***Pak. J. Bot.*, 44(1): 237-246, 2012.**

GENETIC ANALYSIS AND HYBRID VIGOR STUDY OF GRAIN YIELD AND OTHER QUANTITATIVE TRAITS IN AUTOTETRAPLOID RICE

MUHAMMAD QASIM SHAHID[1,3], XU HAI-MING[2], LIN SHUN-QUAN[3], CHEN ZHI-XIONG[1], MUHAMMAD NAEEM[1], LI YA-JUAN[1] AND LIU XIANG-DONG[1*]

[1]State Key Laboratory for Conservation and Utilization of Subtropical Agro-bioresources,
South China Agricultural University, Guangzhou, Guangdong, 510642, China
[2]Department of Agronomy, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310029, China
[3]College of Horticulture, South China Agricultural University, Guangzhou 510642, P.R. China

Abstract

Genetic analysis and genotype-by-environment interaction for important traits of autotetraploid rice were evaluated by additive, dominance and additive × additive model. It was shown that genetic effects had more influence on grain yield and other quantitative traits of autotetraploid rice than genotypic environment interaction. Plant height, panicle length, seed set, grain yield, dry matter production and 1000-grain weight were mainly regulated by dominance variance. Additive and additive × additive gene action constructed the main proportion of genetic variance for heading date (flowering), number of panicles, grains per panicle, grain length, however grain width was supposed to be affected by additive × additive and dominance variance. Flag leaf length and width, fresh weight, peduncle length, unfilled grains and awn length were greatly influenced by genotypic environment interaction. Heading date produced highly negative heterosis over mid parent (H_{pm}) and better parent (H_{pb}), whereas H_{pm} and H_{pb} were detected to be highly positive and significant for grain yield, seed set, peduncle length, filled grains and 1000-grain weight in F_1 and F_2 generations. The results indicated that autotetraploid hybrids 96025 × Jackson (*indica/japonica*), 96025 × Linglun (*indica/indica*) and Linglun × Jackson (*indica/japonica*) showed highly significant hybrid vigor with improved seed set percentage and grain yield. These results suggest that intra-specific autotetraploid rice hybrids have more hybrid vigor as compared to intra-subspecific autotetraploid rice hybrids and autotetraploid rice has the potential to be used for further studies and commercial application.

Introduction

Rice, maize and wheat provide about 50% of the world calories for human beings (Khush, 2003). Rice production will need to increase by further 12% over a decade to cater the demand of rice of rapidly increasing world's population (Normile, 2008). Rice is the second major food crop of Pakistan and plays a crucial role in agriculture and gross domestic product of Pakistan (Akram *et al.,* 2007; Rashid *et al.,* 2007; Ahmad *et al.,* 2008; Rabbani *et al.,* 2010). Rice yield of conventional varieties remained 2 tons hectare^{-1} (1960) to 3.5 tons hectare^{-1} (1970), however with the advent of modern technology rice grain yield has increased up to 6 tons hectare^{-1} (Cheng *et al.,* 2007). Rice yield is stagnant over the past ten years in China (Peng *et al.,* 2009). Hybrid rice has been commercialized in China, Vietnam, India and Philippines (Wang *et al.,* 1994; Virmani and Kumar, 2004). The year of 2008 was critical for rice fed people, because during late April 2008 per pound price of rice hit 24 cents which was double within last 7 months at that time, owing to its shortage.

Phenomenon of heterosis was first described by Darwin (1876) but term heterosis was coined by Shull (1908) which refers to the over expression of F_1 individuals over mid parent (heterosis) (Shull, 1948), better parent (Heterobeltosis) and over commercial variety (useful heterosis) for any of the economically important trait. In rice, heterosis or hybrid vigour was first reported by Jones (1926). Although the cause of this excessive expression has been debated for more than 100 years, yet there is no exact certified explanation. Two pronounced explanations of last century (Allard, 1960) were dominance hypothesis (Davenport, 1908) and over-dominance hypothesis (Shull, 1908; East, 1908); however both hypotheses were based on a single locus theory. On the other hand many scientists have reported that epistasis is the genetic basis of hybrid vigor (Wright, 1968; Fasoulas and Allard, 1992; Fatokun *et al.,* 1992; Lark *et al.,* 1995; Wu *et al.,* 1995; Allard, 1996; Maughan *et al.,* 1996; Yu *et al.,* 1997). Inter-subspecific crosses such as cross between *indica* and *japonica* exhibits vigorous heterosis as compared to other cross combination (Yuan, 1992). Hybrid breeding compiled with variant ploidy level provides an opportunity to cope with current crop breeding problems (Cai *et al.,* 2001). It is reported that hybrids show 15-20% increase in the yield as compared to conventionally inbred varieties (Yuan, 1992).

Polyploidy has abundant advantages over diploid crops such as increased greenness, lushness and biomass yield (Bingham *et al.,* 1994). Autotetraploid rice and autotetraploid cabbage had higher genetic variation than their diploid counterparts (Liu *et al.,* 1997; Luan *et al.,* 2008). Polyploid plants exhibit some new phenotypic changes such as resistance to insect pests and diseases, heading date, increase in biomass production and drought tolerance (Wendell, 2000; Luan *et al.,* 2008). Autotetraploid rice has limitations due to its low seed setting rate and reduction in some other agronomic traits (Xiao *et al.,* 1996; Li and Xu, 2000; Guo *et al.,* 2002; He *et al.,* 2011). Chen *et al.,* (1987) and Song & Zhang (1992) reported the merits and demerits of autotetraploid rice. Their results revealed that increase in 1000-grain weight, better nutrition quality, reduction in plant height and thicker culm, but low seed setting rate, less number of panicle and grains per panicle are the worst characteristics as compared to the advantages of autotetraploid rice. Interestingly, autotetraploid hybrids have higher embryo sac fertility as compared to their diploid hybrids (Hu *et al.,* 2009), but autotetraploid parents have lower embryo sac fertility than diploid parents (Shahid *et al.,* 2010).

---

[*]Corresponding author: Liu Xiang-Dong, Tel.: +86 20 85285752, E-mail address: xdliu@scau.edu.cn

In the present study, statistical approach based on mixed linear model was used which can predict the epistatic effects more efficiently. Additive, dominance, additive × additive (ADAA) model can estimate genetic variance components, heterosis, heritability, genetic effects and their interaction with environment (Xu & Zhu, 1999). It can handle both balanced and unbalanced data. Plant material having best heterotic performance should have dominance type of gene action and are very much feasible for hybrid breeding. This study has the following objectives, (a) to perform the quantitative genetic analysis and to determine the genotype-by-environment interaction among various important traits of autotetraploid rice (b) to determine the heterosis level in autotetraploid rice hybrids and find out suitable autotetraploid hybrids with higher level of heterosis and grain yield.

Materials and Methods

Plant materials and cultivation of rice plants: The experiments were carried out at the farm of South China Agricultural University (SCAU), Guangzhou (23°16N, 113°8E). Eighteen parents were crossed in a half diallel design during March 2005 and 2006, and planted under the field conditions (data not shown). Seed setting rate (percent filled grains) of parents and hybrids was observed during both years, and 5 parents were selected for further investigations (Table 1). These lines were selected because of their varying seed set and contrasting quantitative traits. Four parents were crossed in a complete diallel way (6 hybrids), and 1 hybrid (Jackson × E24) with low seed set percentage was used. All the autotetraploid lines used in this study are genetically stable because they are being investigated in this lab from last 12 years. Five parents, their F_{1s} and F_{2s} were planted under the natural conditions in two different seasons, first planted during 1st March 2007 (early season) and second planted on 25th July, 2007 (late season). Guanglu'ai 4 (diploid cultivar) was used as control during both seasons.

