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Developmental Analysis of Genetic Behavior of Brown Rice Width in indica-japonica Hybrids

ZHANG Xiao-ming [1, 2], SHI Chun-hai [2], YE Shen-hai [1], QI Yong-bin [1]
([1] *Institute of Crop and Nuclear Technology Utilization, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China;*
[2] *College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310029, China*)

Abstract: The developmental genetic behaviors of brown rice width (BRW) have been studied in indica-japonica hybrid rice (*Oryza sativa* L.), in which seven indica male sterile lines and five japonica restorer lines were applied, by using the developmental genetic models and corresponding statistical approaches for quantitative traits of triploid in cereal crops. The BRW of indica-japonica hybrid rice was co-determined by gene expression of triploid endosperm, cytoplasm, diploid maternal plant and their genotype × environmental interaction effects. Unconditional analysis showed that the endosperm additive and maternal additive effects were predominant for the development of BRW from early- to late-stage of the grain development, but the endosperm dominant effect together with maternal effect and cytoplasmic effect became the major factor determing the BRW at the ripening stage. Moreover, conditional analysis found that there were new onset and offset of gene expression at different developmental stages of BRW in indica-japonica hybrid rice. Maternal and cytoplasm general heritabilities and their interaction heritabilities were more important compared to other components of heritability for BRW at all the five developmental stages.

Key words: indica-japonica hybrid rice; developmental genetics; brown rice width; genetic variance; conditional genetic variance; heritability

One of the most effective ways of enhancing rice yield is the utilization of the strong inter-subspecific hybrid heterosis between indica rice and japonica rice in replacement of inter-varietal hybrid heterosis being widely applied. Recently, great progress has been made to increase rice yield in several countries e.g. Japan, Korea, China etc [1]. For example, an indica-japonica hybrid rice combination ‘Xieyou 9308’, which was derived from an indica cytoplasmic male sterile line Xieqingzao A × a japonica restorer line 9308 [C57 (japonica) // 300 (japonica) / IR26 (indica)] by China National Rice Research Institute, reached a grain yield of 12 t / ha [2], being much more compared with inter-varietal hybrids. Moreover, other indica-japonica hybrids such as Xieyou 413, Xieyou 9516, Xieyou 7954 also produced much higher yield [3-4]. Abundant world rice supply has led to renewed interest in improving quality of modern rice varieties or hybrids [5]. The existing tendency can solve the problem of plumpness, which can be helpful in selection of excellent hybrids to meet the world rice demands.

Grain plumpness is one of the major problems of rice production in several rice-producing countries, especially in indica-japonica hybrids, which generally displays incomplete grain filling, and affects the grain shape and size. Though environmental conditions during rice growth, and mechanical factors such as pre- and post-harvest operations can affect the milled rice trait, but variety remains the most important determinant as the market price is judged by grain size, shape and appearance, such as whiteness and translucency [6-7].

In most of previous research, the inheritance of endosperm trait was analyzed by using phenotypic value at maturity [8-13]. These results indicated that the grain width was mostly depended on additive gene effects and their interaction, while the estimation of heritability and genetic advance were fair consistent for grain widths in F_2 and F_3 generations. It can be concluded that pedigree selection would be effective in improving the grain size and biparental mating or reciprocal recurrent selection may be successful [14]. Recently, some quantitative trait analysis softs

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Corresponding author: SHI Chun-hai (chhshi@zju.edu.cn)

generated make developmental genetic analysis possible, but most of the reports are limited to the developmental behaviors of appearance quality of cereal crops [15-19] and very few in indica-japonica hybrid rice. One of the most possible reasons is that such kind of research needs a large number of field labors, and it is difficult to get a huge number of F_1 seeds by cross of indica rice with japonica rice because of incompatibility. In this paper, the genetic behavior of the brown rice width in indica-japonicca hybrids was analyzed by the genetic models and developmental models.

MATERIALS AND METHODS

Plant material

During this experiment seven indica cytoplasmic male sterile lines (A) (Zhe 38A, Xieqingzao A, K17A, Zhenshan 97A, Zhenong 8010A, Jin 23A and II-32A) and their maintainer lines (B), and five japonica wide compatible restorer lines (R) (T748, T42, R1252, Lunhui 422 and Zhong 9308) were used. The seeds used in this experiment were all obtained from previous growing season.

