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不同环境下籼稻糙米重的发育遗传研究

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摘要: 采用包括遗传主效应和基因型与环境互作效应的数量性状发育遗传模型和统计分析方法 ,分析了籼稻 (*Oryza sativa* L.) 稻米 4 个发育时期糙米重的两年资料。结果表明 ,除了三倍体胚乳和二倍体母体植株基因的加性和显性主效应以及细胞质主效应可以控制不同稻米发育时期的糙米重量外 ,基因型与环境互作效应也可明显影响不同发育时期糙米重量。基因加性主效应和加性 ×环境互作效应在整个稻米灌浆过程中起着主要作用 ,对糙米重的选择可以取得良好的改良效果。条件方差分量分析结果表明 ,胚乳和母体植株中控制糙米重表现的基因在多数稻米发育时期均有新的表达 ,且以稻米发育早期为主 ,开花后第 1～7 天是控制糙米重的基因表达最为活跃的时期 ,其次为开花后第 8～14 天。一些基因只在个别发育时期间断表达 ,这在净细胞质主效应和净细胞质 ×环境互作效应以及净显性主效应上表现得尤为明显。稻米不同发育时期的遗传效应预测值表明 ,V20 和作 5 等亲本可以明显提高后代的糙米重量。

关键词: 籼稻 ; 发育遗传 ; 糙米重 ; 遗传方差和条件遗传方差 ; 遗传效应
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Developmental Genetic Analysis of Brown Rice Weight Under Different Environmental Conditions in indica Rice

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Abstract : Analysis of genetic main effects and genotype ×environment (GE) interaction effects for brown rice weight (BRW) at four different filling stages in *indica* rice (*Oryza sativa* L.) was conducted for two-year experimental data by using developmental genetic models and corresponding statistical approaches for quantitative traits of seeds in cereal crops. It was indicated that the genetic main effects and their GE interaction effects of triploid endosperm , cytoplasmic and diploid maternal plant genes were important for BRW at different filling stages of rice , especially for endosperm or maternal additive main effects and their additive interaction effects. Because of the higher additive effects and additive interaction effects for BRW at different filling stages , the better improving effects for this trait could be expected by selection in rice breeding. The results of conditional genetic variance components showed that the new expression of quantitative genes in endosperm and maternal plant for BRW was mostly found at all different filling stages of rice. The gene expression , however , was most active at the early filling stages especially for the first (1 - 7 d) and the second filling stages (8 - 14 d after flowering). The phenomena that some genes were spasmodically expressible among filling stages of rice were detected for some genetic effects especially for net cytoplasmic main effects or its interaction effects and net dominance main effects. Predicted genetic effects at different filling stages of rice showed that some parents such as V20 and Zuo 5 were better than others for improving the BRW.

Key words : *indica* rice (*Oryza sativa*) ; developmental genetics ; brown rice weight ; genetic variances and conditional genetic variances ; genetic effects

Rice grown under natural environments is affected by environmental conditions (e. g. weather , soil , cultivation and management of field) , but the phenotypic variation for many important quality traits of rice is mainly affected by genetic main effects and genotype ×environment (GE) interaction effects. The expression of genes at different filling stages might vary in different environments. So it is necessary to understand the genetic main effects and GE

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interaction effects on the dynamic performances of rice traits in different environments.

Most of the rice traits are controlled by quantitative genes. Many reports have recognized that the performance of endosperm traits of rice could be visibly affected by the genetic main effects and GE interaction effects of triploid endosperm genes, diploid maternal genes and cytoplasmic genes[1-6]. In most of the reports, the final phenotypic value at maturation was used for analysis of the rice endosperm traits. However, little information has been reported so far on the developmental behavior of filling stages in different environments and the influences of environments to the expression of genes. Since the final weight of brown rice is mainly related to the sum-total of the accumulated photosynthates during the whole developmental period of rice at a particular environmental condition, not only do this trait in one special filling stage be controlled by the genetic effects expressed in this special developmental stage, it also be related to the photosynthates accumulated up to this stage from flowering and impregnation. Variance of the expression of endosperm, maternal and cytoplasmic genes and the genetic main effects and GE interaction effects at different filling stages could exist in different environments. So understanding the dynamic gene expression in different environments is a major goal in the research of developmental qualitative genetics.

