



Genetic analysis for protein content in *indica* rice

Chunhai Shi¹, Jun Zhu¹, Xiaoe Yang², Yungui Yu² & Jianguo Wu¹

¹Agronomy Department, and ²Department of Soil Science and Agricultural Chemistry, Zhejiang Agricultural University, Hangzhou 310029, China

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Summary

Analysis of genetic main effects and GE interaction effects for protein content (PC) and protein index (PI) of *indica* rice (*Oryza sativa* L.) was conducted for two year experimental data by using a genetic model for quantitative traits of seeds in cereal crops. Nine cytoplasmic male sterile lines or maintainers as female parents and five restorer lines as male parents were used for a NC II mating design in 1995 and 1996. The results indicated that PC and PI traits were simultaneously controlled by genetic main effects as well as GE interaction effects. For PC and PI of rice, the embryo interaction effects (embryo additive and dominance interaction effects) were important as effects of triploid endosperm, cytoplasm and diploid maternal plant. The estimates of narrow-sense heritability for PC and PI of rice were 85.3% and 77.9%, respectively. The interaction heritability was found to be larger than the general heritability for PC and PI of rice. Significant relationships for components of different genetic effects between PC and PI were found. The GE interaction covariances tended to be positive.

Introduction

Protein in rice (*Oryza sativa* L.) is of importance for the health of people whose main food in daily life is rice. In order to improve the efficiency of breeding for rice nutrient quality, understanding the variation for the expression of genes in different environments is necessary. Studies have shown that protein content of rice is a quantitative trait (Singh et al., 1977, Singh & Singh, 1982; Kaul, 1983; Kambayshi et al., 1984; Sood & Siddiq, 1986; Gupta et al., 1988; Mosina, 1988; Shenoy et al., 1991). Hillerislambers et al. (1973) pointed out that the heritabilities for protein content were 0.130–0.372 due to the genotype \times environment (GE) interaction effects. Results of Tsuzuki & Furusho (1986) and Shenoy et al. (1991) indicated that the heritability of protein content was about 58.8% and 71.0%, respectively. Shi et al. (1996a) found that protein content and protein index were controlled by genetic effects of triploid endosperm, cytoplasm and diploid maternal plant, with the heritabilities being 44.3%, 34.4%, 4.9% for protein content and 30.9%, 34.0%, 19.6% for protein index, respectively. Ge-

netic correlation components have been partitioned for some nutrient quality traits of milled rice (Shi et al., 1996b).

Since rice grain is a new generation, different from maternal plants that provide grain nutrients, maternal and cytoplasmic effects can be important components of the total genetic effect for the performance of rice quality traits. As an important part of seed, the diploid embryo might also have genetic effects affecting the performance of quality traits of rice. Pooni et al. (1992) proposed genetic models that could analyze the endosperm effects and maternal/cytoplasm effects. Foolad & Jone (1992) also suggested genetic models for estimating embryo, endosperm, testa/perisperm and cytoplasmic effects for quantitative traits of endosperm. But these models needed testing individual seed for many generations and also did not include GE interaction effects. Zhu & Weir (1994a, 1994b) proposed genetic models for analyzing diploid embryo and maternal nuclear effects, triploid endosperm effects, and cytoplasm effects, which were extended by including GE interaction effects (Zhu, 1996). Some studies have shown that rice quality traits could be

controlled by gene effects of endosperm, cytoplasm and maternal plant, as well as by their GE interaction effects (Shi et al., 1997, 1998). Yan et al. (1998) found that malting quality traits of barley were controlled by genetic main effects and GE interaction effects were due to diploid embryo genes and triploid endosperm genes.

In the present study, analysis was conducted to determine the genetic main effects and GE interaction effects for protein content and protein index of rice. The objectives of this study were to evaluate the embryo genetic effects, endosperm genetic effects, cytoplasm effects and maternal genetic effects, as well as their GE interaction effects; and to estimate genetic components of variance, heritability, and covariance for protein traits of *indica* rice.

