



## Genetic Effects for Cooking Quality Characters in *Indica-Japonica* Crosses of Rice

CHEN Jian-guo<sup>1</sup> ZHU Jun<sup>2</sup>

(1 Faculty of Life Science, Hubei University, Hubei Wuhan 430062 China)

(2 Department of Agronomy, Zhejiang University, Zhejiang Hangzhou 310029 China)

**Abstract:** Two photo-sensitive genic male sterile (PGMS) lines of *japonica* type and four *indica* varieties are used as parents to make *indica/japonica* crosses in rice (*Oryza sativa* L). Genetic models with genotype  $\times$  environment interactions for triploid endosperm are used for genetic studies of the three cooking quality traits of rice grain, including amylose content, gel consistency and alkali digestion value. The result indicate that the genetic variations of the three characters are mainly attributable to the direct additive and maternal additive effects. Genotype  $\times$  environment (GE) interactions are expressed mainly as dominance  $\times$  environment and cytoplasm  $\times$  environment interactions. Only the interactive maternal heritability is significant for amylose content. Gel consistency has significant general direct heritability and interactive cytoplasmic heritability. Alkali digestion value has highly significant general direct and maternal heritability. The potential values of parental lines for the improvement of rice quality are discussed with respect to the predicted values of genetic effects.

**Key words:** Rice (*Oryza sativa* L); *Indica-japonica* hybridization; Cooking quality; Genetic effect; Genotype  $\times$  environment interaction

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### 0 Introduction

The emphasis on breeding for quality rice has assumed great significance in recent years. To achieve both higher yield and quality, breeders can benefit from understanding the underlying genetic structure of the breeding population and the significance of genotype  $\times$  environment (GE) interactions. The grain of rice is composed of diploid maternal tissues (pericarp and testa), diploid hybrid tissues (embryo), and triploid hybrid tissues (endosperm) like other cereal crops. Hence, the complexity of the gene expression for quality characters of the grain lies in the fact that they may be contributed by several genetic systems (e.g., nuclear genes of maternal plants, nuclear

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genes of endosperms, and cytoplasmic genes), and also affected by environmental factors. Information about the relative importance of the effects of different genetic systems is needed to predict the usefulness of these traits in a breeding program. Several authors developed some genetic models for the estimation of genetic effects of endosperm characters in recent years. The models presented by Foolad and Jones (1992) and Pooni et al. (1992) cannot yield unbiased estimates of the different effects, for linear correlations exist among the genetic parameters. And these methods cannot accommodate the estimation of the genetic variance and covariance components. Therefore further information on other genetic properties of quality traits, such as heritability, genetic correlation and selection response cannot be obtained for the reference population. Furthermore, the above models cannot analyse GE interactions of the effects of different sources in quality traits. Zhu and his colleagues recently proposed a series of models for quantitative traits controlled by triploid endosperm nuclear genes, maternal plant nuclear genes and cytoplasmic genes (Zhu & Weir, 1994b; Zhu, 1996). These models can be used for the estimation of variance and covariance components and for the prediction of genetic effects, and GE interaction effects of different sources.

This study investigates the inheritance of amylose content, alkali digestion value and gel consistency in *indica-japonica* crosses of rice, using genetic model with genotype  $\times$  environment interactions for triploid endosperm developed by Zhu (1996). The objectives are to (1) estimate genetic and genotype  $\times$  environment variances and covariances for deriving statistics, such as heritability, and (2) determine the relative importance of direct genetic effects, maternal genetic effects and cytoplasmic effects in the genetic variations of the three quality characters.

## 1 Materials and Methods

### 1.1 Plant Material and Trait Evaluation

Two *japonica* photo-sensitive genic male sterile (PGMS) lines (N422s, A1073s) and four *indica* varieties (Miyang59, E349, Tx-1 and Miyang56) are used to make non-reciprocal crosses. Crossed ( $F_1$ ) and selfed-seeds are obtained from the same plants. Individuals of these  $F_1$ s and selfed parents were grown at two locations (Lianyungang city in Jiangsu province and Linsui county in Hainan province) during 1994 and 1995. Seeds of parents,  $F_1$ 's and  $F_2$ 's are obtained by self/cross-pollination from entries in two replicates with randomized complete block design.