The objectives of this study were to clarify the developmental dynamics of gene expression for the BRW of *indica* rice in different environments, and explore the mechranism of variations in the developmental expression of triploid endosperm genes, cytoplasmic genes and diploid maternal plant genes by evaluating the conditional and unconditional genetic main effects, as well as their GE interaction effects among filling stages by using the developmental genetic models and statistical methods[7].

1 Materials and Methods

The materials used in this experiment consisted of 7 cytoplasmic male sterile lines (CMS or A) and their maintainer lines (B) of early season *indica* rice (Zhexie 2 (P1), Xieqingzao (P2), Zhenan 3 (P3), Zhenshan 97 (P4), Gangchao 1 (P5), V20 (P6), Zuo 5 (P7)) and 5 restorer lines (R) (T 49 (P8), Cezao 2-2 (P9), 26715 (P10), 102 (P11) and 1391 (P12)). The mating design was a factorial design (7 ×5). All female parents were crossed with male parents to obtain F_1 (A ×R) in 1997. Seedlings of parents and F_1 were planted at the experimental farm at Zhejiang University in 1998 and 1999. The seeds were sown on March 30 in both years. The 31-day old seedlings were individually transplanted at a spacing of 20 cm ×20 cm within rows. There were 36 plants in a plot with two replications. Seed samples of parents and F_2 from F_1 (A ×R) plants were harvested weekly at different filling stages (7, 14, 21 and 28 days after flowering and fertilization) from 16 plants in the middle part of each plot. The F_1 (A ×R) seeds analyzed from different filling stages were obtained by crossing females with males during the same growing season. Brown rice weight (mg) of different filling stages were measured from three replications for each sample of parents, F_1s and F_2s, respectively. According to the developmental stages of rice, we divided the whole rice filling time into early filling stage (1 - 7 d), middle filling stage (8 - 14 d), late filling stage (15 - 21 d), and mature stage (22 - 28 d after flowering).

The genetic models and statistical methods including endosperm, cytoplasmic and maternal effects for quantitative traits of endosperm in cereal crops[8-10] were used to estimate the genetic variance components of endosperm additive (V_A) and dominance variance (V_D), cytoplasmic variance (V_C), maternal additive (V_{Am}) and dominance variance (V_{Dm}), endosperm additive interaction (V_{AE}) and dominance interaction variance (V_{DE}), cytoplasm interaction variance (V_{CE}), maternal additive interaction (V_{AmE}) and dominance interaction variance (V_{DmE}) at different filling stages (from flowering to the special filling stage) for BRW. The developmental genetic models and statistical methods were used to estimate conditional endosperm additive ($V_{A(t,t-1)}$) and dominance variance ($V_{D(t,t-1)}$), conditional cytoplasmic variance ($V_{C(t,t-1)}$), conditional maternal additive ($V_{Am(t,t-1)}$) and dominance variance ($V_{Dm(t,t-1)}$), conditional endosperm additive interaction ($V_{AE(t,t-1)}$) and dominance interaction variance ($V_{DE(t,t-1)}$), conditional cytoplasm interaction variance ($V_{CE(t,t-1)}$), conditional maternal additive interaction ($V_{AmE(t,t-1)}$) and dominance interaction variance ($V_{DmE(t,t-1)}$) at the specific period ($t-1 \rightarrow t$) in rice filling time for BRW[7]. In this experiment, (t, $t-1$) represents the measures at t given the BRW measured at $t-1$ for conditional analysis. The AUP method was used to predict genetic main effects including endosperm additive effect (A), cytoplasmic effect (C), maternal additive effect (Am) as well as their GE interaction effects (AE, CE and AmE)[11,12]. The genetic effects estimated by using the unconditional analysis defined as the total accumulated genetic effects of genes expressed from the initial time (at flowering and fertilization) to time t ($0 \rightarrow t$) of rice filling stage, while

those estimated by using the conditional analysis means the net genetic effects from the genes expressed in the special filling period of time t - 1 to time t. The Jackknife resampling method was employed by sampling generation means of entries to derive the standard errors of estimated components of variances and predictors (genetic effects). All data were analyzed by programs developed by Zhu running on a PC computer[13].

