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Genetic analysis of transparency and chalkiness area at different filling stages of rice (*Oryza sativa* L.)

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Abstract

Seven cytoplasmic male sterile lines and five restorer lines of *indica* rice (*Oryza sativa* L.) were used to analyze genetic effects on transparency and chalkiness area at four filling stages. A developmental genetic model for quantitative traits of triploid endosperm in cereal crops were used for the data analysis. The unconditional analysis showed that the accumulated genetic effects of genes expressed from the initial time (at flowering and fertilization) to the filling time t were all significant for transparency and chalkiness area. These results indicated that the genetic effects of the triploid endosperm, cytoplasmic and diploid maternal plant were all of importance for both traits at various filling stages, especially for maternal additive and dominance effects on transparency. The relatively high endosperm and maternal additive effects on transparency and chalkiness area indicated that the two traits could be improved by selection in early generations. From the conditional analysis for the net genetic effects of genes expressed during time $t-1$ to time t, new expression of genes in endosperm, cytoplasm and maternal plant for transparency and chalkiness area was found at most of the filling stages, especially from 8 to 14 days after flowering for transparency and from 1 to 14 days after flowering for chalkiness area. Predicted genetic effects and conditional genetic effects at different filling stages showed that transparency and chalkiness area of offspring could be improved by using some parents, such as Zuo 5, because of their better endosperm additive and cytoplasmic effects.

Keywords: Rice (*Oryza sativa* L.); Developmental genetics; Transparency; Chalkiness area; Genetic effects

1. Introduction

Transparency and chalkiness area of milled rice are closely related to quality of rice. Consumers usually like rice with better transparency and little or no chalkiness area. To improve the efficiency of breeding for rice quality, it is necessary to understand the variation in the expression of genes for controlling these traits. The genetic factors have been documented in some studies. These have shown that transparency and chalkiness area are quantitative traits which may be controlled by triploid endosperm genetic effects (Choi, 1979; Mckenzie, 1982; Takeda and Saito, 1983; Yang et al., 1986; Li et al., 1987; Jin and Qiu, 1988; Fu et al., 1994), cytoplasmic genetic effect (Yi and Cheng, 1991), diploid maternal plant genetic effects (Choi, 1979; Qi et al., 1983; Yang et al., 1986; Xu and Shen, 1988) or the simultaneous effects of all of these (Bao and Xia, 1999; Chen et al., 1998; Chen and Zhu, 1998; Shi et al., 1996, 1997, 1999; Shi and Zhu, 1998). In most of the reports, the phenotypic values of traits at maturity were used for the endosperm traits analysis. There is little information on

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developmental aspects of the transparency and chalkiness area through grain filling stages. Although final transparency and chalkiness area are mainly determined by the accumulated photosynthates from the whole developmental period, their expression at any one filling stage is related to the genetic effects for that filling stage, and the photosynthates accumulated up to then. Variation might exist for gene expression and genetic effects at the different filling stages. It is necessary, therefore, to understand the dynamics of such gene expression.

Most agronomic and quality traits are complex and controlled by several genes expressed throughout developmental stages. Some studies have shown that for some traits in animals or plants the developmental genetic behavior at different developmental stages is controlled by a single or a few main genes (Kheiralla and Whittington, 1962; Peat and Whittington, 1965; Xu and Shen, 1991; Atchley et al., 1994; Cheverud et al., 1996). Those studies have not however revealed the net genetic effects of gene expression during a developmental stage. According to the theory of developmental genetics, genes are selectively expressed at different growth stages. Therefore, those studies ignored the dissimilar gene actions at different stages which is an important factor influencing the development of the quantitative traits. Seed quality traits are difficult to study the developmental genetic mechanism of genes in any one period $(t-1 \rightarrow t)$ for quantitative traits by using conventional statistical analysis (Henderson, 1985; Cowley and Atchley, 1992; Atchley et al., 1994). The genetic models and statistical analysis methods developed by Zhu (1995) could be effectively used to estimate the conditional genetic variances, and predict conditional genetic effects. By using these models, Atchley and Zhu (1997) and Chen et al. (1999) studied the conditional genetic variances and net genetic effects for weight and tail length of mice, and boll number and yield of cotton, respectively.

