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Modeling covariance structures for genetic and non-genetic effects in cowpea multi-environment trials

Maurício dos Santos Araújo[1] | **Saulo Fabrício da Silva Chaves[1]** |
Kaesel Jackson Damasceno-Silva[2] | **Luiz Antônio dos Santos Dias[1]** |
Maurisrael de Moura de Rocha[2]

[1]Dep. de Agronomia, Univ. Federal de Viçosa, Viçosa, MG, Brazil

[2]Embrapa Meio-Norte, Teresina, PI, Brazil

Correspondence
Maurício dos Santos Araújo, Dep. de Agronomia, Univ. Federal de Viçosa, Viçosa, MG 36570-900, Brazil.
Email: mauricio.araujo@ufv.br

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Abstract

In cowpea breeding, multi-environment trials are conducted to select lines with high yield. The occurrence of genetic and/or statistical imbalance is common in these experiments, in addition to the possibility of (co)variance between genetic and non-genetic effects. We explore the restricted maximum likelihood/best linear unbiased prediction features to select the model with the most appropriated covariance structure and compare the results with the traditional model (homogenous variances and no covariances). Then, 17 inbred lines and three cultivars were evaluated in six experiments during two crop years in the semiarid zone of Northeast Brazil. The trait evaluated was the 100-grain weight. We selected the best model considering the Akaike Information Criterion. The model with diagonal structure for the residual effects and heterogeneous compound symmetry for the genetic effects had the best fit. The predicted genetic gain of lines selected in this model was 1.18% higher compared to the traditional model. Modeling different (co)variance structures for genetic and non-genetic effects is an efficient approach in selecting superior genotypes in multi-environment trials in cowpea breeding.

1 | INTRODUCTION

The World Health Organization (WHO, 2021) estimated that in 2020 about 149 million children under 5 were stunted, 45 million were very thin, and 38.9 million were overweight or obese. These problems are caused by malnutrition of nutrients, for example, protein, vitamins, or minerals, which occurs mainly in poor countries. An alternative to overcome these issues is using nutritive crops in biofortification programs. Cowpea [*Vigna unguiculata* (L.) Walp.], also known as black-eyed pea, southern pea, and crowder pea, is an example of a crop that can be biofortified. Cowpea consumption can provide considerable amounts of protein (24.1%) (Araújo et al., 2021; Dakora & Belane, 2019), vitamins (Gonçalves et al., 2016), and micronutrients, such as iron (61.3 mg kg^{-1}) and zinc (44.7 mg kg^{-1}) (Feitosa et al., 2018). Therefore, biofortification programs are investing in the crop's breeding, aiming at combining grain yield and high nutrient content into the best genotypes.

Cowpea is a food crop of great global importance, mainly for populations of developing countries. Its cultivation is

Abbreviations: AIC, Akaike information criterion; BIC, bayesian information criterion; BLUP, best linear unbiased prediction; CS, compound symmetry; CSH, heterogeneous compound symmetry; GEI, genotype-by-environment interaction; IDH, diagonal structure; IDV, identity variance; LRT, likelihood ratio test; MET, multi-environment trials; REML, restricted maximum likelihood; UN, unstructured; VCU, value cultivation and use; WHO, world health organization.

growing over the years. Some 12.5 million hectares are planted with this crop globally, reaching seven million tons of grain per year (FAOSTAT, 2020). In Brazil, the cultivated area and production are about 1.35 thousand hectares and 716.9 thousand tons, respectively (CONAB, 2021). The interest of companies and family farmers is due to the crop's ability to tolerate abiotic stresses (Goufo et al., 2017; Jayawardhane et al., 2022), low fertilizer requirement, and capacity to perform biological nitrogen fixation (Mndzebele et al., 2020). Providing high-quality food is one of the targets of breeding programs (Gondwe et al., 2019). For this, it is essential to select genotypes that are more productive, with high yield stability (Goa et al., 2022). In addition to these traits, breeding programs prioritizes genotypes with disease resistance (Boukar et al., 2016), nutritional and cook technological quality (Gondwe et al., 2019; Jayathilake et al. 2018), and erect and semi-erect plant architecture, allowing mechanized harvest and expansion of cultivation areas (Guerra et al. 2017).

