.0
PL	3	**RG482–CDO795**	4	G177–RZ590b	3.80			–0.69	8.0
PL	4	*Ph*–G379	6	C235a–G294d	6.95		–0.38*	0.92	14.4
PL	7	CDO497–BCD855	9	RG451–RZ404	4.39			0.77	10.2
SN	2	RZ273–RG139	3	RZ403b–RG482	6.18	0.23*		0.48	9.2
SN	2	RZ260–RZ273	11	RZ797b–RG1094d	3.72			0.35	5.7
SN	2	RG256–RZ260	12	RZ257–RZ797a	3.04			0.32	5.1
SN	3	RG348a–C636x	3	C944a–RZ761	6.30		0.36***	0.47	8.8
SN	4	G177–RZ590b	8	L457a–C1073a	7.40	0.28**		–0.39	6.2
SN	4	G271–C949	11	RZ797b–RG1094d	5.12			0.51	10.4
SF	1	RZ801–RZ14	11	C975–RG1022	6.35			4.0	9.8
SF	1	RG957–RG462	8	L457a–C1073a	6.93			–4.1	10.6
SF	3	**C515–RG348a**	8	CSU754–G104	5.18	–1.7**		2.9	5.2
SF	3	RZ284–RZ403b	6	C236–RG653	8.97		–1.7*	4.9	15.1
SF	3	RZ403b–RG482	12	RG901–G402	5.63			–3.8	8.9
SF	8	C825a–CSU754	11	C975–RG1022	6.05			–3.7	8.4

[a] A_i and A_j are the main effects of the loci *i* and *j*, arising from by the substitution of the Lemont allele by the Teqing allele, and *, **, *** represent the significance levels of the QTL main effects (A_i and A_j) at $P < 0.05$, 0.001, and 0.0001, respectively. AA_{ij} is the epistatic effect between loci *i* and *j*, as defined by Mather and Jinks (1982). R^2 is the proportion of the total phenotypic variation explained by the AA_{ij}, which were all significant at $P < 0.001$. Bold markers are those flanking M-QTLs identified in Table 3

Epistatic QTLs (E-QTLs) detected in the RILs and TC populations

Table 4 shows 30 E-QTL pairs identified in the RILs. These included three pairs accounting for 21.5% of the total variation in HD, five pairs explaining 33.9% of the total variation in PH, four pairs explaining 28.7% of the total variation in FLL, three pairs explaining 19.7% of the total variation in FLW, three pairs explaining 32.6% of total variation in PL, six pairs explaining 45.4% of the total variation in SN and six pairs explaining 58.0% of the total variation in SF, respectively. Of these E-QTLs, three occurred between an M-QTL and a modifying factor, and the remaining interactions occurred between two complementary loci, ten of which also had significant additive effects.

Table 5 shows 34 E-QTL pairs detected in the Z413 TC population. There were six E-QTL pairs identified for HD, including two additive (detected only by the F_1 trait values), one dominant and three overdominant, which together accounted for 48.7% of the TC F_1 variance and 39.9% of the H_{MP} variance, respectively. These included two additive ones (detected only by the F_1 trait values), one showing complete dominance, and three showing overdominance. For PH, the four E-QTLs all appeared to be overdominant and explained 20.7% of the TC F_1 variance and 33.1% of the H_{MP} variance, respectively. For FLL, all five E-QTLs appeared to be overdominant and collectively explained 41.8% of the TC F_1 variance and 34.9% of the H_{MP} variance, respectively. For FLW, one additive and two overdominant E-QTL pairs explained 23.6% of the TC F_1 variance and 22.0% of the H_{MP} variance, respectively. For PL, one dominant and one overdominant E-QTL pair explained 31.3% of the TC F_1 variance and 9.4% of the H_{MP} variance, respectively. For SN, all seven detected E-QTL pairs appeared to be overdominant and explained 49.8% of the TC F_1 variance and 41.5% of the H_{MP} variance, respectively. For SF, four additive and three overdominant E-QTLs explained 72.9% of the TC F_1 variance and 47.0% of the H_{MP} variance, respectively.

