

RESEARCH ARTICLE

Genetic and genotype \times environment interaction effects for the content of seven essential amino acids in *indica* rice

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Abstract

It is necessary for rice breeders to understand the genetic basis of nutrient quality traits of rice. Essential amino acids are most important in determining the nutrient quality of rice grain and can affect the health of people who depend on rice as a staple food. In view of the paucity of genetic information available on essential amino acids in *indica* rice, we estimated the genetic main effects and genotype \times environment ($G \times E$) interaction effects on the content of essential amino acids. Nine cytoplasmic male sterile lines as females and five restorer lines as males were introduced in a North Carolina II design across environments. Estimates of the content of the essential amino acids valine, methionine, leucine and phenylalanine showed that they were mainly controlled by genetic main effects, while the contents of threonine, cysteine and isoleucine were mainly affected by $G \times E$ effects. In the case of genetic main effects, both cytoplasmic and maternal genetic effects were predominant for all essential amino acids, indicating that selection for improving essential amino acid content based on maternal performance would be more effective than that based on seeds. The total narrow-sense heritabilities were high and ranged from 0.72 to 0.83. Since general heritabilities for these essential amino acids (except for cysteine) were found to be much larger than $G \times E$ interaction heritability, the improvement of content of most essential amino acids under selection would be expected under various environments. Rice varieties such as Zhenan 3, Yinchao 1, T49, 26715, 102 and 1391 should be selected as optimal parents for increasing the content of most essential amino acids, while the total genetic effects from Zhexie 2, Xieqingzao, Gangchao 1, V20, Zuo 5 and Zhenshan 97 were mainly negative and these parents could decrease the contents of most essential amino acids.

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Introduction

Half of the world's population depends on rice as the staple food source. Essential amino acids, which humans cannot synthesize but need for physiological requirement, must be supplied from the diet. Therefore, rice nutrient traits for these essential amino acids and protein are very important for human health and well being. The improvement of the nutrient quality of rice grain is one of the main goals for rice breeders. Although the phenotypic variation for many nutrient quality traits of rice might be influenced by environmental conditions, it is mainly affected by genetic main effects and genotype \times environment ($G \times E$) interaction effects during the growth cycle (Chen and Zhu 1999; Shi *et*

al. 1999, 2000). The nutrient quality traits of rice might also be influenced by the different types of cytoplasm (Yi and Cheng 1991, 1992).

The expression of some endospermic traits in the grain of cereal crops are probably controlled by the genotype of the maternal plant (Mo 1995). The contents of non-essential and essential amino acids in barley, another important cereal crop, are controlled by endosperm and maternal genetic effects, and also affected by $G \times E$ interaction effects (Xu *et al.* 1996; Yan *et al.* 1997). The protein content and composition of amino acids in *indica* rice had shown high heritability and significant variation among genotypes (Chai *et al.* 1995). Additionally, QTL loci determining the protein content with mixed genetic effects were detected in rice grain (Tan *et al.* 2001), although this technique cannot distinguish the genetic effects contributed from different genetic systems of endosperm, cytoplasm and maternal plant. Shi *et*

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al. (1996) pointed out that the nutrient quality traits of rice were simultaneously controlled by seed, cytoplasmic, and maternal plant genes.

Furthermore, $G \times E$ interaction effects and their corresponding genetic heritability components for nutrient quality traits of rice have been reported (Chen and Zhu 1999; Shi *et al.* 1999, 2000).

As yet, there is no information about the genetic main effects of endosperm, maternal and cytoplasmic effects and their $G \times E$ interaction effects on essential amino acid contents in rice grain, except for lysine (Lys) (Shi *et al.* 2000). In the present study, $G \times E$ interaction effects on essential amino acids of rice were analyzed.

The objective was to evaluate the genetic main effects including endosperm genetic effects contributed by triploid endosperm, nuclear genes, cytoplasmic genetic effect by cytoplasmic genes and maternal genetic effects by diploid maternal plant nuclear genes, as well as the $G \times E$ interaction effects, and to estimate their narrow-sense heritabilities in *indica* rice and to predict the genetic effects of parents.

