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Genetic analysis for developmental behavior of some seed quality traits in Upland cotton (*Gossypum hirsutum* L.)

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Summary

Analysis of genetic main effects and *GE* interaction effects for oil index (OID), protein index (PID), and lysine index (LID) of Upland cotton (*Gossypium hirsutum* L.) were conducted for 2-yr diallel cross data by using a seed genetic model. Analysis approaches of unconditional and conditional variances and correlations were employed to evaluate developmental behavior of cottonseed. The phenotypic means were relatively larger for F_2 generation than F_1 generation, and larger for all generations in 1993 than in 1994. The results of variance analysis indicated that OID, PID, and LID were simultaneously controlled by seed nuclear, cytoplasm, and maternal nuclear effects. Genetic effects due to maternal nuclear were relatively more important at whole developmental period. *GE* interaction effects were the main contribution to the total variation of OID at first two stages, of PID at the forth stage, and of LID across all four stages, respectively. Not only the phenotypic correlation coefficients but also the coefficients due to different genetic effects varied significantly between traits themselves at various stages. Different genetic effects caused the variation of the correlationship between traits themselves at various stages.

Introduction

The development of the cottonseed is not only an orderly expression process of seed gene in specific physiological and outside environments with the influence of maternal plant, but also the dynamic procedure of biochemistry substances in embryo, such as nucleic acid, protein, fat, starch and so on. Therefore, seed traits may be simultaneously controlled by seed nuclear genes, cytoplasm genes, and maternal nuclear genes. Up to now, there have been lots of reports about developmental physiology (Grindley, 1950; Elmore & Leffler, 1976; Zhou et al., 1991) and genetics (Khattab et al., 1977; Chen et al., 1986; Ramos, 1985; Singh, 1985; Dani & Kohel, 1989; Dani, 1991) of cottonseed and its quality traits. Genetic behavior of cottonseed quality properties was frequently analyzed through estimating genetic variances, genetic effects, heretability, or combining ability with corresponding mating design and established genetic models (Shaver & Dilday, 1982; Ji & Zhu, 1988). Zhu & Weir (1994a,b) proposed genetic models for analyzing cytoplasm 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). But, there were few reports about genetic analysis for developmental behavior of quality traits at various stages, which would be useful to profound understanding of the inheritance during development for plant breeding.

There are now two common methods used for genetic analysis of developmental behavior: one by analyzing the phenotypic value at various periods; the other by using the difference ($y_{(d)} = y_{(t)} - y_{(t-1)}$) between two phenotypic values at time t and t–1. For developmental traits, genetic effect ($G_{(t)}$) measured at time t is the sum of genetic effect ($G_{(t-1)}$) at time (t–1) and the extra genetic effect ($G_{(d)} = G_{(t)} - G_{(t-1)}$), which is usually correlated to $G_{(t-1)}$. Recently, Zhu (1995) developed a conditional analysis method, by

which the net genetic effects at specific time interval could be considered. Up to now, this method has been employed to study the development in cotton (Zhu, 1995), rice (Yan et al., 1998; Cao et al., 2001) and mice (Atchley & Zhu, 1997).

Gene expression of quantitative traits was easily affected by environments. Peacock & Hawkins (1976) reported highly significant contributions of the environment to the development of cottonseed. Environment variation within the season has been shown to be a major factor determining qualitative differences in quality of cottonseed (Kohel & Cherry, 1983). It was suggested that oil and protein content would be affected by genotype, environment, and genotype × environment interaction (Turner et al., 1976; Cherry et al., 1978; Singh et al., 1985). Therefore, interaction of genetic effects and environments should not be ignored when examining the development of the cottonseed quality traits.

In the present study, analysis by unconditional and conditional methods was engaged to consider the variation of genetic effects at different periods. A seed model with genotype × environment (*GE*) interaction effects was employed to investigate the genetic control of oil index, protein index, and lysine index. Correlation coefficients were determined to measure the relationship of accumulated behavior or net genetic effects between traits themselves at various stages.

