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Genetic control of paste viscosity characteristics in *indica* rice (*Oryza sativa* L.)

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Abstract Paste viscosity parameters play an important role in estimating the eating, cooking and processing quality of rice. Four cytoplasmic male-sterile (CMS) lines and eight restorer (R) lines were employed in an incomplete diallel cross to analyze seed effects, cytoplasmic effects and maternal gene effects on the viscosity profiles of *indica* rice. The results indicated that the viscosity profiles of rice were controlled by the direct effects of the seed, by the cytoplasm and by maternal plant. The seed-direct effects ($V_A + V_D$) accounted for over 51% of the total genetic variances ($V_A + V_D + V_C + V_{Am} + V_{Dm}$) for all the traits, suggesting that seed direct effects were more important than maternal effects and cytoplasmic effects. The additive variances ($V_A + V_{Am}$) were much larger than the dominance variances ($V_D + V_{Dm}$), which revealed that additive genetic effects were the major contributors of genetic variation for the paste viscosity profiles, and that selection could be applied for viscosity traits in the early generations. Significant cytoplasmic variance (V_C) was detected for hot paste viscosity (HPV), cool paste viscosity (CPV) and consistency viscosity (CSV). The cytoplasmic effects for these three traits can, therefore, not be neglected in rice breeding. It was also shown that seed heritabilities (h_o^2) tended to be larger than maternal heritabilities (h_m^2) and cytoplasmic heritabilities (h_c^2). Prediction of the main genetic effects for 12 parents showed that CMS lines had highly positive effects on all the traits except for the breakdown viscosity (BDV), and that R lines had both positive and negative effects on the paste viscosity characteristics.

Key words Paste viscosity characteristics · Seed and maternal effects · Cytoplasmic effects · Rapid Visco Analyser · *Indica* rice

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Introduction

In rice improvement programs, amylose content is widely recognized as the most important determinant of the cooking, the processing quality and the edibility of rice. However, it is also agreed that there are secondary differences among varieties that have similar amylose contents, one of which is paste viscosity (Jaliano 1985). Although paste viscosity has long been used in rice-quality breeding to select the desirable eating, cooking and processing properties of new rice varieties, the Brabender Viscoamylograph has not been extensively used for screening promising lines for paste viscosity in rice breeding programs because of the large sample (40 ~ 50 g) and long period (80 min when starting at 50°C or 94 min when starting at 30°C) required per run (Jaliano 1996). A very effective instrument currently available, the Rapid Visco Analyser [(RVA), which is made in Australia (Newport Scientific Pty Ltd., Warriewood, Australia)], is an alternative choice to the traditional Brabender Viscoamylograph (Brabender OHG, Duisberg, Germany). The RVA has become increasingly popular for investigating the viscosity properties of starches of both rice and other cereal crops, because it requires only a small sample size and is easy to operate (Wrigley et al. 1996). Additionally, the RVA is relatively rapid compared with the traditional instrument, making it suitable for breeding programs (Blakeney et al. 1991, 1995; Panozzo et al. 1993; Shu 1996). However, the genetic behavior of the viscosity parameters has so far received little attention, except for the primary research carried out by Gravois and Webb (1997) who found that the inheritance of paste viscosity profiles appeared to be controlled by a single locus with genes with additive effects.

Rice grain represents a new generation different from the maternal plant, so rice quality traits may be controlled by genes of the triploid endosperm, the cytoplasm, and the maternal plant. Shi et al. (1996) showed that the nutrient quality traits (protein and lysine content) were controlled by cytoplasmic and maternal effects as well as by seed direct effects. Cooking quality traits (amylose content, gelatinization temperature and gel consistency) were also found to be mainly controlled by genetic effects and genotype × environment interaction effects with three sets of genetic systems (Shi et al. 1997). In the present paper, the genetic model proposed by Zhu and Weir (1994) for quantitative endosperm traits in cereal crops was employed to dissect the genetic effects of the seed, the cytoplasm and the maternal plant for rice paste viscosity characteristics, and to predict the breeding value of the parents for the quality improvement of rice.

