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Diallel analysis of combining ability and heterosis for yield and yield components in rice by using positive loci

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Abstract Diallel crosses have been widely used for analysis of general combining ability (GCA), specific combining ability (SCA) and heterosis. In the present research, 12 lines were selected from 60 inbred rice bred by International Rice Research Institute with extremely-high or -low yielding records according to the previous three consecutive seasons of yield trial experiments, to construct a half diallel cross. The genetic distances (GDs) revealed by molecular markers for the 12 lines ranged from 0.2288 to 0.7169, averaging at 0.5882; clustering analysis showed the 12 lines were divided into four groups maintaining the original cluster structure of the 60 lines. The positive loci (PLs) including effective-increasing loci (ILs) and effective-decreasing loci (DLs) were screened. The results showed that hybrids derived from those parents with higher GCA effects had better performance for traits of yield and yield components. The SCA effects were strongly correlated to F_1 performance as well as heterosis; the GDs based on ILs were significantly positive correlated to SCA effects and heterosis for yield and yield components while the GDs based on DLs showed the significant negative correlations. Based on this research, a new conception, i.e. general sum of combining ability (GSCA) was conceived, which is defined as the sum of GCAs for two parents of a hybrid. The GSCA and SCA showed similar correlations with traits of yield and yield components. The results illustrated that ILs could be used for further study on prediction of heterosis for traits of yield and yield components; and GSCA may be another considerable parameter combined with ILs for breeders in selecting elite hybrid.

Keywords Rice · Heterosis · General combining ability · Specific combining ability · Effective-increasing loci · Effective-decreasing loci

Introduction

Utilization of heterosis has become a major strategy for increasing productivity of plants, especially in rice, to feed the ever-increasing human population with the decreasing arable land (Masood et al. 2005). There have been a lot of reports on heterosis since Schnell et al. (1982) pointed out that heterosis was a major yield factor in all breeding categories except line breeding. The yield components of F_1 hybrids were usually used to explore methods for the estimation and prediction of yield heterosis in rice (Xangsayasane

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et al. 2010; Melchinger et al. 2008; Gartner et al. 2009; Cho et al. 2004); And a full or partial diallel cross was often conducted to define the heterosis and heterobeltiosis (Zhang et al. 1994; Torres and Geraldi 2007). The heterosis level is clearly a function of the combination of two parents used for offspring production, which may result in a major challenge for plant breeders, as usually several thousand combinations of parents have to be tested for identifying the best combinations (Gartner et al. 2009; Umakanta 2002).

Breeding strategies based on selection of hybrids require expected level of heterosis as well as the specific combining ability (SCA), and the performance of F_1 hybrids depends on choice of parents. But how to choose the parental lines which would result in heterotic combination without necessarily making all possible crosses among the potential parents? Several methods, tried with variable success, include: per se performance, genetic diversity as determined through geographic origin, multivariate analysis using morphological and agronomic traits, isozyme and molecular polymorphism, combining ability, mitochondrial complementation, etc. Among these methods, per se performance is based on the assumption that, in general, high yielding parents produce a larger proportion of high yielding hybrids than do low yielding parents (Mohammadi et al. 2008). And in Melo et al.'s (2001) study, where ten commercial single cross hybrids of different origins were involved, a strong correlation was detected between the per se performances and the SCA, and between the per se performances and heterosis. However, the correlation between SCA and genetic distance was not significant.

Molecular markers have been used in rice to discover the genetic relationships of ecotypes or subspecies and hybrid parents (Xangsayasane et al. 2010; Xiao et al. 1996; Xu et al. 2002). The assessment of genetic diversity is important in plant breeding, Molecular marker based genetic diversity analysis (MMGDA) has potential for assessing changes in genetic diversity over time and space (Duwvick 1984), and studies on MMGDA are also enormous and reflect potential applications in rice (Ravi et al. 2003; Xu et al. 2002), poor relationship between molecular marker-based genetic distance and hybrid performance was observed (Hua et al. 2002). Nevertheless, Xie et al. (2013) defined heterotic groups from 168 tropical *indica* hybrid rice germplasm from International Rice Research Institute (IRRI) using 207 SSR markers, and the result was supported by the eleven IRRI-bred commercial hybrids released in the Philippines showing that the association and prediction could be enhanced when parental groups are formed first by molecular markers.

The objectives of the present research were to (1) evaluate the magnitude of yield heterosis among lines grouped by molecular markers and yield performance; (2) examine the consistency between marker based group and yield performance; (3) analyze combining ability effect for yield and yield components of the selected lines and its hybrids; and (4) explicate the utilization of positive loci (PLs) including effective-increasing loci (ILs) and effective-decreasing loci (DLs) for the prediction of heterosis for yield and yield components.

Materials and methods

Plant materials and field experiments

According to the long-term goal of IRRI's hybrid breeding program, 688 IRRI-inbred lines with six sets of yield trial experiment was conducted by IRRI in previous three consecutive seasons in dry season of 2007 (07DS), wet season of 2007 (07WS) and dry season of 2008 (08DS). And according to its yield performance records (data provided by IRRI was not shown), five lines with the lowest yield record (L group) and five with the top yield record (H group) from each trial set were re-collected resulting 60 lines in total (Huang et al. 2013). Twelve rice lines were further selected based on the unweighted neibhbor-joining tree of 60 IRRI inbred lines as well as its yield performance record (Huang et al. 2013) to establish the 12 × 12 diallel crosses. Table 1 shows the list of the parental lines. They were selected based on the principle (Xie et al. 2013) of lines that can be: (1) representing the original groups clustered from the simple sequence repeat (SSR) and intron length polymorphism (ILP) markers; (2) covering a maximum of the allelic variation of the original 60 lines; and (3) consisting of 6 lines with the highest yield record (H group) and 6 with the lowest yield record (L group) according to the previous yield performance record (Huang et al. 2013). All the possible crosses were made in each except the reciprocal ones; and accordingly, 66 F_1 hybrids were developed from the

Table 1 Rice parents used in the half diallel crosses

Label	Variety	Seed source	Yield* type	Plant type	Yield* (Kg/h)	>CK$ (Kg/h)	Season	Clustering group
HET04	IR 71730-51-2	A3126	L	*Indica*	4,516	−25.6	07DS	I
HET05	IR 04A190	A3135	L	*Indica*	4,925	−18.8	07DS	I
HET07	IR 02A127	A3212	H	*Indica*	6,824	29.9	07DS	IV
HET12	IR 05N269	B3021	L	NPT	4,696	−6.7	07DS	II
HET20	IR 05N170	B3036	H	NPT	7,153	30.1	07DS	V
HET25	IR 04A175	A3130	L	*Indica*	2,374	−41.3	07WS	I
HET26	IR 04A421	A1238	H	*Indica*	5,386	16.5	07WS	IV
HET33	IR 05N211	B3584	L	NPT	2,737	−35	07WS	IV
HET48	IR 02A477	A1146	H	*Indica*	6,409	41	08DS	II
HET53	IR 05N178	B1052	L	NPT	4,813	−2.2	08DS	III
HET58	IR 05N496	B3071	H	NPT	6,707	41.9	08DS	V
HET59	IR 05N346	B1541	H	NPT	7,684	50.9	08DS	V