Material and methods

Materials and field experiment

An 8 × 8 diallel cross was conducted in 1993 and 1994 with 3 cultivars (ZMS 12, ZMS 13, XZ 184) and 5 germplasm (1106, 1109, 1117, 1076, 1065). Seeds of all the parents, F_1, reciprocal crosses (RF_1) and 35 entries of F_2 were analyzed for both years. The experiment was conducted by a randomized complete block design with two replications at Zhejiang University, Hangzhou, China. Fertility and cultivation regimes were consistent with optimum cotton production for this region. Each plot accommodated 26 plants with plot area of 1.33×5 m^2. Cottonseed was sown on 12 April and transplanted on 4 May in both years. From 17 July to 6 August, hand-pollination was conducted to obtain the F_1 seeds.

Oil index (OID = oil weight per 100 kernels), protein index (PID = protein weight per 100 kernels) and lysine index (LID = lysine weight per 100 kernels) were measured on seed kernel sampled randomly at each plot from four stages (20, 30, 40, and 50 days after blooming). All harvested bolls prepared with fixation for 10 min at 105 ° and drying at 50 °. 180 normal seeds (having been ginned and shelled) were selected for the first stage and 120 seeds for the rest. Oil index was calculated from $OID = \frac{(W_1 - W_2) \times KW}{W_1}$, where W_1 and W_2 were the weight of cottonseed power before and after Soxhlet extraction, respectively (AOAC, 1984), *KW* was kernel weight per 100 seeds. Protein index and lysine index were determined by *KW* × protein content (achieved by Lowry method, Lowry et al., 1951) and *KW* × lysine content (achieved by rapid dye-binding procedure, Hurrell, 1979).

Statistical analysis

The genetic model of diploid seeds with genotype × environment interaction effects (Zhu & Weir, 1994a; Zhu, 1996) was employed to study the inheritance of OID, PID, and LID. Unconditional genetic analysis was conducted based on phenotypic value at time *t* ($y_{(t)}$), which can be partitioned as (Zhu, 1992, 1996; Zhu & Weir, 1994a):

$$\begin{aligned} y_{(t)} = {} & \mu_{(t)} + E_{(t)} + A_{(t)} + D_{(t)} + C_{(t)} + Am_{(t)} \\ & + Dm_{(t)} + AE_{(t)} + DE_{(t)} + CE_{(t)} + AmE_{(t)} \\ & + D, E_{(t)} + B_{(t)} + \varepsilon_{(t)} \end{aligned}$$

where $\mu_{(t)}$ = population mean, $E_{(t)}$ = environment effect, $A_{(t)} \sim N(0, V_A)$ = direct additive effect, $D_{(t)} \sim N(0, V_D)$ = direct dominance effect, $C_{(t)} \sim N(0, V_C)$ = cytoplasm effect, $Am_{(t)} \sim N(0, V_{Am})$ = maternal additive effect, $Dm_{(t)}$ = maternal dominance effect, with $Dm_{(t)} \sim N(0, V_{Dm})$, $AE_{(t)} \sim N(0, V_{AE})$ = direct additive × environment interaction effect, $DE_{(t)} \sim N(0, V_{DE})$ = direct dominance × environment interaction effect, $CE_{(t)} \sim N(0, V_{CE})$ = cytoplasm × environment interaction effect, $AmE_{(t)} \sim N(0, V_{AmE})$ = maternal additive × environment interaction effect, $DmE_{(t)} \sim N(0, V_{DmE})$ = maternal dominance × environment interaction effect, $B_{(t)} \sim N(0, V_B)$ = block effect, $\varepsilon_{(t)} \sim N(0, V_\varepsilon)$ = residual effect.