Materials and methods

Plant materials and experimental design

Four cytoplasmic male-sterile (CMS) lines (P1 = Zhenshan 97 A, P2 = Xieqingzao A, P3 = II32 A, and P4 = Longtefu A) and eight restorer (R) lines (P5 = 371, P6 = Minghui 63, P7 = Zhehui No. 3, P8 = Wenhui No. 4, P9 = Milyang 46, P10 = Ce 48-2, P11 = Ce 64-7, P12 = IR36) were used in this experiment. All possible single crosses were made with female CMS lines and male R lines in an incomplete diallel cross (4 × 8) in Hangzhou in September, 1997. The seeds of the parents and F_1s were sown on November 27, 1997, in Hainan province, and a single plant per hill was transplanted to the paddy field at a spacing of 20 × 20 cm on December 19, 1997. The experimental design was a completely randomized block with two replications. There were 36 plants in each plot. Many female plants (CMS) were planted near the plots so that they could be crossed to the male plants during the flowering period to obtain the F_1 seeds by artificial hybridization. One cross combination usually needed 40 CMS plants (about four rows of plants; one row has 12 plants) so that at least 50 g of F_1 seeds would be harvested at maturity in late March, 1998. The parents' seeds and F_2s from F_1s plants were also harvested at the same maturity period from ten plants in the middle part of the plot. The seed samples of each entry were bulked for paste viscosity analysis.

Paste viscosity profiles

The RVA paste viscosity was determined on a Rapid Visco Analyser using the American Association of Cereal Chemists (1995) Standard Method AACC 61-02. This method specifies 3 g of rice flour in 25 ml of water. Rice samples were first milled to white rice using a Satake Rice Machine (Satake Corporation, Japan), they were then ground to flour in a Cyclone Sample Mill (UDY Corporation, Fort Collins, Colorado, USA). The RVA was a RVA-3D model running with a Thermocline Windows control and analysis software, Version 1.2 (Newport Scientific, Sydney, Australia). As required by the standard method, 25 ml of distilled water was dispensed into a clean test canister. The 3 g sample of rice flour was transferred onto the surface of the water. A paddle was placed in the canister, and the blade was vigorously jogged up and down through the sample ten times. The RVA disperses the samples by rotating the paddle at 960 rpm for the first 10 s of the test, after which the viscosity is sensed using a constant paddle rotation speed of 160 rpm. The idle temperature is set to 50°C, and the following 12.5-min test profiles were run: (1) 50°C held for 1.0 min, (2) the temperature is linearly ramped up to 95°C until 4.8 min, (3) The temperature is held at 95°C until 7.5 min, (4) the temperature is linearly ramped down to 50°C at 11 min and (5) held at 50°C until 12.5 min. Heating and cooling were linearly ramped between the profile set points. Rice paste viscosity characteristics can be described by three important parameters of the pasting curve: peak (first peak viscosity after gelatinization), hot paste (paste viscosity at the end of the 95°C holding period), and cool paste viscosity (paste viscosity at the end of the test). In addition, breakdown, setback and consistency can be derived from peak minus hot paste viscosity values, cool paste viscosity minus peak viscosity values, and cool paste viscosity minus hot paste viscosity values, respectively. All the viscosity parameters were measured in Rapid Visco Units (RVU).

Genetic model

The genetic model employed in this experiment, which was proposed by Zhu and Weir (1994), can analyze quantitative endosperm traits in cereal crops. The 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}), co-variance between seed and maternal additive effects ($C_{A.Am}$) and co-variance between seed and maternal dominance effects ($C_{D.Dm}$) were estimated by the MINQUE (0/1) method. The variance of residual effects (Ve) was also estimated. The seed additive effect (A) and dominance effect (D), the cytoplasmic effect (C), and the maternal additive effect (Am) and dominance effect (Dm) were predicted by the Adjusted Unbiased Prediction (AUP) method. Estimations of variances and co-variances were further used for calculating seed heritability, $ho^2 = (V_A + C_{A.Am})/Vp$, cytoplasmic heritability, $hc^2 = V_C/Vp$, and maternal heritability, $hm^2 = (V_{Am} + C_{A.Am})/VP$. Breeding values of the parents were evaluated according to the magnitude of the predictors. The Jackknife method was used to derive the standard errors of the estimated components of variances and of the predicted genetic effects by sampling the generation means of the genetic entries. All data were analyzed by C programs run on an IBM PC computer.