* The letter "L" indicates the yield performance was among the five lowest records in each set of yield trial experiment while "H" indicates the line was among the top five highest yield records

# indicates the record (data provide by International Rice Research Institute was not shown) in previous field trial with all lines in dry season of 2007 (07DS), wet season of 2007 (07WS) and dry season of 2008 (08DS)

$ indicates the difference of yield performance compared to control's; The clustering group was based on the Neighbor joining of the 12 lines in Fig. 2

diallel crosses at IRRI experimental station in 2011 wet season. All F_1 hybrids with its parents were planted in 2011 dry season using random complete block design with 3 replications. Inbred line PSB Rc82 and hybrid combination IR75217H (Mesotiz 3) were used as controls. Each plot contained 36 plants with spacing at 25 × 20 cm. Five plants were randomly chosen for yield and yield components evaluation, i.e. number of effective panicle per plant (NEP) bearing more than 10 grains, total number of grains per panicle (TNGP), filled grain percentage (FGP), thousand kernel weight (TKW) and grain weight per plant (GWP).

Statistical analysis

SSR and thirty six ILP markers were used in this research. Banding profiles generated by all markers were compiled into a data binary matrix based on the presence (1) or absence (0) of the selected band. Only the clear and unambiguous bands were scored. Pair similarity coefficients were calculated for all pairwise combinations of the 12 lines according to the method developed by Nei and Li (1979): $S_{ij} = 2N_{ij}/(N_i + N_j)$, where S_{ij} is the similarity between the genotype i and j; N_{ij} is the number of bands in both i and j, N_i and N_j is the number of bands presented only in i or j, respectively. Genetic distances (GDs) was calculated as $GD = 1-S_{ij}$ (Zhang et al. 2007). Neighbor joining analysis was performed on similarity matrix utilizing the unweighted pair group method with arithmetic averages (UPGMA) method was done by DARwin 5.0 (Perrier et al. 2003). Least-square means, based on a general linear model were used to estimate general combining ability (GCA) and SCA effects of the F_1 crosses according to Griffing's experimental model I, method 4 (Griffing 1956) using the software DIALLEL-SAS05 (Zhang et al. 2005). Heterosis for yield and yield components was calculated as (1) mid-parent heterosis (MPH) = $(F_1-MP)/MP \times 100$, (2) better-parent heterosis (BPH) = $(F_1-BP)/BP \times 100$, and (3) over-CK heterosis (CKH) = $(F_1-CK)/CK \times 100$; where, F_1, BP and CK refers to the performance of F_1 hybrid, better performing parent and control, respectively; $MP = (P_1 + P_2)/_2$ wherein P_1 and P_2 are the performance of the parents.

Screening positive and effect-increasing/decreasing loci

All the F_1 hybrids were divided into two groups, i.e. homozygous group (*HO*) and heterozygous group

(*HE*), according the methods explicated by Zha et al. (2008). If the parents of the F_1 hybrid were homozygous (or heterozygous) at a locus, this F_1 hybrid could be grouped into *HO* (or *HE*). For each locus, the difference of the trait performance between *HE* and *HO* was calculated. The locus was considered as positive locus (PL) for this trait if the difference was statistically significant. And the PL could be further defined as effective-increasing locus (IL) if the *HE*'s performance was significantly higher than *HO*'s, or contrarily, as effective-decreasing locus (DL). The process of these calculations was done by Microsoft Excel 2007 as described by Zha et al. (2008). GDs based on PLs, ILs and DLs were also calculated, respectively. The Pearson correlation coefficient among each type of GDs to the corresponding F_1 performance, heterosis and specific combining abilities was calculated in SAS PROC CORR (SA SInstitute Inc. 2002).

Results

Genetic distances and clustering analysis of parents

An example of the SSR and ILP patterns generated by representative primers RM236 and RI01970 shown in Fig. 1. All responding bands, except the faint and ambiguous ones, were used for the analysis of GDs and clusters. GDs revealed by SSR and ILP markers for the 60 IRRI rice lines ranged from 0.0880 to 0.7771, with an average at 0.6007, and the GDs of the 12 selected samples varied from 0.2288 to 0.7169, averaging at 0.5882, which was slightly lower than that of the 60 lines, but the samples were considered, based on the criteria of parental selection (Xie et al. 2013), as fairly representative of the allelic variation and the cluster structure of the original population (Fig. 2a). The 12 selected lines were distinctly clustered into four groups (Fig. 2b) as lines with low-yield performance (L) record were in group I and III, and these with high yield performance record (H) were in group II and IV (Table 1). Among the groups, the average GD (0.63149) of inter-groups was significantly higher than that (0.3401) of intra-groups ($P <$ s0.001). The highest GD (0.6602) was between group II (H) and III (L) while the lowest (0.2794) was within group IV (H).

Parental and hybrid performance

The performances of yield and yield related traits of 66 hybrids were analyzed (Table 2). The variances for each trait among all the hybrids were significantly different ($p < 0.001$). The five highest record of GWP were found in the hybrids HET53/HET05 (53.4 g), HET25/HET20 (49.3 g), HET58/HET04 (36.9 g), HET59/HET26 (36.6 g) and HET58/HET07 (36.5 g); while the lowest GWP were in HET53/HET04, HET12/HET05, HET48/HET04, HET26/HET04 and HET05/HET04 with the record from 20.6 to 22.8 g. The hybrids derived from parental line HET20, HET25 or HET05 had elite yield performance. The average FGP of all the hybrids was high (84.4 %). Four hybrids, i.e. HET53/HET07, HET26/HET20, HET53/HET26 and HET33/HET07 had the highest record of FGP (>91 %). For TKW, the value differed from 23.0(HET26/HET07) to 28.9 g (HET53/HET20). For TGNP, it ranged from 92.3 (HET05/HET04) to 160.3 (HET58/HET33) with an average of 122.0. For NEP, the average record was 11.4, with the lowest in HET59/HET05 (8.5) and highest in HET53/HET05 (18.7). The performance of hybrids for each trait of yield and yield components was significantly higher than that of control. For the values of each yield components of all hybrids, there was no significant difference between or among the four clustering groups, neither within/among H and L group. This was indicating a poor relationship between yield components performances and clustering groups revealed by molecular markers.

