

XII. METODOLOGIA E TÉCNICAS EXPERIMENTAIS

ESTIMATION OF GENETIC PARAMETERS IN THE SQUARE LATTICE ANALYSIS ⁽¹⁾

JOSÉ MARCELO SORIANO VIANA ⁽²⁾ & ADAIR JOSÉ REGAZZI ⁽³⁾

ABSTRACT

This paper shows how to obtain unbiased estimates of genetic parameters of base populations, e.g., genotypic variance among families, heritability on a family mean basis, genotypic correlation and direct and indirect expected genetic gains, when the sampled families were evaluated in square lattice experiment. The theoretical part presents the variance and covariance components of the intra-block analysis of square lattice and the estimators of the components associated to treatment effect, considering the ordinary least squares method. In the analysis with treatments not corrected for blocks/replications, the estimator of the component due to treatment effect is equal to that of the analysis considering the complete block model. Experimental data from a breeding program of *Eucalyptus pyrocarpa* were used for genetic analysis. The high estimates of narrow sense heritabilities and additive genetic correlation, related to height and diameter, indicate that selection of the superior families will be effective in changing the means of the base population.

Index terms: quantitative genetics, genetic parameters, variance components, covariance components, square lattice.

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⁽²⁾Departamento de Biologia Geral, Universidade Federal de Viçosa, 36570-000 Viçosa (MG).

⁽³⁾Departamento de Informática, Universidade Federal de Viçosa, 36570-000 Viçosa (MG).

RESUMO

ESTIMAÇÃO DE PARÂMETROS GENÉTICOS NA ANÁLISE DE LÁTICE QUADRADO

Neste trabalho, apresenta-se um procedimento para a obtenção de estimativas não viesadas de parâmetros genéticos de populações-base, como variância genotípica entre famílias, herdabilidade em nível de média de família, correlação genotípica entre caracteres e ganhos genéticos esperados, diretos e indiretos, quando as progênies amostradas foram avaliadas no delineamento em látice quadrado. Na parte metodológica, são apresentados os componentes de variância e da covariância da análise intrablocos de látice quadrado e os estimadores dos componentes associados a efeito de tratamento, considerando estimação pelo método dos quadrados mínimos ordinário. Os estimadores dos componentes da variância e da covariância associados a efeito de tratamento da análise com tratamentos não ajustados são iguais aos da análise considerando modelo em blocos. Dados de um experimento de programa de melhoramento de *Eucalyptus pyrocarpa* foram usados para análise genética. Em vista dos elevados valores da herdabilidade em sentido restrito e da correlação genética aditiva, em relação a altura e diâmetro, a seleção das melhores famílias será eficiente em alterar as médias da população base.

Termos de indexação: genética quantitativa, parâmetros genéticos, componentes da variância, componentes de covariância, látice quadrado.

1. INTRODUCTION

The lattice is an incomplete block design in which blocks are arranged in orthogonal replications of treatments. It was introduced by Yates, in 1936, and has been considered appropriate for experiments with a large number of treatments, because the control of the experimental error can be inefficient if very large complete blocks are established (Federer, 1955, and Cochran & Cox, 1957). Since then, the efficiency of the lattice design, with and without recovery of inter-block information, as compared to complete block design and neighbor analysis, has been analyzed by many researchers. The superior accuracy of the lattice design was demonstrated in many studies (Atwood & Garber, 1942; Myers, 1942; Zuber, 1942; Johnson & Murphy, 1943; Wellhausen, 1943; Lin et al., 1993; Saad, 1994a,b). However, in some studies the block design was more efficient (Torrie et al., 1943, and Bancroft & Smith, 1949).

This is an important design for experiments of plant breeding programs in which numerous treat-

ments are evaluated (families, varieties, and so on) (Sahagun-Castellanos & Frey, 1990; Brenner et al., 1991; Beninati & Busch, 1992; Chaves & Miranda Filho, 1992; Singh et al., 1992; Arriel et al., 1993; Marques et al., 1993; Michelini & Hallauer, 1993; Moncada et al., 1993; Ferrão et al., 1994; Naito & Ogawa, 1994; Rezende & Ramalho, 1994; Bisognin et al., 1995, and Bong & Swaminathan, 1995). The objective of experimental evaluation of families sampled from a base population is to assess its genetic structure. Data from these trials are used to draw inferences on genetic variability in the population, in relation to one or more characteristics, on the genic control of these traits, on genotypic correlation between characters etc., favoring the choice of selective procedures able to maximize the expected direct and indirect gains. Such inferences require the estimation of genetic parameters, such as additive genetic variance and genotypic covariance, using estimates of variance and covariance components (Kempthorne, 1957).