The seeds obtained are evaluated for amylose content, alkali digestion value and gel consistency. Amylose content is estimated using the methods developed by Juliano (1971). Alkali digestion value is estimated by use of the alkali digestion test and spreading scores of Little et al. (1958). Test is conducted based on 30 grains per sample. Gel consistency determinations are made by using the procedure outlined by Cagampang et al. (1973). The analysis is repeated two times.

### 1.2 Statistical Analysis

The model used for the analysis is

$$Y_{hijkl} = \mu + E_h + G_{ijk} + GE_{hijk} + B_{l(h)} + e_{hijkl}$$

where  $Y_{hijkl}$  = the phenotypic mean of the  $k$ th mating type of the cross of maternal parent  $i$  and paternal parent  $j$  in the  $l$ th block within the  $h$ th location;  $\mu$  = population mean;  $E_h$  = the environment effect at location  $h$ ;  $G_{ijk}$  = the total genetic effect;  $GE_{hijk}$  = the total genotype  $\times$  environment effect;  $B_{l(h)}$  = the effect of  $l$ th block within location  $h$ ;  $e_{hijkl}$  = the residual error.

The partitioning of genetic effect  $G_{ijk}$  and genotype  $\times$  environment interaction effect  $GE_{hijk}$  depends on specific genetic entry of endosperm. In the present study, seed materials of three generations are used, hence the components of the genetic and genotype  $\times$  environment effects are as follows:

For parent  $P_i$  ( $k = 0$ )

$$G_{ii0} = 3A_i + 3D_{ii} + C_i + 2Am_i + Dm_{ii}$$

$$GE_{hii0} = 3AE_{ii} + 3DE_{hii} + CE_{hi} + 2AmE_{hi} + DmE_{hii};$$

for  $F_{1ij}(P_i \times P_j)$  ( $k = 1$ )

$$G_{ij1} = 2A_i + A_j + D_{ii} + 2D_{ij} + C_i + 2Am_i + Dm_{ii}$$

$$GE_{hij1} = 2AE_{hi} + AE_{hj} + DE_{hii} + 2DE_{hij} + CE_{hi} + 2AmE_{hi} + DmE_{hii};$$

for  $F_{2ij}$  ( $k = 2$ )

$$G_{ij2} = 1.5A_i + 1.5A_j + D_{ii} + D_{jj} + D_{ij} + C_i + Am_i + Am_j + Dm_{ij}$$

$$GE_{hij2} = 1.5AE_{hi} + 1.5AE_{hj} + DE_{hii} + DE_{hjj} + DE_{hij} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}$$

where  $A_i$  is the direct additive effect of endosperm genes from parent  $i$ ;  $D_{ij}$  is the direct dominance effect of endosperm genes from parent  $i$  and  $j$ ;  $C_i$  is the cytoplasm effect of parent  $i$ ;  $Am_i$  is the maternal additive effect of plant nuclear genes from parent  $i$ ;  $Dm_{ij}$  is the maternal dominance effect of plant nuclear genes from parent  $i$  and  $j$ ;  $AE_{hi}$  is the  $A_i \times E_h$  interaction effect;  $DE_{hij}$  is the  $D_{ij} \times E_h$  interaction effect;  $CE_{hi}$  is the  $C_i \times E_h$  interaction effect;  $AmE_{hi}$  is the  $Am_i \times E_h$  interaction effect;  $DmE_{hij}$  is the  $Dm_{ij} \times E_h$  interaction effect.

For the model of seed traits in this study, the phenotypic variance  $V_p$  can be partitioned as

$$V_P = (V_A + V_D) + V_C + (V_{Am} + V_{Dm}) + (V_{AE} + V_{DE}) + V_{CE} + (V_{AmE} + V_{DmE}) + 2(C_{A.Am} + C_{D.Dm}) + 2(C_{AE.AmE} + C_{DE.DmE}) + V_e$$