In the present paper, developmental genetic behavior of transparency and chalkiness area of *indica* rice was analyzed by using a conditional genetic model and statistical methods. The genetic variance components, conditional genetic variance components and net genetic effects for these two endosperm traits at the different filling stages of rice were estimated to explore the expression mechanism of triploid endosperm, cytoplasmic and diploid maternal plant genes.

2. Materials and methods

The mating design used in this experiment was a factorial design with 12 parents—seven cytoplasmic male sterile lines (CMS or A) including four cytoplasmic types and their maintainer lines (B) (P1 = Zhexie 2, P2 = Xieqingzao, P3 = Zhenan 3, P4 = Zhenshan 97, P5 = Gangchao 1, P6 = V_{20} and P7 = Zuo 5) and five restorer lines (R) (P8 = T49, P9 = Cezao 2-2, P10 = 26715, P11 = 102 and P12 = 1391). All female parents were crossed to male parents to obtain the F_1 (A × R) in 1997. Seedlings of the parents and the F_1 were planted at the experimental farm at Zhejiang University in 1998. Seeds were sown on 30 March in 1998 and 31-day-old seedlings individually transplanted at a spacing of 20 cm × 20 cm. There were 36 plants in a plot with two replications. Samples of seeds from the parents and F_1 (A × R) plants (i.e. F_2 seeds) were harvested from the middle part of each plot weekly at different filling stages. Sixteen plants were used in the samples. We retained 40 florets on each panicle which flowered in the same day by removing all other florets. We then labeled the flowering time of each panicle. Subsequent grain samples were made of 7, 14, 21 and 28 days after flowering. The F_1 (A × R) seeds analyzed from different filling stages were obtained by crossing females to males during the same growing season. The two endosperm traits, transparency and chalkiness area, were measured, and the former using a digital photoelectric instrument developed by Zhejiang Academy of Agricultural Sciences, and chalkiness area (%), defined as the percentage of chalkiness area to total area of the milled rice. Since the chalkiness area 7 days after flowering and fertilization cannot be clearly determined for all generations, there was no data for this filling stage.

The genetic model for quantitative traits of endosperm in cereal crops (Zhu and Weir, 1994a,b) was used to estimate the genetic components of endosperm additive variance (V_A), endosperm dominance variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}) and maternal dominance variance (V_{Dm}) at different filling stages for transparency and chalkiness area. An adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996) was employed to predict the genetic effects including the endosperm additive effect (A), the cytoplasmic effect (C) and the maternal additive effect (Am). The

developmental genetic model and statistical methods (Zhu, 1995) were used to estimate conditional endosperm additive variance $(V_{A(t|t-1)})$, conditional endosperm dominance variance $(V_{D(t|t-1)})$, conditional cytoplasmic variance $(V_{C(t|t-1)})$, conditional maternal additive variance $(V_{Am(t|t-1)})$ and conditional maternal dominance variance $(V_{Dm(t|t-1)})$ at the special period $(t-1 \rightarrow t)$ during grain filling for the two traits. Net genetic effects defined as the effects of genes expressed in the period $t-1$ to time t, were detected by using conditional analysis. Genetic effects, defined as the accumulated genetic effects of genes expressed from the initial time (at flowering and fertilization) to time t, were predicted by using unconditional approaches. In this experiment, 7d | 0d or 14d | 0d indicated the cumulative gene expression from the initial time to 7 or 14 days after flowering and fertilization, while 14d | 7d represents the measures at 14 days given the phenotype values measured at 7 days for conditional analysis, and so on.

The Jackknife resampling method (Miller, 1974; Zhu and Weir, 1996) was employed by sampling generation means of 136 genetic entries in 2 years to derive the standard errors of estimated components of variances and covariances or predictors (genetic effects). A t-test with d.f. = 135 was conducted for testing the null hypothesis of zero parameters (variance, covariance, or genetic effect).

3. Results

3.1. Unconditional variance components

Unconditional variances for transparency and chalkiness area at four grain filling stages are summarized in Table 1. The results indicate that genetic variance components, including V_A, V_D, V_C, V_{Am} and V_{Dm}, at 7, 14, 21 and 28 days after flowering and fertilization, were all significant. Transparency and chalkiness area were, therefore, controlled by genetic effects of triploid endosperm genes, cytoplasm genes and diploid maternal plant genes at different filling stages.