In many lattice experiments, however, the estimation of variance and covariance components is based on approximate processes. Sometimes, the design is not taken into account and the analysis is performed considering the complete block model. This is not necessary if the expected mean squares are known or if the software used for the analysis permits the estimation, as is the case with the VARCOMP procedure of the SAS/STAT® (SAS Institute, 1989).

The purpose of this paper is to present a procedure to obtain unbiased estimates of genetic parameters of populations, using the estimates of variance and covariance components of the intra-block analysis of square lattice, considering the ordinary least squares method.

2. THE INTRA-BLOCK ANALYSIS OF SQUARE LATTICE

The complete statistical model is:

$$Y_{ii(j)} = \mu + t_i + r_j + (b|r)_{l(j)} + e_{ii(j)}$$

where:

$Y_{ii(j)}$ is the observation of the treatment i ($i = 1, \dots, v = k^2$), in the block l ($l = 1, \dots, k$) of the replication j ($j = 1, \dots, m$);

μ is a constant common to all observations;
 t_i is the effect of the treatment i ;
 r_j is the effect of the replication j ;
 $(b|r)_{l(j)}$ is the effect of the block l of the replication j ;
 $e_{ii(j)}$ is the error associated to the observation $Y_{ii(j)}$, where $e_{ii(j)} \sim N(0, \sigma)$, independent.

The linear model we consider is:

$$Y = X\Theta + \varepsilon, \text{ where } \varepsilon \sim N(\Phi^2, \sigma^2 I)$$

with:

$$\Theta' = [\mu | t_1 \dots t_v | r_1 \dots r_m | (b|r)_{1(1)} \dots (b|r)_{k(m)}] = [\mu | \tau' | \alpha' | \beta']$$

In the analysis of variance, the orthogonal partitions of the reduction in the total sum of squares due to fitting the complete model will be as follows:

$$R(\mu, \tau, \alpha, \beta) = R(\mu) + R(\alpha|\mu) + R(\beta|\mu, \alpha) + R(\tau|\mu, \alpha, \beta) \\ = R(\mu) + R(\alpha|\mu) + R(\tau|\mu, \alpha) + R(\beta|\mu, \tau, \alpha),$$

where $R(\cdot) = Y'X(X'X)^G X'Y$ is the reduction in the total sum of squares due to fitting a certain model, with rank of $X(X'X)^G X' =$ rank of X degrees of freedom, being $(X'X)^G$ any generalized inverse of $X'X$, and $R(\cdot|\cdot)$ is a difference between two $R(\cdot)$ terms (Searle, 1971; Searle et al., 1992; and Graybill, 1976).

The analyses of variance related to the two partitions of $R(\mu, \tau, \alpha, \beta)$ are shown in Table 1.

Table 1. Analyses of variance of square lattice

Source of variation	Degrees of freedom	Sum of squares	Mean square
Constant	1	$R(\mu)$	$R(\mu)$
Replications	$(m - 1)$	$R(\alpha \mu)$	MSR
Blocks Rep.	$m(k - 1)$	$R(\beta \mu, \alpha)$	MSB R(N.Adj.)
Treatments (Adjusted)	$(v - 1)$	$R(\tau \mu, \alpha, \beta)$	MST(Adj.)
Error	$(k - 1)(mk - k - 1)$	$Y'Y - R(\mu, \tau, \alpha, \beta)$	MSe
Constant	1	$R(\mu)$	$R(\mu)$
Replications	$(m - 1)$	$R(\alpha \mu)$	MSR
Blocks Rep. (Adjusted) ..	$m(k - 1)$	$R(\beta \mu, \tau, \alpha)$	MSB R(Adj.)
Treatments	$(v - 1)$	$R(\tau \mu, \alpha)$	MST(N.Adj.)
Error	$(k - 1)(mk - k - 1)$	$Y'Y - R(\mu, \tau, \alpha, \beta)$	MSe

2.1. The intra-block analysis of the random model

In the random model, with exception of the constant μ , all the effects are random variables. The assumptions associated to the statistical model are:

- (a) $t_i \sim N(0, \sigma_t^2)$, independent;
- (b) $r_j \sim N(0, \sigma_r^2)$, independent;
- (c) $(b|r)_{il(j)} \sim N(0, \sigma_b^2)$, independent;
- (d) $e_{il(j)} \sim N(0, \sigma^2)$, independent;
- (e) $t_i, r_j, (b|r)_{il(j)}$ and $e_{il(j)}$ are independent.

