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# Genetic and heterosis analysis for cooking quality traits of *indica* rice in different environments

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**Abstract** Genetic effects and genotype × environment (GE) interaction effects on the cooking quality traits of *indica* rice (*Oryza sativa* L.) were analyzed based on a genetic model for quantitative traits of triploid endosperm in cereal crops. Nine cytoplasmic male-sterile lines as females and 5 restoring lines as males were used in an incomplete diallel cross over 2 years. The cooking quality traits studied were observed to be mainly controlled by genetic effects, but GE interaction effects, especially for amylose content (AC) and alkali spreading score (ASS), were also indicated. Among the genetic effects, seed direct effects and maternal effects were the main components of AC and ASS, respectively; cytoplasmic effects were the main components of gel consistency (GC). Among the GE interaction effects, AC and ASS were mainly affected by maternal interaction effects and GC by direct interaction effects. Additive effects and/or additive interaction effects were the main factors controlling the performance of rice cooking quality traits except for GC which was affected by dominant interaction effects. For AC and GC, there were seed heterosis and/or maternal heterosis. The predicated genetic effects indicated that four parents were better than the others in improving the rice cooking quality traits of the progenies. It was shown that genetic heterosis and GE interaction heterosis were important, especially for amylose content trait in early season *indica* rice.

**Key words** Cooking quality · Genetic effects · Genotype × environment interactions · Heterosis · *Indica* rice

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## Introduction

In cereal crops, kernel traits have been widely studied. Maternal influences have been detected on oleic and linoleic acid contents or fatty acid compositions of triglycerides and phospholipids in corn (Garwood et al. 1970; Poneleit and Bauman 1970; Weber 1983). Dhaliwal (1977) and Rasyad and Van Sanford (1992) found that maternal effects were important in the inheritance of seed proteins or kernel growth traits of wheat. By means of a reciprocal cross showed (Ullrich and Estick 1978) that there were dosage effects and maternal effects on the protein and lysine contents of seed in barley. Cytoplasmic effects are also involved in the inheritance of yield and grain quality in maize (Rao and Fleming 1978) and wheat (Kofoid and Maan 1982). Qi et al. (1983) observed maternal effects but only small cytoplasmic effects on the rice shape traits, while Poneleit and Egli (1983) observed maternal effects but not cytoplasmic effects on corn kernel growth traits by means of a diallel analysis with four inbred lines. Yu et al. (1992) found that maternal effects and/or cytoplasmic effects are important in the inheritance of some kernel traits in barley. Pooni et al. (1992) suggested that amylose content might be related to the effects of the maternal plant or cytoplasm. Yi and Cheng (1991, 1992) found that some cooking and nutrient quality traits of rice are affected by different types of cytoplasm.

Matzinger et al. (1971) pointed out that a genotype-by-year interaction exists when measuring heterosis and estimating genetic variances. Chauhan et al. (1992) also observed that quality traits like amylose content, milling recovery, water uptake and kernel elongation of rice behave differently to environments. Peterson (1992) found important genotype × environment interaction effects on kernel quality traits in wheat.

Cooking quality traits are closely related to the quality of milled rice. Higher amylose content, harder gel consistency and higher gelatinization temperature are

the main factors influencing the quality of *indica* rice in China. Rice traits will be affected by genetic effects as well as by environmental conditions such as weather, soil and culture management. Both genotype × environment (GE) interaction effects as well as genetic effects on seed traits need to be studied. Although the results of Shi and Zhu (1993, 1994) and Shi et al. (1996a) showed that some rice quality traits are controlled by seed, cytoplasmic and maternal plant genes, GE interaction effects and their influence on heterosis have not been studied for these traits.

In the present paper, genetic models for quantitative traits of endosperm in cereal crops were used to evaluate genetic effects and GE interaction effects of the seed, cytoplasm and maternal plant, and to predict the breeding value of the parents and heterosis in hybrid breeding for cooking quality traits of rice.