The maternal variances $(V_{Gm} = V_{Am} + V_{Dm})$ at four filling stages (7, 14, 21 and 28 days after flowering) accounted for about 52.1, 42.8, 41.3 and 43.0% of total genetic variance $(V_G = V_A + V_D + V_C + V_{Am} + V_{Dm})$ for transparency, respectively, so the main

Table 1
Estimates of variance components for transparency and chalkiness area at different developmental stages in *indica* rice

Parameter	Developmental stages (filling days after flowering and fertilization)						
	Rice transparency ($\times 10^{-2}$)				Rice chalkiness area ($\times 10^{2}$)		
	7d	14d	21d	28d	14d	21d	28d
V_A[a]	0.79**	2.86**	2.54**	1.51**	6.86**	7.56**	6.69**
V_D[b]	0.24**	0.07**	0.38**	0.24**	1.15**	0.17**	1.35**
V_C[c]	0.24**	1.15**	1.48**	1.26**	2.98**	3.82**	1.96**
V_{Am}[d]	1.15**	2.59**	2.59**	1.88**	7.47**	8.23**	5.11**
V_{Dm}[e]	0.23**	0.46**	0.52**	0.38**	1.35**	0.50**	0.92**
$C_{A\cdot Am}$[f]	−0.38	−1.28	−0.79	−0.44	−2.62	−4.63	−1.66
$C_{D\cdot Dm}$[g]	−0.04	−1.11	−0.08	−0.08	−0.22	−3.60	−0.12
V_e[h]	0.01**	0.01**	0.01**	0.01**	0.14**	0.14**	0.14**

[a] Endosperm additive variance.
[b] Endosperm dominance variance.
[c] Cytoplasmic variance.
[d] Maternal additive variance.
[e] Maternal dominance variance.
[f] Additive covariance.
[g] Dominance covariance.
[h] Residual variance.
** Significant at 0.01 probability levels.

genetic effects controlling the performance of this endosperm trait were maternal ones. Among endosperm, cytoplasmic and maternal effects, cytoplasmic effects at all filling stages were the least and the V_C values were about 9.1, 16.2, 19.7 and 23.9% of V_G. Since the ratios of additive variances $(V_A + V_{Am})$ to V_G were about 64.3–76.4% $((V_A + V_{Am})/V_G)$ for all filling stages, endosperm and maternal additive effects were the main factors of genetic effects, and genetic gain could be expected by applying selection for transparency in early generations.

For chalkiness area, the maternal effects at the two filling stages of 14 and 21 days after flowering were the main factors affecting it because of the larger V_{Gm}. However, this was not the last of 28 days since the endosperm variances $(V_{Ge} = V_A + V_D)$ were larger than V_{Gm}. Therefore, it is appropriate to select the single seed with less chalkiness area at the final filling stage because of the difference among seeds. Additive genetic effects were more important than dominance genetic effects for chalkiness area at all filling stages, so selection could be applied for this trait in early generations. As the significant cytoplasmic variances (V_C) were about 12.2–18.8% of V_G for chalkiness area, the cytoplasmic effects could affect performance of the progeny.

Since the covariances between the endosperm and maternal additive effects $(C_{A\cdot Am})$ and between endosperm and maternal dominance effects $(C_{D\cdot Dm})$ were not significant for both transparency and chalkiness area, no relationship was detected between endosperm and maternal genetic effects. It is concluded that these two endosperm traits were mainly determined by genetic effects because of the small values of estimate residual variance (V_e).

3.2. Conditional variance components

From the unconditional variance analysis, it was concluded that expression of genes for transparency and chalkiness area might differ among filling stages. The conditional genetic variances of gene expression for the endosperm traits at one special period could be estimated by using the conditional variance analysis method and the estimates are presented in Table 2.

The results indicate that the new expression of triploid endosperm genes, cytoplasmic genes and maternal plant genes were found at different filling

Table 2
Estimates of conditional variance components for transparency and chalkiness area at different developmental stages in *indica* rice

