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Research Article

Analysis of Genetic Effects of Nuclear-Cytoplasmic Interaction on Quantitative Traits: Genetic Model for Diploid Plants

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Abstract: A genetic model was proposed for simultaneously analyzing genetic effects of nuclear, cytoplasm, and nuclear-cytoplasmic interaction (NCI) as well as their genotype by environment (*GE*) interaction for quantitative traits of diploid plants. In the model, the NCI effects were further partitioned into additive and dominance nuclear-cytoplasmic interaction components. Mixed linear model approaches were used for statistical analysis. On the basis of diallel cross designs, Monte Carlo simulations showed that the genetic model was robust for estimating variance components under several situations without specific effects. Random genetic effects were predicted by an adjusted unbiased prediction (AUP) method. Data on four quantitative traits (boll number, lint percentage, fiber length, and micronaire) in Upland cotton (*Gossypium hirsutum* L.) were analyzed as a worked example to show the effectiveness of the model.

Keywords: Plants traits; genetic model; nuclear-cytoplasmic interaction effects; *GE* interaction; genetic prediction

Various important agronomic traits, such as grain yield and quality, are affected by both nuclear and cytoplasmic genes. Cytoplasmic genes mostly present in mitochondria and chloroplasts of plants. It has been shown that nuclear genes could affect cytoplasmic gene expression and cytoplasmic genome organization[1−3]. Recent reports indicated that nuclear-cy- toplasmic interaction (NCI) effects play vital roles in the development of potato (*Solanum tuberosum* L.) and rice (*Oryza sativa* L.) [4,5], and affect fitness traits of plants, e.g., fertility, viability, and selfing rate, which have considerable importance in evolution[6]. Thus, it is essential to understand the inheritance of NCI in plants.

Beavis *et al.*[7] proposed a method for estimating variance components of nuclear, cytoplasm, and NCI by reciprocal mating designs. However, the main disadvantage of Beavis's approach was that it was unable to obtain unique estimation of cytoplasmic effects. With this respect, Mosjidis *et al.* [8] used weighted least square (WLS) method to estimate effects of cytoplasm and NCI. This method is problematic because accompanying experimental design is rarely used in practice. Yang and Lu [9] and Tao *et al.*[5] conducted a study on NCI of rice (*Oryza sativa* L.) by ANOVA approach, which requires data with balanced structure and can not handle genetic designs with irregular missing combinations.

Moreover, to develop economically important varieties of crops with wide geographical adaptability,

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genotype by environment (*GE*) interaction has been considered as a major concern to breeders and quantitative geneticists[10]. Thus, in addition to the effects of nuclear genes, cytoplasmic genes, and nuclear-cytoplasmic gene interaction[1,5], the genetic model should also address *GE* interaction.

In the present study, a genetic model was proposed to study the inheritance of quantitative traits of diploid plants that are controlled by genetic effects from both nuclear and cytoplasmic genes and their *GE* interaction effects. This model is based on a modified diallel design in the framework of mixed linear model. The validity of the method was evaluated by Monte Carlo simulations, and the data on four quantitative traits in Upland cotton (*Gossypium hirsutum* L.) were used as a worked example to demonstrate the procedure.

1 Model and Methodology

If the genetic experiments are conducted in multiple environments, the phenotypic value (y_{hijkl}) of mating type k of the combination from maternal parent i and paternal parent j in block l within environment h can be generally expressed by the following genetic model

$$y_{hijkl} = \mu + E_h + G_{ijk} + GE_{hijk} + B_{l(h)} + e_{hijkl} \quad (1)$$

where μ is the fixed population mean; E_h is the effect of *h-th* environment (e.g., year, location, etc.); G_{ijk} is the total genetic effect; GE_{hijk} is the $G_{ijk} \times E_h$ interaction effect; $B_{l(h)} \sim (0, \sigma_B^2)$ is the random effect of *l-th* block within *h-th* environment; e_{hijkl} is the effect of random error and $e_{hijkl} \sim (0, \sigma_e^2)$.