Table 1. Autotetraploid rice lines and diploid cultivar used in the study during early season 2007 and late season 2007.

Code	Name	Ploidy	Source	Subspecies
1	96025	4×	ICS-CAA[a]	*indica*
2	Jackson	4×	SCBG- CAS[b]	*japonica*
3	Linglun	4×	Lab[c]	*indica*
4	L202	4×	SCBG- CAS	*japonica*
5	E24	4×	Lab	*japonica*
CK	Guanglu'ai 4	2×	Guangdong, China	*indica*

[a] Institute of Crop Science, Chinese Academy of Agriculture; CAS: Chinese Academy of sciences

[b] South China Botanical Garden, Chinese Academy of sciences

[c] State Key Laboratory for Conservation and Utilization of Subtropical Agro-bioresources, South China Agricultural University, Guangzhou, Guangdong, China

A Randomized Complete Block Design (RCBD) with three replications was used in each season. R × R and P × P distances were kept as 20 and 16.6 cm, respectively. Each plot was 4 m wide and 3.5 m long. Seedlings at four-five leaf stage were planted in the field. Insects, diseases and weeds were controlled as to avoid the yield loss. All other cultural practices were kept according to the recommendation of the area. Thirty plants of each genotype were randomly selected from each replication at maturity and data was recorded for the following traits: Heading date (HD), days to taken for 50% flowering on the whole plot basis, plant height (PH, cm) was measured from ground to top of the panicle. Peduncle length (PD), panicle length (PL), flag leaf length (FL), flag leaf width (FW) and awn length (AL) were measured in centimeters. Number of panicles per plant (NP), number of grains per panicle (GP), filled grains (FG) and unfilled grains per plant (UG) were counted manually. Fresh weight (FWT), dry matter per plant (DM), 1000-grain weight (GWT) and grain yield tons per hectare were measured in grams. For grain yield and dry matter production plants were oven dried at to achieve the constant weight. Grain length (GL) and grain width (GW) of ten randomly selected grains were measured by vernier caliper, and seed set (SS%= filled grains/total number of grains per plant x100) was counted as percentage.

Statistical analysis: Analysis of variance was done by using SAS (Anon., 2006) to check the significance of genotype and genotype by environment interaction effects of the traits. Additive, dominance and additive × additive (ADAA) model (Zhu & Weir, 1996) was used to analyze the data through mixed linear model approaches to estimate each genetic variance components and heritability. Adjusted unbiased prediction (AUP) method (Zhu & Weir, 1996) was used to predict the genetic effects and genotype × environment interaction effects. The jackknife resampling method (Miller, 1974) was applied for testing the significance of each genetic variances and effects (Xu & Zhu, 1999). All these analysis were performed by the QGAStation 1.0 (Chen & Zhu, 2003).

Results

All traits of the individual hybrid were compared with their parents in both seasons (data not shown). A significant difference ($p<0.01$) was found among most of the traits under study in the individual hybrids with their respective parents.

Analysis of variance and heritabilities: Results of variance and heritabilities are explained in Table 2. Ratio of additive variance to phenotypic variance (V_A/V_P) was very highly significant ($p<0.01$) in PL, FG, grain yield, AL, GL and SS, while it was highly significant ($p<0.05$) in DM and GW. In FL and FW significant difference ($p<0.1$) was observed. It meant that there are significant additive effects for these traits. In the remaining traits i.e., HD, PH, FWT, NP, GP, UG, and GWT the V_A/V_P was undetectable and non significant.

Ratio of dominance variance to phenotypic variance (V_D/V_P) was very highly significant ($p<0.01$) in PH, PL, DM, FG, UG, GWT, grain yield and SS while AL was highly significant ($p<0.05$). In PD and FL significant difference ($p<0.1$) was observed. It showed that these traits had significant dominance effects. The V_D/V_P was undetectable and non significant in the remaining traits.

Table 2. Proportion of variance components and heritability of grain yield and other quantitative traits in autotetraploid hybrids.

Parameters	HD	PH	PD	PL	FL	FW	FWT	DM	NP	GP	FG	UG	GWT	Yield	AL	GL	GW	SS
V_A/V_p	0.000	0.000	0.023	0.261^{**}	0.059^{+}	0.136^{+}	0.000	0.144^{*}	0.000	0.000	0.241^{**}	0.000	0.000	0.187^{**}	0.198^{**}	0.385^{**}	0.248^{*}	0.230^{**}
V_D/V_p	0.263	0.713^{**}	0.146^{+}	0.500^{**}	0.223^{+}	0.001	0.000	0.410^{**}	0.000	0.000	0.585^{**}	0.421^{**}	0.741^{**}	0.649^{**}	0.045^{*}	0.000	0.000	0.606^{**}
V_{AA}/V_p	0.599^{**}	0.000	0.253^{*}	0.000	0.000	0.132^{**}	0.256^{*}	0.000	0.470^{**}	0.612^{**}	0.000	0.029	0.000	0.000	0.000	0.542^{**}	0.615^{**}	0.000
V_{AE}/V_p	0.024^{*}	0.050	0.000	0.081	0.000	0.238^{**}	0.187^{**}	0.184^{*}	0.182^{*}	0.072	0.000	0.002	0.020	0.000	0.242^{**}	0.000	0.031^{+}	0.000
V_{DE}/V_p	0.110^{**}	0.130^{+}	0.138^{*}	0.004	0.000	0.348^{**}	0.299^{*}	0.106^{+}	0.266^{**}	0.207^{**}	0.069^{*}	0.483^{**}	0.216^{**}	0.130^{**}	0.473^{**}	0.030^{+}	0.074^{*}	0.000
V_{AAE}/V_p	0.000	0.000	0.236^{**}	0.022	0.383^{**}	0.000	0.000	0.000	0.000	0.000	0.073^{*}	0.000	0.000	0.011	0.000	0.009	0.000	0.151^{**}
V_R/V_p	0.005^{*}	0.107^{**}	0.205^{**}	0.132^{**}	0.335^{**}	0.146^{+}	0.258^{*}	0.157^{**}	0.083^{**}	0.109^{+}	0.032^{**}	0.065^{**}	0.024^{**}	0.023^{**}	0.041^{*}	0.035^{*}	0.033^{**}	0.014^{*}
h^2_G	0.599^{**}	0.112	0.276^{**}	0.262^{**}	0.059^{+}	0.268^{**}	0.223^{*}	0.144^{*}	0.470^{**}	0.612^{**}	0.241^{**}	0.029	0.214^{*}	0.187^{**}	0.198^{**}	0.895^{**}	0.863^{**}	0.230^{**}
H^2_G	0.862^{**}	0.713^{**}	0.422^{**}	0.761^{**}	0.281^{*}	0.269^{**}	0.256^{*}	0.553^{**}	0.527^{**}	0.658^{**}	0.826^{**}	0.450^{**}	0.741^{**}	0.835^{**}	0.244^{**}	0.927^{**}	0.881^{**}	0.836^{**}
h^2_{GE}	0.024^{*}	0.050	0.236^{**}	0.103	0.383^{**}	0.238^{**}	0.187^{**}	0.184^{*}	0.182^{*}	0.072	0.073^{*}	0.002	0.020	0.011	0.242^{**}	0.009	0.031^{+}	0.151^{**}
H^2_{GE}	0.134^{**}	0.181^{*}	0.374^{**}	0.107	0.383^{**}	0.585^{**}	0.486^{**}	0.291^{*}	0.447^{**}	0.279^{*}	0.142^{**}	0.486^{**}	0.235^{**}	0.142^{**}	0.715^{**}	0.038^{*}	0.104^{*}	0.151^{**}

$^{+}$, *, ** Significantly different from zero at $p<0.1$, $p<0.05$ and $p<0.01$, respectively.