Parameter	Developmental stages (filling days after flowering and fertilization)						
	Rice transparency ($\times 10^{-2}$)				Rice chalkiness area ($\times 10^{2}$)		
	7d | 0d	14d | 7d	21d | 14d	28d | 21d	14d | 0d	21d | 14d	28d | 21d
$V_{A(t\|t-1)}$ [a]	0.79**	4.22**	0.81**	3.83**	6.86**	5.12**	5.55**
$V_{D(t\|t-1)}$ [b]	0.24**	0.00	0.25**	0.32**	1.15**	0.76**	4.08**
$V_{C(t\|t-1)}$ [c]	0.24**	1.28**	0.68**	1.43**	2.98**	0.00	0.00
$V_{Am(t\|t-1)}$ [d]	1.15**	3.14**	0.00	1.59**	7.47**	2.37**	0.00
$V_{Dm(t\|t-1)}$ [e]	0.23**	0.47**	0.37**	0.36**	1.35**	0.40**	1.39**
$C_{A\cdot Am(t\|t-1)}$ [f]	−0.38	−1.84	0.00	−0.58	−2.62	−1.41	0.00
$C_{D\cdot Dm(t\|t-1)}$ [g]	−0.04	0.00	−0.05	−0.06	−0.22	−0.05	0.17
$V_{e(t\|t-1)}$ [h]	0.01**	0.01**	0.01**	0.01**	0.14**	0.15**	0.15**

[a] Conditional endosperm additive variance.
[b] Conditional endosperm dominance variance.
[c] Conditional cytoplasmic variance.
[d] Conditional maternal additive variance.
[e] Conditional maternal dominance variance.
[f] Conditional additive covariance.
[g] Conditional dominance covariance.
[h] Conditional residual variance.
** Significant at 0.01 probability levels.

stages, except for conditional endosperm dominance effect ($V_{D(t|t-1)}$) at 14 days or conditional maternal additive effect ($V_{Am(t|t-1)}$) at 21 days after flowering for transparency. Since the total conditional genetic variances including $V_{A(t|t-1)}$ (conditional endosperm additive variance), $V_{D(t|t-1)}$, $V_{C(t|t-1)}$, $V_{Am(t|t-1)}$ and $V_{Dm(t|t-1)}$ (conditional maternal dominance variance) were larger at 14 or 28 days after flowering, the net genetic effects of genes expressed at the filling stages of 8–14 or 22–28 days were more important than at other filling stages. It was shown that many new quantitative genes were activated at these two filling periods, except for the conditional endosperm dominance effect ($V_{D(t|t-1)} = 0$) at 8–14 days filling stage. There was also no expression of new maternal additive effects at 15–21 days filling stage because of the non-significant $V_{Am(t|t-1)}$. Although maternal effects were more important than other genetic effects detected by unconditional variance analysis at all filling stages (Table 1), the results of conditional variance analysis indicated that new expression of triploid endosperm genes were greater than those of maternal plant genes, except for the filling stage 1–7 days after flowering. This result suggests that the larger maternal effects estimated by unconditional variance analysis at various filling stages was caused by the activated genes expressed at early filling stage (1–7 days after flowering) and continually to final filling stage.

For chalkiness area, the results of significant $V_{A(t|t-1)}$, $V_{D(t|t-1)}$ and $V_{Dm(t|t-1)}$ of different developmental stages (1–14, 15–21 or 22–28 days after flowering) showed that new genes were continually activated for endosperm additive and dominance effects or maternal plant dominance effect at these filling stages. There was however no detection of new expression of genes for maternal additive effects at 22–28 days stage or for cytoplasmic effects at 15–21 and 22–28 days stage after flowering, since conditional genetic variances at these stages were not found. The significant unconditional variances at these stages in Table 1 were the results of the continual expression of activated genes at the earlier filling stage(s). It was, therefore, shown that the activation of quantitative genes occurred gradually through all of the filling time and there were some differences in the magnitude or type of genetic effects among the filling stages. These results were difficult to detect by the unconditional genetic variance analysis. Since the conditional dominance variances ($V_{D(t|t-1)}$ and $V_{Dm(t|t-1)}$) were much smaller than conditional additive effects ($V_{A(t|t-1)}$ and $V_{Am(t|t-1)}$) at all filling stages for transparency and chalkiness area, the larger net additive effects showed that the improvement could be expected by selection in early generations.

The conditional additive covariance ($C_{A\cdot Am(t|t-1)}$) and conditional dominance covariance ($C_{D\cdot Dm(t|t-1)}$) was not significant, which suggests that the relationship between the genetic effects expressed by new genes of the triploid endosperm and those of the diploid maternal plant at different filling stages might not be important for transparency and chalkiness area. Significant conditional residual variance ($V_{e(t|t-1)}$) showed that the performance of these two endosperm traits were also influenced by sampling errors.

