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Molecular marker heterozygosity and hybrid performance in indica and japonica rice

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Abstract An essential assumption underlying marker-based prediction of hybrid performance is a strong linear correlation between molecular marker heterozygosity and hybrid performance or heterosis. This study was intended to investigate the extent of the correlations between molecular marker heterozygosity and hybrid performance in crosses involving two sets of rice materials, 9 indica and 11 japonica varieties. These materials represent a broad spectrum of the cultivated rice gene pool including landraces, primitive cultivars, historically important cultivars, modern elite cultivars and parents of superior hybrids. Varieties within each set were intermated in all possible non-reciprocal pairs resulting in 36 crosses in the indica set and 55 in the japonica set. The F_1s and their parents, 111 entries in total, were examined for performance of seven traits in a replicated field trial. The parents were surveyed for polymorphisms using 96 RFLP and ten SSR markers selected at regular intervals from a published molecular marker linkage map. Molecular marker genotypes of the F_1 hybrids were deduced from the parental genotypes. The analysis showed that, with very few exceptions, correlations in the indica dataset were higher than in that of their japonica counterparts. Among the seven traits analyzed, plant height showed the highest correlation between heterozygosity and hybrid performance and heteorsis in both indica and japonica datasets. Correlations were low to intermediate between hybrid performance and heterozygosity (both general and specific) in yield and yield component traits in both indica and japonica sets, and also low to intermediate between specific heterozygosity and heterosis in the indica set, whereas very little correlation was detected between heterosis and heterozygosity (either general or specific) in the japonica set. In comparison to the results from our previous studies, we concluded that the relationship between molecular marker heterozygosity and heterosis is variable, depending on the genetic materials used in the study, the diversity of rice germplasms and the complexity of the genetic basis of heterosis.

Key words *Oryza sativa* · Hybrid rice · Predicting heterosis · Diallel cross · Restriction fragment length polymorphism (RFLP) · Simple sequence repeat (SSR)

Introduction

The recent advances in genome research have generated considerable interest in predicting hybrid performance using molecular markers in crop breeding programs. An essential assumption underlying the prediction of hybrid performance is a strong linear correlation between heterozygosity and heterosis.

Large numbers of studies have been conducted in corn to investigate the relationship between marker-genoype divergence of the parents and performance of hybrids, and these have produced variable results. For example, Lee et al. (1989) and Smith et al. (1990) detected strong correlations between genetic distance based on DNA restriction fragment length polymorphisms (RFLPs) and hybrid performance or heterosis in crosses between elite inbreds from the U.S. Corn Belt. In contrast, Godshalk et al. (1990) and Dudley et al. (1991) observed low correlations between marker distance and yield, whereas the results of Melchinger et al.

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(1990) and Boppenmaier et al. (1993) indicated that the correlations between marker distance and F_1 performance are dependent on the origin of lines studied; the correlations are high for crosses between lines from the same heterotic groups, low between lines from different heterotic groups and intermediate for mixtures consisting of lines both within and between groups. Despite the inconsistency in the correlations, results from all these studies indicate that genetic distances based on marker genotypes are in close agreement with pedigree information and can unambiguously resolve lines into their respective heterotic groups.

Rice is the main staple for a large segment of the world population. Hybrid rice has contributed significantly to the dramatic increase in rice production throughout the world (Yuan 1992), which parallels in many ways the role of hybrid corn in the corn industry. Zhang et al. (1994, 1995) investigated the relationship between marker heterozygosity and hybrid performance and heterosis in a number of characters, including yield and yield component traits, using a diallel cross involving eight elite parental lines commonly used in hybrid rice production in China. They defined two types of heterozygosity for determining such correlations: general heterozygosity, calculated using all the markers included in the study; and specific heterozygosity, based only on markers that detected highly significant effects for each trait. Correlations were mostly low between general heterozygosity and F_1 performance and heterosis. In contrast, very high correlations were detected between midparent heterosis and specific heterozygosity for a number of traits including yield and biomass; and, statistically, these high correlations may have reached the level to be of practical use for predictive purposes.

Rice is also one of the most polymorphic crop species, being composed of a diversity of ecological groups often referred to as subspecies, with their habitats ranging from tropical to subtropical to temperate zones (Oka 1988). The cultivated rice gene pool consists of a wealth of landraces, improved varieties and an increasingly large number of lines for hybrid rice production. Almost all types of the germplasms have been routinely used in various ways in hybrid rice breeding programs. Thus, the potential usefulness of molecular markers in predicting hybrid performance can only be evaluated by investigating the relationships between marker heterozygosity and hybrid performance using a wide range of rice germplasms.

