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C. H. Shi · J. M. Xue · Y. G. Yu · X. E. Yang · J. Zhu

Analysis of genetic effects on nutrient quality traits in *indica* rice

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Abstract Nine cytoplasmic male-sterile lines and five restorer lines were used in an incomplete diallel cross to analyze seed effects, cytoplasmic effects, and maternal gene effects on nutrient quality traits of *indica* rice (*Oryza sativa* L.). The results indicated that nutrient quality traits were controlled by cytoplasmic and maternal effects as well as by seed direct effects. Maternal effects for lysine content (LC), lysine index (LI), and the ratio of lysine content to protein content (RLP) were more important than seed direct effects, while protein content (PC) and protein index (PI) were mainly affected by seed direct effects. Cytoplasmic effects accounted for 2.41–20.80% of the total genetic variation and were significant for all nutrient quality traits. Additive genetic effects were much more important than dominance effects for all of the traits studied, so that selection could be applied for these traits in early generations.

Key words Cytoplasmic effects · Seed and maternal effects · Rice nutrient quality · Heritability · *Indica* rice

Introduction

Rice (*Oryza sativa* L.) provides about one-half of the food energy and protein consumed in China. Consequently, the nutrient quality of rice is of importance in rice breeding. Protein quality is determined by the content of restricted amino acids in the rice grain, with endosperm being the major storage organ of the nutritive materials. Although rice quality traits may be controlled by genes of the triploid endosperm, the rice grain is a new generation that differs from the maternal plants that provide grain nutrients, and as such, material and cytoplasmic effects are important components of extranuclear effects. Qi et al. (1983) observed maternal effects but only small cytoplasmic effects for the rice shape traits. After analyzing the inheritance of amylose content in rice, Pooni et al. (1992) suggested that this trait might be related to the effects of the maternal plant or cytoplasm. The expression of some endospermic traits in the grain of cereal crops are probably controlled by the genotype of the maternal plant (Mo 1995), and some rice quality traits also appear to be influenced by different types of cytoplasm (Yi and Cheng 1991, 1992). The results of Shi and Zhu (1992, 1993, 1994) indicated that significant seed and maternal genetic effects are detectable for rice quality traits.

No studies have yet been reported on the partitioning of the total genetic effect into components of seed, maternal, and cytoplasmic effects on nutrient quality traits of rice grain. Such knowledge would be helpful to our understanding of the genetic effects on rice breeding with respect to improving yield potential and rice nutrient quality. In the research reported here parental lines and their F_1 and F_2 seeds of *indica* rice were used for analyzing the genetic effects of the seed, cytoplasm and maternal plant on nutrient quality traits of milled rice.

Materials and methods

The following varieties of *indica* rice were used in this research: nine cytoplasmic male-sterile (CMS) lines, 'Zhexie 2 A' (P1), 'Xieqingzao A' (P2), 'Zhenan 3A' (P3), 'Gangzaoyang 1 A' (P4), 'Yinzaoyang 1 A' (P5), 'Erjiuqing A' (P6), 'V_{20} A' (P7), 'Zuo 5 A' (P8), 'Zhenshan 97 A' (P9), and five restoring (R) lines, 'T 49' (P10), 'Cezao 2-2' (P11), '26715' (P12), '102' (P13), and '1391' (P14). All possible single crosses were made with female CMS lines and male R lines in an incomplete diallel cross (9 × 5). The seeds of the parents and F_1s were sown on 28 March, 1994, and a single plant per hill was transplanted to the paddy field at Zhejiang Agricultural University on 29 April. There were 24 plants in a plot 20 × 20 cm, with three replications. Seed samples of parents or F_2s were derived at maturity from 8 plants in the middle part of the plot. The F_1 seeds were obtained from crossing CMS lines to restoring lines during the same season. The quantitative traits of the milled rice studied were protein content (PC, %), protein index (milligrams of protein per milled rice, PI), lysine content (LC, %),

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C. H. Shi (✉) · J. M. Xue · Y. G. Yu · X. E. Yang · J. Zhu
Department of Agronomy and Department of Soil Science and Agricultural Chemistry, Zhejiang Agricultural University, Hangzhou 310029, China

lysine index (milligrams of lysine per milled rice, LI), and the ratio of lysine content to protein content (RLP), which were measured with three replications for each sample of parents, F_1s and F_2s.