Results

Estimation of seed, cytoplasmic and maternal genetic variances

Table 1 summarizes the estimated variance and co-variance components of the paste viscosity profiles of rice. Significant seed and maternal genetic variances were detected for all parameters of the paste viscosity profiles studied; thus, the rice paste viscosity profiles were controlled by genetic effects of both the seed and the maternal plant. Seed variances ($V_A + V_D$) accounted for 60.3%, 72.2%, 53.5%, 55.2%, 51.1%, 57.1% of the total genetic variance ($V_A + V_D + V_C + V_{Am} + V_{Dm}$) for each trait, respectively, which indicated that the genetic effects of the seed plant were more important than the maternal plant and the cytoplasmic effects for all the traits. The additive variances ($V_A + V_{Am}$) were much

Table 1 Estimation of genetic variances and co-variances of paste viscosity traits in *indica* rice (*PKV* peak viscosity, *HPV* hot paste viscosity, *CPV* cool paste viscosity, *BDV* breakdown viscosity, *CSV* consistency viscosity, *SBV* setback viscosity)

Parameter	PKV	HPV	CPV	BDV	CSV	SBV
V_A	2738.9**	774.6**	1946.7**	1123.9**	894.5**	1508.1**
V_D	425.4**	130.1**	350.1**	179.8**	150.3**	427.8**
V_C	0.0	50.5**	620.7**	0.0	232.5**	0.0
V_{Am}	1618.5**	233.1**	1124.2**	796.9**	635.5**	921.6**
V_{Dm}	468.7**	67.2**	247.7**	260.1*	132.8**	531.9*
$C_{A.Am}$	– 461.1	– 378.0	158.3	108.2	77.8	1221.2**
$C_{D.Dm}$	– 30.2	– 9.9	– 14.1	– 19.1	2.5	– 5.6
Ve	59.1**	14.9**	51.9*	33.2**	18.4**	25.2**

* and ** at 5% and 1% significance levels, respectively

Table 2 Estimation of heritabilities of paste viscosity traits in *indica* rice

Parameter	PKV	HPV	CPV	BDV	CSV	SBV
h_o^2	0.526**	0.802**	0.455**	0.479**	0.437**	0.467**
h_m^2	0.267**	– 0.293**	0.277**	0.352**	0.321**	0.367**
h_c^2	0.000	0.102^{+}	0.134**	0.000	0.105*	0.000

$^{+,}$* and ** at 10%, 5% and 1% significance levels, respectively

larger than the dominance variances ($V_D + V_{Dm}$), which revealed that additive genetic effects were the major contributors of genetic variation for the paste viscosity profiles. Therefore, selection could be applied for the paste traits in early generations, and commercial rice varieties with desirable viscosity profiles could be developed by selection. Significant additive co-variance ($C_{A.Am}$) was detected for the setback viscosity (SBV), suggesting that the relationship between seed and maternal genetic effects was important for this trait. No other additive co-variances and dominance co-variances ($C_{D.Dm}$) were detected in the experiment, indicating that there were minor relationships between seed additive effects and maternal additive effects and between seed dominance effects and maternal dominance effects among these traits.

Significant cytoplasmic variance (V_C) was detected for hot paste viscosity (HPV), cool paste viscosity (CPV) and consistency viscosity (CSV) traits. The cytoplastic effects comprised about 4.0% for HPV, 14.5% for CPV and 11.4% for CSV, of the total genetic variances, respectively. These three viscosity parameters were significantly controlled by the genetic effects of cytoplasm as well as those of the seed and maternal plant. Hence, the cytoplasmic effects for these traits should not be neglected in rice breeding. Therefore, the paste viscosity profiles of rice varieties or hybrid rice crosses could be improved by selecting a better cytoplasm for these traits.