2 Results

2.1 Unconditional variance component analysis at different filling stages for BRW

It was shown by the results in Table 1 that endosperm, cytoplasmic and maternal genetic main variance and their GE interaction variance components for BRW, including V_A, V_D, V_C, V_{Am}, V_{Dm}, V_{AE}, V_{DE}, V_{CE}, V_{AmE} and V_{DmE} at the filling stages of 7, 14, 21 and 28 d after flowering and impregnation, were significant except for V_D at 14, 21 and 28 d, V_{Dm} at 7, 14 and 28 d, and V_{CE} at 7, 14 and 21 d after flowering. The performance of BRW at different developmental stages was, therefore, controlled by the expression of triploid endosperm, cytoplasmic and/or diploid maternal genes, which could also be affected by the variation of environments.

Table 1 Estimates of variance components for BRW at different developmental stages in *indica* rice

Parameter	Developmental stages of rice			
	7 d	14 d	21 d	28 d
V_G				
V_A	20.39**	17.47**	16.34**	12.27**
V_D	5.69**	0.00	0.00	0.00
V_C	17.18**	7.92**	9.17**	7.41**
V_{Am}	39.11**	18.15**	17.91**	14.45**
V_{Dm}	0.00	0.00	2.30**	0.00
V_{GE}				
V_{AE}	42.96**	16.00**	17.82**	13.66**
V_{DE}	8.64**	5.19**	4.10**	3.71**
V_{CE}	0.00	0.00	0.00	5.02**
V_{AmE}	44.90**	21.12**	13.90**	11.20**
V_{DmE}	12.16**	4.34**	3.02**	2.60**
V_e	0.79**	0.69**	0.40**	0.41**

** significant at 0.01 probability levels. V_G, genetic main variance; V_A, endosperm additive variance; V_D, endosperm dominance variance; V_C, cytoplasmic variance; V_{Am}, maternal additive variance; V_{Dm}, maternal dominance variance; V_{GE}, GE interaction variance; V_{AE}, endosperm additive interaction variance; V_{DE}, endosperm dominance interaction variance; V_{CE}, cytoplasmic interaction variance; V_{AmE}, maternal additive interaction variance; V_{DmE}, maternal dominance interaction variance; V_e, residual variance.

Not only by genetic main effects, the BRW at different developmental stages is also controlled by GE interaction effects. These GE interaction effects belonged to one part of genetic effect inherited among generations besides genetic main effects and were the main reason which caused the variation for BRW of different filling stages in different environments. Compared with the genetic main effects ($V_G = V_A + V_D + V_C + V_{Am} + V_{Dm}$) and GE interaction effects ($V_{GE} = V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}$), the performance of BRW at 7-, 14- and 28-day filling stages were mainly affected by the GE interaction effects and the V_{GE} for these developmental stages were accounted for about 56.88 %, 51.73 % and 51.45 % of total genetic variance ($V_G + V_{GE}$), but BRW at 21 d was mainly controlled by genetic main effects (54.06 %). For the genetic main effects among the different genetic systems, maternal main effects ($(V_{Am} + V_{Dm})/V_G$ = 41.69 % - 47.48 %) were more important at different filling stages, followed by the endosperm main effects ($(V_A + V_D)/V_G$ = 31.66 % - 40.13 %) and cytoplasmic main effects (V_C/V_G = 18.18 % - 21.71 %). For the GE interaction effects, although maternal interaction effects ($(V_{AmE} + V_{DmE})/V_{GE}$ = 52.51 % - 54.58 %) were more important than other GE interaction effects at 7- or 14-day filling stages, the results of unconditional variance analysis indicated that expression of triploid endosperm genes ($(V_{AE} + V_{DE})/V_{GE}$ = 56.42 % - 47.99 %) were more than others at the two filling stages of 21 or 28 d after flowering. The cytoplasmic interaction effect (V_{CE}/V_{GE} = 13.87 %) at 28 d after flowering was smaller for BRW. Therefore, BRW was mainly controlled by the diploid maternal plant nuclear genes, followed by the triploid endosperm nuclear genes, while cytoplasmic effects, especially for cytoplasmic main effect, were also important for BRW at different developmental stages. It was suggested, by the larger additive main variances ($(V_A + V_{Am})/V_G$ = 72.24 % - 81.82 %) and additive interaction variances ($(V_{AE} + V_{AmE})/V_{GE}$ = 68.70 % - 81.66 %) for BRW at different filling stages, that the additive effects were more important than other genetic effects. So the better improving effects could be expected by selection in early generations for BRW.

