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Quantitative analysis of seed genetic model including embryo and endosperm effects in multiple environments

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Abstract

Full seed model was evaluated by using, in multiple environments, mating design of eight parents diallel crosses with F_1's and reciprocal F_1's, F_2's and reciprocal F_2's. Monte Carlo simulations were conducted to calculate Bias, MSE and power value to estimate variance components of embryo genetic effect, endosperm genetic effect, cytoplasm effect, maternal genetic effect and genotype x environment interaction effect. Biases of variance components, σ^2_{Ao}, σ^2_{Do} and σ^2_{Ae}, were found to be around 10% of the parameter values. These variances tend to be well estimated for the full seed model including *GE* interaction effect. If embryo or endosperm genetic effects, when they do exist, are not considered in the model, other genetic variance components could be easily overestimated except σ^2_C, σ^2_{Dm}, σ^2_{CE}, σ^2_{DmE}, and σ^2_ε. If embryo and embryo x environment interaction were ignored, endosperm, maternal genetic variances and genotype x environment genetic variances were overestimated. When endosperm and endosperm x environment interaction were ignored, same phenomena happened to embryo, maternal and GE interaction variances components.

***Key words**:* Full seed model, embryo, endosperm, mixed model, Monte Carlo simulation.

Introduction

Geneticists and breeders are more and more interested to the link between genetic factors and phenotypic variation of quantitative seed traits. Studies of different genetic seed models and the evaluation of genetic effects by estimating genetic variance components become one of the important goals for the understanding of this relation. Cockerham [2] partitioned total genetic effect into several genetic components which were also divided according to the mating type. In addition, statistical methods based on mixed model approaches were merged to general genetic model for analyzing complicated genetic models by using minimum norm quadratic unbiased estimation (MINQUE) method [10, 11]. Most of the plant genetic models were developed for analyzing genetic main effects. In wheat (*Triticum aestivum* L.) maternal effects for seed proteins were found [3]. Foolad and Jones [5] introduced genetic model for analyzing also quantitative seed characters. Some quantitative traits of rice behaved differently across environments [1]. Jansen *et al.* [7] were interested on genotype by environment interaction in genetic mapping of multiple quantitative trait loci. Many problems related to the evaluation of genetic main effects and genotype x interaction (*GE)* effects have still no response. Therefore, what is about the efficiency of the full genetic model including GE interaction effect. In another way, what is the quality of the estimated variance components or their degree of significance if one or several genetic effects are ignored in this model. Simulation analysis of the full seed model was important tool for the answering of these questions. Using the presence or ignorance of some genetic main effects as embryo, endosperm and of genotype x environment interaction effects, the object is to evaluate the full seed model from the estimations of genetic variance components for genetic and *GE* interaction effects and to detect the overestimation. An understanding of this phenotypic variation from genetic main effects and *GE* effects is of fundamental significance in the inheritance and development of plant seeds.

Model and Methodology

By using Cockerham's general genetic model, [12] developed full seed model including embryo genetic effect (Go), endosperm genetic effects (Ge), cytoplasm effect (*C*) and maternal nuclear genetic effect (Gm) as well as their *GE* interaction effects,

$$\begin{aligned} P &= \mu + E + G + GE + B + \varepsilon \\ &= \mu + E + Go + Ge + C + Gm + GoE + GeE + CE + GmE + B + \varepsilon \end{aligned}$$

where μ= population mean, E = environment effect, G = total genotype effect, GE = genotype × environment interaction effect, Go = embryo genetic effect, Ge = endosperm genetic effect, C = cytoplasm effect, Gm = maternal genetic effect, GoE = $Go \times E$ interaction effect, GeE = $Ge \times E$ interaction effect, $CE = C \times E$ interaction effect, GmE = $Gm \times E$ interaction effect, B = block effect, ε = residual effect.