## Materials and methods

Nine cytoplasmic male-sterile (CMS) lines (P1 = Zhexie 2 A, P2 = Xieqingzao A, P3 = Zhenan 3 A, P4 = Gangchao 1 A, P5 = Yinchao 1 A, P6 = Erjiuqing A, P7 = $V_{20}$A, P8 = Zuo 5 A, P9 = Zhenshan 97 A) and 5 restoring lines (P10 = T 49, P11 = Cezao 2-2, P12 = 26715, P13 = 102, P134 = 1391) of early season *indica* rice (*Oryza sativa* L.) were used in this experiment. These CMS and restoring lines were a random sample of parents for a reference population of hybrid rice in China. Seedlings of the parents and $F_1$s of an incomplete diallel cross (9 × 5) with three replications were planted in the experimental farm at Zhejiang Agricultural University in 1994 and 1995. The seeds were sown on March 28 in 1994 and April 3 in 1995, and single plants of 31-day-old seedlings were transplanted at a spacing of 20 × 20 cm. There were 24 plants in each plot. Seed samples from the parents and $F_2$s on $F_1$ plants were derived at maturity from 8 plants located in the middle part of each plot. The $F_1$ seeds used for analyzing were obtained in the same field from CMS lines which had been crossed to the restoring lines during the flowering season. The quantitative traits of rice cooking quality analyzed were amylose content (AC) by the method of Perez and Juliano (1978), gel consistency (GC) by the procedure of Cagampang et al. (1973) and alkali spreading score (ASS, grade) by the method of Little et al. (1958). These traits were measured with three replications for each sample of parents, $F_1$s and $F_2$s.

The genetic model used is an extension of the endosperm model (Zhu and Weir 1994b) by including GE interaction effects (Zhu 1994, 1996a). For a diallel mating from a set of inbred lines, the generation mean ($y_{hijkl}$) of mating type $k$ from maternal line $i$ and paternal line $j$ in block $l$ of environment $h$ can be partitioned as,

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

where $\mu$ = the population mean, fixed; $E_h$ = the environmental effect, fixed; $G_{ijk}$ = genotypic effect; $GE_{hijk}$ = genotype × environment interaction effect; $B_{l(h)}$ = the block effect, random; $e_{hijkl}$ = residual effect, random.

Partitioning of $G_{ijk}$ and $GE_{hijk}$ can be expressed according to different generations:

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

$$G_{ii0} + GE_{hii0} = 3A_i + 3D_{ii} + C_i + 2Am_i + Dm_{ii} + 3AE_{hi} + 3DE_{hii} + CE_{hi} + 2AmE_{hi} + DmE_{hii}$$

$F_{1ij}$ ($k = 1$)

$$G_{ij1} + GE_{hij1} = 2A_i + A_j + D_{ii} + 2D_{ij} + C_i + 2Am_i + Dm_{ii} + 2AE_{hi} + AE_{hj} + DE_{hii} + 2DE_{hij} + CE_{hi} + 2AmE_{hi} + DmE_{hii}$$

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

$$G_{ij2} + GE_{hij2} = 1.5A_i + 1.5A_j + D_{ii} + D_{jj} + D_{ij} + C_i + Am_i + Am_j + Dm_{ij} + 1.5AE_{hi} + 1.5AE_{hj} + DE_{hii} + DE_{hjj} + DE_{hij} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_h$$