Although all residual variances (V_e) were significant for BRW at different filling stages and the performance of BRW could also be influenced by sampling errors, it is concluded that BRW was mainly controlled by genetic effects and/or GE interaction effects of different genetic systems because of the small value of estimated residual variance.

2.2 Conditional variance component analysis at different filling stages for BRW

Since the genetic variances estimated by unconditional variance analysis at different developmental

stages ($0 \rightarrow t$) of rice were the total accumulation genetic effects by genes expressed before time t, the results could not clarify the gene expression in one special developmental stage ($t-1 \rightarrow t$). It is helpful to understand the net genetic effects from the genes expressed in the period of time $t-1$ to time t by using the conditional variance analysis, and the results might effectively explain the dynamic gene expression at different developmental stages of rice.

From the conditional variance analysis (Table 2), it was concluded that the conditional additive variances ($V_{A(t,t-1)}$ and $V_{Am(t,t-1)}$) and the conditional additive interaction variances ($V_{AE(t,t-1)}$ and $V_{AmE(t,t-1)}$) at various rice filling stages were significant except for the conditional endosperm additive interaction variance ($V_{AE(t,t-1)}$) at the middle filling stage (8 - 14 d) or conditional maternal additive interaction variance ($V_{AmE(t,t-1)}$) at mature stage (22 - 28 d after flowering). These results indicated that there were endosperm or maternal additive and additive interaction effects caused by the new expression of genes at most filling stages of rice. While significant conditional dominance variances ($V_{D(t,t-1)}$ and $V_{Dm(t,t-1)}$) and conditional dominance interaction variances ($V_{DE(t,t-1)}$ and $V_{DmE(t,t-1)}$) also showed that there were new gene expression at most filling stages for endosperm or maternal dominance and dominance interaction effects. It is, therefore, shown that the activation of quantitative genes was gradually carried through the continuing filling time and there were some differences for the magnitude or type of genetic effects among the filling stages. These results were difficult to be detected by the unconditional genetic variance analysis. There was no detection of new gene expression for cytoplasmic main effects at the filling stages of 8 - 14, 15 - 21 and 22 - 28 d after flowering, since $V_{C(t,t-1)}$ at these filling stages were not found in this experiment. The significant unconditional cytoplasmic main variances at 14, 21 and 28 d after flowering shown in Table 1 were the result of the continual expression of activated cytoplasmic genes at the early filling stage (1 - 7 d). The results of the significant cytoplasmic interaction effects at middle filling stage and mature stage in Table 2 revealed that the new genetic effects detected by conditional variance analysis could be earlier than those by unconditional variance analysis, since the latter could only find the cytoplasmic interaction effects at the mature stage (28 d after flowering).

The results of conditional variances analysis showed that there were new gene expression of triploid endosperm, cytoplasmic and diploid maternal genetic systems at most filling stages especially for the early filling stage (1 - 7 d after flowering). The conditional variance components of net genetic effects at this special filling stage were significant and most estimates were larger than other filling stages except for $V_{Dm(t,t-1)}$ and $V_{CE(t,t-1)}$. Therefore, the gene expression at this filling stage was more active because of the onset of many new genes, and the genetic effects of different genetic systems at 1 - 7 d after flowering were more important than other filling stages for the development of BRW. Since the conditional variance components were small at the filling stage of 22 - 28 d after flowering, the new gene expression could be visibly reduced near maturation of rice.

Significant conditional residual variances ($V_{e(t,t-1)}$) showed that the performance of BRW at different developmental stages were also influenced by sampling errors.

Table 2 Estimates of conditional variance components for brown rice weight at different developmental stages in *indica* rice

Parameter	Developmental stages of rice			
	7 d, 0 d	14 d, 7 d	21 d, 14 d	28 d, 21 d
$V_{G(t,t-1)}$				
$V_{A(t,t-1)}$	20.39**	23.83**	18.11**	12.50**
$V_{D(t,t-1)}$	5.69**	0.00	0.00	0.38**
$V_{C(t,t-1)}$	17.18**	0.00	0.00	0.00
$V_{Am(t,t-1)}$	39.11**	20.65**	27.78**	10.74**
$V_{Dm(t,t-1)}$	0.00	0.00	1.76**	0.00
$V_{GE(t,t-1)}$				
$V_{AE(t,t-1)}$	42.96**	0.00	13.46**	4.40**
$V_{DE(t,t-1)}$	8.64**	6.03**	4.63**	3.38**
$V_{CE(t,t-1)}$	0.00	19.69**	0.00	7.14**
$V_{AmE(t,t-1)}$	44.90**	20.60**	12.41**	0.00
$V_{DmE(t,t-1)}$	12.16**	4.54**	3.46**	2.15**
$V_{e(t,t-1)}$	0.79**	0.69**	0.40**	0.40**

