Dominance, Over-dominance and Epistasis

Condition the Heterosis in Two Heterotic Rice Hybrids

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ABSTRACT

Two recombinant inbred (RI) populations having 194 and 222 lines each, derived respectively from a highly heterotic inter- (IJ) and intra-subspecific (II) hybrid, were backcrossed to their respective parents. The RI and two backcross populations along with F1 and its two parents of each hybrid were evaluated for nine important traits, including grain yield and other eight yield related traits. A total of 76 quantitative trait loci (QTL) for IJ hybrid and 41 QTL for II hybrid was detected in RI population, mid-parent heterosis of two backcross populations, and two independent sets of data by summation (L1+L2) and by subtraction (L1−L2) of two backcross populations (L1 and L2). The variance explained by each QTL ranged from 2.6% to 58.3%. In IJ hybrid, 42% (32) of the QTL showed an additive effect, 32% (24) a partial-to-complete dominant effect, and 26% (20) an over-dominant effect. In II hybrid, 32% (13) of the QTL demonstrated an additive effect, 29% (12) a partial-to-complete dominant effect, and 39% (16) an over-dominant effect. There were 195 digenic interactions detected in IJ hybrid and 328 in II hybrid. The variance explained by each digenic interaction ranged from 2.0% to 14.9%. These results suggest that the heterosis in these two hybrids is attributable to the orchestrated outcome of partial-to-complete dominance, over-dominance, and epistasis.
Heterosis, a term to describe the superiority of heterozygous genotypes over their corresponding parental genotypes (SHULL 1908), has been under investigation for about 100 years, but no consensus exists about the genetic basis underlying this very important phenomenon. Two contending hypotheses, the dominance hypothesis and over-dominance hypothesis, were proposed to explain this phenomenon about one century ago. The dominance hypothesis attributes heterosis to canceling of deleterious or inferior recessive alleles contributed by one parent, by beneficial or superior dominant alleles contributed by the other parent in the heterozygous genotypes at different loci (DAVENPORT 1908; BRUCE 1910; JONES 1917). Over-dominance hypothesis attributes heterosis to the superior fitness of heterozygous genotypes over homozygous genotypes at single locus (SHULL 1908; EAST 1908).

Molecular markers and their linkage maps have greatly facilitated the identification of individual loci conditioning heterosis and the estimation of gene action of underlying loci. QTL mapping studies aiming at understanding the genetic basis of heterosis have been conducted in rice and other crops (XIAO et al. 1995; YU et al. 1997; LI et al. 1997; LI et al. 2001; LUO et al. 2001; HUA et al. 2002, 2003; SEMEL et al. 2006; MELCHINGER et al. 2007a, 2007b; FRASCAROLI et al. 2007). Evidence from such studies suggests that heterosis may be attributable to dominance (XIAO et al. 1995; Cockerham and ZENG 1996), over-dominance (STUBER et al. 1992; LI et al. 2001; LUO et al. 2001), pseudo-overdominance due to tightly linked loci with beneficial or superior dominant alleles in repulsion phrase (CROW 2000; LIPPMAN and ZAMIR 2007), or epistasis (SCHNELL and COCKERHAM 1992; LI et al. 2001; LUO et al. 2001)
Heterosis is the base of the great success in hybrid rice. Currently, hybrid rice accounts for about 55% of the total planting acreage of paddy rice in China and the annual increased rice production resulting from planting hybrid rice amounts to about 20 million metric tones which can provide a main staple food for more than 70 million people (Lu et al. 2002). Hybrid rice varieties have a yield advantage of 10~20% over the best conventional inbred varieties using similar cultivation conditions (Lu et al. 2002). Besides the large planting in China, hybrid rice varieties are also widely planted in more than 20 countries around the world.

Previous studies indicated the genetic basis of heterosis in rice is very complicated and various depending on study materials and analysis approaches (Xiao et al. 1995; Hua et al. 2002, 2003; Yu et al. 1997; Li et al. 2001). The objective of this study was to identify the main-effect QTL and digenic epistatic loci underlying heterosis of nine important agronomic and economic traits of rice and estimate the gene action of each QTL and interaction using a TTC (triple testcross cross) design to shed light on the understanding of the genetic basis of heterosis in two diverse and highly heterotic rice hybrids.

**MATERIALS AND METHODS**

**Populations:** Two highly heterotic rice hybrids, one inter-subspecific between 9024 (*indica*) and LH422 (*japonica*) and one intra-subspecific between Zhenshan97 (*indica*) and Minghui63 (*indica*), were employed in this study. From the F$_1$ of the inter-subspecific hybrid (designated as *IJ* hybrid hereafter), 194 F$_7$ lines were developed.
by single seed descent. From the F₁ of the intra-subspecific hybrid (designated as II hybrid hereafter), 222 F₁₂ lines were developed through 11 consecutive selfing generations. Each of these F₇ and F₁₂ lines was derived from a different F₂ plant. No positive or negative selection was performed during each of the selfing generations. A single plant from each of these 194 F₇ lines and 222 F₁₂ lines was chosen randomly and backcrossed to each of their two respective parents to produce backcross progeny and selfed to generate F₈ or F₁₃ lines.

**Phenotypic variation:** For IJ hybrid, two backcross populations having 194 lines each, 194 F₈ recombinant inbred lines (RILs), along with the two parental lines and their F₁, were arranged in a field in a randomized complete block design with two replications for phenotypic evaluation in the summer season of 1992 at China National Hybrid Rice Research and Development Center, Changsha, Hunan, China. Twenty-seven plants (three rows × nine plants per row) were planted at a density of 300,000 plants per hectare in each of 1,170 plots. The middle five plants in the central row of each plot were used for phenotypic trait evaluation and data collection.

For II hybrid, the two backcross populations with 222 lines each, the corresponding 222 F₁₃ RILs, along with two parental lines and their F₁, were laid out in a field in a randomized complete block design with two replications for phenotypic evaluation in the summer season of 2006 at the experimental farm of the Huazhong Agricultural University, Wuhan, Hubei, China. Twenty-one-day-old seedlings were transplanted into three-row plots with each plot consisting of a single row of a RIL and two rows of BC hybrids. There were seven plants in each row, with 16.7cm between plants within each row and
26.7 cm between rows. The middle five plants in each row were used for phenotypic trait evaluation and data collection.

Nine quantitative traits of agronomic and economic importance evaluated were heading date (HD in days), plant height (PH in centimeters), tillers per plant (TP), panicle length (PL in centimeters), filled grains per panicle (FGPP), percent seed set (SS), grain density (GD in grain numbers per centimeter of panicle length), 1000-grain weight (KGW in gram) and grain yield (YD in tons/ hectare). Means over replications, for each trait, for RIL and each of two backcross populations, were used for QTL and other analyses.