Table 6 shows 42 E-QTL pairs detected in the IR64 TC population. For HD, one additive, one dominant and four overdominant E-QTLs were identified, which collectively explained 48.7% of the TC F_1 variance and 39.9% of the H_{MP} variance, respectively. For PH, one additive, two dominant and five overdominant E-QTL pairs collectively explained 53.1% of the TC F_1 variance and 49.9% of the H_{MP} variance, respectively. For FLL, one additive and four overdominant E-QTL pairs explained 33.8% of the

Table 5 Digenic epistatic QTL pairs affecting the mean performance and heterosis of heading date (HD), plant height (PH), flag leaf length (FLL) and width (FLW), panicle length (PL), spikelet number per panicle (SN) and spikelet fertility (SF) identified in the Z413F_1s

Trait	Ch.	Marker interval *i*	Ch.	Marker interval *j*	LOD	Testcross F_1			R^2 (%)	LOD	Testcross H_{MP}			R^2 (%)
						A^a_i	A^a_j	AA^a_{ij}			A^a_i	A^a_j	AA^a_{ij}	
HD	1	**C112–RG236**	8	C1073a–G187	5.71			–2.7	7.9					
HD	1	CDO226a–RG811	1	C131–RG472	3.26			2.1	4.8					
HD	2	RG520–RZ446b	7	C586–CDO405	4.45	1.5**	–2.3***	2.8	8.8	4.75	1.0*	–1.1**	1.9	7.7
HD	1	CDO118–CDO455	9	CDO82–CDO226b						7.31			–2.7	15.1
HD	1	CDO348–CDO226a	2	RZ446a–RG654						4.65			–1.8	7.0
HD	1	C131–RG472	5	RG556–*gl1*						3.56			1.6	5.6
PH	2	G45–RZ386a	6	RZ2–*C*	4.18			–4.0	7.4	5.03			–4.4	9.9
PH	4	RZ740–G200b	10	RG1094f–C16	2.53			3.4	5.4	3.22			4.0	7.9
PH	6	C76–RZ516	6	G1468b–RG424	4.06			4.1	7.9	4.57		1.5*	4.6	10.5
PH	3	G249–RG418	12	RZ397–RZ257						3.36	2.3**		2.1	4.8
FLL	1	C944b–RG957	5	*gl1*–Y1049	3.39		–1.04**	–1.62	10.3	3.78		–0.80*	–1.46	9.7
FLL	2	**RG256–RZ260**	6	RZ667–C235a	3.86			–1.26	6.3	2.07			–1.02	4.7
FLL	3	RG944–RG341b	5	*gl1*–Y1049	3.69		–0.61*	1.18	5.5	2.37		–0.72*	0.97	4.5
FLL	3	CDO795a–RZ474	9	R662b–G103a	5.72			1.65	10.6	3.84			1.26	7.2
FLL	4	HHU39–RG143	9	CDO226b–RG570a	3.25			–1.52	9.1	3.47	0.82*		–1.39	8.8
FLW	1	CDO118–CDO455	6	G200a–RZ667	3.3			0.43	6.8	3.83		0.26*	0.40	11.2
FLW	1	C131–RG472	5	RG13-CDSR49	3.36			–0.47	8.0					
FLW	3	RZ403b–RG482	10	RG561–C223	3.51			–0.49	8.8	2.08			–0.39	10.8
PL	3	CDO795a–RZ474	9	G103b–RZ698	6.28			0.96	18.0	2.36			0.65	7.3
PL	4	G379–RZ740	7	G20–RG30	4.51	0.32*		0.83	13.3	2.61	0.36*		0.74	9.4
SN	1	RG462–CDO118	5	R569a–RG13	3.77			–0.47	7.8	3.53			–0.49	6.9
SN	1	RG462–CDO118	6	G200a–RZ667	4.44		0.23*	0.35	4.2	4.73		0.25*	0.40	4.5
SN	1	CDO455–RZ776a	4	**Ph–G379**	3.63			0.37	4.8	2.46			0.35	3.4
SN	1	C131–RG472	4	RG190–RG1094e	3.28			0.43	6.4	2.70			0.44	5.4
SN	2	RG139–C624x	8	C825a–CSU754	4.18			–0.51	9.0	4.56		0.24*	–0.56	8.9
SN	4	G379–RZ740	11	RZ537b–RG16	3.58		–0.22*	–0.50	8.8	2.38			–0.43	5.2
SN	5	*gl1*–Y1049	11	RZ900–G44	4.28		0.28**	0.50	8.8	3.94		0.36**	0.50	7.2
SF	1	RG462–CDO118	4	*Ph*–G379	3.85			–2.6	7.7					
SF	2	RG256–RZ260a	9	RG570a–RG451	3.13			–3.5	14.8					
SF	4	RG214–*Ph*	8	G187–G56a	2.96			–1.9	8.0	5.01			–3.9	18.9
SF	7	**CDO497–BCD855**	11	G2132b–RG1109	3.98			–1.9	8.0					
SF	8	C1073a–G187	10	RG561–C223	3.48			–3.0	10.2	5.58			–3.4	14.8
SF	10	G1084–RZ400	11	RG1094d–RZ900	4.40	1.9*		2.9	9.8					
SF	11	RZ900–G44	11	RZ53–RZ781	5.24			3.5	14.4	3.71			3.2	13.3