Field experiment

In this experiment, an incomplete diallel cross was designed with seven male sterile lines (female parents) and five restorer lines (male parents). All the F_1 seeds were gained by crossing female parents to male parents (A × R) at Hainan Province in spring season of 2001. Seedlings of the parents and F_1s were planted at the experimental farm of Zhejiang Academy of Agricultural Sciences, Hangzhou, Zhejiang Province. Seeds were sown on 25 May in 2001 and 25-day old seedlings were individually transplanted at a spacing of 20 cm×26 cm and 36 plants (6 rows × 6 plants per row) in each plot with two replications. The experiment was also conducted at Hainan Province on 12 December in 2001 using the method described above. Based on the development of rice grain, the whole grain filling period were divided into initial stage (1-7 days after flowering), early stage (8-14 days after flowering), middle stage (15-21 days after flowering), late stage (22-28 days after flowering) and ripening stage (29-35 days after flowering). Seed samples from the parents and F_2s on F_1 plants were collected at 7-, 14-, 21-, 28- and 35-day after flowering from central 16 plants of each plot. The F_1 samples were analyzed and then crossed female parents (A) to male parents (R) during the same growing season. The brown rice width (BRW) was measured with 10 grains by the help of vernier calipers with two replications after seeds were dehulled by hand.

Statistical method

The classic genetic models[21] and developmental genetic models[20] for quantitative traits of endosperm in cereal crops were used to estimate the variance components including genetic main effects and their interaction effects (*GE* genotype × environmental) for BRW at different filling stages.

For unconditional analysis, genetic effects were defined as accumulated effects of genes expressed from flowering (0) to a particular time (*t*). The variance components include endosperm additive variance (V_A), endosperm dominant variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}), maternal dominant variance (V_{Dm}), endosperm additive interaction variance (V_{AE}), endosperm dominant interaction variance (V_{DE}), cytoplasm interaction variance (V_{CE}), maternal additive interaction variance (V_{AmE}), maternal dominant interaction variance (V_{DmE}) and residual variance (V_e). Since partial endosperm genes were derived from maternal plants, there might be covariance between endosperm effects and maternal effects including additive covariance ($C_{A\bullet Am}$), dominant covariance ($C_{D\bullet Dm}$), additive interaction covariance ($C_{AE\bullet Am\mathrm{E}}$), and dominant interaction covariance ($C_{DE\bullet DmE}$).

For conditional analysis, the developmental genetic models and statistical methods could be used to estimate conditional variances during the designated filling periods (t-1→t) for BRW. These conditional variance components were $V_{A(t|t\text{-}1)}$ (conditional endosperm additive variance), $V_{D(t|t\text{-}1)}$ (conditional endosperm dominant variance), $V_{C\ (t|t\text{-}1)}$ (conditional cytoplasmic variance), $V_{Am\ (t|t\text{-}1)}$ (conditional maternal additive variance), $V_{Dm\ (t|t\text{-}1)}$ (conditional maternal dominant variance), $V_{AE(t|t\text{-}1)}$(conditional endosperm additive interaction variance), $V_{DE(t|t\text{-}1)}$ (conditional endosperm dominant interaction variance), $V_{CE(t|t\text{-}1)}$ (conditional cytoplasm interaction variance), $V_{AmE(t|t\text{-}1)}$ (conditional maternal additive interaction variance), $V_{DmE(t|t\text{-}1)}$ (conditional maternal dominant interaction variance), $C_{A\cdot Am(t|t\text{-}1)}$ (conditional additive covariance), $C_{D\cdot Dm(t|t\text{-}1)}$ (conditional dominant covariance), $C_{AE\cdot AmE(t|t\text{-}1)}$ (conditional additive interaction covariance), $C_{DE\cdot DmE(t|t\text{-}1)}$ (conditional dominant interaction covariance) and $V_{e\ (t|t\text{-}1)}$ (conditional residual variance).

