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Genetic basis of heterosis and inbreeding depression in rice (*Oryza sativa* L.)*

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Abstract: The genetic basis of heterosis was studied through mid-parent, standard variety and better parent for 11 quantitative traits in 17 parental lines and their 10 selected hybrids in rice (*Oryza sativa* L.). The characters were plant height, days to flag leaf initiation, days to first panicle initiation, days to 100% flowering, panicle length, flag leaf length, days to maturity, number of fertile spikelet/panicle, number of effective tillers/hill, grain yield/10-hill, and 1000-grain weight. In general the hybrids performed significantly better than the respective parents. Significant heterosis was observed for most of the studied characters. Among the 10 hybrids, four hybrids viz., 17A×45R, 25A×37R, 27A×39R, 31A×47R, and 35A×47R showed highest heterosis in 10-hill grain yield/10-hill. Inbreeding depression of F_2 progeny was also studied for 11 characters of 10 hybrids. Both positive and negative inbreeding depression were found in many crosses for the studied characters, but none was found significant. Selection of good parents was found to be the most important for developing high yielding hybrid rice varieties.

Key words: Heterosis, Inbreeding depression, Rice
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INTRODUCTION

Although rice is a naturally self-pollinated crop, strong heterosis is observed in their F_1 hybrids. Heterosis or hybrid vigor is manifested as improved performance for F_1 hybrids generated by crossing two inbred parents. Heterosis can be defined quantitatively as an upward deviation of the mid-parent, based on the mean values of the two parents (Johnson and Hutchinson, 1993). Heterosis may be positive or negative. Depending upon breeding objectives, both positive and negative heterosis are useful for crop improvement. In general, positive heterosis is desired for yield, and negative heterosis for early maturity. Heterosis is expressed in three ways, depending on the criteria used to compare the performance of a hybrid. The three ways are: mid-parent, standard variety and better parent heterosis. However, from the plant breeder's viewpoint, better parent and/or standard variety is more effective. The former is designated as heterobeltiosis (Fanseco and Peterson, 1968) and the latter as standard heterosis (Virmani, 1994). From a practical point of view, standard heterosis is most important because it is aimed at developing desired hybrids superior to the existing high yielding commercial varieties. Application of heterosis in agricultural production yields multi-billion dollar returns and represents a single greatest applied achievement in the discipline of genetics. Hybrid rice technology has en-

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abled China to increase its rice production significantly during the past 20 years (Virmani, 1988). Good hybrids have the potential for yielding 15%–20% more than the best inbred variety grown under similar condition (Virmani *et al.*, 1997). All these reports led to the conclusion that there was significant occurrence of heterosis, which could be exploited commercially by developing F_1 rice hybrids (Virmani, 1994). Hybrid rice technology could offer great opportunity for increasing food production of rice growing countries.

Inbreeding depression (ID) is usually defined as the lowered fitness or vigor of inbred individuals compared with their non-inbred counterparts. Its converse is heterosis, the 'hybrid vigor' manifested as increased size, growth rate or other parameters resulting from the increase in heterozygosity in F_1 generation crosses between inbred lines. Inbreeding depression, the depressive effect, is the expression of traits arising from increasing homozygosity (Allard, 1960). In quantitative genetics theory, inbreeding depression and heterosis are due to non-additive gene action, and are considered to be two aspects of the same phenomenon (Mather and Jinks, 1982). Li *et al.*(1997b) suggested that hybrid breakdown in rice was part of ID largely related to additive epistasis. In this work, heterosis and inbreeding depression were studied for selecting good materials for developing superior hybrid rice variety.

Experiments were conducted to estimate the effect of heterosis on different yield contributing characters for developing high yielding F_1 hybrid rice variety.