where  $V_A$  is the direct additive variance;  $V_D$  is the direct dominance variance;  $V_C$  is the cytoplasm variance;  $V_{Am}$  is the maternal additive variance;  $V_{Dm}$  is the maternal dominance variance;  $V_{AE}$  is the direct additive  $\times$  environment interaction variance;  $V_{DE}$  is the direct dominance  $\times$  environment interaction variance;  $V_{CE}$  is the cytoplasm  $\times$  environment interaction variance;  $V_{AmE}$  is the maternal additive  $\times$  environment interaction variance;  $V_{DmE}$  is the maternal dominance  $\times$  environment interaction variance;  $C_{A.Am}$  is the covariance between the direct and maternal additive effects;  $C_{D.Dm}$  is the covariance between the direct and maternal dominance effects;  $C_{AE.AmE}$  is the covariance between the direct and maternal additive  $\times$  environment effects;  $C_{DE.DmE}$  is the covariance between the direct and maternal dominance  $\times$  environment effects; and  $V_e$  is the

residual variance.

Variance and covariance components are estimated by MINQUE (0/1) method (Zhu and Weir, 1994a), and then the heritability components are calculated using the method suggested by Zhu (1996). Genetic effects are predicted by the adjusted unbiased prediction (AUP) method (Zhu & Weir, 1996). The potential values of parental lines are then evaluated. Standard errors of the statistics are obtained by the jackknife procedures (Zhu & Weir, 1994a), and *t*-tests are performed for testing null hypothesis of zero parameters.

Table 1 Estimates of Genetic Variances and Covariances of Cooking Quality Characters

Parameters	Amylose Content	Gel Consistency	Alkali Digestion Value
$V_A$	0.00	1490.47**	39.70**
$V_D$	14.73**	0.00	0.00
$V_C$	0.00	0.00	0.88*
$V_{Am}$	0.00	1237.33**	39.95**
$V_{Dm}$	0.00	0.00	0.00
$C_{A.Am}$	0.00	-1265.58**	-34.33**
$C_{D.Dm}$	0.00	0.00	0.00
$V_{AE}$	0.00	0.00	0.00
$V_{DE}$	22.21**	0.00	0.95**
$V_{CE}$	0.00	193.41**	0.00
$V_{AmE}$	45.23**	0.00	0.00
$V_{DmE}$	26.63*	35.78**	0.20*
$C_{AE.AmE}$	0.00	0.00	0.00
$C_{DE.DmE}$	-11.97*	0.00	0.13
$V_e$	0.59	35.94*	0.01

\*\* and \* indicate significant at the 0.01 and 0.05 levels, respectively

## 2 Results

### 2.1 Analysis of Genetic Variance Components and Heritabilities

Significant variances are observed for the three characters, indicating the importance of both direct and maternal genetic effects (Table 1). Genetic variation of amylose content is mainly ascribed to genotype  $\times$  environment interaction variances (including direct dominance  $\times$  environment, maternal additive  $\times$  environment and maternal dominance  $\times$  environment variances). Genetic variations of alkali digestion value and gel consistency are primarily due to the highly significant direct and maternal additive variances, and the negative covariance of the direct and maternal additive effects. Additionally, there are significant cytoplasm variance, direct dominance  $\times$  environment and maternal dominance  $\times$  environment variance for alkali digestion value, but their effects are not important.

Heritability estimates are presented in Table 2. The total heritability consists of the sum of general and interactive heritability component each can be further partitioned in terms of the direct, maternal and cytoplasmic components. General heritabilities of amylose content are not significant, only the interactive maternal heritability component is significant for this trait. Therefore, one would predict that selection for this trait would be more effectively practiced in the optimal environment based on the maternal plant. Gel consistency has significant general direct

heritability and interactive cytoplasmic heritability. Alkali digestion value has highly significant general direct and maternal heritabilities, and these two components are similar in magnitude, hence this trait might be improved through single plant selection and seed selection in various environments.

**Table 2 Heritabilities of Cooking Quality Characters in *Indica-Japonica* Crosses**

Parameters†	Amylose Content	Gel Consistency	Alkali Digestion Value
$h^2_O$	0.00	0.52*	0.40**
$h^2_C$	0.00	0.00	0.07
$h^2_M$	0.00	0.07	0.42**
$h^2_{OE}$	0.00	0.09	0.00
$h^2_{CE}$	0.00	0.45**	0.00
$h^2_{ME}$	0.53**	0.00	0.00

† $h^2_O$  =direct heritability;  $h^2_M$  =maternal heritability;  $h^2_C$  =cytoplasmic heritability;  $h^2_{OE}$  =direct×environment heritability;  $h^2_{ME}$  =maternal×environment heritability;  $h^2_{CE}$  =cytoplasmic×environment heritability.