V_A/V_p, V_D/V_p, and V_{AA}/V_p are ratios of additive variance, dominance variance, and additive × additive variance to phenotypic variance, respectively; V_{AE}/V_p, V_{DE}/V_p, and V_{AAE}/V_p are ratios of interaction variances of additive, dominance, additive × additive with environment to phenotypic variance; V_R/V_p is ratio of residual variance to phenotypic variance; h^2_G and H^2_G are general heritabilities in narrow and broad sense, respectively; h^2_{GE} and H^2_{GE} are interaction heritabilities in narrow and broad sense, respectively.

HD = Heading Date, PH= Plant Height, PD= Peduncle Length, PL= Panicle Length, FL= Flag Leaf Length, FW= Flag Leaf Width, FWT= Fresh Weight, DM= Dry Matter production, NP= Number of Panicles per plant, GP= Number of Grains per Panicle, FG= Filled Grains per plant, UG= Unfilled Grains per plant, GWT= 1000-Grain Weight, Yield= Grain Yield, AL= Awn Length, GL= Grain Length, GW= Grain Width, and SS= Seed Set.

Ratio of additive × additive variance to phenotypic variance (V_{AA}/V_P) was very highly significant ($p<0.01$) in HD, FW, NP, GP, GL and GW, while PD and FWT were just highly significant ($p<0.05$). It showed the presence of significant additive-by-additive epistasis in these traits. In contrast to this V_{AA}/V_P in the other remaining traits was undetectable.

In additive × environment interaction variance to phenotypic variance ratio (V_{AE}/V_P) FW, FWT and AL were very highly significant ($p<0.01$), on the other hand highly significant difference ($p<0.05$) was found in HD, DM and NP, but for the remaining traits it showed non significant differences.

In dominance × environment interaction variance (V_{DE}/V_P) was very highly significant ($p<0.01$) in HD, FW, NP, GP, UG, GWT, grain yield and AL, while PD, FWT, FG and GW was only highly significant ($p<0.05$). In PH, DM and GL significant difference ($p<0.1$) was observed. The V_{DE}/V_P was undetectable and non significant in the remaining traits.

In additive × additive × environment interaction variance to phenotypic ratio (V_{AAE}/V_P) was very highly significant ($p<0.01$) in PD, FL and SS, while FG was only highly significant ($p<0.05$). The V_{AAE}/V_P was non significant in the remaining traits.

General heritability in narrow sense (h^2_G) was non significant in PH and UG whereas in FL was significant ($p<0.05$). FWT, DM and GWT were highly significant ($p<0.05$), while in all other remaining traits h^2_G was very highly significant ($p<0.01$). Similar response was observed for general heritability in broad sense (H^2_G), but PH and UG were also very highly significant ($p<0.01$) as in case of H^2_G. It showed that the latter two traits were mainly influenced by dominance effects, while other traits controlled by both additive and dominance effects.

The interaction heritability in narrow sense (h^2_{GE}) was very highly significant ($p<0.01$) in PD, FL, FW, FWT, AL and SS, while it was highly significant ($p<0.05$) in HD, DM, NP, and FG. In the remaining traits the h^2_{GE} was non significant. Interaction heritability in broad sense (H^2_{GE}) was non significant in PL and highly significant ($p<0.05$) in PH, DM, GP, GL and GW were observed. Remaining traits were very highly significant ($p<0.01$). The general heritability (h^2_G, H^2_G) was higher as compared to interaction heritability (h^2_{GE}, H^2_{GE}) in all traits except FL, FW, FWT, UG and AL.

In summary, the characteristic traits i.e., PH, PL, DM, FG, UG, GWT, grain yield and SS were predominantly affected by the dominance variance, reaching a percentages of 71.3, 50.0, 41.0, 58.5, 42.1, 74.1, 64.9, 60.6 and 46.8%, respectively, of the total variances. Additive × additive variance (V_{AA}) was the main constitute in the genetic variation of HD, PD, NP, GL and GW, exhibiting 59.9%, 25.3%, 47.0%, 54.2% and 61.5% of the total phenotypic variance. FW, FWT and AL were predominantly affected by the dominance × environment interaction variance (V_{DE}), i.e., 34.8%, 29.9% and 47.3%, respectively, while FL was mainly controlled by additive × additive × environment interaction variance (V_{AAE}) i.e., showed 38.3% of the total variance.

Predicted genotypic values and heterosis: The total heterosis of hybrids can be divided into general heterosis (genetic main effect) and interaction heterosis (genotype × environment interaction effect). The general heterosis and the genotypic values declined in the F_2 generation as compared to F_1 (Table 3). Genotypic values of some traits in F_1 and F_2 were found significantly different from the population mean except FL, FWT, and NP. However, all the traits performed different heterotic behavior in different generations.

The lesser the number of days for heading the more desirable it will be. In the present study number of days for heading was less in F_1 than F_2 generations. Negative mean of mid parent heterosis (H_{pm}) and mean of better parent heterosis (H_{pb}) based on population mean were highly significant in both F_1 and F_2 generations, indicating early flowering in autotetraploid hybrids as compared to the parents. For PH, the mean of predicted genotypic values and the H_{pm} were highly significant in F_1, and non significant in F_2. H_{pb} in both generations (F_1 and F_2) was non-significant. Predicted genotypic and the H_{pm} of PD and PL were highly significant in F_1 and F_2 generations, while H_{pb} was highly significant in F_1.

Genotypic values for F_1 and F_2 was non-significant in case of FL and also for predicted F_1 heterosis in case of FW, while significant predicted F_2 heterosis was observed in case of FW. H_{pm} in F_1 and F_2 was significant and non-significant in case of FL and FW, respectively. H_{pb} in F_1 and F_2 was highly significant for FW but non-significant for FL.

The heterosis H_{pm} of FWT was highly significant in both generations, while it was non-significant for H_{pb} and predicted genotypic values. Highly significant results were observed in case of predicted heterosis in F_1, H_{pm} in both generations and H_{pb} in only F_1 generation, while predicted heterosis and H_{pb} in F_2 were found to be non-significant for total dry matter production. H_{pb} (negative) was very highly significant in F_1 and F_2, H_{pm} was significant in F_1 and F_2 while predicted heterosis was non-significant in F_1 and F_2 in case of NP. Predicted heterosis in F_1 and F_2 was highly significant for grains per panicle, while positive H_{pm} and negative H_{pb} were significant in both generations. Predicted heterosis and H_{pm} in both generations and H_{pb} in F_1 were very highly significant for FG, while H_{pb} in F_2 was highly significant.

Highly significant H_{pb} in F_1 and F_2 and significant predicted F_1 genotypic value along with H_{pm} in F_1 and F_2 were found for UG, while genotypic value in F_2 was found to be non-significant. All types of studied heterosis were very highly significant and positive for 1000-grain weight except predicted F_2 genotypic value which was found to be non-significant. Very highly significant and positive heterosis was observed for all types of studied heterosis in case of yield and seed setting percentage. Longer awn length is desirable in rice crop, because it prevents from birds damage and it was very highly significant (negative) in H_{pb} (F_1) while significant in case of Pre (F_1), H_{pm} (F_1 and F_2) and negative H_{pb} (F_2). Pre (F_2) for awn length was found to be non-significant. Negative and non-significant H_{pm} (F_1 and F_2) were observed for grain length, while very highly significant negative H_{pb} and genotypic values were observed in both generations. GW showed very highly positive significant predicted heterosis and H_{pm}, while H_{pb} was very highly significant and negative in both generations. Heterosis in F_2 generation was declined for all the traits except UG and HD.

Table 3. Predicted genotypic values and general heterosis of grain yield and other quantitative traits in autotetraploid rice.