** significant at 0.01 probability levels. $V_{G(t,t-1)}$, conditional genetic main variance; $V_{A(t,t-1)}$, conditional endosperm additive variance; $V_{D(t,t-1)}$, conditional endosperm dominance variance; $V_{C(t,t-1)}$, conditional cytoplasmic variance; $V_{Am(t,t-1)}$, conditional maternal additive variance; $V_{Dm(t,t-1)}$, conditional maternal dominance variance; $V_{GE(t,t-1)}$, conditional GE interaction variance; $V_{AE(t,t-1)}$, conditional endosperm additive interaction variance; $V_{DE(t,t-1)}$, conditional endosperm dominance interaction variance; $V_{CE(t,t-1)}$, conditional cytoplasmic interaction variance; $V_{AmE(t,t-1)}$, conditional maternal additive interaction variance; $V_{DmE(t,t-1)}$, conditional maternal dominance interaction variance; $V_{e(t,t-1)}$, conditional residual variance.

2.3 Unconditional and conditional genetic effects for parents at different filling stages of rice

The results of predicted unconditional and conditional genetic main effects and GE interaction effects from triploid endosperm genes, cytoplasmic genes and maternal plant genes indicated that most predicted genetic effects for CMS lines were positive which could increase the BRW, while most restorer lines were not. Since the

difference of net genetic main effects and net GE interaction effects at early filling stage for BRW among parents were larger than other filling stages, the expression of genes at this stage was more important for the performance of BRW (predicted unconditional and conditional genetic effects for some parents are listed in Table 3).

The variations of net genetic main effects and net GE interaction effects from the expression of genes at different developmental stages were largely existed among parents and environments (years). Although the expression of genes were stable for some parents among different filling stages, the predicted genetic effects of some parents were

Table 3 Predicated unconditional and conditional genetic effects of brown rice weight at different filling stages of *indica* rice

