Research Article

# Analysis of the genetic relationships from different genetic systems between the amylose content and the appearance quality of *indica* rice across environments

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## Abstract

The genetic relationships between amylose content (AC) and appearance quality traits of *indica* rice (*Oryza sativa* L.) were investigated using conditional analysis and unconditional analysis in present experiment. The results from the unconditional analysis indicated that AC of rice positively correlated with brown rice (BR, *i.e.*, dehulled but unmilled rice) length (BRL), width (BRW) and thickness (BRT), but was negatively correlated with the ratio of length to width (RLW). The conditional analysis showed that weight of brown rice (WBR) negatively affected the genetic relationships between AC and the appearance quality traits of rice except between AC and BRW, while the genetic relationships between AC and most appearance quality traits were negatively affected by protein content (PC). However, these influences were not apparent due to the impact of WBR or PC on the most covariance components of the different genetic systems between AC and the appearance quality traits. The conditional analysis showed that it was possible to improve AC while significantly reduce BRL and BRT under maintaining WBR. Furthermore, AC could be improved when BRL was reduced under maintaining PC, but BRW and BRT could be significantly increased.

*Key words:* amylose content, genetic relationships, conditional and unconditional analysis, *indica* rice quality traits.

## Introduction

Rice (*Oryza sativa* L.) is one of the major staple foods, with amylose content (AC) being considered to be one of the most important traits related to the cooking quality of rice. Rice grain shape traits related to the appearance quality of rice are very important in the international market, which usually include length, width, thickness, length to width ratio and length to thickness ratio. Hence, understanding the gene expression and the genetic relationships between AC and the appearance quality traits (AQT) of rice under different environments is necessary for improving both the cooking quality and the appearance quality of rice.

The relationships between the cooking quality and the appearance quality of rice has been well documented, with some studies having shown a negative correlation between AC and AQT (Sood and Siddiq, 1986; Chauhan *et al.*, 1995; Zhao and Xu, 1998; Feng, 1998), while other studies have reported positive correlations between these pairwise traits in rice (Guo *et al.*, 1985; Wang *et al.*, 1992; Chen *et al.*, 1997; Yang *et al.*, 2001). Hussain *et al.* (1987) reported that the correlation coefficient between protein content

(PC) and grain width was $r = -0.881$ (p = 0.05) while between PC and the ratio of grain length to grain width $r = -0.344$ (p = 0.05). Shi and Zhu (1994a) pointed out that in *indica* rice the endosperm and maternal plant genetic effect components were significant between AC and rice width or the ratio of length to width in *indica* rice. The relationships between AC and AQT of rice might be influenced by the weight of brown rice (WBR) and PC, since AC of rice could be affected as PC or WBR increased (Guo *et al.*, 1985; Hussain *et al.*, 1987; Wang *et al.*, 2005).

Although rice quality traits could be affected by the genes of the triploid endosperm, the rice grain is a new generation that differs from its diploid maternal plant which provides the nutrients for the grain development, and, as such, cytoplasmic effect from cytoplasmic genes and maternal effects from the diploid maternal plant nuclear genes are important components of genetic effects for the performance of rice quality traits. Shi and Zhu (1993, 1994b, 1996) found that rice quality traits were subject to significant seed and maternal genetic effects, while Lin *et al.* (2005) reported that the AC of *japonica* rice was not only greatly influenced by the genetic main effects from endosperm, cytoplasm and maternal plant genes but was also affected by genotype environment (GE) interaction effects, because the diversification of gene expression occurred in

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different environments (Bao and Xia, 1999; Shi *et al.*, 1997, 1999). However, genetic effects and relationships between rice quality traits are complex but in the studies discussed above were all directly analyzed using methods based on unconditional analysis, which could not eliminate additional influences from other correlative traits which could affect the relationship between the pairwise traits. For example, the genetic correlations between AC and AQT of rice might be influenced by WBR or PC, but until now little information has been reported on these factors.