The phenotypic value at time *t* conditioned on phenotypic value measured at time (*t*-1) can be partitioned as (Zhu, 1995):

$$\begin{aligned} y_{(t|t-1)} = {} & \mu_{(t|t-1)} + E_{(t|t-1)} + A_{(t|t-1)} + D_{(t|t-1)} \\ & + C_{(t|t-1)} + Am_{(t|t-1)} + Dm_{(t|t-1)} \\ & + AE_{(t|t-1)} + DE_{(t|t-1)} + CE_{(t|t-1)} \\ & + AmE_{(t|t-1)} + DmE_{(t|t-1)} + B_{(t|t-1)} \\ & + \varepsilon_{(t|t-1)} \end{aligned}$$

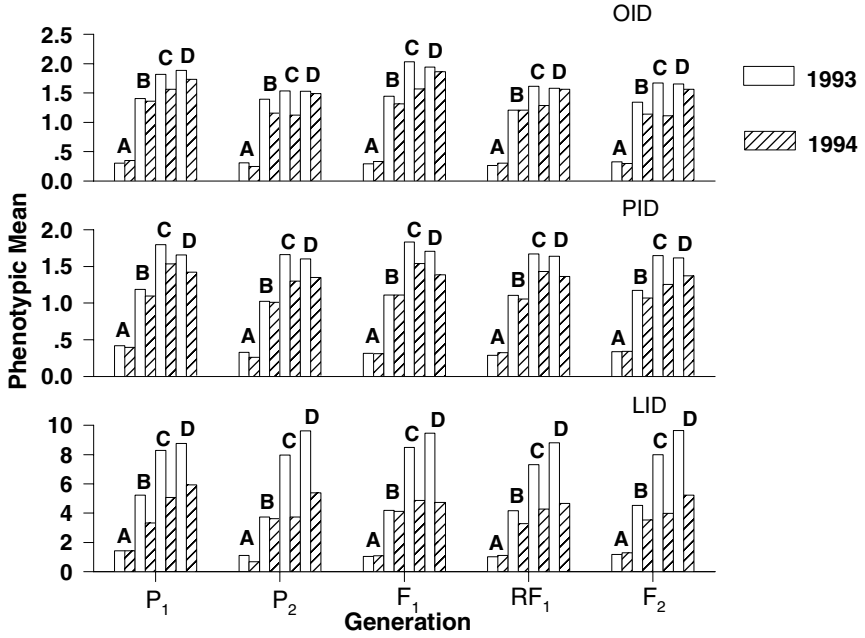

Figure 1. Phenotypic means at four stages in two environments. A, B, C, and D mean 20 days, 30 days, 40 days, and 50 days after flowering, respectively. $F_1 = P_1 \times P2$; $RF_1 = P_2 \times P_1$. E_1 and E_2 mean environment 1 and environment 2, respectively.

with all the parameters defined similar as the unconditional effects.

Both unconditional and conditional variances and covariance were estimated by MINQUE method (Zhu, 1992; Zhu & Weir, 1994a). The conditional variance components measured the variation of net genetic effects at the period from time t to time (t–1). Different correlation coefficients between various developmental stages were calculated for phenotypic correlation coefficient (r_P), correlation coefficients due to genetic main effects (r_A = seed direct additive correlation coefficient, r_D = seed direct dominance correlation coefficient, r_{Am} = maternal additive correlation coefficient, r_{Dm} = maternal dominance correlation coefficient), and the corresponding *GE* interaction correlation coefficients ($r_{AE}, r_{DE}, r_{CE}, r_{AmE}, r_{DmE}$).

Jackknifing was used to estimate standard errors of estimated genetic variances and correlation coefficients (Miller, 1974; Zhu & Weir, 1994a). A t–test with 95 degrees of freedom was employed for testing significance of genetic parameters.

Results

Phenotypic means of generations

Phenotypic values of three seed quality traits differed largely at four stages among different generations over two environments (Figure 1). The means of OID, PID, and LID increased relatively rapid from 20 days to 30 days and from 30 days to 40 days in both years. Only the means of LID maintained the increasing tendency from the initial time to the last stage. The means of F_1 generation for OID were higher at last three stages than that of their parents in both years. The same was observed for PID and LID at 40 days and 50 days in 1993. For all three traits studied, the phenotypic means of F_2 kernel were lower than those of F_1 with the exception of first stage. Phenotypic means of OID, PID, and LID in 1993 were larger than in 1994 for all generations, especially that of LID. It was suggested that variation of these three quality traits could be affected by genotype × environment effects as well as genotype effects.