MATERIALS AND METHODS

Rice germplasm needed for the development of hybrid rice were obtained from IRRI (International Rice Research Institute), Philippines. BRRI dhan 28 developed at Bangladesh Rice Research Institute was used as a standard check. Seventeen parents; CMS lines (17A=IR58025A, 19A=IR62829A, 21A=IR67684A, 25A=IR68280A, 27A=IR68886A, 29A=IR68888A, 31A=IR68897A, 33A=IR68899A and 35A=IR69626A) and restorer lines (37R=IR29723-143-3-2-1R, 39R=IR46R, 43R=IR 60913-42-3-3-2-2R, 44R=IR60919-150-3-3-3-2R, 45R=IR6164-38-19-3-2R, 46R=IR62036-222-3-3-1-2R, 47R=IR62037-12-1-2-2-2R and 49R=IR63870 -7-3-2-3-3R) and their 10 selected.hybrids (17A× 43 R, 17A×45R, 19A×46R, 21A×49R, 25A×37R, 27A ×39R, 29A×44R, 31A×47R, 33A×39R and 35A×47 R) were used in the present investigation. This January to May, 2002, August to December, 2002, and January to May, 2003 experiment was conducted using a randomized complete block design consisting of three replications. Each 10-row plot was 12.5 m×15 m. The row-to-row distance was 50 cm and hill-to-hill distance was 25 cm. There was a 50 cm wide footpath around the field. Observations were recorded for different characters such as plant height (PH), flag leaf length (FLL), panicle length (PL), days to flag leaf initiation (DFLI), days to first panicle initiation (DFPI), days to 100% flowering (D100F), days to maturity (DM), grain yield /10-hill (GY/10H), number of effective tillers/hill (NET/H), number of fertile spikelet/panicle (NFS/P) and 1000-grain weight (1000-GW). The heterosis was calculated as the difference of F_1 from mid parent heterosis (MPH), standard heterosis (STH), and better parents heterosis (BPH). Heterosis was expressed as a percentage increase or decrease over MP, SH and BP. The level of heterosis was tested using Student's "*T*" test.

Heterosis measurement was simple and generally expressed as percentage increase or decrease in the performance of a hybrid in comparison with the reference variety or a parent (Virmani *et al.*, 1997).

Inbreeding depression was measured using F_1 and F_2 means according to the following formula:

$$\text{Inbreeding depression (ID)} = \frac{\overline{F}_1 - \overline{F}_2}{\overline{F}_1}$$

$$T\text{-test of ID} = \frac{\text{Estimated value of ID}}{\text{Standard error of mean}}$$

Where,

$$\text{Standard error of mean} = \sqrt{V\overline{F}_1 + V\overline{F}_2}$$

$V\overline{F}_1$ = *V*ariance of F_1 mean

$V\overline{F}_2$ = *V*ariance of F_2 mean

RESULTS

Heterosis of hybrids over their respective mid-parent, standard variety and better parent for 11 characters is presented in Table 1. For each character, the percentage values of the 10 hybrids were compared with mid parent, standard variety and better parent, the relative superiorities being termed as mid-parent heterosis, standard heterosis and better parent heterosis. The crosses 17A×45R, 21A×49R and 25A×37R showed highly significant positive heterosis for flag leaf length, in three levels of heterosis, except for better parent in 17A×45R, and the highest positive value for both mid-parent (44.41%) and standard (15.23%) level was observed in 17A×45R.

Regarding the characters flag leaf initiation days, first panicle initiation days, days to 100% flowering and days to maturity, negative heterosis was observed in most of the crosses. Among the 10 crosses, highly negative heterosis was observed in 17A×43R, 17A×45R, 27A×39R, 33A×39R for both days to 100% flowering and days to maturity, except mid-parent heterosis in cross 27A×39R, which suggested the possibility of developing early maturity lines from these cross combinations.

In the case of grain yield/10-hill, most of the crosses showed highly significant positive values for the three levels of heterosis. Some crosses showed negative heterosis. The values ranged from –33.70% to 209.82%, –69.71% to 10.11% and –50.79% to 197.51% for mid-parent, standard and better parent heterosis, respectively. Based on heterosis values of grain yield/10-hill, four crosses, 17A×43R, 25A×37R, 31A×47R and 35A×47R, were identified as the most promising combinations for developing high yielding hybrid rice varieties. The highest percent of mid-parent heterosis (209.82%) was observed in cross 31A×47R, followed by 25A×37R (147.77%).

In this investigation, ID was found to occur in F_2 in most of the crosses for the studied characters, but it was not significant (Table 2). Among the different characters, three characters, viz., grain yield/10-hill (0.762), 1000-grain weight (0.106) and fertile spikelets/panicle (0.507) were affected most.