	HD	PH	PD	PL	FL	FW	FWT	DM	NP
Pre(F_1)	77.77(1.044)**	107.800(1.56)**	1.05(0.660)**	31.36(0.350)**	34.26(0.790)	2.008(0.040)	28.62(0.640)	11.43(1.020)**	6.077(0.044)
Pre(F_2)	82.72(1.048)	98.700(1.4)	0.81(0.150)**	28.78(0.120)**	32.22(0.290)	2.04(0.010)*	27.65(0.542)	10.02(0.520)	5.900(0.040)
H_{pm}(F_1)	−0.233(0.005)**	0.138(0.035)**	0.325(0.059)**	0.229(0.022)**	0.098(0.044)$^{+}$	0.033(0.027)	0.147(0.036)**	0.289(0.038)**	0.120(0.020)*
H_{pm}(F_2)	−0.187(0.005)**	0.046(0.039)	0.199(0.030)**	0.088(0.010)**	0.049(0.022)$^{+}$	0.031(0.017)	0.101(0.030)**	0.143(0.019)**	0.095(0.008)*
H_{pb}(F_1)	−0.311(0.007)**	0.078(0.049)	0.087(0.068)**	0.109(0.021)**	0.026(0.053)	−0.08(0.019)**	0.036(0.024)	0.192(0.033)**	−0.247(0.019)**
H_{pb}(F_2)	−0.262(0.007)**	−0.015(0.054)	0.078(0.037)*	0.004(0.013)	−0.06(0.034)	−0.08(0.014)**	0.009(0.017)	0.016(0.017)	−0.325(0.016)**

	GP	FG	UG	GWT	Yield	AL	GL	GW	SS
Pre(F_1)	130.4(0.300)**	478.3(5.640)**	315.4(10.830)$^{+}$	37.1(0.034)**	5.44(0.200)**	1.52(0.029)*	10.03(0.012)**	3.27(0.006)**	59.75(0.710)**
Pre(F_2)	115.9(0.241)**	337.7(5.630)**	335.7(3.280)	34.40(0.030)	3.63(0.210)**	1.35(0.032)	10.00(0.014)**	3.22(0.005)**	43.37(0.350)**
H_{pm}(F_1)	0.089(0.035)*	0.87(0.031)**	-0.303(0.061)$^{+}$	0.156(0.003)**	1.03(0.033)**	0.17(0.041)*	-0.006(0.006)	0.046(0.005)**	0.67(0.025)**
H_{pm}(F_2)	0.081(0.030)*	0.43(0.016)**	-0.162(0.046)$^{+}$	0.077(0.002)**	0.52(0.016)**	0.08(0.021)*	-0.068(0.005)	0.044(0.004)**	0.29(0.013)**
H_{pb}(F_1)	−0.22(0.055)*	0.64(0.064)**	-0.442(0.069)*	0.138(0.003)**	0.79(0.063)**	−0.22(0.031)**	−0.16(0.012)**	−0.196(0.001)**	0.39(0.033)**
H_{pb}(F_2)	−0.26(0.055)*	0.19(0.051)*	-0.276(0.063)*	0.057(0.002)**	0.30(0.050)	−0.3(0.021)*	−0.21(0.012)**	−0.124(0.008)**	0.1(0.021)**

$^{+,*,**}$ Significantly different from zero at $p<0.1$, $p<0.05$ and $p<0.01$, respectively.

The numbers in parentheses are standard errors for parameters.

Pre (F_1) and Pre (F_2) indicate the mean of predicted genotypic values of F_1 and F_2, respectively, H_{pm}: the mean of general heterosis over mid parent based on population mean and H_{pb}: the mean of general heterosis over better parent based on population mean for all crosses.

See foot note of Table 2 for traits abbreviations.

Genotypic-environment interaction heterosis: Genotype × environment interaction heterosis was found to be different among different traits of autotetraploid hybrids during two seasons (Table 4). HD showed almost similar significant negative heterosis behavior in both seasons. In case of PH, results of late season were highly significant for all type of heterosis studied, while in the early season most of the heterosis were non-significant. Almost all type of predicted interaction heterosis studied for PD was highly significant in late season while non-significant in early season. In case of PL, H_{pm} and H_{pb} for F_1 and F_2 were highly significant during late season, while non-significant in early season. A conflicting behavior in two seasons for FL and FW was observed i.e., heterosis in late season was negative and highly significant as compared to non-significant in early season. Rest of the traits FWT, DM, NP, GP, FG, UG, GWT, grain yield, GW and SS did not show remarkable influence of environment. However, traits like AL and GL were seemed to be influenced by different seasons, owing to negative predicted genotypic values (F_1), H_{pm} (F_1 and F_2), H_{pb} (F_1 and F_2) heterosis incase of late season and positive in early season for AL. H_{pm} (F_1 and F_2) and H_{pb} (F_1 and F_2) heterosis was negative in early season but positive in late season in case of GL.

F_1's heterosis and genotypic values of each cross: It is important to know the extent of heterosis in each specific cross of autotetraploid rice. Heterosis and predicted genotypic values of all crosses in F_1 generation are shown in the Table 5. The predicted genotypic values were significantly different from population mean in all crosses for most of the traits except FL, FW, FWT, NP and GP. Highly positive significant genotypic and heterosis values for grain yield over mid and better parent were found in all crosses except 2×5. For PH, all crosses except 1×4 cross showed significant positive heterosis over mid parent, while over better parent two crosses (1×2 and 1×3) showed significant positive heterosis. Six (except 2×4) and four (except 1×4, 2×4 and 2×5) crosses showed significant heterosis for PL over mid and better parents, respectively. Highly significant heterosis was found for PD, FG, UG, GWT, GL, GW, SS and grain yield over both mid and better parents, which indicate the powerful heterosis in autotetraploid hybrids. For HD all the crosses showed highly significant but negative heterosis over both H_{pm} and H_{pb}. The predicted genotypic values of grain yield produced by crosses 1×2, 1×3 and 1×4 were 8.02 tons ha^{-1}, 7.85 tons ha^{-1} and 6.18 tons ha^{-1}, respectively, in F_1 generation. The grain yield of control cultivar was 7.71 tons ha^{-1}. Almost all of the hybrids showed high genotypic values and general heterosis, however among them cross combinations 1×2 (*indica/japonica*) and 1×3 (*indica/indica*) were best performers followed by 1×4, 3×2, 3×4 and 2×4, while 2×5 showed significant reduction in grain yield and seed set. Autotetraploid hybrids exhibited better performance than the control diploid cultivar for most of the traits under study except FWT, DM, NP, FG and SS.

Discussion

Analysis of data following ADAA model represents that plant material studied here exhibited dominance type of gene action for ten important agronomic traits, while remaining were influenced by additive type of gene action.

Heritability analysis proves to be vital in improvement of quantitative traits and magnitude of heritability determined the degree of improvement in traits (Qi *et al.,* 2008). High numerical values of narrow sense heritability represent the additive type of gene action. The traits having low heritability could not be improved by selecting in early generations, where as traits having high heritability indicates direct response to selection even in early segregating generations during conventional pure line breeding. The general heritabilities in broad sense and narrow were found very highly significant in most of the traits indicating that these traits could be improved easily except FL, FW, FWT, AL and UG in which GE interaction constituted the major part of inheritance. Greater interaction heritability indicated larger difference in heritability of these traits during different environments; therefore, different selection strategies should be employed to bring the desirable changes. In this study, high heritability was found for yield in autotetraploid rice and this finding was consistent with previous reports in diploid rice (Mahto *et al.,* 2003; Swati & Ramesh, 2004; Hosseini *et al.,* 2005).