In this study we extended our survey by using two sets of diverse materials including both indica and japonica varieties, which represent a broad spectrum of the cultivated rice gene pool. It is expected that results from this study will provide an estimate for the extent of correlations between marker diversity and hybrid performance or heterosis in rice, which will also permit an assessment on the usefulness of molecular markers in predicting hybrid performance.

Materials and methods

Rice varieties and crosses

The genetic materials used in this study were two sets of varieties of the Asian cultivated rice, *Oryza sativa* L., as listed in Table 1. The first set consisted of nine indica (*O. sativa* ssp. *indica*) varieties from three Asian countries with representatives of landraces, primitive cultivars, historically important cultivars, modern elite cultivars and parents of superior hybrids. The second set, made up of 11 japonica (*O. sativa* ssp. *japonica*) varieties from four countries, also represents a wide range of japonica rice varieties including landraces, cultivars and hybrid parents.

Varieties within each set were intermated in all possible non-reciprocal pairs in the 1992 and 1993 rice growing seasons, resulting in 36 crosses in the indica set and 55 crosses in the japonica set.

Field evaluation

The 91 F_1 hybrids and 20 parents (111 entries in total) were planted in a field following a randomized complete block design (Steel and Torrie 1980) with three replications in the 1994 rice growing season at the Agricultural Research Institute of Jinsha City, Hubei Province. This site represents one of the major hybrid rice growing areas in China. Twenty seedlings were transplanted to each of the 333 two-rowed plots, at distances of 26 cm between plants in a row, and rows were spaced 26 cm apart. Field management followed essentially the practice under normal agricultural conditions.

Five to 10 plants in the middle of each plot were examined for seven quantitative characters: (1) heading date scored as number of days starting on June 16, (2) plant height as the length of the tallest tiller for each plant, (3) panicle length as the average length of all the panicles of each plant, (4) tillers per plant as the number of the seed setting tillers of a plant, (5) seeds per panicle as the total number of seeds threshed from each plant divided by the number of tillers per plant, (6) yield per plant measured as the weight of all filled seeds, and (7) seed weight, which is the total seed weight divided by the total number of seeds per plant.

Table 1 A list of the rice varieties used in this study

Variety	Subspecies	Description	Source
1. Taichung 65	J	Cultivar	China (Taiwan)
2. Mudanjiang 8	J	Cultivar	China
3. Taihu Wanjing	J	Landrace	China
4. Zaoshajing	J	Cultivar	China
5. Balilla	J	Cultivar	Italy
6. Yaso	J	Cultivar	Japan
7. Nongken 58	J	Cultivar	China
8. Akihikari	J	Cultivar	Japan
9. C57	J	Cultivar[a]	China
10. 02428	J	Cultivar[a]	China
11. Ketan Nangka	J	Landrace	Indonesia
12. Nanjing 11	I	Cultivar	China
13. Teqing	I	Cultivar[a]	China
14. Zhaiyeqing 8	I	Cultivar	China
15. Aijiao Nante	I	Cultivar	China
16. Shengli Xian	I	Cultivar	China
17. Minghui 63	I	Cultivar[a]	China
18. Indonesia Paddy Rice	I	Landrace	Indonesia
19. Yuchi 231-8	I	Cultivar	China
20. Dular	I	Landrace	India

[a] Varieties that have been used as parents in hybrid rice production in China

Table 2 Molecular marker polymorphisms resolved by RFLPs and SSRs among the 20 varieties

Sample	Number of varieties	Polymorphic markers	Pieces of non-redundant information	Loci scored as genotypes	Alleles per locus
Indica	9	74	135	81	2.41
Japonica	11	70	125	116	2.37
Total	20	102	241	154	2.78

Molecular marker assay

Tissue for each variety was harvested *en mass* from about 20 seedlings planted in a greenhouse. DNA was extracted following the protocol of Saghai Maroof et al. (1984).

Two classes of markers, restriction fragment length polymorphisms (RFLPs) and simple sequence repeats (SSRs), were used for surveying the DNA polymorphism of the parents. For RFLP analysis, about 5 μg of total cellular DNA for each sample was digested with each of three restriction endonucleases, *Dra*I, *Eco*RI and *Hin*dIII, and probed with each of 96 cloned fragments selected from a published RFLP linkage map at regular intervals (Tanksley et al. 1992). Electrophoresis, blotting, probe labeling and hybridization followed previously described methods (Zhang et al. 1992). SSR polymorphisms were surveyed using 10 pairs of published primer sequences (Wu and Tanksley 1993; Yang et al. 1994).

