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Genetic and genotype × environment interaction effects from embryo, endosperm, cytoplasm and maternal plant for rice grain shape traits of *indica* rice

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Abstract

A seed genetic model with embryo, endosperm, cytoplasmic and maternal effects and genotype × environment (GE) interaction effects was used for analyzing ratio of length-to-width (RLW) and ratio of length-to-thickness (RLT) of *indica* rice (*Oryza sativa* L.). A factorial mating design in two environments was conducted by including nine cytoplasmic male sterile lines (A) and five restorer lines (R) along with their F_1 ($A \times R$), F_2, reciprocal RF_2 and BC_1 ($A \times F_1$). RLW and RLT were found to be controlled mainly by genetic main effects, but also by GE interaction effects. Variance of maternal effects was larger than other variance components. Variance due to embryo effects and embryo × environment interaction effects could also significantly affect the rice grain shape traits. The total narrow-sense heritability for RLW and RLT were about 85.6 and 69.9%, respectively, with the general heritabilities being 62.5 and 61.9% and the interaction heritabilities being 23.1 and 7.9%. It was suggested by the predicted genetic effects that Zhexie 2, Xieqingzao and Cezao 2-2 were better than other parents for improving rice grain shape traits. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Indica* rice; Rice grain shape traits; Genetic variances; Seed embryo effect; Heritability

1. Introduction

The length and width of rice grain are two of the important quantitative traits closely related to the exterior quality of *indica* rice (*Oryza sativa* L.). Rice grain shape has become one of the main goals in rice breeding, because consumers usually prefer milled rice with spindly shape and greater transparency. For rice breeding programs, understanding the inheritance, specifically gene action, for rice grain shape traits is desirable. Genetic analyses of length or width of rice grain have been reported by others and most of the studies have shown that rice grain shape is quantitatively inherited (Kuo and Hsieh, 1982; Qi et al., 1983; Jun, 1986; Yi and Cheng, 1991; Fu et al., 1994; Xu et al., 1996; Chen et al., 1998). It has recently been shown that rice grain shape is simultaneously controlled by triploid endosperm genes, cytoplasmic genes and maternal plant genes (Shi and Zhu, 1996) and their genotype × environment (GE) interaction effects (Chen and Zhu, 1998; Shi et al., 1999), but the genetic effects on the embryo have not previously been demonstrated.

The rice grain is a complex tissue that is composed of embryo, endosperm, testa and carpodermis. Diploid

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embryo and triploid endosperm are two important parts of a grass (poaceae) caryopsis (grain). In barley, Yan et al. (1998, 1999) have shown that the embryo and/or embryo × environment interaction affect the performance of grain quality traits as well as endosperm and endosperm interaction effects. Shi et al. (1999) found that protein content and protein index of rice was affected by GE interaction due to diploid embryo genes. Therefore, effects of diploid embryo genes might also affect the performance of rice grain shape traits in *indica* rice. Since no information on embryo genetic main effects and embryo× environment interaction effects has been reported for rice grain shape traits, it was the purpose of this study to apply a quantitative genetic model to test for these effects. Specifically, the objectives of this study were to evaluate the genetic effects and GE interaction effects for embryo, endosperm, cytoplasm and maternal plant contributions to rice grain shape, to estimate the narrow-sense heritabilities and to predict breeding merit of parents for rice grain shape traits of *indica* rice.