The estimated total narrow-sense heritability (h^2) at different filling stages was differentiated into general heritability (h_G^2) controlled by the genetic main effects and the interaction heritability (h_{GE}^2) controlled by GE interaction effects. The general heritability (h_G^2) can be divided into several components including general endosperm heritability [$h_{Go}^2 = (V_A + C_{A\cdot Am})/V_P$], cytoplasmic heritability ($h_{Gc}^2 = V_C/V_P$) and maternal general heritability [$h_{Gm}^2 = (V_{Am} + C_{A\cdot Am})/V_P$]. The interaction heritability (h_{GE}^2) can also be divided into the different components including endosperm interaction heritability [$h_{GoE}^2 = (V_{AE} + C_{AE\cdot AmE})/V_P$], cytoplasmic interaction heritability ($h_{GcE}^2 = V_{CE}/V_P$) and maternal interaction heritability $h_{GmE}^2 = (V_{AmE} + C_{AE\cdot AmE})/V_P$. The total narrow-sense heritability is $h^2 = h_G^2 + h_{GE}^2 = (h_{Go}^2 + h_{Gc}^2 + h_{Gm}^2) + (h_{GoE}^2 + h_{GcE}^2 + h_{GmE}^2)$.

The Jackknife re-sampling method was employed by sampling generation means of entries for estimating standard errors of estimated components of variances, covariance and heritabilities [22].

RESULTS

Difference of brown rice width (BRW) in parents and their descendants

There were great differences both in sterile lines and in restorer lines for BRW at the five filling stages of rice growth (Table 1), with largest BRW being noted in Zhenshan 97A in the sterile line group and Lunhui 422 in the restorer line group during all developmental stages (Zhenshan 97A and Lunhui 422 reached 2.675 mm and 2.516 mm at the ripening stage, respectively). It also indicated that BRW continuously increased after flowering and the means of BRW were increased 84.42, 8.27, 2.90, 2.48 and 1.93% of their mature widths at the five different developmental stages, respectively. The results of Fig. 1 showed that the mean values of BRW were similar in sterile lines, restorer lines and F_2 at the initial stage, but increased more from early stage to the ripening

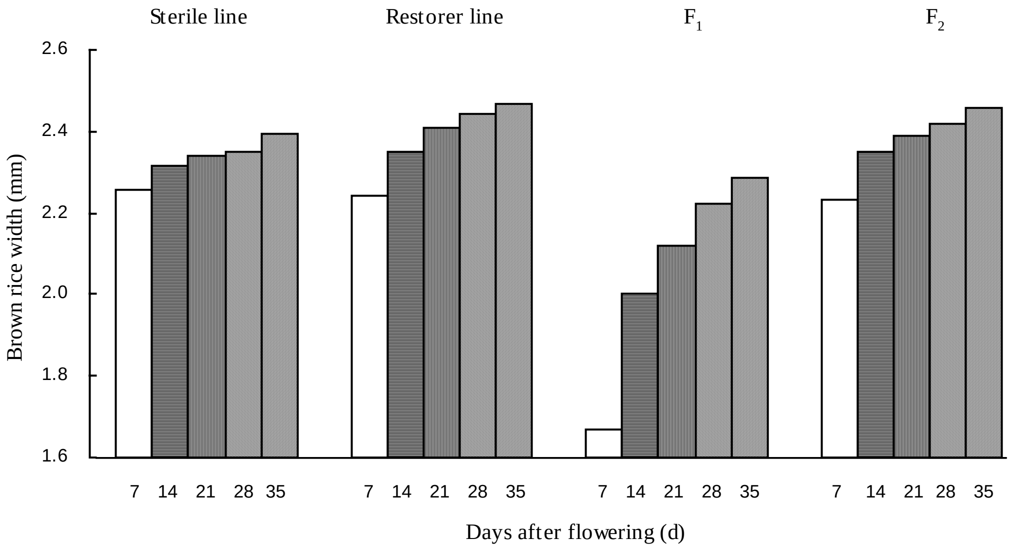

Fig. 1. Mean values of brown rice width (BRW) for sterile line, restorer line, F_1 hybrid and F_2 generation at the five filling stage in indica-japonica hybrid rice crosses.

Table 1. Mean values of BRW in seven sterile lines and five restorer lines at the five different filling stages. mm

Parent	Days after flowering				
	7 d	14 d	21 d	28 d	35 d
Sterile line					
Zhe 38A	2.038	2.095	2.138	2.150	2.20
Xieqingzao A	2.150	2.288	2.313	2.313	2.34
K17A	2.363	2.438	2.450	2.450	2.47
Zhenshan 97A	2.538	2.588	2.600	2.625	2.67
Zhenong 8010A	2.100	2.163	2.200	2.200	2.22
Jin 23A	2.150	2.163	2.163	2.175	2.23
Ⅱ-32A	2.463	2.488	2.525	2.538	2.58
Restorer line					
T748	2.011	2.223	2.290	2.349	2.39
T42	2.004	2.216	2.277	2.340	2.39
R1252	1.967	2.152	2.230	2.288	2.32
Lunhui 422	2.100	2.356	2.485	2.498	2.51
Zhong 9308	1.986	2.188	2.274	2.358	2.41
Mean of total lines	2.010	2.207	2.276	2.335	2.38

stage in restorer lines as well as in F_2. However, in general F_1 expressed some inferiorities at each developmental stage, indicating poor grain plumpness in indica-japonica hybrids.