For a quantitative trait controlled by nuclear genes and cytoplasmic genes, the total genetic effect (G) in model (1) can be further partitioned into nuclear genetic effect (*Go*), cytoplasmic genetic effect (C), and NCI. The nuclear genetic effect *Go* can be further partitioned into additive (A) and dominance (D) nuclear genetic components, and consequently, NCI can be divided into additive nuclear-cytoplasmic interaction effect (AC) and dominance nuclear-cytoplasmic interaction effect (DC).

The partition of total genetic effect G_{ijk} and the total interaction effect GE_{hijk} depends on specific generations. For parents $P_i \times P_j$ ($i = j$ and $k = 0$ the sum of G_{ijk} and GE_{hijk} can be expanded into

$$\begin{aligned} G_{ij0} + GE_{hij0} = {} & 2A_i + D_{ii} + C_i + 2AC_{ii} + DC_{iii} \\ & + 2AE_{hi} + DE_{hii} + CE_{hi} + 2ACE_{hii} + DCE_{hiii} \end{aligned}$$

for F_{1ij} ($k = 1$) from maternal parent i × paternal parent j, it is

$$\begin{aligned} G_{ij1} + GE_{hij1} = {} & A_i + A_j + D_{ij} + C_i + AC_{ii} + AC_{ji} \\ & + DC_{iji} + AE_{hi} + AE_{hj} + DE_{hij} \\ & + CE_{hi} + ACE_{hii} + ACE_{hji} + DCE_{hiji} \end{aligned}$$

for F_{2ij} ($k = 2$) selfed from F_{1ij}, it is

$$\begin{aligned} G_{ij2} + GE_{hij2} = {} & A_i + A_j + 0.25D_{ii} + 0.25D_{jj} + 0.5D_{ij} + C_i \\ & + AC_{ii} + AC_{ji} + 0.25DC_{iii} + 0.25DC_{jji} \\ & + 0.5DC_{iji} + AE_{hi} + AE_{hj} + 0.25DE_{hii} \\ & + 0.25DE_{hjj} + 0.5DE_{hij} + CE_{hi} + ACE_{hii} + ACE_{hji} \\ & + 0.25DCE_{hiii} + 0.25DCE_{hjji} + 0.5DCE_{hiji} \end{aligned}$$

for BC_i ($k = 3$) ($F_{1ij} \times P_i$), it is

$$\begin{aligned} G_{ij3} + GE_{hij3} = {} & 1.5A_i + 0.5A_j + 0.5D_{ii} + 0.5D_{ij} + C_i \\ & + 1.5AC_{ii} + 0.5AC_{ji} + 0.5DC_{iii} + 0.5DC_{iji} \\ & + 1.5AE_{hi} + 0.5AE_{hj} + 0.5DE_{hii} + 0.5DE_{hij} \\ & + CE_{hi} + 1.5ACE_{hii} + 0.5ACE_{hji} \\ & + 0.5DCE_{hiii} + 0.5DCE_{hiji} \end{aligned}$$

and for BC_j ($k = 4$) ($F_{1ij} \times P_j$), it is

$$\begin{aligned} G_{ij4} + GE_{hij4} = {} & 0.5A_i + 1.5A_j + 0.5D_{jj} + 0.5D_{ij} \\ & + C_i + 0.5AC_{ii} + 1.5AC_{ji} + 0.5DC_{jji} \\ & + 0.5DC_{iji} + 0.5AE_{hi} + 1.5AE_{hj} \\ & + 0.5DE_{hjj} + 0.5DE_{hij} + CE_{hi} + 0.5ACE_{hii} \\ & + 1.5ACE_{hji} + 0.5DCE_{hjji} + 0.5DCE_{hiji}. \end{aligned}$$

