

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

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

ABSTRACT

Aiming to demonstrate how to obtain unbiased estimates of genetic parameters of base populations, unaffected by genotype x environment effects, this paper presents the variance and covariance components of the intra-block analysis of a group of square lattice experiments and the estimators of the components associated to treatment effect. Random model and mixed models with environment effect fixed and other effects random are considered. In the analysis with treatments not corrected for blocks/replications/environments, the estimators of the variance and covariance components due to treatment effect are different from those of the analysis considering the complete block model. Data from two experiments of a breeding program of *Eucalyptus pyrocarpa* were used for genetic analysis. The analysis of variance of height and diameter indicated absence of interaction between progeny and environment. Due to this result, the prediction of the direct and indirect genetic gains was based on the mean of the two environments. The high estimates of narrow sense heritabilities and additive genetic correlation indicate that selection of the superior families will be effective in changing the means of the base population for both traits.

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

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⁽²⁾ Engenheiro Agrônomo D.Sc., Departamento de Biologia Geral, Universidade Federal de Viçosa, 36.570-000 Viçosa (MG).

⁽³⁾ Eng.-Agr., D.Sc., Departamento de Informática, Universidade Federal de Viçosa, 36.570-000 Viçosa (MG).

RESUMO

ESTIMAÇÃO DE PARÂMETROS GENÉTICOS NA ANÁLISE DE GRUPO DE EXPERIMENTOS EM LÁTICE QUADRADO

Neste trabalho, discute-se a estimação de parâmetros genéticos de populações-base, quando as famílias amostradas foram avaliadas em dois ou mais ambientes, no delineamento em látice quadrado. Na parte teórica, são apresentados os componentes de variância e covariância da análise intrablocos de grupo de experimentos em 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 covariância da análise com tratamentos não ajustados diferem dos da análise segundo modelo em blocos completos. Além de modelo aleatório, consideram-se também os mistos com efeito de ambiente fixo e demais efeitos aleatórios. Dados de dois experimentos de um programa de melhoramento de *Eucalyptus pyrocarpa* foram usados para análise genética. Como em relação às características altura e diâmetro não houve evidência de interação progênie x ambiente, a predição de ganhos diretos e indiretos foi feita com base na média dos dois ambientes. Os valores elevados da herdabilidade em sentido restrito e da correlação genética aditiva evidenciam que a seleção das famílias superiores será eficiente em alterar as médias da população-base, para as duas características.

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

1. INTRODUCTION

The evaluation of a group of treatments (families, varieties etc.) in more than one environmental condition is common in breeding programs. This allows to study the interaction between treatments and environments (local and/or years, and so on) and, when the treatments are families sampled from a base population, the estimation of genetic parameters not affected by the progeny x environment interaction. Due to its implication on the selective process by decreasing the correlation between phenotypic and genotypic values, the genotype x environment interaction is a complex and widely investigated problem, which must be considered in breeding programs. Since a high number of treatments is normally used in these experiments, the lattice design has been frequently used (Zuber, 1942; Johnson & Murphy, 1943; Torrie et al., 1943; Wellhausen, 1943; Bancroft & Smith, 1949; Sahagun-Castellanos & Frey, 1990; Beninati & Busch, 1992; Chaves & Miranda Filho, 1992; Singh et al., 1992; Arriel et al., 1993; Lin et al., 1993; Michelini

& Hallauer, 1993; Moncada et al., 1993; Oliveira, 1993; Ferrão et al., 1994, and Rezende & Ramalho, 1994), contributing to increase experimental error control efficiency (Cochran & Cox, 1957, and Federer, 1955).

In many cases, however, the joint analysis of lattice experiments and, particularly, the estimation of the variance and covariance components used to estimate genetic parameters, e.g., genotypic variance between families, additive genetic variance, heritability on a family mean basis, genotypic correlation and expected genetic gain (Kempthorne, 1957), involve approximate processes. The lattice design sometimes is not taken into account with the complete block model being considered.

An exact estimation of the variance and covariance components is possible if the expected mean squares are known or if the program used for the analysis makes itself the estimation (for example, the VARCOMP procedure of SAS/STAT® (SAS Institute, 1989)). The purpose of this paper is to show how to estimate genetic parameters of populations, using the

estimates of the variance and covariance components of the intra-block analysis of a group of square lattice experiments, considering the least squares method.

2. THE INTRA-BLOCK ANALYSIS OF A GROUP OF SQUARE LATTICE EXPERIMENTS

The complete statistical model is:

$$Y_{il(j)(g)} = \mu + t_i + (r|a)_{j(g)} + (b|r|a)_{l(j)(g)} + a_g + (ta)_{ig} + e_{il(j)(g)}$$

where:

$Y_{il(j)(g)}$ 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 ($j = 1, \dots, m$), in the environment g ($g = 1, \dots, s$);

μ is a constant common to all observations;

t_i is the effect of the treatment i ;

$(r|a)_{j(g)}$ is the effect of the replication j in the environment g ;

$(b|r|a)_{l(j)(g)}$ is the effect of the block l of the replication j , in the environment g ;

a_g is the effect of the environment g ;

$(ta)_{ig}$ is the effect of the interaction between the treatment i and the environment g ;

$e_{il(j)(g)}$ is the error associated to the observation $Y_{il(j)(g)}$; $e_{il(j)(g)} \sim N(0, \sigma^2)$, independent.