[a]A_i and A_j are the main effects of the loci *i* and *j*, estimated by the difference between two heterozygotes (Z413/Teqing – Z413/Lemont) using the mean F_1 and H_{MP} values and *, **, *** represent significance levels of $P < 0.05$, $P < 0.001$ and $P < 0.0001$, respectively. AA_{ij} were the epistatic effects between loci *i* and *j* defined by Mather and Jinks (1982), which were all significant at $P < 0.001$. Bold markers are those flanking the M-QTLs described in Table 3

Table 6 Digenic epistatic QTL pairs affecting the mean performance and heterosis of heading date (HD), plant height (PH), flag leaf length (FLL) and width (FLW), panicle length (PL), spikelet number per panicle (SN) and spikelet fertility (SF) identified in the IR64F$_1$s

Trait	Ch.	Marker interval *i*	Ch.	Marker interval *j*	LOD	Testcross F_1			R^2 (%)	LOD	Testcross H_{MP}			R^2 (%)
						A_i	A_j	AA_{ij}			A_i	A_j	AA_{ij}	
HD	1	**RG236–RZ801**	6	RZ682–C236	4.60			–1.8	10.5					
HD	1	CDO226a–RG811	3	**RZ761–G249**	4.23			–1.3	5.7	6.30		–0.9**	–1.7	9.5
HD	3	RG341b–C74a	10	RG241a–CDO98	4.46			1.6	8.2	2.49		–1.1**	1.0	5.8
HD	5	R569a–RG13	6	C235a–G294d	4.94			1.7	9.1	3.74		1.1**	1.2	6.9
HD	6	RZ516–RZ2	7	CDO405–CDO497	2.10		–0.9*	1.2	6.3	2.84			1.5	7.3
HD	9	RZ777–CDO82	10	RZ400–RG241a	4.33		–0.9*	–1.7	8.9	4.24		–1.2**	–1.8	10.4
PH	1	C112–RG236	11	G2132b–RG1109	2.68			–1.7	6.7					
PH	1	R210–RZ382	11	RG16–RZ797b	2.57	–1.6*	1.8**	0.9	3.5	4.91			3.7	9.8
PH	1	RG472–RG447	5	CDSR49–RG346	3.23			–3.0	7.6	1.73			–2.2	5.3
PH	2	RG139–C624x	12	**G402–RG20q**	2.54			2.5	5.3	3.04		1.5*	2.0	5.0
PH	3	C944a–RZ761	4	RG1094e–Y1065L	5.53			4.6	18.1	3.38		1.7*	3.3	7.9
PH	3	**RG104–C515**	4	RZ69–RG190						3.60			–2.8	5.5
PH	5	Y1049–R569a	11	RZ781–C975	2.59			2.9	7.2	4.20	1.7*		4.0	11.2
PH	9	C397–G103b1	10	RG241a–CDO98	2.50			1.9	4.7	4.03	1.7*	2.1**	2.7	5.2
FLL	1	RG236–RZ801	3	CDO795a–RZ474	2.77			0.94	5.5	4.28	0.69*		0.95	5.1
FLL	3	RG104–C515	7	RG678–G20	3.57			–1.01	6.3	6.23			–1.35	10.3
FLL	5	CDSR49–RG346	12	RG574–G193	4.15			1.34	11.2					