In present experiment, the unconditional analysis and the conditional analysis techniques were used to examine the genetic relationships from different genetic factors (triploid endosperm genes, cytoplasmic genes and diploid maternal plant genes) between AC and AQT for *indica* rice. The influences from WBR or PC of rice to the genetic relationships between AC and AQT could be disclosed, which could be helpful in understanding the complex relationships between AC and AQT of *indica* rice.

## Materials and Methods

### Field experiment

We used a factorial mating design involving 12 *Oryza sativa* (L.) *indica* rice lines consisting of 7 cytoplasm male sterile (CMS, or A) lines (Zhexie 2, Xieqingzao, Zhenan 3, Zhenshan 97, Gangchao 1, V 20 and Zuo 5) used as females and 5 restorer (R) lines (T 49, Cezao 2-2, 26715, 102 and 1391) used as males. The lines were a random sample of parents for a reference population of *indica* rice, all seed material coming from paddy field in Hangzhou, China. All CMS female parent lines were crossed to five restorer lines to produce $F_1$ seeds in 1997. The derived $F_1$ hybrids, together with their parents, were grown in randomized complete plots with two replications at the experimental farm (120°11'27" E, 30°16'28" N, altitude 12.5 m, semitropical climate, silt loam soil) of Zhejiang University, Hangzhou, China in 1998 and 1999, respectively. In both years, the seeds were sown on 30 March after germination and the 31-day old seedlings were transplanted with a single plant per round and spaced at 20 cm within a row. Each plot consisted of 6 rows with 36 plants. The agricultural practices including the prevention of diseases and insects were followed as other standard paddy fields during the course of the experiments. $F_1$ seeds from A × R crosses used in the analysis were produced by pollinating CMS lines with restorers during the same flowering season. Seeds of both parents and the $F_2$ offsprings from $F_1$ plants were sampled from a batch of 16 mature plants in the middle of each plot. All brown rice was gained from rice grain, which was de-hulled using a sample dehusker (model JLGJ4.5, Taizhou Liangyi Company, China) and milled by sample miller (Model JNMJ3, Taizhou Liangyi Company, China) before grinding to 100-mesh in a model 3010-019 cyclone grinder (Fort Collins, Colorado, USA). The AC and PC of

the rice were measured by near-infrared reflectance spectroscopy using a model 5000 monochromator (NIR Systems Inc, Silver Spring, MD, USA) and 3 g of ground brown rice in a 3.6 cm ring cup (Wu *et al.*, 2002), all samples being duplicated. The weight of brown rice (WBR), the brown rice length (BRL), the brown rice width (BRW), the brown rice thickness (BRT), the ratio of brown rice length to width (RLW) and the ratio of brown rice length to thickness (RLT) were measured using mature de-husked brown rice, all samples being triplicated.

### Statistical methods

The estimated unconditional phenotypic covariance ($C_{P\ (T1)}$) components between AC and AQT of brown rice consisted of the unconditional genetic main covariances ($C_{G\ (T1)}$) and their unconditional GE interaction covariances ($C_{GE\ (T1)}$) and also the unconditional residual covariance ($C_{e\ (T1)}$), which were estimated by the genetic models and statistical methods for quantitative traits of endosperm in cereal crops (Zhu and Weir, 1994). The $C_{G\ (T1)}$ has the components of the unconditional endosperm additive main covariance ($C_{Ae\ (T1)}$), the unconditional endosperm dominance main covariance ($C_{De\ (T1)}$), the unconditional cytoplasmic main covariance ($C_{C\ (T1)}$), the unconditional maternal additive main covariance ($C_{Am\ (T1)}$), the unconditional maternal dominance main covariance ($C_{Dm\ (T1)}$), the unconditional covariance between endosperm and maternal additive effects ($C_{Ae\cdot Am\ (T1)}$), the unconditional covariance between endosperm and maternal dominance effects ($C_{De\cdot Dm(T1)}$). $C_{GE\ (T1)}$ has the components of $C_{AeE\ (T1)}$, $C_{DeE\ (T1)}$, $C_{CE\ (T1)}$, $C_{AmE\ (T1)}$, $C_{DmE\ (T1)}$, $C_{AeE\cdot AmE\ (T1)}$ and $C_{DeE\cdot DmE\ (T1)}$.