The matricial form of the linear model we consider is:

$$Y = X\Theta + e; \quad e \sim N(\Phi, \sigma^2 I)$$

with:

$$Q' = [\mu \mid t_1 \dots t_v \mid (r|a)_{1(1)} \dots (r|a)_{m(s)} \mid (b|r|a)_{1(1)(1)} \dots (b|r|a)_{k(m)(s)} \mid a_1 \dots a_s \mid (ta)_{11} \dots (ta)_{vs}]$$

$$= [\mu \mid \tau' \mid \alpha' \mid \beta' \mid \delta' \mid \tau\delta']$$

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

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

where $R(\cdot) = Y'X(X'X)^GX'Y$ is the reduction in the

total sum of squares due to fitting a certain model, with rank of $X(X'X)^GX' = \text{rank of } X$ 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, 1992, and Graybill, 1976).

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

2.1. The intra-block analysis of random model

The assumptions of the statistical model are:

a) $t_i \sim N(0, \sigma_t^2)$, independent;

b) $(r|a)_{j(g)} \sim N(0, \sigma_r^2)$, independent;

c) $(b|r|a)_{l(j)(g)} \sim N(0, \sigma_b^2)$, independent;

d) $a_g \sim N(0, \sigma_a^2)$, independent;

e) $(ta)_{ig} \sim N(0, \sigma_{ta}^2)$, independent;

f) $e_{il(j)(g)} \sim N(0, \sigma^2)$, independent;

g) $t_i, (r|a)_{j(g)}, (b|r|a)_{l(j)(g)}, a_g, (ta)_{ig}$ and $e_{il(j)(g)}$ are independent.

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

$$V(Y_{il(j)(g)}) = \sigma_t^2 + \sigma_r^2 + \sigma_b^2 + \sigma_a^2 + \sigma_{ta}^2 + \sigma^2 = C_0$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j)(g)}) = \sigma_r^2 + \sigma_b^2 + \sigma_a^2 = C_1 \quad (i \cdot i')$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j')(g)}) = \sigma_r^2 + \sigma_a^2 = C_2 \quad (i \cdot i' \text{ and } l \cdot l')$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j')(g)}) = \sigma_t^2 + \sigma_a^2 + \sigma_{ta}^2 = C_3 \quad (j \cdot j')$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j')(g)}) = \sigma_a^2 = C_4 \quad (i \cdot i' \text{ and } j \cdot j')$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j')(g)}) = \sigma_t^2 = C_5 \quad (g \cdot g')$$

$$\text{Cov}(Y_{il(j)(g)}, Y_{i'l'(j')(g)}) = 0 = C_6 \quad (i \cdot i' \text{ and } g \cdot g')$$

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

$$E(Y'Y) = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + n\sigma_a^2 + n\sigma_{ta}^2 + n\sigma^2$$

$$E[R(\mu)] = n\mu^2 + m\sigma_t^2 + v\sigma_r^2 + k\sigma_b^2 + mv\sigma_a^2 + m\sigma_{ta}^2 + \sigma^2$$

$$E[R(\mu, \tau, \delta, \alpha, \beta)] = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + n\sigma_a^2 + [mks + mk(k-1)]\sigma_{ta}^2 + (v + mks - 1)\sigma^2$$

Considering that the treatments are families sampled from a base population, the two estimators of the variance of the genotypic means of the progenies that can be obtained from the reference population (σ_t^2) are:

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

$$\hat{\sigma}_{t(2)}^2 = \left[\frac{\text{MST(N.Adj.)} - \text{MSe} - m\hat{\sigma}_{ta}^2 - \left(\frac{k}{k+1}\right)\hat{\sigma}_{b(2)}^2}{\text{ms}} \right] \neq \left[\frac{\text{MST (N. Adj.)} - \text{MSTE}_{\text{CB}}}{\text{ms}} \right]$$

where:

$$\hat{\sigma}_{ta}^2 = \left(\frac{k+1}{k}\right) \left(\frac{\text{MSTE} - \text{MSe}}{m}\right)$$

$$\hat{\sigma}_{b(2)}^2 = \left[\frac{\text{ms}}{k(\text{ms} - 1)} \left[\text{MSB} \} \text{R} \} \text{E (Adj.)} - \text{MSe} - \left(\frac{s-1}{s}\right)\hat{\sigma}_{ta}^2 \right] \right]$$

and MSTE_{CB} is the treatments x environments interaction mean square, considering the complete block model.

Therefore, $\hat{\sigma}_{t(2)}^2$ is not the estimator of σ_t^2 of the analysis according to the complete block model.