The phenotypic mean of the *k*-th mating type of genetic entry derived from parents *i* and *j* in the *l*-th block of environment *h* can be partitioned as

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

For Parent *i* ($k = 0$)

$$\begin{aligned} G_{ii0} + GE_{hii0} = 2Ao_i + Do_{ii} + 3Ae_i + 3De_{ii} + C_i + 2Am_i + Dm_{ii} + 2AoE_{hi} \\ + DoE_{hii} + 3AeE_{hi} + 3DeE_{hii} + CE_{hi} + 2AmE_{hi} + DmE_{hii} \end{aligned}$$

For F_1 ($k=1$)

$$G_{ij1} + GE_{hij1} = Ao_i + Ao_j + Do_{ij} + 2Ae_i + Ae_j + De_{ii} + 2De_{ij} + C_i$$
$$+ 2Am_i + Dm_{ii} + AoE_{hi} + AoE_{hj} + DoE_{hij} + 2AeE_{hi}$$
$$+ AeE_{hj} + DeE_{hii} + 2DeE_{hij} + CE_{hi} + 2AmE_{hi} + DmE_{hii}$$

For F_2 ($k=2$)

$$G_{ij2} + GE_{hij2} = Ao_i + Ao_j + 0.25Do_{ii} + 0.25Do_{jj} + 0.5Do_{ij} + 1.5Ae_i + 1.5Ae_j + De_{ii}$$
$$+ De_{jj} + De_{ij} + C_i + Am_i + Am_j + Dm_{ij} + AoE_{hi} + AoE_{hj} + 0.25DoE_{hii}$$
$$+ 0.25DoE_{hjj} + 0.5DoE_{hij} + 1.5AeE_{hi} + 1.5AeE_{hj} + DeE_{hii} + DeE_{hjj} + DeE_{hij}$$
$$+ CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}$$

where Ao_i or Ao_j = embryo additive effect, Do_{ii}, Do_{jj} or Do_{ij} = embryo dominance effect, Ae_i or Ae_j = direct endosperm additive effect, De_{ii}, De_{jj} or De_{ij} = endosperm dominance effect, C_i = cytoplasm effect, Am_i or Am_j = maternal additive effect, Dm_{ij} = maternal dominance effect, AoE_{hi} or $AoE_{hj} = Ao \times E_h$ interaction effect, DoE_{hii}, DoE_{hjj} or $DoE_{hij} = Do \times E_h$ interaction effect, AeE_{hi} or $AeE_{hj} = Ae \times E_h$ interaction effect, DeE_{hjj} or $DeE_{hij} = De \times E_h$ interaction effect, $CE_{hi} = C_i \times E_h$ interaction effect, AmE_{hi} or $AmE_{hj} = Am \times E_h$ interaction effect, $DmE_{hij} = Dm \times E_h$ interaction effect, B_l = block effect, ε_{ijkl} = residual effect

The full seed model can be expressed in a matrix form of mixed linear model

$$\mathbf{y} = \mathbf{Xb} + \mathbf{U}_{Ao}\mathbf{e}_{Ao} + \mathbf{U}_{Do}\mathbf{e}_{Do} + \mathbf{U}_{Ae}\mathbf{e}_{Ae} + \mathbf{U}_{De}\mathbf{e}_{De} + \mathbf{U}_{C}\mathbf{e}_{C} + \mathbf{U}_{Am}\mathbf{e}_{Am}$$
$$+ \mathbf{U}_{Dm}\mathbf{e}_{Dm} + \mathbf{U}_{AoE}\mathbf{e}_{AoE} + \mathbf{U}_{DoE}\mathbf{e}_{DoE} + \mathbf{U}_{AeE}\mathbf{e}_{AeE} + \mathbf{U}_{DeE}\mathbf{e}_{DeE}$$
$$+ \mathbf{U}_{CE}\mathbf{e}_{CE} + \mathbf{U}_{AmE}\mathbf{e}_{AmE} + \mathbf{U}_{DmE}\mathbf{e}_{DmE} + \mathbf{U}_{B}\mathbf{e}_{B} + \mathbf{e}_{\varepsilon}$$
$$= \mathbf{Xb} + \sum_{u=1}^{16} \mathbf{U}_u \mathbf{e}_u$$