DISCUSSION

For developing high yielding hybrid rice varieties, different cross combinations were tested and some were found to be promising. The stability of hybrids was checked through their performance in the F_2 generation, and variable inbreeding depression was noted for the studied characters in different crosses. Inbreeding depression (ID) and heterosis are related phenomena of fundamental importance to evolutionary biology and applied genetics. Inbreeding depression refers to reduced fitness of progenies resulting from inbreeding (Stebbins, 1958; Wright, 1977). In contrast, heterosis or hybrid vigor is defined as the superiority of an F_1 hybrid over its parent (Stuber, 1994).

In the present study, three crosses, 17A×45R, 21A×49R and 25A×34R, showed highly significant positive heterosis for flag leaf length. This indicates that these crosses could be good materials for developing high yielding hybrids, because rice flag leaf length reportedly contributes greatly to high grain yield production (Nuruzzaman *et al.*, 2002). Julfiquar and Tepora (1994) also reported positive heterosis for flag leaf length and panicle length in rice.

Development of high yielding early maturing varieties is desired in rice breeding programs. Among the 10 crosses, highly negative heterosis was observed in 17A×43R, 17A×45R, 27A×39R, 33A×39R for both days to 100% flowering and days to maturity, which indicated the possibility of developing early maturity lines. Negative heterosis for earliness was also reported by Khaleque *et al.* (1977) and Nuruzzaman *et al.*(2002) in rice. Heterosis of hybrids rice was observed to vary in growth duration, ranging from 105 to 135 days (Virmani, 1998).

Of the 10 studied crosses, four crosses, 17A×43R, 25A×37R, 31A×47R and 35A×47R, were identified as the most desired combinations for developing high yielding hybrid rice varieties, because they showed high heterosis value for grain yield/10-hill, 1000-grain yield, number of fertile spikelet/panicle and number of effective tillers/hill. As the highest percentage (209.82%) of heterosis

Table 1 Mid-Parent (MP), standard (ST) and better parent (HP) heterosis are expressed in percent for 11 characters in rice