Parent	Endospern additive effect			Cytoplasmic effect			Maternal additive effect			Total	
	A	AE_1	AE_2	*C*	CE_1	CE_2	*Am*	AmE_1	AmE_2	1998	1999
Unconditional predicted genetic effects											
First developmental stage of rice (WBR1)											
P5	-2.69*	-0.17	0.02	-1.02	-	-	-2.47*	1.29	-1.69	-5.06	-7.85
P6	4.90*	0.49	0.09	2.94	-	-	-1.47	0.47	-0.89	7.33	5.57
P7	6.69*	2.09	-1.30	4.29+	-	-	-0.49	-3.79	2.95	8.80	12.15
P11	-5.22*	3.00+	-3.73+	-3.94	-	-	1.82	-5.33**	5.71*	-9.68	-5.37
Second developmental stage of rice (WBR2)											
P5	-0.28	-0.27	0.13	-0.06	-	-	-1.54*	0.42	-1.40+	-1.72	-3.15
P6	1.26*	0.85	0.06	1.66	-	-	-0.79	1.23	-1.77	4.21	0.43
P7	1.45+	2.01+	-0.96	1.44	-	-	0.73	-3.12	3.57	2.51	6.23
P11	-0.08	-1.08	1.03	-0.24	-	-	-1.08	-0.07	-0.62	-2.55	-0.99
Third developmental stage of rice (WBR3)											
P5	-0.85+	0.08	-0.18	-0.89	-	-	-1.56+	0.56	-1.14	-2.65	-4.61
P6	1.15	1.26*	-0.76	1.89	-	-	0.30	-0.35	0.44	4.26	3.02
P7	2.23+	1.61*	-0.59	2.61+	-	-	-1.01	-2.59*	1.81	2.85	5.05
P11	-1.25	-1.78+	1.44	-0.51	-	-	-1.20	0.93	-1.52	-3.81	-3.04
Fourth developmental stage of rice (WBR4)											
P5	-0.60+	-0.90	-0.17	-0.62	-1.46	1.21	-1.95+	-1.12	-0.55	-6.64	-2.67
P6	0.78*	0.56	0.58	2.45*	2.21	-0.79	-0.10	0.67	-0.77	6.57	2.15
P7	1.47*	1.39	0.82	2.61*	2.73	-1.22	-0.92	-1.85	1.04	5.44	3.80
P11	-1.26	-3.04	0.93	1.43	-2.39	3.00	-1.57	1.97+	-3.17+	-4.87	-0.65
Conditional predicted genetic effects											
Conditional first developmental stage of rice (WBR1, WBR0)											
P5	-2.69*	-0.17	0.02	-1.02	-	-	-2.47*	1.29	-1.69	-5.06	-7.85
P6	4.90*	0.49	0.09	2.94	-	-	-1.47	0.47	-0.89	7.33	5.57
P7	6.69*	2.09	-1.30	4.29+	-	-	-0.49	-3.79	2.95	8.80	12.15
P11	-5.22*	3.00+	-3.73+	-3.94	-	-	1.82	-5.33**	5.71*	-9.68	-5.37
Conditional second developmental stage of rice (WBR2, WBR1)											
P5	0.49	-	-	-	1.78	-1.31	-0.54	0.47	-0.73	2.20	-2.09
P6	1.04	-	-	-	5.79*	-5.56+	-1.94+	0.66	-1.69	5.55	-8.15
P7	0.96	-	-	-	-7.00	6.68	-1.42	-2.58	1.66	-10.04	7.88
P11	0.99	-	-	-	-1.79	2.98+	-2.47+	2.19+	-3.43+	-1.08	-1.93
Conditional third developmental stage of rice (WBR3, WBR2)											
P5	1.04*	0.01	0.17	-	-	-	2.90**	0.51	0.01	4.45	4.11
P6	-0.86*	0.61	-0.72	-	-	-	-2.66**	-0.02	-0.52	-2.92	-4.75
P7	-0.55	0.64	-0.58	-	-	-	-4.93**	-1.37	0.22	-6.20	-5.83
P11	-0.86+	-0.56	0.41	-	-	-	-1.08	-0.04	-0.21	-2.55	1.75
Conditional fourth developmental stage of rice (WBR4, WBR3)											
P5	0.19	-0.92	1.34	-	-1.11	1.33	-0.06	-	-	-1.90	2.81
P6	0.20	0.40	-0.05	-	2.33+	-2.14	-0.54	-	-	2.40	-2.52
P7	0.13	1.45	-1.22	-	2.35	-2.71+	-0.65	-	-	3.27	-4.46
P11	-1.27+	-3.32	0.03	-	-3.98+	5.27+	-3.56*	-	-	-12.13	0.47

+, * and ** were significant at 0.10, 0.05 and 0.01 level, respectively. *A*, endosperm additive effect; *C*, cytoplasmic effect; *Am*, Maternal additive effects; AE_1 and AE_2, endosperm additive interaction effects; CE_1 and CE_2, cytoplasmic interaction effects; AmE_1 and AmE_2, maternal additive interaction effects in 1998 and 1999, respectively. "-" indicates not available of predicted effects because of the corresponding zero estimates of variance components in Table 1 and Table 2.

unconstant and even of positive (or negative) value in the early filling stage(s) and then became negative value (or positive) in the later stage(s). For example, the total genetic effects of P6 (V20) and P7 (Zuo 5) at different developmental stages for BRW were positive by using the unconditional variance analysis, which could increase BRW of offspring, but P5 (Gangchao 1) and P11 (102) were not. We still could find some differences of net genetic effect components among filling stages for these parents. These results suggested, therefore, that the genetic analysis by using the final phenotypic value of BRW might not be suitable to the other filling stages of rice, and it could be more clear to find the genetic variation difference among parents at different developmental stages by using the developmental genetic analysis and using better parents which have better genetic effects at most developmental stages for improving BRW.