2. Materials and methods

The mating design used for this experiment was a factorial design with 14 parents. The materials, which were all early season *indica* rice genotypes, comprised nine cytoplasmic male sterile lines (CMS or A) and their maintainer lines (B) (Zhexie 2, slender shape; Xieqingzao, slender shape; Zhenan 3, bold shape; Gangchao 1, bold shape; Yinchao 1, bold shape; Erjiuqing, bold shape; V_{20}, slender shape; Zuo 5, medium shape and Zhenshan 97, bold shape) and five restorer lines (R) (T 49, medium shape; Cezao 2-2, medium shape; 26715, slender shape; 102, slender shape and 1391, slender shape). All female parents were crossed to male parents to obtain F_1 (A × R) and reciprocal RF_1 (R × B) in 1994. Seedlings of parents, F_1 and RF_1 were planted at the experimental farm of Zhejiang Agricultural University in 1995 and 1996. The seeds were sown on 2nd April in both years and 30-day-old seedlings were individually transplanted at a spacing of 20 cm × 20 cm within rows. There were 24 plants in each plot for parents, F_1 and RF_1. The experiment was laid out in a randomized block design with three field replications. Seed samples were taken at maturity from each of the eight plants in the middle part of each plot for the parent plants, F_1 (A × R) plants (F_2 seed) and RF_1 (R × B) plants (RF_2 seed). Samples of F_1 (A × R) and BC_1 (A × F_1) seeds were obtained during the growing season by using the method of isolated pollination since the females were all CMS lines. The length (mm), width (mm) and thickness (mm) of brown rice with only the lemma and palea removed were measured with vernier calipers for each sample of parents, F_1, F_2, RF_2 and BC_1 from the three replications. Each seed sample came from a single field plot from which three subsamples of 30–50 random seed were measured to provide the plot means used in the analysis. The rice grain shape traits analyzed were ratio of length-to-width of rice (RLW) and ratio of length-to-thickness (RLT).

Analyses of the embryo, endosperm, cytoplasmic and maternal genetic main effects and their GE interaction effects for rice grain shape traits were undertaken by using a genetic model for quantitative traits of seed in cereal crops (Zhu, 1997). This model is derived by combining a diploid seed model (Zhu and Weir, 1994a) and a triploid endosperm model (Zhu and Weir, 1994b) extended to include GE interaction effects (Zhu, 1996). 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

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

where μ is the population mean, fixed; E_h the environmental (year) effect, fixed; G_{ijk} genetic effect with components of embryo additive (Ao) and dominance (Do) effects, endosperm additive (Ae) and dominance (De) effects, cytoplasmic effect (C), maternal additive (Am) and dominance (Dm) effects; GE_{hijk} genotype× environment interaction effect with components of embryo additive interaction (AoE) and dominance interaction (DoE) effects, endosperm additive interaction (AeE) and dominance interaction (DeE) effects, cytoplasmic interaction effect (CE), maternal additive interaction (Am) and dominance interaction (Dm) effects, random; $B_{l(h)}$ the block effect, random; e_{hijkl} residual effect, random.

The MINQUE (1) method (Zhu and Weir, 1996) was used to estimate variance components. Phenotypic variance (V_P) of rice grain shape traits is composed of several genetic components

$$\begin{aligned} V_\mathrm{P} &= V_\mathrm{G} + V_\mathrm{GE} + V_\mathrm{e} \\ &= (V_\mathrm{Ao} + V_\mathrm{Do} + V_\mathrm{Ae} + V_\mathrm{De} + V_\mathrm{C} + V_\mathrm{Am} + V_\mathrm{Dm}) \\ &\quad + (V_\mathrm{AoE} + V_\mathrm{DoE} + V_\mathrm{AeE} + V_\mathrm{DeE} + V_\mathrm{CE} + V_\mathrm{AmE} \\ &\quad + V_\mathrm{DmE}) + V_\mathrm{e} \end{aligned}$$

where V represents the variance due to the effects identified above.

The estimated total narrow-sense heritability consisted of general heritability (h^2_G) due to genetic main effects and interaction heritability (h^2_GE) due to GE interaction effects. The general heritability has components of embryo general heritability ($h^2_\mathrm{Go} = V_\mathrm{Ao}/V_\mathrm{P}$), endosperm general heritability ($h^2_\mathrm{Ge} = V_\mathrm{Ae}/V_\mathrm{P}$), cytoplasmic heritability ($h^2_\mathrm{C} = V_\mathrm{C}/V_\mathrm{P}$), and maternal general heritability ($h^2_\mathrm{Gm} = V_\mathrm{Am}/V_\mathrm{P}$). The interaction heritability (h^2_GE) has components of embryo interaction heritability ($h^2_\mathrm{GoE} = V_\mathrm{AoE}/V_\mathrm{P}$), endosperm interaction heritability ($h^2_\mathrm{GeE} = V_\mathrm{AeE}/V_\mathrm{P}$), cytoplasmic interaction heritability ($h^2_\mathrm{CE} = V_\mathrm{CE}/V_\mathrm{P}$) and maternal interaction heritability ($h^2_\mathrm{GmE} = V_\mathrm{AmE}/V_\mathrm{P}$). The partitioning for the total narrow-sense heritability is