The mixed model approach of conditional genetic analysis for quantitative traits (Zhu, 1995) was used to obtain the conditional phenotypic covariances ($C_{P\ (T1|\ T2)}$) between AC|WBR or AC|PC and the AQT of brown rice. Here, T1|T2 denotes trait 1 conditioned on trait 2, which means the conditional phenotypic value of traits 1, when excluded the impacts of trait 2 on trait 1, AC|WBR or AC|PC means, hence, AC conditioned on WBR or PC, respectively. The conditional phenotypic covariance ($C_{P(T1|T2)}$) components including the conditional endosperm additive main covariance of trait 1 conditioned on trait 2 ($C_{Ae\ (T1|T2)}$), the conditional endosperm dominance main covariance of trait 1 conditioned on trait 2 ($C_{De\ (T1|T2)}$), the conditional cytoplasm main covariance of trait 1 conditioned on trait 2 ($C_{C\ (T1|T2)}$), the conditional maternal additive main covariance of trait 1 conditioned on trait 2 ($C_{Am\ (T1|T2)}$), the conditional maternal dominance main covariance of trait 1 conditioned on trait 2 ($C_{Dm\ (T1|T2)}$), the conditional covariance between endosperm and maternal additive effects of trait 1 conditioned on trait 2 ($C_{Ae\cdot Am\ (T1|T2)}$), the conditional covariance between endosperm and maternal dominance effects of trait 1 conditioned on trait 2 ($C_{De\cdot Dm\ (T1|T2)}$), and their conditional GE interaction covariances $C_{AeE\ (T1|T2)}$, $C_{DeE\ (T1|T2)}$, $C_{CE\ (T1|T2)}$, $C_{AmE\ (T1|T2)}$, $C_{DmE}$

$_{(T1|T2)}$, $C_{AeE \cdot AmE \ (T1|T2)}$, $C_{DeE \cdot DmE \ (T1|T2)}$. And the conditional phenotypic covariance ($C_{P \ (T1|T2)}$) also including the conditional residual covariance of trait 1 conditioned on trait 2 ($C_{e \ (TI|T2)}$). The Jackknife re-sampling method was used with sampling generation means of entries to derive the standard errors of estimated components of unconditional or conditional covariances.

## Results and Discussion

### Covariance analysis between AC and WBR or PC

All the phenotypic covariances ($C_P$) and genotypic covariances ($C_G$) between AC and WBR or AC and PC were significant (Figure 1), indicating that there was true genetic association between AC and WBR or PC because the magnitude of genetic covariance for all the pairwise traits was similar to or larger than the phenotypic covariance between AC and WBR or AC and PC. None of the estimated residual covariances ($C_e$) were significant, so the influences from the sampling errors and microenvironmental factors were not important for the genetic relationships between AC and WBR or AC and PC. Hence, WBR or PC had a close genetic relationship with the AC of *indica* rice, and the conditional analysis method could be used for analyzing the conditional genetic relationship between AC and other traits of *indica* rice.

### Phenotypic and genotypic covariances between AC and AQT

For the unconditional analysis, $C_{P(AC)}$ and $C_{G(AC)}$ values for most of AQT were significantly positive or negative, except for the covariances between AC and BRL or RLT (Table 1). For example, $C_{G(AC)}$ value was 18.09 (p = 0.05) for BRW, 8.58 (p = 0.05) for BRT and -16.13 (p = 0.05) for RLW. Although the $C_{P(AC)}$ for BRL was not significant ($C_{P(AC)}$ = 6.32), $C_{G \ (AC)}$ was significantly positive for BRL ($C_{G \ (AC)}$ = 8.53, p = 0.05) and the genotypic relationship between this pair of traits was clear. It was obvious that AC was positively correlated to most of AQT of rice, except for the RLW and RLT traits. The estimated $C_{e(AC)}$ values for BRL and BRW both significant, indicating that the relationship between AC and both these traits was also influenced by the sampling errors or factors related to

the microenvironment. The small $C_{e(AC)}$ values for these pairwise traits indicated that the correlations between AC and other AQT were mainly controlled by the genetic effects. This suggests that improving AC could simultaneously increase BRL, BRW and BRT.