The following statistical models are considered to estimate covariance components:

$$Y_{il(j)(g)} = \mu_Y + t_{iY} + (r|a)_{j(g)Y} + (b|r|a)_{l(j)(g)Y} + a_{gY} + (ta)_{igY} + e_{il(j)(g)Y} \tag{1}$$

$$X_{il(j)(g)} = \mu_X + t_{iX} + (r|a)_{j(g)X} + (b|r|a)_{l(j)(g)X} + a_{gX} + (ta)_{igX} + e_{il(j)(g)X} \tag{2}$$

$$Y_{il(j)(g)} + X_{il(j)(g)} = (\mu_Y + \mu_X) + (t_{iY} + t_{iX}) + [(r|a)_{j(g)Y} + (r|a)_{j(g)X}] + [(b|r|a)_{l(j)(g)Y} + (b|r|a)_{l(j)(g)X}] + (a_{gY} + a_{gX}) + [(ta)_{igY} + (ta)_{igX}] + (e_{il(j)(g)Y} + e_{il(j)(g)X}) = \mu + t_i + (r|a)_{j(g)} + (b|r|a)_{l(j)(g)} + a_g + (ta)_{ig} + e_{il(j)(g)} \tag{3}$$

where Y and X are random variables.

Let us consider random models and the following assumptions:

- (a) $t_i = (t_{iY} + t_{iX}) \sim (0, \sigma_t^2 = \sigma_{tY}^2 + \sigma_{tX}^2 + 2\sigma_{tYX})$, independent;
- (b) $(r|a)_{j(g)} = [(r|a)_{j(g)Y} + (r|a)_{j(g)X}] \sim (0, \sigma_r^2 = \sigma_{rY}^2 + \sigma_{rX}^2 + 2\sigma_{rYX})$, independent;
- (c) $(b|r|a)_{l(j)(g)} = [(b|r|a)_{l(j)(g)Y} + (b|r|a)_{l(j)(g)X}] \sim (0, \sigma_b^2 = \sigma_{bY}^2 + \sigma_{bX}^2 + 2\sigma_{bYX})$, independent;
- (d) $a_g = (a_{gY} + a_{gX}) \sim (0, \sigma_a^2 = \sigma_{aY}^2 + \sigma_{aX}^2 + 2\sigma_{aYX})$, independent;
- (e) $(ta)_{ig} = [(ta)_{igY} + (ta)_{igX}] \sim (0, \sigma_{ta}^2 = \sigma_{taY}^2 + \sigma_{taX}^2 + 2\sigma_{taYX})$, independent;
- (f) $e_{il(j)(g)} = [e_{il(j)(g)Y} + e_{il(j)(g)X}] \sim (0, \sigma^2 = \sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX})$, independent;
- (g) $t_i, (r|a)_{j(g)}, (b|r|a)_{l(j)(g)}, a_g, (ta)_{ig}$ and $e_{il(j)(g)}$ are independent.

From previous results, the expected mean squares presented in Table 3 are obtained. The two estimators of the covariance between genotypic means of the same family, in relation to Y and X (σ_{tYX}), are:

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

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

where:

$$\hat{\sigma}_{YX} = \frac{MSe(Y+X) - MSe(Y) - MSe(X)}{2}$$

$$\hat{\sigma}_{taYX} = \left(\frac{k+1}{k} \right) \left(\frac{MSTE(Y+X) - MSTE(Y) - MSTE(X) - 2\sigma_{YX}}{2m} \right)$$

$$\hat{\sigma}_{bYX(2)} = \left[\frac{ms}{2k(ms-1)} \right] \left[MSB\{R\}E(Adj.)(Y+X) - MSB\{R\}E(Adj.)(Y) - MSB\{R\}E(Adj.)(X) - 2\hat{\sigma}_{YX} - 2\left(\frac{s-1}{s}\right)\hat{\sigma}_{taYX} \right]$$

2.2. The intra-block analysis of the mixed model with environment effect fixed and other effects random

If the number of environments is reduced they cannot be a representative sample of a population. In these cases and when the researcher is interested in inferring about the chosen environments, their effects should be considered fixed.

2.2.1. Unrestricted mixed model

Generally, when one of the main factors (treatment or environment) is fixed, the sum of the interaction effects in relation to the fixed factor is assumed to be zero. In the unrestricted mixed model, the elements of the covariance matrix of Y are:

$$C_0 = \sigma_t^2 + \sigma_r^2 + \sigma_b^2 + \sigma_{ta}^2 + \sigma^2$$

$$C_1 = \sigma_r^2 + \sigma_b^2$$

$$C_2 = \sigma_r^2$$

$$C_3 = \sigma_t^2 + \sigma_{ta}^2$$

$$C_4 = 0$$

$$C_5 = \sigma_t^2$$

$$C_6 = 0$$

Considering the expectation of quadratic forms, the following expected values and the expected mean squares of the analyses of variance can be demonstrated:

$$E(Y'Y) = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + mv \sum_{g=1}^s a_g^2 + n\sigma_{ta}^2 + n\sigma^2 + 2mv\mu \sum_{g=1}^s a_g$$

$$E[R(\mu)] = n\mu^2 + ms\sigma_t^2 + v\sigma_r^2 + k\sigma_b^2 + \frac{mv}{S} \left(\sum_{g=1}^s a_g \right)^2 + m\sigma_{ta}^2 + \sigma^2 + 2mv\mu \sum_{g=1}^s a_g$$

$$E[R(\mu, \tau, \delta, \alpha, \beta)] = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + mv \sum_{g=1}^s a_g^2 + [mks + mk(k-1)]\sigma_{ta}^2 + (v + mks - 1)\sigma^2 + 2mv\mu \sum_{g=1}^s a_g$$