Generation means were analyzed by the genetic models for quantitative traits of endosperm in cereal crops (Zhu 1992; Zhu and Weir 1994b). Genetic components of seed additive variance (V_A), seed dominance variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}), maternal dominance variance (V_{Dm}), covariance between seed and maternal additive effects ($C_{A.Am}$), and covariance between seed and maternal dominance effects ($C_{D.Dm}$) were estimated by the MINQUE (0/1) method (Zhu and Weir 1994a). The variance of residual effects (V_e) was also estimated. Seed additive effect (A) and dominance effect (D), cytoplasmic effect (C), and maternal additive effect (Am) and dominance effect (Dm) were predicted by the Adjusted Unbiased Prediction (AUP) method (Zhu and Xu 1994). Estimates of variances and covariances were further used for calculating seed heritability $h_o^2 = (V_A + C_{A.Am})/V_p$, cytoplasmic heritability $h_c^2 = V_c/V_p$, maternal heritability $h_m^2 = (V_{Am} + C_{A.Am})/V_p$. Breeding values of the parents were evaluated according to the magnitude of predictors (Zhu et al. 1993; Zhu 1993; Zhu and Weir 1994a,b).

The Jackknife method was used to derive the standard errors of estimated components of variances and of predicted genetic effects by sampling the generation means of genetic entries (Miller 1974; Zhu 1992). All data were analyzed by C programs running on an IBM PC computer.

Results

Estimation of seed, cytoplasmic and maternal genetic variances

Estimates of the variances and covariances components of nutrient quality traits of milled rice are summarized in Table 1. Since highly significant seed and maternal genetic variances were detected for all traits studied, the nutrient quality of milled rice was controlled by genetic effects of the seed and maternal plant. Maternal genetic variances ($V_{Am} + V_{Dm}$) accounted for 50.43%, 44.24%, and 43.14% of the total genetic variances ($V_A + V_D + V_C + V_{Am} + V_{Dm}$) for LC, LI, and RLP, respectively, which indicates that the genetic effects of the maternal plant were more important than the others for these three quality traits. Although PC and PI were mainly affected by seed genetic effects with variances ($V_A + V_D$) around 50.11% and 44.02%, respectively, of the estimated variances, the maternal variances were close to the seed variances. The additive variances (V_A and V_{Am}) were much larger than the dominance variances (V_D and V_{Dm}) for all of the traits studied. It was shown that additive genetic effects were the major contributions of genetic variation for all nutrient quality traits. Therefore, selection could be applied for these traits in early generations, and commercial rice varieties with high nutrient quality could be developed by selection. Significant additive convariance ($C_{A.Am}$) and dominance covariance ($C_{D.Dm}$) were not detected in this experiment. It was suggested that the relationship between seed and maternal genetic effects might not be important for these nutrient quality traits. The small values of the estimated residual variance indicates that nutrient quality traits were mainly affected by genetic effects.

Significant cytoplasmic variances (V_C) comprised about 2.41–20.80% of the total genetic variance for all nutrient quality traits (Table 1). Nutrient quality traits were significantly affected by the genetic effects of cytoplasm as well as those of the seed and maternal plant, and the cytoplasmic effects on nutrient quality traits of milled rice were not negligible in rice breeding. Therefore, the rice quality of varieties or hybrid rice crosses could be improved by selecting a better cytoplasm.

Estimation of seed, cytoplasmic, and maternal heritabilities

Since there are seed, cytoplasmic, and maternal genetic effects, the total narrow-sense heritability can be further partitioned into seed (h_o^2), cytoplasmic (h_c^2), and maternal (h_m^2) heritabilities for all of the nutrient quality traits. Seed heritability (h_o^2) was found to be larger than maternal heritability (h_m^2) for PC (Table 2), but for the other nutrient quality traits, the maternal heritability (h_m^2) was more important. Significant h_o^2 and h_m^2 for LC and h_o^2, h_c^2 and h_m^2 for RLP were detected in this experiment, therefore, selection advances were predictable in the early generations, especially for LC and RLP.

