Genetic Analysis on Gene Effects and GE Interaction Effects for Kernel Nutrient Quality Traits of Upland Cotton

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Abstract　By a genetic model with GE interaction for diploid seeds, gene effects and GE interaction effects for content and index of oil, protein, and lysine of cotton kernel were studied in a mating design with six crosses from five parents. For each cross eight generations (P, F_1, RF_1, BC_i, BC_j, RBC_i and RBC_j) were obtained from two plots of a randomized complete block design in three years from 1991 – 1993. Both gene effects and GE interaction effects were detected for six traits studied. Variances of cytoplasmic and maternal effects as well as their interaction effects were usually larger than that of seed direct effects and their interaction. Heritabilities for gene effects and GE interaction effects were estimated, and h_G^2 was larger than h_{GE}^2 for traits of nutrient index and protein content. Cytoplasmic and maternal heritabilities tended to be larger than direct heritability, so that maternal plant selection could be more efficient than single seed selection. Five parent were evaluated by their gene main effects and GE interaction effects. It was showed that GL-5 was a promising material for improving seed oil and protein. Significantly negative heterosis was discovered for direct and maternal gene effects. Correlation between oil and protein content was negative for r_p, r_{Am}, and r_{CE}, but positive for r_A and r_{AE}. Lysine content had positive correlation with protein content for maternal dominance effects and cytoplasmic by environment interaction effects, but negative correlation for additive by environment interaction effects. Positive correlation was also observed among traits of nutrient index for phenotypic and some of gene effects and GE interaction effects. Partitioning the total response to selection was discussed. Methods of estimating response components and their application in breeding were presented.

Key words　Upland cotton (*Gossypium hirsutum L.*)　kernel nutrient quality variance and covariance　heritability　correlation coefficients GE interaction

1　Introduction

Cotton seeds, which have high content of oil and protein, are an important nutrient resource

for food and forage. Seeds are a new generation resulted from fertilization of female and male gametes, but most of seed nutrients are provided by maternal plants on which seeds bear. Therefore, seed traits may be simultaneously controlled by seed nuclear genes, cytoplasm genes, and maternal plant nuclear genes. Seed direct effects and maternal effects have been detected for seed quantitative traits in some crops such as rape seed (Pleines and Friedt, 1989), and barley (Kaeppler and Rasmusson, 1991). In cotton, maternal effects were found in oil content and seed index (Kohel, 1980, Dani and Kohel, 1989).

Zhu and Weir (1994a, b) proposed genetic models for analyzing cytoplasmic effects, maternal additive and dominance effects as well as direct additive and dominance effects for diploid seeds and triploid endosperm. Several studies have been conducted by using these models to quantitatively analyze maternal effects (Wu *et al*, 1995, Shi *et al*, 1996).

Since gene expressions are evolved under the influence of environments, genes may respond differently to specific environment. Therefore, direct, maternal and cytoplasmic effects may have interaction with environments. But so far, no study has been conducted to partition the genetic variation into components due to seed direct effects, cytoplasmic effects and maternal gene effects as well as genotype × environment interaction effects. Recently Zhu and Weir's models have been extended by including genotype × environment interaction (Zhu, 1994, 1996), so that gene effects and GE interaction effects can be evaluated for seed quantitative traits.

In this study, gene effects and GE interaction effects were analyzed for six kernel nutrient quality traits of Upland cotton (*Gossypium hirsutum* L.). Variance and covariance components and heritabilities were estimated. Predicted genetic effects and GE interaction effects were compared for five parental lines. Correlation among kernel nutrient quality traits was calculated for genetic effects and GE interaction effects.