where direct additive effect $A_i$ or $A_j \sim (0, \sigma^2_A)$; direct dominance effect $D_{ii}$, $D_{jj}$ or $D_{ij} \sim (0, \sigma^2_D)$; cytoplasm effect $C_i \sim (0, \sigma^2_C)$; maternal additive effect $Am_i$ or $Am_j \sim (0, \sigma^2_{Am})$; maternal dominance effect $Dm_{ii}$, $Dm_{jj}$ or $Dm_{ij} \sim (0, \sigma^2_{Dm})$; direct additive interaction effect $AE_{hi}$ or $AE_{hj} \sim (0, \sigma^2_{AE})$; direct dominance interaction effect $DE_{hii}$, $DE_{hjj}$ or $DE_{hij} \sim (0, \sigma^2_{DE})$; cytoplasm interaction effect $CE_{hi} \sim (0, \sigma^2_{CE})$; maternal additive interaction effect $AmE_{hi}$ or $AmE_{hj} \sim (0, \sigma^2_{AmE})$; maternal dominance interaction effect $DmE_{hii}$, $DmE_{hjj}$ or $DmE_{hij} \sim (0, \sigma^2_{DmE})$. There are covariances between direct effects and maternal effects $\mathrm{Cov}(A_i, Am_i) = \mathrm{Cov}(A_j, Am_j) = \sigma_{A.Am}$, $\mathrm{Cov}(D_{ii}, Dm_{ii}) = \mathrm{Cov}(D_{ij}, Dm_{ij}) = \sigma_{D.Dm}$, $\mathrm{Cov}(AE_{hi}, AmE_{hi}) = \mathrm{Cov}(AE_{hj}, AmE_{hj}) = \sigma_{AE.AmE}$, $\mathrm{Cov}(DE_{hii}, DmE_{hii}) = \mathrm{Cov}(DE_{hij}, DmE_{hij}) = \sigma_{DE.DmE}$.

The MINQUE (0/1) method (Zhu and Weir 1994a) was used to estimate variances and covariances. Phenotypic variance ($V_p$) of seed quantitative traits is composed of several genetic components,

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

where $V_A = 4.5\sigma^2_A$, $V_D = 3\sigma^2_D$, $V_C = \sigma^2_C$, $V_{Am} = 2\sigma^2_{Am}$, $V_{Dm} = \sigma^2_{Dm}$, $V_{AE} = 4.5\sigma^2_{AE}$, $V_{DE} = 3\sigma^2_{DE}$, $V_{CE} = \sigma^2_{CE}$, $V_{AmE} = 2\sigma^2_{AmE}$, $V_{DmE} = \sigma^2_{DmE}$, $C_{A.Am} = 3\sigma_{A.Am}$, $C_{D.Dm} = \sigma_{D.Dm}$, $C_{AE.AmE} = 3\sigma_{AE.AmE}$, $C_{DE.DmE} = \sigma_{DE.DmE}$, $V_e = \sigma^2_e$ (Zhu and Weir 1994b).

The AUP method (Zhu 1993; Zhu and Weir 1996) was used to predict genetic effects as well as GE interaction effects with which heterosis over the mean of parents was calculated for $F_2$. In order to compare heterosis for different traits, heterosis was adjusted by population mean $\mu$ ($H = [F_2 - (P_1 + P_2)/2]/\mu$). The partitioning of total heterosis is as

$$H = H_G + H_{GE} = (H_O + H_C + H_M) + (H_{OE} + H_{CE} + H_{ME})$$

where $H_G$ = the genetic heterosis, $H_{GE}$ = the interaction heterosis, $H_O$ = direct heterosis, $H_C$ = cytoplasmic heterosis, $H_M$ = maternal heterosis, $H_{OE}$ = direct interaction heterosis, $H_{CE}$ = cytoplasmic interaction heterosis, $H_{ME}$ = maternal interaction heterosis (Zhu 1996b).

The Jackknife technique (Miller 1974; Zhu 1992; Zhu and Weir 1994a) was applied by sampling generation means of entries for estimating the standard errors of estimated variances or covariances and of predicated genetic effects and heterosis. All data were analyzed on an IBM PC computer by programs written in the C language.

## Results

The estimates of genetic variances, GE interaction variances, residual variances and covariances are presented in Table 1, and the predicated genetic effects and GE

interaction effects on cooking quality traits are listed in Table 2. Heteroses of cooking quality traits of rice are presented in Tables 3 and 4.