FLL	7	CDO405–CDO497	8	RZ143–C825a	4.17			–1.32	10.8	3.99			–1.34	10.2
FLL	4	RG143–G177	12	RZ797a–RG574						5.78	–0.69*	–0.60*	1.16	7.6
FLW	1	RG462–CDO118	9	RG570a–RG451	3.97		–0.22*	0.42	7.3	3.21			0.39	4.7
FLW	1	CDO118–CDO455	7	C285–RG678	3.03			–0.33	4.6	2.39			–0.33	4.1
FLW	2	RZ476b–RG83	4	RZ740–G200b	4.16			–0.46	8.6	5.29			–0.47	6.8
FLW	8	C1073a–G187	9	CDO226b–RG570a	6.41		–0.22*	–0.53	11.5	4.52	0.31**		–0.41	5.1
FLW	3	G249–RG418	7	CDO405–CDO497						2.68			–0.53	8.5
FLW	8	G187–G56a	11	RZ781–C975						3.67	0.24*		–0.35	3.7
PL	1	RZ382–RG532	2	CDO718–RG437	3.23			–0.71	13.3					
PL	2	RZ476a–RZ599	4	RG1094e–Y1065L	2.41			0.49	6.3					
PL	3	RZ403b–RG482	4	G177–RZ590b	1.84			0.35	4.5	3.45			0.68	8.6
PL	2	RZ260a–RZ273	9	CDO395–CDO1081						2.68			–0.59	6.4
PL	4	*Ph*–G379	6	G294d–G294a						3.85		0.29*	–0.60	6.8
SN	1	CDO348–CDO226a	7	CDO385–C285	2.27			–0.28	4.4	2.67			–0.36	5.6
SN	2	RG437–RZ476a	6	RG653–RZ508	4.43			0.43	10.4	3.89		0.24*	0.38	5.8
SN	3	RZ403b–RG482	4	**Ph–G379**	3.50	0.185*		0.31	5.3	3.11			0.34	5.0
SN	4	G177–RZ590b	11	RG16–RZ797b	6.12			0.47	12.6	5.96			0.50	10.8
SN	4	**Ph–G379**	12	G1106–RG901a	3.26			–0.35	6.8	2.52			–0.34	5.0
SN	8	CSU754–G104	11	RZ797b–RG1094d	3.90			0.36	7.1	3.72	0.20*		0.36	5.7
SN	1	CDO226a–RG811	12	RG901a–G402						2.43			–0.34	4.9
SF	1	RZ14–C944b	1	CDO348–CDO226	2.67			–1.7	3.2					
SF	3	RG482–CDO795a	12	RG901a–G402	5.06	–1.1*		–2.8	8.5					
SF	9	G103b1–RZ698	9	CDO226b–RG570	3.09			–2.3	5.8	4.59	–1.7**		–2.9	7.0
SF	4	C949–RG449	11	RG16–RZ797b						5.72	–1.3*	–2.3***	–2.4	4.9
SF	10	RG241a–CDO98	12	**RG91q–RG341a**						3.57			–2.6	6.0

[a]A_i and A_j are the main effects of the loci *i* and *j*, estimated by the difference between two heterozygotes (IR64/Teqing–IR64/Lemont) using the mean F_1 and H_{MP} values and *, **, *** represent significance levels of $P < 0.05$, $P < 0.001$ and $P < 0.0001$, respectively. AA_{ij} were the epistatic effects between loci *i* and *j* defined by Mather and Jinks (1982), which were all significant at $P < 0.001$. Bold markers are those flanking the M-QTLs described in Table 3

