Genetic analysis of cytoplasmic and maternal effects for milling quality traits in *indica* rice

CHUNHAI SHI and JUN ZHU

Agronomy Department, Zhejiang Agricultural University, Hangzhou, 310029, China

Summary

Analysis of cytoplasmic and maternal effects of maternal plant as well as seed effects controlled by nuclear genes of endosperm cells was conducted for milling quality traits of *indica* rice (*Oryza sativa* L.). Nine cytoplasmic male sterile lines as females and five restorer lines as males were used in an incomplete diallel cross. The results indicated that milling quality traits were controlled by seed, cytoplasmic and maternal genetic effects. Maternal effects for brown rice recovery (BRR) and milled rice recovery (MRR) were more important than seed effects. But brown rice weight (BRW), milled rice weight (MRW) and head milled rice recovery (HMRR) were mainly controlled by seed effects. Cytoplasmic effects accounted for 4.1 to 37.3% of total genetic variation and were significant for all milling quality traits. BRW, MRW and HMRR were mainly controlled by seed and cytoplasmic heritabilities, but MRR was affected by seed and maternal heritabilities. Additive correlation was more important between BRW and MRW, BRW and MRR, BRW and HMRR, MRW and MRR. Estimates of seed additive, maternal additive and cytoplasmic effects showed that V_{20} A was better than other parents for improving the milling quality of rice grain.

Introduction

Yield of rice is closely related to milling quality including brown rice recovery, milled rice recovery, head milled rice recovery, brown rice weight and milled rice weight. It is important to breed new varieties with good milling quality. Although milling quality traits could be affected by environmental factors, they were mainly controlled by genetic effects (Shi and Zhu, 1992). Since rice seeds are a new generation different from their maternal plants which provide grain nutrients, rice quality traits may be affected by endosperm and/or maternal plant genes (Qi, Li, Yang and Wu, 1983; Shi and Zhu, 1992, 1993, 1994; Pooni, Kumar and Khush, 1992), or of cytoplasm (Yi and Cheng, 1991, 1992). But up to now, the genetic effects have not been partitioned into the effects of seed, maternal plant and cytoplasm for milling quality traits of rice grain.

In this paper, the genetic model for quantitative traits of endosperm in cereal crops (Zhu, 1992; Zhu and Weir, 1994) was used to determine the genetic effects of seed, maternal plant and cytoplasm on milling quality traits of rice grain by using the generation means.

Materials and methods

Materials

Nine cytoplasmic male sterile (CMS) lines (Zhexie 2 A (P1), Xieqingzao A (P2), Zhenan 3 A (P3), Gangzao 1 A (P4), Yinzao 1 A (P5), Erjiuqing A (P6), V_{20} A (P7), Zuo 5 A (P8), Zhenshan 97 A (P9)), and five restorer (R) lines (T 49 (P10), Cezao 2-2 (P11), 26715 (P12), 102 (P13), 1391 (P14)) of *indica* rice were used in an incomplete diallel cross (9 × 5). These CMS and restorer lines were randomly sampled from a reference population and some of them have applied in making hybrid rice crosses in China. Seedlings of parents and F_1s were planted in the field of experimental farm at Zhejiang Agricultural University during early in 1994. The seeds were sown on 28 March and single plants were transplanted at spacings of 20 × 20 cm on 29 April. There were 24 plants in each plot with three replications. Seed samples of parents or F_2s on F_1's plants were derived at maturity from eight plants in the middle part of the plot. The F_1 seeds used for analyzing were obtained by crossing CMS lines to restorer lines at flowering during the early season. Quantitative traits studied were brown rice weight, milled rice weight, brown rice recovery, milled rice recovery and head milled rice recovery, which were measured with three replications for each sample of parents, F_1s and F_2s.

Methods

MINQUE(0/1) method (Zhu, 1992; Zhu and Weir, 1994) was used to estimate genetic components of seed additive (V_A) and dominance (V_D) variances, maternal additive (V_{Am}) and dominance (V_{Dm}) variances, cytoplasmic variance (V_c), and covariances between seed and maternal additive effects ($C_{A.Am}$) and between seed and maternal dominance effects ($C_{D.Dm}$). The variance of residual effects (V_e) was also estimated. Estimates of variances and covariances were further used for calculating seed heritability $h_o^2 = (V_A + C_{A.Am})/V_P$, maternal heritability $h_m^2 = (V_{Am} + C_{A.Am})/V_p$, and cytoplasmic heritability $h_C^2 = V_c/V_p$.