## 2.2 Evaluation of Genetic Effects in Parents

Genetic effects are evaluated for two traits, gel consistency and alkali digestion value (Table 3). The highest positive general additive effect ( $A + Am$ ) for gel consistency is observed in Miyang59, followed by Miyang56 and Tx-1. The lowest values are observed for N422s. For alkali digestion value, only A1073s show significant negative values for direct additive effects, the others are positive. The highest positive direct additive effect is exhibited by Miyang59, and the lowest by E349. Miyang59 might therefore be the best parental line aiming at lower gelatinization temperature and softer gel consistency.

**Table 3 Predicted Genetic Effects of Cooking Quality Characters in Parents**

Traits	Effects†	Parental Varieties					
		A1073s	N422s	Miyang59	E349	Tx-1	Miyang56
Gel Consistency	$A$	11.69**	-34.21**	39.67**	-24.51**	5.06**	230
	$Am$	-46.42**	-48.75**	69.89**	7.39**	4.61**	46.27**
Alkali digestion Value	$A$	-2.57**	1.44**	2.25**	0.79**	2.18**	0.92**
	$Am$	-3.13**	0.84**	2.54**	2.77**	2.46**	1.52**

† $A$  =direct additive effect,  $Am$  =maternal additive effect

## 3 Discussion

The results in this study reveal that the genetic control of cooking quality characters in *indica-japonica* hybrids involve the direct genetic effects of endosperm genes, the maternal genetic effects and the cytoplasm effects, and the genetic parameters are influenced by genotype × environment interactions. In summary, direct and maternal additive effects are the main factors for the three cooking quality characters and, selection for these traits would be effective in progenies of *indica-japonica* crosses. The direct additive × environment variances are nonsignificant for the three traits, and the maternal additive variances are nonsignificant for gel consistency and alkali digestion value. This indicates that the additive effects are comparatively stable across environments, hence selections for cooking quality traits in *indica-japonica* crosses could be effectively

performed in various environments. The genotype  $\times$  environment interactions for cooking quality characters are operated mainly via dominance (including direct and maternal dominance) effects. Therefore heterosis of these traits might vary with environments. These results indicate that the partitioning of genotype  $\times$  environment interactions of the cooking quality traits into different components in terms of the different genetic systems is significant for the prediction of the usefulness of these traits in a breeding program.

Roach and Wulff (1987) considered three different effects as maternal effects: cytoplasmic genetic, endosperm nuclear and maternal phenotypic effects. This may increase the complexity of the interpretation and design of genetic studies for seed traits. For the cooking quality characters in the present study, maternal effects are defined as the genetic effects on seed traits of the nuclear genes of the maternal plant, which bear the seeds. The dosage effects of the endosperm nuclear genes in Roach and Wulff's (1987) can be regarded as the direct additive genetic effects of the seed.

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## 籼粳交稻米蒸煮品质性状的遗传效应分析

陈建国<sup>1</sup> 朱军<sup>2</sup>

(1 湖北大学 生命科学学院, 湖北 武汉 430062; 2 浙江大学 农学系, 浙江 杭州 310029)

**摘要:** 以 2 个粳型光温敏核不育系和 4 个籼稻品种为材料, 配制籼粳交组合, 用包括基因型  $\times$  环境互作效应的胚乳性状遗传模型对 3 个蒸煮品质性状 (直链淀粉含量、胶稠度、碱消值) 进行了遗传研究, 结果表明: 直接加性和母体加性效应对三个性状的遗传变异起主要作用。基因型  $\times$  环境互作主要表现为显性  $\times$  环境以及细胞质  $\times$  环境互作。直链淀粉含量的普通遗传率都不显著, 只有较高的互作母体遗传率; 胶稠度具有显著的普通直接遗传率和互作细胞质遗传率; 碱消值的普通直接遗传率和普通母体遗传率都极显著。根据遗传效应预测值对供试亲本的利用价值作了评价。

**关键词:** 水稻; 籼粳杂交; 蒸煮品质; 遗传效应; 基因型  $\times$  环境互作