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Genotype × environment interaction effect and genotypic correlation for nutrient quality traits of *indica* rice (*Oryza sativa*)

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ABSTRACT

The genetic effects and genotype × environment interaction effect on nutrient quality traits of *indica* rice (*Oryza sativa* L.) was studied during 1994–95 by using genetic models for quantitative traits of triploid endosperm. Nine cytoplasmic male sterile lines as females and 5 restoring lines as males were included in a factorial design for 2 years. Results indicated that the nutrient quality traits of protein content, protein index and lysine content were mainly controlled by genetic effect but lysine index was mainly affected by genotype × environment (GE) interaction effects. Maternal effects were the main genetic effects for protein content, lysine content and lysine index, but not for protein index. Cytoplasmic effects were significant for protein content and protein index only. Among the GE interaction effects, protein content and lysine content traits were mainly affected by seed interaction effects and protein index and lysine index by maternal interaction effects. Direct additive and maternal additive effects primarily controlled the performance of the rice nutrient quality traits. Direct and maternal additive interaction effects were more important for protein content and protein index. The nutrient quality traits were controlled by direct and maternal dominance effects, and their environment interaction effects especially for lysine content and lysine index. The cytoplasmic interaction effects were significant for all nutrient quality traits studied. The genotypic correlations among nutrient quality traits could be further partitioned into genetic correlations and GE interaction correlations. Significant correlations for the pairwise nutrient quality traits, especially for direct additive correlations and cytoplasmic interaction correlations, were noted.

Key words : genetic effects, genotype × environment interaction effects, genetic correlations, nutrient quality traits, *indica* rice

Rice (*Oryza sativa* L.) is one of the main staple foods in the world. To improve the nutrient quality of rice, understanding the variation for the expression of genes in different environments is a major goal in rice breeding. Rice grown under natural environments will be affected by environmental conditions (eg weather, soil, cultural and management of field) but the phenotypic variation for many important nutrient quality traits of rice will be affected mainly by genetic main effects and genotype × environment (GE) interaction effects. The rice grain itself is a new generation and differs from the maternal plant while the endosperm of rice is a triploid tissue. Although rice nutrient quality traits may be controlled by genes of the triploid endosperm, since maternal plants supply assimilates for rice grain filling, the gene effects of maternal plant and cytoplasm may be important components of genetic effects for rice nutrient quality traits. Significant maternal effects instead of small cytoplasmic effects for rice shape traits were noted (Qi *et al.* 1983). Some cooking and nutrient quality traits of rice might be related to the effects of maternal plant or different types of cytoplasm (Pooni *et al.* 1992, Yi and Cheng 1991, 1992). Amylose content, milling recovery, water uptake and kernel elongation of rice behaved differently to environment (Chauhan *et al.* 1992). The analysis of different genetic systems have shown that nutrient quality traits of rice were controlled by seed, cytoplasmic, and maternal plant genes (Shi *et al.* 1996a) and milling quality traits or cooking quality traits of rice were affected by genetic effects and GE interaction effects (Shi *et al.* 1997, 1998). Direct additive and dominance correlations, cytoplasmic correlations, and maternal additive and dominance correlations existed for some nutrient quality traits of milled rice (Shi *et al.* 1996b).

Genotype × environment interaction effects and their associations for nutrient quality traits of rice were analyzed. The objectives was to evaluate the seed genetic effects (direct additive or dominance effects) controlled by triploid endosperm nuclear genes, cytoplasmic genetic effects controlled by cytoplasmic genes and maternal genetic effects (maternal additive or dominance effects) controlled by diploid maternal plant nuclear genes, as well as the GE interaction

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Table 1 Phenotypic value of 14 parents, 45 F_1s and 45 F_2s for nutrient quality traits of *indica* rice

