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Analysis of Genetic Effects and Genotype × Environment Interaction Effects for Apparent Quality Traits of Indica Rice

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籼稻稻米外观品质性状的遗传主效应和环境互作效应分析

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摘　要：利用不同环境条件下的试验资料分析了遗传主效应和环境互作效应对籼稻5个外观品质性状的影响。结果表明，糙米长、糙米长宽比和糙米长厚比主要受制于遗传主效应，而糙米宽和糙米厚的表现则主要受到环境互作效应的影响。其中糙米长、糙米长宽比和糙米长厚比3个性状的遗传主效应以母体效应为主，而糙米宽和糙米厚的遗传主效应则以细胞质效应为主。在环境互作效应中，所有外观品质性状均以母体互作效应为主。基因的加性效应和加性互作效应是影响糙米长、糙米长宽比和糙米长厚比表现的主要因子，而糙米宽和糙米厚则主要受制于基因的显性效应。遗传效应预测值结果表明，浙协2号A、协青早A、V20A、测早2-2等是改良杂交后代稻米外观品质性状的良好亲本，其中浙协2号A亲本的外观品质性状预测值在两年中的环境互作效应较为一致，不易受到外界条件的影响。

关键词：稻米；外观品质；基因型环境互作；遗传效应；种子直接效应；细胞质效应；母体效应

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Abstract: Genetic and genotype × environment interaction effects were studied for apparent quality traits, including brown rice length (BRL), brown rice width (BRW), brown rice thickness (BRT), ratio of length to width of brown rice (RLW) and ratio of length to thickness of brown rice (RLT), of indica rice in different environments. Results indicated that BRL, RLW and RLT were mainly controlled by genetic effects, and BRW and BRT were mainly influenced by genotype × environment interaction effects. Among the genetic effects, maternal effects were the principal components for BRL, RLW, and RLT, while cytoplasmic effects were the principal components for BRW and BRT. Among the genotype × environment interaction effects, all apparent quality traits were mainly affected by maternal × environment interaction effects. Additive effects and additive by environment interaction effects primarily controlled the performance of rice apparent quality traits, except for BRW and BRT which were affected by dominance effects. The predicted genetic effects indicated that the genetic effects of Zhexie 2A, Xieqingzao A, V20 A, and Cezao 2-2 were better parents for improving rice apparent quality traits of progenies. The predicted genotype × environment interaction effects showed that the genetic stability of Zhexie 2A in different environments were expected.

Key words: apparent quality traits; cytoplasmic effects; genetic effects; genotype × environment interaction; maternal effects; rice; seed direct effects

Agronomic characteristics of crops are affected by genetic effects and environment conditions such as weather, soil, cultivation and management of field. Variation for gene expression will be observed in different environments. Thus, it is necessary to study the genotype × environment interaction effects. Gravois *et al*. found that genotype × year variance was the most important source of variation for head rice yield[1]. Chauhan *et al*. observed that amylose content, milling recovery, water uptake, and kernel elongation of rice had different responses to the environment[2]. Oosato *et al*. have found genotype × environment interactions were significant for palatability trait of rice[3]. Guo *et al*. showed that there was genotype × site interaction effects for head rice recovery of most tested varieties[4]. The results of Shi *et al*. pointed out that milling and cooking quality traits of indica rice were simultaneously controlled by seed, cytoplasmic, maternal plant genes and genotype × environment interaction effects[5,6].

In this paper, the genetic models for quantitative traits of endosperm in cereal crops[7,8] were used to rate the genetic effects of seed, cytoplasm and maternal plant, and the genotype × environment interaction effects, and to predict the breeding value of parents based on apparent quality traits of indica rice.