Materials and methods

Plant materials

The mating design used in this experiment was a North Carolina II design (Comstock and Robinson 1952) with 9 females mating to 5 males. The nine cytoplasmic male sterile lines and their maintainer lines used as females were Zhexie 2 (P_1), Xieqingzao (P_2), Zhenan 3 (P_3), Gangchao 1 (P_4), Yinchao 1 (P_5), Erjiuqing (P_6), V20 (P_7), Zuo 5 (P_8) and Zhenshan 97 (P_9). The five restorer lines were T49 (P_{10}), Cezao 2-2 (P_{11}), 26715 (P_{12}), 102 (P_{13}) and 1391 (P_{14}). The F_1 generation was obtained by crossing all female parents with male parents in 1994.

The seeds of parents and F_1 were sown on April 2 in both 1995 and 1996. Single 30 day old seedlings were transplanted at spaces of 20×20 cm in the field of the experimental farm at Zhejiang Agricultural University. The experiment was laid out in a randomized block design with three-fold replication in each block. There were 24 plants in each plot for parents and F_1 . Seed samples of parents and F_2 s from F_1 plants were collected at maturity from eight plants in the middle of each plot. The seeds of F_1 s were obtained by crossing females to males during the flowering season.

Determination of amino acids

All seeds including F_1 s, F_2 s and their parents were dehulled by using electrical dehuller (model B-76, Huangyan, Zhejiang province, China) and milled by sample miller (model JB-20, Huangyan, Zhejiang province, China). The milled rice samples were further ground with a cyclone grinder (model 3010-019, Fort Collins, Colorado, USA) equipped with a 100-mesh screen. About 10 mg of each

flour sample was weighed and collected for chemical analysis by amino acid autoanalyzer (model L-8500, Hitachi, Japan) (Wu *et al.* 2002). Duplicated determinations of the contents of essential amino acids were made for each sample.

Statistical analysis

The genetic main effects and the $G \times E$ interaction effects of triploid endosperm, cytoplasm, and diploid maternal plant on the content of essential amino acids were analyzed by an extension of the triploid endosperm model for quantitative traits of seed in cereal crops (Zhu and Weir 1994; Zhu 1996). According to this model, the phenotypic variance (V_P) can be partitioned into corresponding components including endosperm additive variance (V_A), endosperm dominance variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}), maternal dominance variance (V_{Dm}), endosperm additive interaction variance (V_{AE}), endosperm dominance interaction variance (V_{DE}), cytoplasmic interaction variance (V_{CE}), maternal additive interaction variance (V_{AmE}), maternal dominance interaction variance (V_{DmE}) and residual variance (V_e). The covariance between endosperm and maternal effects could also be divided into covariance between endosperm and maternal additive effect (C_{A-Am}), covariance between endosperm and maternal dominance effect (C_{D-Dm}), covariance between endosperm and maternal additive interaction effect (C_{AE-AmE}), and covariance between endosperm and maternal dominance interaction effect (C_{DE-DmE}). The genetic variance and covariance components described above were estimated by MINQUE(0/1) method (Zhu and Weir 1994).

As the total genetic effect can be divided into components for genetic main effects and $G \times E$ interactions, the total narrow-sense heritability (h^2), consequently, consisted of general heritability (h_G^2) with components of endosperm general heritability ($h_{Go}^2 = (V_A + C_{A-Am})/V_P$), cytoplasm general heritability ($h_{Gc}^2 = V_C/V_P$) and maternal general heritability ($h_{Gm}^2 = (V_{Am} + C_{A-Am})/V_P$), and interaction heritability (h_{GE}^2) with endosperm interaction heritability ($h_{GoE}^2 = (V_{AE} + C_{AE-AmE})/V_P$), cytoplasmic interaction heritability ($h_{GcE}^2 = V_{CE}/V_P$) and maternal interaction heritability ($h_{GmE}^2 = (V_{AmE} + C_{AE-AmE})/V_P$).

Genetic effects of each parent were predicted by the adjusted unbiased prediction (AUP) method (Zhu and Weir 1996). The standard errors of estimated variances, heritabilities and predicted genetic effects were estimated by the Jackknife procedure (Miller 1974; Zhu 1993; Zhu and Weir 1996), and *t*-tests were performed for testing null hypothesis of zero parameter values.

Results

Phenotypic values in the assay generations

The contents of seven essential amino acids showed large variations among parents and hybrid (F_1) crosses (table 1),

Table 1. Phenotype means of seven essential amino acid contents (%) of parents and their F₁ and F₂ generations in *indica* rice.