2   Materials and Analysis Methods

This experiment was conducted in Zhejiang Agricultural University during the years 1990 – 1993. Five parents of Upland cotton were employed: P_1 (ZHONG7), P_2 (HG-H-12), P_3 (PD0111), P_4(PD0458) and P_5(GL-5). In 1990, these five parents were mated to produce six F_1 crosses: $(P_1 \times P_3)$, $(P_1 \times P_4)$, $(P_2 \times P_3)$, $(P_2 \times P_4)$, $(P_3 \times P_5)$ and $(P_4 \times P_5)$. In the following years from 1991 to 1993, these five parental lines and six F_1 s were used to produced eight generations (P, $F_1 = P_i \times P_j$, $RF_1 = P_j \times P_i$, F_2, $BC_i = F_1 \times P_i$, $BC_j = F_1 \times P_j$, $RBC_i = P_i \times F_1$, $RBC_j = P_j \times F_1$) for each cross. However there were several genetic entries missing for some crosses. Each generation was assigned in a plot ($1.33 \times 2.5m^2$) by a randomized complete block design with two replications. Kernel oil content (Oil%), oil index (OilID= oil weight of 100 seeds, g), protein content (Pro%), protein index (ProID= protein weight of 100 Seeds, g), lysine content (Lys%) and lysine index (LysID= lysine weight of 100 Seeds, g) were measured by sampling seeds at random from each plot.

The genetic model for diploid seeds with genotype × environment interaction (Zhu, 1994, 1996) was employed to study the inheritance of seed kernel nutrient quality characters. The

MINQUE (0/1) method (Zhu and Weir, 1994a) was used to obtain the unbiased estimates of variance and covariance components for each trait. After obtaining estimates of variances and co-variances, heritabilities were then calculated (Zhu, 1996). By the same procedure of variance estimation, covariances among different traits were also estimated (Zhu and Weir, 1994a). Correlation coefficients were calculated for genetic and GE interaction effects as well as for phenotypic effects. An adjusted unbiased prediction (AUP) method (Zhu, 1993, Zhu and Weir, 1996) was employed to predict genetic effects and genotype × environment interaction effects. With the Jack-knife procedure by sampling genetic entry (Zhu and Weir, 1994a), standard errors of estimates and predicted values were obtained for significance test by a *t*-test. All the data were analyzed on a PC with C programs.

3 Results and Analysis

3.1 Phenotypic mean of kernel nutrient quality traits of parents and their hybrids

The phenotypic means of six kernel nutrient quality traits of parents and their hybrids based on the average of six crosses are presented in Fig 1.
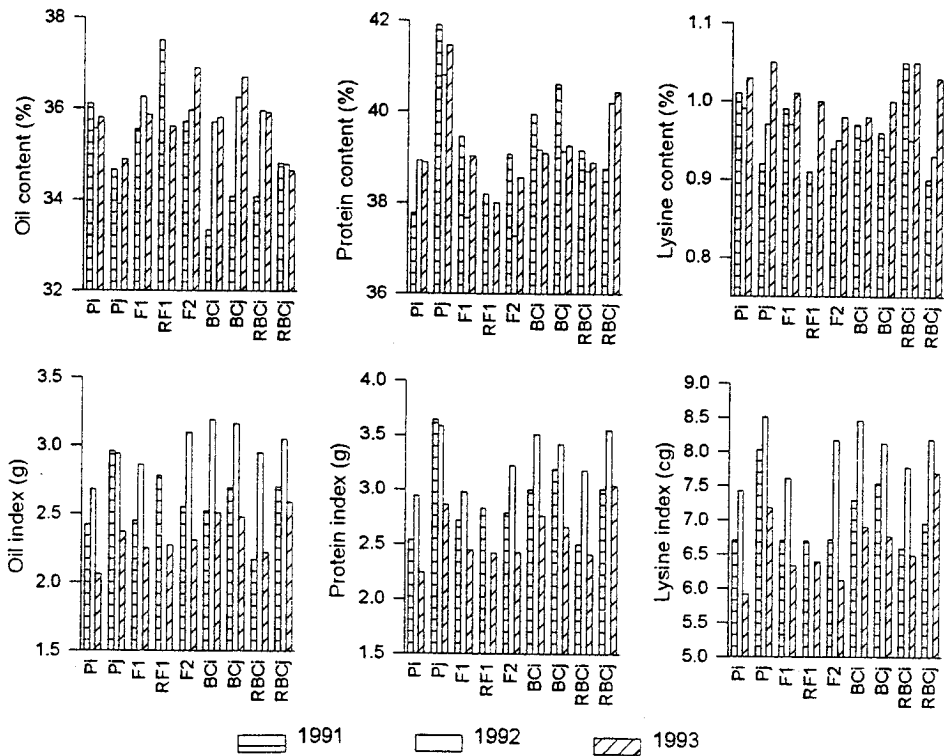