1 Materials and Methods

Nine indica type cytoplasmic male sterile (CMS) lines, i.e. Zhexie 2A (P_1), Xieqingzao A (P_2), Zhenan 3A (P_3), Gangchao 1A (P_4), Yinchao 1A (P_5), Erjiuqing A (P_6), V20 A (P_7), Zuo 5A (P_8), Zhenshan 97A (P_9), and five indica type restoring lines, i.e. T49 (P_{10}), Cezao 2-2 (P_{11}), 26715 (P_{12}), 102 (P_{13}), 1391 (P_{14}), were used in an incomplete diallel cross (9×5). The CMS and restoring lines were randomly sampled from a reference population and some of them have

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been used in making hybrid rice crosses in China. Seedlings of parents and F_1s were planted in the field of experimental farm at Zhejiang Agricultural University in 1994 and 1995. The seeds were sown on 28 March for 1994 and 3 April for 1995, and single plants of 31-day seedlings were transplanted at spacings of 20 cm × 20 cm. There were 24 plants in each plot with three replications. Seed samples of parents and F_2s in F_1's plants were collected at maturity from eight plants in the middle part of the plot. The F_1 seeds used for analyzing were obtained by crossing CMS lines to restoring lines at flowering during the growing season. Quantitative traits of rice apparent quality, i.e. brown rice length (BRL), brown rice width (BRW), brown rice thickness (BRT), ratio of length to width of brown rice (RLW) and ratio of length to thickness of brown rice (RLT), were measured with three replications for each sample of parents, F_1s and F_2s.

The genetic variances or covariance and genotype × environment interaction variances or covariance components of rice apparent quality traits were estimated by using the genetic models including genetic effects and genotype × environment interaction effects for quantitatively inherited traits of triploid endosperm in cereal crops[7,8], MINQUE (0/1) method[9,10] was used to estimate the genetic variance (V_G) components of seed direct additive variance (V_A), seed direct dominance variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}), maternal dominance variance (V_{Dm}), and genotype × environment interaction variances (V_{GE}) components for seed direct additive by environment interaction variance (V_{AE}), seed direct dominance by environment interaction variance (V_{DE}), cytoplasmic by environment interaction variance (V_{CE}), maternal additive by environment interaction variance (V_{AmE}), maternal dominance by environment interaction variance (V_{DmE}). The genetic convariance components analyzed were covariances between seed direct additive and maternal additive effect ($C_{A \cdot Am}$) or between seed direct dominance and maternal dominance effect ($C_{D \cdot Dm}$), and environment interaction covariances between seed direct additive by environment interaction effect and maternal additive by environment interaction effect ($C_{AE \cdot AmE}$) or between seed direct dominance by environment interaction effect and maternal dominance by environment interaction effect ($C_{DE \cdot DmE}$). Residual variances (V_e) were also estimated. The AUP method was used to predict genetic effects and genotype × environment interaction effects[11].

The Jackknife technique was applied by sampling generation means of entries for estimating the standard errors of estimated variances or covariances and of predicted genetic effects[9,12].

2 Results

The estimates of genetic variances, genotype × environment interaction variances, residual variances and covariances are presented in Table 1. BRL, RLW and RLT were found to be mainly controlled by genetic effects and the genetic variances ($V_G = V_A + V_D + V_C + V_{Am} + V_{Dm}$) accounted for about 57.9%, 85.06% and 77.42% of the total genetic variances ($V_G + V_{GE}$), respectively. But BRW and BRT were mainly influenced by genotype × environment interaction effects, and the genotype × environment interaction variances ($V_{GE} + V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}$) accounted for about 78.10% and 89.65% of total genetic variances, respectively. Therefore, environment interaction effects for BRW and BRT were larger than those of other apparent quality traits.

2.1 Estimation of variances and covariances

Genetic variances were significant for apparent quality traits but not for V_A of BRW and BRT, V_D of BRT, V_C of RLT, and V_{Am} of BRW and BRT (Table 1). Therefore, most of the apparent quality traits were controlled by genetic effects of seed, cytoplasm as well as maternal plant. The maternal variances ($V_{Am} + V_{Dm}$) were 83.55%, 78.53% and 91.53% of genetic variances (V_G) for BRL, RLW and RLT, respectively. Therefore, the maternal effects were the largest genetic effects for BRL, RLW and RLT. The proportion of cytoplasmic variances to total genetic variances (V_C/V_G) were 84.19% for BRW and 82.81% for BRT, so the cytoplasmic effects were the most important genetic effects for these two traits. Cytoplasmic effects were also important for other apparent quality traits except for RLT.