Prediction of genetic effects

Predicted seed additive effects (A) and maternal additive effects (Am) are listed in Table 3. The results indicate that seed additive effects were mostly positive and the

Table 1 Estimation of genetic variances and covariances of nutrient quality traits in *indica* rice (*PC* protein content, *PI* protein index, *LC* lysine content, *LI* lysine index, *RLP* ratio of lysine content to protein content)

Parameter	PC	PI	LC ($\times 10^{-3}$)	LI ($\times 10^{-3}$)	RLP ($\times 10^{-3}$)
V_A	18.171**	0.344**	10.253**	0.363**	0.047**
V_D	2.433**	0.064**	2.920**	0.084**	0.014**
V_c	0.934**	0.121**	3.179**	0.259**	0.035**
V_{Am}	16.291**	0.363**	13.429**	0.457**	0.048**
V_{Dm}	0.964**	0.035**	3.204**	0.104**	0.025**
$C_{A.Am}$	−9.745	−0.154	−2.858	−0.109	−0.004
$C_{D.Dm}$	−0.166	−0.004	−0.245	−0.006	−0.001
V_e	0.063**	0.005**	0.070**	0.003**	0.001**

** At 1% significance level

Table 2 Estimation of heritabilities of nutrient quality traits in *indica* rice

Parameter	PC	PI	LC	LI	RLP
h_o^2	0.443	0.309	0.275*	0.244	0.266**
h_m^2	0.344	0.340	0.394**	0.335	0.275**
h_c^2	0.049	0.196	0.118	0.249	0.221**

* and ** At 5% and 1% significance level, respectively

maternal additive effects mostly negative for male parents (P10–P14) for PC, PI, and LC. The seed additive effects of these males could increase the nutrient quality traits for PC, PI and LC of milled rice, but the maternal additive effects would decrease these traits. In the female parents (P1–P9), negative seed additive effects were detected, and the maternal additve effects were almost positive for PC, PI and LC. Therefore, the genetic effects on males and females were different. In the traits of LI and RLP, only some parents had significant seed or maternal additive effects. Estimates of seed additive and maternal genetic effects showed that P11 was better than the other parents for improved nutrient quality of milled rice. The seed additive effects of P11 could significantly increase PC, PI, LC, and LI, while only the maternal additive effect could decrease PC of milled rice.

For PC, the cytoplasmic effects were significantly positive in P1, P4 and P8, while the others were negative (Table 4). It may be that the cytoplasmic effects of P1, P4 and P8 could highly increase the PC of milled rice. The cytoplasmic effects of most parents could improve PI, but those of P4 and P5 could reduce this trait. For LC and LI, the cytoplasmic effects were positive for most of the parents, with the exception of P3, P4, and P7. There were significant cytoplasmic effects for RLP in P1 and P5, and RLP could be improved by the cytoplasmic effects of these two parents.

Differences were found between CMS lines with different cytoplasm for some nutrient quality traits (Table 4). P1 and P2 with different cytoplasms and the same nuclear genes had different cytoplasmic effects, especially for PC and RLP. The cytoplasmic genetic effects of P1 could significantly increase PC and RLP, but those of P2 were negative for these two traits. Although there were positive cytoplasmic effects for PI, LC and LI in the crosses of P1 × Pi and P2 × Pi, significant effects were only found in the crosses of P1 × Pi. We could also find differences in some nutrient quality traits, except for LC between crosses of P4 × Pi and P5 × Pi, which had the same nuclear genes and different cytoplasm for female parents. In these two group of crosses, the cyto-plasmic effects of P4 could significantly increase PC and reduce