$$\begin{aligned} h^2 = h^2_\mathrm{G} + h^2_\mathrm{GE} &= (h^2_\mathrm{Go} + h^2_\mathrm{Ge} + h^2_\mathrm{C} + h^2_\mathrm{Gm}) \\ &\quad + (h^2_\mathrm{GoE} + h^2_\mathrm{GeE} + h^2_\mathrm{CE} + h^2_\mathrm{GmE}) \end{aligned}$$

An adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996) was used to predict components of genetic main effects and GE interaction effects. The Jackknife method (Miller, 1974; Zhu and Weir, 1996) was applied by sampling generation means of entries to derive the standard errors of estimated variances, heritabilities and predicted genetic effects. All data were analyzed by the programs of Zhu (1997).

3. Results

3.1. Phenotypic means of the generations

The means and ranges of generations showed that there was large variation for the two rice grain shape traits among materials studied (Table 1). The means of restorer lines were all larger than those of CMS lines in both years, while those of F_2 and RF_2s were intermediate between the female and male parents. The performance of F_1s and BC_1s were, however, close to the means of females because these F_1s and BC_1s' seeds grew on the female plants. Although the mean of each generation of rice grain shape traits was not much different between 1995 and 1996, the range of each generation differed detectably for these traits over years. The temperature in June was much higher in 1996 than in 1995, while that in July was not. There was much rainfall in 1996 and a significant difference between the 2 years for rain days at flowering and filling period of rice, and there were also some water and manure management differences of the field between the 2 years. Therefore, these climatic factors or cultural differences could affect the differential expression of genes in the 2 years.

3.2. Variance components for genetic main effects and GE interaction effects

Estimates for phenotypic variance, components of genetic main effect variance, GE interaction variance

Table 1
Phenotypic means (ranges) of generations of 14 parents or 45 crosses for rice grain shape traits in 1995 and 1996

Generation	RLW[a]		RLT[b]	
	1995	1996	1995	1996
CMS lines (female parent)	2.60 (2.10–3.13)	2.62 (2.12–3.36)	3.34 (2.88–3.91)	3.30 (2.86–3.88)
Restore lines (male parent)	2.99 (2.69–3.33)	3.08 (2.78–3.58)	3.77 (3.55–4.11)	3.73 (3.46–4.08)
F_1	2.51 (2.02–3.31)	2.59 (1.89–3.63)	3.21 (2.76–4.27)	3.11 (2.47–4.15)
F_2	2.69 (2.25–3.36)	2.74 (2.04–3.41)	3.47 (2.95–3.90)	3.46 (2.69–4.13)
Reciprocal RF_2	2.72 (2.22–3.38)	2.78 (2.31–3.61)	3.52 (3.11–3.92)	3.56 (3.12–4.48)
BC_1	2.64 (2.00–3.81)	2.59 (1.96–3.38)	3.26 (2.61–4.00)	3.16 (2.51–3.78)

[a] The length-to-width ratio of rice.

[b] The length-to-thickness ratio of rice.

Table 2
Estimated variance components for rice grain shape traits in *indica* rice ($\times10^{-2}$)[a]

Genetic main effect variance (V_G)			GE interaction variance (V_{GE})		
Component	RLW	RLT	Component	RLW	RLT
V_{Ao}	3.61*	0.00	V_{AoE}	5.79**	0.61*
V_{Do}	2.89*	2.80*	V_{DoE}	0.20*	0.80***
V_{Ae}	0.00	2.93*	V_{AeE}	0.00	0.00
V_{De}	0.00	0.00	V_{DeE}	0.42*	0.00
V_C	3.81*	0.00	V_{CE}	0.70*	0.84*
V_{Am}	16.52*	10.94*	V_{AmE}	2.37*	0.33*
V_{Dm}	0.54*	1.58*	V_{DmE}	0.29*	0.23*