**Analysis of field data and of heterosis:** For each hybrid, data of RI and BC populations were analyzed separately. SAS PROC GLM (SAS institute 1996) was used to test the differences among RILs and the corresponding BC hybrids. Heterosis was evaluated in BC populations by Hmp. Hmp= F₁ – (RIL + recurrent parent)/2. F₁’s are mean trait values of individual BC hybrids while RIL is the corresponding RIL parent for each of the BC hybrids, and recurrent parent is 9024 or LH422 in the IJ hybrid and Zhenshan 97 or Minghui 63 in the II hybrid. To distinguish one from another, the RIL in is designated as RILij in IJ hybrid and as RILii in II hybrid.

Following KEARSEY et al. (2003) and FRASCAROLI et al. (2007), the crosses of the n RILs to the two recurrent parents are referred as ‘L₁i’ and ‘L₂i’ (i=1~n), respectively. The two independent sets of data by summation (L₁i + L₂i) and by subtraction (L₂i – L₁i) of two BC populations’ values hereafter are referred to the “SUM” data set and the “DIFF” data set, respectively. Variation within the SUM data set is due to additive
effects and variation within the DIFF data set is due to dominance effects when combined over two BC populations.

In this study, for *I* hybrid, the L_{1i} and L_{2i} represent the n=194 RILs to 9024 and LH422, respectively; while for *II* hybrid, the L_{1i} and L_{2i} represent the n=222 RILs to Zhenshan97 and Minghui63, respectively. To distinguish one from another, the two data sets SUM and DIFF in the *I* hybrid are referred as SUMij and DIFFij; and in the *II* hybrid as SUMii and DIFFii.

**NCIII and TTC analysis:** ANOVA was used to test for additive (L_{1i} + L_{2i} ) and dominance (L_{2i} – L_{1i} ) variation by following the standard North Carolina III (NC III) design and for epistatic variation (L_{1i} + L_{2i} – P ) following extending TTC (triple testcross cross) design as described by KEARSEY *et al.* (1968) with P indicated as RI population in this study. Additive (V_A) and dominance (V_D) components of genetic variance were estimated and used to calculate the average degree of dominance, [as \sqrt(2V_D/V_A)], which is a weighted mean of the level of dominance over all segregating loci (KEARSEY and POONI 1996).

**Genetic linkage maps:** For *I* hybrid, a subset of 141 polymorphic RFLP markers was selected from the rice high-density molecular map (CAUSSE *et al.* 1994) to construct the linkage map of the recombinant inbred (RI) population by XIAO *et al.* (1995). For *II* hybrid, a linkage map was constructed by XING *et al.* (2002), which consisted of 221 marker loci and covered a total of 1,796 cM.
QTL mapping and detection of dominance degree of main-effect QTL and epistatic-effect QTL:

QTL mapping: QTL analysis was performed separately for the RI, the mid-parental heterosis (Hmp) of two backcross populations and two independent set data “SUM” and “DIFF” in IJ hybrid and II hybrid. In the absence of epistasis, the analysis of RIL and SUM data set identifies QTL with an additive effect \( (a) \), whereas the analysis of Hmp, and DIFF data sets detect QTL with a dominance effect \( (d) \) (FRASCAROLI et al. 2007).

Analysis of main-effect QTL (M-QTL) was conducted in each mapping population by composite interval mapping using WinQTLcart (ZENG 1994). A LOD score of 2.0 was selected as the threshold for the presence of a main-effect QTL based on the total map distance and the average distance between markers. QTL detected in different populations or for different traits were considered as common if their estimated map position was within a 20 cM distance (GROH et al. 1998), which is a common approach in comparative mapping. Following FRASCAROLI et al. (2007), in the absence of epistasis, the expectation of genetic effects in RIL, SUM, Hmp and DIFF data was \( a, a, d/2 \) and \( d \).

Analysis of digenic interaction was conducted in each mapping population by the mixed linear approach and by the use of the computer software QTLMAPPER ver.1.0 (WANG et al. 1999). The analysis was first conducted without considering epistasis to confirm the QTL detected with the method previously described, then with epistasis considered in the model. A threshold of \( \text{LOD} \geq 3.0 \) \( (P<0.001) \) was used for declaring the presence of a putative pair of epistatic QTL.

Genetic analysis methods for estimating QTL dominance degree: In 1952, NCIII
design (North Carolina Design III) was put forward by Comstock and Robison. In a NCIII design, male progeny from generation 2 (F2, which were treated as a base population) of two inbred strains are backcrossed to their grandmothers (marked as L1 and L2), and their progeny are arranged in a completely randomized block design (Comstock and Robison 1952). In 1968, NCIII design was developed by Kearsey and Pooni. In their theory, the F3, F4...Fn, DH and RIL also can be treated as base populations. Following Kearsey, the base population was crossed to the two parents (P1 and P2) indicated as L1 and L2. With the data of L1+L2 and L1 – L2, the genetic parameters of QTL such as additive effect, dominant effect, and the degree of dominance could be estimated.

Based on the correlation analysis of detected M-QTL and digenic interaction proposed by Hu et al. (1995, 2002), regression and variance analysis of two data L1+L2 and L1 – L2 when base population was DH population could be deduced as follows (Table1 and Table2).

Based on the methodology proposed, we developed a software QTLIII (not published yet), which is suitable for analyzing the additive effect, dominant effect and dominance degree of QTL (including one factor, two factor and three factor ANOVA, see in Table 1 and Table 2). In this study, it was used to estimate dominance degree of main-effect and epistatic effect QTL.

The degree of dominance of a M-QTL was estimated as |d/a|. For this purpose, for all QTL declared as significant within any data set, dominant and additive effects were estimated in SUM and DIFF data sets by QTLIII with ANOVA analysis. These estimates were used to calculate |d/a| and classify the QTL as additive (A, |d/a| < 0.2), partial
dominance (PD, $0.2 \leq |d/a| < 0.8$), dominance (D, $0.8 \leq |d/a| < 1.2$), and over-dominance (OD, $|d/a| \geq 1.2$) according to STUBER et al. (1987).

Genetic expectations of the parameters estimated in the epistatic models differ based on genetic composition of data sets analyzed. For SUM data set, the estimated interaction is expected to be predominantly of the additive $\times$ additive ($aa$), whereas for DIFF data set it is expected to be predominantly of the dominance $\times$ dominance ($dd$). In this study, $|dd/aa|$, defined as epistasis dominance degree (EDD), was estimated by the software QTLIII with ANOVA analysis. These estimates were used to calculate $|dd/aa|$ to classify the epistatic QTL as additive (A, $|dd/aa| < 0.2$), partial dominance (PD, $0.2 \leq |dd/aa| < 0.8$), dominance (D, $0.8 \leq |dd/aa| < 1.2$) and over-dominance (OD, $|dd/aa| \geq 1.2$).