Combining ability effects

The GCA effect, which determines the average performance of a parent in crosses, and is an estimate of its breeding value was estimated for each parental line (Table 3). For NEP, HET05 and HET25 from group I showed the significant positive GCA effect while HET12 from group III and HET59 from group IV had the significant negative effect. We found that hybrids derived from the parents with higher GCA effect also had higher NEP values; for TNGP, FGP and TKW, the similar phenomenon was also found. For GWP, HET04 showed the significant negative effect, while HET20, HET05 and HET 25 had positive GCA effect but not significant.SCA effect was further calculated for the judgment of the usefulness of a particular cross in exploiting

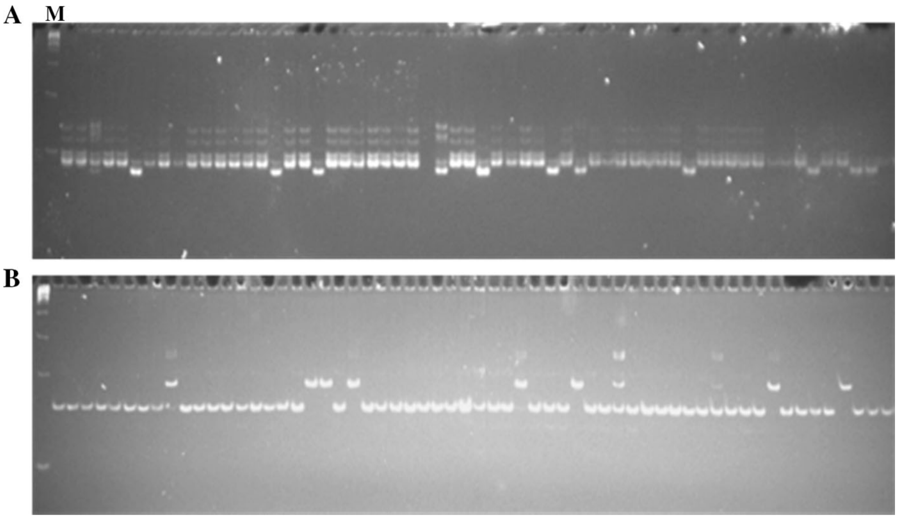

Fig. 1 SSR (**a**. RM236) and ILP (**b**. RI01970) profiles of the 60 *lines* generated with primers. M is the DNA marker 1000

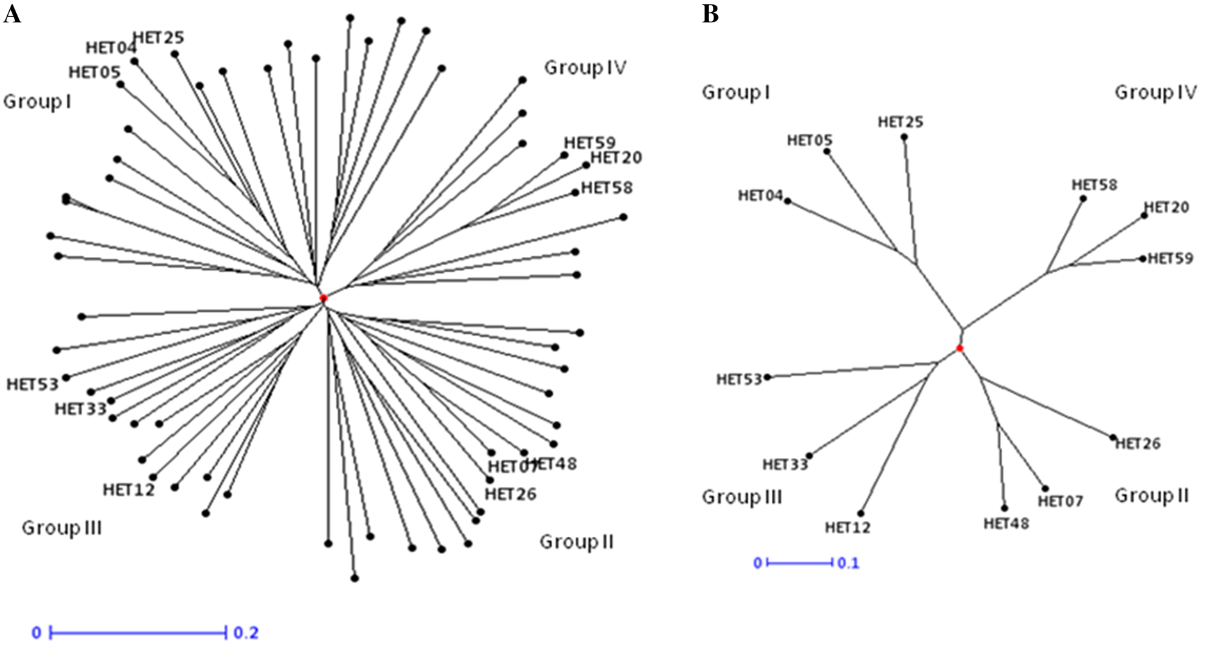

Fig. 2 Unweighted neighbor joining tree of **a** the 60 IRRI *rice lines* and **b** the 12 selected for *diallel crosses* respectively, based on Nei's genetic similarity derived from 70 SSR and 36 ILP markers

heterosis. The result was given in Table 4. For GWP, four of the top five positive SCA effect values for the hybrids of HET48 crossed with HET05, HET12, HET53 and HET59, were statistically significant; while the SCA effect of the cross between HET48 and HET20 was significant negative as the minimum value. This illuminated that HET48 could be used to select elite hybrids in a special combination with other parents. For FGP, the maximum SCA effect values (significant positive) were found in the crosses of HET12/HET25, HET07/HET33, HET07/HET25 and HET26/HET59, while the minimum values (significant negative) were in HET07/HET20 and HET20/HET25. For TKW and NEP, SCA effect was not significant excluding the maximum positive values in HET07/HET25 and HET05/HET53 (TKW) and the minimum negative value in HET26/HET59 (NEP).

