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Multi-trait multi-environment models for selecting high-performance and stable eucalyptus clones

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ABSTRACT. Multi-trait multi-environment (MTME) models were fitted to eucalyptus breeding trials data to assess residual variance structure, genetic stability and adaptability. To do so, 215 eucalyptus clones were evaluated in a randomized complete block design with 30 replicates and one plant per plot in four environments. At 36 months of age, tree diameter at breast height (DBH) and pilodyn penetration (PP) were measured. Two MTME models were fitted, for which residuals were considered homoscedastic and heteroscedastic, with the best MTME model selected using Bayesian information criterion. The harmonic mean of the relative performance of the genotypic values (HMRPGV) was used to determine stability and adaptability. Of the two models, the heteroscedastic MTME model had better fit and provided greater accuracy. In addition, genotype-by-environment interaction was complex, and there was low genetic correlation between DBH and PP. Rank correlation between the clones selected by the MTME models was high for DBH but low for PP. The HMRPGV facilitated clone selection through simultaneous evaluation of stability, adaptability, and productivity. Thus, our results suggest that heteroscedastic MTME model / HMRPGV can be efficiently applied in the genetic evaluation and selection of eucalyptus clones.

Keywords: quantitative genetics; genotype-by-environment interaction; multivariate analysis; genetic selection; tree breeding; eucalyptus breeding.

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Introduction

Eucalyptus L'Hér species are commercially important trees in tropical and subtropical regions around the world (Castro, Resende, Bhering, & Cruz, 2016). The widespread use of these species in plantations is due primarily to their beneficial silvicultural and industrial properties, along with the success of breeding programs (Ramalho, Marques, & Lemos, 2021). In Brazil, for instance, nearly 7 million hectares have been planted with eucalypt, constituting ~ 77 % of the country's total planted forest area (IBGE, 2019).

Multi-environment trials (MET) are often employed in eucalyptus breeding programs to determine genotype-by-environment interactions (GEI) (van Eeuwijk, Bustos-Korts, & Malosetti, 2016). Indeed, MET are particularly important for eucalyptus breeding because these species are farmed in a diverse range of environments, each of which presents a unique suite of soil and climatic conditions (Binkley et al., 2017; Elli, Sentelhas, & Bender, 2020). Such variation in environmental conditions can in part account for the often large discrepancies in yield among plantations across regions (Elli, Sentelhas, Freitas, Carneiro, & Alvares, 2019).

Because of the wide range of conditions in which eucalyptus plantations are situated, data acquired from MET may contain substantial heterogeneous residual variance (Shalizi & Isik, 2019). In addition, trials conducted in different environments may be statistically and genetically unbalanced. To ensure the accuracy of genotype evaluation, statistical methods must therefore account for both heteroscedasticity and missing data (Melo et al., 2020; Smith & Cullis, 2018). However, homogeneous residual variance and statistical and genetic balance are assumptions of several methods commonly used to measure GEI, including ANOVA-based methods: AMMI (additive main effects and multiplicative interaction), and GGE biplots (the genotype main effects plus GEI effects) (van Eeuwijk et al., 2016; Yan, Hunt, Sheng, & Szlavnics, 2000; Zobel, Wright, &

Gauch, 1988). Methods capable of capitalizing on heteroscedasticity and imbalance are thus preferable to more conventional approaches (Li, Suontama, Burdon, & Dungey, 2017; Smith & Cullis, 2018).

One such example is the use of mixed models via restricted maximum likelihood (REML) and best linear unbiased prediction (BLUP) (van Eeuwijk et al., 2016). Estimation of variance components using REML (Patterson & Thompson, 1971) and prediction of genetic values using BLUP (Henderson, 1975) offer several advantages over traditional methods, such as the ability to overcome complex data structures (e.g., statistical and genetic imbalance), comparison of individuals over time and space, and correcting for environmental trends (Isik, Holland, & Maltecca, 2017; Resende, 2016).