In the covariance matrix of Y, $Cov(Y) = E\{[Y - E(Y)][Y - E(Y)]'\} = \Sigma_{(n)} \neq \sigma^2 I, n = mk^2$, the elements are:

$$V(Y_{il(j)}) = \sigma_t^2 + \sigma_r^2 + \sigma_b^2 + \sigma^2$$

$$Cov(Y_{il(j)}, Y_{i'l'(j)}) = \sigma_r^2 + \sigma_b^2 \quad (i \neq i')$$

$$Cov(Y_{il(j)}, Y_{i'l'(j)}) = \sigma_r^2 \quad (i \neq i' \text{ and } l \neq l')$$

$$Cov(Y_{il(j)}, Y_{i'l'(j')}) = \sigma_t^2 \quad (j \neq j')$$

$$Cov(Y_{il(j)}, Y_{i'l'(j')}) = 0 \quad (i \neq i' \text{ and } j \neq j')$$

Using the property of mathematical expectation of quadratic forms (Searle, 1971; Searle et al., 1992, and Graybill, 1976), the expected values below and those of the mean squares described in Table 2, can be demonstrated:

$$E(Y'Y) = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + n\sigma^2$$

$$E[R(\mu)] = n\mu^2 + m\sigma_t^2 + v\sigma_r^2 + k\sigma_b^2 + \sigma^2$$

Each analysis (Table 1) provides an estimate of the variance component associated to treatment effect (σ_t^2). The two estimators are:

$$\hat{\sigma}_{t(1)}^2 = \left(\frac{k+1}{k}\right) \left[\frac{MST(Adj.) - MS\epsilon}{m} \right]$$

$$\hat{\sigma}_{t(2)}^2 = \left[\frac{MST(N.Adj.) - MSe}{m} \right] \left[\frac{MSB|R(Adj.) - MSe}{(k+1)(m-1)} \right]$$

$$= \left[\frac{MST(N.Adj.) - MSe_{CB}}{m} \right]$$

where MSe_{CB} is the error mean square of the analysis according to the complete block model.

Therefore, the estimator $\hat{\sigma}_{t(2)}^2$ is identical to that of the analysis considering the complete block model.

In the analysis of experiments with progenies sampled from a base population, the variance component associated to treatment effect is the variance of the genotypic means of the families that can be obtained from the reference population, and it is used to estimate genetic parameters. The estimation of genotypic correlation depends on the estimation of the covariance among treatment effects, in relation to two traits .

Table 2. Expected mean squares of the analyses of variance of square lattice, considering the random model

Source of variation	E(M.S.)
Replications	$\sigma^2 + k\sigma_b^2 + v\sigma_r^2$
Blocks Rep.	$\sigma^2 + \sigma_t^2 + k\sigma_b^2$
Treatments (Adjusted)	$\sigma^2 + \left(\frac{k}{k+1}\right) m\sigma_t^2$
Error	σ^2
Replications	$\sigma^2 + k\sigma_b^2 + v\sigma_r^2$
Blocks Rep. (Adjusted)	$\sigma^2 + \left(\frac{m-1}{m}\right) k\sigma_b^2$
Treatments	$\sigma^2 + \left(\frac{k}{k+1}\right) \sigma_b^2 + m\sigma_t^2$
Error	σ^2

Let us consider the following statistical models in which Y and X are random variables:

$$Y_{i(j)} = \mu_Y + t_{iY} + r_{jY} + (b|r)_{i(j)Y} + e_{i(j)Y} \quad (1)$$

$$X_{i(j)} = \mu_X + t_{iX} + r_{jX} + (b|r)_{i(j)X} + e_{i(j)X} \quad (2)$$

$$\begin{aligned} Y_{i(j)} + X_{i(j)} &= (\mu_Y + \mu_X) + (t_{iY} + t_{iX}) + (r_{jY} + r_{jX}) + [(b|r)_{i(j)Y} \\ &\quad + (b|r)_{i(j)X}] + (e_{i(j)Y} + e_{i(j)X}) \\ &= \mu + t_i + r_j + (b|r)_{i(j)} + e_{i(j)} \quad (3) \end{aligned}$$