Unconditional variance component analysis for BRW

Genetic variances for endosperm, cytoplasm and maternal effects and their *GE* interactions on the 7th, 14th, 21st, 28th and 35th day after flowering are given in Table 2. It indicated that BRW was controlled by genetic main effects (V_A + V_D + V_C + V_{Am} + V_{Dm}) except for maternal dominant effects (V_{Dm}) at the initial stage, endosperm dominant effect (V_D) at the early- and mid-stage and endosperm additive effects (V_A) at the ripening stage and controlled by *GE* interaction effects except for endosperm dominant interaction effects (V_{DE}) at the initial- and early-stage and maternal dominant interaction effects (V_{DmE}) at the mid- and ripening-stage.

Among endosperm, cytoplasmic and maternal effects, BRW was mainly controlled by additive effects both in main genetic effects and in *GE* interaction effects during the whole filling period, which accounted for 87.14, 84.94, 81.26, 70.97 and 68.71% of total variances [$(V_A+V_{Am}+V_{AE}+V_{AmE})$ / (V_G+V_{GE})] at the five different filling stages, but the values were declined with the development of rice grains. Performance of BRW could be influenced by sampling errors due to significant residual variances (V_e). But in comparison with the genetic parameters, the values of V_e were rather lower, which occupied only 0.38, 0.62, 1.48, 0.97 and 2.63% of total variances [V_e / $(V_G+V_{GE}+V_e)$]. As shown in Table 2, there was no relationship between the expression of endosperm and maternal genes at all different filling stages, since the genetic main covariances ($C_{A\cdot Am}$ or $C_{D\cdot Dm}$) or *GE* interaction covariances ($C_{AE\cdot AmE}$ or $C_{DE\cdot DmE}$) between the endosperm and maternal effects were all not significant.

Table 2. Estimates of unconditional variance components for brown rice width in indica-japonica hybrid rice.

Parameter	Developmental stage of grain (Days after flowering)				
	7 d	14 d	21 d	28 d	35 d
V_A	0.451 **	0.205 **	0.119 **	0.044 **	0.000
V_D	0.053 **	0.000	0.000	0.007 **	0.015 **
V_C	0.046 **	0.037 **	0.034 **	0.030 **	0.029 **
V_{Am}	0.499 **	0.216 **	0.136 **	0.056 **	0.059 **
V_{Dm}	0.000	0.009 **	0.010 **	0.009 **	0.011 **
V_{AE}	0.540 **	0.129 **	0.088 **	0.056 **	0.078 **
V_{DE}	0.000	0.000	0.007 **	0.005 **	0.012 **
V_{CE}	0.155 **	0.064 **	0.050 **	0.034 **	0.040 **
V_{AmE}	0.556 **	0.138 **	0.095 **	0.064 **	0.098 **
V_{DmE}	0.048 **	0.012 **	0.000	0.005 **	0.000
$C_{A\cdot Am}$	-0.166	-0.111	-0.056	-0.002	0.000
$C_{D\cdot Dm}$	0.000	0.000	0.000	-0.008	-0.005
$C_{AE\cdot AmE}$	-0.185	-0.038	-0.020	-0.017	-0.038
$C_{DE\cdot DmE}$	0.000	0.000	0.000	0.000	0.000
V_e	0.009 **	0.005 **	0.008 *	0.003 **	0.009 *

*,** Significant at the 0.05 and 0.01 levels, respectively.

Conditional variance component analysis for BRW at different filling stages

BRW genes in indica-japonica hybrids might be expressed in different ways during grain filling stages since the genetic variances estimated by unconditional analyses at time *t* revealed the variation of accumulated genetic effects expressed from flowering (time = 0) to time *t* $(0 \rightarrow t)$, and thus the results could not clarify gene expression in each developmental stage $(t-1 \rightarrow t)$. Hence, conditional analysis approaches were used in order to more effective explanation of the dynamic gene expressions at all filling stages.