3.3. Genetic effects for parents at different developmental stages

Analysis for genetic effects for parents at different filling stages would be helpful to clarify the dynamic changes of breeding value among the filling stages of rice. The plotted values including endosperm additive effects, cytoplasmic effects and maternal additive effects, predicted by unconditional or conditional genetic analysis for each parent, are shown in Figs. 1 and 2.

The predicted unconditional genetic effects (Fig. 1) for transparency indicated that the variations of genetic effects at different filling stages largely existed for most parents. The predicted genetic effects of some parents even were positive (or negative) in the early filling stage(s) and then became negative (or positive) in the later stage(s) such as the endosperm additive effect of P10 (26715) and cytoplasmic effect of P6 (V_{20}). These results indicate that the genetic analysis based only on the phenotypic data at maturity might not represent other filing stage(s) of rice. In the 12 parents, the endosperm additive effects or cytoplasmic effects of P3 (Zhenan 3) and P7 (Zuo 5) for transparency were all positive at various filling stages and might improve the transparency of offspring by using these two parents.

The genetic effects detected in a special period $(t\,|\,t-1)$ by using the conditional genetic analysis were the net genetic effects for the parents, expressed from the genes at one special filling stage of rice

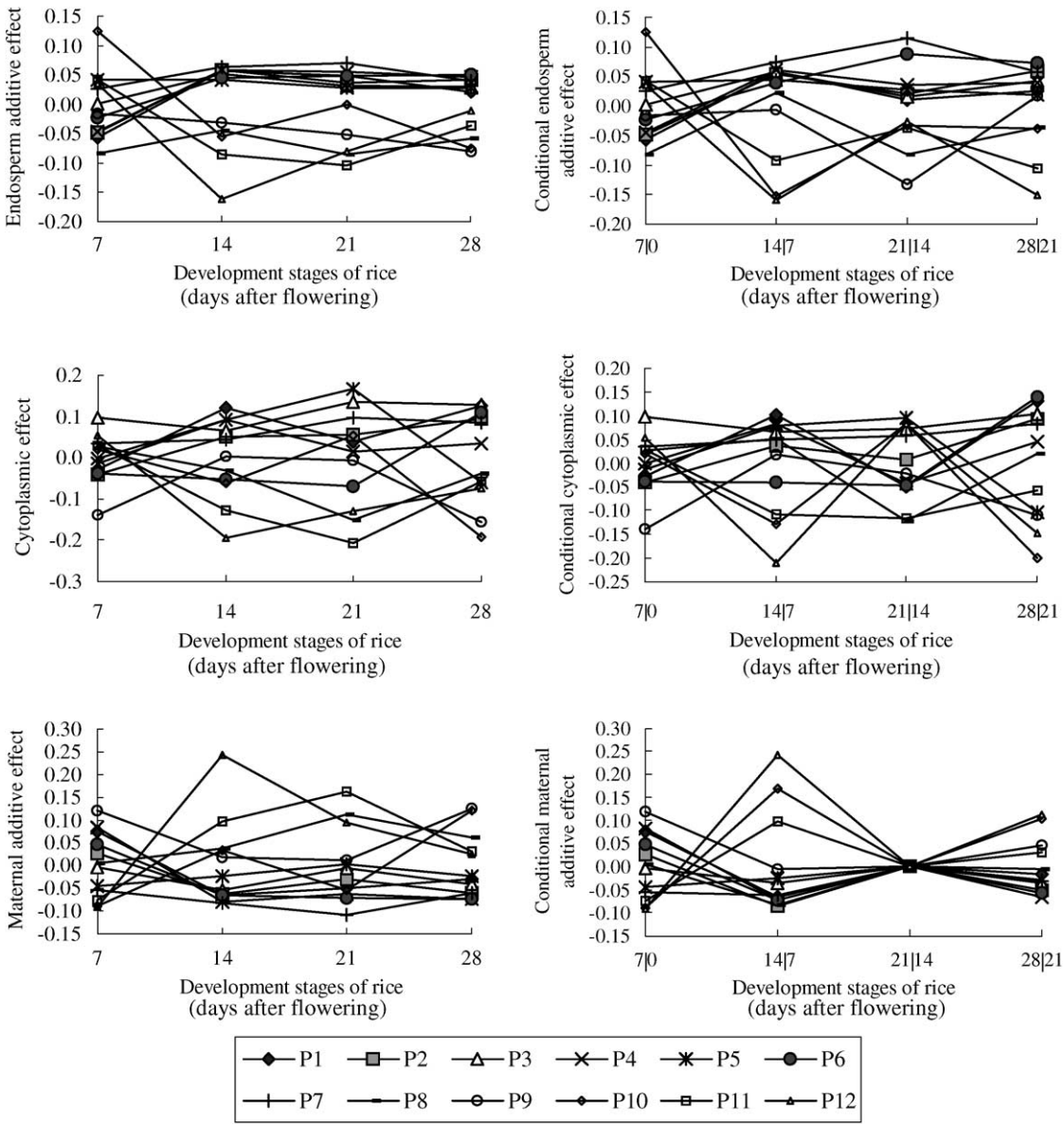

Fig. 1. Predicted genetic (left) and conditional genetic (right) effects for transparency at different development stages of rice.

through time $t-1$ to t. The net genetic effects, including conditional endosperm additive effects and conditional cytoplasmic effects for transparency, indicated that there was new expression of genes at different filling stages (Fig. 1). There was however no new expression of maternal additive effect at the 15–21 days filling stage. Those genetic effects detected by unconditional analysis at this stage were due to the expression of activated genes at the early filling stages (1–14 days). Besides, there are other differences between genetic effects predicted by unconditional and conditional analysis for the parents studied. For example, the unconditional maternal additive effects of P8 (T49) for transparency at four filling stages were 0.006, 0.037, 0.112, 0.061, respectively, and were much higher than those (0.006, −0.084,

