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Analysis of the genetic behavior of some starch properties in *indica* rice (*Oryza sativa* L.): thermal properties, gel texture, swelling volume

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Abstract Starch comprises about 90% of milled rice, so that the eating and cooking quality of rice is mainly affected by the starch properties. In the present paper, we analyzed the genetical behavior of gelatinization temperature tested by differential scanning calorimetry (DSC), gel texture, and the swelling volume (SV) of *indica* rice with an incomplete cross of 4×8 parents. A genetic model which can dissect the effects of triploid seed, the cytoplasm, and the maternal plant on the endosperm traits was used. The results indicated that peak temperature (T_p), conclusion temperature (T_c) and enthalpy (ΔH) were controlled by three types of genetic effects: seed direct (endosperm) effects, cytoplasmic effects and maternal effects. No cytoplasmic effects for the onset temperature (T_o), hardness and SV, and no maternal effects for cohesiveness were found. The additive variances (V_A+V_{Am}) were larger than the dominance variances (V_D+V_{Dm}) for all the traits except for T_c, which suggested that selection could be applied for the starch properties in early generations. The total narrow-sense heritability for each parameter was over 60%, indicating that selection advances were predictable in the early generations for these traits.

Keywords Starch · Differential scanning calorimetry · Gel texture · Swelling volume · Rice

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Introduction

Rice is the main staple food for over half of the world's population. In China, rice breeders presently focus on rice quality improvement, especially eating and cooking quality. Because starch comprises about 90% of milled rice, rice eating and cooking quality is mainly affected by the starch properties. Therefore, understanding the genetic behavior of starch properties will definitely contribute to success in breeding programs.

Some studies have been documented in the literature for the genetic control of amylose content, gelatinization temperature (GT), gel consistency (McKenzie and Rutger 1983; Shi et al. 1997; He et al. 1999), and paste viscosity characteristics (Bao and Xia 1999). The other important starch traits such as thermal properties during gelatinization, gel texture and swelling volume (SV), however, have been little studied to-date.

GT is generally indirectly tested by alkali digestibility following the method of Little et al. (1958). This method cannot differentiate the temperature at which rice starch gelatinization starts and ends, and the energy input required. The differential scanning calorimetry (DSC) instrument can determine gelatinization temperature, the heat energy required for gelatinization, and the degree of starch gelatinization. It allows simulation of the rice-cooking process and can yield valuable information to the rice processor (Marshall 1994). At present, the inheritance of GT has not been understood fully. One to three genes with several modifiers were reported to control this trait (see Hue and Choi 1973; Chang and Li 1991). On the other hand, quantitative inheritance was indicated by Ghosh and Govindaswamy (1972). McKenzie and Rutger (1983) found that alkali spreading value in one cross was probably controlled by a single gene, while in another five crosses, segregation patterns did not conform to any identifiable genetic model. Puri and Siddiq (1983) reported that additive gene action played the major role in expression of this trait, although some crosses did show predominantly non-additive gene action. Shi and Zhu (1994) found GT was only controlled by seed direct dominant gene effects, but in another experiment (Shi et al. 1997), GT was found to be controlled mainly by maternal additive effects and cytoplasmic effects.

Rice textural quality largely determines the palatability of cooked rice and its consumer acceptability (Juliano 1991). Many studies on relationships between amylose and protein contents, paste viscosity and instrumental measurements of textural properties have been conducted (Juliano et al. 1981; Del Mundo et al. 1989; Hamaker and Griffin 1990; Sandhya and Bhattacharya 1995; Bhattacharya et al. 1999; Champagne et al. 1999). When starch is heated to a critical temperature in the presence of excess water, the granules imbibe water, swell, and some starch leaches out into the solution. The degree of swelling depends on the extent of chemical bonding within the granules (Tian et al. 1991). The swelling volume of starch tested at a temperature of 92.5°C provides a rapid, small-scale method to predict the eating quality of wheat, rice and starch noodles (Crosbie et al. 1992; Collado and Corke 1997; Bhattacharya et al. 1999). Questions, such as what kinds of genetic effects control these traits and whether these traits have high heritabilities, are not clear.

Rice grain represents a new generation different to the maternal plant, so inheritance of rice quality traits is more complicated than that of other agronomic traits due to epistasis, maternal and cytoplasmic effects, and the triploid nature of the endosperm (Pooni et al. 1992; Zhu and Weir 1994; Mo 1995). The nutritional quality traits (protein and lysine content), cooking quality traits (amylose content, gelatinization temperature and gel consistency) and paste viscosity parameters seem to be controlled by cytoplasmic and maternal effects as well as by seed direct (endosperm) effects (Shi et al. 1996, 1997; Bao and Xia 1999). In the present paper, the genetic model proposed by Zhu and Weir (1994) for quantitative traits of endosperm in cereal crops was employed to dissect the genetic effects of the seed, cytoplasm and the maternal plant for rice DSC thermal properties, gel texture and SV.