Generation	Thr	Cys	Val	Met	Ile	Leu	Phe
Female parent	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.482	0.511	0.103	0.042	0.852	0.884
Male parent	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.478	0.068	0.041	0.036	0.149	0.136
F ₁	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.486	0.527	0.100	0.096	0.889	0.964
F ₂	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.485	0.524	0.118	0.071	1.024	0.956
Spearman rank correlation coefficient ^a	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.447	0.462	0.090	0.039	0.790	0.825
Spearman rank correlation coefficient ^a	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.466	0.057	0.040	0.042	0.119	0.102
Spearman rank correlation coefficient ^a	1995	1996	1995	1996	1995	1996	1995
	1996	1995	1996	1995	1996	1995	1996
	Mean	0.427**	0.009	0.009	0.497**	0.128	0.491**

**Significant at 0.01 level.

^a Correlation coefficient between means in 1995 and in 1996.

which indicated that it was possible to improve the nutrient traits of hybrid rice. The means of amino acid contents, except for cysteine (Cys) and methionine (Met), were larger in male parents (restorer lines) than those in female parents (cytoplasmic male sterile lines), both in 1995 and 1996. There was significant heterosis for these amino acid contents because of the larger means in F_1 s, while the means in F_2 s were less than those in their F_1 s or parents, except for Met, in the two assay years.

Considering the total data of all generations in both years, amino acids with high contents were leucine (Leu, 1.029%) and valine (Val, 0.898%), whereas the lower ones were Cys (0.082%) and Met (0.098%). Based on the amount of amino acids, the growth environment of 1996 appeared to have been beneficial for the performance with regard to the content of these amino acids, except for Cys, in rice grain. Spearman rank correlation analysis on amino acid content in 1995 and 1996 was performed separately for each of the amino acids studied. In the case of Val, Ile, Leu, threonine (Thr) and phenylalanine (Phe), the contents in 1995 and 1996 were not strongly correlated, suggesting that content of these five amino acids was likely to be influenced more by environmental conditions rather than genotype. The correlation coefficients between the contents of Cys and Met in the two years were not significant, suggesting that variation in content of these two amino acids could be affected markedly by environmental conditions.

Genetic variance and covariance components analysis

Estimates of genetic main effect variances, $G \times E$ interaction variances, covariances and residual variances are sum-

marized in table 2. All genetic variances were significant for the contents of the seven essential amino acids. Therefore, the genetic main effects and their environmental interaction effects could simultaneously affect the performance of these nutrient traits in rice. Compared with the $G \times E$ interaction effects ($V_{GE} = V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}$), the performance of the contents of Val, Met and Leu was mainly controlled by the genetic main effects ($V_G = V_A + V_D + V_C + V_{Am} + V_{Dm}$) with value as high as 79.59%, 62.45% and 78.97% of the total genetic variance ($V_G + V_{GE}$), respectively. Since most of the genetic main variance components were significant, the contents of these amino acids were controlled by genetic main effects of endosperm, cytoplasm as well as maternal plant. Cytoplasmic and maternal additive effects, which possessed the proportions $((V_C + V_{Am})/V_G)$ of 67.23%, 61.4% and 66.5%, had played important role in genetic main effects for these amino acids. Thus, genetic improvement for these amino acids could be effectively achieved by selection based on maternal performance. Furthermore, the environmental interaction effects could not be neglected in utility of heterosis due to high percentage of dominance interaction effects $(V_{DE} + V_{DmE})/V_{GE}$ with respective values of 100%, 44.6% and 100% for the three amino acids.

For the traits of threonine (Thr) and isoleucine (Ile), the $G \times E$ interaction effects were more important than genetic main effects, since V_{GE} for these two traits accounted for 51.66% and 50.66% of total genetic variances ($V_G + V_{GE}$). But for Phe, genetic main effect (V_G) was more important with a value of 58.13% of the total. Moreover, the performances of Thr, Ile and Phe were mainly contributed by the additive and cytoplasmic main effects with the values of

Table 2. Estimation of genetic variance and covariance components of seven essential amino acid contents in *indica* rice ($\times 10^{-2}$).