Variance components

Total phenotypic variance (V_P) consists of variance components of genotypic, *GE* interaction and residual effects ($V_P = V_G + V_{GE} + V_\varepsilon$). Among genotypic

Table 1. Estimation of unconditional and conditional variances at four stages

Para.	20D	30D	40D	50D	20D|initial	30D|20D	40D|30D	50D|40D
OID (10^{-3})								
V_A	4.66**	0.00	48.91**	55.70**	4.66**	0.00	48.72**	0.00
V_D	0.46**	10.36**	11.21**	0.00	0.46**	9.66**	0.00	0.00
V_C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V_{Am}	2.60**	55.85**	120.17**	78.99**	2.60**	48.65**	131.89**	167.45**
V_{Dm}	2.75**	32.12**	79.59**	62.28**	2.75**	29.15**	52.20**	92.72**
V_{AE}	0.00	40.98**	29.33**	0.00	0.00	35.38**	0.00	0.00
V_{DE}	2.86**	0.00	25.63**	35.48**	2.86**	6.13**	22.98**	18.45**
V_{CE}	6.68**	69.57**	53.52**	0.00	6.68**	49.70**	0.00	0.00
V_{AmE}	0.00	0.00	0.00	29.40**	0.00	0.00	0.00	25.59**
V_{DmE}	0.00	52.88**	0.00	0.00	0.00	55.46**	32.37**	0.00
V_ε	8.33**	27.95**	70.43**	79.05**	8.33**	23.49**	61.62**	8.57**
V_G	10.48**	98.32**	256.88**	196.97**	10.48**	87.46**	23.28**	26.02**
V_{GE}	9.54**	163.42**	108.49**	64.88**	9.54**	146.66**	55.36**	44.04**
PID (10^{-3})								
V_A	7.40**	19.35**	67.53**	0.00	7.40**	17.86**	57.20**	15.27**
V_D	1.74**	0.00	0.00	0.00	1.74**	0.00	0.00	0.00
V_C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.54**
V_{Am}	4.33**	17.41**	45.66**	11.18**	4.33**	15.67**	42.95**	9.50**
V_{Dm}	2.03**	21.91**	39.27**	8.72**	2.03**	22.91**	48.53**	0.00
V_{AE}	0.04**	0.00	0.00	0.00	0.04**	0.00	0.00	0.00
V_{DE}	1.88**	13.40**	40.17**	15.39**	1.88**	12.93**	28.07**	13.97**
V_{CE}	7.04**	0.00	38.73**	0.00	7.04**	0.00	25.88**	9.16**
V_{AmE}	5.97**	0.00	0.00	15.68**	5.97**	0.00	36.80**	16.89**
V_{DmE}	0.00	45.59**	0.00	0.00	0.00	45.80**	0.00	0.00
V_ε	6.28**	13.17**	10.43**	7.12**	6.28**	7.43**	31.84**	7.53**
V_G	15.51**	58.67**	152.46**	19.90**	15.51**	56.45**	148.69**	38.32**
V_{GE}	14.92**	58.99**	78.90**	31.07**	14.92**	58.73**	90.75**	40.02**
LID (10^{-1})								
V_A	1.42**	0.00	33.91**	0.00	1.42**	0.00	30.89**	0.00
V_D	0.00	2.08**	3.91**	10.55**	0.00	1.85**	0.00	10.83**
V_C	0.79**	0.00	17.51**	0.00	0.79**	0.00	17.39**	0.00
V_{Am}	0.72**	10.80**	17.33**	0.00	0.72**	9.46**	14.64**	0.00
V_{Dm}	0.50**	8.62**	0.00	31.59**	0.50**	6.67**	0.00	31.25**
V_{AE}	0.96**	25.09**	40.22**	0.00	0.96**	23.97**	36.39**	0.00
V_{DE}	0.50**	0.00	9.80**	0.00	0.50**	0.00	12.53**	0.00
V_{CE}	0.87**	17.69**	0.00	64.73**	0.87**	15.55**	0.00	56.28**
V_{AmE}	0.00	9.60**	0.00	0.00	0.00	5.28**	0.00	0.00
V_{DmE}	1.20**	0.00	53.61**	0.00	1.20**	0.00	48.21**	0.00
V_ε	0.54**	48.50**	48.63**	16.91**	0.54**	4.44**	16.20**	15.26**
V_G	3.43**	21.50**	72.66**	42.14**	3.43**	17.98**	62.92**	42.08**
V_{GE}	3.53**	52.38**	103.63**	64.73**	3.53**	44.80**	97.13**	56.28**