Material and methods

Plant materials

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 May 1998, and a single plant per hill was transplanted to the paddy field at a spacing of 20×20 cm. The experiments were planted in a randomized complete block design with two replications. There were 36 plants in each plot. Many CMS lines were planted nearby the plots so that they could be crossed to the male plants during the flowering period to obtain the F_1 seeds by artificial pollination. The seeds of maternal plants, of F_1s on the maternal plants and of F_2s on the F_1 plants were harvested at maturity from ten plants in the middle part of the plot. Rice samples were firstly milled to white rice using a Satake Rice Machine (Satake Corporation, Japan), then ground to flour on a Cyclone Sample Mill (UDY Corporation, Fort Collins, Colo., USA) through a 100-mesh sieve.

Thermal properties

The thermal properties of milled rice flour were analyzed with a DSC 2920 thermal analyser (TA Instruments, Newcastle, Del., USA) equipped with DSC standard and dual sample cells. Rice flour (1.0 mg) was weighed into an aluminum pan and 10 µl of distilled water was added; the pan was then sealed with a lid and was heated at a rate of 10°C/min from 30°C to 110°C. A sealed empty pan was used as a reference. The onset (T_o), peak (T_p), conclusion (T_c) and enthalpy (ΔH) of gelatinization were calculated automatically by a Universal Analysis Program, Version 1.9D (TA Instruments, Newcastle, Del., USA).

Texture profiles

The resulting flour gels from Rapid Visco Analyser analysis experiments (Bao and Xia 1999; Bao et al. 2000) were kept in the canister, sealed with Parafilm and held at room temperature (20–25°C) for 24 h (Wu et al. 1995). Texture profile analysis was carried out on a TA-XT2*i* Texture Analyzer (Texture Technologies Corp., Scarsdale, N.Y./Stable Micro Systems, Godalming, Surrey, U.K.) equipped with a Texture Expert software program (Version 5.16). A standard two-cycle program was used to compress the gels for a distance of 10 mm at a 4 mm/s speed using a 3-mm cylindrical probe with a flat end. Texture parameters of hardness (the maximum force, *g*), and cohesiveness (the ratio of the positive force area during the second compression to that during the first compression) were derived from the instrument software.

Swelling volume

Starch swelling volume was determined according to the method of Crosbie et al. (1992). Flour samples (0.4 g, d.b.) were mixed with 12.5 ml of water in 125×16-mm Pyrex culture tubes, equilibrated at 25°C for 5 min and then heated to 92.5°C and held at that temperature for 30 min. The samples were cooled in an ice water bath for 1 min, equilibrated at 25°C for 5 min and then centrifuged at 1,000 *g* for 15 min. The swelling volume was calculated by converting the height of the resultant gels to a volume basis, and the results were expressed in ml/g of dry flour.

Genetic model

The genetic model used in this experiment, which was proposed by Zhu and Weir (1994), can analyze the genetic effects of quantitative traits of endosperm in cereal crops with unbalanced data. The variance component for seed additive (V_A), seed dominance (V_D), cytoplasmic (V_C), maternal additive (V_{Am}), maternal dominance (V_{Dm}), phenotypic (V_P), and residual (V_e) effects were estimated by the MINQUE(0/1) method with the jack-knife procedure (Miller 1974; Zhu 1992; Zhu and Weir 1994). Variances were further used for calculating seed heritability $h^2o=V_A/V_P$, cytoplasmic heritability $h^2c=V_C/V_P$, and maternal heritability $h^2m=V_{Am}/V_P$ (Shi et al. 1996, 1997). Seed additive effect (A), cytoplasmic effect (C) and maternal additive effect (Am) were predicted by the Adjusted Unbiased Prediction (AUP) method with the jack-knife procedure (Miller 1974; Zhu 1993). All data were analyzed by C programs (supported by Prof. Zhu Jun at Zhejiang University) running on an IBM PC computer.