Since the relationships between AC and AQT could be significantly influenced by WBR or PC (Figure 1), the conditional analysis method was used to further detect the genetic correlations between the pairwise traits between AC and AQT. When AC was conditional on WBR (AC|WBR), the conditional phenotypic covariance ($C_{P(AC|WBR)}$) and the conditional genotypic covariance ($C_{G(AC|WBR)}$) between AC|WBR and BRL or AC|WBR and BRT changed to significantly negative (Table 1). $C_{P(AC|WBR)}$ and $C_{G(AC|WBR)}$ between AC|WBR and BRW ceased to be significantly positive as compared to the significantly positive $C_{P(AC)}$ and $C_{G(AC)}$ values produced by unconditional analysis. $C_{P(AC|WBR)}$ and ($C_{G(AC|WBR)}$) between AC|WBR and RLW or RLT were significantly negative and the values were larger than those produced by unconditional analysis. It therefore appears that the influence of WBR on the relationships between AC and AQT was complex in that WBR could positively affect the relationship between AC and

**Table 1** - Estimated phenotypic and genotypic covariance components from the unconditional and conditional analysis between amylose content (AC) and the appearance quality traits (AQT), including brown rice length (BRL), brown rice width (BRW), brown rice width (BRT), ratio of brown rice length to width (RLW) and ratio of brown rice length to thickness (RLT).

| Covariance parameters[†] | Appearance quality traits | | | | |
|---|---|---|---|---|---|
| | BRL | BRW | BRT | RLW | RLT |
| $C_{P(AC)}$ | 6.32 | 17.53[*] | 8.41[*] | -16.38[*] | -12.69 |
| $C_{P(AC|WBR)}$ | -65.19[**] | 5.68 | -6.43[*] | -33.20[**] | -22.65[**] |
| $C_{P(AC|PC)}$ | -27.97[*] | 28.25[**] | 8.34[**] | -42.53[**] | -31.16[**] |
| $C_{G(AC)}$ | 8.53[*] | 18.09[*] | 8.58[*] | -16.13[*] | -11.78 |
| $C_{G(AC|WBR)}$ | -63.70[**] | 5.94 | -6.44[*] | -32.90[**] | -21.82[**] |
| $C_{G(AC|PC)}$ | -25.85[*] | 28.94[**] | 8.60[**] | -42.46[**] | -30.48[**] |
| $C_{e(AC)}$ | -2.22[**] | -0.56[**] | -0.17 | -0.26 | -0.91 |
| $C_{e(AC|WBR)}$ | -1.49 | -0.25 | 0.01 | -0.30 | -0.84 |
| $C_{e(AC|PC)}$ | -2.12 | -0.69 | -0.27 | -0.07 | -0.68 |

[†]WBR, weight of brown rice; PC, protein content; $C_{P(AC)}$, unconditional covariance between AC and the appearance quality traits; $C_{P(AC|WBR)}$, conditional phenotypic covariance between AC|WBR and the appearance quality traits; $C_{P(AC|PC)}$, conditional phenotypic covariance between AC|PC and the appearance quality traits; $C_{G(AC)}$, unconditional genotypic covariance between AC and the appearance quality traits; $C_{G(AC|WBR)}$, conditional genotypic covariance between AC|WBR and the appearance quality traits; $C_{G(AC|PC)}$, conditional genotypic covariance between AC|PC and the appearance quality traits; $C_{e(AC)}$, unconditional residual covariance between AC and the appearance quality traits; $C_{e(AC|WBR)}$, conditional residual covariance between AC|WBR and the appearance quality traits; $C_{e(AC|PC)}$, conditional residual covariance between AC|PC and the appearance quality traits.
*Significant at the p = 0.05 by the t-test.
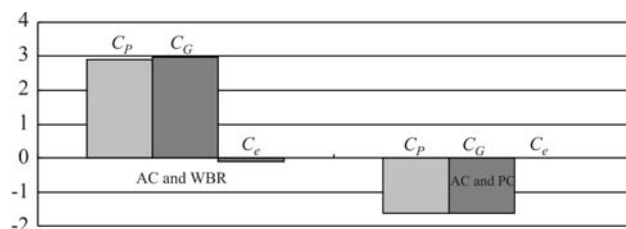**Significant at the p = 0.01 by the t-test.