Table 2 Record of number of effective panicle per plant (NEP), total number of grains per panicle (TNGP), filled grain percentage (FGP), thousand kernel weight (TKW) and grain weight per plant (GWP) for all hybrids from the 12 × 12 diallel crosses

Cross*	NEP#	TNGP	FGP (%)	TKW (g)	GWP (g)
1 × 2	12.3 ± 1.6 BCDEF	92.3 ± 3.9 J	80 ± 2.7 FGHIJKLMN	24.8 ± 0.8 HIJKLMNOP	22.8 ± 4.9 CD
1 × 3	10.9 ± 1.9 BCDEF	119 ± 20.1 BCDEFGHIJ	87.9 ± 2.3 ABCDEFGH	26.7 ± 0.6 ABCDEFGHIJK	31.1 ± 10.8 CD
1 × 4	9.1 ± 0.5 EF	121.8 ± 17.8 BCDEFGHIJ	82.9 ± 1.9 CDEFGHIJKLMN	26 ± 1 BCDEFGHIJKLMN	24.2 ± 5.7 CD
1 × 5	11.9 ± 3.6 BCDEF	113.6 ± 19.6 BCDEFGHIJ	86 ± 3.8 ABCDEFGHIJKL	27.6 ± 1 ABCDEFG	33.4 ± 15.3 CD
1 × 6	13.9 ± 1.5 BCD	111.3 ± 10.4 BCDEFGHIJ	77.8 ± 3.1 KLMN	24.9 ± 1.8 FGHIJKLMNOP	30 ± 4.1 CD
1 × 7	10.6 ± 1.6 BCDEF	110 ± 4.2 CDEFGHIJ	77.2 ± 5.2 LMN	25.2 ± 1.2 EFGHIJKLMNOP	22.6 ± 1.9 CD
1 × 8	11.2 ± 1.9 BCDEF	139.7 ± 36.2 ABCD	80.1 ± 7.7 FGHIJKLMN	26.2 ± 2.4 ABCDEFGHIJKLM	33.8 ± 14.9 BCD
1 × 9	9.7 ± 1.9 CDEF	103.3 ± 10.2 GHIJ	79.8 ± 6.3 GHIJKLMN	26.1 ± 0.6 BCDEFGHIJKLMN	21.5 ± 7.7 CD
1 × 10	8.9 ± 1.9 EF	96.4 ± 10 IJ	80.8 ± 3.2 FGHIJKLMN	28.9 ± 0.4 A	20.6 ± 7.1 D
1 × 11	13 ± 4.4 BCDEF	125.4 ± 17.5 BCDEFGHIJ	86.1 ± 2.9 ABCDEFGHIJKL	26.7 ± 1.6 ABCDEFGHIJK	37 ± 10.6 BC
1 × 12	9.9 ± 2.1 BCDEF	128.6 ± 3.3 ABCDEFGHI	74.1 ± 4.8 N	27.7 ± 0.2 ABCDEF	25.8 ± 4.1 CD
2 × 3	12.5 ± 1.1 BCDEF	125.3 ± 13.8 BCDEFGHIJ	86.7 ± 2 ABCDEFGHIJ	26.4 ± 0.2 ABCDEFGHIJKL	35.8 ± 5.4 BCD
2 × 4	10 ± 0.8 BCDEF	106 ± 21.9 DEFGHIJ	78.7 ± 7.3 IJKLMN	25.8 ± 0.5 BCDEFGHIJKLMNO	21.4 ± 3.9 CD
2 × 5	12 ± 2.7 BCDEF	118 ± 13.5 BCDEFGHIJ	90.7 ± 1.4 ABCD	28.3 ± 0.2 AB	36.1 ± 7.1 BCD
2 × 6	13.1 ± 3.3 BCDE	111.7 ± 6.2 BCDEFGHIJ	86.1 ± 2.1 ABCDEFGHIJK	25.5 ± 2.1 DEFGHIJKLMNOP	32.4 ± 10 CD
2 × 7	12.4 ± 3.1 BCDEF	110.8 ± 13.8 CDEFGHIJ	90.2 ± 6.2 ABCDE	25.2 ± 1 EFGHIJKLMNOP	31.2 ± 9.6 CD
2 × 8	10.8 ± 1.8 BCDEF	126.6 ± 26.1 ABCDEFGHIJ	83.9 ± 5.8 CDEFGHIJKLM	27.3 ± 0.5 ABCDEFGHI	31.6 ± 9.1 CD
2 × 9	13.5 ± 1.8 BCDE	103.6 ± 14.9 EFGHIJ	88.7 ± 5.3 ABCDEF	24.9 ± 0.3 GHIJKLMNOP	30.4 ± 1.6 CD
2 × 10	18.7 ± 7.5 A	115.2 ± 12.2 BCDEFGHIJ	88.2 ± 3.2 ABCDEFG	28.3 ± 0.6 AB	53.4 ± 21.1 A
2 × 11	11.1 ± 2.7 BCDEF	106.2 ± 16.7 DEFGHIJ	87.8 ± 2.8 ABCDEFGH	27.5 ± 3.5 ABCDEFG	28 ± 6.6 CD
2 × 12	8.5 ± 1.3 F	119.5 ± 11.3 BCDEFGHIJ	88.9 ± 2.5 ABCDEF	27.9 ± 0.5 ABCDE	25 ± 3.6 CD
3 × 4	10.8 ± 2.3 BCDEF	145.3 ± 20.8	84.9 ± 4.9 ABCDEFGHIJKLM	23.2 ± 0.5 OP	31 ± 8.3 CD
3 × 5	10.1 ± 2.3 BCDEF	111.3 ± 20.3 BCDEFGHIJ	86 ± 4.7 ABCDEFGHIJKL	26.7 ± 0.3 ABCDEFGHIJK	26.3 ± 10.9 CD
3 × 6	13.1 ± 2.7 BCDE	124.1 ± 32.8 BCDEFGHIJ	85.5 ± 5.7 ABCDEFGHIJKLM	23.6 ± 3 MNOP	31.5 ± 3.8 CD
3 × 7	14.1 ± 4.1 BC	126.6 ± 19.7 ABCDEFGHIJ	81.7 ± 6.7 EFGHIJKLMN	23 ± 0.8 P	33.9 ± 13.4 BCD
3 × 8	10.5 ± 1.2 BCDEF	132.4 ± 14.7 ABCDEFGH	91.1 ± 2.3 ABC	26.7 ± 1.4 ABCDEFGHIJK	33.8 ± 5.6 BCD
3 × 9	10.7 ± 1.1 BCDEF	125.9 ± 3.2 BCDEFGHIJ	82.1 ± 1 DEFGHIJKLMN	23.2 ± 0.4 OP	25.6 ± 2.7 CD
3 × 10	10.9 ± 1.5 BCDEF	115.3 ± 20.4 BCDEFGHIJ	93.4 ± 4.7 A	25.5 ± 0.8 DEFGHIJKLMNOP	29.6 ± 5.5 CD
3 × 11	12.1 ± 3.2 BCDEF	140.2 ± 14.7 ABCD	88.9 ± 2.6 ABCDEF	23.8 ± 0.4 LMNOP	36.5 ± 12.8 BC
3 × 12	10.8 ± 1.6 BCDEF	137.2 ± 17.7 ABCDEFG	86 ± 2.4 ABCDEFGHIJKL	24.8 ± 1 HIJKLMNOP	31.1 ± 2.3 CD
4 × 5	11 ± 2.1 BCDEF	125.9 ± 16.9 BCDEFGHIJ	86.9 ± 1.1 ABCDEFGHI	25.4 ± 0.3 DEFGHIJKLMNOP	30.9 ± 9.4 CD
4 × 6	12.9 ± 4.3 BCDEF	120.4 ± 5.1 BCDEFGHIJ	78.6 ± 2.9 IJKLMN	26.2 ± 0.8 ABCDEFGHIJKLM	32.1 ± 12.2 CD
4 × 7	9.2 ± 0.7 EF	125.7 ± 10.6 BCDEFGHIJ	85.7 ± 4 ABCDEFGHIJKL	24.2 ± 0.4 JKLMNOP	23.9 ± 2.2 CD
4 × 8	10.3 ± 1.5 BCDEF	139.7 ± 15.4 ABCD	80.1 ± 3.8 FGHIJKLMN	25.3 ± 0.3 EFGHIJKLMNOP	29 ± 4.1 CD