Besides the genetic effects of seed, cytoplasmic and maternal plant genes, the apparent quality traits were also controlled by genotype × environment interaction effects (Table 1). These interaction effects were the main cause of the genetic difference of the traits between the two years (environments). Because maternal interaction variances (V_{AmE} and V_{DmE}) account for about 60.07%—72.01% of V_{GE} for BRL, RLW and RLT, the maternal interaction effects were more important than other environment interaction effects for these traits. Therefore, the expression of maternal plant genes were more easily influenced by environments than that of seed genes. The proportion of seed interaction variances ($V_{AE} + V_{DE}$) to total genetic × environment interaction variances (V_G) were 47.66% for BRW and 46.71% for BRT, so seed inter-

Table 1. Estimation of genetic and genotype × environment interaction variances and covariances of apparent quality traits in indica rice.

Parameter	BRL $/10^{-2}$	BRW $/10^{-3}$	BRT $/10^{-3}$	RLW $/10^{-3}$	RLT $/10^{-2}$
V_A	6.248^{*}	0.000	0.000	20.409^{*}	0.661^{*}
V_D	0.814^{*}	0.770^{*}	0.000	4.463^{*}	0.390^{*}
V_C	0.006^{+}	5.052^{+}	3.961^{*}	6.526^{+}	0.000
V_{Am}	32.811^{*}	0.000	0.000	109.135^{*}	10.451^{*}
V_{Dm}	3.086^{*}	0.179^{*}	0.822^{+}	5.687^{*}	0.906^{+}
$C_{A \cdot Am}$	−2.526	0.000	0.000	−4.218	−0.607
$C_{D \cdot Dm}$	−0.229	0.991^{*}	0.000	1.710^{*}	0.088^{+}
V_{AE}	9.019^{*}	7.695^{*}	17.972^{*}	2.192	0.410^{*}
V_{DE}	0.673^{*}	2.505^{*}	1.389^{*}	1.854^{*}	0.323^{*}
V_{CE}	2.758^{*}	0.000	0.000	4.633^{*}	0.280^{*}
V_{AmE}	17.532^{*}	9.306^{+}	21.753^{*}	14.328^{*}	2.236^{*}
V_{DmE}	1.198^{*}	1.896^{*}	0.336^{*}	2.669^{*}	0.369^{*}
$C_{AE \cdot AmE}$	−14.922	−9.602	−21.343	−11.707	−1.447
$C_{DE \cdot DmE}$	−0.347	−1.327	−0.503	−0.805	−0.179
V_e	2.884^{*}	5.520^{*}	3.450^{*}	8.643^{*}	1.317^{*}

$^{+}$, * and ** indicate significance at 0.10, 0.05, and 0.01 levels, respectively.

action effects were important for these two traits. Cytoplasmic interaction effects were not found for BRW or BRT in this experiment.

Except for the large cytoplasmic effects of BRW and BRT in genetic effects, additive effects or additive by environment interaction effects were the main factors for the apparent quality traits of rice (Table 1). As a result of the large V_{Am} and V_{AmE} for most of apparent quality traits, the maternal additive effects and maternal additive interaction effects were more important than seed additive effects and seed additive interaction effects. Therefore, it is possible to increase apparent quality traits of rice by selecting maternal plants in early generations. But these traits still could be influenced by dominance effects and dominance interaction effects because of the significant V_D, V_{Dm}, V_{DE} and V_{DmE}.

Significant positive dominance covariances ($C_{D \cdot Dm}$) showed that seed dominance effects and maternal dominance effects for BRW, RLW and RLT were in the same direction. There were significant positive correlations between two dominance effects for these traits. $C_{D \cdot Dm}$ of BRL or BRT and $C_{A \cdot Am}$, $C_{AE \cdot AmE}$ or $C_{DE \cdot DmE}$ of all apparent quality traits were not significant in this experiment. No significant relationship was found between these seed and maternal effects, or between seed interaction effects and maternal interaction effects.

Since all residual variances (V_e) of apparent quality traits were significant, the total genetic effects of apparent quality traits were also influenced by sampling errors. It is concluded that apparent quality traits of rice were mainly controlled by genetic effects and /or genotype by environment interaction effects because of the small value of estimated residual variance.

2. 2 Prediction of genetic and genotype by environment interaction effects

Genetic and genotype by environment interaction effects with significant variances in Table 1 were predicted for evaluating breeding values of parents (Table 2). This will help breeders to find the best parent(s) for improving rice apparent quality.