Results

Phenotypic performance of the parents and their offspring

Differences among 12 parents for four DSC parameters, two gel-texture parameters and swelling volume (SV) were significant (Table 1). Of the DSC parameters, Minghui 63 (P6) exhibited the highest T_o (72.1°C), T_p (76.9°C), T_c (82.3°C) and ΔH (8.53 J/g) values, Longtefu A (P4) showed the lowest values for T_o (58.2°C), T_p (64.4°C) T_c (70.9°C) and ΔH (5.72 J/g) (Table 1). For gel texture, the gels of P4 (Longtefu A) and P9 (Milyang 46) were the hardest (25.0 g) and softest (6.0 g) respectively, while the cohesiveness ranged from 0.525 (P6) to 0.652 (P10). The SV of parents ranged from P7 (11.7 ml/g) to P9 (17.5 ml/g). Wide segregations were found for all parameters in F_1s and F_2s, some traits in F_1s were greater than their respective parent, while most traits in the F_2s were between their parents (data not shown).

Estimation of genetic variances and heritabilities

The estimated variance and heritability components of the seven starch properties of *indica* rice are listed in Table 2.

For T_o, hardness and SV, significant seed and maternal genetic variances were detected, so these parameters were controlled significantly by genetic effects of the seed and maternal plant. Three types of genetic systems were identified as controlling the T_p, T_c and ΔH, but no maternal additive effects were identified for T_p and T_c, and no seed dominance effects for ΔH (Table 2). For cohesiveness, only seed direct variances and cytoplasmic variances were significant. Seed variances (V_A+V_D) accounted for 57.2%, 53.1%, 55.5% and 65.6% of the total genetic variances ($V_A+V_D+V_C+V_{Am}+V_{Dm}$) for T_o, T_p, hardness and cohesiveness, respectively, which indicated that the genetic effects of the triploid seed were a little more important than maternal plant effects and cytoplasmic effects. It seemed that ΔH and SV were mainly controlled by the maternal effects (Table 2). However, cytoplasmic effects on T_p, T_c, ΔH and cohesiveness could not be neglected because they accounted for 34.1%, 48.5%, 37.6% and 34.4% of the total variances, respectively. These parameters of rice varieties or hybrid rice could be improved by selecting a better cytoplasm. The additive variances (V_A+V_{Am}) were larger than the dominance variances (V_D+V_{Dm}) for all the traits except for T_c, which revealed that additive genetic effects were the major contributors of genetic variation to these traits. Therefore, selection could be applied for the starch properties in early generations, and commercial rice varieties with desirable starch properties could be developed by selection. Significant residual variances (V_e) were detected for all the traits, but they accounted for a small proportion of the total variance.

Table 1 Phenotypic differences of the starch properties among 12 parents. Different small letters in each column are at the 5% significance level

Parents	T_o (°C)	T_p (°C)	T_c (°C)	ΔH (J/g)	Hardness(*g*)	Cohesiveness (×10^{-1})	SV (ml/g)
P1	66.2 e	71.9 d	77.0 e	6.43 bc	19.6 bc	5.38 bc	12.2 f
P2	69.6 bc	74.6 b	80.0 bcd	6.39 bc	24.6 a	5.65 bc	14.2 d
P3	68.3 d	74.3 bc	79.3 d	6.97 abc	20.4 b	5.50 bc	11.8 f
P4	58.2 h	64.4 f	70.9 g	5.72 c	25.0 a	5.59 bc	13.4 e
P5	62.2 fg	68.5 e	75.0 f	7.05 abc	6.3 e	5.73 b	16.8 bc
P6	72.1 a	76.9 a	82.3 a	8.53 a	6.6 e	5.25 c	17.1 ab
P7	69.2 c	74.7 b	80.7 b	7.53 ab	20.7 b	5.59 bc	11.7 f
P8	69.3 bc	74.5 b	79.7 cd	7.31 abc	19.7 bc	5.74 b	13.7 de
P9	62.4 f	68.5 e	74.4 f	6.07 bc	6.0 e	6.46 a	17.5 a
P10	61.7 g	68.0 e	74.7 f	7.15 abc	6.1 e	6.52 a	16.2 c
P11	70.0 b	74.8 b	80.0 bcd	7.20 abc	15.6 d	5.85 b	11.8 f
P12	68.1 d	73.7 c	80.2 bc	6.78 bc	17.0 d	5.62 bc	13.2 e

Table 2 Estimation of the genetic variances and heritabilities of the starch properties in *indica* rice

Item	T_o	T_p	T_c	ΔH	Hardness	Cohesiveness	SV
Genetic variance							
V_A	10.30**[a]	4.87**	3.78**	0.13**	31.51**	0.24**	0.00
V_D	2.42**	2.59**	2.79**	0.00	12.66**	0.16**	0.70**
V_C	0.00	4.79**	8.37**	1.38**	0.00	0.21**	0.00
V_{Am}	8.51**	0.00	0.00	1.26**	30.15**	0.00	4.01**
V_{Dm}	1.02**	1.80**	2.30**	0.89**	5.26**	0.00	0.44**
V_e	0.62**	0.17**	0.34**	0.75**	1.37**	0.13^{+}	0.23**
Heritabilities							
h^2o	0.450**	0.343**	0.215**	0.030^{+}	38.900**	32.100**	0.000
h^2c	0.000	0.337**	0.476**	0.312**	37.200**	0.000	0.000
h^2m	0.372**	0.000	0.000	0.285**	0.000	28.600**	0.745**