Dominance effects were more pronounced on PH, PL, DM, GWT, grain yield and SS. The traits having stronger dominance effects are not useful for direct selection but having trends to produce stronger heterosis, and selection of these traits in later generations would be useful to achieve the genetic improvement in these traits. Dominance variance constituted a large proportion of the total variance for grain yield and its associated traits in wheat (Inamullah *et al.,* 2006; Iqbal *et al.,* 2007), rice (Verma & Srivastava, 2004) and maize (Wardyn *et al.,* 2007).

Epistasis plays an important role in genetic variation of populations and phenotypic expressions of genes, and it has significant effect on quantitative traits (Fasoulas & Allard, 1962; Li *et al.,* 1997; Liu *et al.,* 2003). Population genetic analysis has also demonstrated that epistatic effect have its function in the maintenance and assembling of favorable multilocus genotypes which ultimately led to better adaptedness of various plant species (Carson *et al.,* 1984; Allard, 1996). HD, NP, GP, FG, GL and GW were mostly influenced by additive × additive type of gene action. These genetic components can be easily controlled and the selection of these traits in advanced generations would be more effective to bring the suitable changes in these important traits of autotetraploid rice. Epistatic effects had strong influence on flowering and growth duration of spring wheat and soybean (Nanda *et al.,* 1981; Sheikh *et al.,* 2000, Martin *et al.,* 2009).

Table 4. Predicted genotype × environment values and interaction heterosis for grain yield and other quantitative traits under two environments.

Parameters	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
	HD		**FG**		**FW**		**GL**		**PH**		**UG**	
Pre(F_1)	−3.198	−2.499	10.15^{+}	66.42	0.155	−0.007	0.040	0.078	4.452	5.647^{**}	40.60	69.06
Pre(F_2)	−0.474	−0.577	7.769	2.338	0.017	0.017	0.021	0.015	1.595	0.965	0.488	0.326
$H_{pm}(F_1)$	-0.065^{+}	-0.046^{*}	0.130^{*}	0.811^{*}	0.110	−0.018	−0.020	0.018	0.035	0.068^{**}	0.240	0.414^{+}
$H_{pm}(F_2)$	-0.032^{+}	-0.023^{*}	0.022	0.595^{*}	0.042	−0.006	−0.019	0.012	0.006	0.021^{**}	0.120	0.206^{+}
$H_{pb}(F_1)$	-0.088^{*}	-0.060^{**}	0.169	0.58^{+}	0.063	-0.114^{*}	-0.034^{*}	0.001	0.007	0.041^{*}	0.083	0.513^{*}
$H_{pb}(F_2)$	-0.056^{**}	-0.037^{*}	−0.177	0.365	−0.006	-0.102^{**}	-0.038^{**}	−.006	-0.035^{**}	−0.006	−0.037	0.307^{*}
	FWT		**GW**		**PD**		**GWT**		**DM**		**SS**	
Pre(F_1)	5.867	13.451^{*}	0.026	−0.025	−0.411	2.202^{+}	0.521^{*}	1.877^{+}	0.607	3.754	1.426	0.437
Pre(F_2)	1.006	0.667	−0.024	−0.030	0.144	0.214	0.129	0.142	0.510	−0.008	1.341	0.411
$H_{pm}(F_1)$	0.046	0.112^{*}	0.03	0.003	-0.132^{+}	0.428^{**}	0.123^{*}	0.101^{*}	0.006	0.229^{+}	0.014	0.388^{*}
$H_{pm}(F_2)$	0.004	-0.021^{*}	0.015	0.002	-0.100^{+}	0.312^{**}	0.011	0.050^{*}	0.003	0.115^{+}	0.001	0.361^{*}
$H_{pb}(F_1)$	-0.080^{*}	0.088^{*}	−0.015	-0.045^{**}	-0.213^{*}	0.317^{**}	0.003	0.068^{+}	-0.139^{*}	0.104	−0.198	0.179
$H_{pb}(F_2)$	-0.090^{+}	-0.045^{**}	−0.030	-0.047^{**}	-0.181^{**}	0.200^{**}	−0.009	0.017	−0.142	−0.01	−0.214	0.157
	PL		**Yield**		**NP**		**FL**		**AL**		**GP**	
Pre(F_1)	0.213	0.593	0.267^{+}	3.480^{*}	0.593^{+}	0.331	0.308	−0.745	0.783	−0.561	4.790	7.810
Pre(F_2)	0.202	0.627	0.155	1.097	0.093	0.145	0.281	−0.781	0.156	−0.179	2.780	4.348
$H_{pm}(F_1)$	0.020	0.035^{**}	0.056^{*}	0.878^{*}	0.164^{+}	0.161^{*}	0.188^{*}	−0.072	0.925^{+}	−0.564	0.037	0.051
$H_{pm}(F_2)$	0.018	0.036^{*}	0.025	0.559^{*}	0.082	0.031	0.172^{*}	−0.085	0.462^{+}	−0.282	0.018	0.018
$H_{pb}(F_1)$	−0.032	-0.093^{*}	−0.076	0.713^{+}	0.117	-0.311^{*}	0.057	-0.248^{*}	0.585	-0.836^{*}	−0.039	−0.121
$H_{pb}(F_2)$	−0.035	-0.088^{*}	−0.087	0.391^{+}	0.036	-0.38^{**}	0.051	-0.262^{*}	0.123	-0.554^{*}	−0.058	-0.154^{*}

$^{+,*,**}$ Significantly different from zero at $p<0.1$, $p<0.05$ and $p<0.01$, respectively

Pre (F_1) and Pre (F_2) indicate the mean of predicted genotypic values of F_1 and F_2 in specific environment, respectively, H_{pm}: the mean of general heterosis over mid parent and H_{pb}: the mean of general heterosis over better parent based on population mean for all crosses

E_1, E_2 stand for the two environments viz. Early season 2007 and Late season 2007, respectively

See foot note of Table 2 for traits abbreviations

Table 5. Genotypic values and heterosis of seven autotetraploid hybrids and one diploid cultivar (CK) for grain yield and other quantitative traits in the F$_1$ generation.