**Significant at $p < 0.01$.

variance ($V_G = V_O + V_C + V_M$), variance of direct effects ($V_O = V_A + V_D$) measures genetic variation contributed by the seed gene effects across different environments, variance of cytoplasm effects (V_C) and maternal nuclear effects ($V_M = V_{Am} + V_{Dm}$) reveals the contribution of maternal plant through effects of cytoplasm and maternal nucleolus genes. *GE* interaction variance ($V_{GE} = V_{OE} + V_{CE} + V_{ME}$=($V_{AE}$ + V_{DE})+V_{CE}+(V_{AmE} + V_{DmE})) assesses the different behavior of genotype under distinctive macro-environment effects. Residual variance (V_ε) covers the remaining unexplainable random effects, most of which are due to the micro-environment effects around cotton plants.

Estimates of unconditional and conditional variance components were summarized in Table 1. Relatively small residue variance (except at last stage for LID) indicated that the genetic effects and *GE* interaction effects were the predominant source of variation. Seed quality was mainly controlled by V_{GE} at second stages for OID, and at forth stage for PID. For LID, both unconditional V_{GE} and conditional $V_{GE(t|t-1}$ were the main component across four stages. Therefore, the expression of genes for LID was mainly affected by environments, which indicating the inefficiency of selection under specific situation for general genetic gain across different environments.

Significant unconditional and conditional variances of maternal additive and dominance effects were noticeably detected at most developmental stages for OID, PID, and LID. It was indicated that net genetic effects of maternal plant were existed through the whole development period. Both unconditional and conditional interaction variances for $Am\times E$ and $Dm\times E$ effects varied largely for different traits, suggesting that macro-environment could have various effects on seed quality traits at different developmental periods. For example, both unconditional and conditional variances of these two components were only significantly detected at last stage, and 30 days after blooming (also third stage for conditional $V_{DmE(t|t-1)}$), respectively. Therefore, the gene expression of maternal plant was relatively stable. Unconditional and conditional variances of cytoplasm effects for OID and PID (except $V_{C(50D|40D}$ for PID) had not been detected across four stages, but variances of *CE* interaction effects had been observed at some stages. This revealed that cytoplasm had no main effects on the behaviors of oil and protein index except in some specific environments. But for LID, significant variances of cytoplasm effects were observed at first and third stages, indicating that cytoplasm could affect the variation of LID at some developmental periods. At most stages, PID had significant variances for direct additive effects and *DE* interaction effects. It was implied that genetic selection on seeds could be quite effective to improving protein index at various stages but heterosis was more important in some specific environments.

Since development is a dynamic procedure, gene expression should not always be the same ways for developmental quantitative traits (Zhu, 1995). For instance, new additive effects due to the seed gene expression could affect oil index and lysine index at the first stage (from initial to 20 days) and the third stage (from 30 days to 40 days), but affect protein index at all four periods. Dynamic consequences of genetic effects could be revealed by the combination of conditional and unconditional methods for different developmental traits at specific periods. For example, there actually had no new effects of gene expression at forth period (from 40 days to 50 days) but significant unconditional maternal dominant variance of PID was still observed, due to accumulated results of early stages. Although no significant unconditional V_C was detected at four stages, there had net genetic effects of cytoplasm from 30 days to 40 days, which might accumulate not large enough to be detected by unconditional method. Thus, the conditional analysis method could help to have a glimpse of the genetic effects of new gene expression before being detected by unconditional method.