Materials and methods

The experiments were conducted in 1995 and 1996. The mating design used by this experiment was a NC II design with 14 parents. Nine cytoplasmic male sterile (CMS or A) lines and their maintainer lines (B) were Zhexie 2, Xieqingzao, Zhenan 3, Gangchao 1, Yinchao 1, Erjiuqing, V₂₀, Zuo 5 and Zhenshan 97. Five restorer lines (R) were T 49, Cezao 2-2, 26715, 102 and 1391. All female parents were crossed to male parents to obtain F₁ (A × R) and reciprocal F₁ (R × B) in 1994. Seedlings of parent, F₁ and reciprocal F₁ with three replications were planted in the field of experimental farm at Zhejiang Agricultural University in 1995 and 1996. The seeds were sown on April 2 in both years. Single plants of 30-day seedlings were transplanted at spaces of 20 × 20 cm. Seed samples of parents, F₂s from F₁ plants and reciprocal F₂s from reciprocal F₁ plants were collected at maturity from 8 plants in the middle part of each plot with 24 seedlings. The seeds of F₁ (A × R) and BC₁ (A × F₁) were obtained by crossing females to males at flowering during the same growing season. Quantitative traits of rice quality analyzed were protein content (PC, %) determined by Kjeldahl extraction methods (Southwest Agric. Univ. & China South Agric. Univ., 1992) and protein index (PI, mg protein per milled rice), which were measured from three replications for each sample of parents, F₁s, F₂s, reciprocal F₂s, and BC₁s.

The genetic main effects and their GE interaction effects of diploid embryo, triploid endosperm, cytoplasm and diploid maternal plant were analyzed for rice protein traits by using the full genetic model for

quantitative traits of seed in cereal crops (Zhu, 1997). This model is derived by combining diploid seed model (Zhu & Weir, 1994a) and triploid endosperm model (Zhu & Weir, 1994b) with extension of including GE interaction effects (Zhu, 1996). According to the model, the phenotypic variance (V_P) or covariance (C_P) can be partitioned into several components. Partitioning for the phenotypic variance is:

$$\begin{aligned} V_P &= V_G + V_{GE} + V_\varepsilon \\ &= V_{Ao} + V_{Do} + V_{Ae} + V_{De} + V_C + V_{Am} \\ &\quad + V_{Dm} + V_{AoE} + V_{DoE} + V_{AeE} + V_{DeE} \\ &\quad + V_{CE} + V_{AmE} + V_{DmE} + V_\varepsilon \end{aligned}$$

where V_G = genetic main variance, V_{GE} = GE interaction variance, V_{Ao} = embryo additive variance, V_{Do} = embryo dominance variance, V_{Ae} = endosperm additive variance, V_{De} = endosperm dominance variance, V_C = cytoplasm variance, V_{Am} = maternal additive variance, V_{Dm} = maternal dominance variance, V_{AoE} = embryo additive interaction variance, V_{DoE} = embryo dominance interaction variance, V_{AeE} = endosperm additive interaction variance, V_{DeE} = endosperm dominance interaction variance, V_{CE} = cytoplasm interaction variance, V_{AmE} = maternal additive interaction variance, V_{DmE} = maternal dominance interaction variance, and V_ε = residual variance. Phenotype covariance can be partitioned and defined the same way as variance,

$$\begin{aligned} C_P &= C_G + C_{GE} + C_\varepsilon \\ &= C_{Ao} + C_{Do} + C_{Ae} + C_{De} + C_C + C_{Am} \\ &\quad + C_{Dm} + C_{AoE} + C_{DoE} + C_{AeE} + C_{DeE} \\ &\quad + C_{CE} + C_{AmE} + C_{DmE} + C_\varepsilon \end{aligned}$$

Since the total genetic effect can be partitioned into components for genetic main effects and GE interaction effects, the total narrow-sense heritability (h^2) should also be differentiated into general heritability ($h_G^2 = V_G/V_P$) for genetic main effects and interaction heritability ($h_{GE}^2 = V_{GE}/V_P$) for GE interaction effects:

$$\begin{aligned} h^2 &= h_G^2 + h_{GE}^2 \\ &= h_{Go}^2 + h_{Ge}^2 + h_C^2 + h_{Gm}^2 + h_{GoE}^2 + h_{GeE}^2 \\ &\quad + h_{CE}^2 + h_{GmE}^2 \end{aligned}$$

The general heritability (h_G^2) has components of embryo general heritability ($h_{Go}^2 = V_{Ao}/V_P$), endosperm general heritability ($h_{Ge}^2 = V_{Ae}/V_P$), cytoplasm general heritability ($h_C^2 = V_C/V_P$), and maternal general