Seed additive (A) and dominance (D) effects, cytoplasmic effect (C), maternal additive (Am) and dominance (Dm) effects for milling quality traits were predicted by Adjusted Unbiased Prediction (AUP) method (Zhu and Xu, 1994). Breeding values of parents and heteroses of F_1s were evaluated according to the magnitude and direction of predictors. If the standard dominance direction ($\Delta o = -\sum \hat{D}o_{ii} / \sqrt{n\sigma_{\hat{D}o}^2}$) or ($\Delta m = -\sum \hat{D}m_{ii} / \sqrt{n\sigma_{\hat{D}m}^2}$) was larger than 0, the positive heterosis was expected for seed or maternal plant (Zhu, 1993; Zhu, Ji and Xu, 1993). Seed additive correlation (r_A), seed dominance correlation (r_D), cytoplasmic correlation (r_c), maternal plant additive correlation (r_{Am}), maternal dominance correlation (r_{Dm}) and residual correlation (r_e) for pairwise traits of milling quality were also estimated.

The Jackknife method (Miller, 1974) was applied by sampling generation means of entries for estimating the standard errors of estimated components of variances or correlation coefficients, and of predicted genetic effects.

Results and analysis

Estimation of genetic variances and heritabilities
Milling quality traits studied were controlled by genetic effects of seed, maternal plant and cytoplasm. Significance was detected at 1% level for all variances in MRR, and for V_D, V_C and V_{Dm} in BRR (Table 1). Maternal variances accounted for 51.3% and 43.0% of estimated variance for MRR and BRR, respectively. Genetic variances of maternal plant for MRR and BRR were larger than those of seed. It was shown that additive variances (V_A and V_{Am}) were larger than dominance variances (V_D and V_{Dm}) in MRR. It is possible to increase MRR in rice varieties by selection. Since additive variances for BRR were not found in this experiment, BRR was mainly controlled by dominance effects. BRR could be increased through heterosis in *indica* hybrid rice. BRW, MRW and HMRR were mainly controlled by seed genetic effects with variances (V_A and V_D) around for 41.9 to 49.7% of total genetic variance ($V_A + V_D + V_C + V_{Am} + V_{Dm}$). Additive genetic effects were more important than dominance genetic effects for BRW, MRW and HMRR so that selection could be applied for these traits in early generations. As significant cytoplasmic variances (V_c) were about 4.1 to 37.3 % of total genetic variance for all traits, the cytoplasmic effects could influence the milling quality performance of the progeny. Additive covariance ($C_{A.Am}$) and dominance covariance ($C_{D.Dm}$) were not detected. No relationship was detected between seed and maternal genetic effects on these milling quality traits. It is concluded that milling quality traits were mainly affected by genetic effects because of the small values of estimate residual variance.

Since there are three types of genetic effects (seed, maternal plant and cytoplasm), the narrow-sense heritability can be further partitioned into seed heritability (h^2_0), maternal plant heritability (h^2_m) and cytoplasmic heritability (h^2_C). h^2_0 and h^2_C were significant for BRW, MRW and HMRR (Table 1). Therefore, selection advances were predictable in the early generations for BRW, MRW and HMRR. Seed additive variance (V_A) was larger than maternal additive variance (V_{Am}), therefore h^2_0 was larger than h^2_m for these three traits. Significant h^2_0 and h^2_m for MRR indicated that selection in early generations was applicable. BRR was mainly controlled by seed and maternal dominance effects or cytoplasmic effects. It was suggested to increase BRR by selection in latter generations or by utilizing heterosis.

Prediction of genetic effects
The predicted seed additive effects (A), maternal additive effects (Am), and cytoplasmic effects (C) were shown in table 2 for milling quality traits. The results showed that seed additive effects of five restorer lines (P10, P11, P12, P13 and P14) were negative for BRW, MRW, MRR and HMRR. Cytoplasmic effects of these parents were also negative for BRW, MRW, BRR and MRR, except for BRW of P14. Therefore, seed additive and/or cytoplasmic effects of five restorer lines could reduce these milling quality performance of the progeny. But positive maternal additive effects of P10, P11 and P12 could increase BRW and/or MRW. In HMRR, significant positive cytoplasmic effects

483

Table 1. Estimation of genetic variances, covariances and heritabilities of milling quality traits in *indica* rice for brown rice weight (BRW), milled rice weight (MRW), brown rice recovery (BRR), milled rice recovery (MR), and head milled rice recovery (HMRR).