Correlation coefficients

Genetic variation analyzed in foregoing section could only get insight into the gene action of specific period. It would be useful to examine the correlation between seed quality traits with themselves (e.g., between 20 and 30 days for OID). This could facilitate the understanding about the interaction of the gene effects, and whether the genetic association pattern would be altered by various gene expression of each trait at specific time intervals.The estimation of unconditional and conditional correlation coefficients indicated that relations of the seed quality traits with themselves at different stages varied considerably (Tables 2–4), suggesting that the genetic effects of early stages not always in the same way as that of the later stages.

For OID, it was relatively large positive correlation ($r_{Am(20D)/(30D)} = 0.16^{**}$, $r_{Am(20D)/(40D)} = 0.16^{*}$, $r_{A(20D)/(50D)} = 0.22^{**}$, $r_{Am(30D)/(40D)} =$

Table 2. Estimates of unconditional and conditional correlation coefficients of OID at four stages

Stage 1	Stage 2	R_P	R_A	R_D	R_{Am}	R_{Dm}	R_{AE}	R_{DE}	R_{CE}	R_{DmE}
20D	30D	0.04	0.00	–0.31**	–0.10*	0.16**	0.00	0.00	0.14**	0.00
	40D	0.02	0.04	–0.42**	0.05	0.16*	0.00	0.09	0.13*	0.00
	50D	0.17*	0.22**	0.00	0.20**	0.13*	0.00	–0.07$^+$	0.00	0.00
30D	40D	0.18**	0.00	–0.27**	0.50**	0.34**	0.20**	0.00	0.23**	0.00
	50D	0.17*	0.00	0.00	0.40**	0.12*	0.00	0.00	0.00	0.00
40D	50D	0.21**	0.50**	0.00	0.67**	0.27**	0.00	0.38**	0.00	0.00
20|initial	30D|20D	–0.02	0.00	–0.18**	–0.18**	0.12	0.00	0.14**	–0.05	0.00
	40D|30D	0.07	0.08	0.00	0.27**	0.03	0.00	0.14**	0.00	0.00
	50D|40D	0.18*	0.00	0.00	0.11$^+$	–0.04	0.00	–0.28**	0.00	0.00
30D|20D	40D|30D	–0.12*	0.00	0.00	–0.68**	0.01	0.00	0.26**	0.00	0.10$^+$
	50D|40D	–0.01	0.00	0.00	–0.43**	–0.27**	0.00	–0.28**	0.00	0.00
40D|30D	50D|40D	0.05	0.00	0.00	0.11	–0.35**	0.00	–0.03	0.00	0.00

* Significant at $p < 0.05$; ** Significant at $p < 0.01$.

Table 3. Estimates of unconditional and conditional correlation coefficients of PID at four stages

Stage 1	Stage 2	R_P	R_A	R_{Am}	R_{Dm}	R_{DE}	R_{CE}	R_{AmE}
20D	30D	–0.04	–0.03	–0.29**	0.13*	0.13**	0.00	0.00
	40D	0.15*	0.21**	0.30**	0.20**	0.10$^+$	0.02	0.00
	50D	0.19**	0.00	1.00**	–0.15**	0.15**	0.00	–0.65**
30D	40D	–0.06	0.24**	–0.32**	–0.15**	0.36**	0.00	0.00
	50D	–0.06	0.00	–0.39**	–0.08	0.55**	0.00	0.00
40D	50D	0.36**	0.00	0.57**	0.16**	0.49**	0.00	0.00
20|initial	30D|20D	–0.09	–0.33**	–0.31**	0.08$^+$	0.04	0.00	0.00
	40D|30D	0.15*	0.29**	0.31**	0.19**	–0.03	–0.24**	0.18**
	50D|40D	0.18**	0.82**	1.00**	0.00	0.25**	0.08	–0.67**
30D|20D	40D|30D	–0.03	–0.01	–0.10	–0.12*	–0.06	0.00	0.00
	50D|40D	–0.08	–0.43**	–0.22**	0.00	0.37**	0.00	0.00
40D|30D	50D|40D	0.06	0.11	0.02	0.00	–0.16**	–0.12*	0.16**

* Significant at $p < 0.05$; ** Significant at $p < 0.01$.