If the inbred parents are randomly sampled from a reference population, the above genetic effects are considered to be random effects. A_i (or A_j) $\sim (0, \sigma_A^2)$ is the cumulative additive effect of nuclear genes

from line i (or line j); D_{ij} (or D_{ii}, or D_{ij}) ~ (0, σ^2_D) is the cumulative dominance effect of nuclear genes from line i × line j ($i \leq j$); C_i ~ (0, σ^2_C) is the cumulative cytoplasmic effect; AC_{ji} (or AC_{ii}) ~ (0, σ^2_{AC}) is the cumulative AC between additive effect from line j (or line i) and cytoplasmic effect from line i; DC_{iii} (or DC_{iji}, or DC_{jji}) ~ (0, σ^2_{DC}) is the cumulative DC between the D_{ii} (or D_{ij} or D_{jj}) and C_i; AE_{hi} (or AE_{hj}) ~ (0, σ^2_{AE}), DE_{hij} (DE_{hii} or DE_{hjj}) ~ (0, σ^2_{DE}) and CE_{hi} ~ (0, σ^2_{CE}) are the interaction effect between the environment and additive, dominance, cytoplasm effect, respectively. ACE_{hji} (or ACE_{hii}) ~ (0, σ^2_{ACE}) is the interaction effect of AC_{ji} (or AC_{ii}) × E_h, and DCE_{hiii} (or DCE_{hiji} or DCE_{hjji}) ~ (0, σ^2_{DCE}) is the interaction effect of DC_{iii} (or DC_{iji} or DC_{jji}) × E_h.

Therefore, the phenotypic variance (V_P) can be partitioned as

$$\begin{aligned} V_P &= V_G + V_{GE} + V_\varepsilon \\ &= (V_A + V_D + V_C + V_{AC} + V_{DC}) \\ &\quad + (V_{AE} + V_{DE} + V_{CE} + V_{ACE} + V_{DCE}) + V_\varepsilon \end{aligned} \tag{2}$$

where V_G is genetic variance with components of additive variance V_A, dominance variance V_D, cytoplasmic variance V_C, AC variance V_{AC} and DC variance V_{DC} . V_{GE} is GE interaction variance with components of A × E interaction variance V_{AE}, D × E interaction variance V_{DE}, C × E interaction variance V_{CE}, AC × E interaction variance V_{ACE}, DC × E interaction variance V_{DCE}. V_ε is the residual variance.

A minimum norm quadratic unbiased estimation (MINQUE) method is applicable to estimate variance components in the framework of mixed linear model[11]. An adjusted unbiased prediction (AUP) method is suitable for predicting random genetic effects [12]. A *t*-test following Jackknife resampling technique is used to detect the significance of variances and various genetic effects [12].

2 Results

2.1 Monte Carlo simulation

The simulations were based on modified diallel crosses with three randomized complete block designs.

These designs included three different constructions: 1) parents, F_1s, RF_1s, F_2s, RF_2s; 2) parents, F_1s, RF_1s; and 3) parents, F_2s, RF_2s. For each case, 200 simulations were conducted to obtain the estimates of sample means and power value for variances, and to predict the means and variances for all the random effects.

Simulation results of bias and power for variance components were summarized in Table 1. Most absolute values of the bias were less than 5% of the parameter values, which was the conventional criterion for unbiased estimation. For the second and the third types of designs, a small number of absolute values of bias were larger than 5% and smaller than 10% of the parameter values, which was well estimated. For the first type of seven-parent modified diallel crosses, the significance of nonzero $\sigma^2_A, \sigma^2_{AC}, \sigma^2_{AE}, \sigma^2_\varepsilon$ can be detected with a probability of more than 70%, and significant $\sigma^2_D, \sigma^2_C, \sigma^2_{DC}, \sigma^2_{DE}, \sigma^2_{CE}, \sigma^2_{ACE}, \sigma^2_{DCE}$ was detected with a probability of more than 50%. For the second and the third types of designs, the significance of some nonzero variance components was detected with relatively lower powers. When there were no NCI ($\sigma^2_{AC} = \sigma^2_{DC} = \sigma^2_{ACE} = \sigma^2_{DCE} = 0$) or no dominance variation ($\sigma^2_D = \sigma^2_{DC} = \sigma^2_{DE} = \sigma^2_{DCE} = 0$), other effects can be estimated with similar bias, and power value as when the NCI or dominance variation was present. It was indicated that the genetic model was robust for estimating variance components even in the absence of NCI or dominance effects. As the mean values of predicted effects are zero and their variances approach to preset value, the AUP method gave prediction with unbiased means and variances (Table 2).