Characters	Heterosis	Crosses									
		17A×43R	17A× 45R	31A×46R	21A × 49R	25A×37R	27A×39R	29A×44R	31A×47R	33A×39R	35A×47R
PH (cm)	MPH	–05.62***	02.18***	02.21	–02.61*	26.23***	–14.69**	12.09***	–18.33***	00.03	–77.03***
	STH	–15.96***	–10.21***	26.43***	–27.58***	02.17	–29.18***	–20.17***	–23.62***	–12.89***	–21.58***
	BPH	–10.17***	–03.36*	–05.18**	–04.10**	25.29***	–18.63***	–20.00***	–30.05***	–04.74**	–86.82***
NFS/P	MPH	–08.19***	–04.53**	–11.56***	–05.72**	46.60***	–41.44**	–21.18***	–06.96***	–04.18**	–04.52
	STH	–26.14***	–26.44***	–41.94***	–38.19***	00.32	–55.12***	–43.80***	–25.47***	–24.49***	–17.76***
	BPH	–17.72***	–10.66***	–15.16***	–08.88***	43.94***	–47.04***	26.42***	12.36***	06.22***	–00.64
NET/H	MPH	12.06***	–16.27***	17.69***	–28.60***	16.51***	23.26***	31.81***	13.38***	–15.38***	19.52***
	STH	31.52***	–25.15***	–35.15***	–39.09***	07.27***	–30.00***	32.12***	21.52***	–20.00***	28.18***
	BPH	33.14***	–24.46***	–22.74***	–41.40***	31.54***	–38.07***	–45.76***	–34.60***	–29.41***	37.63***
PL (cm)	MPH	–01.71	11.05***	–02.11	07.76***	19.89***	00.56	02.89*	05.50**	–07.94***	–00.92
	STH	–18.55***	–06.79***	–23.76***	16.74***	–03.85**	–19.00**	–15.38***	–11.09***	–13.12***	–20.81***
	BPH	–06.01***	04.83**	–05.34**	–0055	19.72***	–02.45*	–04.35**	03.97**	–06.08***	–03.31
FLL (cm)	MPH	02.23	44.41***	–17.91***	19.30***	19.03***	–01.98	–01.93	05.92**	–10.22***	–07.53**
	STH	–22.56***	15.23***	–31.95***	10.53***	03.01***	–20.86***	–23.68***	–14.29***	–18.42***	–16.92***
	BPH	01.73***	–35.32***	–19.02***	10.09***	17.27***	–04.32***	–07.94***	01.79	–02.25***	–15.94***
DFLI	MPH	–19.58***	–22.87***	–06.91***	–00.90	09.60***	–04.62***	–03.64*	05.50**	–01.57	–11.23**
	STH	–16.76***	–28.14***	–08.65***	–07.83***	06.01***	–29.42***	–21.58***	–16.12***	–23.04***	–21.04***
	BPH	–28.87***	–25.71***	–12.17***	–00.80	06.79***	–26.75***	–25.58***	01.88	–20.13***	–03.13
DFPI	MPH	–18.27***	–19.51***	–06.57***	–01.60**	17.33***	–22.28***	09.27***	05.62**	14.63***	–02.10
	STH	–12.79***	–23.98***	–04.09**	–04.71**	04.00*	–09.53***	–03.73**	–16.52***	–10.21***	–17.32***
	BPH	–27.04***	–20.96***	–12.27***	–04.45**	–01.76	–08.72***	–01.63	06.43**	–04.23**	–08.79**
D100%F	MPH	–12.42***	–16.2***	–10.94***	–03.56*	–09.67***	–10.68***	–09.99***	–01.17	–14.36***	03.31
	STH	–14.64***	–21.34***	–16.68***	–15.16***	00.59	–24.94***	–019.43***	–22.00***	–23.18***	–20.75***
	BPH	–20.82***	–21.28***	–19.56***	–06.18***	–06.96***	–24.72***	–20.31***	–01.21	–23.01***	–20.75***
DM	MPH	–08.32***	–09.00***	–02.78	–00.31	00.62	03.70	00.53	02.50	–00.55	01.81
	STH	–21.52***	–21.30***	–18.30***	–20.13***	–15.13***	–17.30***	–15.96***	–21.47***	–19.47***	–21.91***
	BPH	–14.90***	–16.07***	–10.64***	–01.98	–03.30*	–03.13*	–07.07**	–01.08	–05.42**	00.093
GY10/H (g)	MPH	105.76***	88.09***	20.44***	59.58***	147.77***	–33.70***	07.90**	209.82***	21.67***	80.41***
	STH	03.21*	–16.71***	–49***	–38.20***	04.26*	–69.71***	–38.93***	10.11***	–38.00***	26.22***
	BPH	55.81***	50.91***	19.65***	19.59***	135.44***	–50.79***	–13.97***	197.51***	03.62*	76.12***
1000-GW (g)	MPH	04.41**	8.08***	09.07***	4.17**	08.65***	–03.92*	–00.31	01.64	00.79	00.01
	STH	00.02	4.22**	0.31	–01.82	01.95	–00.65	01.62	–01.62	–00.84	00.84
	BPH	–02.22	0.63	–00.19	–05.67**	00.96	–05.55*	–01.88	00.33	–01.48	–02.32

*, ** and *** Indicates the significant level at 5%, 1% and 0.1%, respectively.

PH=Plant height, FLL= Flag leaf length, PL= Panicle length, DFLI= Days to flag leaf initiation, DFPI= Days to first panicle initiation, D100F= Days to 100% flowering, DM= Days to maturity, GY/10H= Grain yield/10-hill, NET/H= Number of effective tillers/hill, NFS/P= Number of fertile spikelet/panicle, 1000-GW= 1000-grain weight.

Table 2 Estimation of inbreeding depression in F_2 from F_1's for eleven characters in rice (*T*-test of ID is expressed as TT)