Data processing and statistical analyses

The molecular marker data were scored and processed as described by Zhang et al. (1994). Briefly, banding patterns of RFLPs resolved by the majority of probe/enzyme combinations (PEs) and SSRs that corresponded to single locus variation were scored as genotypes, and RFLPs and SSRs that did not agree with single locus variation (multiple variable bands) were scored by the presence or absence of individual bands. In cases where redundant data were obtained within a probe among different enzymes, data from only one of the enzymes were used to avoid redundancy. The same data processing scheme was also applied to those PEs and SSRs whose variation was scored by bands.

The marker genotype of an F_1 hybrid was inferred from the parental genotypes. Heterozygosity of an F_1 hybrid was measured as the percentage difference of marker genotypes between the two parents. The effect of a chromosomal region, as marked by a molecular marker, on a trait was assessed with an one-way analysis of variance using marker types (genotypes or bands) as groups and entries within marker types as the error term. Markers that detected significant effects on a trait at the 0.01 probability level were referred to as positive markers for that trait.

Results

Marker polymorphisms

A number of statistics pertaining to the level of polymorphism of the parental varieties are given in Table 2. A few words are necessary to clarify the estimation. Over all, 92 of the 96 probes detected RFLPs with at least one of the three enzymes, and SSR polymorphisms were resolved with all ten primer pairs. We refer to these 92 RFLPs and ten SSRs as 102 "markers" (Table 2), which generated 241 pieces of non-redundant information including 154 scored as genotypes and 87 by bands. The estimates for the number of alleles were based only on the 154 pieces of information scored as genotypes. As can be seen from Table 2, although the japonica set contained 2 more varieties than the indica set, the japonica set still appeared to be less polymorphic than the indica set.

Variation of the traits among the parents

There was a wide range of variation in all seven traits among the parents (Table 3). The most variable characters were heading date and grain yield per plant, which showed a more than sixfold difference among the 20 parents. Two- to fourfold differences were also detected among the parents for plant height, tillers per plant and seeds per panicle. The least variable trait was seed weight, which only showed approximately a 30% difference between the lowest and the highest parent. It is also clear from Table 3 that, in contrast to the marker polymorphisms, the parents in the japonica set were more variable than those in the indica set for all characters except plant height.

Heterosis of the hybrids

Indica set

The amounts of heterosis differed drastically among the 36 crosses in this set and also varied widely from one trait to another (Fig. 1). Grain yield showed the highest heterosis among the seven traits, ≥100% heterosis was observed in 7 of the 36 crosses, and another 19 crosses expressed ≥50% heterosis. Among the three yield component traits, tillers per plant and seeds per panicle showed intermediate and approximately equal levels of heterosis, and very little heterosis was observed in seed weight (Fig. 1). Small negative heterosis for heading date was observed in 12 of the 36 crosses.

Among the 7 crosses expressing ≥100% heterosis for yield, 3 had var 'Nanjing 11' as one of the parents and another 3 crosses had 'Dular' as one of the parents, whereas none of the crosses involving 'Minghui 63' or 'Teqing', both of which are widely used as parents in hybrid rice production, expressed high heterosis. In the most extreme case, a cross between 'Shengli Xian', the most popular cultivar in China before the advent of semi-dwarf varieties, and 'Teqing' expressed moderate negative heterosis for all the characters.

Table 3 Measurements of the seven characters for the 20 parents used in this study