Table 1. Analyses of variance of group of square lattice experiments

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

Constant	1	$R(\mu)$	$R(\mu)$
Replications Environment	$s(m - 1)$	$R(\alpha \mu, \delta)$	MSR E
Blocks Rep. Env. (Adjusted) ..	$sm(k - 1)$	$R(\beta \mu, \tau, \delta, \alpha)$	MSB R E(Adj.)
Treatments	$(v - 1)$	$R(\tau \mu, \delta, \alpha)$	MST(N.Adj.)
Environments	$(s - 1)$	$R(\delta \mu)$	MSE
Treatments x Environments ...	$(v - 1)(s - 1)$	$R(\tau\delta \mu, \tau, \delta, \alpha, \beta)$	MSTE
Error	$s(k - 1)(mk - k - 1)$	$Y'Y - R(\mu, \tau, \alpha, \beta, \delta, \tau\delta)$	MSe

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

Source of variation	E(M.S.)
Replications Environment	$\sigma^2 + k\sigma_b^2 + v\sigma_b^2$
Blocks Rep. Env.	$\sigma^2 + \sigma_{ta}^2 + \sigma_t^2 + k\sigma_b^2$
Treatments (Adjusted)	$\sigma^2 + \left(\frac{k}{k+1}\right)m\sigma_{ta}^2 + \left(\frac{k}{k+1}\right)ms\sigma_t^2$
Environments	$\sigma^2 + m\sigma_{ta}^2 + v\sigma_r^2 + k\sigma_b^2 + mv\sigma_a^2$
Treatments x Environments	$\sigma^2 + \left(\frac{k}{k+1}\right)m\sigma_{ta}^2$
Error	σ^2

Replications Environment	$\sigma^2 + k\sigma_b^2 + v\sigma_r^2$
Blocks Rep. Env. (Adjusted)	$\sigma^2 + \left(\frac{s-1}{s}\right)\sigma_{ta}^2 + \left(\frac{ms-1}{ms}\right)k\sigma_b^2$
Treatments	$\sigma^2 + m\sigma_{ta}^2 + \left(\frac{k}{k+1}\right)\sigma_b^2 + ms\sigma_t^2$
Environments	$\sigma^2 + m\sigma_{ta}^2 + v\sigma_r^2 + k\sigma_b^2 + mv\sigma_a^2$
Treatments x Environments	$\sigma^2 + \left(\frac{k}{k+1}\right)m\sigma_{ta}^2$
Error	σ^2