Table 2 continued

Cross*	NEP#	TNGP	FGP (%)	TKW (g)	GWP (g)
4 × 9	9.9 ± 1.2 BCDEF	125.1 ± 13.6 BCDEFGHIJ	90.3 ± 1.1 ABCDE	23.7 ± 2.6 LMNOP	26.4 ± 3.7 CD
4 × 10	11.4 ± 2 BCDEF	127.5 ± 12.4 ABCDEFGHI	83 ± 1.5 CDEFGHIJKLMN	26.1 ± 0.7 BCDEFGHIJKLMN	31.2 ± 3.6 CD
4 × 11	10.7 ± 1.7 BCDEF	136 ± 28.6 ABCDEFG	84.7 ± 5.5 ABCDEFGHIJKLM	23.4 ± 1.1 NOP	28.1 ± 1.4 CD
4 × 12	10.1 ± 1.3 BCDEF	125.4 ± 11.9 BCDEFGHIJ	83.7 ± 2.2 CDEFGHIJKLM	24 ± 0.4 KLMNOP	25.5 ± 5.3 CD
5 × 6	14.4 ± 4.2 AB	135.3 ± 31 ABCDEFG	84.9 ± 4.4 ABCDEFGHIJKLM	28.2 ± 0.7 ABC	49.3 ± 26 AB
5 × 7	11.1 ± 2.8 BCDEF	116 ± 37.4 BCDEFGHIJ	93.2 ± 3.5 AB	26 ± 0.7 BCDEFGHIJKLMN	31.6 ± 13.5 CD
5 × 8	11.1 ± 0.8 BCDEF	131 ± 8.7 ABCDEFGH	83.8 ± 5.2 CDEFGHIJKLM	24.7 ± 3.3 HIJKLMNOP	30 ± 5.3 CD
5 × 9	11.6 ± 2.5 BCDEF	105.9 ± 14.1 DEFGHIJ	90.1 ± 1.8 ABCDE	25.5 ± 2.2 CDEFGHIJKLMNOP	28.4 ± 8 CD
5 × 10	11.7 ± 2.1 BCDEF	103.1 ± 15.5 FGHIJ	78.9 ± 7.1 IJKLMN	28.9 ± 0.3 A	27.5 ± 7.4 CD
5 × 11	12.2 ± 3.9 BCDEF	103 ± 9.9 GHIJ	84.2 ± 2.8 CDEFGHIJKLM	26.8 ± 0.6 ABCDEFGHIJ	29 ± 12.3 CD
5 × 12	10.7 ± 2.6 BCDEF	116.6 ± 10.4 BCDEFGHIJ	84.2 ± 3.9 CDEFGHIJKLM	27.4 ± 0.9 ABCDEFGH	29.3 ± 10.1 CD
6 × 7	10.5 ± 1.8 BCDEF	136.1 ± 27.8 ABCDEFG	87 ± 4.9 ABCDEFGHI	25.3 ± 0.7 EFGHIJKLMNOP	31.7 ± 9.2 CD
6 × 8	9.5 ± 1 DEF	114.6 ± 7.6 BCDEFGHIJ	80.3 ± 5.4 FGHIJKLMN	27.7 ± 0.8 ABCDE	24.4 ± 5.4 CD
6 × 9	13.3 ± 1.5 BCDE	109.1 ± 16.6 CDEFGHIJ	86.1 ± 1.6 ABCDEFGHIJKL	26 ± 2.7 BCDEFGHIJKLMN	31.9 ± 1.1 CD
6 × 10	10.5 ± 0.9 BCDEF	121 ± 11.4 BCDEFGHIJ	83.1 ± 1.4 CDEFGHIJKLM	28.1 ± 1 ABCD	29.5 ± 3.3 CD
6 × 11	10 ± 1.2 BCDEF	135.8 ± 20.1 ABCDEFG	79.2 ± 7.2 HIJKLMN	26.7 ± 1.2 ABCDEFGHIJK	29.4 ± 10.7 CD
6 × 12	10.5 ± 0.8 BCDEF	128.2 ± 15.5 ABCDEFGHI	77.6 ± 3 KLMN	27.4 ± 0.6 ABCDEFGH	28.3 ± 1.2 CD
7 × 8	10.6 ± 1.3 BCDEF	137.9 ± 13.3 ABCDE	88.4 ± 1.2 ABCDEFG	23.9 ± 1.7 LMNOP	30.6 ± 2.4 CD
7 × 9	12.5 ± 4 BCDEF	112.5 ± 4.6 BCDEFGHIJ	83.8 ± 2.4 CDEFGHIJKLM	24.7 ± 0.5 HIJKLMNOP	29.4 ± 11.3 CD
7 × 10	11.7 ± 2.1 BCDEF	102.6 ± 10.2 GHIJ	91.7 ± 1.3 ABC	26.8 ± 0.2 ABCDEFGHIJ	29.4 ± 5.8 CD
7 × 11	11.3 ± 0.5 BCDEF	133.3 ± 12.1 ABCDEFG	86 ± 3.3 ABCDEFGHIJKL	23.8 ± 0.5 LMNOP	30.7 ± 2.1 CD
7 × 12	12.7 ± 2.6 BCDEF	140.7 ± 11.8 ABC	84.1 ± 5.8 CDEFGHIJKLM	24.6 ± 0.8 IJKLMNOP	36.6 ± 4.4 BC
8 × 9	10.1 ± 1.7 BCDEF	111.2 ± 12.8 BCDEFGHIJ	86.5 ± 1.3 ABCDEFGHIJK	24.8 ± 0.5 HIJKLMNOP	24.3 ± 6.1 CD
8 × 10	12.8 ± 2 BCDEF	126.9 ± 15.5 ABCDEFGHI	84.4 ± 2.9 BCDEFGHIJKLM	26.7 ± 0.6 ABCDEFGHIJK	36.4 ± 5.7 BCD
8 × 11	11.6 ± 2.8 BCDEF	160.3 ± 14.7 A	80.1 ± 3 FGHIJKLMN	23 ± 1.3 P	33.6 ± 3.7 BCD
8 × 12	10.9 ± 2.2 BCDEF	142.5 ± 19.7	77.8 ± 2.4 JKLMN	25.5 ± 0.2 CDEFGHIJKLMNOP	30.5 ± 3.9 CD
9 × 10	10.4 ± 0.9 BCDEF	97.9 ± 6 HIJ	89.8 ± 1 ABCDE	26.7 ± 0.7 ABCDEFGHIJK	24.4 ± 2.8 CD
9 × 11	11.1 ± 1.3 BCDEF	126.6 ± 8.8 ABCDEFGHIJ	86.3 ± 3 ABCDEFGHIJK	23.2 ± 0.9 OP	28.3 ± 5.1 CD
9 × 12	12.5 ± 1.9 BCDEF	142.2 ± 17.1	76.8 ± 4.5 MN	25.4 ± 2.3 DEFGHIJKLMNOP	34.3 ± 5 BCD
10 × 11	10.8 ± 0.3 BCDEF	124.2 ± 8.4 BCDEFGHIJ	81.4 ± 1.5 EFGHIJKLMN	26.4 ± 1.2 ABCDEFGHIJKL	28.8 ± 2 CD
10 × 12	10.1 ± 0.6 BCDEF	108.5 ± 14.9 CDEFGHIJ	81.6 ± 6.6 EFGHIJKLMN	27.4 ± 2.7 ABCDEFGH	24.5 ± 5.4 CD
11 × 12	11.2 ± 1 BCDEF	137.5 ± 14.2 ABCDEF	86.5 ± 9 ABCDEFGHIJK	24.5 ± 1 JKLMNOP	32.7 ± 5.8 CD