Even though significant residual variances (Ve) were detected for all the traits, they accounted for little of the total variances ($V_A + V_D + V_C + V_{Am} + V_{Dm}$). It was clear that the paste viscosity profiles of rice were mainly affected by genetic effects.

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 rice paste viscosity traits. Significant seed heritabilities and maternal heritabilities were detected; seed heritabilities were found to be larger than maternal heritabilities for all traits in this experiment (Table 2). Cytoplasmic heritabilities were only detected in the CPV and CSV traits and were smaller than those of seed and maternal heritabilities. Because of the significant narrow-sense heritabilities identified, selection advances were predictable in the early generations for all traits. However, the negative maternal heritabilities for HPV would reduce selection efficiencies for this trait, while others would increase the selection efficiencies.

Prediction of genetic effects for the parents

Prediction of the genetic effects of the parents involved in this experiment, for all the parameters, indicated that seed-direct additive (*A*) and maternal additive (*Am*) effects of CMS lines tend to increase all the viscosity profiles except for BDV. The male parents, on the other hand, gave both positive and negative effects of both the direct additive and the maternal additive kind on the paste viscosity profiles. It was generally accepted that all the CMS lines employed in this experiment had poor quality characteristics. Their paste profiles were characterized by small BDV, greater SBV and CSV.

Table 3 Predicted seed and maternal and cytoplasmic genetic effects of paste viscosity

Patent	PKV		HPV			CPV			BDV		CSV			SBV	
	A	Am	A	Am	C	A	Am	C	A	Am	A	Am	C	A	Am
P1	3.1*	−10.1*	4.6**	−1.3	5.2**	7.7**	1.9	6.8**	−1.5^{+}	−8.8**	3.1**	3.2*	1.6	4.7**	11.6**
P2	2.7	1	5.1**	4.0*	3.2^{+}	7.6**	15.5**	−0.2	−2.4	−3.3	2.4	11.5**	−3.3	4.9^{+}	14.6**
P3	1.5	3.7*	3.8**	2.5**	2.5**	8.0**	7.3**	4.4**	−2.2*	1.2	4.2**	4.7**	1.9^{+}	6.5**	3.5**
P4	4.1	−7.3^{+}	7.9**	−4.1	−10.1	14.1**	6.0^{+}	−11.6	−3.8**	−3.3	6.2**	10.1**	−1.6	10.0**	13.4**
P5	2	12.3**	1.0	1.8*		−8.8**	2.3		1.0	10.5**	−9.8**	0.6		−10.7**	−10.2**
P6	7.1*	10**	−2.9	0.3		−14.3**	−1.7		10.2**	9.6**	−11.4**	−2.0		−21.3**	−11.9**
P7	−22.7**	13.9	−13.0**	6.0*		−12.6**	−1.8		−9.6*	7.9	0.4	−7.8*		9.3	−14.7
P8	−10.9**	0.5	−8.0**	1.0		−8.5**	0.5		−2.7	−0.7	−0.5	−0.5		2.7	−0.3
P9	7**	0.5	−0.6	0.4		−4.8	−6.2		7.8**	−0.1	−4.2	−6.6^{+}		−11.8*	−6.8
P10	−5.2	5.5	−0.3	1.3		−6.9*	5.0		−4.7*	4.1	−6.6**	3.7^{+}		−1.6	−0.6
P11	−1.9	−14.1**	−3.2*	−9.2**		1.7	−18.9**		0.1	−3.5^{+}	4.9	−9.7*		3.6	−4.8^{+}
P12	13.3**	−16.1**	5.7**	−2.7		16.9**	−9.9*		7.8**	−13.6**	11.2**	−7.2*		3.7*	6.2**

$^{+}$,* and ** at 10%, 5% and 1% significance levels, respectively

The genetic analysis of this experiment also showed that all the female parents displayed similarly to smaller BDV, and higher SBV and CSV, which are considered to be indicators of lower quality. The divergent effects of R lines indicated that the paste viscosity of hybrid rice could be improved by selecting a better restorer with different additive effects to that of CMS lines. In the eight male parents, P5 and P6 seemed to be better lines for the first choice. The cytoplasmic effect (*C*) of the CMS lines also showed that P1 and P3 could increase HPV and CPV significantly, which are also not conductive to quality improvement.