Table 1. Phenotypic means (range) of generations for protein content (PC) and protein index (PI) in 1995 and 1996

Generation	PC (%)		PI (mg)	
	1995	1996	1995	1996
Female parent	13.76 (10.99 ~ 18.21)	14.09 (11.79 ~ 18.07)	2.34 (1.95 ~ 3.09)	2.67 (1.84 ~ 3.43)
Male Parent	14.21 (12.82 ~ 15.22)	14.42 (12.68 ~ 15.60)	2.28 (2.02 ~ 2.73)	2.71 (2.27 ~ 3.25)
F ₁	14.43 (11.06 ~ 18.52)	15.44 (10.27 ~ 20.72)	2.37 (1.89 ~ 3.01)	2.84 (1.95 ~ 3.95)
BC ₁	14.58 (11.09 ~ 19.78)	15.07 (9.92 ~ 20.88)	2.37 (1.87 ~ 3.03)	2.75 (1.66 ~ 4.07)
F ₂	13.16 (11.52 ~ 16.62)	13.25 (11.45 ~ 15.38)	2.27 (1.91 ~ 2.75)	2.59 (1.73 ~ 3.22)
Reciprocal F ₂	13.35 (11.28 ~ 15.26)	13.08 (11.20 ~ 15.32)	2.29 (1.90 ~ 2.86)	2.64 (2.13 ~ 3.07)

heritability ($h_{Gm}^2 = V_{Am}/V_P$). The interaction heritability (h_{GE}^2) has components of embryo interaction heritability ($h_{GoE}^2 = V_{AoE}/V_P$), endosperm interaction heritability ($h_{GeE}^2 = V_{AeE}/V_P$), cytoplasm interaction heritability ($h_{CE}^2 = V_{CE}/V_P$), and maternal interaction heritability ($h_{GmE}^2 = V_{AmE}/V_P$).

Variances and covariances were estimated by MINQUE(1) method (Zhu & Weir, 1996). The Jackknife technique (Miller, 1974; Zhu & Weir, 1996) was applied by sampling means of genetic entries for estimating the standard errors of estimated variances, heritabilities and covariances.

Results

Phenotypic means of the generations

The results of means and ranges of generations showed that there was large variation among materials studied (Table 1). The variation ranges of CMS lines were larger than those of restorer lines in both years. The means of F₁ and BC₁ were higher, in both years, than those of their parents and it was suggested that there could exist heterosis in F₁ seeds for two quality traits studied. Performance of PC and PI of rice for parents, F₁s, F₂s, reciprocal F₂s, and BC₁s in two years was different with means in 1995 smaller than those in 1996. This revealed that the variation of the PC and PI of rice could be affected by genotype effects as well as GE interaction effects.

Estimation of components for genetic main variance and GE interaction variance

Estimates of the variance components for PC and PI of milled rice are summarized in Table 2. The contributions of V_G and V_{GE} to total genetic variance were 34.24% and 65.76% for PC, and 26.09% and 73.91% for PI, respectively. Therefore, the expression of genes for PC and PI could be mainly affected by environments. It was suggested that GE interaction effects cannot be neglected in improving protein traits for nutrient quality breeding. For genetic main effects, significant endosperm additive (V_{Ae}) and dominance (V_{De}) variances, maternal additive (V_{Am}) and dominance (V_{Dm}) variances existed. But embryo additive (V_{Ao}) and dominance (V_{Do}) variances, and cytoplasmic variance (V_C) were not found. The genetic main effects of PC and PI were mostly contributed by endosperm effects, since V_{Ae} and V_{De} were larger than V_{Am} and V_{Dm} . For GE interaction effects, the embryo interaction effects were much more important than the other interaction effects. Embryo additive interaction (V_{AoE}) and dominance interaction (V_{DoE}) variances were accounted for about 59.41% and 60.41% of GE interaction variances for PC and PI, respectively. Since embryo effects were not found in genetic main effects, the expression of diploid embryo genes were more easily affected by environments than those of triploid endosperm genes, cytoplasm genes or diploid maternal plant genes.