TC F_1 variance and 33.2% of the H_{MP} variance, respectively. For FLW, all six E-QTLs appeared to be overdominant and collectively explained 32.0% of the TC F_1 variance and 32.9% of the H_{MP} variance, respectively. For PL, two additive and three overdominant E-QTL pairs explained 25.1% of the TC F_1 variance and 21.8% of the H_{MP} variance, respectively. For SN, all seven E-QTL pairs appeared to be overdominant and explained 46.6% of the TC F_1 variance and 42.8% of the H_{MP} variance, respectively. For SF, two additive and three overdominant E-QTLs explained 17.5% of the TC F_1 variance and 17.9% of the H_{MP} variance, respectively.

Discussion

The unique use of a set of RILs together with their TC hybrids for QTL mapping allowed the direct measurements of heterosis for all measured traits and maximized the ability to more accurately resolve different types of gene action for identified QTLs that were responsible for trait performance and heterosis (Liu et al. 1996). For instance, the RILs allowed more recombination of linked QTLs and thus were more powerful in dissecting QTLs having both additive and non-additive gene actions. We realized that the M-QTL main effects detected in the TC populations could not be clearly defined genetically, and actually represented the differential intralocus interactions between the parental alleles of the RILs and the tester allele, or the difference between the two heterozygotes (Lemont/tester – Teqing/tester). Thus, if the tester allele is dominant to the parental alleles, no QTLs would be detectable. In cases where the tester has the same allele as one of the parents, the QTL effect estimated from the mean values of the TC hybrids was expected to contain both additive and dominance effects, while that estimated from the H_{MP} values was the QTL dominance effect. Overdominance could be inferred as long as $A_i(H_{MP})$ or $AA_{ij}(H_{MP}) >> ½A_i(TCF_1)$ or $½AA_{ij}(TCF_1)$ (Melchinger et al. 1998).

Our design was also expected to have increased the power to identify more QTLs and even multiple alleles at QTL loci because of the inclusion of the testers as additional parents of the mapping populations. This was particularly true since the two testers were genetically divergent. We noted that the trait variation of the RILs was similar to that of the $Z413F_1$s and only slightly greater than that of the $IR64F_1$s. Indeed, we were able to identify a total of 32 M-QTLs (or 4.6 per trait) and 106 E-QTL pairs (or 15.1 per trait), which was much more than those identified from any of the single mapping populations. As will be discussed below, this increased power of our design in detecting more QTLs could largely be attributed to the fact that QTLs with different types of gene action (additive, dominant and over- or under-dominant QTLs) could be detected in the TC populations.

The most striking finding of this study was the presence of two predominant types of identified QTLs, the additive QTLs and the overdominant QTLs, with only a few exceptional QTLs showing complete or partial dominance. For instance, the total number of the identified additive QTLs was 24 (13 from the RILs, 7 from $Z413F_1$s, and 4 from $IR64F_1$s) and 44 (30 from the RILs and 14 from the TC populations) for E-QTLs, respectively. The total number of the identified overdominant QTLs was 12 (7 from $Z413F_1$s and 5 from $IR64F_1$s) for the M-QTLs and 57 (25 from $Z413F_1$s and 32 from $IR64F_1$s) for E-QTLs, respectively. Only four M-QTLs (two for HD and two for FLW) and five E-QTL pairs (two for HD, two for PH and one for PL) appeared to be dominant in the TC populations. As a result, approximately 19.4% (22.4% for $Z413F_1$s and 16.3% for $IR64F_1$s) of the total trait variation in the TC population was attributable to additive gene action and 32.9% (36.1% for $Z413F_1$s and 29.7% for $IR64F_1$s) was attributable to non-additive gene action resulting largely from the overdominant QTLs (Table 7). kata The relative importance of different types of gene action differed significantly across the measured traits and the mapping populations. In the $Z413F_1$s, both additive and non-additive gene actions contributed almost equally to the total F_1 phenotypic variation for HD, SF and FLW, while for the remaining traits, non-additive gene action was more important. In the $Z413F_1$s, the relative importance of the non-additive vs additive gene action in a descending order was SN > FLW > FLL > PL > PH > HD > SF. The high importance of non-additive gene action for SN was consistent with prior reports (Li et al. 2001; Luo et al. 2001) that non-additive gene action is crucial to grain yield and its components, since SN is the primary contributor to yield.