It was shown by the prediction that Zhexie 2 (P_1) could significantly increase BRL of rice by the seed direct additive effects (A) and seed direct additive by environment interaction effects in 1994 ($AE1$) or 1995 ($AE2$), cytoplasmic by environment interaction effects in 1995($CE2$), maternal additive effects (Am) and maternal additive by environment interaction effects in 1995($AmE2$). Since A, $AE1$ and $AE2$ were all positive, they could increase the brown rice length in both years (environments). Positive Am (0. 12$^+$) and $AmE2$ (0. 44$^+$) could significantly increase BRL, but no significance was found for $AmE1$(−0. 32) in this experiment. Therefore, $AmE1$ and $AmE2$ were different in two years or environments and the effects of increasing BRL for maternal plant genes in 1995 were higher than those in 1994. Cytoplasmic effect was significantly positive in 1995 ($CE2$=0. 21*). Since most significant predicted genetic effects and genotype × environment interaction effects were all positive for BRT, RLW, RLT but negative for BRW, P_1 could make the rice shape of progenies more slender. In other parents, most of the predicated merits of Xieqingzao A (P_2), V20A(P_7) and Cezao 2-2(P_{11}) were similar to P_1 and they could be applied in rice breeding to improve the apparent quality of indica rice. The genetic effects and genotype × environment interaction effects of four parents, i. e. Gangchao 1A(P_4), Yinchao 1A(P_5), Erjiuqing A(P_6), and Zhenshan 97A(P_9) could significantly decrease the apparent quality traits except for BRW. Although the predicted genotype × environment interaction effects for Gangchao 2A(P_4) and Yinchao 1A (P_5) were stable in two years except for BRT, they were not suitable parents for improving the rice shape because most of the AE, CE and AmE were significantly negative for apparent quality traits. The differences between $AE1$ and $AE2$, $CE1$ and $CE2$ or $AmE1$ and $AmE2$ for T49(P_{10}) or 1391 (P_{14}) were larger than other parents, so that these two parents were unsuitable for improving rice shape. Zhexie 2A (P_1) and Xieqingzao A (P_2) were parents with the same nuclear genes and different cytoplasms. There were some differences between these two parents for the apparent quality traits. BRW or RLT of P_1 could be significantly decreased by C (−0. 05$^+$) or increased by Am (0. 20$^+$), but those of P_2 could not (C=−0. 06 and Am=0. 25). Some genotype×environment interaction effects were also significantly different, such as $AE1$ of P_1 and P_2 for BRW were −0. 04 and −0. 03*, respectively. So the different cytoplasms would cause changes of some rice quality traits.

3 Discussion

Although the apparent quality traits of rice can be influenced by the environmental effects (E), they were mainly controlled by genetic effects (G) and genotype×environment interaction effects (GE). Because GE is the deviation of genetic effects in different environments, it is different from E which was caused by environments. When there are genotype × environment interaction effects, experiments should be conducted in different years or locations. Genetic models including G and GE for estimating unbiased genetic effects and environment interaction effects[8] would be useful. Because G can be further partitioned into seed direct additive effect(A), seed direct dominance effect (D), cytoplasmic effect (C), maternal additive effect (Am) and maternal dominance effect (Dm), the GE can also be further partitioned into seed direct additive by environment interaction effect (AE), seed direct dominance by environment interaction effect (DE), cytoplasmic by environment interaction effect (CE), maternal additive by environment interaction effect (AmE) and maternal dominance by environment interaction effect (DmE). According to the magnitude of G and GE components, the genetic mechanism can be further illustrated for seed quality traits. In general, if GE had the same direction as G did, selection could significantly improve seed quality traits. Breeders could select breeding materials suitable to different environments for the traits with small GE. If GE was large for seed quality traits, breeders could only obtain breeding materials suitable to specific environment.

Besides the genetic main effects, we found genotype × environment interaction effects were important for the

Table 2. Predicted genetic effects and genetic × environment interaction effects of apparent quality traits of parents in indica rice.