[a] RLW, length-to-width ratio of rice; RLT, length-to-thickness ratio of rice; V_G, genetic main variance; V_{GE}, genotype × environment interaction variance; V_{Ao}, embryo additive variance; V_{Do}, embryo dominance variance; V_{Ae}, endosperm additive variance; V_{De}, endosperm dominance variance; V_C, cytoplasmic variance; V_{Am}, maternal additive variance; V_{Dm}, maternal dominance variance; V_{AoE}, embryo additive interaction variance; V_{DoE}, embryo dominance interaction variance; V_{AeE}, endosperm additive interaction variance; V_{DeE}, endosperm dominance interaction variance; V_{CE}, cytoplasmic interaction variance; V_{AmE}, maternal additive interaction variance; V_{DmE}, maternal dominance interaction variance; V_P, phenotypic variance (0.3829* and 0.2238* for RLW and RLT, respectively) and V_ε, residual variance (0.0115** and 0.0134** for RLW and RLT, respectively).

* Significant at 0.05 probability levels.

** Significant at 0.01 probability levels.

*** Significant at 0.10 probability levels.

and residual variance are summarized in Table 2. RLW and RLT traits were controlled by the embryo, endosperm, cytoplasmic and maternal genetic main effects as well as the corresponding GE interaction effects. Since the genetic main effect variance ($V_G = V_{Ao} + V_{Do} + V_{Ae} + V_{De} + V_C + V_{Am} + V_{Dm}$) accounted for about 73.7 and 86.7% of the total genotypic variances ($V_G + V_{GE}$, where $V_{GE} = V_{AoE} + V_{DoE} + V_{AeE} + V_{DeE} + V_{CE} + V_{AmE} + V_{DmE}$) for RLW and RLT, respectively, the genetic main effects for rice grain shape traits were much more important than GE interaction effects.

For genetic main effects, variance components $V_{Ao}, V_{Do}, V_C, V_{Am}, V_{Dm}$ for RLW and $V_{Do}, V_{Ae}, V_{Am}, V_{Dm}$, for RLT were significant. Therefore, these two traits were simultaneously controlled by genetic main effects of embryo, endosperm, cytoplasm and maternal plant. Since the maternal variances (V_{Am} and V_{Dm}) were the largest component ($(V_{Am} + V_{Dm})/V_G = 62.3\%$ for RLW and 68.6% for RLT), the maternal genetic main effects were most important for these two traits. The embryo genetic effects were also important in genetic main effects, since the embryo variances ($V_{Ao} + V_{Do}$) accounted for about 23.7% of V_G for RLW and 15.3% of V_G for RLT, respectively. For GE interaction effects, embryo× environment interaction variances (V_{AoE} and V_{DoE}) were about 61.6 and 50.2% of V_{GE} for RLW and RLT traits, respectively. It was indicated that the expression of embryo genes could be more affected by environments. Therefore, the embryo genetic main effects and embryo × environment interaction effects should not be neglected. In addition to embryo× environment interaction effects, GE interaction effects of endosperm, cytoplasm and maternal plant were also important for rice grain shape because of the significant components V_{DeE}, V_{CE}, V_{AmE} and V_{DmE} (V_{DeE} was not found for RLT). The additive effects and cytoplasmic effect are important in selection breeding of rice, while dominance effects will be lost in later generations. Therefore, genetic gain could be expected by applying selection for RLW and RLT traits in early generations, because of the large proportions of V_{Ao}, V_C and V_{Am} to V_G (87.5%) and of V_{AoE}, V_{CE} and V_{AmE} to V_{GE} (90.7%) for RLW or large proportions of V_{Ae} and V_{Am} to V_G (76.0%) and of V_{AoE}, V_{CE} and V_{AmE} to V_{GE} (63.4%) for RLT. Commercial rice cultivar with desired rice grain shape could be obtained by selecting under different environments because of the substantial main genetic effects. The small V_ε suggested that rice grain shape was mainly affected by genetic main effects and GE interaction effects.