Table 1 Bias and power value of variance estimation by MINQUE(1) for modified diallel crosses

Parameter	True value	Parents, F_1s, RF_1s, F_2s, RF_2s		Parents, F_1s, RF_1s		Parents, F_2s, RF_2s	
		Bias	Power [a]	Bias	Power [a]	Bias	Power [a]
σ^2_A	20	–0.882	0.880	0.968	0.825	–0.055	0.865
σ^2_D	10	0.899[b]	0.660	0.240	0.690	–0.083	0.560
σ^2_C	30	0.859	0.650	1.716[b]	0.680	2.136[b]	0.710
σ^2_{AC}	20	–0.011	0.900	–0.329	0.750	0.321	0.670
σ^2_{DC}	30	–0.183	0.900	0.735	0.750	0.272	0.585
σ^2_{AE}	10	–0.233	0.925	0.047	0.865	–0.031	0.865
σ^2_{DE}	15	0.421	0.675	0.560	0.925	–1.174[b]	0.475
σ^2_{CE}	10	–0.690[b]	0.755	–0.171	0.510	–0.492	0.545
σ^2_{ACE}	10	0.244	0.790	0.625[b]	0.570	0.947[b]	0.415
σ^2_{DCE}	10	–0.142	0.655	–0.943[b]	0.520	–0.185	0.385
σ^2_ε	20	–0.078	1.000	0.139	1.000	0.120	1.000

[a] Probability of rejecting the null hypothesis of no variation by the *t*-test at $\alpha = 0.05$ significance level;

[b] Bias > 5% and < 10% of the true value.

Table 2 Variance of predicted genetic effects by AUP for modified diallel crosses [a]

Parameter	Variance	Parents, F_1s, RF_1s, F_2s, RF_2s	Parents, F_1s, RF_1s	Parents, F_2s, RF_2s
A	20	21.14	19.19	20.20
D	10	9.98	11.62	11.79
C	30	30.58	30.77	27.35
AC	20	20.05	21.90	21.54
DC	30	29.85	31.62	32.88
AE	10	10.24	9.95	10.04
DE	15	14.58	14.44	16.67
CE	10	10.96	10.72	10.63
ACE	10	9.76	9.79	9.70
DCE	10	10.21	11.48	11.04

[a] Mean values of parameter and prediction of each random genetic effect are zero and 10^{-2}–10^{-6}, respectively.

2.2 Worked example

Four plant traits in cotton, *i.e*., boll number (BN), lint percentage (LP), fiber length (FL), and micronaire (Mic), were analyzed. The experiments were conducted at Zhejiang University Experimental Farms (Hangzhou) with three randomized complete blocks in 1994, and two blocks in 1995, respectively. Seven varieties (three glanded P_1, P_2, and P_3 vs four glandless cultivars P_4, P_5, P_6, and P_7) of Upland cotton were used in this experiment. Crosses of cotton varieties between glanded and glandless cultivars were arranged in a 3 × 4 diallel design. The mating design involved seven parents, F_1s and F_2s, but didn't contain reciprocal F_1s and F_2s. The Jackknife technique was used for estimating the standard errors of the estimated variances and the predicated genetic effects.

The estimates of the variance components are shown in Table 3. The contributions of V_G and V_{GE} to total genetic variance were 74.38% and 25.62% for BN, 73.62% and 26.38% for LP, 78.54% and 21.46%

for FL, and 62.73% and 37.27% for Mic, respectively. These traits were, therefore, controlled mainly by genotypic effects and were less affected by *GE* interaction effects. The variances of additive effects (V_A) and cytoplasmic effects (V_C) were both significant for the three traits (BL, LP, and FL) and only the significant V_A was detected for Mic. The DC interaction variance (V_{DC}) was important for BL and LP, and the dominance variance (V_D) was significant for FL and Mic. However, there was no significant AC interaction variance (V_{AC}) for all the traits. For the *GE* interaction effects, most of the additive interaction variance (V_{AE}) was significant for these traits. Significant variance of *CE* interaction (V_{CE}) was detected for BN and LP, and that of ACE interaction (V_{ACE}) for FL and Mic, respectively. However, the DCE interaction variance (V_{DCE}) was negligible for all these four traits.