Table 4. Estimates of unconditional and conditional correlation coefficients of LID at four stages

Stage 1	Stage 2	R_P	R_A	R_D	R_C	R_{Am}	R_{Dm}	R_{AE}	R_{DE}	R_{CE}	R_{DmE}
20D	30D	0.05	0.00	0.00	0.00	–0.20**	0.32**	0.05	0.00	0.02	0.00
	40D	–0.03	–0.09	0.00	–0.58**	–0.21**	0.00	–0.12*	–0.30**	0.00	–0.46**
	50D	–0.06	0.00	0.00	0.00	0.00	0.32**	0.00	0.00	–0.09$^+$	0.00
30D	40D	0.07	0.00	–0.17**	0.00	0.24**	0.00	0.24**	0.00	0.00	0.00
	50D	0.08	0.00	–0.04	0.00	0.00	–0.12$^+$	0.00	0.00	0.02	0.00
40D	50D	0.02	0.00	–0.17**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
20|initial	30D|20D	0.05	0.00	0.00	0.00	0.12*	0.04	0.11*	0.00	0.10	0.00
	40D|30D	–0.03	–0.18**	0.00	–0.69**	–0.16*	0.00	0.02	–0.21**	0.00	–0.43**
	50D|40D	–0.06	0.00	0.00	0.00	0.00	0.42**	0.00	0.00	–0.03	0.00
30D|20D	40D|30D	0.07	0.00	0.00	0.00	–0.12*	0.00	0.06	0.00	0.00	0.00

* Significant at $p < 0.05$; ** Significant at $p < 0.01$.

0.50^{**}, $r_{Am(30D)/(50D)} = 0.40^{**}$, $r_{Am(40D)/(50D)} = 0.67^{**}$) that contributed mostly to the performances of between corresponding stages. Negative conditional r_P was noticeable between second and third, second and last, third and last periods, which were largely due to the $r_{Am(30D|20D)/(40D|30D)}$, and $r_{Am(30D|20D)/(50D|40D)}$, and $r_{Dm(30D|20D)/(50D|40D)}$ and $r_{Dm(40D|30D)/(50D|40D)}$, respectively. Although there existed negative unconditional $r_{D(20D)/(40D)}$ with relatively large magnitude, zero conditional correlation between the first and the third periods was observed, caused by the zero conditional V_D at third period. The unconditional positive r_{Am}, and r_{Dm} were significantly detected, only with the exception of $r_{Am(20D)/(30D)}$ and $r_{Am(20D)/(40D)}$. But the noticeable negative conditional $r_{Am(30D|20D)/(40D|30D)}$, $r_{Am(30D|20D)/(50D|40D)}$, $r_{Dm(30D|20D)/(50D|40D)}$ and $r_{Dm(40D|30D)/(50D|40D)}$ indicated that extra effects of new maternal gene expression at these development interval had contrary function on OID.

For PID, both unconditional and conditional phenotypic correlation coefficients between the second and third period were not significant from zero. It seemed that positive r_A, r_{DE} and negative r_{Am}, r_{Dm} were the main contributions. But actually, nearly every conditional correlation coefficient between the second and third periods was not significant from zero, which indicating that effects of new gene expression at the second period had no relationship with that at the third period. It was showed by significantly positive unconditional $r_{Am(20D)/(50)}$ and conditional $r_{Am(20D|\text{initial})/(50D|40D)}$ that genetic effects due to maternal plant at initial period could ultimately affect the performance of protein index at maturing stage and could intimately influence the maternal additive effects adapting PID at last period. Although there had no significant unconditional and conditional correlation of direct dominance, unconditional r_{DE} between various stages were notable. It was indicated, by the significant conditional r_{DE} between final period and other three periods, that net genetic effects of $D \times E$ at first three period.