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

Source of variation	E(M.S.)
Replications Env.	$[\sigma_Y^2 + k\sigma_{bY}^2 + v\sigma_{rY}^2] + [\sigma_X^2 + k\sigma_{bX}^2 + v\sigma_{rX}^2] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks R E	$[\sigma_Y^2 + \sigma_{taY}^2 + \sigma_{tY}^2 + k\sigma_{bY}^2] + [\sigma_X^2 + \sigma_{taX}^2 + \sigma_{tX}^2 + k\sigma_{bX}^2] + 2[\sigma_{YX} + \sigma_{taYX} + \sigma_{tYX} + k\sigma_{bYX}]$
Treatments (Adj.)	$[\sigma_Y^2 + (\frac{k}{k+1})m\sigma_{taY}^2 + (\frac{k}{k+1})ms\sigma_{tY}^2] + [\sigma_X^2 + (\frac{k}{k+1})m\sigma_{taX}^2 + (\frac{k}{k+1})ms\sigma_{tX}^2] + 2[\sigma_{YX} + (\frac{k}{k+1})m\sigma_{taYX} + (\frac{k}{k+1})ms\sigma_{tYX}]$
Environments	$[\sigma_Y^2 + m\sigma_{taY}^2 + v\sigma_{rY}^2 + k\sigma_{bY}^2 + mv\sigma_{aY}^2] + [\sigma_X^2 + m\sigma_{taX}^2 + v\sigma_{rX}^2 + k\sigma_{bX}^2 + mv\sigma_{aX}^2] + 2[\sigma_{YX} + m\sigma_{taYX} + v\sigma_{rYX} + k\sigma_{bYX} + mv\sigma_{aYX}]$
Treat. x Env.	$[\sigma_Y^2 + (\frac{k}{k+1})m\sigma_{taY}^2] + [\sigma_X^2 + (\frac{k}{k+1})m\sigma_{taX}^2] + 2[\sigma_{YX} + (\frac{k}{k+1})m\sigma_{taYX}]$
Error	$[\sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX}]$
Replications Env.	$[\sigma_Y^2 + k\sigma_{bY}^2 + v\sigma_{rY}^2] + [\sigma_X^2 + k\sigma_{bX}^2 + v\sigma_{rX}^2] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks R E (Adj.)	$[\sigma_Y^2 + (\frac{s-1}{s})\sigma_{taY}^2 + (\frac{ms-1}{ms})k\sigma_{bY}^2] + [\sigma_X^2 + (\frac{s-1}{s})\sigma_{taX}^2 + (\frac{ms-1}{ms})k\sigma_{bX}^2] + 2[\sigma_{YX} + (\frac{s-1}{s})\sigma_{taYX} + (\frac{ms-1}{ms})k\sigma_{bYX}]$
Treatments	$[\sigma_Y^2 + m\sigma_{taY}^2 + (\frac{k}{k+1})\sigma_{bY}^2 + ms\sigma_{tY}^2] + [\sigma_X^2 + m\sigma_{taX}^2 + (\frac{k}{k+1})\sigma_{bX}^2 + ms\sigma_{tX}^2] + 2[\sigma_{YX} + m\sigma_{taYX} + (\frac{k}{k+1})\sigma_{bYX} + ms\sigma_{tYX}]$
Environments	$[\sigma_Y^2 + m\sigma_{taY}^2 + v\sigma_{rY}^2 + k\sigma_{bY}^2 + mv\sigma_{aY}^2] + [\sigma_X^2 + m\sigma_{taX}^2 + v\sigma_{rX}^2 + k\sigma_{bX}^2 + mv\sigma_{aX}^2] + 2[\sigma_{YX} + m\sigma_{taYX} + v\sigma_{rYX} + k\sigma_{bYX} + mv\sigma_{aYX}]$
Treat. x Env.	$[\sigma_Y^2 + (\frac{k}{k+1})m\sigma_{taY}^2] + [\sigma_X^2 + (\frac{k}{k+1})m\sigma_{taX}^2] + 2[\sigma_{YX} + (\frac{k}{k+1})m\sigma_{taYX}]$
Error	$[\sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX}]$

The expected mean squares are identical to those presented for the random model, with

$$\begin{aligned} \phi_a &= \left(\frac{1}{s-1} \right) \left[\sum_{g=1}^s a_g^2 - \frac{\left(\sum_{g=1}^s a_g \right)^2}{s} \right] = \left(\frac{1}{s-1} \right) \sum_{g=1}^s \left[a_g - \frac{\sum_{g=1}^s a_g}{s} \right]^2 \\ &= \left(\frac{1}{s-1} \right) \sum_{g=1}^s (a_g - \bar{a})^2 \end{aligned}$$

in the place of σ_a^2 . Therefore, the estimators of the component σ_t^2 are identical to those of the random model.

As seen, the statistical models (1), (2) and (3) are considered to estimate the covariance component due to treatment effect (σ_{tYX}), with a_{gY} , a_{gX} and $a_g = a_{gY} + a_{gX}$ as fixed effects. Using previous results and since

$$\begin{aligned} \phi_a &= \left(\frac{1}{s-1} \right) \left[\sum_{g=1}^s (a_{gY} + a_{gX})^2 - \frac{\left[\sum_{g=1}^s (a_{gY} + a_{gX}) \right]^2}{s} \right] = \\ &= \left(\frac{1}{s-1} \right) \left[\sum_{g=1}^s a_{gY}^2 - \frac{\left(\sum_{g=1}^s a_{gY} \right)^2}{s} \right] + \left(\frac{1}{s-1} \right) \left[\sum_{g=1}^s a_{gX}^2 - \frac{\left(\sum_{g=1}^s a_{gX} \right)^2}{s} \right] \\ &+ 2 \left(\frac{1}{s-1} \right) \left[\sum_{g=1}^s (a_{gY} a_{gX}) - \frac{\left(\sum_{g=1}^s a_{gY} \right) \left(\sum_{g=1}^s a_{gX} \right)}{s} \right] = \\ &= \phi_{aY} + \phi_{aX} + 2\phi_{aYX} \end{aligned}$$

the expected mean squares of the analyses of variance of the variable $Y + X$ are demonstrated. The expected mean squares are identical to those presented for the random model, with ϕ_{aY} , ϕ_{aX} and ϕ_{aYX} in the place of σ_{aY}^2 , σ_{aX}^2 and σ_{aYX} , respectively. Therefore, the estimators of σ_{tYX} are equal to those of the random model.

2.2.2. Restricted mixed model

In the mixed model with the restriction

$$\sum_{g=1}^s (ta)_{ig} = 0, \text{ to all } i,$$

not all effects of interaction between treatment and environment are independent random variables.