**Figure 1** - The unconditional analysis covariance components between amylose content (AC) and weight of brown rice (WBR) or AC and protein content (PC). Figure shows phenotypic covariance ($C_P$), genotypic covariance ($C_G$) and residual covariance ($C_e$).

BRW but negatively affect the relationship between AC and the other appearance quality traits. While AC was conditional on PC (AC|PC), all $C_{P(AC|PC)}$ and $C_{G(AC|PC)}$ between AC|PC and AQT were significantly positive or negative (Table 1). Among them, $C_{P(AC|PC)}$ and ($C_{G(AC|PC)}$) between AC|PC and BRL became significantly negative, while those between AC|PC and BRW, BRT, RLW, RLT were all significantly positive or negative by conditional analysis. However, the conditional analysis values were generally notably larger than those produced by unconditional analysis, the exception being the pairwise traits between AC|PC and BRT, which were similar to the unconditional analysis values. It was found that PC could negatively affect most of the genetic relationships between AC and the appearance quality traits, especially for the relationship between AC and BRL. Since none of the small $C_{e(AC|WBR)}$ or $C_{e(AC|PC)}$ values from the conditional analysis were significant, the conditional genetic correlations between AC and AQT were not influenced by sampling errors or microenvironmental factors when AC was conditioned on WBR or PC.

## Analysis of AC and AQT covariance components from different genetic systems

Since rice quality traits were simultaneously controlled by the genes from the triploid endosperm, cytoplasm and diploid maternal plant, the genetic main effects as well as their GE interaction effects were important for the performance of rice quality. The covariance components from the different genetic systems between AC and AQT could be evaluated by the unconditional analysis method and conditional analysis method (Table 2).

The unconditional analysis results in Table 2 shows that $C_{Ae\,(AC)}$ between AC and BRL or AC and RLW was significantly negative, while $C_{C\,(AC)}$ between AC and BRL or AC and BRW and $C_{Ae\cdot Am\,(AC)}$ between AC and BRL were significantly positive. For the GE interaction covariance, only $C_{DeE\,(AC)}$ and $C_{DeE\cdot DmE\,(AC)}$ between AC and RLT were significantly negative. Since other covariance parameters from different genetic systems between AC and AQT were not significant, the genetic relationships from endosperm, cytoplasmic and maternal plant effects were not visible for most of the pairwise traits between AC and AQT.

For the conditional analysis, when AC was conditional on WBR (AC|WBR) almost all the covariance components from the different genetic systems between AC|WBR and AQT were not significant, except for the significant positive $C_{AeE(AC|WBR)}$ and significant negative $C_{DeE(AC|WBR)}$ between AC|WBR and RLT (Table 2.). For AC conditional on PC (AC|PC), the GE interaction covariances including $C_{DmE(AC|PC)}$, $C_{DeE\text{-}DmE(AC|PC)}$ between AC|PC and BRT or $C_{DeE\text{-}DmE(AC|PC)}$ between AC|PC and RLT were significantly correlated. The influence of WBR or PC on the covariances from different genetic system was not large, because only small endosperm, cytoplasmic or maternal

covariance parameters were detected significant between AC and AQT by conditional analysis method.