## Estimation of genetic variances and covariances

For the three cooking quality traits studied, no significant relationships were found between direct and maternal effects, or between direct interaction effects and maternal interaction effects (Table 1). There existed small but significant residual effects for these three traits.

Amylose content of milled rice was mainly controlled by direct additive effects ($A$) and direct additive interaction effects ($AE$). Maternal additive interaction effects ($AmE$) were also important for amylose content. Cytoplasmic effects ($C$) were detectable but small for amylose content. Although dominance effects ($D$ and $Dm$) and their environment interaction effects ($DE$ and $DmE$) were significant, they were smaller than their additive counterparts. Therefore, it is possible to improve the amylose content of rice by selecting seeds or plants of early generations.

For the gel consistency of milled rice, cytoplasmic effects ($C$) and maternal additive effects ($Am$) were the two largest components among genetic and GE interaction effects. There were small but significant direct additive effects ($A$) and direct dominance interaction effects ($DE$) for gel consistency. It has been suggested that improving gel consistency of milled rice is more efficient when selection is conducted on cytoplasm and plants than on seeds.

The alkali spreading score of milled rice was mainly controlled by maternal additive effects ($Am$), followed by cytoplasmic effects ($C$) and its environment interaction effects ($CE$). Direct additive effects ($A$) and direct interaction effects ($AE$ and $DE$) were relatively smaller. Therefore, the alkali spreading score could be improved more easily by selecting plants and cytoplasm rather than by screening seeds.

**Table 1** Estimation of variance and covariance components for genetic effects and genotype × environment interaction effects of cooking quality traits in *indica* rice

| Parameter | Amylose content | Gel consistency | Alkali spreading score |
|---|---|---|---|
| $V_A$ | 35.63* | 87.86† | 0.45† |
| $V_D$ | 2.68* | 0 | 0 |
| $V_C$ | 4.50* | 691.69* | 2.04* |
| $V_{Am}$ | 0 | 280.04* | 4.00* |
| $V_{Dm}$ | 1.09* | 20.75* | 0 |
| $V_{AE}$ | 12.67* | 0 | 0.47* |
| $V_{DE}$ | 2.48* | 52.99* | 0.58* |
| $V_{CE}$ | 0 | 29.1† | 2.08* |
| $V_{AmE}$ | 13.23* | 0 | 1.82* |
| $V_{DmE}$ | 8.21** | 48.27* | 0.94* |
| $C_{A.Am}$ | 0 | − 392.13 | − 2.46 |
| $C_{D.Dm}$ | − 0.47 | 0 | 0 |
| $C_{AE.AmE}$ | − 14.14 | 0 | − 1.81 |
| $C_{DE.DmE}$ | − 0.26 | − 18.4 | − 0.03 |
| $V_e$ | 1.08* | 2.62† | 0.06* |

†, * and ** are significant at the 0.10, 0.05 and 0.01 levels, respectively

**Table 2** Predicated genetic effects and genotype × environment interaction effects of some parents for cooking quality traits in *indica* rice ($A$ seed additive effects. $C$ cytoplasmic effects. $Am$ maternal additive effects. $AE_1$ and $AE_2$ seed direct additive interaction effects. $CE_1$ and $CE_2$. cytoplasmic interaction effects. $AmE_1$ and $AmE_2$ maternal additive interaction effects in 1994 and 1995, respectively)