Table 3
Estimated components of heritability (%) for rice grain shape traits in *indica* rice[a]

General heritability			Interaction heritability		
Parameter	RLW	RLT	Parameter	RLW	RLT
h^2_{Go}	9.43*	0.00	h^2_{GoE}	15.11**	2.71***
h^2_{Ge}	0.00	13.08***	h^2_{GeE}	0.00	0.00
h^2_{C}	9.95**	0.00	h^2_{CE}	1.83***	3.76*
h^2_{Gm}	43.13**	48.84**	h^2_{GmE}	6.19**	1.47*

[a] RLW, length-to-width ratio of rice; RLT, length-to-thickness ratio of rice; h^2_{Go}, embryo general heritability; h^2_{Ge}, endosperm general heritability; h^2_{C}, cytoplasmic heritability; h^2_{Gm}, maternal general heritability; h^2_{GoE}, embryo interaction heritability; h^2_{GeE}, endosperm interaction heritability; h^2_{CE}, cytoplasmic interaction heritability; h^2_{GmE}, maternal interaction heritability.

* Significant at 0.05 probability levels.

** Significant at 0.01 probability levels.

*** Significant at 0.10 probability levels.

3.3. Estimation of general heritabilities and interaction heritabilities

Estimates of the narrow-sense heritability components are presented in Table 3 for general heritability, which is applicable to multiple environments, and interaction heritability, which is only applicable to specific environments. The total narrow-sense heritability values (h^2) for RLW and RLT were about 85.6 and 69.9%, respectively, with the general heritability values being 62.5 and 61.9%, respectively, and interaction heritability values being 23.1 and 7.9%, respectively. Selection advance for RLW and RLT traits could be expected in the early generations and the expression of genes was stable in different environments. With regard to the components of general heritability, maternal general heritability were much more important for RLW ($h^2_{\mathrm{Gm}} = 43.1\%$) and RLT ($h^2_{\mathrm{Gm}} = 48.8\%$). Therefore, it was suggested that improving rice grain shape would be more efficient when selection is based on maternal plants than on seed in early generations. Components of interaction heritability, except of h^2_{GoE} and h^2_{GmE} for RLW, were relatively small and could be negligible in rice breeding.

4. Prediction of embryo, endosperm, cytoplasmic and maternal effects and their GE interaction effects

In breeding for rice quality, breeders can be aided by understanding the inheritance patterns, but also by predicting the genetic merit of parents. By evaluating predicted breeding value of genetic main effects and GE interaction effects in different environments (years) for parents, breeders could select better parent(s) for a breeding program. It was shown, by predicted embryo additive effect (Ao), endosperm additive effect (Ae), cytoplasmic effect (C), maternal additive effect (Am), embryo additive interaction effect (AoE), cytoplasmic interaction effect (CE) and maternal additive interaction effect (AmE) of parents, that genetic main effects as well as GE interaction effects could affect rice grain shape traits of offspring (Table 4). There were detectable differences for the genetic main effects and GE interaction effects between CMS lines and restorers. In general, the genetic main effects of restorer lines were better than those of CMS lines for improving the rice cultivar with spindly shape of milled rice. The total genetic main effects and GE interaction effects of some CMS lines, such as Zhexie 2 and Xieqingzao could also significantly increase RLW and RLT, but those of other CMS lines were mostly negative, which would decrease these rice grain shape traits of offspring. Among genetic main effects, Am was more important than Ao, Ae, or C for most parents, especially for improving RLW. In GE interaction effects, AoE, CE, or AmE of most parents were variable in direction between 2 years. Although the predicted genetic main effects showed that Yinchao 1 was not a good parent for improving RLW, the direction of GE interaction effects of this parent was consistent for 2 years and was more stable than those of other parents. The results indicted that Zhexie 2, Xieqingzao or Cezao

Table 4
Predicted genetic main effects and GE interaction effects of parents for rice grain shape traits in *indica* rice[a]