The results in Table 3 show that there were some differences between the genetic main effects and GE interaction effects predicted by unconditional variance analysis or conditional variance analysis. Since the conditional genetic effects and conditional GE interaction effects of new gene expression at the late filling stage (15 - 21 d) for P6 (V20) and P7 (Zuo 5) were mainly negative and some conditional GE interaction effects at the middle (8 - 14 d) and mature filling stage (22 - 28 d after flowering) were also not the same direction between two years, the expression of new activated genes was more sensitive to the variation of environments. The positive genetic effects detected in 1998 and 1999 by unconditional variance analysis for these two parents at different developmental stages were mainly caused by the sequentially positive expression of the activated genes at the early filling stage (1 - 7 d after flowering). The expression of the new activated genes at various filling stages for P5 (Gangchao 1) and P11 (102) could reduce BRW of offsprings because of their negative predicted conditional genetic effects and conditional GE interaction effects at 4 special filling stages, but the stability of gene expression at different filling stages for these two parents was better than other parents. There was no new gene expression for conditional cytoplasmic main effect at the middle, late, and mature filling stages; conditional endosperm additive interaction effect at the middle filling stage, and conditional maternal additive interaction effect at mature stage for these parents, so those genetic main effects or GE interaction effects detected by unconditional analysis at these filling stages were the sequentially expression of activated genes at the early filling stage(s). The conditional cytoplasmic interaction effects expressed at the middle filling stages also showed that some genetic effects of parents by using the conditional variance analysis could be found earlier than those by unconditional variance analysis. So there was spasmodically expressible phenomenon for some genetic effects of parents in gene expression and it could be effectively detected by the conditional quantitative genetic analysis at all filling stages of rice.

3 Discussion

Most of the quantitative traits of crops are simultaneously controlled by genetic main effects and GE interaction effects besides environmental effects. Although the genetic effects estimated by using the final phenotypic data of quantitative traits could provide the cumulative genetic effects of many quantitative genes expressed at the developmental stages from the initial time to the final time, these results could not clarify the gene expression at one specific period ($t - 1 \rightarrow t$) in the whole developmental period. It is more difficult to study the developmental genetic mechanism of gene onset or offset at the specific period for these traits by using the conventional statistical analysis[14,15]. There was also no information about the developmental genetic mechanism of quantitative traits studied by molecular genetics. The theory of developmental genetics indicated that genes are expressed selectively at different growth periods and there might be that some genes were activated and others are not or being closed at a specific developmental stage. Since the performance of quantitative traits would be controlled by the gene expression, regulation and reaction during growth periods and also be influenced by environments, it is difficult to study the developmental genetics of quantitative traits. It is necessary, therefore, to understand the dynamics of gene expression and variation of genetic effects at different developmental stages for the quantitative traits in different environments by using the new genetic models and statistical approach. The genetic models and statistical approach developed by Zhu[7] could be used for estimating the conditional genetic variance components, predicting the conditional genetic effects, analyzing the developmental quantitative genetics and the gene expression at specific developmental period of quantitative traits. By using these genetic models, Atchley and Zhu[16] have effectively analyzed the developmental behavior in mice and Chen *et al*[17] in cotton for quantitative traits.

Since most of the rice endosperm traits were quantitative traits, the quantitative genes for the rice grain were expressed selectively at different developmental

periods from the zygote, which could also be influenced by environments. Otherwise, rice endosperm quantitative traits were simultaneously controlled by different genetic systems including triploid endosperm nuclear genes, cytoplasmic genes and diploid maternal plant nuclear genes, which were different from the agronomy traits[1-6]. It is helpful to clarify the developmental genetic mechanism of genes and to improve the rice endosperm traits by studying the genetic effects of different genetic systems and the variation of gene expression at different filling stages for these quantitative traits in various environments. By using the unconditional variance or conditional variance analysis, we have studied the endosperm, cytoplasmic and maternal genetic effects of quantitative gene expression for BRW from flowering to one filling time $(0 \rightarrow t)$ or at one specific filling stage $(t-1 \rightarrow t)$ in different environments. The results have revealed some developmental genetic characters for BRW and found that the activation of quantitative genes was gradually carried through the continuing filling time and there was a phenomenon of intercurrent gene expression among the filling stages especially for cytoplasmic genes. The gene expression was more active at the early filling stage (1-7 d after flowering) and the genetic effects were more important than those at other filling stages for the development of BRW. So there could be greater physiological change at the early filling stage of rice. It would be helpful to increase BRW by using the varieties with better genetic effects as parents in rice breeding and by better cultural management of field at this filling stage. The results above have clarified the dynamic expression of quantitative genes and the dynamic change of genetic effects and the net genetic effects expressed at the specific developmental stage(s) for BRW in different environments. It could provide some basis for quantitative trait loci (QTLs) analysis and marker assisted selection (MAS) of rice endosperm quality traits improvement at different developmental stages.

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