Variety	Heading date (days after 6/15)	Plant height (cm)	Tillers/plant	Panicle length (cm)	Seeds/panicle	1000 seed weight (g)	Yield/plant (g)
Taichung 65	59.1	103.4	6.3	21.3	77.9	24.0	11.8
Mudanjiang 8	11.3	70.7	7.5	13.6	36.4	23.1	6.3
Taihu Wanjing	72.1	102.6	6.6	21.6	107.0	21.7	15.3
Zoashajing	42.2	95.4	16.5	18.1	57.8	25.7	24.5
Balilla	40.8	88.7	12.2	16.9	65.1	24.5	19.5
Yaso	40.9	106.1	6.7	21.1	54.0	30.1	10.9
Nongken 58	75.5	103.3	12.2	23.0	101.0	26.1	32.2
Akihikari	43.1	84.7	10.7	16.7	62.5	24.2	16.2
C57	57.1	99.7	8.9	22.6	134.8	23.3	28.0
02428	59.1	85.2	6.3	21.9	142.9	21.3	19.2
Ketan Nangka	59.5	112.1	8.6	22.7	106.4	24.1	22.1
Nanjing 11	55.1	95.4	14.5	21.0	88.7	22.5	28.9
Teqing	56.1	108.3	11.3	19.5	137.6	24.6	38.3
Zhaiyeqing 8	31.3	69.9	14.2	18.1	54.1	24.2	18.6
Aijiao Nante	35.1	70.9	16.7	20.1	65.8	22.0	24.2
Shengli Xian	48.5	135.4	15.5	28.4	94.1	27.3	39.8
Minghui 63	56.4	110.1	12.3	24.1	119.2	22.9	33.6
Indonesia paddy rice	33.3	80.5	12.6	20.6	74.2	25.1	23.5
Yuchi 231–8	47.9	114.3	15.6	22.7	66.7	26.3	27.3
Dular	46.4	148.9	10.4	27.5	113.6	25.8	30.5

Japonica set

The overall level of heterosis in the japonica set was higher than in the indica set (Fig. 1). Again, yield demonstrated the highest heterosis among the seven traits, followed by seeds per panicle and tillers per plant. Very little heterosis was detected for seed weight and heading date.

The range of heterosis was much wider among the crosses in the japonica set than among those in the indica set. For example, heterosis for yield varied from a low of -26% in the hybrid between 'Balilla' and 'Akihikari' to a high of 237% in the cross between 'Mudanjiang 8' and 'Taihu Wanjing'. However, there was a highly significant negative correlation between heterosis and midparent value ($r = -0.443$, $P < 0.01$), indicating that a large portion of the heterosis resulted from poor performing parents and that high heterosis does not necessarily mean high performance. For example, 'Taichung 65' and 'Taihu Wanjing', with a yield of 11.8 and 15.3 g per plant, respectively (Table 3), produced the largest proportions (6/10 for both varieties) of highly heterotic ($>100\%$) hybrids. The highest heterosis was observed in a cross between the 2 parents with the poorest performance ('Mudanjiang 8' and 'Taihu Wanjing'). In contrast, very small proportions of heterotic crosses were obtained from high-performing parents. For example, only 2 of the 10 crosses resulting from var 'C57', a commonly used parental line in japonica hybrid rice production, expressed more than 100% heterosis; and none of the crosses involving 'Nongken 58', which showed the highest yield among the japonica parents, expressed strong heterosis.

Correlations of heterozygosity with performance and heterosis

Two measurements of heterozygosity were used in calculating the correlations of molecular-marker distances with hybrid performance and heterosis: general heterozygosity and specific heterozygosity. General heterozygosity of an F_1 hybrid refers to the distance between the 2 parents calculated using all the markers employed in the study, and specific heterozygosity for a particular trait of an F_1 hybrid refers to the distance between the 2 parents based only on the markers that detected significant effects (positive markers) on that trait.

Indica set

There was considerable variation among the seven traits in the level of correlations between general heterozygosity and hybrid performance (Table 4). Four of the seven correlation coefficients were significant at the 0.01 probability level, and two of the remaining three were significant at the 0.05 probability level. The correlation was the highest for plant height (0.773) followed by panicle length (0.536) and heading date (0.515). Correlations of general heterozygosity with yield and yield component traits were low in general.

Correlations of general heterozygosity with heterosis were much lower than those with performance for almost all the traits. The coefficient was significant at the 0.01 probability level only for plant height, and at the 0.05 probability level for heading date.

When specific heterozygosity was used in the calculation, the levels of all the correlations, except for the