In this model:

$$V \left[\sum_{g=1}^s (ta)_{ig} \right] = s\sigma_{ta}^2 + 2 \sum_{g=1}^s \sum_{g'=1}^s \text{Cov}[(ta)_{ig}, (ta)_{ig'}] = 0,$$

assuming that $\text{Cov}[(ta)_{ig}, (ta)_{ig'}] = E[(ta)_{ig}(ta)_{ig'}] = \sigma$, to all i, g and g' ($g \cdot g'$), we have:

$$\sigma = - \left(\frac{1}{s-1} \right) \sigma_{ta}^2$$

Therefore, in the matrix Σ ,

$$C_0 = \sigma_t^2 + \sigma_r^2 + \sigma_b^2 + \sigma_{ta}^2 + \sigma^2$$

$$C_1 = \sigma_r^2 + \sigma_b^2$$

$$C_2 = \sigma_r^2$$

$$C_3 = \sigma_t^2 + \sigma_{ta}^2$$

$$C_4 = 0$$

$$C_5 = \sigma_t^2 - \left(\frac{1}{s-1} \right) \sigma_{ta}^2$$

$$C_6 = 0$$

Using the expectation of quadratic forms, the expected values below and those presented in Table 4 can be obtained:

$$E(Y'Y) = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + mv \sum_{g=1}^s a_g^2 + n\sigma_{ta}^2 + n\sigma^2 + 2mv\mu \sum_{g=1}^s a_g$$

$$E[R(\mu)] = n\mu + ms\sigma_t^2 + v\sigma_r^2 + k\sigma_b^2 + \frac{mv}{s} \left(\sum_{g=1}^s a_g \right)^2 + 2mv\mu \sum_{g=1}^s a_g$$

$$E[R(\mu, \tau, \delta, \alpha, \beta)] = n\mu^2 + n\sigma_t^2 + n\sigma_r^2 + n\sigma_b^2 + mv \sum_{g=1}^s a_g^2 + mks\sigma_{ta}^2 + (v + mks - 1) \sigma^2 + 2mv\mu \sum_{g=1}^s a_g$$

The estimators of σ_t^2 are:

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

$$\hat{\sigma}_{t(2)}^2 = \left[\frac{\text{MST}(\text{N. Adj.}) - \text{MSe} - \left(\frac{k}{k+1} \right) \hat{\sigma}_{b(2)}^2}{\text{ms}} \right] \neq \left[\frac{\text{MST}(\text{N. Adj.}) - \text{MSe}_{\text{CB}}}{\text{ms}} \right]$$

where:

$$\hat{\sigma}_{b(2)}^2 = \left[\frac{\text{ms}}{k(\text{ms}-1)} \right] \left[\text{MSB} \{R\} E(\text{Adj.}) - \text{MSe} - \left(\frac{s-1}{s} \right) \left(\frac{k+1}{k} \right) \left(\frac{\text{MST} - \text{MSe}}{m} \right) \right]$$

and MSe_{CB} is the error mean square, considering the complete block model. Therefore, $\hat{\sigma}_{t(2)}^2$ is not the estimator of σ_t^2 of the analysis according to the complete block model.

The statistical models (1), (2) and (3) are adjusted to estimate the covariance component σ_{tYX} .

Based on previous results and on the assumptions about the restricted mixed model, and since not all effects $(\text{ta})_{ig} = (\text{ta})_{igY} + (\text{ta})_{igX}$ are independent, the expected mean squares presented in Table 5 are demonstrated. The estimators of σ_{tYX} are:

Table 4. Expected mean squares of the joint analyses of variance of square lattices, considering restricted mixed model¹ with environment effect fixed and other effects random

Source of variation	E(M.S.)
Replications Environment	$\sigma^2 + k\sigma_b^2 + v\sigma_b^2$
Blocks Rep. Env.	$\sigma^2 + \sigma_{ta}^2 + \sigma_t^2 + k\sigma_b^2$
Treatments (Adjusted)	$\sigma^2 + \left(\frac{k}{k+1} \right) \text{ms}\sigma_t^2$
Environments	$\sigma^2 + \left(\frac{s}{s-1} \right) \text{m}\sigma_{ta}^2 + v\sigma_r^2 + k\sigma_b^2 + mv\phi_a^2$
Treatments x Environments	$\sigma^2 + \left(\frac{s}{s-1} \right) \left(\frac{k}{k+1} \right) \text{m}\sigma_{ta}^2$
Error	σ^2
Replications Environment	$\sigma^2 + k\sigma_b^2 + v\sigma_r^2$
Blocks Rep. Env. (Adjusted)	$\sigma^2 + \sigma_{ta}^2 + \left(\frac{\text{ms}-1}{\text{ms}} \right) k\sigma_b^2$
Treatments	$\sigma^2 + \left(\frac{k}{k+1} \right) \sigma_b^2 + \text{ms}\sigma_t^2$
Environments	$\sigma^2 + \left(\frac{s}{s-1} \right) \text{m}\sigma_{ta}^2 + v\sigma_r^2 + k\sigma_b^2 + mv\phi_a^2$
Treatments x Environments	$\sigma^2 + \left(\frac{s}{s-1} \right) \left(\frac{k}{k+1} \right) \text{m}\sigma_{ta}^2$
Error	σ^2

¹Under the restrictions $\sum_{g=1}^s (\text{ta})_{ig} = 0$, to all i.