Item	P_1	P_2	P_3	P_4	P_5	P_6	P_7	P_8	P_9	P_{10}	P_{11}	P_{12}	P_{13}	P_{14}
Brown rice length/mm														
A	0.21*	0.19*	0.01	-0.18*	-0.18*	-0.14*	0.20*	0.16*	-0.06^{+}	-0.06^{+}	0.05*	-0.04*	-0.10^{+}	-0.04^{+}
*AE*1	0.23*	0.23*	0.06^{+}	-0.09^{+}	-0.10^{+}	-0.06	0.29*	0.28*	0.03	-0.22^{+}	-0.04	-0.25*	-0.20	-0.16*
*AE*2	0.15^{+}	0.11^{+}	-0.05^{+}	-0.23*	-0.24*	-0.20*	0.08^{+}	0.02	-0.15*	0.10^{+}	0.14^{+}	0.18*	0.01	0.08^{+}
*CE*1	0.06	0.20^{+}	-0.01	-0.06	-0.07	0.13*	0.42*	0.22^{+}	0.12^{+}	-0.16*	-0.42^{+}	-0.15	-0.22	-0.04
*CE*2	0.21*	0.01	-0.03	-0.20^{+}	-0.19	-0.20*	-0.08	-0.07	0.06	0.14*	0.42^{+}	-0.22*	0.30*	-0.16
Am	0.12^{+}	0.21^{+}	-0.04	-0.57^{+}	-0.83^{+}	-0.79^{+}	0.06	0.28	-0.68^{+}	0.49^{+}	0.73^{+}	0.80^{+}	-0.12	0.34^{+}
*AmE*1	-0.32	-0.41^{+}	0.30*	-0.34^{+}	-0.58^{+}	0.55^{+}	-0.33^{+}	-0.01	-0.46^{+}	0.59^{+}	0.79^{+}	0.66^{+}	0.27	0.38^{+}
*AmE*2	0.44^{+}	0.62^{+}	-0.34^{+}	-0.26^{+}	-0.29^{+}	-0.28^{+}	0.39^{+}	0.30^{+}	-0.24	-0.07	-0.03	0.18^{+}	-0.40	-0.03
Brown rice width/mm														
*AE*1	-0.04	-0.03*	0.01	0.06*	0.06*	0.08*	0.02	0.05*	0.04^{+}	0.06*	-0.04	-0.11*	-0.07^{+}	-0.07*
*AE*2	0.15^{+}	-0.02^{+}	0.00	-0.00	-0.02	-0.02	-0.04*	-0.02	0.04*	-0.01	0.05^{+}	0.01	0.04^{+}	0.00*
C	-0.05^{+}	-0.06	0.09	0.07	0.07	0.07^{+}	0.07	0.04	0.09	-0.10^{+}	0.06*	0.02	-0.25	-0.12^{+}
*AmE*1	-0.06	-0.18^{+}	-0.04	0.09	-0.02	-0.08^{+}	0.01	0.03^{+}	0.06	-0.05	0.01	0.09^{+}	0.08	0.06*
*AmE*2	-0.05^{+}	0.07^{+}	0.07	-0.04	0.08	0.17^{+}	0.00	0.09	0.06	0.09^{+}	-0.14	-0.26^{+}	-0.01	-0.13^{+}
Brown rice thickness/mm														
*AE*1	0.03^{+}	0.04	0.01	0.05*	0.07^{+}	0.08*	0.06*	0.08^{+}	0.06^{+}	-0.02	-0.03^{+}	-0.21^{+}	-0.05	-0.18*
*AE*2	0.01	0.01	-0.04^{+}	-0.06*	-0.09^{+}	-0.03^{+}	-0.01	-0.02	-0.04^{+}	-0.02	-0.00	0.17^{+}	0.01^{+}	0.11*
C	0.10^{+}	0.11^{+}	-0.06*	-0.07	-0.09	0.08^{+}	0.14^{+}	0.08	0.04	-0.07	-0.04	-0.08	-0.11^{+}	-0.03
*AmE*1	-0.12	-0.07	-0.12^{+}	-0.07^{+}	-0.04	-0.20^{+}	-0.15^{+}	0.02	-0.08*	0.11^{+}	0.13^{+}	0.23	0.14	0.22^{+}
*AmE*2	0.02	-0.02	0.14^{+}	0.06^{+}	0.08^{+}	0.09^{+}	0.21^{+}	0.24^{+}	0.06^{+}	-0.12^{+}	-0.11	-0.23^{+}	-0.17	-0.25^{+}
Ratio of length to width of brown rice														
A	0.12^{+}	0.12*	-0.01	-0.11*	-0.10*	-0.10*	0.09^{+}	0.04^{+}	-0.08*	-0.05^{+}	0.01	0.06^{+}	-0.02	0.03*
*CE*1	0.08**	0.10^{+}	-0.03	-0.06*	-0.04	-0.07*	0.14*	0.03	0.09*	-0.09*	-0.12*	-0.08^{+}	0.00	0.05*
*CE*2	0.05^{+}	0.02	-0.04	-0.10*	-0.11*	-0.02	-0.06*	0.01	-0.12**	0.15*	0.08*	-0.04	0.20*	-0.02