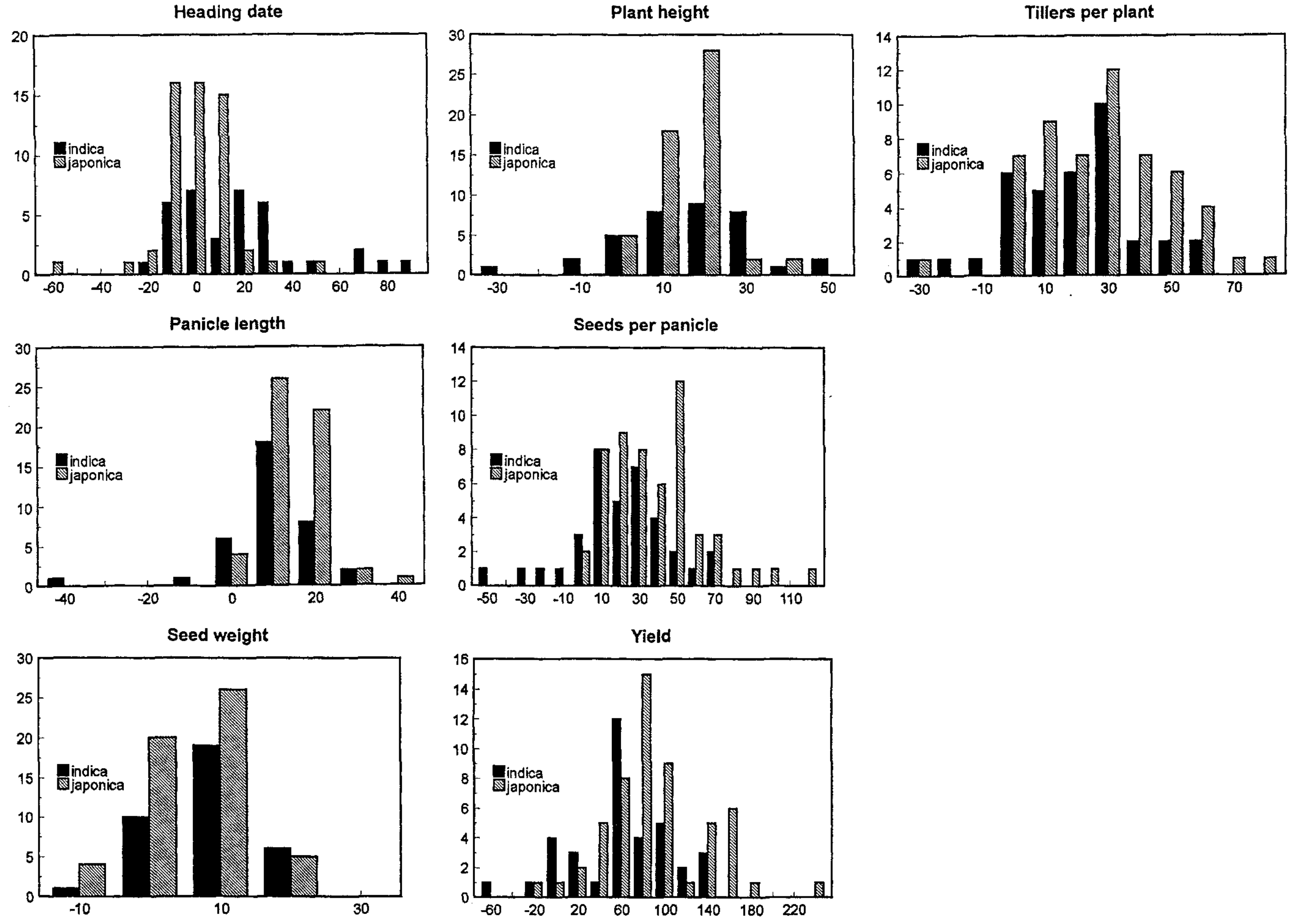

Fig. 1 Distribution of midparent heterosis of the seven traits in the indica and japonica sets of diallel crosses. The *horizontal axis* of each chart is the percentage of heterosis, and the *vertical axis* is the number of crosses.

performance of plant height, were increased compared to those based on general heterozygosity (Table 4). The correlations of specific heterozygosity with performance became significant at the 0.01 probability level for all the traits except tillers per plant; correlations between specific heterozygosity and heterosis for four of the seven traits became significant at the 0.01 probability level.

Japonica set

Correlations of general heterozygosity with performance (Table 4) were significant at the 0.01 probability level for four of the seven traits. Highly significant correlations were also detected between specific heterozygosity and performance for four traits. However, there was little correlation between heterosis and heterozygosity (either general or specific); it was significant at the 0.01probability level only for one trait (plant height), and at the 0.05 probability level for another trait (panicle length).

Discussion

The present study was intended to investigate the extent of correlations between marker heterozygosity and various attributes of hybrid performance and heterosis. The varieties selected for this study represent a wide range of cultivated rice germplasm of both indica and japonica rice, including landraces, historically important cultivars and parents of superior hybrids.