Parameter	Thr	Cys	Val	Met	Ile	Leu	Phe
V_A	1.353**	0.000	7.527**	3.161**	2.410**	14.992**	2.218**
V_D	0.000	0.000	0.000	0.781**	0.000	0.000	0.000
V_C	1.428**	0.402**	4.917**	2.539**	2.164**	8.638**	1.917**
V_{Am}	2.360**	0.661**	10.523**	3.724**	3.780**	21.126**	3.709**
V_{Dm}	0.000	0.000	0.000	0.000	0.667**	0.000	0.382**
V_{AE}	2.023**	0.808**	0.000	0.000	3.389**	0.000	2.068**
V_{DE}	0.411**	0.287**	2.091**	1.398**	0.582**	4.912**	0.439**
V_{CE}	0.000	0.423**	0.000	3.459**	0.000	0.000	0.000
V_{AmE}	2.098**	0.000	0.000	0.000	4.022**	0.000	2.477**
V_{DmE}	0.963**	0.359**	3.799**	1.280**	1.269**	7.010**	0.942**
C_{A-Am}	-0.580	0.000	-4.553	-2.194	-0.710	-9.080	-1.52
C_{D-Dm}	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C_{AE-AmE}	-0.519	0.000	0.000	0.000	-1.460	0.000	-0.55
C_{DE-DmE}	-0.025	-0.030	-0.516	-0.091	-0.010	-0.930	-0.02
V_e	0.136**	0.026**	0.230**	0.039**	0.253**	0.108**	0.304**

** significantly different from zero, at 0.01 level.
See text for description of parameters

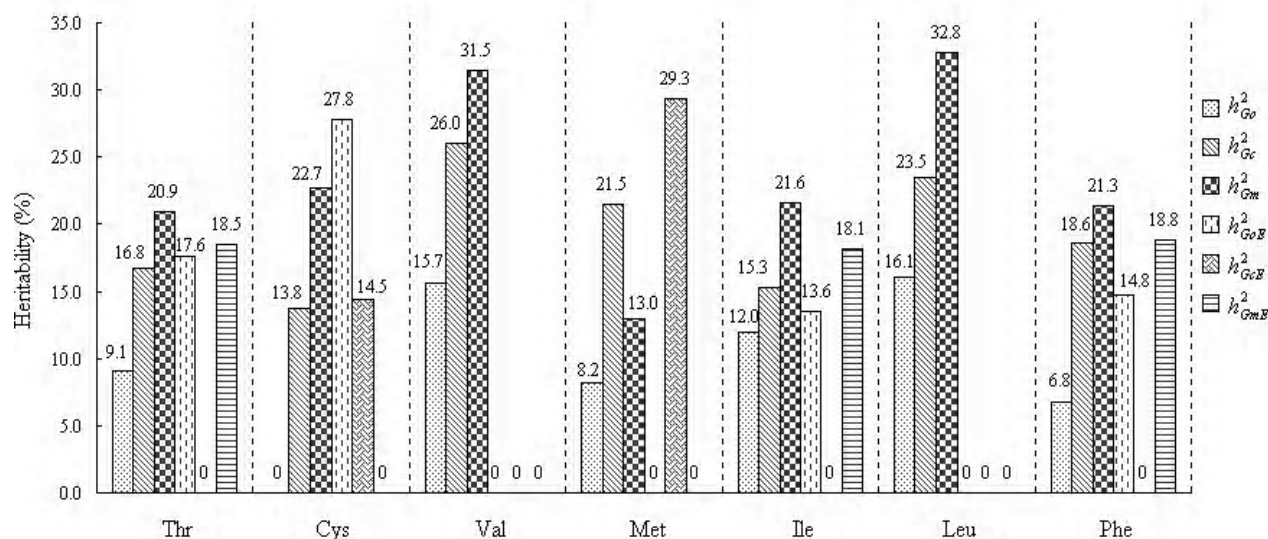


Figure 1. Estimates of heritability (%) of essential amino acids in *indica* rice. Heritability component values are listed upon corresponding columns. h^2_{Go} = endosperm general heritability, h^2_{Gc} = cytoplasmic general heritability, h^2_{GmE} = maternal general heritability, h^2_{GoE} = endosperm interaction heritability, h^2_{GcE} = cytoplasm interaction heritability and h^2_{GmE} = maternal interaction heritability.

100%, 92.61% and 95.36% ($V_A + V_C + V_{Am}$)/ V_G), and their interaction variances with the values of 75%, 80.02% and 76.70% ($V_{AE} + V_{CE} + V_{AmE}$)/ V_{GE}), respectively. Selection for improving these amino acids would, consequently, be effective in early generations. But for Thr and Ile, the different environmental influences should not be neglected due to large value of $G \times E$ interaction. Since no endosperm main effects (V_A and V_D) were detected, the trait of Cys was also mainly affected by the cytoplasmic and maternal effects, which were predominant with the ratio of V_G as high as 100%. The $G \times E$ interaction effects for Cys were more important than genetic main effects, accounting for 63.84% of the total genetic effects.