Fig 1 Phenotypic means of six kernel nutrient quality traits of parents and their hybrids based on the average of six crosses

For Pro% , the phenotypic mean of F_2 kernel was lower than that of F_1 kernel which had lower Pro% than their parents, it suggested that both negative direct heterosis and negative maternal heterosis existed. Genotype × environment interaction might exist because the phenotypic means fluctuate among three years. The phenotypic means of Oil ID, Pro ID and Lys ID of F_2 kernel were higher than that of F_1 kernel only in 1992 but not in other two years, whith indicting

the existing of maternal dominance × environment interaction. The presence of maternal effects could be insinuated by the fact that phenotypic mean of RBC_i was similar to their maternal parent P_i and so was that of RBC_j. Since this kind of tendency changed a bit in different years, it suggested the existence of maternal × environment interaction effects.

3.2 Estimation of genetic variance and covariance components

Estimates of variance and covariance components for genetic effects and genotype × environment interaction effects are listed in Table 1 for six kernel nutrient quality traits.

For Oil% maternal additive variance (V_{Am}) was the major component of total genetic variance, followed by direct additive (V_A) and dominance (V_D) variances. Both direct genetic variances (V_A & V_D), cytoplasmic variance (V_C) and maternal genetic variances (V_{Am} & V_{Dm}) were significant for Pro%, positive covariances of additive effects ($C_{A.Am}$) and dominance effects ($C_{D.Dm}$) were also detected. Cytoplasmic effects was found to be the most important contribution to the genetic variation of Lys%. There were significant V_{AE} and V_{CE} for these three nutrient content, but only V_{DmE} for Oil% and V_{DE} for Lys% were found to be significant. The existence of significant additive covariance ($C_{A.Am}$) for Pro% and Pro ID implied that there had strong positive correlation between direct additive effects and maternal additive effects. This relationship was useful for improving seed protein content and protein index.

Table 1　　Estimated genetic variance and covariance components for kernel nutrient traits in Upland cotton

Parameter	Oil%	Pro%	Lys%	Oil ID	Pro ID	Lys ID
V_A	1.485**	1.586**	0.000	0.053**	0.068**	0.289**
V_D	0.426**	0.478**	0.000	0.000	0.000	0.000
V_C	0.000	1.692**	0.010**	0.000	0.000	1.078**
V_{Am}	3.154**	1.881**	0.000	0.111**	0.274**	1.408**
V_{Dm}	0.000	0.777**	0.001**	0.000	0.000	0.000
$C_{A.Am}$	−1.083	0.673**	0.000	0.016	0.053*	0.227
$C_{D.Dm}$	0.000	0.170*	0.000	0.000	0.000	0.000
V_{AE}	1.227**	1.702**	0.004**	0.000	0.095**	0.419**
V_{DE}	0.000	0.000	0.002**	0.025**	0.000	0.000
V_{CE}	1.908**	2.688**	0.006**	0.107**	0.118**	1.704**
V_{AmE}	0.000	0.000	0.000	0.000	0.000	0.000
V_{DmE}	1.977**	0.000	0.000	0.071**	0.061**	0.363**
$C_{AE.AmE}$	0.000	0.000	0.000	0.000	0.000	0.000
$C_{DE.DmE}$	0.000	0.000	0.000	−0.004	0.000	0.000
V_e	0.956**	0.591**	0.002**	0.032**	0.048**	0.361**

* Sgnificant at P<0.05, ** Significant at P<0.01.