Parent	PC (%)	PI (mg)	LC (%)	LI (mg)
Female				
'Zhexie 2 A'	10.092	1.813	0.249	0.045
'Xieqingzao A'	10.690	1.891	0.302	0.053
'Zhenan 3 A'	15.845	2.628	0.396	0.066
'Gangchao 1 A'	12.605	1.930	0.399	0.061
'Yinchao 1 A'	12.332	1.883	0.345	0.053
'Erjiuqing A'	13.080	2.127	0.398	0.065
'V20 A'	10.813	1.912	0.358	0.064
'Zuo 5 A'	10.425	2.124	0.250	0.051
'Zhenshan 97 A'	13.738	2.358	0.371	0.064
Mean	12.180±1.884	2.074±0.269	0.341±0.060	0.058±0.008
Range	10.092~15.845	1.813~2.628	0.294~0.399	0.045~0.066
Male				
'T 49'	12.522	2.219	0.322	0.057
'Cezao 2-2'	11.248	2.103	0.296	0.055
'26715'	12.338	1.850	0.439	0.066
'102'	12.977	1.887	0.341	0.050
'1391'	13.157	1.965	0.390	0.058
Mean	12.448±0.748	2.005±0.154	0.358±0.057	0.057±0.006
Range	11.248~13.157	1.850~2.219	0.296~0.439	0.050~0.066
F_1				
Mean	14.504±1.827	2.305±0.271	0.386±0.082	0.061±0.013
Range	10.770~19.750	1.580~3.230	0.183~0.563	0.036~0.091
F_2				
Mean	12.338±1.261	2.143±0.224	0.349±0.053	0.060±0.009
Range	9.170~16.620	1.660~2.752	0.239~0.463	0.039~0.083

effects and to estimate genetic correlations for nutrient quality traits of protein content, protein index, lysine content and lysine index in *indica* rice.

MATERIALS AND METHODS

Experiment was conducted in 1994–95. The mating design used for this experiment was a factorial design with 9 females mating to 5 males. Nine cytoplasmic male sterile lines used as females were 'Zhexie 2 A', 'Xieqingzao A', 'Zhenan 3 A', 'Gangchao 1 A', 'Yinchao 1 A', 'Erjiuqing A', 'V$_{20}$ A', 'Zuo 5 A' and 'Zhenshan 97 A'. Five restorers used as males were 'T 49', 'Cezao 2–2', '26715', '102' and '1391'. These cytoplasmic male sterile lines and restorers were randomly sampled from a reference population of *indica* rice being used for hybrid rice production in China. All female parents were crossed to male parents in 1993. Seedlings of parents and F_1s were planted at the experimental farm of the University, Hangzhou. The seeds were sown on 28 March 1994 and 3 April 1995 and single 31-day-old seedlings were transplanted at 20 cm × 20 cm spaces. Each plot had 24 plants with 3 replications. Seed samples of parents and F_2s on F_1s' plants were derived at maturity from 8 plants in the middle part of the plot. The F_1 seeds analyzed were obtained by crossing cytoplasmic male sterile lines to restores. The nutrient quality traits studied were protein content (%) determined by Kjeldahl extraction method, protein index (mg protein/milled rice), lysine content (%) determined by colorimetrically method, and lysine index (mg lysine/milled rice) of milled rice measured with three replications for each sample of parents, F_1s and F_2s.

The genetic and GE interaction effects of rice nutrient quality traits were analyzed by an extension of the triploid endosperm model for quantitative traits of cereal crops (Zhu and Weir 1994a,b, Zhu 1996). MINQUE (0/1) method (Zhu and Weir 1994a,b) was used to estimate variances and covariances which included direct additive variance (V_A), direct dominance variance (V_D), cytoplasm variance (V_C), maternal additive variance (V_{Am}), maternal dominance variance (V_{Dm}), direct additive interaction variance (V_{AE}), direct dominance interaction variance (V_{DE}), cytoplasm interaction variance (V_{CE}), maternal additive interaction variance (V_{AmE}), maternal dominance interaction variance (V_{DmE}), covariance between direct additive and maternal additive effects ($C_{A\cdot Am}$), covariance between direct dominance and maternal dominance effects ($C_{D\cdot Dm}$), covariance between direct additive interaction effects and maternal additive interaction effects ($C_{AE\cdot AmE}$), covariance between direct dominance interaction effect and maternal dominance interaction effects ($C_{DE\cdot DmE}$) and residual variance (V_e). The components of genotypic correlation (r_G) included direct additive correlation (r_A), direct dominance correlation (r_D), cytoplasm correlation (r_C), maternal additive correlation (r_{Am}), maternal dominance correlation (r_{Dm}). The components of GE interaction correlation (r_{GE}) were direct additive interaction correlation (r_{AE}), direct dominance interaction correlation (r_{DE}), cytoplasmic interaction correlation (r_{CE}), maternal additive interaction correlation (r_{AmE}), and maternal dominance interaction correlation (r_{DmE}). Residual correlations (r_e) for rice nutrient quality traits were also estimated.