Parent	Ao	AoE_1	AoE_2	Ae	C	CE_1	CE_2	Am	AmE_1	AmE_2	Total	
											1995	1996
RLW												
CMS lines												
Zhexie 2	-0.23^{***}	0.00	-0.31^{***}	–	0.29^{***}	0.05	0.13	0.55^{***}	0.06	0.27^{***}	0.72	0.70
Xieqingzao	−0.06	-0.22^{*}	0.14^{*}	–	0.17^{***}	0.10^{***}	0.01	0.36^{***}	0.14^{***}	0.08^{***}	0.49	0.70
Zhenan 3	−0.03	-0.15^{*}	0.10^{***}	–	−0.01	0.02	−0.03	−0.13	0.03^{***}	-0.11^{***}	−0.27	−0.21
Gangchao 1	0.31^{*}	0.51^{**}	−0.08	–	-0.55^{***}	-0.33^{*}	−0.04	-0.63^{***}	-0.26^{***}	−0.12	−0.95	−1.11
Yinchao 1	0.20^{***}	0.03	0.26^{*}	–	-0.48^{***}	-0.09^{***}	-0.23^{***}	-0.55^{***}	-0.09^{***}	-0.24^{***}	−0.98	−1.04
Erjiuqing	0.09^{***}	-0.13^{**}	0.26^{**}	–	−0.15	0.05	−0.16	-0.50^{***}	−0.05	-0.25^{***}	−0.69	−0.71
V_{20}	-0.21^{*}	0.28^{**}	-0.57^{**}	–	0.18	−0.04	0.16^{***}	0.44^{***}	-0.14^{*}	0.40^{***}	0.51	0.40
Zuo 5	0.08	−0.06	0.17	–	−0.05	−0.02	−0.01	−0.06	0.07^{***}	−0.10	−0.04	0.03
Zhenshan 97	0.05	0.15^{*}	−0.08	–	-0.14^{***}	-0.18^{***}	0.08	-0.38^{***}	-0.14^{***}	−0.09	−0.64	−0.56
Restorer lines												
T 49	−0.02	-0.11^{*}	0.08^{*}	–	0.25	0.08^{*}	0.09	0.04	0.04^{***}	-0.02^{***}	0.28	0.42
Cezao 2-2	-0.06^{***}	-0.09^{*}	0.00	–	0.31^{***}	0.17^{***}	0.05	0.33^{***}	0.10^{***}	0.10^{***}	0.76	0.73
26715	0.00	-0.06^{*}	0.06^{***}	–	−0.03	-0.06^{*}	0.04^{**}	0.27^{***}	0.17^{***}	−0.01	0.29	0.33
102	−0.05	-0.13^{*}	0.06^{***}	–	0.12^{***}	0.06	0.02	0.01	0.00	0.01	0.01	0.17
1391	-0.08^{***}	−0.03	-0.08^{*}	–	0.10	0.18^{***}	−0.10	0.23^{***}	0.07^{***}	0.07^{***}	0.47	0.14
RLT												
CMS lines												
Zhexie 2	–	−0.01	−0.02	0.09	–	0.08^{*}	0.11	0.30^{***}	0.06	0.04	0.52	0.52
Xieqingzao	–	−0.08	0.06	0.14	–	−0.01	0.13^{*}	0.19	0.10	−0.02	0.34	0.50
Zhenan 3	–	−0.04	0.02	-0.17^{***}	–	0.26^{***}	0.04	−0.06	0.02^{*}	-0.05^{*}	0.01	−0.22
Gangchao 1	–	0.14	−0.08	−0.12	–	-0.28^{***}	0.17^{***}	-0.37^{***}	−0.13	-0.01^{*}	−0.76	−0.41
Yinchao 1	–	0.01	0.08	−0.08	–	0.04	−0.18	-0.55^{***}	-0.08^{*}	−0.12	−0.66	−0.85
Erjiuqing	–	−0.08	0.07	−0.26	–	0.07	−0.14	-0.36^{***}	−0.02	−0.11	−0.65	−0.80
V_{20}	–	0.04	−0.01	0.08	–	-0.05^{*}	0.10^{*}	0.02	−0.04	0.05	0.05	0.24
Zuo 5	–	0.08	−0.01	0.08	–	−0.11	0.04	-0.15^{***}	−0.06	0.01	−0.16	−0.03
Zhenshan 97	–	0.03	0.06	−0.08	–	−0.17	0.23	-0.39^{***}	−0.04	-0.11^{***}	−0.65	−0.29
Restorer lines												
T 49	–	0.01	−0.03	0.10	–	0.07	−0.14	0.21^{***}	0.02	0.06^{***}	0.41	0.20
Cezao 2-2	–	0.01	−0.05	0.15	–	0.19	−0.08	0.39^{***}	0.05^{***}	0.09	0.79	0.50
26715	–	−0.02	−0.04	0.07	–	-0.13^{***}	0.01	0.36^{***}	0.06	0.07	0.34	0.47
102	–	−0.05	0.02^{*}	0.00	–	−0.08	−0.01	0.11^{***}	0.01^{**}	0.03	−0.01	0.15
1391	–	−0.03	−0.07	0.00	–	0.13^{**}	-0.28^{*}	0.32^{***}	0.04	0.09^{***}	0.46	0.06