**Relationship between genome-wide or chromosome-wide molecular marker heterozygosity and phenotypic trait performance and heterosis:** GGT (VAN 1999) was used to calculate genome ratios (percentage of total genome originated from one parental genome) for each line in the RI population, initially for the whole genome and then for each chromosome. Relationship between molecular marker heterozygosity and phenotypic performance was tested by regressing phenotypic performance on whole genome heterozygosity in two backcross populations in both $II$ and $II$ hybrids. Meanwhile, in order to elucidate the relationship between observed heterosis and heterozygosity, (i) the Hmp and DIFF values were respectively regressed against heterozygosity across the whole genome using linear regression. When the DIFF data set was used as a dependent variable, genome heterozygosity of the each backcross population was the independent variable; (ii) the Hmp values were regressed against
heterozygosity on individual chromosomes by multiple regression.

**RESULTS**

**F1 Heterosis:** In *IJ* hybrid, LH422 showed significant higher mean trait values than 9024 (Table 3). All the nine traits except heading date in F1 had a higher value than both parents. For mid-parental heterosis, yield showed the strongest significant heterosis (25.58%), followed by 1000-grain weight (15.82%), plant height (15.34%), panicle length (9.42%), tillers per plant (8.00%), seed set (4.06%), and heading date (1.74%). However, the F1 hybrid had a lower trait value for filled grains per panicle and grain density than the parental lines, with negative heterosis 2.08% and 10.17%, respectively.

In *II* hybrid, the parent Minghui63 had significant higher phenotypic value than Zhenshan97 for all the nine traits investigated (Table 3). F1 hybrid had 91 days to heading, similar to Minghui63, which took more days to heading than Zhenshan97. The values of the other traits were significant higher in F1 than both parents. The mid-parental heterosis of the F1 plants was strongest for yield (83.09%), followed by filled grains per panicle (29.13%), plant height (21.94%), heading date (17.46%), seed set (16.68%), grain density (13.86%), panicle length (13.42%), tillers per plant (11.09%), and 1000-grain weight (8.21%).

**Heterosis in RI and BC populations:** RIL and parental inbred mean values (Table 3) were not significantly different for any trait in both *IJ* and *II* hybrids.

Significant heterosis for yield was observed in *II* hybrid BC populations, but not in *IJ* hybrid BC populations. Most of other traits did not show significant heterosis in BC
populations of both $IJ$ and $II$ hybrids

For $IJ$ hybrid, the mean values of the 9024BC and LH422BC populations were 80.96 and 81.21 for heading date, 107.28 and 110.83 for plant height, 10.38 and 9.55 for tillers per plant, 24.60 and 25.27 for panicle length, 83.20 and 98.28 for filled grains per panicle, 60.66 and 62.75 for seed set, 5.60 and 6.25 for grain density, 26.31 and 24.45 for 1000-grain weight, and 6.14 and 6.18 for yield. The heterosis was 24.45 (29.5%) and 3.12 (7.0%) for heading date, 6.45 (6.4%) and 5.1 (4.6%) for plant height, −0.3 (−2.8%) and 0.28 (3.0%) for tillers per plant, 1.65 (7.2%) and 1.36 (5.5%) for panicle length, −5.9 (−6.6%) and −1.56 (−1.8%) for filled grains per panicle, −7.39 (−10.9%) and 4.62 (6.9%) for seed set, 0.62 (12.5%) and 0.97 (20.8%) for grain density, 2.19 (9.1%) and 1.58 (5.9%) for 1000-grain weight, and −0.16 (−2.5%) and 0.14 (2.3%) for yield, in the 9024BC and LH422BC populations, respectively.

For $II$ hybrid, the mean values of the Zhenshan97BC and Minghui63BC populations were 75.44 and 85.44 for heading date, 113.11 and 113.50 for plant height, 11.99 and 12.00 for tillers per plant, 23.32 and 24.81 for panicle length, 121.81 and 126.15 for filled grains per panicle, 79.42 and 81.29 for seed set, 5.22 and 5.09 for grain density, 26.26 and 26.74 for 1000-grain weight, and 6.73 and 7.56 for yield. The heterosis values were −11.53 (−15.9%) and −1.53 (−1.8%) for heading date, 1.72 (1.7%) and 2.11 (1.9%) for plant height, 0.59 (1.1%) and 0.59 (0.9%) for tillers per plant, −0.75 (−3.5%) and 0.74 (3.1%) for panicle length, 4.7 (4.5%) and 9.04 (7.7%) for filled grains per panicle, 4.89 (10.7%) and 8.75 (13.6%) for seed set, 0.34 (7.1%) and 0.21 (4.3%) for grain density, −1.64 (−0.64%) and −0.16 (−0.6%) for 1000-grain weight, and 1.82 (36.9%) and 1.04 (15.9%) for yield, the Zhenshan97BC and Minghui63BC populations, respectively.
**NCIII and TTC analysis:** TTC analysis allows to test non-allelic interactions. Significant additive × additive ([*aa*]) epistasis was detected for all traits in both *II* and *II* hybrids (Table 4). The epistasis due to additive × dominance or dominance × dominance ([*ad*] and [*dd*]) was significant for all traits in *II* hybrid and all the traits except tillers per plant in *II* hybrid.

In this study, NCIII analysis led to the estimates of *V_A* (additive variance) and *V_D* (dominance variance), which were always highly significant (*P*<0.005) in both hybrids, except for the *V_D* of tillers per plant in *II* hybrid which was significant at *P*<0.05 (Table 4).

**Main-effect QTL (M-QTL):** QTL detected in RIL, SUM, two Hmp and the DIFF data set in *II* and *II* hybrids are shown in Table 5 and Table 6, respectively.

In total, 76 and 41 QTL were revealed in five data sets of *II* and *II* hybrids, respectively. Most of these QTL explained less than 10% of variation individually. Five QTL (6.76%) in *II* hybrid and four (9.76%) in *II* hybrid accounted for more than 20% phenotypic variation individually.

**Heading date (HD):** In *II* hybrid, 10 QTL were detected. Three showed an additive effect, four a partial-to-complete dominant effect, and three an over-dominant effect. Six of the nine QTL showing a dominant effect identified in Hmp and DIFFij were negative, with alleles from 9024 increasing the trait value. In *II* hybrid, eight QTL were found. Three exhibited an additive effect and five a partial-to-complete dominant effect. Four of the five QTL displaying a dominant effect revealed in Hmp and DIFFii were positive,
with alleles form Minghui63 increasing the trait value.