Traits	Parameters	1×2	1×3	1×4	2×4	2×5	3×2	3×4	Control
HD (Days)	Pre(F$_1$)	74.12**	82.01	79.63	71.38**	74.55**	84.85**	77.89**	86
	H_{pm}(F$_1$)	−0.225**	−0.044**	−0.216**	−0.353**	−0.420**	−0.141**	−0.232**	
	H_{pb}(F$_1$)	−0.421**	−0.166**	−0.293**	−0.392**	−0.424**	−0.242**	−0.237**	
PH (cm)	Pre(F$_1$)	108.07	110.79*	106.93	105.6*	103.47	111.4**	108.5*	95.8
	H_{pm}(F$_1$)	0.209**	0.14	0.128	0.053*	0.142**	0.198*	0.094*	
	H_{pb}(F$_1$)	0.143	0.110	0.051	0.035	0.035	0.087	0.088	
PD (cm)	Pre(F$_1$)	2.52**	1.31**	1.06*	0.71**	0.32**	0.86**	0.58*	1.02
	H_{pm}(F$_1$)	0.339**	0.416**	0.312**	0.259*	0.044**	0.16**	0.464**	
	H_{pb}(F$_1$)	0.321**	0.077*	0.069*	0.127	0.047**	0.075*	0.142*	
PL (cm)	Pre(F$_1$)	32.57**	36.64**	32.12**	24.09	28.32	31.28	34.50**	23.9
	H_{pm}(F$_1$)	0.251**	0.324**	0.262**	−0.055	0.151**	0.181*	0.206*	
	H_{pb}(F$_1$)	0.197**	0.196*	0.134	−0.08	0.044	0.150*	0.119*	
FL (cm)	Pre(F$_1$)	36.83	43.12	37.63	26.57	30.36	30.52	34.78	29.1
	H_{pm}(F$_1$)	0.296**	0.404*	0.102*	−0.091	-0.065	-0.012	0.058	
	H_{pb}(F$_1$)	0.239*	0.260	0.074	-0.138	−0.163*	-0.067	-0.024	
FW (cm)	Pre(F$_1$)	1.996	2.205	2.273**	1.960	1.882	1.969	2.098	1.9
	H_{pm}(F$_1$)	0.017	0.044	0.048	0.033	0.045*	0.007	0.039	
	H_{pb}(F$_1$)	−0.041	−0.092	−0.057	−0.087*	−0.098**	−0.054	−0.145**	
FWT (Tons/ha)	Pre(F$_1$)	29.73	31.71*	28.59	25.70	27.74	28.98	27.86	30.7
	H_{pm}(F$_1$)	0.183*	0.171*	0.151*	0.143*	0.105*	0.070*	0.205*	
	H_{pb}(F$_1$)	0.099	0.167*	0.047*	−0.008	0.013	−0.101	0.041	
DM (Tons/ha)	Pre(F$_1$)	13.54*	16.46*	11.38*	8.94	9.17	8.53*	11.95**	14.7
	H_{pm}(F$_1$)	0.472**	0.616**	0.308**	0.171	0.128	0.002	0.329**	
	H_{pb}(F$_1$)	0.331**	0.505**	0.197**	0.137	0.086	−0.061	0.147	
NP	Pre(F$_1$)	6.526	6.205	6.101	4.826	6.162	7.090	5.628	9.1
	H_{pm}(F$_1$)	−0.073*	−0.144	0.157	0.093	0.304**	0.282**	0.224**	
	H_{pb}(F$_1$)	−0.714**	−0.766**	−0.166**	−0.067	0.010	−0.095	0.064	
GP	Pre(F$_1$)	120.69**	140.4**	144.3**	119.8	117.7	133.8*	135.9**	133
	H_{pm}(F$_1$)	0.077	0.038	0.048	−0.030	0.303**	0.334**	0.147	
	H_{pb}(F$_1$)	−0.148	−0.458**	−0.258**	−0.106	−0.072	0.010	−0.465**	
FG	Pre(F$_1$)	686.4**	673.8**	558.6**	403.1**	14.54**	540.9**	470.6**	1074
	H_{pm}(F$_1$)	1.316**	1.506**	0.853**	0.664**	−0.259*	0.991**	0.994**	
	H_{pb}(F$_1$)	1.163**	1.151**	0.704*	0.546**	−0.720**	0.914**	0.753**	
UG	Pre(F$_1$)	101.2**	197.2**	321.8	175.1**	710.9**	407.6**	294.1	138.2
	H_{pm}(F$_1$)	−0.914**	−1.139**	−0.766**	−0.637**	1.468**	0.502**	−0.635*	
	H_{pb}(F$_1$)	−1.401**	−1.166**	−0.793**	−0.751**	1.400**	0.491**	−0.876**	
GWT (g)	Pre(F$_1$)	38.951**	38.809**	36.849	36.642**	32.660*	37.740**	38.093**	23.7
	H_{pm}(F$_1$)	0.215**	0.230**	0.175**	0.125**	−0.013	0.171**	0.195**	
	H_{pb}(F$_1$)	0.209**	0.229**	0.144**	0.114**	−0.065*	0.155**	0.179**	
Yield (Tons/ha)	Pre(F$_1$)	8.02**	7.85**	6.18**	4.43**	0.142**	6.12**	5.38**	7.71
	H_{pm}(F$_1$)	1.541**	1.777**	0.988**	0.769**	−0.191*	1.119**	1.214**	
	H_{pb}(F$_1$)	1.351**	1.467**	0.579**	0.624**	−0.577**	1.059**	1.017**	
AL (cm)	Pre(F$_1$)	2.562**	2.207**	1.901**	1.401	1.145*	1.010**	0.415**	0.25
	H_{pm}(F$_1$)	0.573**	0.451*	0.216*	−0.012	0.150*	0.097	−0.234*	
	H_{pb}(F$_1$)	−0.162	−0.425*	−0.235**	−0.199	0.037	0.031	−0.563**	
GL (cm)	Pre(F$_1$)	10.885**	9.335**	9.925**	10.524**	9.156**	9.659	10.71**	7.61
	H_{pm}(F$_1$)	0.012*	0.014	0.007	−0.006	−0.033*	−0.043**	0.007	
	H_{pb}(F$_1$)	−0.029**	−0.106**	−0.045**	−0.281**	−0.207**	−0.155**	−0.262**	
GW (cm)	Pre(F$_1$)	3.027**	4.087**	3.324**	2.847**	3.142**	3.194**	3.255*	3.12
	H_{pm}(F$_1$)	0.071**	0.022	0.040	0.053	0.008	0.110**	0.015	
	H_{pb}(F$_1$)	−0.130**	−0.140**	−0.131**	−0.188**	−0.293**	−0.103**	−0.386**	
SS (%)	Pre(F$_1$)	87.15**	77.36**	63.45**	69.72**	2.004**	57.03**	61.54**	88.3
	H_{pm}(F$_1$)	1.070**	1.215**	1.230**	0.751**	−0.605**	0.239**	0.820**	
	H_{pb}(F$_1$)	1.063**	0.916**	0.308**	0.743**	−0.979**	0.154**	0.518**	

*,** Significantly different from zero at p<0.05 and p<0.01, respectively

Pre (F$_1$) indicates the predicted genotypic values of F$_1$, H_{pm}: General heterosis over mid parent and H_{pb}: General heterosis over better parent based on population mean for each cross

See foot note of Table 2 for traits abbreviations

Study of genotype × environment interaction plays a crucial role in plant breeding and evolution. To date, a lot of research has been done to understand the mystery of GE interaction, with a purpose to investigate the stability of different crops especially in diploid species (Shi *et al.,* 1997; Yang & Zhu, 2005). The model of Xu & Zhu (1999) predicted the general heterosis and genotypic environment interaction from the parents, F$_1$ and F$_2$. Most of the quantitative traits of autotetraploid rice were largely affected by the genotype as compared to environment, in contrast, some other studies showed the significant influence of environment on diploid rice

(Young & Virmani, 1990; Shi *et al.,* 1997; Dwivedi *et al.,* 1998; Shahid *et al.,* 2011), Indian mustard (Lionneton *et al.,* 2004), Chinese vegetable mustard (Qi *et al.,* 2008) and cotton (Ye *et al.,* 2008). The stronger effect of GE interaction variance to phenotypic variance on FL, FW, FWT, AL and UG represents the pronounced influence of environment than genetic components representing that above mentioned traits might grow better in one environment.

Hybrids of diploid rice, maize and sorghum have been successfully developed and are under cultivation, but autotetraploid rice hybrids have limitations due to its low seed set percentage and yield (Li & Xu, 2000). Genetic basis of heterosis is very complicated because environment has great influence on it and it varied frequently under different environments (Knight, 1973; Young & Virmani, 1990; Virmani, 1999). Autotetraploid rice hybrids depicted higher level of heterosis for most of the traits under study, and higher genotypic values and general heterosis were found in F_1 as compared to F_2. H_{pm} and H_{pb} was highly significant (negative) for HD in both generations which indicated early heading date of hybrids as compared to their parents. Grain yield and SS showed highly significant positive heterosis for H_{pm} and H_{pb} in F_1 and F_2 generations. Therefore, grain yield and SS could be successively improved using this material, proving to be a breakthrough in autotetraploid hybrid rice breeding. Previous studies reported high heterosis for various traits of diploid rice including total dry matter, panicle number, spikelet number, 1000-grain weight, plant height, heading date and grain yield (Young & Virmani, 1990; Dwivedi *et al.,* 1998). Not only grain yield but quality of rice grains also very important and autotetraploid rice had better nutritional quality than diploid rice (Song & Zhang, 1992). Li & Rutger (2007) registered two genetic stock lines TG_1 (SY×L202) and TG_2 (SY×Jackson) of autotetraploid rice. We also found promising results with Jackson and L202.