[a] RLW, ratio of length-to-width of rice; RLT, ratio of length-to-thickness of rice; Ao, embryo additive effects; Ae, endosperm additive effect; C, cytoplasmic effects; Am, maternal additive effects; AoE_1 and AoE_2, embryo additive interaction effect; CE_1 and CE_2, cytoplasmic interaction effects; and AmE_1 and AmE_2, maternal additive interaction effects in 1995 and 1996, respectively; '–' indicate non-availability of predicted effects because of the corresponding zero estimates of variance components in Table 2.

* Significant at 0.05 level.

** Significant at 0.01 level.

*** Significant at 0.10 level.

2-2 were better parents for improving rice grain shape because of the larger total predicted genetic effects ($Ao + AoE_{1/2} + Ae + C + CE_{1/2} + Am + AmE_{1/2}$), which were 0.72, 0.49 or 0.76 in 1995 and 0.70, 0.70 or 0.73 in 1996 for RLW, and 0.52, 0.34 or 0.79 in 1995 and 0.52, 0.50 or 0.50 in 1996 for RLT, respectively (Table 4).

5. Discussion

Inheritance of rice quality traits has been widely studied in recent decades, but these efforts failed to partition the total genetic effects into embryo, endosperm, cytoplasmic and maternal genetic effects and GE interaction effects because there was no suitable genetic models and statistical methods for analyzing the data. Although Foolad and Jones (1992) introduced genetic models for analyzing quantitative traits including testa, cytoplasm and embryo effects as well as endosperm effects, it is difficult to use this model because of the need to measure single seed of eight selfed and ten hybrid or backcross generations in the experiment. Furthermore, these models cannot analyze GE interaction effects of quantitative quality traits. Rice breeders usually cannot afford very large sample sizes in conducting genetic research because F_1 or backcross seed must be produced by manual hybridization. Therefore, for analyzing rice quality traits, a more useful genetic model should consist of different genetic effects and GE interaction effects due to diploid embryo nuclear genes, triploid endosperm nuclear genes, cytoplasmic genes and diploid maternal plant nuclear genes. Zhu (1997) proposed a genetic model for quantitative traits controlled by embryo, endosperm, cytoplasmic and maternal genetic effects as well as their GE interaction effects. This model only needs the means of not more than six generations from a set of crosses among six or seven parents evaluated in multiple environments. By using this model, RLW and RLT grain shape traits were found to be affected by embryo effects and embryo × environment interaction effects besides endosperm, cytoplasmic and maternal genetic effects and their GE interaction effects. Therefore, the diploid embryo nuclear genes were also important for the performance of rice grain shape traits of *indica* rice as well as endosperm, cytoplasmic and maternal plant genes, but the expression of embryo genes was subject to environmental affects, probably due to the climatic differences between different years (environments). The genetic model and statistical analysis method used in this experiment might be useful to other cereal crops for studying quantitative seed quality traits.

According to the magnitude of genetic main effects and GE interaction effects, the genetic patterns of parents can be further illustrated for rice grain shape traits, which are of importance in improving rice shape through selection breeding. Breeders could select breeding materials suitable to different environments for the traits with small GE. If GE was large for seed traits, breeders could only obtain breeding materials suitable to specific environment. In rice breeding, breeders could improve grain shape traits by selecting better parent(s) in pure-line breeding, or by selecting better CMS lines or restorer lines with superior dominance effects in hybrid breeding. In the present study, it was showed that some parents such as Zhexie 2, Xieqingzao and Cezao 2-2 had better breeding values due to genetic main effects and GE interaction effects.

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