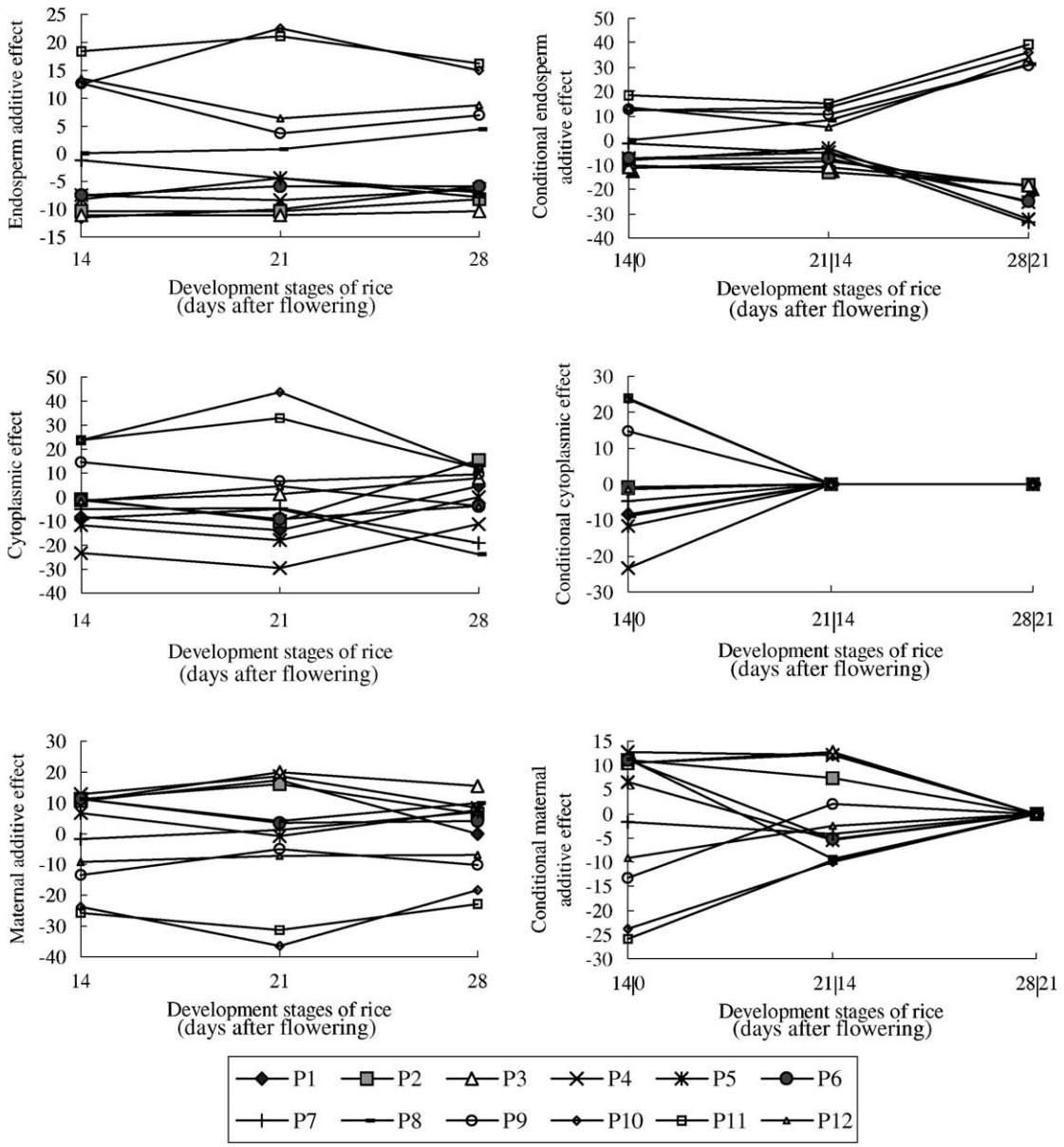

Fig. 2. Predicted genetic (left) and conditional genetic (right) effects for rice chalkiness area at different development stages of rice.

0.000, −0.005, respectively) predicted by conditional analysis except for the first filling stage. There was, therefore, spasmodic expression of some genetic effects of parents in new (or net) expression of gene(s) and it could be effectively detected by the method of conditional genetic analysis at all filling stages.

For chalkiness area, the genetic effects were more constant among different filling stages (Fig. 2). The endosperm additive effects and cytoplasmic effects of P4 (Zhenshan 97) could clearly reduce chalkiness area of offspring at different filling stages, but the maternal additive effects for this parent could significantly increase chalkiness area. Similar results existed for

some other parents, especially for P10 (26715) and P11 (102), of which the genetic effects at various filling stages could increase or reduce chalkiness area. The results suggest that the developmental genetic analysis was effective in identifying the parent(s) which have better genetic effects at all developmental stages for improving the endosperm quantitative traits. The net endosperm additive effect predicted by conditional analysis for chalkiness area showed that there were new (or net) expression of gene(s) at four filling stages (Fig. 2). There was no new expression of cytoplasmic genes at the 15–21 or 22–28 days filling stages after flowering in parents and the new expression from maternal plant genes for maternal additive effect was not found at the 22–28 days filling stage. Therefore, the differences for new (or net) expression of gene(s) were clearly existed at different filling stages, and among different genetic systems, especially for the cytoplasmic genes and diploid maternal nuclear genes.

4. Discussion

Understanding the dynamic variation in the expression of genes at different developmental stages across environments is a major goal in developmental qualitative genetics. The genetic mechanisms which controls the performance of complex quantitative traits varies in different developmental stages. In this experiment, the developmental genetic mechanism