During the breeding process, it is most natural to evaluate the candidates in multi-environment trials (MET). MET aims at identifying the behavior of genotypes when facing the genotype-by-environment interaction (GEI). Predicting GEI allows the identification of optimal gene combinations for target environments. In other words, neglecting GEI disregards the genotypes' adaptability and, consequently, reduces the genetic gain (Heslot et al., 2014; Jarquín et al., 2014; Millet et al., 2016). Thus, it is necessary to evaluate the performance of genotypes in MET (Islam et al., 2016). Nevertheless, MET have experimental and statistical peculiarities that cannot be ignored. The different environmental conditions and management decreases the chance of homoscedasticity of variance (Silva et al., 2019; Souza et al., 2021). Moreover, METs are more susceptible to genetic and/or statistical imbalance (Elias et al., 2016; Schmidt et al., 2019).

These peculiarities hinder the usage of traditional methods in the statistical analysis of MET data, such as the ordinary least squares. As an alternative, the breeder may employ methodologies that are flexible enough to deal with heteroscedasticity, imbalance, and/or non-orthogonality. In this context, the use of the residual maximum likelihood method (REML) (Patterson & Thompson, 1971) to estimate the best linear unbiased predictors (BLUP) (Henderson, 1975) is an interesting alternative. The REML/BLUP method allows modeling the covariance structure of the random effects, providing the model with flexibility and adequacy to diverse situations (Melo et al., 2020). Despite the aforementioned advantages, the use of this methodology in cowpea data analysis is still limited.

In this article, we explore the REML/BLUP features to select the model with the most appropriated covariance structure and compare the results with the traditional model, that is, homogeneous variances. In addition, we select the supe-

Core ideas

- Multi-environment trials have peculiarities that must be accounted for in the statistical modeling.
- The genetic and residual homoscedasticity assumption is unlikely to be true.
- By modeling the covariance structures of a mixed model random effects, there are higher accuracy and gains.
- The cowpea breeder must not ignore this step in the breeding process.

rior cowpea genotypes for 100-grain weights based on the best-fitted model.

2 | MATERIALS AND METHODS

2.1 | Experimental conditions and plant material

We evaluated 20 genotypes, being 17 inbred lines and three commercial cultivars (Table S1), from the value for cultivation and use (VCU) trials of color type. These 17 inbred lines are candidates for new cultivars of the Cowpea Breeding Program of Embrapa Meio-Norte, Piauí state, Brazil. These genotypes were evaluated in four locations from semi-arid zone of Piauí State, and in two crop-years (Table 1).

The trials were established in a randomized complete block design, with four replications. Each treatment was represented by a plot of four rows of 5.0 m, with spacing between rows of 0.50 m and with spacing between plants within row of 0.25 m. The two central rows were the useful plot. The soil of the four sites were Red-Yellow Podzolic type. The evaluated trait was 100-grain weight taken at random from the useful plot.

Management practices followed the technical recommendations for the crop (Freire-Filho et al., 2011). The soils of the trials were prepared and then harrowing was performed. Soon after, pre-emergence herbicide based on s-metolachlor (1 L ha^{-1}) was applied and weed control was done at 20 and 30 days. We also applied insecticides based on dimethoate (1 L ha^{-1}) and thiamethoxam (100 g ha^{-1}) for aphid control. We harvested at 70 days after planting.

2.2 | Statistical analyses

All statistical procedures are based on the REML (Patterson & Thompson, 1971), for estimation of the variance components; and on the BLUP for genotypic values prediction

TABLE 1 Localization and environmental conditions of the trials located in Piauí, during two crop seasons: 2019/2020 and 2020/2021

| ID | Sites | Year | Geographic coordinates | | Altitude (m) | Temperature | |
			Latitude	Longitude		Min. (°C)	Max. (°C)
IP	Ipiranga do Piauí	2020	6°49′ S	41°44′ W	410	22	28
PI1	Pio IX	2019	6°50′ S	40°35′ W	513	18	36
PI2	Pio IX	2020	6°50′ S	40°35′ W	513	19	36
MH1	Monsenhor Hipólito	2019	7°00′ S	41°01′ W	262	25	38
MH2	Monsenhor Hipólito	2020	7°00′ S	41°01′ W	262	21	38
SM	São Miguel do Tapuio	2019	5°29′ S	41°18′ W	272	20	32

Abbreviations: Min., minimum; Max., maximum.