The results of the conditional variance analysis showed a new onset and offset of gene expressions in triploid endosperm, cytoplasm and diploid maternal genetic systems. Moreover, the results in Table 3 showed there were endosperm additive, maternal additive, endosperm dominant and cytoplasmic effects ($V_{A(7|0)}$,$V_{Am(7|0)}$,$V_{D(7|0)}$ and $V_{C(7|0)}$) at the initial stage, endosperm additive, maternal additive, maternal dominant and cytoplasmic effects ($V_{A(14|7)}$, $V_{Am(14|7)}$, $V_{Dm(14|7)}$ and $V_{C(14|7)}$) at the early stage, endosperm dominant and maternal dominant effects ($V_{D(21|14)}$ and $V_{Dm(21|14)}$) at the middle stage, endosperm dominant, maternal additive and cytoplasmic effects ($V_{D(28|21)}$, $V_{Am(28|21)}$ and $V_{C(28|21)}$) at the late stage and maternal additive, maternal dominant and cytoplasmic effects ($V_{Am(35|28)}$, $V_{Dm(35|28)}$ and $V_{C(35|28)}$) at the ripening stage for controlling the development of BRW, respectively.

Comparing with conditional results in Table 3, the unconditional endosperm additive, maternal additive and cytoplasmic effects at the mid filling stage (21 days after flowering), unconditional endosperm additive and maternal dominant effects at the late filling stage (28 days after flowering) and unconditional endosperm dominant effect at the ripening stage (35 days after flowering) (Table 2) might be due to the continual expression of activated genes at the previous stages. On the contrary, conditional dominant effect ($V_{D\,(21|14)}$) at the middle stage was found by conditional analyzing (Table 3), but not in unconditional analyzing (Table 2). It could be due to the conditional analysis as the expression of genes in conditional analysis method is a bit earlier than unconditional analysis. Furthermore, the results in Table 3 also revealed a phenomenon of new expression of genes being interrupted during different filling stages such as the conditional endosperm dominant effect. The genetic main variances ($V_{A(t|t-1)}$ + $V_{D(t|t-1)}$ + $V_{C(t|t-1)}$ + $V_{Am(t|t-1)}$ + $V_{Dm(t|t-1)}$) at the five different filling stages were 1.049,

Table 3. Estimates of conditional variance components for brown rice width in indica-japonica hybrid rice.

Parameter	Developmental stage of grain (Days after flowering)				
	7 d | 0 d	14 d | 7 d	21 d | 14 d	28 d | 21 d	35 d | 28 d
$V_{A\,(t\mid t-1)}$	0.451**	4.080**	0.000	0.000	0.000
$V_{D\,(t\mid t-1)}$	0.053**	0.000	2.068**	0.046**	0.000
$V_{C\,(t\mid t-1)}$	0.046**	0.261**	0.000	0.013**	2.067**
$V_{Am\,(t\mid t-1)}$	0.499**	2.722**	0.000	0.062**	1.024**
$V_{Dm\,(t\mid t-1)}$	0.000	0.231**	0.059*	0.000	0.423**
$V_{AE\,(t\mid t-1)}$	0.540**	0.000	0.000	0.037**	15.623**
$V_{DE\,(t\mid t-1)}$	0.000	4.006**	1.995*	0.017**	4.638**
$V_{CE\,(t\mid t-1)}$	0.155**	0.000	0.000	0.000	0.000
$V_{AmE\,(t\mid t-1)}$	0.556**	0.000	0.000	0.049**	3.413**
$V_{DmE\,(t\mid t-1)}$	0.048**	0.082**	0.120**	0.005**	0.741**
$C_{A\bullet Am\,(t\mid t-1)}$	-0.166	-0.721	0.000	0.000	0.000
$C_{D\bullet Dm\,(t\mid t-1)}$	0.000	0.000	-0.126	0.000	0.000
$C_{AE\bullet AmE\,(t\mid t-1)}$	-0.185	0.000	0.000	-0.032	-6.880
$C_{DE\bullet DmE(t\mid t-1)}$	0.000	-0.143	0.021	-0.001	0.617**
$V_{e(t\mid t-1)}$	0.009**	0.004**	0.006^{+}	0.002**	0.020**

$^{+}$, *, ** significant at 0.10, 0.05 and 0.01 probability levels, respectively.