Assuming that:

(a) $t_i = (t_{iY} + t_{iX}) \sim (0, \sigma_t^2 = \sigma_{tY}^2 + \sigma_{tX}^2 + 2\sigma_{tYX})$, independent;

(b) $r_j = (r_{jY} + r_{jX}) \sim (0, \sigma_r^2 = \sigma_{rY}^2 + \sigma_{rX}^2 + 2\sigma_{rYX})$, independent;

(c) $(b|r)_{i(j)} = [(b|r)_{i(j)Y} + (b|r)_{i(j)X}] \sim (0, \sigma_b^2 = \sigma_{bY}^2 + \sigma_{bX}^2 + 2\sigma_{bYX})$, independent;

(d) $e_{i(j)} = [e_{i(j)Y} + e_{i(j)X}] \sim (0, \sigma^2 = \sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX})$, independent;

(e) $t_i, r_j, (b|r)_{i(j)}$ and $e_{i(j)}$ are independent;

and from previous results, we have the mathematical expectations presented in Table 3.

Therefore, two estimates of the covariance component σ_{tYX} can be obtained from the analyses of variance of Y, X and Y + X. The estimators are:

Therefore, $\hat{\sigma}_{tYX(2)}$ is the estimator of the analysis considering the complete block model. When the treatments are families sampled from a base population, σ_{tYX} is the covariance between genotypic means of the same family, in relation to the traits Y and X.

3. APPLICATION

Table 4 presents the analysis of variance of height and diameter of 49 half-sib families of *Eucalyptus pyrocarpa*, obtained from a non inbred population, evaluated in a 7 x 7 simple lattice. The SAEG (System for Statistical Analyses) program, developed by the Universidade Federal de Viçosa, was used for the analysis. There is genetic variability for height and diameter in the base population. Estimates of some genetic parameters, obtained from the estimates of the genotypic variance between families and the covariance between genotypic means of the same half-sib progeny, are shown in Table 5. The slight difference between the estimates of $\sigma_{t(1)}^2$ and $\sigma_{t(2)}^2$ and of $\sigma_{t(1)}$

$$\hat{\sigma}_{tYX(1)} = \left(\frac{k+1}{k} \right) \left\{ \frac{[MST(Adj.)(Y+X) - MST(Adj.)(Y) - MST(Adj.)(X)] - [MSe(Y+X) - MSe(Y) - MSe(X)]}{2m} \right\}$$

$$\hat{\sigma}_{tYX(2)} = \left\{ \frac{[MST(N.Adj.)(Y+X) - MST(N.Adj.)(Y) - MST(N.Adj.)(X)] - [MSe(Y+X) - MSe(Y) - MSe(X)]}{2m} \right\}$$

$$- \left\{ \frac{[MSB|R(Adj.)(Y+X) - MSB|R(Adj.)(Y) - MSB|R(Adj.)(X)] - [MSe(Y+X) - MSe(Y) - MSe(X)]}{2(k+1)(m-1)} \right\}$$

$$= \left\{ \frac{[MST(N.Adj.)(Y+X) - MST(N.Adj.)(Y) - MST(N.Adj.)(X)] - [MSe_{CB}(Y+X) - MSe_{CB}(Y) - MSe_{CB}(X)]}{2m} \right\}$$

Table 3. Expected mean squares of the analyses of variance of square lattice, considering the random model, in relation to the Y+X variable

Source of variation	E(M.S.)
Replications	$[\sigma^2_Y + k\sigma^2_{bY} + v\sigma^2_{rY}] + [\sigma^2_X + k\sigma^2_{bX} + v\sigma^2_{rX}] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks Rep.	$[\sigma^2_Y + \sigma^2_{tY} + k\sigma^2_{bY}] + [\sigma^2_X + \sigma^2_{tX} + k\sigma^2_{bX}] + 2[\sigma_{YX} + \sigma_{tYX} + k\sigma_{bYX}]$
Treatments (Adj.)	$[\sigma^2_Y + (\frac{k}{k+1})m\sigma^2_{tY}] + [\sigma^2_X + (\frac{k}{k+1})m\sigma^2_{tX}] + 2[\sigma_{YX} + (\frac{k}{k+1})m\sigma_{tYX}]$
Error	$\sigma^2_Y + \sigma^2_X + 2\sigma_{YX}$
Replications	$[\sigma^2_Y + k\sigma^2_{bY} + v\sigma^2_{rY}] + [\sigma^2_X + k\sigma^2_{bX} + v\sigma^2_{rX}] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks Rep. (Adj.)	$[\sigma^2_Y + (\frac{m-1}{m})k\sigma^2_{bY}] + [\sigma^2_X + (\frac{m-1}{m})k\sigma^2_{bX}] + 2[\sigma_{YX} + (\frac{m-1}{m})k\sigma_{bYX}]$
Treatments	$[\sigma^2_Y + (\frac{k}{k+1})\sigma^2_{bY} + m\sigma^2_{tY}] + [\sigma^2_X + (\frac{k}{k+1})\sigma^2_{bX} + m\sigma^2_{tX}] + 2[\sigma_{YX} + (\frac{k}{k+1})\sigma_{bYX} + m\sigma_{tYX}]$
Error	$\sigma^2_Y + \sigma^2_X + 2\sigma_{YX}$