(Henderson, 1975). First, we tested the normality assumption using the quantile–quantile plot, as recommended by Kozak and Piepho (2018). We assumed the residual independency, and the heteroscedasticity will be accounted for in the modeling of the residual covariance matrix. Once we were assured of data normality, we performed individual analyses for each environment, using the following model:

$$\mathbf{y} = \mathbf{Xm} + \mathbf{Zg} + \mathbf{e}$$

where $\mathbf{y}$ is the phenotypic data vector, $\mathbf{m}$ is the vector of fixed effects (effects of replications and the intercept), $\mathbf{g}$ is the vector of the genotypic effect, considered random [$\mathbf{g} \sim \mathrm{N}(0, \mathbf{I}\sigma_g^2)$], and $\mathbf{e}$ is the vector of random residual effects [$\mathbf{e} \sim \mathrm{N}(0, \mathbf{I}\sigma_e^2)$]. $\mathbf{X}$ and $\mathbf{Z}$ are the incidence matrices for $\mathbf{m}$ and $\mathbf{g}$, respectively. Individual analyses were performed to assess the significance of the genotypic effect, using the likelihood ratio test (LRT) (Wilks, 1938):

$$LRT = -2 \left(\mathrm{Log}\, L - \mathrm{Log}\, L_R \right)$$

where L is the maximum point of residual likelihood function of the complete model and L_R is the same for the reduced model, that is, without the effect to be tested. The LRT value was compared with a tabulated value based on the chi-square table, with one degree of freedom and 0.95 probability.

Then, we performed the joint analysis, considering all the environments, using the following model:

$$\mathbf{y} = \mathbf{Xm} + \mathbf{Zg} + \mathbf{Wge} + \mathbf{e}$$

where $\mathbf{m}$ is the vector of fixed effects (effects of environments, replications and their combinations, added to the overall mean); $\mathbf{g}$ is the vector of the genotypic effect, considered random [$\mathbf{g} \sim \mathrm{N}(0, \mathbf{G_g})$]; $\mathbf{ge}$ is the vector of the random GEI effects [$\mathbf{ge} \sim \mathrm{N}(0, \mathbf{I}\sigma_{ge}^2)$]; and $\mathbf{e}$ is the vector of random errors effect [$\mathbf{e} \sim \mathrm{N}(0, \mathbf{R})$]. $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are the incidence matrices for $\mathbf{m}$, $\mathbf{g}$, $\mathbf{ge}$, respectively. $\mathbf{G_g}$ and $\mathbf{R}$ refer to the covariance matrices for genotype and residual effects, respec-

tively. The model above was the basis for the elaboration of other models, with different covariance structures for $\mathbf{G_g}$ and $\mathbf{R}$.

The $\mathbf{R}$ matrix was modeled using two different structures. The first was the identity of variances (IDV), which considers homoscedasticity between environments. The second was the diagonal structure (IDH), which assumes that different environments have distinct residual variances. The genetic effects were modeled after residual effects. We tested four structures. The first one, contained in the base model, is the homogeneous compound symmetry (CS), which considers a single genetic variance for all environments and an explicit variance attributed to the GEI. The second one was the diagonal (IDH). The third one was heterogeneous compound symmetry (CSH), which considers heterogeneity of genetic variances between environments and the presence of covariance between them. Finally, we tested the unstructured model (UN), which considers each environment as a different trait. Table 2 compiles the structure of the random effects of each model.

The best-fit model was selected based on Akaike information criterion (AIC) (Akaike, 1973) and the Bayesian information criterion (BIC), given by, respectively:

$$\mathrm{AIC} = -2\mathrm{Log}\,L + 2p$$

$$\mathrm{BIC} = -2\mathrm{Log}\,L + p\mathrm{Log}\,[n - r(x)]$$

where L is the maximum point of the residual likelihood function, p is the number of estimated parameters, and $r(x)$ is the rank of the fixed effects incidence matrix. The smaller the AIC and BIC values, the better the fit.

From the best-fit model, were estimated the generalized heritability $\{ H_g^2 = 1 - \frac{V[\Delta(g_i - g_{i'})]}{2\sigma_g^2}$, where $V[\Delta(g_i - g_{i'})]$ is the mean variance of the difference between two BLUPs [Cullis et al., 2006]}, and the selective accuracy [$r_{\hat{g}g} = \sqrt{1 - (\frac{\mathrm{PEV}}{\sigma_g^2})}$, where PEV is the variance of the prediction