Information on dominance to phenotypic variance, additive to phenotypic variance, heritability studies, and heterotic performance of the studied traits exhibited predominantly additive type of gene action for half of the traits, but remaining supposed to be controlled by non-additive type of gene action. The plant material examined here having significant non-additive type of gene action could be efficiently used in autotetraploid hybrid rice breeding. The present study infers that seed set and grain yield of autotetraploid rice can be meliorated by using different autotetraploid lines and autotetraploid rice has the potential to be used on commercial scale.

Acknowledgements

The authors thank Ms. Shu-Hong Yu, Ou Zhimiao, and Liu Shichang for their help in laboratory and field. We are thankful to Dr. Li Jin-Quan, Dr. Syed Muhammad Zaka and Prof. Liu Gui-fu for valuable suggestions in analysis. This research was supported by the National Science Foundation of China (30771328).

References

Ahmad, S., M.Z. Haq, M. Imran, S. Iqbal, J. Iqbal and M. Ahmad. 2008. Determination of residual contents of pesticides in rice (*Oryza sativa* L.) crop from different regions of Pakistan. *Pak. J. Bot.,* 40(3): 1253-1257.

Akram, M., S.U. Ajmal and M. Munir. 2007. Inheritance of traits related to seedling vigor and grain yield in rice *(Oryza sativa* L.). *Pak. J. Bot*., 39(1): 37-45.

Allard, R.W. 1960. *Principles of plant breeding* (Wiley, New York).

Allard, R.W. 1988. Future direction in plant population genetics, evolution and breeding. In: *Plant population genetics and germplasm resources*. (Eds.): A.H.D. Brown, M.T. Clegg, A.L. Kahler and B.S. Weir. Sinauer Associates Inc. Sunderland, Massachusetts, pp 1-19.

Allard, R.W. 1996. Genetic basis of the evolution of adaptedness in plants. *Euphytica,* 92: 1-11.

Bingham, E.T., R.W. Groose, D.R. Woodfield and K.K. Kidwell. 1994. Complementary gene interactions in alfalfa are greater in autotetraploids than diploids. *Crop Sci.,* 34: 823-829.

Cai, D.T., L.P. Yuan and X.G. Lu. 2001. A new strategy of rice breeding in the 21st century: II.searching a new pathway of rice breeding by utilization of double heterosis of wide cross and polyploidization. *Acta Agron. Sin.,* 27: 110-116.

Carson, H.L. and A.R. Templeton. 1984. Genetic revolutions in relation to speciation phenomenon: The founding of new populations. *Annual Rev. Ecol. Syst.,* 15: 97-131.

Chen, G.B. and J. Zhu. 2003. Department of Agronomy, Zhejiang University, Hangzhou, China. http://ibi.zju.edu.cn/software/qga/index.htm.

Chen, Z.Y., D.Y. Wu, W.C. Song, Y.H. Zhang, R.Z. Qin and W.K. Bao. 1987. Recent advances in autotetraploid rice breeding. *Sci. Agric. Sin.,* 20: 20-24.

Cheng, S.H., J.Y. Zhuang, Y.Y. Fan, J.H. Du and L.Y. Cao. 2007. Progress in research and development on hybrid rice: A Super-domesticate in China. *Ann. Bot.,* 100: 959-966.

Darwin, C.R. 1876. The effects of cross and self-fertilization in the vegetable kingdom (1st ed.), John Murray.

Davenport, C.B. 1908. Degeneration, albinism and inbreeding. *Science,* 28: 454-455.

Dwivedi, D.K., M.P. Pandey, S.K. Pandey and R.B. Li. 1998. Heterosis in inter and intrasubspecific crosses over three environments in rice. *Euphytica*, 99: 155-165.

East, E.M. 1908. Inbreeding in corn. Reports of the connecticut agricultural experimental station for years 1907-1908, pp. 419-428.

Fasoulas, A.C. and R.W. Allard. 1962. Nonallelic gene interactions in the inheritance of quantitative characters in barley. *Genetics,* 47: 899-907.

Fatokun, C.A., D.I. Menancio-Hautea, D. Danesh and N.D. Young. 1992. Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. *Genetics,* 132: 841-846.

Guo, X.P., R.Z. Qin and X. Chen. 2002. Factors affecting production of autotetraploid rice. *J. Plant Genet. Resour.,* 3: 30-33.

He, J.H., M.Q. Shahid, Y.J. Li, H.B. Guo, X.A. Cheng, X.D. Liu and Y.G. Lu. 2011. Allelic interaction of F_1 pollen sterility loci and abnormal chromosome behaviour caused pollen sterility in intersubspecific autotetraploid rice hybrids. *J. Exp. Bot.,* 62: 4433-4445.

Hosseini, M., R.H. Nejad and A.R. Tarang. 2005. Gene effects, combining ability of quantitative characteristics and grain quality in rice. *Iranian J. Agric. Sci.,* 36: 21-32.

Hu, C.Y., Y.X. Zeng, Y.G. Lu, J.Q. Li and X.D. Liu. 2009. High embryo sac fertility and diversity of abnormal embryo sacs detected in autotetraploid *indica/japonica* hybrids in rice by whole-mount eosin B-staining confocal laser scanning microscopy. *Plant Breed.,* 128: 187-192.

Inamullah, H. Ahmad, F. Mohammad, S. Din, G. Hassan and R. Gul. 2006. Diallel analysis of the inheritance pattern of agronomic traits of bread wheat. *Pak. J. Bot.,* 38: 1169-1175.

Iqbal, M., A.R. Navabi, F.S. Donald, R.C. Yang, M.M. Brenda, S.M. Steve and S. Dean. 2007. Genetic analysis of flowering and maturity time in high latitude spring wheat. *Euphytica,* 154: 207-218.

Jones, J.W. 1926. Hybrid vigour in rice. *J. Am. Soc. Agron.,* 18: 423-428.

Khush, G.S. 2003. Productivity improvement in rice. *Nutr. Rev.,* 61: 114-116.

Knight, R. 1973. The relation between hybrid vigour and genotype×environment interaction. *Theor. Appl. Genet.,* 43: 318-322.

Lark, K.G., K. Chase, F. Adler, L.M. Mansur and J.H. Orf. 1995. Interactions between quantitative traits loci in soybean in which trait variation at one locus is conditional upon a specific allele at another. *Proc. Nat. Acad. Sci.,* 92: 4656-4660.

Li, Y.Q. and J.N. Rutger. 2007. Registration of two tetraploid rice genetic stocks. *J. Plant Regis.,* 1: 173-174.

Li, Y.Q. and Q.S. Xu. 2000. Research on the hybrid vigor of autotetraploid intersubspecies. In: Proc. of studying on two lines hybrid rice supported by 863-Project in Hainan in 2000.

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

Lionneton, E., G. Aubert, S. Ochatt and O. Merah. 2004. Genetic analysis of agronomic and quality traits in mustard (*Brassica juncea*). *Theor. Appl. Genet.,* 109: 792-799.

Liu, H.J., H. Wang and L.H. Gao. 1997. Comparisons of isoenzymes between autotetraploid and diploid Chinese cabbage varieties of different ecotypes. *J. Nanjing Agric. Uni.,* 20: 26-30.