Table 3 Predicted seed and maternal genetic effects of nutrient quality traits

Parent	PC (%)		PI (mg)		LC (%)		LI (mg)		RLP	
	A	Am	A	Am	A	Am	A	Am	A	Am
P1	-1.335*	0.365	-0.146*	-0.116	-0.038	0.036	-0.004	0.002	0.000	0.001
P2	-1.256*	0.184	-0.092	-0.198	-0.040^{+}	0.041	-0.004	0.002	-0.000	0.002
P3	-1.500^{+}	3.800**	-0.157	0.602**	-0.005	0.028	0.000	0.007	0.001	-0.002
P4	-1.471**	2.746**	-0.204**	-0.341*	-0.006	0.034	-0.001	0.005	0.003*	-0.002
P5	-1.610*	3.159*	-0.213*	0.312*	-0.008	-0.003	-0.002	-0.004	0.002^{+}	-0.003
P6	-1.141*	1.651*	-0.093^{+}	0.100	-0.014	-0.005	-0.001	-0.005^{+}	0.001	-0.002
P7	-0.974**	-1.254**	-0.070	-0.278**	-0.022	0.004	-0.001	-0.001	0.001	0.001
P8	-1.523**	1.053	-0.116	-0.052	-0.025	-0.011	0.002	-0.011	0.002	-0.002
P9	-0.878**	0.113	-0.069	0.020	-0.006	-0.009	0.001	-0.002	0.001	-0.001
P10	2.824**	-3.725**	0.443**	-0.476**	0.051^{+}	-0.077^{+}	0.009	-0.011	-0.002	0.000
P11	2.960**	-2.482**	0.388*	-0.126	0.079*	-0.053	0.011^{+}	-0.001	-0.000	0.000
P12	1.117	0.963	-0.094	0.591*	-0.045	0.107*	-0.015	0.031^{+}	-0.006*	0.003
P13	2.892**	-4.104**	0.352*	-0.499**	0.060^{+}	-0.071	0.008	-0.012	-0.001	0.001
P14	1.894^{+}	-2.468*	0.072	-0.222	0.018	-0.021	-0.004	0.000	-0.002	0.001

$^{+}$, * and ** At 10%, 5% and 1% significance level, respectively

Table 4 Predicted cytoplasmic genetic effects of nutrient quality traits in crosses

Cytoplasmic effect	PC (%)	PI (mg)	LC (%)	LI (mg)	RLP
P1	0.173**	0.189^{+}	0.043**	0.012**	0.003**
P2	-0.634^{+}	0.435	0.011	0.011	-0.001
P3	-0.467**	0.069	-0.021*	-0.001	-0.001
P4	1.349*	-0.276^{+}	-0.029	-0.007**	-0.000
P5	-0.102	-0.019	0.086	0.012**	0.007*
P6	-0.370*	0.138^{+}	0.006	0.003	-0.000
P7	-0.087	0.352^{+}	-0.061	-0.007^{+}	-0.008
P8	1.736*	0.222*	0.088	0.034*	0.012
P9	-0.356**	0.187	0.013^{+}	0.006*	0.001

$^{+}$, * and ** At 10%, 5%, and 1% significance level, respectively

PI and LI and that of P5 could significantly improve LI and RLP. In general, the cytoplasmic effects of P1 and P8 were better than those of the other female parents for improving the quality of milled rice.

Discussion

The protein and lysine content of milled rice is related to its nutrient value. Breeders in China are now paying much more attention than in the past for improving rice quality. It is necessary for breeders to understand the inheritance of nutrient quality traits for endosperm. From the results of this study, we found that nutrient quality traits in *indica* rice were controlled by cytoplasmic genetic effects as well as by seed and maternal genetic effects and that the additive effects of the genes were more important than dominance effects. Therefore, the triploid models for seed direct genetic effects (Gale 1975; Bogyo et al. 1988; Mo 1988) would give biased estimates for quantitative endospermic traits with maternal and/or cytoplasmic effects. By using the new genetic models for quantitative traits of triploid endosperm (Zhu 1992; Zhu and Weir 1994ab), we could evaluate the seed, cytoplasmic, and maternal effects that control the quality traits of milled rice.

Although rice artificial emasculation and pollination are very labor intensive, especially for analyzing endospermic quality traits, the method of this study only needs the means of three generations of parents, F_1s, and F_2s with two or three replications in a set of diallel crosses, without the requirement of measuring single seed or plant. Since cytoplasmic male-sterile lines have been used for producing hybrid seeds in rice, a mating design with CMS lines as female parents and R lines as males can be used for the estimation of variance and covariance components and for the prediction of genetic effects. In comparison with other genetic models, the method used in this experiment for analyzing the genetic effects of triploid endosperm is unbiased and applicable.

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