There was little overlap between QTLs identified in the RILs and those detected in the TC populations, in contrast to the 53% overlap for the M-QTLs detected in the RILs and their BCF_1 populations (unpublished data). Only one M-QTL (*QFlw4*) was detected in all three populations, but the dominance effects estimated from the two TC populations were in opposite directions, suggesting the presence of multiple alleles at this locus. Two dominant M-QTLs (*QHd3* and *QHd8*) were detected in both RILs and $Z413F_1$s, as well as in the BCF_1 populations (unpublished data) and in the original F_2–F_4 population (Li et al. 1995). It is not surprising that RILs and $Z413F_1$s shared more M-QTLs since the tester, Z413, is more closely related to one of the parents of the RILs, Teqing. These results were consistent with the results of the correlation analyses (Table 2), and the same pattern was observed for grain yield and its components in the same RI and TC populations (Li et al. 2001; Luo et al. 2001), i.e. the higher the trait heritability was, the less-pronounced inbreeding depression the RILs displayed and the less-pronounced heterosis the TC hybrids exhibited.

The predominance of additive and overdominant QTLs detected in the TC populations was also true in the two BCF_1 populations (the RILs × parents) (unpublished data), suggesting that additive gene action is largely independent from the non-additive gene action in the genetic control of quantitative traits of rice. In a similar

Table 7 Summarized results on gene action of QTLs affecting seven traits in the Lemont/Teqing RILs and two testcross populations

Trait	RILs		Z413 testcross							IR64 testcross							
	No.	R^2	Additive		Complete or partial dominance			Over- or under-dominance			Additive		Complete or partial dominance			Over- or under-dominance		
			No.	$R^2(F_1)$	No.	$R^2(F_1)$	$R^2(H_{MP})$	No.	$R^2(F_1)$	$R^2(H_{MP})$	No.	$R^2(F_1)$	No.	$R^2(F_1)$	$R^2(H_{MP})$	No.	$R^2(F_1)$	$R^2(H_{MP})$
M-QTLs																		
HD	2	15.4	3	18.2	2	32.5	30.0									1	8.3	7.7
PH	3	37.8						3	30.2	25.2						1	8.6	10.3
FLL	1	18.7	1	11.5				1		13.2								
FLW	4	41.3	1	6.1	1	24.7	15.5						1	5.8	10.0			
PL			1	11.3				1		15.6	1	8.5						
SN	3	28.0						2	7.2	14.6								
SF			1	6.6							3	26.2				3	8.8	33.9
Mean	1.9	20.2	1.0	7.7	0.4	8.2	6.5	1.0	5.3	9.8	0.6	5.0	0.1	0.8	1.4	0.7	3.7	7.4
E-QTLs																		
HD	3	21.5	2	12.7	1	8.8	7.7	3		27.7	1	10.5	1	8.2	5.8	4	30.0	34.1
PH	5	33.9						4	20.7	33.1	1	6.7	2	25.7	13.2	5	20.7	36.7
FLL	4	28.7						5	41.8	34.9	1	11.2				4	22.6	33.2
FLW	3	19.7	1	8.0				2	15.6	22.0						6	32.0	32.9
PL	3	32.6			1	18.0	7.3	1	13.3	9.4	2	19.6				3	4.5	21.8
SN	6	45.4						7	49.8	41.5						7	46.6	42.8
SF	6	59.0	4	40.3				3	32.6	47.0	2	11.7				3	5.8	17.9
Mean	4.3	34.4	1.0	8.7	0.3	3.8	2.1	3.6	24.8	30.8	1.0	8.5	0.4	4.8	2.7	4.6	23.2	31.3

R^2 (in %) was the proportion of total trait phenotypic variances explained

QTL mapping of maize using TC progenies (F_3 lines testcrossed with a tester), M-QTLs for two traits, with moderate to high heritability, protein content and kernel weight identified in the TC progeny, only partially overlapped with those identified in the F_3 progeny per se (Schön et al. 1994); and those overlapping QTLs had similar effects in both magnitude and direction, suggesting they were additive QTLs. The importance of apparent overdominance was unexpected from what is generally believed from numerous classical quantitative genetic studies, i.e. most genes contributing to quantitative trait variation are partially dominant, which was apparently due to the summed effects of additive and overdominant loci based on our observations. Thus, our observation may have important implications in plant breeding if it is confirmed to be generally true for gene actions of QTLs in plants.