V_A = additive variance, V_D = dominance variance, V_C = cytoplasm variance, V_{Am} = maternal additive variance, V_{Dm} = maternal dominance variance, $V_{A.Am}$ = additive covariance, $V_{D.Dm}$ = dominance covariance, V_{AE} = additive × environment interaction variance, V_{DE} = dominance × environment interaction variance, V_{CE} = cytoplasm × environment interaction variance, V_{AmE} = maternal additive × environment interaction variance, V_{Dm} = maternal dominance × environment interaction variance, $C_{AE.AmE}$ = additive × environment interaction covariance, $C_{DE.DmE}$ = dominance × environment interaction covariance, V_e = residual variance.

The inheritance of nutrient index (Oil ID, Pro ID, or Lsy ID) was a little diffferent. Their maternal additive effects (Am) and cytoplasm × environment interaction effects (CE) were the

major components followed by maternal dominance × environment interaction effects (DmE) and direct additive effects (A). Significant V_{AE} was detected for Pro ID and Lys ID, and so did V_{DE} for Oil ID. Cytoplasmic effects (C) was also important for Lys ID.

Additionally, error variance components were all significant for traits studied. It showed that errors existed obviously in experimental process such as planting condition, sampling and measuring methods.

3.3 Heritability Analysis

Since analysis of variances and covariances revealed the existence of genotype × environment interaction, the general and interaction heritabilities are listed in Table 2 for kernel nutrient quality traits studied.

The total general heritability ($\hat{h}_G^2 = \hat{h}_O^2 + \hat{h}_C^2 + \hat{h}_M^2$) was higher than the total interaction heritability ($\hat{h}_{GE}^2 = \hat{h}_{OE}^2 + \hat{h}_{CE}^2 + \hat{h}_{ME}^2$) for Pro% ($\hat{h}_G^2 = 0.497 > \hat{h}_{GE}^2 = 0.336$), Oil ID ($\hat{h}_G^2 = 0.464 > \hat{h}_{GE}^2 = 0.254$), Pro ID ($\hat{h}_G^2 = 0.583 > \hat{h}_{GE}^2 = 0.276$) and Lys ID($\hat{h}_G^2 = 0.531 > \hat{h}_{GE}^2 = 0.349$), respectively. It was suggested that selection improvement could be expected across different environments for these traits. Oil% ($\hat{h}_G^2 = 0.276 < \hat{h}_{GE}^2 = 0.350$) and Lys% ($\hat{h}_G^2 = 0.392 < \hat{h}_{GE}^2 = 0.414$) had lower value of the general heritability than that of the interaction heritability. Therefore, more difficulties were expected in improving Oil% and Lys% over several environments.

For improving seed quantitative traits, selection can be applied based on measuring individual seeds (single seed selection) or a sample of seeds from maternal plant (maternal plant selection). For Oil%, Pro% and Oil ID, maternal plant selection was more efficient than single seed selection, because the major component of h_G^2 was h_M^2 for Oil% and Oil ID and was ($h_M^2 + h_C^2$) for Pro%. This might not be true for Pro ID and Lys ID, since significance of h_M^2 or h_C^2 was not detected for these two traits. As h_{CE}^2 was the main components of h_{GE}^2 for all the traits studied, selection based on cytoplasm interaction effects could result in genetic gain in specific environment.

Table 2   Heritabilities of kernel nutrient traits in Upland cotton

Heretability	Oil%	Pro%	Lys%	Oil ID	Pro ID	Lys ID
h_O^2	0.045	0.173**	0.000	0.163**	0.158**	0.085**
h_C^2	0.000	0.129**	0.392	0.000	0.000	0.177
h_M^2	0.231**	0.195**	0.000	0.301**	0.425	0.269
h_{OE}^2	0.137**	0.130**	0.167**	0.000	0.123**	0.069**
h_{CE}^2	0.213**	0.206**	0.247**	0.254**	0.153**	0.280**
h_{ME}^2	0.000	0.000	0.000	0.000	0.000	0.000

** Significant at P<0.01.

h_O^2 = direct heritability, h_C^2 = cytoplasm heritability, h_M^2 = maternal heritability,

h_{OE}^2 = direct × environment interaction heritability, h_{CE}^2 = cytoplasm × environment interaction heritability, h_{ME}^2 = maternal × environment interaction heritability.