Discussion

Paste viscosity profiles are very important predictors of the eating, cooking and processing quality characteristics of rice (Jaliano 1985; Shu et al. 1998). Any information leading to our understanding of the genetic mechanisms of these traits will improve the breeding process. Even though Gravois and Webb (1997) have analyzed the genetic behavior of rice viscosity and shown that peak, hot paste and cool paste viscosities were controlled by one major gene with additive effects, maternal plant and cytoplasmic effects were neglected as were the triploid properties of the endosperm of the cereal.

A number of genetic models and corresponding statistical methods have been proposed (Bogyo et al. 1988; Mo 1988, 1995; Pooni et al. 1992; Foolad et al. 1992). These models either give a biased estimation, as the traits involved were controlled by seed-direct, cytoplasmic and maternal-plant effects, or else the experiment are very difficult to carry out (Shi et al. 1996, 1997). For instance, the model proposed by Foolad et al. (1992) analyzing seed-direct and cytoplasmic and maternal effects for endosperm traits, requires measurements on a single kernel and then 17 further generations. Using this model is labor intensive and time-consuming (Shi et al. 1997). Moreover, these models cannot be applied to an analysis of the viscosity traits since the viscometric instruments are not able to determine the viscosity characteristics of a single kernel. RVA needs about 3 g of rice flour while the Brabender Amylograph needs nearly 50 g of rice flour. The genetic model and statistical method proposed by Zhu and Weir (1994) is suitable for genetic analysis of the paste viscosity traits of rice. This model allows the use of bulked flour samples (suitable for RVA testing) as well as unbalanced data with missing crosses, suitable for genetic analysis (Zhu and Weir 1994).

Based on this model with three sets of genetic systems, we analyzed the genetic control of the paste viscosity parameters of rice. The results indicated that these traits were controlled by seed-direct, cytoplasmic and maternal-plant genes. The seed-additive and maternal-additive effects accounted for over 70% of the total variance, and the cytoplasmic effects comprised about 4.0% for HPV, 14.5% for CPV and 11.4% for CSV of the total variance. The inheritance of cytoplasmic genes was through the maternal plants. These facts indicated that early selection would improve rice quality. However, because of RVA's being unable to test the viscosities of a single kernel, and the fact the variance of seed-additive effects were more than the total of maternal-additive effects and cytoplasmic effects for every trait, early selection for RVA profiles in rice breeding programs should be based on a single plant so that the selection efficiency would not be as much as expected. The qualities of most of the *indica* CMS lines in China are generally poor, and the CMS lines involved in this experiment are higher in amylose content (data not shown) and have characteristics of small BDV, higher SBV and CSV, which are not desirable parental varieties for quality improvement. It was shown that all the female parents tended to increase all the parameters of rice viscosity except for BDV, while the male parents had both positive and negative effects on the viscosity profiles. Therefore, selecting a better restorer line would improve the paste profiles of hybrid rice quality. However, the most effective way to improve hybrid rice is to breed a better CMS line with improved quality parameters.

Unfortunately, the experiment was performed in only one environment. Chauhan et al. (1992) observed that quality traits like amylose contents, milling recovery, water uptake and kernel elongation of rice behaved differently to environments. Shi et al. (1997) also demonstrated that the amylose content and alkali-spreading score were affected by different environmental interactions, although these traits were mainly controlled by genetic effects. Therefore, the heritability of the paste viscosity parameters of rice obtained in this study might be over-estimated if there were genotype by environment interactions.

We are now carrying out QTL (quantitative trait locus) mapping work for the paste viscosities in rice. QTL mapping will not only dissect the complex quantitative traits into Mendelian factors but we hope, as well, to learn what kind of genes, major or minor, and how many genes, control these traits (Yano et al. 1997). Other work underway is the early selection for paste viscocities in both the $F_{2:3}$ generations and the $BC_{1:2}$ generations in our *indica* rice-breeding program. We expect this work to further confirm the results arising from the present paper and to accelerate improvements in rice quality in the future.

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