| Parent | $A$ | $AE_1$ | $AE_2$ | $C$ | $CE_1$ | $CE_2$ | $Am$ | $AmE_1$ | $AmE_2$ |
|---|---|---|---|---|---|---|---|---|---|
| *Amylose content* (%) | | | | | | | | | |
| P1 | 1.35† | 0.03 | 1.34† | 0.88† | – | – | – | 2.91† | − 1.96† |
| P2 | 3.38† | 1.10† | 2.32† | 3.21† | – | – | – | 0.50 | − 2.10 |
| P4 | 2.12† | 0.57† | 1.57† | 0.56† | – | – | – | − 1.95† | 2.21† |
| P5 | 2.33† | 0.57 | 1.79† | 1.59† | – | – | – | 1.09 | − 3.56† |
| P12 | − 7.05† | − 2.62† | − 4.50† | − 6.14† | – | – | – | − 2.53 | − 0.85 |
| *Gel consistency* (*mm*) | | | | | | | | | |
| P1 | − 1.83† | – | – | − 14.00† | − 1.98 | − 3.03† | 3.71† | – | – |
| P2 | − 3.69† | – | – | − 18.27† | − 3.34† | − 3.19† | 3.36† | – | – |
| P4 | − 4.01† | – | – | − 20.53† | − 5.35† | − 1.96† | 7.19† | – | – |
| P5 | − 4.54† | – | – | − 22.85† | − 3.72† | − 4.43† | 3.99† | – | – |
| P12 | 17.99† | – | – | 99.78† | 19.80† | 15.93† | − 49.67† | – | – |
| P14 | 5.77† | – | – | 58.61† | 19.27† | 1.57 | 13.70 | – | – |
| *Alkali spreading score* | | | | | | | | | |
| P1 | − 0.16 | − 0.24† | 0.11† | − 1.58† | 0.32† | − 1.88† | 1.71† | 1.97† | − 0.65† |
| P2 | − 0.16 | − 0.08 | − 0.06* | − 1.74† | 1.39† | − 3.11† | 0.97† | − 1.30† | 2.05† |
| P4 | 0.23 | − 0.05† | 0.24† | − 0.46† | 0.87† | − 1.33† | 1.71† | 0.53† | 0.79† |
| P5 | − 0.07 | − 0.22† | 0.16† | − 2.38† | − 0.12 | − 2.23† | 1.86† | 1.61† | − 0.17 |
| P7 | 0.20† | − 0.15† | 0.31† | 1.13† | − 0.23† | 1.35† | 0.60† | − 0.59† | 1.05† |
| P8 | 0.30† | − 0.42† | 0.66† | 0.60† | − 0.71† | 1.30† | 0.12† | 0.35* | − 0.25* |

† and * are significant at the 0.10 and 0.05 levels, respectively

**Table 3** Mean (range) of heteroses for cooking quality traits of $F_2$ seed in *indica* rice

| Parameter | Genetic heterosis | Interaction heterosis in 1994 | Interaction heterosis in 1995 |
|---|---|---|---|
| *Amylose content* | | | |
| Direct heterosis | − 0.03 (− 0.14–0.07) | 0.01 (− 0.18–0.14) | − 0.04 (− 0.12–0.07) |
| Cytoplasmic heterosis | 0.05 (− 0.07–0.16) | 0 | 0 |
| Maternal heterosis | 0.02 (− 0.11–0.09) | − 0.03 (− 0.59–0.33) | 0.10 (− 0.23 − 0.33) |
| *Gel consistency* | | | |
| Direct heterosis | 0 | − 0.13 (− 0.71–0.50) | − 0.02 (− 0.49–1.04) |
| Cytoplasmic heterosis | − 0.80 (− 2.30–0.13) | − 0.20 (− 0.52–0.07) | − 0.07 (− 0.38–0.22) |
| Maternal heterosis | − 0.24 (− 1.25–0.33) | − 0.37 (− 1.26–0.99) | − 0.10 (− 1.67–1.40) |
| *Alkali spreading score* | | | |
| Direct heterosis | 0 | 0.16 (− 0.18–0.43) | − 0.14 (− 0.44–0.22) |
| Cytoplasmic heterosis | − 0.29 (− 0.58–0.11) | 0.10 (− 0.08–0.40) | − 0.38 (− 0.96–0.11) |
| Maternal heterosis | 0 | 0.04 (− 0.43–0.59) | − 0.35 (− 1.08–0.40) |