Plant height (PH): In *IJ* hybrid, 12 QTL were found. Six were classified as additive, three as partial-to-complete dominance, and four as over-dominance. In *II* hybrid, four QTL were detected. Three were found to be additive, and one in Zhenshan97Hmp to be over-dominant. No QTL was identified in SUMii.

Tillers per plant (TP): In *IJ* hybrid, four QTL were identified with two showing an additive effect, one an over-dominant effect, and one a partial dominant effect. No QTL was found in LH422Hmp and DIFFij data set. In *II* hybrid, five QTL were detected with two exhibiting an additive effect, one a dominant effect, and two an over-dominant effect.

Panicle length (PL): In *IJ* hybrid, 11 QTL were found with five classified as an additive effect, four an over-dominant effect, and two a partial-to-complete dominant effect. In *II* hybrid, two QTL in RIL and one QTL in SUMii were detected, displaying an additive effect and with alleles from Minghui63 increasing the trait value.

Filled grains per panicle (FGPP): In *IJ* hybrid, six QTL were found with three behaving like an additive effect, two a partial-dominant effect, and one an over-dominant effect. In *II* hybrid, two QTL were detected with one appearing to be an over-dominant effect and one a partial-dominant effect. No QTL was revealed in Hmp and DIFFii.

Seed set (SS): In *IJ* hybrid, 10 QTL were found with four displaying an additive effect, four a partial dominant effect, and two an over-dominant effect. In *II* hybrid, only one QTL was detected in DIFFii data, showing over-dominant effect, and the alleles from Zhenshan 97 increased the trait value.

Grain density (GD): In *IJ* hybrid, seven QTL were identified with two exhibiting an additive effect, two a partial-to-complete dominant effect, and three an over-dominant effect.
effect. No QTL was detected in 9024Hmp. In II hybrid, four QTL were revealed with two showing an additive effect, one a partial-dominant effect, and one an over-dominant effect. No QTL was found in Minghui63Hmp and DIFFii data set.

1000-grains weight (KGW): In IJ hybrid, 10 QTL were revealed with five displaying an additive effect, three a partial-dominant effect, and two an over-dominant effect. No QTL was found in 9024Hmp. In II hybrid, eight QTL were detected with two showing an additive effect, three a partial-to-complete dominant, and three an over-dominant effect.

Yield (YD): In IJ hybrid, six QTL were identified with two exhibiting an additive effect, three a dominant effect, and one an over-dominant effect. No QTL was found in SUMij and LH422Hmp. In II hybrid, six QTL were detected with one showing an additive effect and five an over-dominant effect. No QTL was found in Zhenshan97Hmp and SUMii data set.

**Digenic interaction:** Table 7 shows the digenic interactions detected in DIFFij data in IJ hybrid. A total of 46 digenic interactions were found in DIFFij data. No significant interaction was found for yield. The variation explained by individual interaction ranges from 2.0% to 10.1%. The proportion of total variation explained by all digenic interaction was about 30% in most traits. The highest value of total variation was observed for panicle length in the DIFFij data set (45.1%), which mainly reflected the dominance × dominance digenic interactions.

Table 8 shows the digenic interaction identified in DIFFii data in II hybrid. In total, 81 digenic interactions were revealed. Each interaction generally showed modest $R^2$ of
less than 10% for all significant interactions except one interaction with 18.1%. However, in \( IJ \) hybrid, the total variation explained by all digenic interactions was more than 40% for most of the traits. The highest value of total \( R^2 \) was observed for SS in the DIFFii data set (52.7%).

Table 9 summarizes the digenic interaction detected in RIL, SUM, Hmp and DIFF data sets of \( IJ \) and \( II \) hybrids. Most of the detected interactions involved QTL without a significant main effect and each interaction showed a modest \( R^2 \) of less than 10% for all traits. However, it should be noted that an interaction occurred between two significant M-QTL in Minghui63Hmp for 1000-grain weight, which explained 43.4% of phenotypic variation (data not shown here).

In \( IJ \) hybrid, the number of digenic interactions detected for each trait varies from none to 10 in RILij population with an average of 3.22, and the variance explained \((R^2)\) by each pair was up to 39.1% with an average of 16.4%. The number of digenic interactions detected in SUMij data set varies from none to seven with an average 3.44, and the \( R^2 \) of each pair varies from 10.9% to 44.7% with an average of 21.8%. For digenic interaction of dominance \( \times \) dominance, on average, 1.11, 1.11 and 2.00 with additive effect were detected in 9024Hmp, LH422Hmp and DIFFij and had a contribution rate of 6.0%, 6.4% and 12.2%, respectively; 2.11, 2.44 and 2.22 QTL pairs with partial-to-complete dominance were detected in 9024Hmp, LH422Hmp and DIFFij and had a contribution rate of 14.7%, 15.2% and 13.3%, respectively; and 1.67, 1.33 and 0.89 QTL pairs with over-dominance were detected in 9024Hmp, LH422Hmp and DIFFij, and had a contribution rate of 10.6%, 8.4% and 4.5%, respectively.

For \( II \) hybrid, the number of digenic interactions identified for each trait varies from
none to 12 in RILii population with an average of 8.11, and had a contribution rate ($R^2$) up to 87.0%, with an average of 47.9%. The number of digenic interactions detected in SUMii data set varies from none to 14 with an average 7.44, and each pair had a $R^2$ up to 59.4% with an average of 40.4%. For digenic interaction of dominance × dominance, on average, 1.44, 0.11 and 1.22 QTL pairs with additive effect were detected in Zhenshan97Hmp, Minghui63Hmp and DIFFii and had a contribution rate of 7.0%, 0.7% and 7.4%, respectively; 5.44, 1.56 and 2.44 QTL pairs with partial-to-complete dominance were detected in Zhensha97Hmp, Minghui63Hmp and DIFFii and had a contribution rate of 27.7%, 13.8% and 11.8%, respectively; and 2.44, 0.89 and 5.33 QTL pairs with over- dominance were detected in Zhenshan97Hmp, Minghui63Hmp and DIFFii and had a contribution rate of 12.2%, 5.3% and 25.3%, respectively.

**Relationship between trait performance and genome-wide or chromosome-wide marker heterozygosity:** The correlation coefficients (Table 10) between level of genome-wide heterozygosity and performance *per se* of the two backcross populations were not significant for most of traits in both *IJ* and *II* hybrids (except plant height in 9024BC and 1000-grain weight in Minghui63BC). The analysis of the relationship between level of heterozygosity and of heterosis (as evaluated in Hmp and DIFF) showed that correlation coefficients, for several traits, were slightly higher than those previously shown, but still not significant for most of traits. The significant correlation coefficients were found for plant height, heading date, 1000-grain weight in *IJ* hybrid and for tillers per plant in *II* hybrid.