In addition, REML/BLUP procedure can account for covariance among traits when a multi-trait BLUP is fitted (Alves et al., 2018; Henderson & Quaas, 1976, Imai et al., 2016), which is essential when traits are correlated because selection bias may arise when traits are analyzed individually. Within the context of MET, a multi-trait multi-environment BLUP (MTME-BLUP) has the capacity to incorporate bits of information simultaneously, thereby taking into consideration both genetic and non-genetic covariances (Mathew, Léon, & Sillanpää, 2018; Resende, Silva, & Azevedo, 2014).

The MTME-BLUP output (genotypic values) can be used to assess both genotypic stability and adaptability. The stability refers to a genotype's predictability of its phenotypic performance, whereas adaptability refers to a genotype's capacity to effectively respond to its environmental conditions (Finlay & Wilkinson, 1963; Eberhart & Russell, 1966). The harmonic mean of the relative performance of the genotypic value (HMRPGV) is a useful method for identifying genotypes that respond well to favorable environments, are largely unaffected by unfavorable conditions, and produce high yields (Chaves et al., 2021; Dias et al., 2018; Ferreira et al., 2021).

In this study, our main objective was to examine the effectiveness of using MTME-BLUP models for genetic assessment of eucalypt, highlighting the importance of residual variance structure, and stability and adaptability analyses in eucalyptus clone selection.

Material and methods

Genetic material, experimental design, and assessed traits

Two hundred and fifteen clones of different eucalyptus species and hybrids (Table 1) were evaluated under four different environmental conditions (Table 2). The experimental design consisted of a randomized complete block with 30 replicates and a single-tree plot with spacing dimensions of 3.5 m between rows × 2.6 m between trees.

Table 1. Hybrids of *Eucalyptus* evaluated in four environments (CB, CP, FZ, and SJ).

Two-way cross	Three-way cross	Four- Way crosss
E. grandis × *E. urophylla*	*E. urophylla* × (*E. grandis* × *E. urophylla*)	(*E. grandis* × *E. kirtoniana*) × (*E. robusta* × *E. tereticornis*)
E. urophylla × *E. maidenii*	*E. globulus* × (*E. grandis* × *E. urophylla*)	(*E. grandis* × *E. urophylla*) × (*E. urophylla* × *E. globulus*)
E. pellita × *E. grandis*	*E. grandis* × (*E. grandis* × *E. urophylla*)	
E. grandis × *E. maidenii*	*E. urophylla* × (*E. camaldulensis* × *E. grandis*)	
E. grandis × *E. dunnii*	*E. saligna* × (*E. grandis* × *E. urophylla*)	
E. grandis × *E. saligna*	*E. robusta* × (*E. grandis* × *E. urophylla*)	
E. urophylla × *E. saligna*	*E. grandis* × (*E. dunnii* × *E. grandis*)	
E. urophylla × *E. globulus*	*E. maidenii* × (*E. grandis* × *E. urophylla*)	
E. grandis × *E. globulus*	*E. saligna* × (*E. urophylla* × *E. grandis*)	
E. globulus × *E. tereticornis*	*E. urophylla* × (*E. grandis* × *E. globulus*)	
E. urophylla × *E. deanei*	*E. urophylla* × (*E. tereticornis* × *E. saligna*)	
E. urophylla × *E. tereticornis.*	*E. urophylla* × (*E. urophylla* × *E. grandis*)	

Locations: CB: Minas do Leão – Rio Grande do Sul State, Brazil (Forest Garden Cambará); CP: Encruzilhada do Sul – Rio Grande do Sul State, Brazil (Forest Garden Capivara); FZ: Dom Feliciano – Rio Grande do Sul State, Brazil (Forest Garden Fortaleza) and SJ: Vila Nova do Sul – Rio Grande do Sul State, Brazil (Forest Garden São João).

Table 2. Geographic location (GL) and annual climatic conditions (ACC) of each environment (E).