Parameter	BRW	MRW	BRR	MRR	HMRR
V_A	8.285**	4.184**	0.000	19.181**	160.667**
V_D	0.499**	0.335**	2.236**	6.494**	45.132**
V_C	2.340**	2.128**	2.598**	2.373**	169.232**
V_{Am}	5.308**	2.863**	0.000	19.630**	0.000
V_{Dm}	1.257**	1.270**	3.648**	9.913**	79.054**
$C_{A.Am}$	−4.264	−1.547	0.000	−0.402	0.000
$C_{D.Dm}$	−0.300	−0.233	−1.329	−3.863	−19.051
V_e	0.183**	0.146**	1.011**	1.334**	5.033**
h_o^2	0.460**	0.358**	0.000	0.373*	0.382**
h_m^2	0.119	0.179	0.000	0.382*	0.000
h_c^2	0.268*	0.289*	0.380	0.047	0.402**

* and ** at 5% and 1% significance level, respectively.

were detected only for P12 and P14 among five restorer lines, so these two lines might be good candidates for parents of increasing HMRR as female in other rice breeding plans. In CMS lines, the positive seed additive and/or cytoplasmic effects were significant for P1, P2, P3, P7, P8 and P9, but significant negative maternal additive effects were also found for P1, P2, P4, P5, P6 and P8 in BRW, MRW, BRR and/or MRR, respectively. The genetic effects could increase and/or reduce these quality traits. Seed additive effects of P8 was 5.848* and cytoplasmic effects of P1 and P9 were −25.724* and −23.869* for HMRR, respectively. So the genetic effects could reduce HMRR of the progeny using these three CMS parents as females. In all parents studied, estimates of seed additive, maternal additive and cytoplasmic effects showed that V_{20} A (P7) was better than other parents for improving the milling quality of rice grain.

Differences were found between CMS lines with the same cytoplasm or with different cytoplasm for some milling quality traits (Table 2). P1 and P2 with the same nuclear genes and different cytoplasm had no differant cytoplasmic effects for BRW, MRW and MRR, but different for BRR and HMRR. There were no differences in all milling quality traits between P4 and P5 which had the same nuclear genes but different cytoplasm. In CMS lines of P3, P6, P7 and P9 with the same cytoplasm and different nuclear genes, differences could still be detected in cytoplasmic effects for the traits studied.

Negative seed standard dominance direction Ao (−2.815** for BRW, −1.263* for MRW, −0.870* for MRR, −2.495** for HMRR) and positive maternal standard dominance direction Am (3.249* for BRW, 3.121** for MRW, 1.577* for BRR, 1.328[+] (10% significant level) for MRR) were found. These results indicated different direction of heterosis for seed and maternal plant in milling quality traits.

Analysis of genetic correlations
Correlation components of total genetic correlation include those of seed additive corre-

Table 2. Predicted genetic effects of milling quality traits in *indica* rice for brown rice weight (BRW), milled rice weight (MRW), brown rice recovery (BRR), milled rice recovery (MRR), and head milled rice recovery (HMRR).

Parent	BRW			MRW			BRR	MRR			HMRR	
	A	C	Am	A	C	Am	C	A	C	Am	A	C
P1	2.706*	0.041	-1.555**	1.162*	0.383	-0.767*	-0.446	-1.231	-1.501	0.559	7.077	-25.724*
P2	1.643*	1.374	-1.059	1.472**	1.120	-0.923*	2.679**	0.602	3.482	-1.104	5.710	-5.238
P3	0.636	0.280	-0.310	-0.205	1.581*	-0.259	1.680	3.174	1.973	-2.810	6.547	2.686
P4	0.321	-0.190	-0.717**	-0.059	-0.606	-0.314*	-1.340	2.238	0.067	-1.537	8.949	-11.427
P5	1.321	-1.803	-1.230**	0.336	-1.212	-0.633**	-0.473	1.205	1.375	-0.392	-0.397	0.056
P6	0.400	0.567	-0.701*	0.537	0.199	-0.509*	0.525	0.985	0.560	-0.410	6.822	4.597
P7	1.057*	2.463**	-0369	0.866**	1.891**	-0.227	1.614*	0.389	-0.067	-0.366	-0.867	-0.644
P8	3.185**	0.986	-1.312*	2.651**	1.784	-1.081	0.853	-0.059	1.480*	-0.515	-5.848*	-2.092
P9	0.249	1.306**	-0.093	-0.377	1.337*	0.254	2.040*	0.641	0.676	-0.033	6.819	-23.869*
P10	-2.055**	-2.689	2.041**	-0.552	-1.202	0.925	-0.275	-0.298	-2.269	0.045	-3.358	-3.541
P11	-2.292**	-0.296	2.390**	-1.005*	-0.421	1.464*	-0.874	-0.058	0.579	-0.897	-5.412	3.709
P12	-3.316**	-1.538	2.690**	-2.262**	-2.292	1.681*	-3.058*	-1.775	-1.087	1.781	-10.829	29.951*
P13	-1.359**	-1.358	-0.559	-0.626	-1.772	-0.277	0.120	-2.407	-1.628	2.205	-8.897	15.595
P14	-2.508**	0.852*	0.774	-1.944**	-0.796	0.658	-3.954*	-3.425	-3.648	3.452	-6.325	15.932*