**Table 4** Mean (range) of heteroses with significant value for cooking quality traits of $F_2$ seed in *indica* rice

| Parameter | Genetic heterosis | | Interaction heterosis in 1994 | | Interaction heterosis in 1995 | |
|---|---|---|---|---|---|---|
| | NC[a] | Mean (Range) | NC | Mean (Range) | NC | Mean (Range) |
| *Amylose content* | | | | | | |
| Direct heterosis | 10 | 0.04 (0.01–0.07) | 14 | 0.07 (0.02–0.14) | 7 | 0.04 (0.01–0.07) |
| | 28 | − 0.06 (− 0.14– − 0.02) | 11 | − 0.08 (− 0.18– − 0.03) | 23 | − 0.08 (− 0.12 − –0.02) |
| Cytoplasmic heterosis | 28 | 0.09 (0.03–0.16) | – | – | – | – |
| | 7 | − 0.04 (− 0.07– − 0.02) | – | – | – | – |
| Maternal heterosis | 24 | 0.06 (0.01–0.09) | 7 | 0.18 (0.10–0.33) | 18 | 0.24 (0.10–0.33) |
| | 8 | − 0.05 (− 0.11– − 0.02) | 14 | − 0.19 (− 0.59– − 0.03) | 11 | − 0.12 (− 0.23– − 0.06) |
| *Gel consistency* | | | | | | |
| Direct heterosis | – | – | 7 | 0.16 (0.05–0.50) | 13 | 0.34 (0.07–1.04) |
| | – | – | 19 | − 0.34 (− 0.71– − 0.04) | 19 | − 0.25 (− 0.49– − 0.07) |
| Cytoplasmic heterosis | 5 | 0.08 (0.04–0.13) | 5 | 0.04 (0.02–0.07) | 13 | 0.11 (0.03–0.22) |
| | 39 | − 1.00 (− 2.30– − 0.11) | 31 | − 0.27 (− 0.52– − 0.06) | 24 | − 0.18 (− 0.38– − 0.01) |
| Maternal heterosis | 7 | 0.16 (0.08–0.33) | 6 | 0.30 (0.05–0.99) | 15 | 0.38 (0.07–1.40) |
| | 33 | − 0.34 (− 1.25– − 0.04) | 26 | − 0.59 (− 1.26– − 0.09) | 16 | − 0.54 (− 1.67– − 0.10) |
| *Alkali spreading score* | | | | | | |
| Direct heterosis | – | – | 30 | 0.23 (0.04–0.43) | 4 | 0.15 (0.09–0.22) |
| | – | – | 4 | − 0.10 (− 0.18– − 0.04) | 32 | − 0.21 (− 0.44– − 0.04) |
| Cytoplasmic heterosis | 3 | 0.07 (0.05–0.11) | 29 | 0.15 (0.01–0.40) | 2 | 0.11 (0.11–0.11) |
| | 40 | − 0.33 (− 0.58– − 0.05) | 4 | − 0.05 (0.08– − 0.01) | 38 | − 0.46 (− 0.96– − 0.06) |
| Maternal heterosis | 0 | – | 15 | 0.30 (0.05–0.59) | 9 | 0.19 (0.03–0.40) |
| | 0 | – | 7 | − 0.24 (− 0.42– − 0.10) | 16 | − 0.75 (− 1.08– − 0.25) |

[a] NC, Number of crosses with a significant positive or negative value

It was shown that total genetic variance ($V_G = V_A + V_D + V_C + V_{Am} + V_{Dm}$) was larger than total GE interaction variance ($V_{GE} = V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}$) for amylose content and gel consistency of milled rice. These two traits were, therefore, controlled mainly by genetic effects and less by GE interaction effects. For the alkali spreading score of milled rice, GE interaction effects were as equally important as genetic effects, indicating that environments can shape the genetic behavior of genes in the endosperm, cytoplasm and plant.