GL / ACC	CB	CP	FZ	SJ
Geographic coordinates	Latitude: 30°11'09" S Longitude: 52°00'10" W	Latitude: 30°29'45" S Longitude: 52°19'35" W	Latitude: 30°27'19" S Longitude: 52°39' 53" W	Latitude: 30°14'46" S Longitude: 53°49'7" W
Altitude (m)	141	378	250	301
Average temperature (ºC)	17.5	16	17	16.8
Absolute minimum temperature (ºC)	-0.9	-1.7	-0.6	0.0
Absolute maximum temperature (ºC)	32.3	30.7	33.3	34.7
Rainfall (mm)	1422	1564	1368	1133

Locations: CB: Minas do Leão – Rio Grande do Sul State, Brazil (Forest Garden Cambará); CP: Encruzilhada do Sul – Rio Grande do Sul State, Brazil (Forest Garden Capivara); FZ: Dom Feliciano – Rio Grande do Sul State, Brazil (Forest Garden Fortaleza) and SJ: Vila Nova do Sul – Rio Grande do Sul State, Brazil (Forest Garden São João).

Tree diameter at breast height (DBH, in cm) and pilodyn penetration (PP, in mm) were determined at 36 months of age. DBH was measured using a diameter measuring tape, and PP was measured with a pilodyn, a device that fires a 2.5 mm metallic pin into a tree at a preset force, with wood density estimated from the inverse proportional relationship between the depth of penetration and the hardness of the wood in the direction transverse to the tree stem (Hasnikova & Kuklík, 2013). For PP, two measurements were made at a height of 1.3 m, one on the north and another on the south cardinal aspects of each tree, with the average value of these two measurements used in the analyses.

Statistical analyses

REML/MTME-BLUP procedure (Henderson & Quaas, 1976; Patterson & Thompson, 1971) was used to estimate the variance components and predict genotypic values. The MTME model was calculated as:

$$y = X\beta + Z\alpha + W\theta + Q\rho + e,$$

where y is the vector of phenotypic data; β is the vector of environment effects (assumed to be fixed) added to the overall mean, α is the vector of genotypic effects (assumed to be random) [$\alpha \sim N(0, \Sigma_G \otimes I)$, where Σ_G represents the genotypic covariance matrix], θ is the vector of GEI effects (random) [$\theta \sim N(0, \Sigma_{GEI} \otimes I)$, where Σ_{GEI} is the GEI covariance matrix], ρ is the vector of replications effects (assumed to be random) [$\rho \sim N(0, \Sigma\_\rho \otimes I)$, where Σ_ρ represents the replications covariance matrix], and e is the vector of residuals (random) [$e \sim N(0, \Sigma_R)$, where Σ_R is the residual covariance matrix]; I is an identity matrix and $\otimes$ is the Kronecker product. The uppercase letters X, Z, W, and Q represent the incidence matrices for β, α, θ, and ρ, respectively.

Residual variance structures (homogeneous and heterogeneous) were compared via Bayesian information criterion (BIC) (Schwarz, 1978), based on the equation:

$$BIC = -2LogL_F + pLog[n - r(x)],$$

where $LogL_F$ is the logarithm of the restricted likelihood function, p is the number of estimated parameters, n is the number of observations, and $r(x)$ is the rank of the fixed effects incidence matrix. The significance of the random effects of the MTME models was tested using the confidence interval, considering the t distribution and a confidence level of 95% (Type I error of 5%) (Burdick & Graybill, 1992).

Phenotypic variance ($\hat{\sigma}^2_{p_j}$, Equation 1), broad-sense individual heritability (h^2_{gj}, Equation 2), selective accuracy ($r_{\hat{g}g_j}$, Equation 3), reliability ($r^2_{\hat{g}g_j}$, squared selective accuracy), type B genotypic correlations across environments (r^2_{gei}, Equation 4), and the coefficient of determination of the GEI effects (c^2_{gei}, Equation 5) were estimated using the following equations: Equation 1:

$$\sigma^2_{p_j} = \sigma^2_g + \sigma^2_{gei} + \sigma^2_{e_j} \qquad (1)$$

where σ^2_g é the genotypic variance, σ^2_{gei} is the GEI variance and σ^2_{ej} is the residual variance, one value for the homoscedastic model and four values (one for *each* j^{th} environment) in the heteroscedastic model; Equation 2: Equation 3:

$$h^2_{g_j} = \sigma^2_g / \sigma^2_{p_j} \qquad (2)$$

$$r_{\hat{g}g_j} = \sqrt{1 - \frac{PEV}{\sigma^2_g}} \qquad (3)$$

where PEV is the prediction error variance, extracted from the diagonal of the generalized inverse of the coefficient matrix of the mixed model equation (Resende et al., 2014) Equation 4:

$$r^2_{gei} = \frac{\sigma^2_g}{\sigma^2_g + \sigma^2_{gei}} \qquad (4)$$

and

$$c^2_{gei} = \frac{\sigma^2_{gei}}{\sigma^2_{p_j}} \qquad (5)$$

The genotypic covariance between traits ($\sigma_{gDBH,PP}$) was used to estimate the genotypic correlations between traits ($r_{DBH,PP}$), by the following expression:

$$r_{DBH,PP} = \frac{\sigma_{g_{DBH,PP}}}{\sqrt{\sigma^2_{g_{DBH}}\,\sigma^2_{g_{PP}}}},$$

The harmonic mean of the relative performance of genotypic values (HMRPGV), a value that reflects clones' stability and adaptability associated to its productivity (Resende, 2004), was estimated by:

$$HMRPGV_i = \frac{E}{\sum_{j=1}^{E}\frac{1}{\frac{GV_{ij}}{\mu_j}}},$$

where E is the number of environments, GV_{ij} is the genotypic value (BLUP) of the i^{th} clone in the j^{th} environment and μ_j is the phenotypic mean of the j^{th} environment.

To select simultaneously for both traits, the Additive Index (AI) was used:

$$AI_i = \sum_1^2 CV_g \frac{HMRPGV_{ic}}{\sigma_{g_c}},$$

where CV_g is the genotypic coefficient of variation ($CV_{g_c} = \left(100\sigma_{g_c}\right)/\mu$), used as weight and σ_{g_c} is the genotypic standard-deviation of the trait c. The assignment of weights were positive weight for DBH and negative weights for PP.

The gain with selection (GS), was predicted (considering four different selection intensities: 5, 10, 15, and 20%) by the following equation:

$$GS(\%) = \left(\sum_{i=1}^{S} GV_i\right)/S,$$

where S is the number of selected clones.

The rank correlation (Spearman's rank correlation) (r_r) between the two models (homoscedastic MTME and heteroscedastic MTME) were calculated based on the HMRPGV rank, and was given by:

$$r_r = 1 - \frac{6\sum D^2}{n(n^2-1)},$$

where D is the difference between ranks and n is the number of pairs of data.

All statistical analyses were performed using ASReml-R (Butler, Cullis, Gilmour, Gogel, & Thompson, 2018).

Results

BIC comparison suggested that the best-fit model for DBH and PP had a heterogeneous residual variance structure (Table 3).

Table 3. Fitted model, likelihood logarithm (LogL), number of parameters (NP) related to the R (residue effects) and G (genotypic, GEI and replications effects) covariance matrices, Bayesian information criterion (BIC) and accuracy of each model for the traits diameter at breast height (DBH) and pilodyn penetration (PP) evaluated in eucalyptus clones.

Model	LogL	NP		BIC	Selective accuracy	
		G	R		DBH	PP
Homoscedastic residue	-55214.5	9	3	110535.9	0.97	0.99
Heteroscedastic residue[†]	-54094.5	9	12	108424.4	0.97	0.99

[†]The most suitable model.

Both genotypic and GEI effects were significant, according to their confidence intervals (Table 4), indicating the existence of genetic variability and GEI. Broad-sense individual heritability was low for DBH and moderate for PP in all four environments (Table 4). Despite heritability, reliability was high for all traits across the four environments. In general, PP exhibited greater reliability than DBH, and the second environment displayed better selection conditions for both traits.

Evaluating the significance of the GEI effects and differences in the residual variances, heritabilities, and reliabilities between environments improves understanding of the moderate and high genotypic correlations across environments for DBH and PP, respectively (Table 4). Variation in the magnitude of parameters among traits might account for the low correlation between DBH and PP. Such results would prove an obstacle to indirect selection.

Based on the predicted genotypic values, HMRPGV was calculated to identify the most stable, adaptable, and better performing (i.e., high DBH and low PP) genotypes. To illustrate differences in trait estimates when the residual variance was considered homogeneous and when it was considered heterogeneous, BLUP for DBH and PP were determined for both models, and an additive index was used to achieve gains for both traits, which were found to be similar regardless of selection intensity (Table 5). The high-ranking correlations underscore the similarities between the two models, and, in this case, shows the extent to which the different residual variance structures affected clone rankings (Table 5). A high correlation was found between the two rankings for both traits, indicating lower model influence.