where $\mathbf{e}_u$ are the random effects with $\mathbf{e}_{Ao} \sim (\mathbf{0}, \sigma^2_{Ao}\mathbf{I})$, $\mathbf{e}_{Do} \sim (\mathbf{0}, \sigma^2_{Do}\mathbf{I})$, $\mathbf{e}_{Ae} \sim (\mathbf{0}, \sigma^2_{Ae}\mathbf{I})$, $\mathbf{e}_{De} \sim (\mathbf{0}, \sigma^2_{De}\mathbf{I})$, $\mathbf{e}_{C} \sim (\mathbf{0}, \sigma^2_{C}\mathbf{I})$, $\mathbf{e}_{Am} \sim (\mathbf{0}, \sigma^2_{Am}\mathbf{I})$, $\mathbf{e}_{Dm} \sim (\mathbf{0}, \sigma^2_{Dm}\mathbf{I})$, $\mathbf{e}_{AoE} \sim (\mathbf{0}, \sigma^2_{AoE}\mathbf{I})$, $\mathbf{e}_{DoE} \sim (\mathbf{0}, \sigma^2_{DoE}\mathbf{I})$, $\mathbf{e}_{AeE} \sim (\mathbf{0}, \sigma^2_{AeE}\mathbf{I})$, $\mathbf{e}_{DeE} \sim (\mathbf{0}, \sigma^2_{DeE}\mathbf{I})$, $\mathbf{e}_{CE} \sim (\mathbf{0}, \sigma^2_{CE}\mathbf{I})$, $\mathbf{e}_{AmE} \sim (\mathbf{0}, \sigma^2_{AmE}\mathbf{I})$, $\mathbf{e}_{DmE} \sim (\mathbf{0}, \sigma^2_{DmE}\mathbf{I})$, $\mathbf{e}_{B} \sim (\mathbf{0}, \sigma^2_{B}\mathbf{I})$, $\mathbf{e}_{\varepsilon} \sim (\mathbf{0}, \sigma^2_{\varepsilon}\mathbf{I})$; $\mathbf{U}_u$ are known coefficient matrix and $\mathbf{I}$ is the identity matrix.

In this full seed model, genetic entries $i \times j$ (for $i, j = 1, 2, ..., 8$) were employed by using mating design of diallel crosses with F_1's and reciprocal F_1's, F_2's and reciprocal F_2's. Randomized complete block design was used with three replications in each environment. There were a total of 120 genetic entries in each block. In multiple environments, a total of 1080 entries was used for 3 environments. Environment effects were assumed as fixed with values of 50, 100, and 150 for 3 environments. Genetic effects were assumed independent and random. The genetic entries were assigned at random within each block. Variance components were estimated by MINQUE (1) method. Jackknifing over block method [4, 9] was conducted for estimating standard error. Pseudo-random normal deviates with zero mean and unit variance (0,1) were generated by the method of Kinderman and Monathan [8]. Five hundred simulations were used for computing sample mean of estimate, bias, MSE and power value. Bias is calculated as $\hat{\theta} - \theta$. If $\text{bias}/\theta \leq 5\%$, the estimate $\hat{\theta}$ is considered as unbiased [6]. Sampling variance of estimates is calculated by $\text{var}(\hat{\theta}) = \frac{1}{n-1}\sum(\hat{\theta} - \bar{\hat{\theta}})^2$. MSE is calculated by, $(\text{bias})^2 + \text{var}(\hat{\theta})$ which is usually used as a main criterion for comparing efficiency of estimation methods. The null hypothesis of no variation was tested by a *t*-test with 0.05 significant level. Power value (the probability of rejecting the null hypothesis) was obtained by five hundred runs of simulation.

Results and Discussion

All genetic components of genetic and genotype x environment effects were included in the full seed model. Embryo, endosperm, cytoplasm, maternal, and GE interaction effects compose the full seed model. By including or ignoring genetic effects or *GE* interaction effects, the full genetic model can be evaluated. Efficiency and variance components were analyzed according to the degree of the overestimation. The evaluation of the full seed model gave interesting results and information about the estimations of variance components of the different genetic effects (Table 1). Biases of variance components, $\sigma^2_{Ao}, \sigma^2_{Do}$ *and* σ^2_{Ae} were found to be around 10% of the parameter values. These variances tend to be well estimated for the full seed model including *GE* interaction effects. This model is employed especially when both embryo and endosperm are considered to be able to have effects on the quantitative studied seed traits. However, all the other estimated variance components were quite unbiased with reasonable power values. Estimated variance components of σ^2_C, σ^2_{Dm}, σ^2_{CE}, σ^2_{DmE} and σ^2_{ε} were highly unbiased. The present results indicated that the choice between full seed model including GE and without *GE* interaction effects must be based on the fundamental agronomic information about genetic main effects and *GE* interaction effects.