Since all the covariances including $C_{A:Am}$, $C_{D:Dm}$, $C_{AE:AmE}$ and $C_{DE:DmE}$ were all non-significant in the present experiment, we can deduce that there was no significant relationship between the endosperm and maternal main effects or between endosperm and maternal interaction effects. The residual variances of essential amino acids were all significant, indicating that the performance of these nutrient traits could be influenced by sampling errors or other factors in the genetic control of these traits.

Estimation of heritabilities

The total narrow-sense heritability (h^2) is a combination of two components: general heritability (h^2_G) which can be applied on various environments (locations or years), and interaction heritability (h^2_{GE}) applied only on the specific environment. Each of these component heritabilities can further be partitioned in terms of the endosperm, cytoplasmic and maternal components. The estimates of $h^2(h^2_G +$

$h^2_{GE})$ were high and ranged from 72.0 to 82.9% for essential amino acids (figure 1). Since high general heritabilities (h^2_G) without interaction heritabilities (h^2_{GE}) for Val and Leu were found, the selection advance could be expected in early generations in different years. Moreover, the h^2_G for Thr, Met, Ile and Phe were estimated to be much larger than their h^2_{GE} , suggesting that selection for screening high contents of these amino acids can be effective in early inbred lines. But, selection for Cys might be affected by environmental condition of years because of the larger h^2_{GE} .

As regards the components of general heritability, cytoplasmic and maternal general heritability for all essential amino acids were much more important than endosperm general heritability. Thus, it was evident that selection methods based on maternal plants would be more capable of improving essential amino acids of rice than those based on seeds. For the contents of Cys and Met, the cytoplasmic interaction heritability (h^2_{GE}) was significant, showing that selection for these two amino acids would be influenced by the cytoplasm in specific environments. There also existed maternal interaction heritability (h^2_{GmE}) for the contents of Thr, Ile and Phe, indicating the need for breeders to pay attention to the maternal performance in multiple environments when evaluating plant material.

Evaluation of genetic effects in parents

In order to improve nutrient quality traits of rice, breeders would be interested in genetic merits of parents and therefore make a decision as to which parents are more suitable for breeding projects. Parental genetic effects, including endosperm additive effects (A), cytoplasmic effects (C) and

Table 3. Genetic effect predictions of essential amino acid contents (%) for parents of *indica* rice ($\times 10^{-1}$) in different environments^a (test years).

Parent	Thr		Cys		Val		Met		Ile		Leu		Phe	
	T_1	T_2	T_1	T_2	T_1	T_2	T_1	T_2	T_1	T_2	T_1	T_2	T_1	T_2
P_1	-0.1922	-0.444	-2.580	4.088	-1.198	-1.198	0.033	2.035	-0.184	0.395	-0.525	-0.525	-0.771	-0.303
P_2	-1.014	-0.446	-1.912	1.243	-1.788	-1.788	0.788	1.335	-1.284	-1.281	-1.695	-1.695	-1.289	-0.784
P_3	-0.140	1.561	1.647	-0.761	0.777	0.777	-1.719	-3.145	0.555	2.032	1.044	1.044	0.450	2.320
P_4	-0.054	0.163	-0.078	-1.806	-0.251	-0.251	1.560	-1.441	-0.265	-0.610	-0.793	-0.793	-0.120	-0.373
P_5	0.215	0.562	0.522	-2.583	0.920	0.920	5.686	0.135	-0.497	0.264	-0.154	-0.154	0.067	0.156
P_6	0.164	0.080	0.702	-3.011	0.492	0.492	-3.145	-2.017	1.745	0.476	-0.019	-0.019	0.754	0.139
P_7	-0.256	-0.453	1.297	-1.783	-0.761	-0.761	-2.728	-2.914	-0.095	-1.300	-1.424	-1.424	-0.469	-1.030
P_8	-1.450	-1.480	1.313	-1.971	-1.542	-1.542	3.961	-1.226	-1.192	-2.087	-1.090	-1.090	-1.151	-1.867
P_9	-1.346	-1.401	-0.704	-2.310	-2.561	-2.561	-4.503	-1.560	-0.811	-1.444	-3.137	-3.137	-1.151	-1.572
P_{10}	1.204	0.480	-0.642	2.866	1.350	1.350	3.950	3.820	1.186	0.076	1.425	1.425	1.296	0.331
P_{11}	1.074	-0.541	-0.226	2.416	0.256	0.256	-0.736	2.041	0.486	-0.465	0.583	0.583	0.964	-0.637
P_{12}	0.594	0.607	0.151	1.263	1.319	1.319	-1.454	1.405	0.163	1.728	1.345	1.345	0.549	1.347
P_{13}	1.400	0.340	-0.058	0.931	2.003	2.003	-0.340	1.701	1.213	1.011	2.976	2.976	1.218	0.946
P_{14}	0.354	0.972	0.566	1.450	1.020	1.020	-1.350	-0.165	-0.994	1.231	1.496	1.496	-0.303	1.350