[a] $^{+}$ and ** are at the 10% and 1% significance levels, respectively

Table 3 Predicted seed, maternal and cytoplasmic genetic effects of starch properties for each parent

Parent	T_o (°C)		T_p (°C)		T_c (°C)		ΔH (J/g)			Hardness (*g*)		Cohesiveness		SV (ml/g)
	A	Am	A	C	A	C	A	C	Am	A	Am	A	C	Am
P1	–0.38	2.54**	–0.04	4.03**	0.04	4.53**	0.29**	0.20	0.74**	1.90**	–2.89	–0.01	0.05	0.01
P2	–0.06	2.19**	0.30	3.46**	0.54	3.11**	–0.25**	1.11	–1.11	3.18**	–4.54	–0.01	–0.02	–2.03**
P3	–0.34**	1.50**	0.14	1.82**	0.20	2.16**	–0.03	0.08	0.47	1.85**	–2.42	–0.01	0.03	–0.77
P4	–2.14**	0.33	–1.26**	4.25**	–1.46	4.05	1.99**	–1.74	–0.61	2.91**	–1.88	0.00	0.03	–1.30**
P5	–1.13**	–1.70**	–0.26		–0.50		0.86**		–0.92**	–1.50*[a]	–1.53	0.02		0.85**
P6	1.52**	–0.08	0.63		0.17		–0.48**		0.74	–2.28^{+}[a]	–2.67	0.02		3.33**
P7	1.72**	–0.78	0.94**		1.03		–0.30**		0.94**	–1.82	6.65	–0.01		–0.95**
P8	1.38**	–0.19	0.80**		0.84		–1.38**		1.16	–1.29^{+}	4.67	–0.04^{+}		–0.15
P9	–0.62	–3.08**	–0.94**		–1.19		0.42**		1.18**	–4.03*	3.32	0.04		0.75**
P10	–1.54**	–1.22	–1.47**		–0.70		–0.20		–1.01	–0.45	–4.73	0.02		0.98^{+}
P11	0.42	1.67**	0.53**		0.37		0.12		–0.30	0.35	2.30	–0.01		–1.21**
P12	1.15**	–1.20**	0.60**		0.65		–1.04**		–1.27**	1.18	3.72	–0.01		0.49

[a] $^{+}$, * and ** are at the 10%, 5% and 1% significance levels, respectively

Because the seed, cytoplasmic and maternal genetic effects were significant for the starch property parameters, the total narrow-sense heritability can be further partitioned into seed (h^2o), cytoplasmic (h^2c) and maternal (h^2m) heritabilities. The total heritabilities of T_o, T_p, T_c, ΔH, hardness, cohesiveness and SV were 82.2%, 68%, 69.1%, 62.7%, 76.1% 60.7% and 74.5% respectively, indicating that early selection for these parameters should be effective in rice quality breeding programs (Table 2). Because the inheritance of cytoplasmic effects was through the maternal plant, the total of maternal heritabilities and cytoplasmic heritabilities for T_c, ΔH and SV (47.6%, 59.7% and 74.5%, respectively) were larger than the seed direct heritabilities, suggesting that selection based on a single plant would be more effective for these traits. For T_o, T_p, hardness and cohesiveness, seed direct heritabilities were comparable to the maternal heritabilities or cytoplasmic heritabilities, so selection based on a single seed would be as effective as that based on a single plant.

Prediction of genetic effects for the parents

Table 3 summarizes the genetic effects of the seed direct additive effect (A), maternal additive effect (Am) and cytoplasmic effect (C) for 12 parents. It seemed that some parents had significant seed direct additive effects, while others had significant maternal additive effects or cytoplasmic effects. For example, the maternal effects of P1 and P2 were significant for T_o, but seed direct effects of P4 were significant, while both were significant for P3. Some of the parents had two significant effects with a different direction (positive/negative) such as P3 for T_o, which would offset its genetic effects when using this parent in breeding; these parents were not suitable for quality improvement. However, a trend existed that the sum of all the significant genetic effects of a parent was positively correlated with the phenotypic performance of the parent. For example, when the sum of significant A and Am of each parent for T_o was calculated, we found that the sum of P4, P5, P9, P10 and P12 was negative indicating that these parents in breeding tended to decrease T_o (Table 3). We also found that the T_o values of these parents were less than that of the others (Table 1). This norm was true for many traits except ΔH and T_p of P4. Although the T_p of P4 was the lowest among 12 parents (Table 1), the cytoplasmic effects of P4 would increase the value of its progeny by 4.25°C, while the seed direct additive effects would decrease it by 1.26°C (Table 3). The net effects of P4 on its progeny were positive. It was noted that seed direct additive effects of four CMS lines tended to increase hardness while the male parents P5 and P9 gave negative effects, and all the maternal effects were non-significant. Both seed additive effects and cytoplasmic effects were non-significant for cohesiveness (Table 3), so these parents could contribute little to improve the cohesiveness of gel texture.