In this study, Hmp value was regressed against heterozygosity on individual
chromosomes using multiple linear regression (Table 11). The hybrid performance was also poorly associated with marker heterozygosity in most chromosomes. There were eight, six, eight, and five significant regressions between trait value and marker heterozygosity in individual chromosomes resolved in 9024Hmp, LH422Hmp, Zhenshan97Hmp and Minghui63Hmp, respectively. Nineteen of these 27 (70.3%) significant regressions were associated with one or two M-QTL and/or digenic interaction. In \( IJ \) hybrid, \( F \)-test value was significant for panicle length and grain density in 9024Hmp and for plant height and heading date in LH422Hmp. While in \( II \) hybrid, \( F \)-test value was significant for plant height in Zhenshan97Hmp and for yield in Minghui63Hmp. The coefficients \((r^2)\) for most of traits were less than 0.10 in both \( IJ \) and \( II \) hybrids.

**DISCUSSION**

**Choice of the experimental design and statistical methods:** NCIII and TTC designs are most suitable for studies of heterosis in the presence of epistasis because they provide estimates of augmented dominance effects (KUSTERER et al. 2007a, 2007b). Meanwhile, compared with \( F_2 \) or \( F_3 \) population, RILs as parents for producing testcross progenies offer few advantages. Firstly, the effects of linkage are reduced because linkage disequilibrium between tightly linked loci is almost half of that in \( F_2 \) population. Secondly, use of homozygous parents (RIL) maximizes the genetic variance among testcross progenies and leads to an increased power in \( F \)-tests and reduced standard errors of variance component and dominance effect estimates since RILs are homozygous at almost all of the genetic loci while \( F_2 \) plants have 50% heterozygous loci. Thirdly, RILs are immoral and testcross progeny can be repeatedly generated and tested as needed.
Up to now, several studies have been conducted to try to understand the genetic basis of heterosis in rice (XIAO et al. 1995; LI et al. 2001; LUO et al. 2001; HUA et al. 2002, 2003). However, the causes underlying this important phenomenon have remained unclear and none of these studies quantified the gene action of QTL. In present study, with two derived data sets (SUM and DIFF) and the software developed by ourselves, we resolved the dominance degree for all of the M-QTL and digenic interaction. The statistical method employed in this study is much more precise and informative to understand the causes of heterosis in rice since it classifies underlying QTL into additive (A), partial dominance (PD), dominance (D) and over-dominance (OD) based on degree of dominance.

It should be noted that, the A, PD, D and OD referred in this study is different from the additive effect, dominant effect and over-dominant effect in traditional dominant-additive model. In fact, as well as in hybrid F₁, since each locus is heterozygosis, only gene action of dominance, dominance × dominance, dominance × dominance × dominance, etc. existed in Hmp and DIFF. Therefore, in this study, the A, PD, D and OD were only treated as a scale for quantifying the degree of dominance ($d$) or dominance × dominance ($dd$) effect.

**Heterosis for the traits studied:** In the two hybrids investigated here, grain yield showed the strongest heterosis among the nine traits studied (25.58% in IJ hybrid, 83.09% in II hybrid), consistent with the findings of previous studies conducted on rice (LI et al. 2001; LUO et al. 2001) as well as other cereal crops (TOLLENAAR et al. 2004; HOECKER et al. 2006). Heterosis for the other traits was less than 20% in IJ hybrid and
less than 30% in II hybrid. Negative heterosis for filled grains per panicle and grain density was observed in II hybrid. These results confirm that heterosis of yield components were much less than grain yield itself (Li et al. 2001).

For II hybrid, the Hmp of some backcross lines was stronger than that of F₁, while some other backcross lines expressed an Hmp in the opposite direction. This result is in harmony with the study conducted by Mei et al. (2005) in which an indica/japonica hybrid was also used. It can be concluded that heterosis was generally related to the average level of heterozygosity in a hybrid population but poorly correlated with heterozygosity at the individual level (Zhang et al. 1995; Yu et al. 1997). This conclusion also can be confirmed by the fact that the correlation between marker heterozygosity and trait expression is negligible.

For II hybrid, the heterosis in BC populations was much lower than F₁. This may be due to the fact that the two intra-specific parents are more genetically similar than the two inter-specific parents of II hybrids. The reduction in the proportion of heterozygous loci in the BCF₁ population probably caused the reduced average level of heterosis in the BCF₁s compared to the hybrid between two parents.

**NCIII and TTC analysis:** For the traits showing highly significant epistasis, Vₐ and Vₐ estimates are to some extent biased (Kearsey and Pooni 1996) and so are the average degree of dominance estimates. In II hybrid, highly significant [aa], [ad] and [dd] epistasis were observed for all the traits studied. In II hybrid, the average degree of dominance for most traits was less than 1.00, except for plant height (1.18) and grain yield (1.20), suggesting an important contribution of over-dominance to the heterosis of
these two traits. For epistasis conducted by TTC analysis, $[aa]$ was highly significant ($P \leq 0.005$) for all traits, and $[ad]$ and $[dd]$ for most of traits, except for yield and grain density (significant at $P \leq 0.01$), panicle length (significant at $P \leq 0.05$) and tillers per plant (not significant). Therefore, epistasis appeared to be of more importance than intra-locus interaction in affecting heterosis in these two elite hybrids. A similar conclusion was drawn in Arabidopsis by KUSTERER et al. (2007a) in which a TTC family derived from the Arabidopsis C24 × Col-0 was analyzed and found that epistasis across environments was more important for most traits. However, in the TTC design with recombinant inbred lines of the maize B73 × H99 (FRASCAROLI et al. 2007), the epistasis was found not significant for most traits.

**Genetic basis of heterosis in two highly heterotic hybrids of rice:** Our analyses allowed the identification of several QTL for each of the traits investigated. Most individual QTL explained modest variation (<10%), only four QTL in IJ hybrid and five QTL in II hybrid contributed more than 20% variation individually (Tables 5 and 6), confirming that the heterosis is a polygenic phenomenon (HALLAUER and MIRANDA 1981; KUSTERER et al. 2007a).

The proportion of QTL with an additive or a dominant effect is different between the two hybrids. Among the 74 main-effect QTL detected in IJ hybrid, 24 (32%) showed a gene action of partial-to-complete dominance, 20 (26%) over-dominance, and 32 (42%) additive effect; while among the 41 main-effect QTL identified in II hybrid, 12 (29%) exhibited partial-to-complete dominance, 16 (39%) over-dominance, and 13 (32%) additive effect. These results indicate that dominance and over-dominance played an
important role in conditioning the heterosis in these two hybrids. Also, the results from the dominance degree ($|d/a|$) of main-effect QTL estimated by QTLIII with regression analysis and by WinQTLcart (Zeng 1994) show that, although the dominance degree was not exactly consistent with each other by the three approaches (ANOVA, regression analysis, WinQTLcart), the proportion of QTL detected with dominance and with over-dominance were more than 25% each.