3.4 Prediction of gene effects and genotype × environment interaction effects

The genetic merit of parents can be evaluated based on both gene main effects and genotype × environment interaction effects. The predicted A & AE effects, and C & CE effects of the five parents are presented in Fig 2,3.
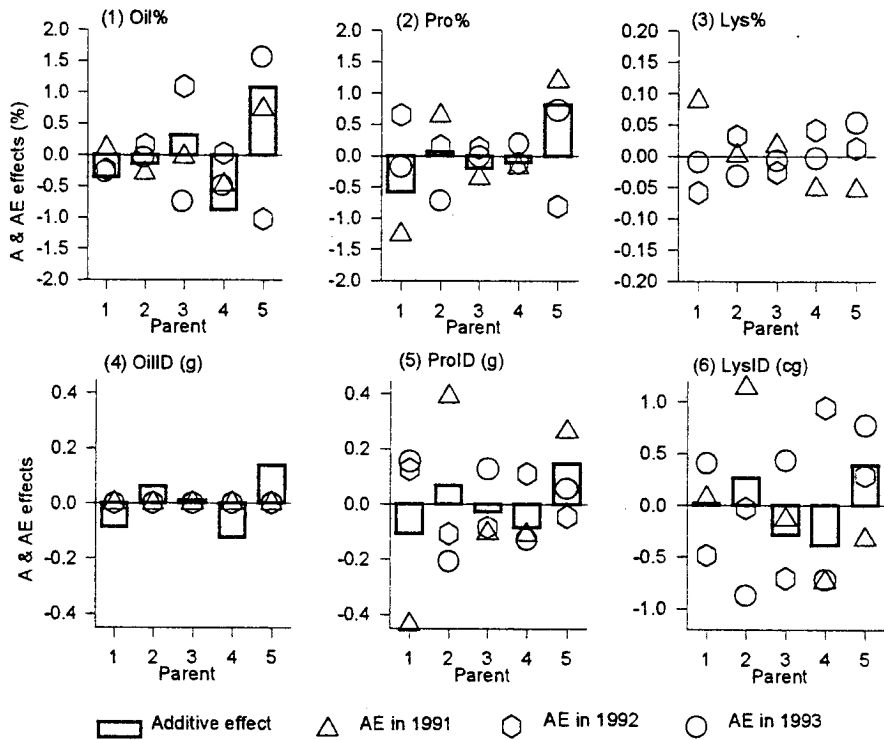
Fig 2   Additive effects and additive × environment interaction effects in three years for six kernel nutrient quality traits of parents.

There was no additive main effects for Lys% or additive × environment interaction effects for Oil ID. For other four traits, both A and AE effects were existed. P_5(GL-5) had the highest A effect and relatively high AE effects in the years 1991 and 1993 for Oil%, Pro% and Pro ID. P_5 also had the highest A effects for Oil ID and Lys ID. Therefore A & AE effects of P_5 could be utilized for improving nutrient traits of oil and protein, especially in environments like the years 1991 and 1993.

The main and interaction effects of cytoplasm are important criteria for selecting maternal parent. Since there were no cytoplasm main effects for Oil% and Oil ID, the expected good maternal parent for improving oil trait was P_5 in environment like the year 1991 but P_2(HG-H-12) in environments like the years 1992 and 1993. Although both P_2 and P_5 had high A effects for Pro% and fluctuating AE effects for Pro% and Pro ID, P_5 was overall better than P_2 for serving as a maternal parent in protein selection. P_1(ZHONG-7) could be utilized as maternal parent for improving lysine since it had the highest values of A & AE in the year 1991 for Lys% and Lys ID. P_5 was the second candidate but P_2 was the worst one for lysine selection.