Am	0.18^{+}	0.21^{+}	-0.06	-0.29^{+}	-0.41^{+}	-0.43^{+}	0.01	-0.03	-0.40^{+}	0.16^{+}	0.46^{+}	0.54^{+}	-0.14^{+}	0.19^{+}
*AmE*1	-0.04	0.03	0.10^{+}	-0.14^{+}	-0.13^{+}	-0.09	-0.08^{+}	-0.03*	-0.15^{+}	0.18^{+}	0.18^{+}	0.12^{+}	0.01	0.04
*AmE*2	0.15^{+}	0.10	-0.13^{+}	-0.04^{+}	-0.12^{+}	-0.18^{+}	0.09^{+}	0.01	-0.09	-0.08^{+}	0.10^{+}	0.21^{+}	-0.10^{+}	0.08^{+}
Ratio of length to thickness of brown rice														
A	0.06*	0.05*	0.02**	-0.06*	-0.06*	-0.07*	0.05*	0.03*	-0.04*	-0.01	0.03*	0.01	-0.02	0.01
*AE*1	0.04**	0.03**	0.01	-0.03	-0.05*	-0.05*	0.03^{+}	0.02	-0.02	-0.03	-0.00	0.05	-0.02	0.04^{+}
*AE*2	0.02	0.02	0.01	-0.02	-0.01	-0.03*	0.02^{+}	0.02	-0.01*	0.03	0.03*	-0.04^{+}	-0.00	-0.02
*CE*1	0.02*	0.05	-0.01	-0.02	-0.06	-0.05	0.08	0.05	-0.03	0.04	-0.07	0.01	-0.02	0.01
*CE*2	-0.01	-0.06	0.05^{+}	-0.03	0.02	-0.05	-0.08	-0.08	0.07*	0.06	0.11	-0.07^{+}	0.12	-0.05
Am	0.20^{+}	0.25	-0.04	-0.31^{+}	-0.53^{+}	-0.33^{+}	-0.04	-0.15^{+}	-0.36^{+}	0.28^{+}	0.38^{+}	0.44^{+}	-0.02	0.24
*AmE*1	-0.00	-0.07	0.23*	-0.08	-0.20^{+}	-0.06	0.01	-0.02^{+}	-0.12	0.12^{+}	0.19	0.04^{+}	-0.01	-0.03
*AmE*2	0.15^{+}	0.25^{+}	-0.27^{+}	-0.15^{+}	-0.18^{+}	-0.18^{+}	-0.04	-0.10^{+}	-0.15^{+}	0.09	0.09^{+}	0.28^{+}	-0.01	0.20^{+}

$^{+}$, * and ** were significant at 0.10, 0.05 and 0.01 levels, respectively. *A*=Seed direct additive effects; *C*=Cytoplasmic genetic effects; *Am*=Maternal plant additive effects; *AE*1 and *AE*2=Seed direct additive by environment interaction effects in 1994 and 1995; *CE*1 and *CE*2=Cytoplasmic by environment interaction effects in 1994 and 1995; and *AmE*1 and *AmE*2=Maternal plant additive by environment interaction effects in 1994 and 1995, respectively.

apparent quality traits of indica rice. It could not be negligent for GE especially for maternal by environment interaction effects. For BRW and BRT, which were mainly influenced by GE, breeders should consider the influences of GE for improving these quality traits. According to the predicted breeding value of G and GE in different environments (years) for parents, the breeders could select better parent(s) such as Zhexie 2A to improve the selection advance for quality traits. The genetic models and statistical analysis methods used in this experiment only need three generations (parents, F_1 and F_2) in several environments, so it is also useful for other cereal crops for studying quantitative seed quality traits.

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