Characters		17A× 43R	17A× 45R	31A× 46R	21A × 49R	25A× 37R	27A× 39R	29A× 44R	31A× 47R	33A× 39R	35A× 47R
PH (cm)	ID	−0.135	−0.085	−0.098	−0.081	−0.164	0.005	−0.134	−0.076	0.010	−0.049
	TT	−0.060	−0.034	−0.056	−0.058	−0.073	0.004	−0.099	−0.079	0.006	−0.028
NFS/P	ID	0.001	0.171	0.244	0.201	−0.033	0.072	−0.303	0.071	0.373	0.507
	TT	0.000	0.012	0.018	0.015	−0.006	0.003	−0.007	0.012	0.021	0.095
NET/H	ID	−0.109	0.313	0.318	0.386	0.123	0.607	0.181	0.121	0.568	0.207
	TT	−0.387	0.254	0.540	0.168	0.166	0.994	0.247	0.066	0.288	0.208
PL (cm)	ID	0.054	0.089	−0.028	0.313	0.053	0.177	0.072	0.015	0.166	0.126
	TT	0.077	0.088	−0.060	1.024	0.110	0.093	0.086	0.011	0.187	0.058
FLL (cm)	ID	0.000	0.152	−0.073	0.092	−0.087	0.153	−0.139	0.043	0.164	−0.082
	TT	0.000	0.122	−0.028	0.103	−0.057	0.046	−0.143	0.063	0.078	−0.081
DFLI	ID	−0.320	−0.236	−0.178	−0.096	−0.191	−0.201	−0.196	−0.217	−0.477	−0.331
	TT	−0.391	−0.289	−0.218	−0.118	−0.166	−0.246	−0.152	−0.266	−0.584	−0.574
DFPI	ID	−0.281	−0.422	−0.325	−0.192	−0.254	0.183	−0.176	−0.079	−0.060	−0.329
	TT	−0.218	−0.517	−0.398	−0.235	−0.312	0.224	−0.136	−0.097	−0.052	−0.403
D100%F	ID	−0.236	−0.233	−0.262	−0.108	−0.224	−0.171	−0.265	−0.370	−0.289	−0.262
	TT	−0.183	−0.286	−0.227	−0.133	−0.275	−0.296	−0.325	−0.286	−0.017	−0.321
DM	ID	−0.123	−0.215	−0.192	−0.089	−0.204	−0.170	−0.137	−0.250	−0.282	−0.195
	TT	−0.095	−0.068	−0.118	−0.043	−0.091	−0.104	−0.106	−0.070	−0.047	−0.119
GY/10H (g)	ID	0.553	0.762	0.490	0.635	0.391	0.644	0.433	0.525	0.634	0.678
	TT	0.010	0.082	0.076	0.091	0.081	0.125	0.062	0.053	0.160	0.147
1000-GW (g)	ID	0.013	0.021	0.006	0.059	−0.015	0.019	0.106	0.216	0.023	0.092
	TT	0.037	0.029	0.006	0.065	−0.041	0.050	0.216	0.411	0.018	0.586

T = 2.10 (at 5% level) for df = 18

PH = Plant height, FLL= Flag leaf length, PL= Panicle length, DFLI= Days to flag leaf initiation, DFPI= Days to first panicle initiation, D100F= Days to 100% flowering, DM= Days to maturity, GY/10H= Grain yield/10-hill, NET/H= Number of effective tillers/hill, NFS/P= Number of fertile spikelet/panicle, 1000-GW= 1000-grain weight

for mid-parent was observed in cross 31A×47R, this cross could be used for developing good hybrid varieties. High percentage (91.8 to 150.4) of heterosis for yield per plant was also reported by Zhang *et al.*(1994) and Alzona and Arrauadeau (1995). Li *et al.*(1997a) suggested epistasis might be an importance genetic basis of heterosis in rice. Exploitation of heterosis for increasing grain yield in rice was reported by Virmani *et al.*(1991).

ID was not found to be significant in most of the crosses for the studied character, because the calculated *t*-test values of ID were lower than the corresponding tabulated *t*-value 2.10 at 5% level for df 18 (Table 2). The characters of grain yield/10-hill, 1000-grain weight and number of fertile spikelet/panicle showed positive ID in F_2 generation, indicating inbreeding resulted in loss of hybrid vigor. Among the studied hybrids, 25A×37R, 29A×44R, and 31A×46R exhibited a low level of inbreeding depression for yield characters (GY/10-hill and 1000-grain weight) indicating their high level of stability as F_1 variety. The presence of hybrid breakdown in self-pollinated plant species, such as rice, has been observed by many researchers (Stebbins, 1958; Li *et al.*, 1997a; 1997b).