Most rice quality traits are complex quantitative traits, which are not only controlled by genetic main effects, GE interaction effects and environmental conditions but can also be influenced by other traits. Hence, analyzing the genetic correlations for pairwise quality traits of rice should consider these factors. In general, the quantitative traits can affect each other in the developmental period of rice, which also can interfere with the genetic relationships between the quality traits. To understand the true genetic correlations between rice quality traits, it is better to exclude the extra factors which can affect the relationship between pairwise traits. Although some genetic models and statistical analysis methods have been proposed for analyzing the genetic correlations between complex quantitative traits they do not effectively exclude the influences of the other trait(s) on the relationship between two quantitative traits (Mo, 1985; Zhu, 1992; Zhu and Weir, 1994). Hence, the choice of genetic models and statistical analysis methods are very important when researching quantitative traits. Zhu (1995) proposed a new statistical method for analyzing conditional genetic effects and conditional genetic variance components based on the genetic models for quantitative traits with contribution measure for each component to the complex traits. By using this conditional analysis method, the causal influences from the extra trait which affected the genetic relationships between AC and AQT of rice can be excluded and the actual genetic correlation between the pairwise traits can be found. This conditional analysis method can also estimate the genetic main effects as well as their GE interaction effects from the triploid endosperm, cytoplasm and diploid maternal plants.

Our results presented in present experiment indicate that under the influenced of WBR or PC, AC was positively correlated to BRL, BRW or BRT, but was negatively correlated to RLW or RLT. The results of conditional analysis revealed that WBR could positively affect the relationship between AC and BRW, but negatively affect the relationships for other pairwise traits, while PC could negatively affect the relationships between AC and most of the appearance quality traits. Among the genetic correlations from different genetic systems including endosperm, cytoplasmic and maternal effects for the pairwise quantitative traits, only some significant covariance components were detected between AC and AQT of rice analyzed by both the unconditional or conditional methods, with WBR or PC having little impact on the covariance components of different genetic systems between the pairwise traits of *indica* rice.

Comparing the results from the unconditional and conditional analysis, it appears that, for the same brown rice weight, it is possible to improve the amylose content and simultaneously noticeably reduce the brown rice length and brown rice thickness. Furthermore, if breeders improve

**Table 2** - Estimated covariance components from the unconditional and conditional analysis between amylose content (AC) and the appearance quality traits (AQT) including brown rice length (BRL), brown rice width (BRW), brown rice width (BRT), ratio of brown rice length to width (RLW) and ratio of brown rice length to thickness (RLT).