^a T_1 ($A+AE_1+C+CE_1+Am+AmE_1$) and T_2 ($A+AE_2+C+CE_2+Am+AmE_2$) were the total genetic values for 1995 and 1996, respectively.

maternal additive effects (Am) as well as their $G \times E$ interaction effects (AE , CE and AmE), were therefore predicted for the contents of seven essential amino acids and the total values ($T_1 = A + AE_1 + C + CE_1 + Am + AmE_1$ in 1995 and $T_2 = A + AE_2 + C + CE_2 + Am + AmE_2$ in 1996) are presented in table 3. The results showed that the cytoplasmic interaction effects (CE) for all amino acids, except for Cys and Met, were not detectable. Furthermore, the endosperm additive interaction effects (AE) for the contents of Val, Met and Leu, and maternal additive interaction effects (AmE) for the contents of Cys, Val, Met and Leu were not found in all parents. As most genetic main effects including A , C and Am were significant, parents could affect the essential amino acid of offspring dramatically (data not shown).

According to the total predicted genetic values, the performance of Val and Leu in all parents was stable in both years due to the genetic effects with the same positive or negative values. Parents P_3 , $P_{10} \sim P_{14}$ with positive genetic effects were suitable for improving these two traits, while parents P_1 , P_2 , P_4 , $P_7 \sim P_9$ with negative ones were unsuitable. P_6 could increase the Val content and decrease the Leu content. As for the other amino acid contents, parents showed varying performance, some were stable and others unstable for the same amino acid across the two test years. In general, the total genetic effects of P_1 , P_2 , P_4 and $P_7 \sim P_9$ were mainly negative and these parents would decrease the contents of most essential amino acids, while those of P_3 , P_5 , P_{10} and $P_{12} \sim P_{14}$ were mainly positive and such parents should be selected as optimal parents for increasing the most essential amino acids. However, P_6 and P_{11} could be considered as parents for improving the contents of some specific amino acids, such as P_6 for increasing the contents of Thr, Val, Ile and Phe.

Discussion

The contents of essential amino acids are closely related to nutrient values of milled rice. Breeders in the world now need to focus on improving nutrient quality traits in rice grain after the significant breakthrough of the yield of hybrid rice. For this, we need a better understanding of the inheritance of nutrient quality traits for milled rice (endosperm). Since rice grain is a new generation, and differs from its maternal plant that provide assimilates for seed development, the essential amino acid traits might be controlled by genes of triploid endosperm and be simultaneously affected by maternal and cytoplasmic effects. For example, various nutrient quality traits, such as protein content and lysine content, were found to be controlled by endosperm genetic effects, cytoplasm genetic effects as well as maternal effects in rice (Shi and Zhu 1996; Chen and Zhu 1999; Shi *et al.* 2000). So far, studies on the genetics of essential amino acid content in rice grain were limited to classical genetic analysis, thus only simple genetic information was reported using ANOVA method or simple cor-

relation analysis (Chai *et al.* 1995; Liu and Lü 1995; Yang *et al.* 1997). Such studies might possibly mislead breeders in understanding the genetic behavior of these traits due to mixed genetic component effects obtained via classical analysis. In the present study, more detailed information was obtained about endosperm, cytoplasmic and maternal effects, which affected these nutrient traits of milled rice via new genetic models for quantitative traits of triploid endosperm. The performance of essential amino acid contents was found to be contributed by the genes of seed endosperm, cytoplasm and maternal plant nucleus, except for Cys, without seed endosperm effects in genetic main effects (table 2). Furthermore, cytoplasmic and maternal genetic effects for all these traits were predominant in genetic main effects, indicating that selection for increasing these traits based on maternal performance would be more effective than that based on seeds.

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