Maternal additive effects were the most important component of genetic effects for five traits in this study, while maternal additive × environment interaction effects were not detectd for all the traits studied. It implied that gene expression for maternal additive effects was not influenced by environments. In this study, P_5 had the highest values of maternal additive effects for Pro% (1.088 **), Oil ID (0.214 *), Pro ID (0.450 **) and Lys ID (1.010 **), but the lowest value
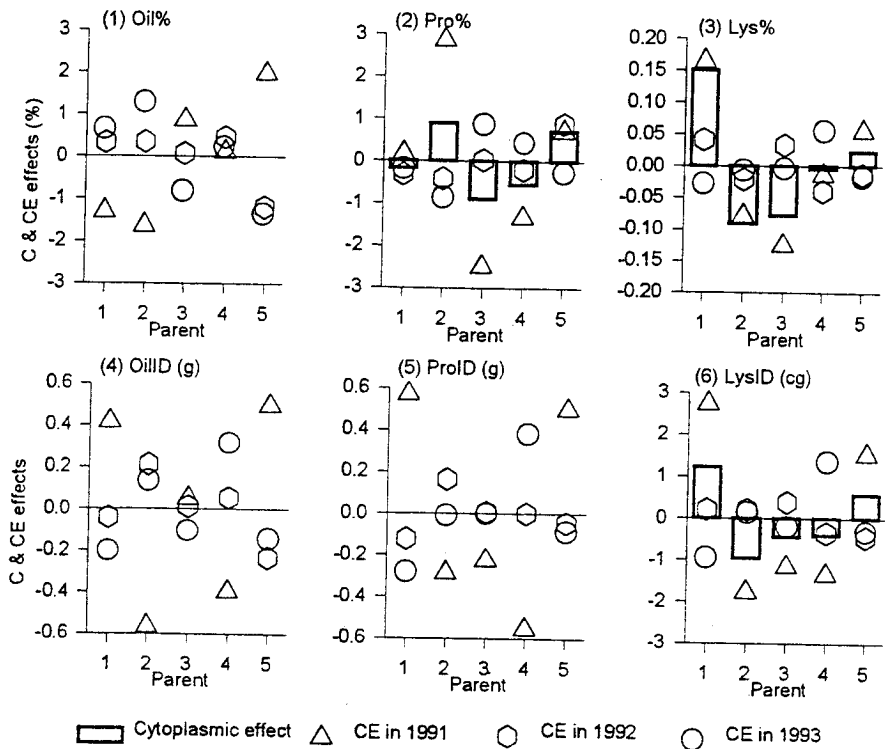
Fig 3　Cytoplasmic effects and cytoplasmic × environment interaction effects in three years for six kernel nutrient quality traits of parents.

for Oil% (-1.374^{**}). It suggested that P_5 can be used in breeding to increase protein content and index for oil, protein and lysine.

The statistic $\hat{\Delta} = \sum_{i=1}^{n} \hat{D}_{ii} / \sqrt{n\hat{\sigma}_D^2}$ can be used to judge direct heterosis (Zhu *et al*, 1993).

Similarly, $\hat{\Delta}_M = - \sum_{i=1}^{n} \hat{D}m_{ii} / \sqrt{n\hat{\sigma}_{Dm}^2}$, $\hat{\Delta}_{QE} = - \sum_{i=1}^{n} \hat{DE}_{ii} / \sqrt{n\hat{\sigma}_{DE}^2}$, and $\hat{\Delta}_{ME} = - \sum_{i=1}^{n} \hat{D}mE_{ii} / \sqrt{n\hat{\sigma}_{DmE}^2}$ can be used to certify maternal heterosis, direct interaction heterosis, and maternal interaction heterosis, respectively. In this study, Pro% had negative direct heterosis($\hat{\Delta} = -1.411^{**}$) and negative maternal heterosis ($\hat{\Delta}_M = -1.355^{**}$). This elucidated the reason of $F_2 < F_1 < MP$ for phenotypic means of protein content as showed in Fig 1. Other Δ's were not significant for the kernel nutrient traits studied.