| Unconditional or conditional AC† | Traits | Genetic covariance parameters | | | | | | | | | | | | | |
| | | Genetic main covariance | | | | | | | GE interaction covariance | | | | | | |
| | | $C_{Ae}$ | $C_{De}$ | $C_C$ | $C_{Am}$ | $C_{Dm}$ | $C_{Ae.Am}$ | $C_{De.Dm}$ | $C_{AeE}$ | $C_{DeE}$ | $C_{CE}$ | $C_{AmE}$ | $C_{DmE}$ | $C_{AeE.AmE}$ | $C_{DeE.DmE}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AC | BRL | -31.99* | 0.21 | 16.58* | -88.80 | 6.03 | 58.96* | -0.54 | 35.07 | 2.48 | -8.94 | 36.72 | -4.29 | -35.63 | -0.08 |
| AC\|WBR | | -24.35 | -1.89 | 10.42 | 4.53 | 4.02 | -15.60 | 0.78 | 18.16 | 0.27 | -23.26 | 27.32 | -1.04 | -24.46 | 0.33 |
| AC\|PC | | -55.07 | 7.43 | -13.33 | 26.83 | 5.21 | -0.96 | -1.92 | -60.56 | -5.57 | 17.38 | -100.50 | -1.13 | 78.98 | 0.63 |
| AC | BRW | 10.42 | 0.00 | 21.43* | -2.04 | -3.88 | -4.68 | 1.70 | 12.13 | 1.38 | -3.72 | 4.44 | 5.99 | -8.45 | -2.60 |
| AC\|WBR | | -0.86 | -0.45 | 10.96 | -2.43 | -3.55 | -0.76 | 0.98 | -15.44 | 1.28 | -3.53 | 3.44 | 5.15 | 7.42 | -1.95 |
| AC\|PC | | 9.10 | -0.20 | 6.08 | 10.70 | -7.71 | -4.68 | 3.54 | -32.20 | 4.64 | 3.14 | -60.32 | 14.69 | 47.95 | -6.31 |
| AC | BRT | 0.24 | -0.60 | 14.52 | -5.84 | -2.47 | 0.26 | 1.07 | -2.94 | 4.23 | -4.66 | -0.42 | 5.27 | 1.49 | -2.21 |
| AC\|WBR | | -3.64 | -0.58 | 4.48 | -3.26 | -1.93 | -1.35 | 0.56 | -22.88 | 3.73 | -8.33 | -1.78 | 5.06 | 13.76 | -1.63 |
| AC\|PC | | 0.91 | 1.23 | -0.24 | 1.34 | -6.31 | -1.92 | 2.31 | 5.51 | 4.95 | 5.00 | -13.96 | 13.45* | 3.48 | -5.51* |
| AC | RLW | -27.26* | 0.50 | -21.75 | -36.13 | 6.63 | 33.78 | -2.05 | 6.50 | -1.47 | 1.33 | 16.57 | -7.22 | -11.33 | 2.69 |
| AC\|WBR | | -6.78 | 0.05 | -9.82 | 5.23 | 5.49 | -6.44 | -0.77 | 28.10 | -2.22 | -5.51 | 11.82 | -5.01 | -22.09 | 2.18 |
| AC\|PC | | -23.75 | 2.83 | -13.18 | 9.78 | 10.08 | -4.49 | -4.48 | -5.09 | -6.38 | -0.43 | 6.50 | -14.89 | -1.68 | 6.69 |
| AC | RLT | -20.13 | 1.47 | -19.29 | -36.72 | 7.40 | 32.21 | -2.19 | 23.38 | -6.27* | 4.96 | 19.70 | -11.04 | -21.43 | 3.78* |
| AC\|WBR | | -5.20 | 0.07 | -2.84 | 9.39 | 5.42 | -7.18 | -0.55 | 50.36* | -6.75* | 3.08 | 16.86 | -9.09 | -36.81 | 2.97 |
| AC\|PC | | -32.15 | 1.49 | -5.41 | 10.19 | 13.86 | 4.07 | -5.09 | -45.70 | -10.20 | -4.30 | -28.97 | -24.22 | 38.50 | 9.99* |

†$C_{Ae}$, the endosperm additive main covariance; $C_{De}$, the endosperm dominance main covariance; $C_C$, the cytoplasmic main covariance; $C_{Am}$, the maternal additive main covariance; $C_{Dm}$, the maternal dominance main covariance; $C_{Ae.Am}$, the covariance between endosperm and maternal additive effects; $C_{De.Dm}$, the covariance between endosperm and maternal dominance effects; $C_{AeE}$, the endosperm additive interaction covariance; $C_{DeE}$, the endosperm dominance interaction covariance; $C_{CE}$, the cytoplasmic interaction covariance, $C_{AmE}$, the maternal additive interaction covariance; $C_{DmE}$, the maternal dominance interaction covariance; $C_{AeE.AmE}$, interaction covariance between endosperm and maternal additive effect; $C_{DeE.DmE}$, interaction covariance between endosperm and maternal dominance effect.

*Significant at the p = 0.05 by the t-test.

**Significant at the p = 0.01 by the t- test.

the rice amylose content while maintaining the same protein content, the brown rice length could be reduced while simultaneously increasing the brown rice width and the brown rice thickness.

The mixed model approaches of conditional genetics analysis for quantitative traits described in present paper provides a new analysis method and strategy for research on the relationship between quantitative traits and might be useful not only for rice but for other cereal crops.

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