* The number from 1 to 12 represents the parent HET04, HET05, HET07, HET12, HET20, HET25, HET26, HET33, HET48, HET53, HET58 and HET59, respectively

\# Different letters mean significant difference at 1 % level

Table 3 Estimates of general combining ability (GCA) of parents for number of effective panicle per plant (NEP), total number of grains per panicle (TNGP), filled grain percentage (FGP), thousand kernel weight (TKW) and grain weight per plant (GWP)

Parent	NEP	TNGP	FGP (%)	TKW(g)	GWP (g)
HET04	−0.339	−8.019**	−3.617**	0.689**	−2.886*
HET05	0.988*	−10.616**	2.124**	0.806**	1.645
HET07	0.141	6.108*	2.539**	−1.024	1.467
HET12	−0.952*	5.731	−0.924	−1.044	−2.762
HET20	0.268	−6.166*	1.989**	1.179	2.022
HET25	0.674*	0.618	−2.265**	0.576*	1.895
HET26	0.168	1.097	2.005**	−1.111	−0.001
HET33	−0.552	12.134	−1.237	−0.198	0.643
HET48	0.034	−7.834**	1.148	−0.961	−2.658
HET53	0.281	−10.296**	0.756	1.592	0.375
HET58	0.008	8.691**	0.232	−0.784**	1.058
HET59	−0.719*	8.549**	−2.749**	0.282	−0.798

* $P < 0.05$

** $P < 0.01$

Screening of PLs, ILs and DLs

A total number of 337 loci were detected from the parents, the number of PLs, increasing-effective loci (ILs) and DLs were further screened. The number of PLs ranged from 15 (NETP) to 81 (TKW) (Table 4). The PLs were consisting of ILS and DLs. Only five ILs were screened for NEP while 29 for TKW, as the highest number, were screened; 5 DLs for GWP as the lowest number and 52 as the highest number were screened.

Relationships of GDs with F_1 performance and SCA effect

In this study, the Nei's GDs were calculated based on four types of loci, i.e. PLs, ILs, DLs and all loci. The Pearson correlation coefficients of GDs with values of F_1 phenotypic performance and SCA effect were estimated shown in Table 5. It was obvious that the correlations of GDs based on DLs with F_1 phenotypic value and SCA effect were negative; correlations of GDs based on ILs with F_1 phenotypic value and SCA effect were significant positive. GDs based on PLs or all loci showed significant positive correlations with F_1 phenotypic value and SCA effect only for TKW and GWP. The results indicated the usefulness of ILs for predicting positive SCA effect and phenotypic values of yield and yield components.

Relationships between GDs and heterosis

Since heterosis is a general phenomenon in the entire plant kingdom, a promising approach is to investigate its molecular basis in rice, as a model species. Therefore, correlations of heterosis with GDs based on the four types of loci for yield and yield components were assessed (Table 6). In the 12 × 12 diallel crosses, GDs based on DLs for NEP were significantly negative correlated to the three types of heterosis, i.e. BPH, CKH and MPH (Table 7). GDs based on ILs were significantly positive correlated to heterosis excluding BPH and MPH for both FGP and GWP. It was noted that the correlation between GD based on ILs and CKH for TKW was strong as $r = 0.671$ ($P < 0.01$). While the GDs based on PLs or all loci showed poor correlation to heterosis excluding CHK and MPH for TKW. Obviously, GDs based on ILs presented higher correlations to heterosis than that based on PLs or all loci showing that ILs could be used for the further study on the prediction of heterosis for yield and yield related traits.

Discussion

Diallel mating designs are important tools in plant breeding programs to obtain information on the inheritance of quantitative traits. A partial diallel

Table 4 Estimates of specific general combining ability (SCA) of each cross for number of effective panicle per plant (NEP), total number of grains per panicle (TNGP), filled grain percentage (FGP), thousand kernel weight (TKW) and grain weight per plant (GWP)