Table 4. Estimates of variance components (± confidence interval) and genetic parameters for the traits diameter at breast height (DBH) and pilodyn penetration (PP) evaluated in eucalyptus in four environments† (E1, E2, E3 and E4), by the heteroscedastic multi-trait multi-environment model.

Components/Parameters	DBH				PP			
	E1	E2	E3	E4	E1	E2	E3	E4
σ^2_g	--------- 0.910 ± 0.220 ---------				--------- 3.601 ± 0.716 ---------			
σ^2_{gei}	--------- 0.799 ± 0.106 ---------				--------- 0.551 ± 0.078 ---------			
σ^2_r	--------- 0.129 ± 0.039 ---------				--------- 0.629 ± 0.168 ---------			
σ^2_e	4.89	3.44	2.87	6.52	3.91	2.48	5.72	3.65
σ^2_{pj}	6.73	5.28	4.71	8.36	8.70	7.27	10.51	8.43
h^2_{gj}	0.14	0.17	0.19	0.11	0.41	0.50	0.34	0.43
$r_{\hat{g}g}$	0.90	0.93	0.91	0.84	0.97	0.98	0.98	0.96
$r^2_{\hat{g}g_j}$	0.82	0.88	0.84	0.78	0.95	0.97	0.96	0.94
r^2_{gei}	-------------- 0.53 --------------				-------------- 0.87 --------------			
c^2_{geij}	0.12	0.15	0.17	0.10	0.06	0.08	0.05	0.07
μ_j	14.11	13.21	12.64	14.55	17.41	20.07	18.26	18.69
$r_{DBH,PP}$	---------------------------------- 0.167 ----------------------------------							

σ^2_g: genotypic variance; σ^2_{gei}: genotype-by-environment interaction (GEI) variance; σ^2_e: residual variance; σ^2_{pj}: phenotypic variance; h^2_{gj}: broad-sense individual heritability: reliability; r_{GEI}: type B genotypic correlation across environments; c^2_{GEIj}: coefficient of determination the GEI effects; μ: phenotypic mean; and $r_{DBH,PP}$: genetic correlation between DBH and PP. †E1: Minas do Leão (Rio Grande do Sul State, Brazil); E2: Encruzilhada do Sul (Rio Grande do Sul State, Brazil); E3: Dom Feliciano (Rio Grande do Sul State, Brazil); E4: Vila Nova do Sul (Rio Grande do Sul State, Brazil).

Table 5. Selection gains in percentage (GS %) for diameter at breast height (DBH) and pilodyn penetration (PP) evaluated in eucalyptus considering the additive index value, four selective intensities and assuming homogeneous and heterogeneous residual variance structures.

Traits	Selection intensity (%)	Selection gains (%)		Ranking correlations
		Homoscedastic residue	Heteroscedastic residue	
DBH	5	13.57%	13.57%	0.99
	10	11.33%	11.33%	0.99
	15	9.46%	9.46%	0.99
	20	6.77%	6.77%	0.99
PP	5	-17.16%	-17.16%	0.99
	10	-14.47%	-14.47%	0.99
	15	-12.11%	-12.11%	0.99
	20	-9.39%	-9.39%	0.99

For PP, lower values indicate greater gains with selection.

Discussion

Residual effects encompassed all non-controllable factors in the trials. When considering residual homoscedasticity, it is usually presumed that environmental influences are the same in all locations, an assumption that clearly does not reflect real-world conditions (Coelho et al., 2020; Silva, Oliveira, Nuvunga, Pamplona, & Balestre, 2019). In truth, differing edaphoclimatic and management conditions will have distinct impacts on the same genotype, driving performance variability across regions (Elli et al., 2019; Isik et al., 2017; Peixoto et al., 2020). Two fundamental factors of MET can thus be derived: i) at the experimental level, MET models must be established in representative regions, both in terms of prevailing edaphoclimatic conditions and management type; and ii) at the genetic-statistical level, model residues must be tested for homoscedasticity in order to select models that better simulate real-world conditions (Atlin, Cairns, & Das, 2017; Ceccarelli, 2015; Isik et al., 2017). Both conditions were met in this study.