The importance of dominance and overdominance conditioning the heterosis of these two hybrids seems different. In $IJ$ hybrid, the proportion of QTL showing a gene action of over-dominance is less than with partial-to-complete dominance. This result was also found by the study conducted by Xiao et al. (1995) using the same materials, a different analysis method. However, in $II$ hybrid, the proportion of QTL exhibiting a gene action of over-dominance is more than those having a gene action of partial-to-complete dominance. This result is in harmony with other studies, especially the work conducted on the $F_{2:3}$ families derived from the cross between Zhenshan97 and Minghui63 by Yu et al. (1997). However, although a relatively higher portion of QTL demonstrated over-dominance in $II$ hybrid, QTL exhibiting high over-dominant effects are not necessarily indicative of true over-dominance, but rather they can be the result of dominant alleles linked in repulsion (pseudo-over-dominance).

Compared to M-QTL detected in these two hybrids, only two QTL for heading date were found in similar genomic region bordered by the same molecular markers. This may be due to the fact that very few markers were common across these two linkage maps. On chromosome 1, one QTL was detected between RG811 and RG173 in $IJ$ hybrid, showing an additive effect. One QTL between RM243 and RG173 was detected in $II$ hybrid,
displaying a partial-dominant effect. On chromosome 8, one QTL between RG333 and RZ562 in \( IJ \) hybrid and one between C1121 and RG333 in \( II \) hybrid were exhibiting an additive effect. Thus suggesting that, even in the same or similar genomic region bordered by the same molecular markers in different hybrids, the gene action of QTL could be different due to interaction of different alleles at the QTL. It should be noted that, for the two hybrids were planted in different environments, the type of gene action maybe influenced by environment effect, the type of gene action maybe influenced by environment effect.

Various levels of negative dominance were observed at some QTL for each trait, indicating that heterozygosity was not necessarily always favorable for the expression of the trait even in highly heterotic hybrids. For both hybrids studied here, dominant effects of the detected QTL were always bidirectional, resulting in the cancellation of positive and negative dominant effects contributed by different QTL controlling the trait, which explains the poor relationship observed between marker heterozygosity and trait expression” in the revised manuscript. A good consistency was also found in other studies of rice (Yu et al. 1997; Mei et al. 2005), but in contrast with the study (Frascaroli et al. 2007) in maize.

There was a large number of digenic interactions found to have effects on the traits of the two hybrids studied here. Two pronounced features were noticeably found for the epistasis in the present study. First, although individual interaction had a modest \( R^2 \) (phenotypic variation), less than 10% in most cases (data not shown here) for each trait of the two hybrids, the total variation explained by all the significant digenic interactions for the trait was much greater than that by all the M-QTL affecting the same trait for most
traits.

Similar to a large number of empirical studies in other selfing and outcrossing plant species (ALLARD 1988; LI et al. 2001; MEI et al. 2005), most epistasis occurred between complementary loci with no detectable main effects. In many fewer cases, epistasis occurred between a M-QTL and a complementary locus, and in only seven cases in II hybrid and two in II hybrid between M-QTL. By using the same population of II hybrid reported here, XIAO et al. (1995) was unable to detect epistasis due to the unavailability of appropriate mapping methodology (LI et al. 2001).

It should be noted that, the two digenic interactions in II hybrid occurred between M-QTL accounting for a large variation for 1000-grain weight detected in Minghui63Hmp and for panicle length detected in Zhenshan97BC, explaining 43.4% and 23.8% of the variation, respectively (data not shown here). When a M-QTL was involved in the epistatic interaction, the effect of the single-locus QTL is mostly dependent on the genotypes of other locus and can sometimes be negated by the genotypes of a second locus. Thus an attempt for utilization of the QTL in the breeding programs needs to consider such epistatic effects, especially the interaction occurring between two significant M-QTL and having a high phenotypic variation.

Another feature of digenic interaction in this study is that both partial-to-complete dominance and over-dominance played an important role in conditioning heterosis. Shown in Table 9 is the relative importance of additive and non-additive gene action of digenic interaction summarized by comparing the genetic effects detected in the SUM and DIFF data set by QTL with ANOVA analysis.

For the additive x additive digenic interactions, there were an average 3.22 and 3.44
pairs detected in RILij and SUMij data set for each trait in \textit{I}I \ hybrid, contributing 16.4\% and 21.8\% phenotypic variation, respectively; while in \textit{II} \ hybrid, an average 8.11 and 7.44 pairs were detected in RILii and SUMii data set for each trait, explaining 47.9\% and 40.4\% of the phenotypic variation, respectively.

There was a total of 135 and 188 digenic interactions of dominance $\times$ dominance interaction detected in Hmp and DIFF in \textit{I}I \ and \textit{II} \ hybrids, respectively. The proportion of digenic interaction displaying partial-to-complete dominance was a little more than that showing over-dominance in both hybrids. There were 62 (45.2\%) and 85 (45.2\%) digenic interactions that behaved like partial-to-complete dominance, 36 (26.7\%) and 78 (41.5\%) digenic interactions exhibited over-dominance, and 37 (28.1\%) and 25 (13.3\%) digenic interactions displayed additive effect, in \textit{I}I \ and \textit{II} \ hybrids, respectively.

The poor relationship between total genome-wide molecular marker heterozygosity and phenotypic trait performance was observed for almost all the traits in this study (Table 10). This result is different from the study of maize performed by FRASCAROLI \textit{et al.} (2007) in which they found that there was a high relationship between marker heterozygosity level and performance \textit{per se} and heterosis (as evaluated in Hmp and DIFF) for most of traits. To further investigate the relationship between observed heterosis and heterozygosity, Hmp value was regressed against heterozygosity on individual chromosomes using multiple linear regression. As shown in Table 11, the hybrid performance was also poorly associated with marker heterozygosity in most chromosomes, although it was relatively significant than that with whole genome heterozygosity. Nineteen of the 27 (70.4\%) significant regressions by individual chromosomes were associated with one or two M-QTL and/or digenic interaction,
indicating that marker heterozygosity in individual chromosomes in QTL regions was important for phenotypic variation. This finding is consistent with SYED’s (2005) result of the relationship between heterozygosity and heterosis in Arabidopsis. Therefore, the hybrid vigor is poorly related to heterozygosity of whole genome and on individual chromosomes in rice, which further confirms that the genetic basis or mechanism of heterosis of rice is different from that of maize.

Our results indicate that heterosis in rice is very complex, reflected by the large number of loci involved, their wide genomic distribution, and complex epistatic relationships and that the non-allelic interactions (epistasis) play a relatively more important role than allelic interactions (M-QTL) in conditioning the heterosis of these two highly heterotic hybrids, implicating that marker-assisted selection in heterosis breeding to significantly enhance the heterosis of desirable traits may be very challenging.