Table 2. Estimation of variance components for genetic main effects and GE interaction effects of protein content (PC) and protein index (PI) in *indica* rice

Parameter	PC	PI	Parameter	PC	PI
V_G	8.758	0.342	V_{GE}	16.821	0.968
V_{Ao}	0.000	0.000	V_{AoE}	8.341*	0.441*
V_{Do}	0.000	0.000	V_{DoE}	1.653 ⁺	0.143*
V_{Ae}	4.643*	0.233*	V_{AeE}	0.000	0.000
V_{De}	0.953 ⁺	0.102*	V_{DeE}	0.000	0.000
V_C	0.000	0.000	V_{CE}	3.593*	0.159*
V_{Am}	2.794*	0.000	V_{AmE}	2.773*	0.206*
V_{Dm}	0.368*	0.007*	V_{DmE}	0.461**	0.019**
			V_ϵ	0.381**	0.025**

+ , * and ** were significant at 0.10, 0.05 and 0.01 level, respectively. V_G = genetic main variance, V_{GE} = GE interaction variance, V_{Ao} = embryo additive variance, V_{Do} = embryo dominance variance, V_{Ae} = endosperm additive variance, V_{De} = endosperm dominance variance, V_C = cytoplasm variance, V_{Am} = maternal additive variance, V_{Dm} = maternal dominance variance, V_{AoE} = embryo additive interaction variance, V_{DoE} = embryo dominance interaction variance, V_{AeE} = endosperm additive interaction variance, V_{DeE} = endosperm dominance interaction variance, V_{CE} = cytoplasm interaction variance, V_{AmE} = maternal additive interaction variance, V_{DmE} = maternal dominance interaction variance, and V_ϵ = residual variance.

Table 3. Estimation of heritability components (%) for protein content (PC) and protein index (PI) in *indica* rice

Parameter	PC	PI	Parameter	PC	PI
h_{Go}^2	0.00	0.00	h_{GoE}^2	32.13**	33.06**
h_{Ge}^2	17.89**	17.49**	h_{GeE}^2	0.00	0.00
h_C^2	0.00	0.00	h_{CE}^2	13.84**	11.90**
h_{Gm}^2	10.77**	0.00	h_{GmE}^2	10.68**	15.41**

** was significant at 0.01 level. h_{Go}^2 = embryo general heritability, h_{Ge}^2 = endosperm general heritability, h_C^2 = cytoplasmic heritability, h_{Gm}^2 = maternal general heritability, h_{GoE}^2 = embryo interaction heritability, h_{GeE}^2 = endosperm interaction heritability, h_{CE}^2 = cytoplasmic interaction heritability, h_{GmE}^2 = maternal interaction heritability.

Estimation of components for general heritability and interaction heritability

The estimates of total narrow-sense heritability were 85.3% and 77.9% for PC and PI, respectively (Table 3). The interaction heritability (h_{GE}^2) for PC and PI were found to be larger than the general heritability (h_G^2). Therefore, selection efficiency could be affected by the environments. For the general heritability, only significant h_{Ge}^2 and h_{Gm}^2 for PC existed, and h_{Ge}^2 for PI. For the interaction heritability, because of the large and significant V_{AoE} for PC and PI (Table 2), the embryo interaction heritability h_{GoE}^2 was 32.13% and 33.06% for these two traits, respectively. There

also significant cytoplasm interaction heritability h_{CE}^2 and maternal interaction heritability h_{GmE}^2 for PC and PI existed, but they were all less than h_{GoE}^2 .

Analysis of components for genetic main covariance and GE interaction covariance

For breeding a new rice variety, breeders are more concerned with the overall performance of multiple traits in the selection programs. Genetic covariance components could reveal the genetic relationships among different traits of rice. The total covariance was partitioned into its components (Table 4). Although the total genetic covariance ($C_G + C_{GE} = 0.565$) was not significant, there still existed some significant components of genetic main covariance (C_G) or GE interaction covariance (C_{GE}) between PC and PI. Components of genetic main covariance were found to be significant for embryo additive covariance (C_{Ao}), endosperm additive covariance (C_{Ae}), cytoplasm covariance (C_C), maternal additive covariance (C_{Am}) and maternal dominance covariance (C_{Dm}). These results indicated that there was a significant relationship for these genetic effects between PC and PI. The relationship for endosperm additive effects ($C_{Ae} = 1.764^+$) between PC and PI was positive. It was indicated that simultaneously improving PC and PI could be expected in indirect selection. For GE interaction covariance, the additive and cytoplasm interaction covari-