Note: * and ** at the 5% and 1% significance level, respectively. A = seed additive effect, C = cytoplasmic effect, and Am = maternal additive effect.

485

lation (r_A), seed dominance correlation (r_D), cytoplasmic correlation (r_c), maternal additive correlation (r_{Am}) and maternal dominance correlation (r_{Dm}). Estimates of the genetic correlation components and residual correlation (r_e) among milling quality traits are listed in Table 3.

Significantly positive correlations between BRW and MRW or between MRW and MRR were detected for r_A, r_D, r_c, r_{Am} and r_{Dm} with (r_A, r_{Am} and r_c) > (r_D and r_{Dm}). The relationship between BRW and MRW or between MRW and MRR was mainly controlled by additive and cytoplasmic effects. These results indicted that increasing BRW, MRW and MRR could be accomplished in rice breeding. Positive r_D or r_{Dm} suggested that simultaneous improvement of BRW, MRW and MRR could be obtained for hybrids. Although there existed positive additive correlations (r_A and r_{Am}) between BRW and MRR, BRW and HMRR, MRW and HMRR or between MRR and HMRR, the indirect

Table 3. Correlation components betw.een milling quality traits in indica rice for brown rice weight (BRW), milled rice weight (MRW), brown rice recovery (BRR), milled rice recovery (MRR) and head milled rice recovery (HMRR).

Trait		BRW	MRW	BRR	MRR	HMRR
BRW	r_A		0.720**	0.000	0.596**	0.486**
	r_D		0.540**	−0.093*	−0.334**	−0.126**
	r_C		0.477**	0.378**	0.135**	−0.253**
	r_{Am}		0.509**	0.000	0.311**	0.000
	r_{Dm}		0.426**	0.032	−0.001	0.041
	r_e		0.100	0.159*	−0.118	0.123*
MRW	r_A			0.000	0.364**	0.174**
	r_D			−0.251**	0.009	0.175**
	r_C			0.571**	0.453**	−0.349**
	r_{Am}			0.000	0.145**	0.000
	r_{Dm}			0.075	0.119**	0.066
	r_e			−0.136	0.344**	0.123*
BRR	r_A				0.000	0.000
	r_D				0.258**	−0.172**
	r_C				0.496**	−0.393**
	r_{Am}				0.000	0.000
	r_{Dm}				0.264**	−0.157**
	r_e				0.269**	−0.059
MRR	r_A					0.314**
	r_D					0.208**
	r_C					−0.310**
	r_{Am}					0.000
	r_{Dm}					0.182**
	r_e					−0.008

Note: r_A = seed additive correlation, r_D = seed dominance correlation, r_C = cytoplasmic correlation, r_{Am} = maternal additive correlation, r_{Dm} = maternal dominance correlation and r_e = residual correlation.

selection in early generations could be influenced by negative r_D, r_{Dm} or r_c. Significant r_D and r_{Dm} between BRR and MRR showed that high BRR and MRR in *indica* hybrid rice cross could be obtained. The relationship between BRW and BRR, or between MRW and BRR, was mainly controlled by cytoplasmic effects. There were negative r_D, r_{Dm} and r_C between BRR and HMRR. Therefore, it will be difficult to breed a variety or cross with high BRR and HMRR. Residual correlation was detected between BRW and BRR, BRW and HMRR, MRW and MRR, MRW and HMRR, BRR and MRR.