The Jackknife technique (Miller 1974, Zhu and Weir 1994a) was applied by sampling generation means of entries for estimating the standard errors of estimated variances, covariances and correlation.

RESULTS AND DISCUSSION

Phenotypic value of parents and crosses for nutrient quality traits of rice

Phenotypic value of 14 parents, 45 F_1s and 45 F_2s for protein content, protein index, lysine content and lysine index are presented in Table 1. Differences between parents or hybrid rice crosses indicated the possibility of improving hybrid rice for nutrient quality traits and studying the genetic mechanism involved. In the F_1, protein content, protein index, lysine content and lysine index of rice were 14.50%, 2.31mg, 0.39% and 0.061mg for 45 hybrid rice crosses respectively. These means were much larger than those of cytoplasmic male sterile lines or restorers and there were significant heterosis for these nutrient quality traits. But the means of nutrient quality traits for F_2 were less than those of F_1, and were 12.34%, 2.14 mg, 0.35% and 0.060 mg for protein content, protein index, lysine content and lysine index respectively.

Estimation of variances and covariances of nutrient quality traits of rice

According to the magnitude of each genotypic variance component, we could find the major contribution effects affecting the nutrient quality traits of indica rice. Estimates for genotypic variances, GE interaction variances, covariances and residual variances are presented in Table 2. The results indicated that the traits of protein content, protein index and lysine content were mainly affected by genetic main effects of genes and the genotypic variance ($V_G=V_A+V_D+V_C+V_{Am}+V_{Dm}$) accounted for about 75%, 62% and 62% of the total genotypic variances [V_G+V_{GE} ($V_{GE}=V_{AE}+V_{DE}+V_{CE}+V_{AmE}+V_{DmE}$)], respectively. The lysine index was mainly affected by GE interaction effects with V_{GE} accounting for about 53% of total genetic variances (V_G+V_{GE}). Therefore, GE interaction effects were more important for lysine index than for the other nutrient quality traits.

Table 2 Estimates of genetic and genotype × environment interaction variances and covariances of nutrient quality traits in *indica* rice

Parameter	PC	PI	LC ($\times 10^{-2}$)	LI ($\times 10^{-4}$)
Main genetic effect				
V_A	8.779*	0.157*	0.727*	1.050*
V_D	0.084**	0.002*	0.046*	0.294*
V_C	0.345*	0.016*	0.000	0.000
V_{Am}	13.024*	0.136*	1.139*	1.680*
V_{Dm}	0.325*	0.004*	0.019*	0.131*
$C_{A\cdot Am}$	—10.848	—0.157	—0.903	—1.300
$C_{D\cdot Dm}$	—0.275	—0.004	—0.016	—0.133
GE interaction effect				
V_{AE}	1.628+	0.000	0.000	0.000
V_{DE}	1.932*	0.047*	0.470*	1.150*
V_{CE}	0.732+	0.042*	0.289*	1.110*
V_{AmE}	2.388+	0.084*	0.000	0.000
V_{DmE}	0.820*	0.023*	0.422*	1.340*
$C_{AE\cdot AmE}$	—2.729	0.000	0.000	0.000
$C_{DE\cdot DmE}$	—0.205	—0.004	—0.132	—0.322
V_e	0.049+	0.006*	0.02*	0.094*