TABLE 2 Models and covariance structures used in the **R** and **G**$_g$ matrices and their respective linear representations

| Model | Matrix R | | Matrix G$_g$ | |
	Structure	Representation	Structure	Representation
M1	IDV	$\sigma_e^2 \mathbf{I}_a \otimes \mathbf{I}_n$	CS	$(\sigma_g^2 \mathbf{J} + \sigma_{gs}^2 \mathbf{I}) \otimes \mathbf{I}_t$
M2	IDH	$\oplus_{j=1}^a \sigma_e^2 \mathbf{I}_a \otimes \mathbf{I}_n$	CS	$(\sigma_g^2 \mathbf{J} + \sigma_{gs}^2 \mathbf{I}) \otimes \mathbf{I}_t$
M3	IDH	$\oplus_{j=1}^a \sigma_e^2 \mathbf{I}_a \otimes \mathbf{I}_n$	IDH	$\oplus_{i=1}^g \sigma_g^2 \mathbf{I}_g \otimes \mathbf{I}_t$
M4	IDH	$\oplus_{j=1}^a \sigma_e^2 \mathbf{I}_a \otimes \mathbf{I}_n$	CSH	$\{\mathbf{D}[\mathbf{I}_a + \rho(\mathbf{J} - \mathbf{I}_a)]\mathbf{D}\} \otimes \mathbf{I}_t$
M5	IDH	$\oplus_{j=1}^a \sigma_e^2 \mathbf{I}_a \otimes \mathbf{I}_n$	UN	$\sum \otimes \mathbf{I}_t$

Note: σ_e^2, residual variance; σ_g^2, genetic variance; $\mathbf{I}_a$, $\mathbf{I}_t$, and $\mathbf{I}_n$, identity matrices of size $a \times a$, $t \times t$, and $n \times n$, respectively, where a is the number of environments and t the number of genotypes and n is the number of observations; **D**, $a \times a$ diagonal matrix of standard deviations; **J**, $a \times a$ matrix of ones; Σ, full covariance matrix; $\otimes$, Kronecker product; $\oplus$, direct sum.

Abbreviations: CS, compound symmetry; CSH, heterogeneous compound symmetry; IDH, diagonal structure; IDV, identity variance; UN, unstructured.

TABLE 3 Likelihood ratio test for genotypic effect on each environment and genotypes-by-environment interaction effect for all the environments

Effect	Environment[a]	LogL	Deviance	LRT
Genotype	SM	−56.8461	−113.692	16.388**
	PI1	−79.9993	−159.999	15.829**
	MH1	−78.8114	−157.623	21.055**
	IP	−96.9116	−193.823	0.4912
	MH2	−73.4207	−146.841	0.7452
	PI2	−88.2007	−176.401	0.0138
GEI	—	−503.7645	−1007.53	27.288**

Abbreviation: GEI, genotype-by-environment interaction.

[a]See Table 1 for explanation of environments.

TABLE 4 Akaike information criterion (AIC) and Bayesian information criterion (BIC) values of five fitted models with different covariance structures for genetic (G$_g$) and residual (R) effects

| Model | Covariance structures[a] | | AIC | BIC |
	Matrix G$_g$	Matrix R		
M1	CS	IDV	986.2409	998.58
M2	CS	IDH	947.2736	980.20
M3	IDH	IDH	951.8634	1001.25
M4	*CSH*	*IDH*	*921.1129*	*974.61*
M5	UN	IDH	—	—

Note: In italic, the best fit model, according to AIC and BIC, the model M5 did not converge.

Abbreviations: CS, compound symmetry; CSH, heterogeneous compound symmetry; IDH, diagonal structure; IDV, identity variance; UN, unstructured.

[a]See Table 2 for explanation of structures.

error, obtained from the diagonal of the generalized inverse of the coefficient matrix of the mixed model equations]. We also estimated the selection gains ($SG = \frac{BLUP_s}{\mu_0} \times 100$, where $BLUP_s$ are the selected genotypes BLUP and μ_0 is the overall mean), considering the top five genotypes. We estimated the aforementioned parameters for the first, traditional model (M1), and for the best-fitted model, for comparison purposes. The genotype ranking between models was compared with Spearman correlation coefficient [$\rho = 1 - \frac{6\sum_{i=1}^n d^2}{n(n^2-1)}$, in which d is the difference between ranking and n is the number of observations]. All analyses were performed in R software (R Core Team, 2022), using the ASReml-R package (Butler et al., 2018).

3 | RESULTS

The genetic variance was significant ($p < 0.001$) only in the trials evaluated in year one. The GEI was also significant, indicating that genotypes performed differently across trials (Table 3).

The model that the genotypic and residual effects were modeled using the CSH and IDH structures (M4), respectively, had the best fit according to AIC and BIC (Table 4).