for transparency and chalkiness area was investigated for unconditional genetic effects $(0 \rightarrow t)$ and conditional net genetic effects in a specific period $(t-1 \rightarrow t)$. The total rice filling time was divided into four stages: early filling (1–7 days after flowering), middle filling (8–14 days after flowering), late filling (15–21 days after flowering) and maturity (22–28 days after flowering).

The results indicate that the genetic effects of triploid endosperm genes, cytoplasmic genes and maternal plant genes affect transparency and chalkiness area at maturity. This finding support the previous work (Shi and Zhu, 1993; Chen and Zhu, 1998; Shi et al., 1999). In addition, however, the results show that these genes affect the traits in other filling stages. These results, therefore, support the theory that genes are selectively expressed at different growth stages, even for rice quality traits, and variation exists for the genetic effects at the different filling stages. Since transparency and chalkiness area were mainly affected by gene expression for the whole filling period, the genetic effects expressed in the intermediate filling stage(s) were important for that stage and stages that followed. Since the main genetic effects for these traits were additive effects, including endosperm and maternal additive effects, improvement could be expected by selection in early generations for rice quality breeding. The results of conditional genetic variances analysis revealed that there was new expression of genes in most filling stages for endosperm, cytoplasmic and maternal genetic systems, especially for the middle filling stage (8–14 days after flowering for transparency or 1–14 days for chalkiness area). The gene expression at this filling stage was therefore more active. It was implied, by the detection of different genetic variances at different filling stages, that genes controlling transparency and chalkiness area might be differently expressed during the various stages of whole filling period. Since the performance of endosperm quality traits might be affected by genotype × environment interaction, further evaluation in different environments is required.

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