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

$$\hat{\sigma}_{tYX(2)} = \left[\frac{\text{MST(N.Adj.)}(Y+X) - \text{MST(N.Adj.)}(Y) - \text{MST(N.Adj.)}(X) - 2\hat{\sigma}_{YX} - 2\left(\frac{k}{k+1}\right)\hat{\sigma}_{bYX(2)}}{2ms} \right]$$

where:

$$\hat{\sigma}_{YX} = \frac{\text{MSe}(Y+X) - \text{MSe}(Y) - \text{MSe}(X)}{2}$$

$$\hat{\sigma}_{bYX(2)} = \left[\frac{ms}{2k(ms-1)} \right] [\text{MSB}\neq\text{R}\neq\text{E(Adj.)}(Y+X) - \text{MSB}\neq\text{R}\neq\text{E(Adj.)}(Y) - \text{MSB}\neq\text{R}\neq\text{E(Adj.)}(X) - 2\hat{\sigma}_{YX} - 2\hat{\sigma}_{taYX}]$$

$$\hat{\sigma}_{taYX} = \left(\frac{s-1}{s} \right) \left(\frac{k+1}{k} \right) \left(\frac{\text{MSTE}(Y+X) - \text{MSTE}(Y) - \text{MSTE}(X) - 2\hat{\sigma}_{taYX}}{2m} \right)$$

3. APPLICATION

The results of the analyses of variance for height and diameter of 49 half-sib families of *Eucalyptus pyrocarpa*, from a non inbred population, evaluated in a 7 x 7 simple lattice in two different environmental conditions, are shown in Table 6. The SAEG (System for Statistical Analyses) program, developed by the Universidade Federal de Viçosa, was used for the analyses.

Considering unrestricted mixed model, the analyses of variance show, at a level of 5% of significance, absence of interaction between families and environments, for height and diameter. There is no difference between the means of the reference population in the two environments (two levels of fertilization were used). In the base population there is genetic variability for both characters. As there is evidence of absence of progeny x environment interaction, selection can be done considering the means

of the families in the two levels of fertilization, favoring the choice of those with desired performance in different environments. Estimates of the genotypic variance between progenies, of the covariance between genotypic means of same family, and of some other genetic parameters are presented in Table 7. The equality between the estimates of $\sigma_{t(1)}^2$ and $\sigma_{t(2)}^2$ and of $\sigma_{t(1)}$ and $\sigma_{t(2)}$, reveals homogeneity between blocks within replication within environment.

In relation to both characters, the differences between the additive genetic values of the individuals in the base population account for a relevant portion of the variance of the phenotypic means of the families. The magnitude of the two heritabilities indicates that the families with greater phenotypic mean should have a common parent with greater additive genetic value (greater number of genes which increase each trait). The estimates of the correlation between the phenotypic mean of the family and the additive

Table 5. Expected mean squares of the joint analyses of variance of square lattices, considering restricted mixed model¹ with environment effect fixed and other effects random, in relation to the variable Y+X