+, * and ** were significant at P = 0.10, 0.05 and 0.01 level respectively. PC, Protein content, PI, protein index, LC, lysine content, LI, lysine index; V_A, additive variance; V_D, dominance variance; V_C, cytoplasmic variance; V_{Am}, maternal additive variance; V_{Dm}, maternal dominance variance; V_{AE}, additive interaction variance; V_{DE}, dominance interaction variance; V_{CE}, cytoplasmic interaction variance; V_{AmE}, maternal additive interaction variance; V_{DmE}, maternal dominance interaction variance; $C_{A.Am}$, covariance between additive and maternal additive effects; $C_{D.DmE}$, covariance between dominance and maternal dominance effects; $C_{AE.AmE}$, covariance between additive interaction effects and maternal additive interaction effects; $C_{DE.DmE}$, covariance between direct dominance interaction effects and maternal dominance interaction effects and V_e, residual variance

Genotypic variances were significant for all nutrient quality traits except for cytoplasm variances (V_C) of lysine content and lysine index. Therefore, nutrient quality traits were controlled by genetic effects of seed, cytoplasm as well as maternal plant. The maternal variance ($V_{Am}+V_{Dm}$) were about 59%, 60% and 57% of genotypic variances (V_G) for protein content, lysine content and lysine index, respectively. Seed direct variance (V_A+V_D) for protein index of rice was around 50% of V_G. Since the cytoplasm variances (V_C) were only significant for protein content and protein index, the cytoplasmic effects were also important genetic main effects for these two traits but not for lysine content and lysine index. The proportions of direct additive variances and maternal additive variances to genotypic variances ((V_A+V_{Am})/V_G) were about 87–97% for all nutrient quality traits of rice. Therefore, direct and maternal additive effects were the main factors of genetic main effects.

Not only by the seed, cytoplasm and maternal genetic effects, the nutrient quality traits were also controlled by GE interaction effects. Since maternal interaction effects (V_{AmE} and V_{DmE}) accounted for about 55% and 37% of GE interaction variances (V_{GE}) for protein index and lysine index, respectively, the maternal interaction effects were more important than other GE interaction effects for these traits. The proportions of direct

Table 3 Correlations of genetic components of nutrient quality traits in *indica* rice

Correlation	PC and PI	PC and LC	PC and LI	PI and LC	PI and LI	LC and LI
r_G	0.54**	0.45**	0.25**	0.15**	0.26**	0.64**
r_A	0.96**	1.00**	1.00**	0.93**	1.00**	1.00**
r_D	1.00**	–0.69*	–0.13	1.00**	0.38*	1.00**
r_C	–0.53*	0.00	0.00	0.00	0.00	0.00
r_{Am}	0.97**	0.80**	0.61**	0.71**	0.57**	0.94**
r_{Dm}	0.88**	0.35*	–0.08	1.00**	0.64*	0.93**
r_{AE}	0.00	0.00	0.00	0.00	0.00	0.00
r_{DE}	0.84**	0.46**	0.35**	0.29**	0.39**	0.94**
r_{CE}	1.00**	1.00**	1.00**	1.00**	1.00**	1.00**
r_{AmE}	0.54**	0.00	0.00	0.00	0.00	0.00
r_{DmE}	1.00**	0.17**	0.05	0.10+	0.21**	1.00**
r_e	0.52*	–0.02	0.03	0.02	0.55**	0.78**

+, *,** were ignificant at $P = 0.10$, 0.05 and 0.01 level respectively. PC, Protein content; PI, protein index; LC, lysine content and LI, lysine index; r_A, direct additive correlation; r_D, direct dominance correlation; r_c, cytoplasmic correlation; rAm, maternal additive correlation; r_{Dm}, maternal dominance correlation; r_{AE}, direct additive interaction correlation; r_{DE}, direct dominance interaction correlation; r_{CE}, cytoplasmic interaction correlation; r_{AmE}, maternal additive interaction correlation; r_{DmE}, maternal dominance interaction correlation and r_e, residual correlations

additive and dominance interaction variances to GE interaction variance ($(V_{AE} + V_{DE}) / V_{GE}$) were about 47% for protein content and 40% for lysine content. Cytoplasmic interaction effects were important for nutrient quality traits of milled rice especially for lysine content and lysine index. The large direct additive interaction variances (V_{AE}) and maternal additive interaction variances (V_{AmE}) for protein content and protein index indicated that the direct and maternal additive interaction effects were more important than direct and maternal dominance interaction effects. It was indicated, by the fact of no significant V_{AE} and V_{AmE} for lysine content and lysine index in this experiment, that additive effects were stable in different environments. But, lysine content and lysine index were affected by larger direct dominance interaction variances (V_{DE}) and maternal dominance interaction variances (V_{DmE}).