7.294, 2.217, 0.121 and 3.514, respectively, which accounted for 7.44, 51.71, 15.08, 0.86 and 24.91% of total variance, indicating that the genetic main effects were rather higher at the early stage and with more active genes to control BRW in indica-japonica hybrids. These results were difficult to be detected by the unconditional genetic variance analysis.

For the conditional interaction analysis, similar results were observed as in unconditional analysis. The endosperm additive interaction variance and maternal additive interaction variance at the early- and mid-stage, maternal dominant interaction variance at the middle stage and cytoplasmic interaction variance from early to ripening stage were found by unconditional analysis (Table 2), but could not be found by conditional analysis (Table 3), which were probably from the continual expression of activated genes at the previous stages. At the early stage, the conditional interaction variance only accounted for 35.92% of the total variance [$V_{GE(14|7)}$ / ($V_{G(14|7)}$+ $V_{GE(14|7)}$)], which confirmed that BRW was mostly controlled by genetic main effects.

There was no significant relationship between the new gene expression from endosperm and maternal plants at all filling stages by unconditional analysis (Table 2), but the relationship between dominant interaction and maternal dominant interaction ($C_{DE \cdot DmE(35|28)}$) at the ripening stage was significant by conditional analysis (Table 3). These results implied that some variances or relationship were hard to be detected by unconditional analysis but they could be detected by conditional analysis. Thus, we can get more information by using both unconditional and conditional analyses. There was a significant conditional residual variances ($V_{e(t|t\text{-}1)}$), which revealed that the new expression of BRW genes at a special filling stage could be influenced by sampling errors, while comparing with other genetic parameters, the values of V_e were rather lower and only occupied 0.38, 0.04, 0.14, 0.87 and 0.07% of total variances [V_e / (V_G + V_{GE} + V_e)].

Estimation of heritabilities at different filling stages

The results from Table 4 showed that general heritability components in cytoplasm and endosperm genetic systems were only observed at the late developmental stage and maternal genetic system at the ripening stage, whereas the endosperm interaction heritabilities were noted at the mid- and late-stages. However, the cytoplasmic interaction heritability observed at the late stage and maternal interaction heritabilities at all the five different developmental stages. With regard to the components of heritability, maternal, and cytoplasm general heritabilities and their interaction heritabilities were more important for BRW at all the developmental stages ($h^2_{Gm} + h^2_{Gc} + h^2_{GmE} + h^2_{GcE}$ = 58.63, 62.24, 64.64, 67.05 and 82.19%, respectively).

DISCUSSION

The development and quality of rice grain could be directly affected by climatic factors, e.g. solar radiation, temperature, humidity, etc. The soil and crop management practices may indirectly affect the rice

Table 4. Estimates of heritability components for brown rice width in indica-japonica hybrid rice.

Parameter	Developmental stage of grain (Days after flowering)				
	7 d	14 d	21 d	28 d	35 d
General heritability					
h^2_{Go}	0.172	0.181	0.160	0.163**	0.000
h^2_{Gc}	0.028	0.071	0.087	0.115**	0.107**
h^2_{Gm}	0.201	0.202	0.203	0.211	0.222**
Interaction heritability					
h^2_{GoE}	0.214	0.177	0.172*	0.150**	0.153
h^2_{GcE}	0.094	0.124	0.127	0.131**	0.151
h^2_{GmE}	0.224**	0.193**	0.190**	0.180**	0.226**

*, ** significant at 0.05 and 0.01 probability levels, respectively.

pests and diseases resulting in lower grain yield and quality. Though physical quality of rice can be influenced by above environmental effects (*E*), it mainly controlled by genetic main effects (*G*) and *GE* interactions [6]. Such kind of *GE* interaction is different from *E*, caused by environments, as *GE* serves as the deviation of genetic effects at different environments. Thus, the genetic models including *G* and *GE* for estimating unbiased genetic effects and environmental interaction effects would be useful.

During this experiment, the genetic behaviors of brown rice width was controlled by endosperm, maternal and cytoplasm effects, while the genes were expressed during each developmental stage due to conditional genetic variance analysis. BRW controlled by genetic main effects with high heritabilities. The results of conditional genetic variance analysis of BRW indicated a phenomenon of intercurrent expression for some genes during grain filling, but the differences of grain widths among hybrid combinations were obvious. The generation of ‘Xieqingzao A / R1252’ attained higher values despite of low expressions from their parents. Therefore, it could be suggested that under certain genetic backgrounds, some external supplementary genes could improve the grain plumpness.