As compared to OID and PID, the correlation due to different genetic effects varied relatively stable for LID except for the relationship between the first and third stages (or periods). There was not many negative conditional correlation observed at various periods. Unconditional r_{Dm} was positive between first and second, first and last stages. But conditional analysis revealed that actually only extra maternal dominance effects of first and last periods were positively correlated.

Discussion

The genetic complexity of seed quantitative traits largely enhanced the difficulties in genetic analysis for developmental behavior. Previously developed methods such as diallel cross method and generation mean method can not simultaneously analyze component effects due to seed nuclear, cytoplasm, and maternal nuclear. A method was proposed to estimate the effects due to these three genetic systems with the data collected from 18 generations and measuring single seeds (Foolad & Jones, 1992). Therefore, most of the former reports only discussed the additive and dominant effects due to seed nuclear (Ji & Zhu, 1988; Singh et al., 1985). But maternal nuclear and cytoplasm effects had been detected for seed traits. Oil content of cottonseed could be affected by maternal effects (Dani & Kohel, 1989; Ramos, 1985), and significant cytoplasm effects were observed in protein content of maize (Singh & Hadley, 1972). Furthermore, correlations due to different genetic effects existed (Wang et al., 1996a,b). Zhu & Weir (1994a,b) proposed a new seed model with genotype $\times$ environment interaction effects to unbiased estimating the variances and covariance due to seed nuclear, maternal cytoplasm, and maternal nuclear by only using several generation means. And with the combination of conditional analysis approach (Zhu, 1995), the performance of net genetic effects at different periods and the relationship between them could be obtained for developmental behavior of the quantitative traits.

In the present study, genetic characteristics of cottonseed quality traits exhibited great complexity during the development, which was represented by the variation of magnitude and significance of the genetic variances and correlation coefficients. One possible reason might be that polygene system of quantitative traits could have specific expression pattern at different developmental periods. Dissimilar categories and activity of isozyme were found during the development of embryo and endosperm in maize (Yang & Zeng, 1984). The nuclear DNA content in endosperm changed dynamically during the development in maize, and had significant correlation with seed weight and volume (Gao, 1994). Furthermore, various developmental periods might be controlled by different loci of the polygene system. Wu & Stettler (1994)

reported that different QTLs could modify the growth of the *Populus* at the first and second years. The other reason might be that different position of boll setting would have effects on the variation of the traits of seed quality, due to different environment conditions of sunshine, temperature, humidity, and so on. According to Zhu et al. (1993) and Jenkins et al. (1990), significant variation was observed at various positions in upland cotton. It was suggested that quality of cottonseeds was affected by position of the cotton boll (Zhao et al., 1994; Conkerton et al., 1993; Merwade & Katarki, 1985).

It was obvious that genetic effects due to maternal plant ($V_C + V_{Am} + V_{Dm}$, and $V_{CE} + V_{AmE} + V_{DmE}$) were the main cause of the genetic variation for three quality traits during the whole developmental period. Therefore, oil index, protein index, and lysine index could be improved more efficiently based on selecting maternal plants instead of on individual seeds. In order to further explore the distinctly decreasing unconditional V_{Am} and $V_{Am(t|t-1)}$ large conditional for OID at last stage, genetic effects of eight parents were predicted with adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu & Weir, 1996). It was mainly due to the reverse direction of net genetic effects of new gene expression at later stage (at the third stage $Am1_{(40D)} = 0.14^{*}$, $Am2_{(40D)} = 0.17^{*}$, $Am3_{(40D)} = 0.18^{**}$, $Am7_{(40D)} = -0.23^{**}$, $Am8_{(40D)} = -0.44^{**}$; at the period from 40D to 50D $Am1_{(50D|40D)} = -0.16^{*}$, $Am2_{(50D|40D)} = -0.34^{**}$, $Am3_{(50D|40D)} = -0.18^{+}$, $Am7_{(50D|40D)} = 0.22^{*}$, $Am8_{(50D|40D)} = 0.52^{**}$).

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