No significant relationships were found between these direct and maternal effects or between direct interaction effects and maternal interaction effects, since no significant covariances ($C_{A \cdot Am}$, $C_{D \cdot Dm}$, $C_{AE \cdot AmE}$ and $C_{DE \cdot DmE}$) of nutrient quality traits were noted. Small but significant residual effects for these nutrient quality traits existed.

Analysis of genetic correlations

Since the total genetic effects could be further partitioned into genotypic effects and GE interaction effects, the correlations consisted of components due to genotypic correlation and GE interaction correlation. According to the magnitude of these components, the mechanism of correlation can be illustrated for nutrient quality traits in indica rice.

Significantly genotypic relationships (r_G) among the nutrient quality traits existed, especially for protein content and protein index ($r_G \triangleq 0.54^{**}$), protein content and lysine content ($r_G \triangleq 0.45^{**}$), and lysine content and lysine index ($r_G \triangleq 0.64^{**}$) (Table 3). Of genotypic correlation, direct additive (r_A) and maternal additive (r_{Am}) correlations were significantly positive for the nutrient quality traits. It was concluded that simultaneously improving these pairwise traits of rice was possible in rice breeding. Cytoplasm correlation (r_C) was –0.53* between protein content and protein index, but not found for other pairwise traits in this experiment. Direct dominance (r_D) and maternal dominance (r_{Dm}) correlations were not significant between protein content and protein index, but significantly positive for other pairwise traits, except for the r_D (-0.69^{*}) between protein content and lysine content. Of GE interaction correlations, no additive interaction relationship (r_{AE}) for the pairwise nutrient quality traits of rice was noted, since the additive interaction effects for protein index, lysine content and lysine index were not found in this experiment (Table 2). Only significant maternal interaction correlation ($r_{AmE} \triangleq 0.54^{**}$) between protein content and protein index were noted. Possibility of simultaneously improving these nutrient quality traits of milled rice was expected in rice breeding because of the significant positive cytoplasmic interaction correlations (r_{CE}). From the results of direct interaction dominance (r_{DE}) and maternal interaction dominance (r_{DmE}) correlations, there was significantly positive relationship for these nutrient quality traits in indica hybrid rice, except between protein content and lysine index. It was suggested that simultaneously improving some pairwise nutrient quality traits of rice could be obtained in indica hybrid crosses since r_D, r_{Dm}, r_C, r_{DE} and r_{DmE} between protein content and protein index, protein index and lysine content, protein index and lysine index, and lysine content and lysine index were each significantly positive.

Since residual correlations (r_e) for protein content and protein index, protein index and lysine index, and lysine content and lysine index were significant, the relationships of these nutrient quality traits of milled rice were also influenced by sampling errors.

Although the results showed that nutrient quality traits of *indica* rice were controlled by seed, cytoplasm and maternal genetic effects (Shi and Zhu 1996), we have further found that GE interaction effects were also important for nutrient quality traits in our study. GE interaction effects were important, especially for maternal interaction effects of protein index and lysine index and for direct interaction effects of protein content and lysine content in milled rice. Since we also found that genetic effects and GE interaction effects existed for milling and cooking quality traits of rice (Shi *et al.* 1997, 1998), rice breeders should consider variation of rice quality traits in different environments.

For breeding new rice genotypes with improved nutrient traits, breeders have been concerned with the combination of multiple traits in selection processes. Indirect selection could be effectively applied in rice breeding according to an understanding of genotypic and GE interaction correlation components. Breeders could simultaneously improve nutrient quality traits with higher additive correlations (r_A, r_{Am} and/or r_{AE}, r_{AmE}) and cytoplasm correlation (r_C and/or r_{CE}). The non-additive relationship between two traits (r_D, r_{Dm} and/or r_{DE}, r_{DmE}) could also be used in indica hybrid rice breeding to improve the quality of milled rice. Therefore, it may be helpful for breeders to understand genetic mechanisms of quantitative nutrient quality traits in milled rice from analysis of effects and correlations of genes in different environments.

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