The analysis showed that, with very few exceptions, correlations of molecular-marker heterozygosity with hybrid performance and heterosis were higher in the indica dataset than their japonica counterparts. Of the seven traits analyzed, correlations of marker heterozygosity (either general or specific) with hybrid performance and heterosis of plant height were the highest in both indica and japonica datasets. Among yield and yield component traits, there were low-to-intermediate correlations between hybrid performance and heterozygosity (both general and specific) in both indica and japonica sets, and also low-to-intermediate correlations between specific heterozygosity and heterosis in the indica set, whereas very little correlation was detected between heterosis and heterozygosity (either general or specific) in the japonica set. The lack of correlation in the

Table 4 Correlations of general (GH) and specific (SH) heterozygosity with hybrid performance and heterosis in the indica and japonica diallel sets

	Heading date	Plant height	Panicle length	Tillers per plant	Seeds per panicle	Seed wieght	Yield per plant
Indica[a]							
GH & performance	0.515	0.773	0.536	−0.135	0.468	0.365	0.425
GH & heterosis	0.356	0.537	0.162	0.165	0.236	0.140	0.338
SH & performance	0.631	0.770	0.578	0.265	0.570	0.610	0.443
SH & heterosis	0.549	0.604	0.254	0.299	0.323	0.541	0.445
Japonica[a]							
GH & performance	0.117	0.502	0.520	0.118	0.422	−0.083	0.484
GH & heterosis	−0.028	0.496	0.367	0.167	0.117	−0.037	0.165
SH & performance	−0.072	0.563	0.342	0.515	0.683	0.260	0.585
SH & heterosis	0.069	0.505	0.347	−0.029	0.125	−0.050	0.093

Critical values: $r_{0.05} = 0.325$ and $r_{0.01} = 0.418$ for the indica set; $r_{0.05} = 0.273$ and $r_{0.01} = 0.354$ for the japonica set

japonica set may have resulted from the very different length of growth duration among the parents, largely due to the presence or absence of genes for photoperiod response that regulate the shift from vegetative growth to reproductive growth, hence conferring the enormous variation in phenotypes of the parents and their hybrids (Vergara and Chang 1976).

In this connection, it is interesting to compare the results of this study with those from the previous report of Zhang et al. (1994) using a set of eight parental lines of superior hybrids commonly used in rice production in China. In that study, Zhang et al. also observed low-to-intermediate correlations of general heterozygosity with hybrid performance and heterosis. However, a striking difference between their results and the results of the present investigation is the high correlations that they observed between specific heterozygosity and heterosis for seeds per panicle and yield per plant. An even higher correlation was found later between specific heterozygosity and heterosis for plant height and biomass (Zhang et al. 1995).

A general feature that emerged from these analyses is that the correlations of heterozygosity with performance and heterosis differed greatly from one trait to another and also varied widely with the genetic materials used in the studies. As far as yield and yield component traits are concerned, there are low-to-intermediate correlations between general heterozygosity and performance or heterosis in all three datasets. There are also intermediate correlations between specific heterozygosity and hybrid performance in all three datasets. However, the levels of correlation between specific heterozygosity and heterosis are highly variable: they are low in the mixture of japonica varieties (this study), intermediate in the mixture of indica varieties (this study) and high in the set of parents of superior hybrids (Zhang et al. 1994).

There have been several suggestions for obtaining a better correlation between marker heterozygosity and heterosis by making use of informative markers in the calculation. For example, Charcosset et al. (1991) and Bernardo (1992), based on their theoretical computations, suggested that heterosis may be better predicted using a subset of informative markers or markers that are significantly associated with traits of interest. Similar suggestions have also been made by Melchinger et al. (1990) and Boppenmaier et al. (1993) who studied correlations between marker distance and hybrid performance using different inbreds of corn. In our studies, we found that using pre-selected (positive) markers indeed increased the correlations between marker heterozygosity and heterosis in the two indica datasets. However, the increments in correlation resulting from the use of positive markers in the mixed set of varieties used in the present study were much less than those in the set of superior hybrid parents as observed in our previous study, whereas no increase in correlation was obtained by using positive markers in the japonica dataset. Thus, the effectiveness of pre-selected markers on improving the correlations also varied from one set of materials to another.

In summary, the results from our studies suggest that the relationships between marker heterozygosity and hybrid performance are complex. This was expected because of the diversity of the rice germplasms (Oka 1988) and also because of the complexity of the genetic basis of hybrid performance and heterosis, which has just started to be characterized (Zhang et al. 1994; Xiao et al. 1995). Thus, there is a great need for detailed characterization of the rice germplasms and for in-depth comprehension of the genetic basis of heterosis. The knowledge gained from such studies will certainly facilitate the utilization of molecular markers to improve the efficiency of hybrid rice breeding programs.

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