## Prediction of genetic effects and genotype × environment interaction effects

The genetic effects and GE interaction effects with significant variances in Table 1 were used to predict the merit values of the parents used in this experiment (Table 2).

It was shown by this prediction that additive ($A$) and cytoplasmic ($C$) effects of CMS lines tended to increase the amylose content of rice but that the reverse was true for restoring lines. Because high amylose content was

one of the factors reducing the cooking quality of milled rice, P12 was a better parent than the others for reduced amylose content. The interaction effects of $AE_1$ and $AE_2$ had the same direction as the direct additive effects ($A$). The different sign of $AmE_1$ and $AmE_2$ for some parents suggested that environments could affect the gene expression of the maternal plant in opposite ways for amylose content.

Cytoplasmic effects ($C$) and their interaction effects ($CE$) as well as direct additive effects ($A$) could significantly reduce gel consistency for CMS lines but increase that for restoring lines. Maternal additive effects ($Am$) tended to increase gel consistency for CMS lines but decrease that for restoring lines. P12 and P14 were better than other parents for an improved gel consistency.

Maternal additive effects ($Am$) could increase the alkali spreading score of milled rice. Cytoplasmic effects would decrease the score value of alkali spreading for CMS lines but increase the value for restoring lines. Environments could affect gene expression in different ways for additive, cytoplasmic and maternal interaction effects. Environmental effects on direct additive interaction ($AE$) had a tendency to enlarge the score value of alkali spreading in 1995, but reduce it in 1994. This tendency was not observed for cytoplasmic interaction ($CE$) and maternal additive interaction ($AmE$). But it was obvious that environments in 1994 and 1995 had different effects on gene expression in the cytoplasm and maternal plant for the alkali spreading score of milled rice.

### Analysis of direct, maternal and cytoplasmic heterosis

The heterosis of cooking quality traits in rice can be partitioned into genetic heterosis ($H_G$) and interaction heterosis ($H_{GE}$). According to the magnitude of the heterosis components, the genetic mechanism can be illustrated for heterosis of cooking quality traits in early season *indica* hybrid rice (Tables 3 and 4).

For amylose content, the average cytoplasmic heterosis was about 5% (Table 3) in 45 hybrids of which 28 hybrids had a significant positive heterosis with an average of 9% (Table 4). The direct heterosis and its interaction heterosis had different signs as compared to the maternal counterparts. The direct heterosis had an average of −6% for 28 hybrids, and the direct interaction heterosis was −8% for 23 hybrids in 1995 but 7% for 14 hybrids in 1994. Although positive heterosis was observed for maternal heterosis (2%) and maternal interaction heterosis in 1995 (10%), negative heterosis was found for maternal heterosis (−5% in 8 hybrids) and maternal interaction heterosis (−19% in 14 hybrids from 1994 and −12% in 11 hybrids from 1995).

The gel consistency in early season *indica* hybrid rice tended to have negative heterosis. The average heterosis of 45 hybrids was −80% for cytoplasm effects and −24% for maternal effects (Table 3). The environment interaction could have had more effects on negative heterosis in 1994 than that in 1995 for gel consistency.

The average genetic heterosis of the alkali spreading score was −29% for 45 hybrids of which 40 hybrids showed significant negative genetic heterosis (−33%). Environments tended to cause positive interaction heterosis in 1994 but negative interaction heterosis in 1995. Interaction heterosis in 1994 was 23% for direct interaction heterosis of 30 hybrids, 15% for cytoplasmic interaction heterosis of 29 hybrids and 30% for maternal interaction heterosis of 15 hybrids. Meanwhile, interaction heterosis in 1995 was −21% for direct interaction heterosis of 32 hybrids, −46% for cytoplasmic interaction heterosis of 38 hybrids and −75% for maternal interaction heterosis of 16 hybrids.