3.5　Correlation analysis

The estimates of correlation coefficients among content and index of kernel nutrient traits are listed in Table 3 for phenotypic correlation and correlation for différent gene main effects and genotype × environment interaction effects.

Between oil and protein content, very weak negative r_p was observed, which might mainly due to the negative r_{Am}, r_{CE} and r_e. Direct additive effects had positive correlation between oil and protein content ($\hat{r}_A = 0.278^{**}$). Although there was no significant phenotypic correlation between oil and lysine content, negative correlation coefficients was observed ($\hat{r}_{CE} = -0.115^*$ and $\hat{r}_e = -0.131^{**}$). For protein and lysine content, there were both positive correlation ($\hat{r}_{Dm} = $

0.281^* and $\hat{r}_{CE} = 0.188^{**}$) and negative correlation ($\hat{r}_{AE} = -0.238^*$ and $\hat{r}_e = -0.173^{**}$) resulting in negligible phenotypic correlation.

There was highly significant phenotypic correlation among traits of kernel nutrient index. The contributions to positive r_p were mainly due to the direct and maternal additive effects (A and Am) as well as the interaction effects (CE and DmE). Positive residual correlation was also considerable.

Table 3   Correlation coefficients for kernel nutrient traits in Upland cotton

Paramete	Oil% & Pro%	Oil% & Lys%	Pro% & Lys%	Oil ID & Pro ID	OilID & Lys ID	Pro ID & Lys ID
r_p	-0.130^{**}	-0.059	0.063^*	0.359^{**}	0.315^{**}	0.357^{**}
r_A	0.278^{**}	0.000	0.000	0.155^{**}	0.150^{**}	0.127^{**}
r_D	-0.093^*	0.000	0.000	0.000	0.000	0.000
r_C	0.000	0.000	-0.095^*	0.000	0.000	0.000
r_{Am}	-0.327^{**}	0.000	0.000	0.453^{**}	0.429^{**}	0.529^{**}
r_{Dm}	0.000	0.000	0.281^{**}	0.000	0.000	0.000
r_{AE}	0.309^{**}	0.046	-0.238^{**}	0.000	0.000	-0.100^*
r_{DE}	0.000	0.000	0.000	0.000	0.000	0.000
r_{CE}	-0.266^{**}	-0.115^*	0.188^{**}	0.415^{**}	0.502^{**}	0.517^{**}
r_{AmE}	0.000	0.000	0.000	0.000	0.000	0.000
r_{DmE}	0.000	0.000	0.000	0.361^{**}	0.371^{**}	0.144^{**}
r_e	-0.415^{**}	-0.132^{**}	-0.173^{**}	0.841^{**}	0.752^{**}	0.797^{**}

* Significant at $P<0.05$, ** Significant at $P<0.01$.

r_A = additive correlation, r_D = dominance correlation, r_C = cytoplasm correlation, r_{Am} = maternal additive correlation, r_{Dm} = maternal dominance correlation, r_{AE} = additive × environment interaction correlation, r_{DE} = dominance × environment interaction correlation, r_{CE} = cytoplasm × environment interacction correlation, r_{AmE} = maternal additive × environment interaction correlation, r_{DmE} = maternal dominance × environment interaction correlation, r_e = residual variance.