Therefore, what is about the efficiency and the overestimation of the different variance components if some genetic effects such as embryo, endosperm are to be ignored in the model. In addition, what is the degree of significance of the overestimated variances involved by each genetic and genotype by environment interaction effects. When embryo and embryo x environment interaction were ignored, endosperm and maternal genetic variances σ^2_{Ae}, σ^2_{De}, σ^2_{Am}, σ^2_{AeE}, σ^2_{DeE}, σ^2_{AmE} were highly increased. When the true value is equal to 30, Bias, MSE and power value of σ^2_{Ae} vary respectively from 3.45, 4233.76, 0.63 to 77.98, 11387.00, 0.98. If endosperm and endosperm x environment interaction were ignored, we observed the same phenomena for variance components such as σ^2_{Ao}, σ^2_{Do} σ^2_{Am}, σ^2_{AoE}, σ^2_{DoE}, σ^2_{AmE}. When the true value is equal to 80, these Bias, MSE and power value of σ^2_{Ao} increased respectively from -5.68, 5690.12, 0.80 to 27.73, 6050.85, 0.98.

Experiment of this genetic model should be conducted carefully. Since seeds are the offspring of maternal plants, the realizations of artificial emasculation and pollination need caution. Parent lines and F_1's are randomized within blocks to produce seeds of Parents, F_1 and F_2. The full seed model needs more control, more entries and replications in the experimental design especially when *GE* interaction effect is included. In this research of balanced eight parents modified diallel crosses, the significance of non-zero σ^2_C was detected with a probability over 99%. For the modified diallel crosses with F_1's and reciprocal F_1's, F_2's and reciprocal F_2's, size of eight parents was reasonable to obtain unbiased estimation. When more parents are involved in mating, power value of tests to detect significance could be increased. However, plant breeders usually can not use large sample size in conducting genetic research since seeds of F_1's should be produced by manual hybridization.

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Table 1. Bias, MSE and power value for variance components for full seed model with embryo and endosperm effects in multiple environments.

Parameter	True value	With embryo and endosperm effects			Ignoring embryo & embryo × environment			Ignoring endosperm & endosperm × environment		
		Bias	MSE	Power	Bias	MSE	Power	Bias	MSE	Power
σ^2_{Ao}	80	–5.68	5690.12	0.80	—	—	—	27.73	6050.85	0.98
σ^2_{Do}	50	5.29	32582.50	0.53	—	—	—	81.31	8672.84	1.00
σ^2_{Ae}	30	3.45	4233.76	0.63	77.98	11387.00	0.98	—	—	—
σ^2_{De}	20	–1.00	1995.34	0.61	12.83	293.68	1.00	—	—	—
σ^2_{C}	40	–0.20	621.03	0.99	–0.20	620.97	0.99	–0.19	621.34	0.99
σ^2_{Am}	25	0.12	677.12	0.77	22.37	1518.30	0.96	13.22	988.82	0.93
σ^2_{Dm}	25	0.00	69.41	1.00	0.00	69.46	1.00	–0.01	69.40	1.00
σ^2_{AoE}	20	1.07	456.18	0.70	—	—	—	20.08	757.34	1.00
σ^2_{DoE}	25	1.97	4254.95	0.47	—	—	—	59.84	3872.53	1.00
σ^2_{AeE}	20	–0.90	482.42	0.70	20.24	766.31	1.00	—	—	—
σ^2_{DeE}	15	–0.53	269.54	0.66	6.21	56.77	1.00	—	—	—
σ^2_{CE}	20	0.09	64.57	1.00	0.10	64.57	1.00	0.08	64.63	1.00
σ^2_{AmE}	20	0.42	110.60	0.98	7.53	194.69	1.00	8.90	218.92	1.00
σ^2_{DmE}	15	–0.05	10.85	1.00	–0.07	10.87	1.00	–0.02	10.85	1.00
σ^2_{ε}	10	0.00	0.26	1.00	–0.03	0.26	1.00	0.02	0.27	1.00