Cross	NEP	TNGP	FGP (%)	TKW(g)	GWP (g)
HET04/HET05	0.328	−10.977	−2.924	−2.529**	−6.093*
HET04/HET07	−0.225	−1.071	4.518*	1.201	2.379
HET04/HET12	−0.932	2.1	2.994	0.555	−0.299
HET04/HET20	0.581	5.826	3.171	−0.102	4.131
HET04/HET25	2.241	−3.285	−0.741	−2.132**	0.845
HET04/HET26	−0.585	−4.997	−5.628*	−0.145	−4.699
HET04/HET33	0.735	13.626	0.481	−0.092	5.857
HET04/HET48	−1.319	−2.836	−2.211	0.571	−3.063
HET04/HET53	−2.365	−7.25	−0.739	0.785	−7.049
HET04/HET58	1.975	2.729	5.019*	0.995	8.641*
HET04/HET59	−0.019	6.135	−2.363	0.785	2.521
HET05/HET07	−1.392	7.899	−6.887	0.271	−7.63*
HET05/HET12	−0.612	−11.097	2.103	0.548	2.306
HET05/HET20	0.115	12.866	1.828	−1.715*	−1.287
HET05/HET25	−0.112	−0.221	1.591	−0.329	−0.537
HET05/HET26	−0.992	−1.604	−1.404	0.925	−0.875
HET05/HET33	1.088	3.166	0.971	−0.745	1.266
HET05/HET48	6.041	0.057	0.913	0.101	21.193**
HET05/HET53	−1.285	14.123	1.041	1.711*	−4.85
HET05/HET58	0.255	−13.861	−1.142	−0.499	2.182
HET05/HET59	−1.699	−0.352	−3.005	0.745	−7.335
HET07/HET12	0.961	11.479	0.76	−1.752*	−2.001
HET07/HET20	2.401	−10.644	−7.267**	−0.699	2.255
HET07/HET25	−0.479	−4.582	5.341*	2.155**	1.517
HET07/HET26	−0.865	−2.511	−5.98**	−0.582	−3.329
HET07/HET33	−0.912	−7.774	5.669**	−0.902	−2.388
HET07/HET48	0.561	5.674	1.736	−0.159	3.869
HET07/HET53	0.328	−2.444	1.388	−0.502	1.54
HET07/HET58	1.788	3.395	−2.694	0.868	2.867
HET07/HET59	−1.372	0.578	0.199	0.555	−3.437
HET12/HET20	0.481	4.426	−2.146	0.708	1.026
HET12/HET25	−0.505	−7.874	5.676**	−0.129	1.68
HET12/HET26	0.715	−3.057	−1.229	−0.249	3.481
HET12/HET33	0.255	−0.154	0.919	−0.539	−0.323
HET12/HET48	2.101	5.248	0.733	0.678	15.217**
HET12/HET53	−0.725	10.123	4.739	0.131	−0.574
HET12/HET58	−0.005	−0.334	−1.349	−2.082**	−2.778
HET12/HET59	−0.059	−10.861	2.53	−0.485	−1.131
HET20/HET25	−0.239	18.919*	−8.318**	0.295	−5.043
HET20/HET26	0.568	−0.87	−2.471	0.605	−4.26
HET20/HET33	−1.665	3.089	2.854	0.035	−0.34
HET20/HET48	−2.012	−2.086	−0.651	1.521*	−8.317
HET20/HET53	1.201	−2.36	2.778	0.585	2.523

Table 4 continued

Cross	NEP	TNGP	FGP (%)	TKW(g)	GWP (g)
HET20/HET58	−1.845	−21.441*	0.16	0.131	−2.883
HET20/HET59	−2.039	−7.725	−3.233	1.075	−3.699
HET25/HET26	−0.372	12.439	3.156	−0.625	−0.188
HET25/HET33	0.908	−20.088*	−3.822	0.971	1.906
HET25/HET48	−0.139	−5.633	4.453*	0.551	−1.127
HET25/HET53	−0.265	8.732	−0.69	−0.072	−0.483
HET25/HET58	−0.705	4.492	2.183	0.125	−3.778
HET25/HET59	1.715	−2.899	0.411	−0.495	5.256
HET26/HET33	0.788	2.756	−3.381	−1.785**	1.806
HET26/HET48	−1.272	−2.696	3.473	0.235	−3.477
HET26/HET53	−0.265	−10.143	0.464	−0.855	−0.213
HET26/HET58	−0.432	1.599	−3.94	0.895	−0.649
HET26/HET59	−3.159*	9.082	5.132*	0.978	−6.014
HET33/HET48	0.021	−15.046	1.734	−0.292	0.331
HET33/HET53	0.381	3.07	2.923	−1.039	−1.087
HET33/HET58	−0.239	17.506*	0.48	0.171	−2.071
HET33/HET59	−0.845	−0.152	−1.792	0.708	−2.923
HET48/HET53	1.928	−5.972	0.415	−0.372	7.226**
HET48/HET58	0.848	3.764	−2.64	−0.352	0.475
HET48/HET59	1.795	19.526*	−6.062**	0.311	7.616**
HET53/HET58	−0.845	3.803	−3.974	−0.209	−2.773
HET53/HET59	−0.852	−11.681	−0.82	−0.242	−5.19
HET58/HET59	0.555	−1.652	4.571*	−0.765	2.287

* $P < 0.05$

** $P < 0.01$

consisting of crosses between two parents groups is useful when there are distinct groups of populations and the breeder is not interested in evaluating the crosses between parents of the same group. Variety diallel crosses have widely used in plant breeding as practical means for the evaluation of combining ability and heterotic patterns of varieties or inbred lines in cross combinations. In this research, half diallel crosses were used for analysis of combining ability effect and heterosis for agronomic traits. We found that the hybrids derived from the parents with high GCA for GWP, TKW and FGP, had high performance for the corresponding traits. Based on the results, GCA may be used as a direction for breeding elite hybrid combinations when GCA values are estimated under the same conditions, or may be used to predict heterosis for specific breeding target. Hybrid breeding can be also called as GCA breeding, many reports support this concept, especially in the prediction for yield performance (Gopal et al. 2008; Worku et al. 2008), disease resistance and drought tolerance (Yanchuk 1996), etc. Even those with low GCA could be used as test lines in breeding (Lobato-Ortiz et al. 2010).

SCA was also reported to be used to predict heterosis (Ahangar et al. 2008; Ni et al. 2009; Torres and Geraldi 2007). In the present study, strong correlations were found between SCA and heterosis for most of the yield and yield related traits. Nevertheless, it is impractical to use SCA for the heterosis prediction. SCA is for specific cross between two parents. Once we obtain the SCA values for all the crosses through our experiments such as diallel crosses, we actually have already obtained all the phenotypic values for the hybrid crosses, so it will be unnecessary to do the correlation analysis between SCA and heterosis. While GCA is different from SCA, which is to describe the parent’s combining ability for

Table 5 Pearson correlation of genetic distances based on four types of loci (DLs, ILs, PLs and all loci) with phenotypic values and SCA effect values derived from the 12 × 12 diallel crosses

	Traits	Genetic distance			
		Based on DLs	Based on ILs	Based on PLs	Based on All loci
Pheno-typic value	NEP	−0.430**	0.358**	−0.106	−0.044
	TNGP	−0.383**	0.385**	0.081	0.139
	FGP	−0.368**	0.378**	0.195	0.011
	TKW	−0.166	0.656**	0.471**	0.455**
	GWP	−0.297*	0.431**	0.356**	0.254*
SCA effect value	NEP	−0.388*	0.332*	−0.091	−0.025
	TNGP	−0.213	0.261*	0.088	0.096
	FGP	−0.247*	0.306*	0.195	0.054
	TKW	−0.041	0.586*	0.448*	0.433*
	GWP	−0.258*	0.352*	0.282*	0.236*