Moreover, the predicted genetic effects were also presented for these four traits (Table 4, 5). Among the seven parental varieties, there were significantly positive additive and cytoplasmic effects of P_1 and P_2 on BN of P_7 on LP, and of P_1 and P_5 on FL. There were significantly negative additive effects of P_1 on the Mic. Parents P_1 and P_2 might be more superior to other varieties for increasing BN and P_7 might be a suitable parent for increasing LP. The P_1 might be a suitable parent for increasing FL and decreasing Mic. In addition, the NCI of $DC_{37.3}$ on BN and LP were significantly positive. It might be inferred that the P_3 (♀) × P_7 (♂) cross could obtain extra genetic gain from NCI for high BN and LP.

Table 3 Estimates of variance components for cotton boll number (BN)**, lint percentage** (LP)**, fiber length** (FL)**, and micronaire** (Mic)

Variance components	BN	LP	FL	Mic
V_A	6.795**	2.048**	1.983**	0.055**
V_D	0.000	0.108	0.685**	0.039**
V_C	23.069**	6.807**	3.585*	0.044
V_{AC}	0.000	0.000	0.000	0.000
V_{DC}	4.230*	1.055*	0.000	0.000
V_{AE}	1.407**	0.420**	0.310*	0.006
V_{DE}	3.574**	1.183**	1.031**	0.059**
V_{CE}	6.764**	1.986**	0.000	0.000
V_{ACE}	0.000	0.000	0.368**	0.017**
V_{DCE}	0000	0.000	0.000	0.000
V_ε	3.323**	1.083**	0.552**	0.034**

* and ** indicates significance at the 0.05 and 0.01 levels, respectively.

Table 4 Predicted of additive and cytoplasmic effects of parents for cotton boll number (BN)**, lint percentage** (LP)**, fiber length** (FL) **and micronaire** (Mic)

Additive effects					Cytoplasmic effects			
Parameter	BN	LP	FL	Mic	Parameter	BN	LP	FL
A_1	2.297**	0.829**	1.057**	– 0.283**	C_1	1.628**	–0.761**	1.070**
A_2	2.147**	–2.092**	0.801**	–0.072*	C_2	3.526**	3.582**	–1.194**
A_3	2.777**	0.270	0.870**	0.059	C_3	–2.174**	–1.453**	–0.756**
A_4	–2.351**	1.373**	–1.282**	0.327**	C_4	– 0.069	–0.255**	–0.131**
A_5	–2.503**	–0.507**	0.777**	–0.221**	C_5	–0.828**	–2.155**	1.140**
A_6	–1.534**	–1.227**	–0.466*	0.230**	C_6	– 0.023	–1.250**	1.069**
A_7	–0.833**	1.355**	–1.758**	–0.040	C_7	– 2.059**	2.292**	–1.197**

* and ** indicates significance at the 0.05 and 0.01 levels, respectively.

Table 5 Predicted of dominance nuclear-cytoplasmic interaction effect (DC) **for cotton boll number** (BN) **and lint percentage** (LP)