## Discussion

Rice cooking quality is one of the important characteristics of rice varieties and is a restricting factor in rice breeding in China. Therefore, any knowledge that can be gained on the genetic mechanism of cooking quality traits will be helpful in improving the breeding efficiency of *indica* rice. Since seeds are the progenies of maternal plant and the nutrient materials of rice also come from the maternal plant, some quality traits will be affected by genetic effects and GE interaction effects of the seed, maternal plant and cytoplasm.

Although the models and statistical methods proposed by Bogyo (1988) and Mo (1988) could be used for analyzing the additive and dominance effects of seed endosperm genes, biased estimation would be obtained when analyzing the endosperm quantitative traits controlled by seed direct, cytoplasmic and maternal effects. Pooni et al. (1992) proposed a model which can analyze the seed direct effects and maternal/cytoplasm effects of endosperm traits, but this model can not differentiate the maternal and cytoplasm effects. Although the genetic model proposed by Foolad and Jone (1992) can estimate seed direct, cytoplasmic and maternal effects for quantitative traits of endosperm, it is very difficult to use this model as it requires the measurement of single seeds and 17 generations. If there was no GE interaction effects for quantitative traits of endosperm, the seed direct, cytoplasmic and maternal genetic effects for endosperm quantitative traits could be estimated using the models proposed by Zhu and Weir (1994b). When the GE interaction effects are really important for the quantitative traits of endosperm, the triploid models without GE interaction would give biased estimates. Therefore, when GE interaction effects for the quantitative traits of endosperm exist we need to use genetic models which are biological

meaningful and can be appropriately analyzed by statistical methods. The experiment should also be conducted in different environments.

The genetic model and statistical analysis method (Zhu 1994, 1996) used in this experiment can estimate genetic effects and GE interaction effects for quantitative traits of endosperm by using only three generations (Parents, $F_1$ and $F_2$) in a set of crosses in two environments. In comparison to other genetic models for triploid, this method, which can differentiate the genetic effects and GE interaction effects, is simple, convenient and applicable. On the basis of the magnitude of the genetic effects and GE interaction effects, it was able to illustrate the genetic mechanism of endosprem quality traits which were important in improving rice quality in rice breeding. In general, if GE interaction effects have the same direction as genetic effects, selection could significantly improve seed quality traits. Breeders could select breeding materials suitable to different environments for the traits with small GE interaction effects. If GE interaction effects are larger or GE interaction effects in different environments are not in the same direction for endosperm quality traits, breeders could only obtain breeding materials suitable to a specific environment. The present results indicated that cooking quality traits of *indica* rice are mainly controlled by genetic effects but are also affected by GE interaction effects. GE interaction effects, cannot be neglected especially for maternal interaction effects on amylose content and alkali spreading score, and for seed direct interaction effects on the gel consistency of milled rice.

Not only do breeders need to understand the inheritance mechanism of seed quality traits, they also want to know the genetic merit of parents or the heterosis of crosses for improving rice quality. According to the predicted breeding value of genetic effects and GE interaction effects in different environments (years) for parents, the breeders could select better parent(s) for improving quality traits. In the present study, it was shown that P7, P8, P12 and P14 had better genetic effects and GE interaction effects for rice cooking quality traits. Therefore, these varieties would be the better parents cross(es) for improving some of cooking quality traits and could be used as parents in rice breeding.

It is important to use heterosis of traits in hybrid rice breeding. Although the seeds of the $F_1$ plant were the progenies that differed from their maternal plant, the nutrients in endosperm come from maternal plant. Therefore, heterosis of endosperm traits such as rice nutrient quality traits could be simultaneously influenced by seed direct, cytoplasmic and maternal effects (Shi et al. 1996b). We have studied the genetic effects and GE interaction effects for heterosis of cooking quality traits using data from different environments. The results indicated that the heterosis of cooking quality was influenced by genetic effects and GE interaction effects, especially for the amylose content trait of early season *indica* rice. Rice breeders should therefore pay more attention to the variation of heterosis of cooking quality of rice in different environments or years.

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