4   Discussion

As an important resource of oil and protein, increasing nutrient in cotton seeds has been paid remarkable attention. In order to improve seed kernel nutrient, which has become an important objective of cotton breeding, profound understanding of genetic basis of seed traits is necessary. Because the growth and development of seeds depend on the maternal plants which provide most of nutrients and physiological substances, seed traits may be controlled by three genetic systems (seed nuclear genes, nuclear and cytoplasm genes of maternal plant). However previously developed methods such as diallel cross method and generation mean method can not simultaneously analyze component effects of these three genetic systems. Comparison of generation mean and differences of reciprocal crosses can only obtain a simple certainty for the existence of maternal and cytoplasmic effects, not on the quantitative basis. Foolad and Jones (1992) proposed a method that can estimate cytoplasmic and maternal effects as well as seed effects, but this method needs of 18

generations and measuring single seeds. New methods (Zhu and Weir 1994a , b) have been proposed for unbiased estimation of variance components for direct additive and dominance effects, cytoplasmic effects, maternal additive and dominance effects by only using several generation means. These methods have been extended to estimate all the variance components of genotype × environment interaction for seed quantitative traits (Zhu 1994, 1996). Covariances and correlation coefficients were also estimable among seed traits. At the same time, unbiased prediction of genetic and genotype × environment interaction effects were obtainalbe (Zhu, and Weir, 1994a, b, Zhu, 1994, 1996).

In kernel nutrient quality traits of Upland cotton, previous studies failed to analyze direct effects, maternal effects and GE interaction effects (Ji and Zhu 1988; Malm, 1979; Dani, 1989a, 1989b; Dani and Kohel, 1989). In this study maternal effects and maternal × environment interaction effects were detected to a certain extent in six traits studied. Maternal effects are the important genetic factors for most of the seed kernel nutrient quality traits, and also are the main cause of differences between reciprocal crosses. This may due to the fact that maternal plants furnish the nutrients for seed and also provide environment and substratum in which seeds are developed (Choudhry, 1982; Meredith, 1984). In addition, maternal plants provide much RNA (Choudhry, 1982) and cytoplasmic gene which control photosynthesis and respiration. The mechanism of maternal effects might involve a series of biochemical and physiological reaction.

In plant and animal breeding, heritability is usually used in predicting response to selection ($R = ih^2 \sqrt{V_p}$ with intensity of selection i). Since the total heritability has components due to gene main effects (general heritability h_G^2) and gene by environment interaction effects (interaction heritability h_{GE}^2), the total response to selection also consists of general response (R_G) and interaction response (R_{GE}) which can be further partitioned into different components for seed quantitative traits,

$$
\begin{aligned}
R &= R_G + R_{GE} \\
&= (R_O + R_C + R_M) + (R_{OE} + R_{CE} + R_{ME}) \\
&= (ih_O^2 \sqrt{V_p} + ih_C^2 \sqrt{V_p} + ih_M^2 \sqrt{V_p}) + (ih_{CE}^2 \sqrt{V_p} + ih_{CE}^2 \sqrt{V_p} + ih_{ME}^2 \sqrt{V_p}),
\end{aligned}
$$

Where R_O = direct general response, R_C = cytoplasmic general response, R_M = maternal general response, R_{OE} = direct interaction response, R_{CE} = cytoplasmic interaction response, R_{ME} = maternal interaction response.

When R_G is much larger than R_{GE}, selection in one environment may gain response in other environments. If R_G is much smaller than R_{CE}, selection in one environment is only adaptable to that specific environment. In this study, response to selection was calculated with $i = 2.06$ for 5% proportion selected. R_G is very close to R_{GE} for content of oil, protein, and lysine, but considerably larger for index traits. Since seed quantitative traits may controlled by different gene systems, selection based on direct additive effects, cytoplasmic effects or maternal additive effects is not equally efficient for every trait. Considering protein content as an example ($\hat{R}_O = 1.276^{**}$, $\hat{R}_C = 0.956^{**}$, $\hat{R}_M = 1.443^{**}$), selecting maternal plant for both cytoplasmic and maternal ad-

ditive effects $(R_C + R_M)$ is more efficient than single seed selection. This study revealed that maternal plant selection, which is also easily conducted, could result in more response than single seed selection in improving kernel nutrient quality traits.

5 Acknowledgments

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