NEP number of effective panicle per plant, *TNGP* total number of grains per panicle, *FGP* filled grain percentage, *TKW* thousand kernel weight, *GWP* grain weight per plant, *SCA* specific combining ability, *DLs* the decreasing-effective loci, *ILs* increasing-effective loci, *All loci* all the loci from all the molecular markers used in this research

* $P < 0.05$

** $P < 0.01$

Table 6 Pearson correlation of genetic distances based on four types of loci (DLs, ILs, PLs and all loci) with heterosis for yield and yield components derived from the 12 × 12 diallel crosses

Trait	Genetic distance			
	Based on DLs	Based on ILs	Based on PLs	Based on all loci
Better-parent heterosis (BPH)				
NEP	−0.427**	0.352**	−0.108	−0.047
TNGP	−0.168	0.275*	0.152	0.154
FGP	−0.001	−0.033	−0.016	0.078
TKW	−0.078	0.247*	0.151	0.146
GWP	−0.135	0.058	0.043	0.115
Over-CK heterosis (CKH)				
NEP	−0.351**	0.308**	−0.075	−0.054
TNGP	−0.363**	0.347**	0.063	0.053
FGP	−0.395**	0.296*	0.116	0.011
TKW	−0.221	0.671**	0.462**	0.442**
GWP	−0.265*	0.277*	0.22	0.198
Mid-parent heterosis (MPH)				
NEP	−0.449**	0.326**	−0.14	−0.032
TNGP	−0.265*	0.351**	0.155	0.133
FGP	0.063	0.025	0.072	0.085
TKW	0.029	0.407**	0.319**	0.280*
GWP	−0.148	0.093	0.069	0.216

NEP number of effective panicle per plant, *TNGP* total number of grains per panicle, *FGP* filled grain percentage, *TKW* thousand kernel weight, *GWP* grain weight per plant, *DLs* the decreasing-effective loci, *ILs* increasing-effective loci, *All loci* all the loci from all the molecular markers used in this research

* $P < 0.05$

** $P < 0.01$

Table 7 Pearson correlations between GSCA and SCA effect derived from the 12 × 12 diallel crosses

Correlations		NEP	TNGP	FGP	TKW	GWP
GSCA vs	SCA	0.281*	0.380**	0.410**	0.440**	0.329**
SCA vs	Pheno-value	0.945**	0.894**	0.921**	0.850**	0.941**
GSCA vs	Pheno-value	0.413**	0.624**	0.583**	0.750**	0.453**
SCA vs	BPH	0.638**	0.509**	0.540**	0.424**	0.638**
	CKH	0.828**	0.773**	0.871**	0.780**	0.829**
	MPH	0.667**	0.506**	0.674**	0.549**	0.666**
GSCA vs	BPH	0.334**	0.340**	0.121	0.344**	0.247*
	CKH	0.459**	0.773**	0.628**	0.805**	0.431**
	MPH	0.342**	0.352**	0.2	0.404**	0.141

GSCA the sum of general combining ability effect for the two parents of a hybrid, *SCA* specific combining ability; *NEP* number of effective panicle per plant, *TNGP* total number of grains per panicle, *FGP* filled grain percentage, *TKW* thousand kernel weight, *GWP* grain weight per plant, *BPH* better-parent heterosis, *CKH* over-CK heterosis, *MPH* mid-parent heterosis

* $P < 0.05$

** $P < 0.01$

a trait. Usually, GCA is considered to be controlled by additive genes (Vacaro et al. 2002; Yang et al. 1997). GCA can be easily recombined and accumulated through gene flow; and the inheritance of GCA is high (Lu 1999). Thus we conceived a new conception, i.e. general sum of combining ability (GSCA) to substitute SCA. The value of GSCA is the sum of GCAs for the two parents of a hybrid. Using the GCAs in Table 3 for the twelve parents, we assessed all the GSCAs of the 66 hybrids for the five traits. The correlations between SCA and GSCA were hence estimated including their correlations considering the aspects of phenotypic value and the three types of heterosis for each corresponding trait (Table 7). The correlation between GSCA and SCA for the each trait of yield and yield components was statistically significant. The correlations between GSCA and phenotypic value, between SCA and phenotypic value, between GSCA and heterosis, between SCA and heterosis, were all significant. It is expected to use GSCA to substitute SCA to predict the promising combinations from the parental lines. The obvious advantage of GSCA over SCA is that it is estimated from GCA not from the complicated crosses design. Breeders usually have many breeding lines with known GCA values, when they exchange their lines with others, the GSCA can be directly calculated to estimate their SCA values. This may need more evidence to support since it is mainly based on the 12×12 half diallel crosses.

Prediction of heterosis in rice breeding is of great meaning for breeders. How to make it come true with a high efficiency and veracity is of their concerns. Many methodologies were attempted but no one was ideal. Scientists used the heterozygosity of positive molecular loci to predict heterosis. Zhang et al. (1994)-pointed out that PLs presented strong correlations to yield and yield related traits, among which the heterozygous PLs were strongly correlated to mid-heterosis for yield and other traits. Zha et al. (2008) screened ILs and DLs from PLs in two sets of diallel crosses indicating that the GDs based on ILs were significantly correlated to the performances of F_1s for most of traits with an average correlation of 0.76. The correlations were stable over different environments except GWP. He et al. (2002) reported that ILs could used to predict the heterosis for yield and yield related traits. Although the correlation coefficients between DLs or ILs and the values of phenotypic (SCAs or heterosis) were statistically significant, the magnitude was low, so the DLs or ILs could not be directly used for heterosis prediction. But when stable DLs and ILs can be revealed from different sets of diallel crosses under different environments, they may be useful in prediction for breeding.

In the present research we found that ILs and DLs were significantly correlated to heterosis except for a few traits. And the frequencies of ILs for yield and yield related traits screened from all the loci were calculated. ILP marker RI00297 had 9 ILs detected in the diallel crosses, RM149 had 6 ILs, RM514, RM276, RM252, RM232 and RM216 had 5. The ILs with high frequencies detected from SSR marker were reported to be as QTLs for yield and yield components, such as RM149 and RM216 (Cho et al. 1991; Jiang et al. 2004), RM232 (Xiao et al. 1998), RM252(Xu et al. 2001), RM276 (Temnykh et al. 2000), RM514 (Moncada et al. 2001) and RM213 (Brondani et al. 2002). According this research, the ILs could be used for the further study on prediction of heterosis for yield and yield related traits; GSCA may be another considerable parameter combined with ILs for breeders in selecting elite hybrid.

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