Residual variances were particularized (one for each environment) in the heteroscedastic MTME, which, as noted, BIC comparison indicated was the best-fit model. The significance of GEI and differences in residual variance observed across environments justified the care taken to account for model selection. Following the detection of genetic variability, its suitability for population selection was tested. In the presence of GEI, selection can be undertaken individually or jointly for each environment, taking into account the GEI effects (Alves et al., 2020). Ideally, the choice of selection strategy will depend on breeding program objectives, with selection based solely on identification of genotypes that perform better under the specific conditions of each location; however, logistical problems and lack of necessary resources often limit options. In such cases, selection of genotypes exhibiting broader adaptability and stability should be prioritized (Ewing, Runck, Kono, & Kantar, 2019; Hardner, 2017), a strategy that was used in this study.

Individual broad-sense heritability estimates were low for DBH (< 0.15) and moderate for PP (0.15-0.50) (Resende & Alves, 2020). Given that this parameter represents the proportion of the heritable portion of the trait in the phenotypic variance (Falconer & MacKay, 1996), the low values observed for DBH are indicative of the substantial influence that environmental conditions have on phenotypic expression, which can be a complicating factor in selection. GEI is linked to the unequal expression of genes in each environment in response to the particular conditions of each location (Leon, Jannink, Edwards, & Kaeppler, 2016; van Eeuwijk et al., 2016). Reliability, an auxiliary parameter to heritability, is a measure of the degree to which experimental precision and results are consistent (Bernardo, 2020). Here, reliability differed between traits, with PP having higher values than DBH, likely due to trait measurement process.

Genotypic correlations across environments were moderate for DBH (0.533) and high for PP (0.867) (Resende & Alves, 2020), suggesting that environmental conditions have a greater effect on DBH than on PP. Moreover, the GEI for PP was relatively simple (i.e. genotypes best suited for one environment were also the best-suited for other environments; Li et al. (2017), whereas GEI for DBH was found to be more complex.

MTME-BLUP enables more accurate estimates of genetic and non-genetic (co)variance between traits and environments. Because it considers correlations between traits among genotypes, use of multi-trait BLUP reduces selection bias and increases selective accuracy (Montesinos-López et al., 2016; Sun et al., 2017). For MET, MTME-BLUP also considers the specificities of environmental conditions by accounting for residual heteroscedasticity (Volpato et al., 2019), which is especially relevant in instances of high correlation among traits (Imai et al., 2016). However, this was not the case in our study ($r_{DBH,PP} = 0.167$), suggesting that the genes that determine both DBH and PP are not pleiotropic, or that several genes are in linkage disequilibrium (Montesinos-López et al., 2019). Nonetheless, quantifying this relationship, even if inconsequential, may be beneficial for improving the accuracy of model projections.

MTME-BLUPs were used to estimate HMRPGV, which penalizes genotype instability and prioritizes adaptability across different environments (Peixoto et al., 2021); that is, this approach selects for clones responsive to the most suitable environments (Bocianowski & Liersch, 2021), an effective strategy for selecting genotypes that grow under a wide range of environmental conditions (Chaves et al., 2021).

Although no differences were observed between homoscedastic and heteroscedastic MTME model gains, our results lead us to conclude that the heteroscedastic MTME model is more suitable for both parameter estimation and genetic selection, particularly because the heteroscedastic model maximized accuracy. This highlights the importance of modeling residual variance structure and reducing the probability of erroneous selection by the breeder, which could lead to additional problems in the future.

Conclusion

The results of our analyses suggested that, for eucalyptus genotype selection, a heteroscedastic MTME model was more suitable for MET data analysis, as reflected by the lower BIC for this model version. Combining multi-trait and multi-environment information via an MTME-BLUP allowed for wider interpretation of the results through greater consideration of the relationships between both environments and traits, enhancing genotypic evaluation accuracy. Finally, application of HMRPGV facilitated simultaneous assessment of stability, adaptability, and productivity among eucalyptus genotypes.

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