CONCLUSION

In conclusion, some promising lines, in both CMS and restorer, were found to be useful for developing high yielding hybrid rice varieties. The identified lines are: CMS (17A, 25A, 29A, 31A and 35A) and restorer (37R, 43R, 44R, 46R and 47R). For further increasing of grain yield in F_1 hybrid rice, different types of CMS and restoral lines can be evaluated and then exploited.

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References

Allard, R.W., 1960. Principles of Plant Breeding. John Wiley and Sons, Inc., NewYork.

Alzona, A.V., Arraudeau, M.A., 1995. Heterosis in yield components of upland rice. *Philippine J. Crop Sci.*, **17**: 13.

Fanseco, S., Peterson, F.L., 1968. Hybrid vigor in a seven parent diallel cross in common wheat (*T. aestivum* L.). *Crop Sci*, **8**:85-88.

Johnson, T.E., Hutchinson, F.W., 1993. Absence of strong heterosis for life span and other life history traits in *Caenorhabditis elegans*. *Genetics*, **134**:465-474.

Julfiquar, A.W., Tepora, N.M., 1994. Heterosis in some quantitative characters in F_1 hybrid rice (*Oryza sativa* L.). *Clsu Sci. J*, **12**:30-36.

Khaleque, M.A., Jorder, O.I., Eunus, A.M., 1977. Heterosis and combining ability in diallel cross of rice (*Oryza sativa* L). *Bangla. J. Agril. Sci*, **4**:137-145.

Li, Z.K., Pinson, S.R.M., Paterson, A.H., Park, W.D., Stansel, J.W., 1997a. Epistasis for three grain yield components in rice (*Oryza sativa* L.). *Genetics,* **145**:453-465.

Li, Z.K., Pinson, S.R.M., Paterson, A.H., Park, W.D., Stansel, J.W., 1997b. Genetics of hybrid sterility and hybrid breakdown in an inter-sub specific rice (*Oryza sativa* L.) population. *Genetics*, **145**:1139-1148.

Mather, K., Jinks, J.L., 1982. Biometrical Genetics, Ed., 3. Chapman and Hall, London, New York.

Nuruzzaman, M., Alam, M.F., Ahmed, M.G., Shohael, M.A., Biswas, M.K., Amin, M.R, Hossain, M.M., 2002. Studies on parental variability and heterosis in rice (*Oryza sativa* L.). *Pak. J. Biol. Sc.*, **5**(10):1006-1009.

Stebbins, G.L., 1958. The inviability weakness and sterility of interpecific hybrids. *Adv. Genet*, **9**:147-215.

Stuber, C.W., 1994. Heterosis in plant breeding. *Plant Breed. Rev.*, **12**:227-251.

Virmani, S.S., 1994. Heterosis and Hybrid Rice Breeding. Springer-Verlag, Berlin Heidelberg, Germany.

Virmani, S.S., 1998. Hybrid Rice Research and Development in the Tropics. *In*: Virmani, S.S., Siddiqe, E.A., Muralidharan K; editors. Advances in Hybrids Rice Technology. Proceeding of the 3rd International Symposium on Hybrid Rice, 1996, Hydarabad, Manila, Philippines, International Rice Research Institute, India, p.35-49.

Virmani, S.S., Young, J.B., Moon, H.P., Kumar, I., Finn, J.C., 1991. Increasing Rice Yields through Exploitation of Heterosis. IRRI. Los Baños, Laguna, Philippines, p.12.

Virmani, S.S., Viraktamath, B.C., Casal, C.L., Toledo, R.S., Lopez, M.T., Manalo, J.O., 1997. Hybrid Rice Breeding Manual. International Rice Research Institute, Los Banos, Laguna, Philippines, p.7.

Wright, S., 1977. Evaluation and the Genetics of Populations. University of Chicago Press, Chicago.

Yu, S.B., Li, J.X., Xu, C.G., Tan, Y.F., Gao, Y.J., Li, X.H., Qifa, Z., Saghi, M.A., 1997. Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. *Proc. Natl. Acad. Sci.*, **94**:926-931.

Zhang, Q., Gao, Y.J., Yang, S.H., Ragab, R.A., Maroof, M.A.S., Li, Z.B., 1994. A diallel analysis of heterosis in elite hybrid rice based on RFLPs and microsatellites. *Theor. Appl. Genetics*, **89**:185-192.