Table 4. Estimation of covariance components for genetic main effects and GE interaction effects between protein content (PC) and protein index (PI) traits of *indica* rice

Parameter	Covariance	Parameter	Covariance
C_{Ao}	-1.179 ⁺	C_{AoE}	1.862*
C_{Do}	-0.184	C_{DoE}	0.443 ⁺
C_{Ae}	1.764 ⁺	C_{AeE}	-2.611 ⁺
C_{De}	0.428	C_{DeE}	-0.785
C_C	-0.362 ⁺	C_{CE}	0.664 ⁺
C_{Am}	-0.311 ⁺	C_{AmE}	0.770 ⁺
C_{Dm}	0.039*	C_{DmE}	0.027
		C_ε	-0.393

⁺ and * were significant at 0.10 and 0.05 level, respectively. C_{Ao} = embryo additive covariance, C_{Do} = embryo dominance covariance, C_{Ae} = endosperm additive covariance, C_{De} = endosperm dominance covariance, C_C = cytoplasm covariance, C_{Am} = maternal additive covariance, C_{Dm} = maternal dominance covariance, C_{AoE} = embryo additive interaction covariance, C_{DoE} = embryo dominance interaction covariance, C_{AeE} = endosperm additive interaction covariance, C_{DeE} = endosperm dominance interaction covariance, C_{CE} = cytoplasm interaction covariance, C_{AmE} = maternal additive interaction covariance, C_{DmE} = maternal dominance interaction covariance, and C_ε = residual covariance.

ance components were significantly positive (C_{AoE} = 1.862*, C_{AmE} = 0.770⁺ and C_{CE} = 0.664⁺). These relationships might be helpful for improving both PC and PI by selection in specific environments.

Discussion

As important parts in seeds of cereal crops, embryo and endosperm are different generations from their maternal plant. Embryo is a diploid tissue and endosperm is a triploid tissue. In dicotyledon crops such as cotton and rape, which have no endosperm in their seed, the main part of seed is embryo (cotyledon), which consists of genes affecting the performance of seed quality traits (Thomas & Kondra, 1973; Wu et al., 1995). In monocotyledon barley, the results of Yan et al. (1998) have shown that the embryo and endosperm effects and their interaction effects could affect the performance of diastatic power, alpha-amylase activity, beta-amylase activity and malt nitrogen content. Results of the present experiment have also shown that the embryo genetic effects as well as endosperm, cytoplasm and maternal genetic effects could affect PC and PI traits of *indica* rice. But the expression of embryo genes could be easily affected by environments. PC and PI of rice were mainly affected by

embryo interaction effects including embryo additive interaction effects and embryo dominance interaction effects. Therefore, embryo effects for some nutrient quality traits could not be ignored in quality trait improvement.

Seeds of cereal crop such as rice, wheat or barley are usually very small and difficult to be produced by artificial emasculation and pollination in field experiments. Although, Pooni et al. (1992) proposed models for analyzing endosperm effects and maternal/cytoplasm effects of endosperm traits, this model could not differentiate the maternal and cytoplasm effects. The genetic model proposed by Foolad & Jone (1992) included effects of embryo, endosperm, testa/perisperm and cytoplasm for quantitative traits of endosperm, but this model is difficult to be used because of the requirement for measuring single seeds of 18 generations (8 selfing and 10 crossing). Otherwise, these models and statistical methods (Pooni et al., 1992; Foolad & Jone, 1992) could not be used to analyze the genotype x environment interaction effects for quantitative traits of endosperm. If there are GE interaction effects, those triploid models without GE interaction will give biased estimates. The new genetic models based on mixed linear model approaches (Zhu & Weir, 1994a, 1994b; Zhu, 1996; Zhu, 1997) can analyze genetic main effects and GE interaction effects for diploid embryo, triploid endosperm, cytoplasm and diploid maternal plant. According to the magnitude of embryo, endosperm, cytoplasmic and maternal genetic effects and GE interaction effects, it was able to illustrate the genetic mechanism of endosperm nutrient traits, which are of importance in improving rice quality through breeding.

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