There is a clear difference between the variance components and genetic parameters of M1 and M4. In the traditional model, M1 (CS for the genetic effect and ID for the residual effect), one would not observe the differences between the genetic variance of the two evaluated years. By particularizing the variances, there is no generalization in the reckoning of the accuracy and heritability. Note that the accuracies and heritabilites of the environments where the genetic variance was significant are higher than the generalized value indicated by M1. This emphasizes that the non-significant trials were biasing the estimation of these parameters (Table 5).

The aforementioned differences reflect in the genotypes ranking, according to their breeding value (BLUPs) (Figure 1). Modeling of G and R cause a 25% change in the rankings. Considering the top five genotypes the expected genetic gains change from 2.60% in M1 to 3.78% in M4 (Table 5).

TABLE 5 Variance components and genetic parameters estimated from the traditional model (M1) and best fit model (M4)

Component/Parameter	M1	M4 Environments					
		SM	PI1	MH1	IP	MH2	PI2
σ_g^2	0.140	0.931	2.322	1.949			
σ_{ge}^2	0.662	—	—	—	—	—	—
σ_r^2	2.158	0.880	1.506	1.312	4.069	2.188	3.376
σ_f^2	2.961	1.810	3.828	3.261	4.096	2.242	3.376
H_g^2	0.356	0.875	0.894	0.891	—	—	—
r_{gg}	0.596	0.866	0.888	0.885	—	—	—
SG (%)	2.60%	3.78%					
Spearman correlation				0.75			

Abbreviations: σ_g^2, genotypic variance; σ_{ge}^2, genotypes-by-environment interaction variance, σ_r^2, residual variance; σ_f^2, phenotypic variance; H_g^2, broad-sense mean heritability; r_{gg}, selective accuracy.
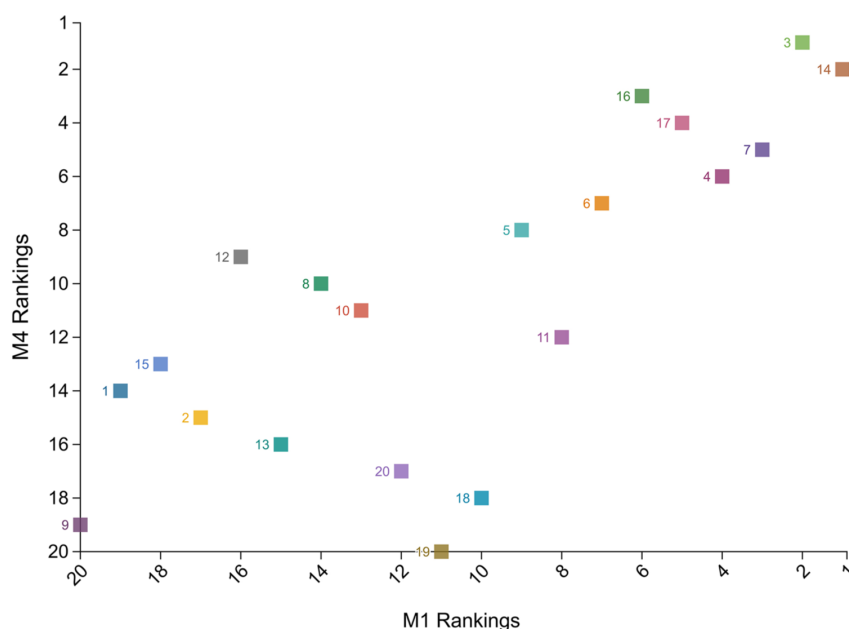
FIGURE 1 Genotypes' ranking according to their genotypic values in M1 and M4. The values are averaged across environments.

4 | DISCUSSION

In this study, we tested different statistical models with distinct covariance structures for 100-grain weight. The results showed that by modeling the random effects, one could improve cowpea's genetic evaluation by elevating the preciseness of the results.

The existence of genetic variability for the evaluated trait indicates the population's potential for selection (Owusu et al., 2021a). According to Alidu et al. (2020) and Owusu et al. (2021b), cowpea has wide genetic variability for almost all traits of agronomic and nutritional interest, which facilitates the breeding actions. Among the yield components, 100-grain weight is one of the most important traits for selecting superior genotypes for grain yield (Ajayi & Gbadamosi, 2020; Ezin et al., 2021; Marinho et al., 2021).