Source of variation	E(M.S.)
Replications Env.	$[\sigma_Y^2 + k\sigma_{bY}^2 + v\sigma_{rY}^2] + [\sigma_X^2 + k\sigma_{bX}^2 + v\sigma_{rX}^2] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks R E	$[\sigma_Y^2 + \sigma_{taY}^2 + \sigma_{tY}^2 + k\sigma_{bY}^2] + [\sigma_X^2 + \sigma_{taX}^2 + \sigma_{tX}^2 + k\sigma_{bX}^2] + 2[\sigma_{YX} + \sigma_{taYX} + \sigma_{tYX} + k\sigma_{bYX}]$
Treatments (Adj.)	$[\sigma_Y^2 + (\frac{k}{k+1})ms\sigma_{tY}^2] + [\sigma_X^2 + (\frac{k}{k+1})ms\sigma_{tX}^2] + 2[\sigma_{YX} + (\frac{k}{k+1})ms\sigma_{tYX}] + 2[\sigma_{YX} + (\frac{k}{k+1})ms\sigma_{tYX}]$
Environments	$[\sigma_Y^2 + (\frac{s}{s-1})m\sigma_{taY}^2 + v\sigma_{rY}^2 + k\sigma_{bY}^2 + mv\phi_{aY}] + [\sigma_X^2 + (\frac{s}{s-1})m\sigma_{taX}^2 + v\sigma_{rX}^2 + k\sigma_{bX}^2 + mv\phi_{aX}] + 2[\sigma_{YX} + (\frac{s}{s-1})m\sigma_{taYX} + v\sigma_{rYX} + k\sigma_{bYX} + mv\phi_{aYX}]$
Treat. x Env.	$[\sigma_Y^2 + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taY}^2] + [\sigma_X^2 + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taX}^2] + 2[\sigma_{YX} + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taYX}]$
Error	$\sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX}$
Replications Env.	$[\sigma_Y^2 + k\sigma_{bY}^2 + v\sigma_{rY}^2] + [\sigma_X^2 + k\sigma_{bX}^2 + v\sigma_{rX}^2] + 2[\sigma_{YX} + k\sigma_{bYX} + v\sigma_{rYX}]$
Blocks R E (Adj.)	$[\sigma_Y^2 + \sigma_{taY}^2 + (\frac{ms-1}{ms})k\sigma_{bY}^2] + [\sigma_X^2 + \sigma_{taX}^2 + (\frac{ms-1}{ms})k\sigma_{bX}^2] + 2[\sigma_{YX} + \sigma_{taYX} + (\frac{ms-1}{ms})k\sigma_{bYX}]$
Treatments	$[\sigma_Y^2 + (\frac{k}{k+1})\sigma_{bY}^2 + ms\sigma_{tY}^2] + [\sigma_X^2 + (\frac{k}{k+1})\sigma_{bX}^2 + ms\sigma_{tX}^2] + 2[\sigma_{YX} + (\frac{k}{k+1})\sigma_{bYX} + ms\sigma_{tYX}]$
Environments	$[\sigma_Y^2 + (\frac{s}{s-1})m\sigma_{taY}^2 + v\sigma_{rY}^2 + k\sigma_{bY}^2 + mv\phi_{aY}] + [\sigma_X^2 + (\frac{s}{s-1})m\sigma_{taX}^2 + v\sigma_{rX}^2 + k\sigma_{bX}^2 + mv\phi_{aX}] + 2[\sigma_{YX} + (\frac{s}{s-1})m\sigma_{taYX} + v\sigma_{rYX} + k\sigma_{bYX} + mv\phi_{aYX}]$
Treat. x Env.	$[\sigma_Y^2 + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taY}^2] + [\sigma_X^2 + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taX}^2] + 2[\sigma_{YX} + (\frac{s}{s-1})(\frac{k}{k+1})m\sigma_{taYX}]$
Error	$\sigma_Y^2 + \sigma_X^2 + 2\sigma_{YX}$

⁽¹⁾ Under the restrictions $\sum_{g=1}^s (ta)_{ig} = \sum_{g=1}^s [(ta)_{igY} + (ta)_{igX}] = 0$, to all i.

Table 6. Joint analyses of variance of height and diameter of 49 half-sib families of *Eucalyptus pyrocarpa*

Source of variation	Degrees of freedom	Mean square	
		Height	Diameter
Replications Env.	2	6.7455	0.5862x10 ⁻³
Blocks Rep. Env. (Adj.)	24	1.9398	0.2496x10 ⁻³
Families (Adj.)	48	6.0997**	0.7704x10 ⁻³ **
Environments	1	13.0885 ^{ns}	0.1046x10 ⁻² ^{ns}
Families x Environments	48	2.3549 ^{ns}	0.2987x10 ⁻³ ^{ns}
Error	72	1.7297	0.2148x10 ⁻³

** : P < 0.01. ns: not significant at 5%.

Table 7. Estimates of variance and covariance components and of some other genetic parameters¹, in relation to height and diameter of half-sib families of a population of *Eucalyptus pyrocarpa*, evaluated in two environments

Parameter	Estimate	Trait
	m	
$\sigma^2_{t(1)}$	Height	1.07
	Diameter	0.13 x 10 ⁻³
$\sigma^2_{t(2)}$	Height	1.03
	Diameter	0.13 x 10 ⁻³
$\sigma_{t(1)}$	–	0.01
$\sigma_{t(2)}$	–	0.01
Population mean	Height	14.02
	Diameter	0.117
Mean of the selected families (selection based on height)	Height	15.49
	Diameter	0.134
Mean of the selected families (selection based on diameter)	Height	15.38
	Diameter	0.134
h^2	Height	0.61
	Diameter	0.59
ΔG	Height	6.58%
	Diameter	8.52%
r_A	–	0.89

¹The values of h^2 (heritability in 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.

genetic value of the common parent (Viana, 1996b) are $\sqrt{0.61} = 0.78$ and $\sqrt{0.59} = 0.77$, for height and diameter, respectively. Thus, the choice of the superior families will alter the genotypic means of height and diameter of the base population, in the desirable direction. In relation to height, the predicted direct genetic gain with selection and recombination of the 15 best families (selection intensity of approximately 1.138) is of 6.58%. In relation to diameter, the expected direct gain is 8.52%. The magnitude of the additive genetic correlation between the two traits (Viana, 1996a) shows that the direct selection based on one trait will determine indirect gain in relation to the other. The selection based on height should determine a change in the mean diameter of the base population of $(0.134 - 0.117) (0.59) .100 / 0.117 = 8.57\%$. Evidently, there is no difference between the direct and indirect gains in relation to diameter (because of the equality between direct and indirect selection differentials). With selection considering diameter, the expected indirect gain for height is of $(15.38 - 14.02) (0.61) .100 / 14.02 = 5.92\%$.

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