Table 4. Analysis of variance of height and diameter of 49 half-sib families of *Eucalyptus pyrocarpa*

Source of variation	Degrees of freedom	Mean square	
		Height	Diameter
		m	m
Replications	1	5.1796	0.3984 x 10 ⁻³
Blocks Rep. (Adj.)	12	1.9872	0.1893 x 10 ⁻³
Families (Adj.)	48	5.0499**	0.6203 x 10 ^{-3**}
Error	36	2.0041	0.2579 x 10 ⁻³

** : P < 0.01.

and $\sigma^2_{t(2)}$, for both characters, reflects homogeneity between blocks within replication.

A relevant portion of the variance of the phenotypic means of the families is ascribed to the differences between the additive genetic values of their common parents, indicating that the genotypic means of height and diameter, in the base population, can be changed by selection. For each trait, the magnitude of the estimate of the heritability in the narrow sense indicates that the families with greater phenotypic means should have the common parent with greater additive genetic value (greater number of genes that increase the character). The correlation between mean

phenotypic value of the family and the additive genetic value of its common parent is $\sqrt{0.60} = 0.77$ for height and $\sqrt{0.59} = 0.77$ for diameter (Viana, 1996b), indicating that the selection based on height or diameter will be efficient in changing the population mean.

In relation to height, the selection of the 15 best families (selection intensity of approximately 1.138) can induce genetic gain of 8.17%, considering recombination occurring only with selected families. The predicted direct gain in relation to diameter is 10.67%. The correlation between genotypic means of same half-sib family, in relation to two traits, is the correlation between additive genetic values of the

individuals in the reference population (Viana, 1996a). The high additive genetic correlation between the traits shows that the population plants with greater additive genetic value for height should have greater additive genetic value for diameter. Therefore, the direct selection based on one characteristic will alter the genotypic mean of the population in relation to the other character in the same direction. The expected indirect gain in relation to diameter, due to selection based on height, is $(0.139 - 0.119) \cdot (0.59) \cdot 100 / (0.119) = 9.92\%$. If the selection is based on diameter, the predicted indirect gain in relation to height is $(15.99 - 14.27) \cdot (0.60) \cdot 100 / (14.27) = 7.23\%$.

Table 5. Estimates of variance and covariance components associated to treatment effects and of some other genetic parameters⁽¹⁾, in relation to height and diameter of *E. pyrocarpa* population half-sib families

Parameter	Trait	Estimate
	m	
$\sigma^2_{t(1)}$	Height	1.74
	Diameter	0.21×10^{-3}
$\sigma^2_{t(2)}$	Height	1.59
	Diameter	0.20×10^{-3}
$\sigma_{t(1)}$		0.018
$\sigma_{t(2)}$		0.017
Population mean	Height	14.27
	Diameter	0.119
Mean of the selected families (selection based on height)	Height	16.12
	Diameter	0.139
Mean of the selected families (selection based on diameter)	Height	15.99
	Diameter	0.141
h^2	Height	0.60
	Diameter	0.59
ΔG	Height	8.17%
	Diameter	10.67%
r_A	–	0.97

⁽¹⁾The values of h^2 (heritability in the narrow sense, on a family mean basis), ΔG (expected genetic gain due to selection and recombination of the 15 best families, expressed as percentage of the mean of the base population) and r_A (additive genetic correlation between height and diameter), were obtained considering the estimates of $\sigma^2_{t(1)}$ and $\sigma_{t(1)}$. The variance of the phenotypic means of the families was estimated using the estimator $MST (Adj.) / (k / (k+1))ms$.

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