Parameter	BN	LP
$DC_{11.1}$	0.032**	–0.355**
$DC_{44.1}$	0.144**	0.003
$DC_{55.1}$	–0.453**	–0.124**
$DC_{66.1}$	–1.367**	–0.565**
$DC_{77.1}$	0.788**	–0.440**
$DC_{14.1}$	–0.123**	–0.028**
$DC_{15.1}$	0.494**	0.230**
$DC_{16.1}$	1.350**	0.128**
$DC_{17.1}$	–0.392**	0.915**
$DC_{22.2}$	0.137**	–0.334**
$DC_{44.2}$	–0.223**	0.365**
$DC_{55.2}$	0.747**	0.405**
$DC_{66.2}$	–0.640**	0.649**
$DC_{77.2}$	–0.026	0.705**
$DC_{24.2}$	0.136**	–0.025*
$DC_{25.2}$	–0.544**	–0.057**
$DC_{26.2}$	1.339**	–0.605**
$DC_{27.2}$	0.095**	0.004
$DC_{33.3}$	–0.598**	–0.771**
$DC_{44.3}$	–1.363**	0.090**
$DC_{55.3}$	–1.239**	0.069**
$DC_{66.3}$	0.522**	0.262**
$DC_{77.3}$	–0.830**	–1.815**
$DC_{34.3}$	1.487**	0.182**
$DC_{35.3}$	0.903**	0.130**
$DC_{36.3}$	–0.633**	–0.235**
$DC_{37.3}$	1.664**	1.639**

* and ** indicates significance at the 0.05 and 0.01 levels, respectively.

3 Discussion

It has been well known that NCI made significant contribution to the genetic variance of quantitative traits for many diploid plants, such as soybean (*Glycine max* L.) and barley (*Hordeum vulgare* L.) [13, 14], and also for some nondiploid plants, such as maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) [15, 16]. In fact, the present model could also be used for allopolyploid plants that have similar meiotic behavior as diploid plants. In this worked example, four plant traits of cotton were analyzed through the present genetic model. The results showed that DC effects could affect the two yield traits (BN and LP), and similarly ACE effects could affect the two quality traits (FL and Mic).

In breeding practice, the NCI is used in some breeding programs to improve crop yield and its components. So it is important to develop an efficient breeding strategy to appropriately dissect different sources of variation for these traits. The present model can partition the total genetic effects into genetic main effects of nuclear, cytoplasm, NCI, and their *GE* interactions. It was shown that model has the ability of robustness for estimating each of these variance components. Even if there were no NCI or dominance effect, the other variance components can still be well estimated. The model proposed by Beavis *et al.*[7] could not obtain unbiased estimates of cytoplasm or NCI by quadratic analysis. Moreover, their model requires that the reciprocal mating design need to include all possible reciprocal crosses of a single set of parental lines[17]. But for some plants, because of the existence of intercrossing barriers in nature, intercrossing is possible in only one direction [18], and it might be impossible to conduct experiments for all reciprocal crosses mating design. Although the model advocated by Mosjidis *et al.* [8] could provide unbiased estimation of NCI, it was still difficult for application because it required the measurement of single seed for 15 generations. The ANOVA could estimate variance component of NCI, but it needed at least seven backcrosses nuclear-plasmic replacement lines [5, 9]. In the present model, hybridization with CMS (cytoplasmic male–sterile lines) at large scale became much easier [19,20]. The diallel crosses mating design could involve the CMS lines and the restores and require only three generations. Monte Carlo simulations showed that most variance components could be well estimated. In addition, genetic effects of breeding material were sometimes more interesting to the breeder in plant breeding, and the genetic effects predicted by the AUP method were of importance.

References

1 Leon P, Arroyo A, Mackenzie S. Nuclear control of plastid and mitochondrial development in higher plants. *Annu Rev Plant Physiol Plant Mol Biol*, 1998, 49(1): 453–480.

2 Strand A. Plastid–to–nucleus signalling. *Curr Opin Plant Biol*, 2004, 7(6): 621–625.

3 Nott A, Jung HS, Koussevitzky S, Chory J. Plastid-to-nucleus retrograde signaling. *Annu Rev Plant Biol*, 2006, 57(3): 739–759.

4 Scotti N, Monti L, Cardi T. Organelle DNA variation in parental *Solanum spp* genotypes and nuclear-cytoplasmic interactions in *Solanum tuberosum* (+) *S. commersonii* somatic hybrid–backcross progeny. *Theor Appl Genet*, 2004, 108(1): 87–94.

5 Tao D, Hu F, Yang J, Yang G, Yang Y, Xu P, Li J, Ye C, Dai L. Cytoplasm and cytoplasm–nucleus interactions affect agronomic traits in *japonica* rice. *Euphytica*, 2004, 135(3): 129–134.