Liu, P.Y., J. Zhu, X.Y. Lou and Y. Lu. 2003. A method for marker-assisted selection based on QTLs with epistatic effects. *Genetica,* 119: 75-86.

Luan, L., X. Wang, W.B. Long, Y.H. Liu, S.B. Tu, Z.P. Zhao, F.L. Kong and M.Q. Yu. 2008. Microsatellite analysis of genetic variation and population genetic differentiation in autotetraploid and diploid rice. *Bioche. Genet.,* 46: 248-266.

Mahto, R.N., M.S. Yadava and K.S. Mohan. 2003. Genetic variation, character association and path analysis in rainfed upland rice. *Ind. J. Dryland Agri. Res. Dev.,* 18: 196-198.

Martin, S.K. St., F.T. Xie, H.J. Zhang, W. Zhang and X.J. Song. 2009. Epistasis for quantitative traits in crosses between soybean lines from China and the United States. *Crop Sci.,* 49: 20-28.

Maughan, P.J., M.A.S. Maroof and G.R. Buss. 1996. Molecular-marker analysis of seed-weight: genomic locations, gene action and evidence for orthologous evolution among three legume species. *Theor. Appl. Genet.,* 93: 574-579.

Miller, R.G.Jr. 1974. The Jackknife, a review. *Biometrika,* 61: 1-15.

Nanda, G.S., G.N. Hazarika and K.S. Gill. 1981. Inheritance of heading date, plant height, ear length and spikelets per spike in an intervarietal cross of wheat. *Theor. Appl. Genet.,* 60: 167-171.

Normile, D. 2008. Reinventing Rice to Feed the World. *Science,* 321: 330-333.

Peng, S., Q.Y. Tang and Y.B. Zou. 2009. Current status and challenges of rice production in China. *Plant Prod. Sci.,* 12: 365-380.

Qi, X.H., J.H. Yang, J.Q. Yu and M.F. Zhang. 2008. Genetic and heterosis analysis for important agronomic traits of Chinese vegetable mustard (*Brassica juncea*) in different environments. *Genetica,* 136: 89-95.

Rabbani, M.A., M.S. Masood, Z.K. Shinwari and Y.S. Kazuko. 2010. Genetic analysis of basmati and non-basmati pakistani rice (*Oryza sativa* l.) Cultivars using microsatellite markers. *Pak. J. Bot*., 42(4): 2551-2564.

Rashid, M., A. A. Cheema and M. Ashraf. 2007. Line x tester analysis in basmati rice. *Pak. J. Bot*., 39(6): 2035-2042.

Anonymous. 2006. SAS system for windows. Version 9.1. SAS Inst., Cary, NC

Shahid, M.Q., G.F. Liu, J.Q. Li, M. Naeem and X.D. Liu. 2011. Heterosis and gene action study of agronomic traits in diploid and autotetraploid rice. *Acta Agr. Scand. B-S. P.,* 61: 23-32.

Shahid, M.Q., J.F. Sun, C.M. Wei, P. Zhang and X.D. Liu. 2010. Studies on the abnormality of embryo sac and pollen fertility in autotetraploid rice during different growing seasons. *Pak. J. Bot.,* 42(1): 7-19.

Sheikh, S., I. Singh and J. Singh. 2000. Inheritance of some quantitative traits in bread wheat (*Triticum aestivum* L.). *Ann. Agri. Res.,* 21: 51-54.

Shi, C H., J. Zhu, R.C. Zang and G.L. Chen. 1997. Genetic and heterosis analysis for cooking quality traits of *indica* rice in different environments. *Theor. Appl. Genet.,* 95: 294-300.

Shull, G.H. 1908. The composition of a field of maize. *Amer. Breed. Asso. Rep.,* 4: 296-301.

Shull, G.H. 1948. What is "heterosis"? *Genetics,* 33: 439-446.

Song, W.C. and Y.H. Zhang. 1992. Rice tetraploidy and its effect on agronomic traits and nutritional constituents. *Acta Agro. Sin.,* 18: 137-144.

Swati, P.G. and B.R. Ramesh. 2004. The nature and divergence in relation to yield traits in rice germplasm. *Ann. Agr. Res.,* 25: 598-602.

Tu, S.B., L. Luan, Y.H. Liu, W. Long, F.L. Kong, T. He, Q.F. Xu, W.G. Yan and M.Q. Yu. 2007. Production and heterosis analysis of rice autotetraploid hybrids. *Crop Sci.,* 47: 2356-2363.

Verma, O.P. and H.K. Srivastava. 2004. Genetic component and combining ability analyses in relation to heterosis for yield and associated traits using three diverse rice-growing ecosystems. *Field Crops Res.,* 88: 91-102.

Virmani, S.S. 1999. Exploitation of heterosis for shifting the yield frontier of rice. p. 423-438. In J. G. Coors and S. Pandey eds., The genetics and exploitation of heterosis in crops. ASA, CSSA, SSSA, Madison, WI.

Virmani, S. . and I. Kumar. 2004. Development and use of hybrid rice technology to increase rice productivity in the tropics. *Inter. Rice. Res. Notes*, 29: 10-19.

Wang, G.J., S. Castiglione, J. Zhang, R.Z. Fu, J.S. Ma, W.B. Li, Y.R. Sun and F. Sala. 1994. Hybrid rice (*Oryza sativa* L.): identification and parentage determination by RAPD fingerprinting. *Plant Cell Rep.,* 14: 112-115.

Wardyn, B.M., J.W. Edwards and K.R. Lamkey. 2007. The genetic structure of a maize population: The role of dominance. *Crop Sci.,* 47: 467-476.

Wendel, J.F. 2000. Genome evolution in polyploids. *Plant Mol. Bio.,* 42: 225-249.

Wright, S. 1968. Evolution and genetics of populations (Univ. Chicago Press, Chicago), Vol. 1.

Wu, P., G. Zhang, J.K. Ladha, S.R. McCouch and N. Huang. 1995. Molecular-marker-facilitated investigation on the ability to stimulate N_2 fixation in the rhizosphere by irrigated rice plants. *Theor. Appl. Genet.,* 91: 1177-1183.

Xiao, J., J. Li, L.P. Yuan and S.R. McCouch. 1996. Genetic diversity and its relationship to hybrid performance and heterosis in rice as revealed by PCR based markers. *Theor. Appl. Genet.,* 92: 637-643.

Xu, Z.C. and J. Zhu. 1999. An approach for predicting heterosis based on additive, dominance and additive×additive model with environment interaction. *Heredity,* 82: 510-517.

Yang, J. and J. Zhu. 2005. Methods for predicting superior genotypes under multiple environments based on QTL effects. *Theor. Appl. Genet.,* 110: 1268-1274.

Ye, Z.H., Y.J. Mei, K.Q. Zou, X.S. Fu and L.S. Jiang. 2008. Genetic dissection of net effects between yield and its components in sea island cotton (*Gossypium barbadense* L.). *Agri. Sci. China,* 7: 1052-1060.

Young, J.B. and S.S. Virmani. 1990. Heterosis in rice over environments. *Euphytica,* 51: 87-93

Yu, S.B., J. X. Li, C.G. Xu, Y.F. Tan, Y.J. Gao, X.H. Li, Q. Zhang and M.A.S. Maroof. 1997. Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. *Proc. Nat. Acad. Sci.,* 94: 9226-9231.

Yuan, L.P. 1992. Development and prospects of hybrid rice breeding, pp. 97-105 in agricultural biotechnology, Proceeding of Asian-Pacific conference on agricultural biotechnology, edited by C. B. You and Z. L. Chen. China Agriculture Press, Beijing.

Zhu, J. and B.S. Weir. 1996. Diallel analysis for sex-linked and maternal effects. *Theor. Appl. Genet.,* 92: 1-9.

(Received for publication 14 February 2011)