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REFERENCES

1 Peng S, Khush G S, Cassman K G. Evolution of new plant ideotype for increased yield potential. *In*: Cassman K G. Breaking the Yield Barrier. Manila: IRRI, 1994: 5-20.

2 Dai C M, Xia R D. Characteristic and cultural points of hybrid rice Xieyou 9308. *J Zhejiang Agric Sci,* 2000 (1): 12-13, 24.

3 Dong W Q, Shi S H, Dong Y J, Wang J J. Breeding and utility of a new hybrid rice Xieyou 9516. *J Zhejiang Agric Sci*, 1999 (5): 211-213.

4 Zhang Z X, Li C S, Xu K S, Bao F S, Chen J T, Yang X W. Performance of Xieyou 7954 in experimental cultivation at Jinhua, Zhejiang and its high-yielding cultural practices. *Hybird Rice*, 2002 (1): 43-44.

5 Khush G S, Virk P S. Rice breeding: achievements and future strategies. *Crop Improve*, 2000, **27**: 115-144.

6 Juliano B O. Varietal impact on rice quality. *Cereal Foods World*, 1998, **43**: 207-211, 214-216, 218-222.

7 Kunze O R. Effect of environment and variety on milling quality of rice. *In*: Rice Grain Quality and Marketing. Manila: IRRI, 1985: 37-48.

8 Chauhan J S, Chauhan V S, Lodh S B. Environment influence on genetic parameters of quality component in rainfed upland rice. *Indian J Agric Sci*, 1992, **62**: 773-775.

9 Matzinger D F, Wernsman E A, Ross H F. Diallel crosses among barley varieties of *Niccotiana tabacum* L. in the F_1 and F_2 generation. *Crop Sci*, 1971, **11**: 275-279.

10 Osato K F, Hamachi Y, Matsue Y. Genotype × environment interaction of palatability in rice. *Japan J Crop Sci*, 1996, **65**: 585-589.

11 Shi C H, Zhu J, Wu J G, Fan L J. Genetic and genotype × environment interaction effects from embryo, endosperm, cytoplasm and maternal plant for rice grain shape traits of indica rice. *Field Crops Res*, 2000, **68**: 191-198.

12 Tan Y F, Xing Y Z, Li J X, Yu S B, Xu C G, Zhang Q F. Genetic bases of appearance quality of rice grains in Shanyou 63, an elite rice hybrid. *Theor Appl Genet*, 2000, **101**: 823-829.

13 Xu C W, Mo H D, Zhang A H, Zhu Q S. Genetic control of quality traits of rice grains in indica-japonica hybrids. *Acta Genet Sin*, 1995, **22**: 192-198.

14 Roy A. Genetics of yield and yield components in rice. *Crop Improv*, 1994, **25**: 223-225.

15 Fan L J, Shi C H, Wu J G, Zhu J, Wu P. Developmental genetic analysis of brown rice thickness of indica rice (*Oryza sativa* L.). *Acta Genet Sin*, 2000, **27**: 870-877.

16 Shi C H, Wu J G, Wu P. Developmental behavior of gene expression for brown rice thickness under different environments. *Genesis*, 2002, **33**: 185-190.

17 Shi C H, Wu J G, Lou X B, Zhu J, Wu P. Genetic analysis of transparency and chalkiness area at different filling stages of rice (*Oryza sativa* L.). *Field Crops Res*, 2002, **76**: 1-9.

18 Shi C H, Wu J G, Zhang X M, Wu P. Developmental analysis on genetic behavior of brown rice recovery in indica rice across environments. *Plant Sci*, 2002, **163**: 555-561.

19 Shi C H, Wu J G, Wu P. Genetic analysis of developmental behavior for amylose content in filling process of rice. *J Sci Food & Agric*, 2005, **85**: 791-796.

20 Zhu J. Analysis of conditional genetic effects and variance components in developmental genetics. *Genetics*, 1995, **141**: 1633-1639.

21 Zhu J, Weir B S. Analysis of cytoplasm and maternal effects: II. Genetic models for triploid endosperms. *Theor Appl Genet*, 1994. **89**: 160-166.

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