So far almost all of the documented studies on revealing the genetic basis of heterosis are limited to classical quantitative genetics and QTL mapping using molecular markers. The advancements in functional genomics create a novel avenue to study the genetic basis of heterosis at the gene expression level. DNA microarrays can quantify expression of tens of thousands of genes on a single DNA chip (SCHENA et al. 1998). The timing, level, relationship of the transcription of two different alleles of the same gene in the hybrids can be compared with that of their corresponding parental lines by using microarrays (SWANSON et al. 2006; STUPAR et al. 2006). Functional genomics approaches to elucidating the genetic basis of heterosis would turn the study of this very important and still controversial issue into a new chapter. Evidence from functional
expression studies of genes underlying heterosis would elevate our understanding of the genetic basis of heterosis to a new level.

We gratefully acknowledge the expert technical assistance of Prof. Qifa Zhang on trial design and analysis, and the skillful assistance of Prof. Yingguo Zhu in field trials. We are indebted to thank Prof. Jinhua Xiao and Prof. Yunchun Song for valuable suggestions for improving the manuscript. This work was financially supported by the 973 Program (No. 2006CB101707), the 863 Program (No. 2003AA207160), the National Natural Science Foundation of China (No. 30270760), and the Key grant Project of Chinese Ministry of Education (No. 307018).

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### TABLE 1

Genetic expectation of regression coefficients of $L_1+L_2$ and $L_1-L_2$ when the base population was DH population

|                  | $L_1+L_2$ | $L_1-L_2$ | $|(L_1-L_2) / (L_1+L_2)|$ |
|------------------|-----------|-----------|--------------------------|
| $b'_1$           | $(1-2r_1)a_1$ | $-(1-2r_1)d_1$ | $d_1/a_1$               |
| $b''_2$          | $(1-2r_1)(1-2r_2)i_{a1a2}$ | $(1-2r_1)(1-2r_2)l_{d1d2}$ | $l_{d1d2}/i_{a1a2}$   |
| $b'_{111}$       | $\left[\prod_{m=1}^{3} (1-2r_m) \right]_{i_{a1a2}}$ | $(-1)^3\left[\prod_{m=1}^{3} (1-2r_m) \right]_{l_{d1d2}}$ | $l_{d1d2}/i_{a1a2}$   |
| $b'_{K}$         | $\left[\prod_{m=1}^{K} (1-2r_m) \right]_{i_{a1...aK}}$ | $(-1)^K\left[\prod_{m=1}^{K} (1-2r_m) \right]_{l_{d1...dK}}$ | $l_{d1...dK}/i_{a1...aK}$ |

$b'_i$ (i=1~K, K is the total number of markers in linkage map) indicated as regression coefficient. $a_i$ (i=1~K) and $d_i$ (i=1~K) denoted as the additive effect and dominant effect, respectively; $i_{a1a2}$ was the additive $\times$ additive epistatic effect, $i_{a1a2a3}$ was the additive $\times$ additive $\times$ additive epistatic effect, etc. $l_{d1d2}$ was the dominance $\times$ dominance epistatic effect, $l_{d1d2d3}$ was the dominance $\times$ dominance $\times$ dominance epistatic effect, etc. $r_m$ denotes the recombinant value. For RI population, the expectations were similar to those in the DH population except for $r_m$ which was
replaced by \( 2r_m' / (1 + 2r_m') \) and \( 4r_m'' / (1 + 6r_m'') \), respectively. The \( r_m' \) and \( r_m'' \) were recombinant values for two RI population (selfing population and sib-mating population), respectively (Hu et al. 2002). \( d_1/a_1 \) indicated as dominant degree of main-effect QTL, \( l_{d_1d_2}/l_{a_1a_2} \) as epistasis dominance degree (EDD), \( l_{d_1d_2d_3}/l_{a_1a_2a_3} \) as epistasis dominance degree among three markers etc.
### TABLE 2

Genetic expectation of variance components of $L_1+L_2$ and $L_1-L_2$ when the base population was DH population

<table>
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<tr>
<th>ANOVA</th>
<th>$L_1+L_2$</th>
<th>$L_1-L_2$</th>
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<td>one way</td>
<td>$\sigma^2 = (1-2r_1)^2 a_1^2$</td>
<td>$\sigma^2 = (1-2r_1)^2 d_1^2$</td>
<td>$d_1/a_1$</td>
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<td>two way</td>
<td>$\sigma^2 = (1-2r_2)^2 (a_1 + j_{a_4d_2})^2$</td>
<td>$\sigma^2 = (1-2r_2)^2 (d_1 + j_{d_4a_2})^2$</td>
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<tr>
<td></td>
<td>$\sigma^2 = (1-2r_2)^2 (a_2 + j_{a_4d_2})^2$</td>
<td>$\sigma^2 = (1-2r_2)^2 (d_2 + j_{a_4d_2})^2$</td>
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<tr>
<td></td>
<td>$\sigma^2 = (1-2r_2)^2 (1-2r_2)^2 i_{a_4d_2}^2$</td>
<td>$\sigma^2 = (1-2r_2)^2 (1-2r_2)^2 l_{d_4x_2}^2$</td>
<td>$l_{d_4x_2} / i_{a_4d_2}$</td>
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<td>three way</td>
<td>$\sigma^2 = (1-2r_1)^2 (a_1 + j_{a_4d_2} + j_{a_4d_4d_2_4} + j_{a_4d_4d_2_4})^2$</td>
<td>$\sigma^2 = (1-2r_1)^2 (d_1 + j_{d_4a_2} + j_{d_4a_2a_4} + j_{d_4a_2a_4})^2$</td>
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<td></td>
<td>$\sigma^2 = (1-2r_2)^2 (a_2 + j_{a_4d_2} + j_{a_4d_4d_2_4} + j_{a_4d_4d_2_4})^2$</td>
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\[ \sigma_{13}^2 = (1-2r_1)^2(1-2r_3)^2(i_{\alpha_1} + j_{\alpha_1})^2 \]

\[ \sigma_{23}^2 = (1-2r_2)^2(1-2r_3)^2(i_{\alpha_2} + j_{\alpha_2})^2 \]

\[ \sigma_{123}^2 = (1-2r_1)^2(1-2r_2)^2(1-2r_3)^2 i_{\alpha_1}^2 + j_{\alpha_2}^2 + j_{\alpha_3}^2 \]

\[ \sigma_{123}^2 = (1-2r_1)^2(1-2r_2)^2(1-2r_3)^2 l_{d_1d_2d_3} l_{d_1d_2d_3} \]

\[ \sigma_i^2 (i=1\sim K), \sigma_{ij}^2 (i<j, i=1\sim K, j=2\sim K), \sigma_{ijl}^2 (i<j<l, i=1\sim K, j=2\sim K, l=3\sim K) \] denoted as variance component of single marker, two markers and three markers. The other parameters were the same as in Table 1.
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<th>HD</th>
<th>PH</th>
<th>TP</th>
<th>PL</th>
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<th>SS</th>
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For a description of agronomic traits see MATERIALS AND METHODS.
### TABLE 4
NCIII and TTC analyses of the two rice hybrids

<table>
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<tr>
<th>Parameter</th>
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*\(P \leq 0.05, **P \leq 0.01, ***P \leq 0.005.\)*

\(^a\) Estimates of additive (\(V_A\)) and dominance (\(V_D\)) variance, average degree of dominance (a.d.d.), and tests for additive × additive ([\(aa\)]) and additive × dominance and dominance × dominance ([\(aa\)], [\(dd\)]) epistasis.