The breeder needs genetic variability in a breeding program to practice selection of superior genotypes. We identified that the genotypic effect was significant only in the first year of trials. In year two, the non-controllable effects at these locations may have been intense. Without a significant genetic variance, it is impossible to differentiate the genotypes'

performance (Simion et al., 2018; Gerrano et al., 2019). In cowpea, edaphoclimatic variables such as minimum temperature, solar radiation, rainfall, wind speed, length of crop growth cycle, and altitude can affect the performance of genotypes in different environments (Oliveira et al., 2020). Bear in mind that 100-grain weight is a quantitative trait, so it is expected that the greatest variation in this trait is due to the environmental effects (Mekonnen et al., 2022).

GEI also plays an important role in 100-grain weight expression (Caro et al., 2017). The significance of GEI indicates a differential genotypic performance across environments. When this effect is crossover, selection and recommendation of new cultivars with broad stability are difficult, due to the differential response of genotypes to different environments (Kang, 1997; Enyew et al., 2021). Furthermore, MET may exhibit high levels of heterogeneity of variances and covariances (Gouveia et al., 2020). When this heterogeneity is not considered, it can cause inflation or deflation of Type I statistical error rates for genotype comparisons. This fluctuation depends on some factors, such as the level of heterogeneity and assumptions about the effects of environments (whether fixed or random) (Hu et al., 2013).

The M4 model had the best fit according to AIC. In this model, the residual and genetic covariance matrices were structured using the block diagonal (IDH) and CSH variance structures. In the CSH structure, the magnitude of the covariances is based on the product of genetic standard deviations multiplied by a single correlation coefficient. Thus, correlation over environments is constant, but covariances differ depending on the differences in standard deviations (Milliken & Johnson, 2001). One may interpret the magnitude of GEI from the genetic correlation coefficient across environments. Note that this model is more parsimonious than the unstructured model (M5), the most complete and parameterized, which did not converge in our study.

ANOVA-based analyses assumes that all observations have a common error, that is, there is residual homoscedasticity. However, MET may not fulfill this assumption, since each trial is subjected to a different environmental condition, according to the location and year. Bear in mind that each location has its own dynamics of edaphoclimatic conditions, water availability, and incidence of pests and diseases. Furthermore, these conditions may change drastically on an yearly basis in tropical environments, such as the ones in this study. Thus, as expected, this was the tendency herein since the model with IDH had the best fit. The IDH covariance structure assumes that there are important differences between non-controllable effects (Isik et al., 2017). Rocha et al. (2019) and Melo et al. (2020) obtained similar results for common bean (*Phaseolus vulgaris* L.). Therefore, in MET context, modeling genetic and non-genetic covariances structure can enable greater reliability for the statistical models (Smith et al., 2005, 2015).

In M1, one cannot observe the population behavior in each environment, for neither genetic nor residual effects. The CS structure in M1 divides the genetic effects into the genotypic variance and the GEI variance, lowering the heritability and the selective accuracy. On the other hand, the structure employed in M4 allows the particularization of the population performance in each environment. As the CSH structures do not have the GEI variance, heritabilities and selective accuracies are considerably higher. From this, Spearman's correlation (0.75) revealed differences in the ranking of genotypes, culminating in a 1.18% difference between the expected genetic gains of M1 and M4.

In this study, we validate the necessity of modeling the covariance matrix structure of a linear mixed model's random effects. Although the CSH for genetic effects and IDH for the residual effects were the most appropriate for the 100-grain weight trait, one cannot take this fact as truth for all cases. In other words, the best covariance structure will differ according to the peculiarities of each data set, such as the number of evaluated genotypes, the number of environments, and the evaluated trait. Thus, the breeder must do the testing for all cases.

AUTHOR CONTRIBUTIONS

Maurício dos Santos Araújo: Conceptualization; formal analysis; methodology; validation; writing—original draft; writing—review and editing. **Saulo Fabrício da Silva Chaves**: Formal analysis; investigation; methodology; validation; writing—original draft; writing—review and editing. **Kaesel Jackson Damasceno-Silva**: Conceptualization; funding acquisition; supervision; validation; writing—review and editing. **Luiz Antônio dos Santos Dias**: Conceptualization; methodology; writing—original draft; writing—review and editing. **Maurisrael de Moura Rocha**: Conceptualization; supervision; validation; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Maurício dos Santos Araújo https://orcid.org/0000-0002-7728-2590
Saulo Fabrício da Silva Chaves https://orcid.org/0000-0002-0694-1798
Kaesel Jackson Damasceno-Silva https://orcid.org/0000-0001-7261-216X

Luiz Antônio dos Santos Dias https://orcid.org/0000-0002-1828-6938

Maurisrael de Moura de Rocha https://orcid.org/0000-0001-5817-2794

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SUPPORTING INFORMATION

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