Discussion

Starch properties have great effects on rice eating and cooking quality. There are some reports on the genetic basis for amylose content, gelatinization temperature, gel consistency and pasting viscosity (McKenzie and Rutger 1983; Shi et al. 1997; Bao and Xia 1999; He et al. 1999). We are not aware of any reports on the genetic basis for starch thermal properties, gel texture and swelling volume. These starch parameters serve as significant indicators for rice eating and cooking quality. The thermal properties tested on DSC can simulate the rice-cooking process and yield valuable information to the rice processor (Marshall 1994). The gel texture, similar to gel consistency, can differentiate the degree of hardness of the cooked rice, similar to that perceived during chewing. The SV reflects the water-holding ability of starch, and has become a rapid, small-scale method to predict the eating quality of wheat, rice and starch noodles (Crosbie et al. 1992; Collado and Corke 1997; Bhattacharya et al. 1999). However, the genetic behavior of these parameters is little understood and, thus, is the objective of the present paper. Any information leading to our understanding of the genetic mechanisms of these traits will improve the breeding process. It is generally recognized that triploid endosperm traits may be controlled by seed direct (endosperm) effects, maternal plant effects and cytoplasmic effects (Pooni et al. 1992; Zhu and Weir 1994; Mo 1995). In a previous study, starch pasting viscosity parameters were found to be controlled by the direct effects of seed, by cytoplasm and by the maternal plant (Bao and Xia 1999). We find that T_p, T_c, ΔH are also controlled by the three sets of genetic effects; except that no cytoplasmic effects for T_o, hardness and SV, and no maternal effects for cohesiveness were found (Table 2). The heritabilities for each trait are relatively high, suggesting that early selection in rice quality breeding would be effective. Further dissection of the total heritabilities into seed direct heritabilities, maternal heritabilities and cytoplasmic heritabilities can direct selection strategies in breeding programs. In selection practice, selection on a single seed can begin with F_2 seed, generally using half the seed for testing, and the other part of the seed with the embryo to germinate to advance generations when a desirable trait is found. Selection on a single plant can begin with F_3 seed, with half the seeds for test and the rest for planting to form $F_{3:4}$ generations if a desirable plant is found in the $F_{2:3}$. For T_c and ΔH, testing part of single seed by DSC is possible, because only a small sample is needed. But for traits impossible to test with a single seed, such as cohesiveness, selection could be delayed to select $F_{3:4}$ plants. In such cases where a trait should be selected on a single seed (according to genetic analysis), but with no test method available (i.e. presently needed to test on the bulk sample from a single plant), the selection efficiencies would not be as high as theoretically possible.

Rice germplasm diversity is very important in rice breeding, and screening for desirable germplasm is necessary in breeding work. The genetic effects with significant variances in Table 2 were used to predict the merit values of the parents employed in this experiment (Table 3). The genetic effects of the parent with a larger phenotypic value tend to increase this trait, and the smaller one to decrease it, which implies the importance of wide diversity for breeding. However, the reverse relationships also existed, suggesting that even if the parent has good phenotypic performance, its genetic effects might be disadvantageous to its progeny. Xiao et al. (1996) found via quantitative trait locus mapping that wild rice with low yield has genetic loci which could improve the yield potential of commercial rice. The reverse is also true from the present quantitative genetic analysis.

The present experiment was performed in only one environment. Chauhan et al. (1992) observed that quality traits like amylose content, milling recovery, water uptake and kernel elongation of rice are subject to environmental effects. It is also noted that the amylose content, gel consistency, alkali spreading score (Shi et al. 1997; Bao 1999) and paste viscosity parameters (Bao 1999; Bao et al. 2000) were affected by different environmental interactions, although these traits were mainly controlled by genetic effects. The heritability of starch properties estimated in the present study might be over-estimated if there were genotype by environment interactions. Therefore, further investigations on these parameters in different environments are needed.

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