Although less pronounced than for grain yield and its components (Li et al. 2001; Luo et al. 2001), the relative contribution to the total trait variation by the identified E-QTL pairs was much greater than that of the detected M-QTLs for all traits except HD and FLW in the $Z413F_1$s (Table 7). In the RILs, the mean R^2 was 20.2% (ranging from 0.0 for PL and SF to 41.3% for FLW) for M-QTLs and 34.4% (ranging from 19.7% for FLW to 59.0% for SF) for E-QTLs, respectively. In the $Z413F_1$s, the mean R^2 was 21.2% for M-QTLs and 37.3% for E-QTLs, respectively. In the $IR64F_1$s, the mean R^2 was 9.5% for M-QTLs and 36.5% for E-QTLs, respectively. Furthermore, most detected E-QTLs (80.0% in the RILs, 88.2% in the $Z413F_1$s and 89.2% in the $IR64F_1$s) occurred between two complementary loci, and the remainder occurred between an M-QTL and a modifying factor, with only one interaction between two M-QTLs for HD in the RILs. This result was consistent with what we observed in the BC populations and the grain yield components in the TC and BC populations, as well as in the early generation of the Lemont/Teqing cross (Li et al. 1997a, 2001), providing compelling evidence that epistasis plays an important role in the genetic control of quantitative traits in rice (Yu et al. 1997).

Evolutionarily, dominance for increased fitness would expectedly be favored by selection for genes affecting fitness traits. Contrary to this expectation, four of the six SF M-QTLs identified in the TC populations had main effects for reduced fertility, including two under-dominant QTLs. This was also observed in the early generation of the Lemont/Teqing cross (Li et al. 1997b, who inferred that these QTLs might represent the genomic regions where there are cryptic chromosomal aberrations, which are responsible for the hybrid sterility commonly observed in intersubspecific crosses of rice. Similarly, most epistatic effects of the recombinant type (Tables 5 and 6) tended to result in reduced SF, lending strong support to the result that incompatible interactions between *japonica* and *indica* alleles at many E-QTL pairs were responsible for the hybrid breakdown observed in the RILs and early generation of the Lemont/Teqing cross (Li et al. 1997b).

The presence of multiple alleles with known or potential functional differences has been well documented for disease resistance loci, self incompatibility loci and some isozyme loci in many plants including rice, and has important implications in selecting appropriate candidate alleles/QTLs in marker-aided trait manipulations. However, it has been difficult to identify multiple alleles at QTLs since most QTL-mapping in plants is based on bi-parental populations. It has been observed that many QTLs affecting the same phenotypes map to the same or similar genomic regions in rice populations derived from different parental lines (Xiao et al. 1994, 1996; Li et al. 1995; Yu et al. 2002), but comparison across different mapping populations to infer the presence of multiple alleles at the QTL level is imprecise, both due to the difference in genetic maps, genetic backgrounds and to possible QTL × environment interactions (Xing et al. 2002). We detected the presence of multiple alleles at one M-QTL, *QFlw4*, by comparing its effects estimated from different TC populations with those from the RILs and two BC populations. *QFlw4* behaved as an additive M-QTL detected in the RI and Teqing BCF_1 populations (unpublished data), but was an overdominant QTL in the $Z413F_1$s and an underdominant QTL in the $IR64F_1$s. Thus, identification and characterization of multiple functional alleles at QTLs remain a largely unexploited but very important area, if the results from QTL mapping studies are to be applied to the genetic improvement of quantitative traits.

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