Discussion

Milling quality is related to the yield of brown rice or milled rice. Breeders in China are now paying much more attention to improve rice quality, including milling quality. Qi et al. (1983) pointed out that rice seed shape may be controlled by maternal plant genes, and that cytoplasmic effects were very small. Yi and Cheng (1992) found that milling quality traits were also influenced by different types of cytoplasm. The results of Shi and Zhu (1992) indicated that significant seed and maternal genetic effects were existed in some milling quality traits. In this study, we have found that seed, maternal and cytoplasmic genetic effects could influence milling quality traits. Maternal effects for BRR and MRR were more important than seed effects, and BRW, MRW and HMRR were mainly controlled by seed effects. All milling quality traits were also affected by cytoplasmic effects. In rice breeding, when traits are mainly controlled by maternal and cytoplasm genetic effects with high maternal and cytoplasmic heritabilities, they can be improved by selecting maternal plant. However, for those traits controlled mainly by seed genetic effects with high seed heritabilities, it is applicable to select the single seed with good quality because of the difference among seeds. In hybrid rice, when traits are mainly influenced by maternal dominance effects, the F_2 seeds grown on F_1 plants will have no apparent segregation. But traits affected mainly by seed dominance effects will have segregation in F_2 seeds. It is necessary for breeders to understand the genetic mechanism of quantitative traits for endosperm.

Indirect selection can also be used in rice breeding. Although genetic correlation can be used in measuring the relationship between pairwise traits, it can not provide information about additive and dominance correlations. When traits can not be easily measured or their heritabilities are low, it is better to indirectly select other highly correlated traits. Our results showed that additive correlations were more important between BRW and MRW, BRW and MRR, BRW and HMRR, and between MRW and MRR in genetic correlation, so indirect selection could be applied for these pairwise traits in rice breeding. Breeding for hybrid rice could be expected to improve BRR and MRR or BRR and HMRR due to the dominance correlations.

Because these nine CMS lines and five restorer lines were randomly sampled from a reference population, the results or information of this experiment and the method of analysis could be applied in rice breeding or making *indica* hybrid rice crosses in general. It is also useful for other cereal crops to introduce this genetic model and analysis method for studying quantitative seed quality traits.

Acknowledgements

References

Miller, R. G. (1974). The Jackknife, a review. *Biometrika*, **61**, 1–15.

Pooni, H. S., Kumar, I. and Khush, G. S. (1992). A comprehensive model for disomically inherited matrical traits expressed in triploid tissues. *Heredity*, **69**, 166–174.

Qi, Z. B., Li, B. J., Yang, W. G. and Wu, X. F. (1983). A study on the genetics of exterior quality and fat of the rice grains. *Acta Genetica Sinica*, **10**(6), 452–458.

Shi, C. H. and Zhu, J. (1992). Genetic analysis of milling quality characters in indica hybrid rice. *Chin. J. Biomath.*, **7**(4), 37–45.

Shi, C. H. and Zhu, J. (1993). Analysis of seed and maternal genetic effects for exterior quality characters in indica hybrid rice. *Acta Agri. Univ. Pekinensis*, **19** (supplement), 69–74.

Shi, C. H. and Zhu, J. (1994). Analysis of seed and maternal genetic effects for characters of cooking quality in indica rice. *Chin. J. Rice Sci.*, **8**(3), 129–134.

Yi, X. P. and Cheng, F. Y. (1991). A study on the genetic effect of cytoplasm on quality character of indica hybrid rice. I. The analysis of out-looking characters and contents of amino acids. *J. Guangxi Agri. College*, **10**(1), 25–32.

Yi, X. P. and Cheng, F. Y. (1992). Genetic effect of different cytoplasm types on rice cooking, milling and nutrient qualities in indica type hybrid rice. *Chin. J. Rice Sci.*, **6**(4), 187–189.

Zhu, J. (1992). Mixed model approaches for estimating variances and covariances. *Chin. J. Biomath.*, **7**(1), 1–11.

Zhu, J., Ji, D. F. and Xu, F. H. (1993). A genetic approach for analyzing inter-cultivar heterosis in crops. *Chin. J. Genet.*, **20**(3), 183–191.

Zhu, J. and Xu, H. F. (1994). A genetic model and analysis methods for endosperm traits. *Acta Agronomica Sinica*, **20**(3), 164–270.

Zhu, J. (1993). Methods of predicting genotype value and heterosis for offspring of hybrids. *Chin. J. Biomath.*, **8**(1), 32–44.

Zhu, J. and Weir, B. S. (1994). Analysis of cytoplasmic and maternal effects. I. Genetic models for triploid endosperm. *Theor. Appl. Genet.*, **89**, 160–166.