\(^b\) \(V_A\) was highly significant (\(P \leq 0.005\)) for all traits; \(V_D\) was highly significant for all traits, except TP (significant at \(P \leq 0.05\)) in II hybrid.
# TABLE 5

Main-effect QTL resolved in *IJ* hybrid

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<th>SUMij</th>
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<th>LH422Hmp</th>
<th>DIFFij</th>
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**TP**

| 3-1| RG1356-CDO87     | -0.27  | 5.00  |       | A     |
| 4-5| RG214-CDO539     | 0.27   | 8.70  |       | A     |
| 5-11| CDO1160-CDO202 | 0.2    | 5.10  |       | OD    |
| 9-9| XNPB295-RZ404    | -0.38  | 5.10  |       | PD    |

**PL**

<p>| 1-9| RG233-XNPB302    | 0.63   | 5.80  |       | OD    |
| 2-4| CDO1091-CDO395   | 0.46   | 4.10  |       | A     |
| 3-8| RZ993-CDO1081    | 0.42   | 5.20  |       | A     |
| 4-13|RZ602-CDO456     | -0.42  | 6.70  |       | OD    |
| 5-4| RZ296-RG573      | -0.49  | 7.00  |       | PD    |
| 5-11| CDO1160-CDO202 | -0.36  | 4.70  | -0.54 | 5.60  | D     |</p>
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| FGPP | 3-8 | RZ993-CDO1081 | -7.02 | 12.50 | -7.52 | 9.80 | A |
|      | 4-2 | RG143-RZ590 | -5.36 | 5.50 | A |
|      | 4-5 | RG214-CDO539 | -7.8 | 15.70 | A |
|      | 5-2 | RZ556-RG360 | -3.64 | 6.90 | 6.31 | 6.90 | PD |
|      | 5-3 | RG360-RZ296 | 5.96 | 9.00 | PD |
|      | 8-1 | RG333-RZ562 | 5.52 | 5.80 | OD |

<p>| SS | 2-9 | RZ599-RG152 | -2.63 | 4.10 | A |
|    | 3-8 | RZ993-CDO1081 | -2.44 | 5.10 | PD |
|    | 4-9 | RZ565-XNPB271 | 2.38 | 4.80 | A |
|    | 5-3 | RG360-RZ296 | 2.9 | 7.20 | A |
|    | 6-17 | RG653-RZ828 | -1.44 | 7.50 | PD |
|    | 7-9 | CDO533-RG528 | -4.41 | 12.30 | PD |
|    | 7-10 | RG528-RG417 | 2.78 | 4.60 | PD |</p>
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Effects estimated in 9024Hmp and LH422Hmp were multiplied by two, and the values estimated in LH422Hmp and the DIFF were multiplied by (−1).

*a* chr-In represent chromosome number-interval of the QTL detected in the study.

*b* A and D represent additive effect and dominance effect of M-QTL.

*c* The degree of dominance for all M-QTL declared as significant in any data set was determined after estimating their additive and dominance effects, respectively, in SUM and DIFF data sets. QTL were classified according to their \(|d/a|\) ratio as additive (A; \(|d/a|<0.2\)), partial dominance (PD; \(0.2\leq|d/a|<0.8\)), dominance (D; \(0.8\leq|d/a|<1.2\)), and over-dominance (OD; \(|d/a|\geq1.2\)) (STUBER et al. 1987).
TABLE 6

Main-effect QTL resolved in II hybrid

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<th>SUMii A&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Zhenshan97Hmp D&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Minghui63Hmp D&lt;sup&gt;b&lt;/sup&gt;</th>
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Effects obtained in Zhenshan97Hmp and Minghui63Hmp were multiplied by two, and the values obtained in LH422Hmp and the DIFF were also multiplied by (−1).

*See footnotes Table 5 for explanation.*
### TABLE 7

Digenic interactions in DIFFij data set in IJ hybrid

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*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.0001.

*a* Chri and Chrj represent the chromosome of loci i and loci j located on, respectively.

*b* Ai and Aj are the main effects of the loci i and loci j, and AAij is the epistatic effect between loci i and j.

*c* Percentage of the total variation explained by the AAij.

*d* The epistasis dominance degree (EDD) of digenic interaction. Digenic interaction were classified according to their |dd/aa| ratio as additive (A; |dd/aa| < 0.2), partial dominance (PD; 0.2 ≤ |dd/aa| < 0.8), dominance (D; 0.8 ≤ |dd/aa| < 1.2), and over-dominance (OD; |dd/aa| ≥ 1.2).
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**TABLE 8**

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*a~d see footnotes of Table 7 for explanation.
### TABLE 9

**Summaries of digenic interaction in five data sets of the two hybrids**

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\(^a\) In I hybrid, Hmp (1) and Hmp (2) represent 9024Hmp and LH422Hmp, respectively; while in II hybrid, Hmp (1) and Hmp (2) represent Zhenshan97Hmp and Minghui63Hmp, respectively.

\(^b\) The total variation explained by each trait (%).
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<th>Heterosis</th>
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DIFF (1) and DIFF (2) represent that, in IJ hybrid, when the DIFF data set was used as a dependent variable, genome heterozygosity of the 9024BC, LH422BC hybrids was the independent variable, respectively. While in IJ hybrid, DIFF (3) and DIFF (4) represent that when the DIFF data set was used as a dependent variable, genome heterozygosity of the Zhenshan97BC, Minghui63BC hybrids was the independent variable, respectively.

* $P \leq 0.05$, ** $P \leq 0.01$. 

TABLE 10

Correlation coefficients between genome-wide molecular marker heterozygosity and phenotypic values
TABLE 11

Significant regression coefficients of mid-parent values of backcross populations on individual chromosomes marker heterozygosity for the indicated traits

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*F*-test value.
determination coefficients.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Boldface indicates the presence of a QTL on a particular chromosome.