6 Gregorius HR, Ross MD. Selection with gene–cytoplasm interactions. I. Maintenance of cytoplasm polymorphisms. *Genetics*, 1984, 107(1): 165–178.

7 Beavis WD, Pollak E, Frey KJ. A theoretical model for quantitatively inherited traits influenced by nuclear-cytoplasmic interaction. *Theor Appl Genet*, 1987, 74(5): 571–578.

8 Mosjidis JA, Waines JG, Yermanos DM, Rosielle AA. Methods for the study of cytoplasmic effects on quantitative traits. *Theor Appl Genet*, 1989, 77(2): 195–199.

9 Yang RC, Lu HR. A study on effects of nucleo–cytoplasmic interaction in *Oryza* L. *Scientia Agricultura Sinca*, 1989, 22(2): 56–63 (in Chinese with an English abstract).

10 Falconer DS, Mackay Trudy FC. Introduction to quantitative genetics. 4th ed. Longman Press, New York, 1996.

11 Rao CR. Estimation of variance and covariance components MINQUE theory. *J Multivar Anal*, 1971, 1(2): 257–275.

12 Zhu J, Weir BS. Mixed model approaches for diallel analysis based on a bio–model. *Genet Res*, 1996, 68(3): 233–240.

13 Peng YH, Yang GB, Yuan JZ, Mei DS, Li W. Characteristic analysis of a planting time–sensitive male sterile soybean. *Acta Agronomic Sinica*, 1998, 24(6): 1010–1013 (in Chinese with an English abstract).

14 Goloenko IM, Lukhanina NV, Shimkevich AM, Aksyonova EA, Danilenko NG, Davydenko OG. The productivity characteristics of substituted barley lines with marked chloroplast and mitochondrial genomes. *Cell Mol Biol Lett*, 2002, 7(2): 483–491.

15 Rao AP, Fleming AA. Cytoplasmic–genetypic effect in the GT 112 maize inbred with four cytoplasms. *Crop Sci*, 1978, 18(4): 935–937.

16 Murai K, Takumi S, Koga H, Ogihara Y. Pistillody, homoeotic transformation of stamens into pistil–like structures, caused by nuclear-cytoplasmic interaction in wheat. *Plant J*, 2002, 29(2): 169–181.

17 Cockerham CC, Weir BS. Quadratic analysis of reciprocal crosses. *Biometrics*, 1977, 33(1): 187–203.

18 Eijlander R, Laak W, Hermsen JGT, Ramanna MS, Jacobsen E. Occurrence of self-compatibility, self-incompatibility and unilateral incompatibility after crossing diploid *S. tuberosum* (SI) with *S. verrucosum* (SC): I. Expression and inheritance of self–compatibility. *Euphytica*, 2000, 115(2): 127–139.

19 Schnable PS, Wise RP. The molecular basis of cytoplasmic male sterility and fertility restoration. *Trends Plant Sci*, 1998, 3(5): 175–180.

20 Touzet P, Hueber N, Brkholz A, Barnes S, Cuguen J. Genetic analysis of male fertility restoration in wild cytoplasmic male sterility G of beet. *Theor Appl Genet*, 2004, 109(3): 240–247.

数量性状的核质互作遗传效应分析：二倍体植株遗传模型

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摘 要：提出了能分析二倍体植株数量性状核质互作效应的遗传模型，该模型把控制数量性状总的遗传效应分为核效应、质效应和核质互作效应，以及它们分别与环境作用的效应。其中，核质互作效应可进一步分解为加性核质互作与显性核质互作。基于平衡与非平衡两种双列杂交试验设计，蒙特卡罗模拟结果表明：采用混合线性模型方法进行统计分析，可以有效地估计各项遗传效应值及其方差分量。此外，运用该模型对棉花的 4 个数量性状（单株铃数、衣分、2.5% 跨长和麦克隆值）进行了遗传分析。

关键词：植株性状；遗传模型；核质互作；基因型×环境互作；预测

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