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ARTICLE

Modeling spatial trends and selecting tropical wheat genotypes in multi-environment trials

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Abstract: *In many cases, traditional analysis of breeding trials based on analysis of variance (ANOVA) do not allow a suitable genetic evaluation. Alternatively, mixed model-based approaches create the possibility of dealing with unbalanced data and modeling spatial trends. The aims of this study were to compare the goodness-of-fit of the model and the genotype ranking through different residual modeling approaches and to select the best performing tropical wheat genotypes based on the best-fitting model. A panel of tropical wheat genotypes was evaluated in three field trials conducted between 2020 and 2021 for grain yield. Linear mixed model analyses were used on the data to estimate the genetic parameters and to predict the genotypic values in analyses of single- and multi-environment trials. Accounting for spatial trends in the analyses of single- and multi-environment trials provides better outcomes than the compound symmetry model does.*

Keywords: *BLUP, mixed-model, spatial analysis*, Triticum aestivum L.

INTRODUCTION

Elite wheat selection candidates need to be evaluated in multi-site multi-year breeding trials to be recommended. Generally, data from multi-environment trials (MET) are unbalanced and have heterogeneous variances due to differences in environmental conditions, factors that hamper ordinary least square-based inferences. These difficulties are easily overcome using linear mixed models (Henderson 1975). This method deals with statistical and genotypic imbalance, and allows the modeling of covariance structures. Using linear mixed models, all decisions are based on restricted maximum likelihood (REML) estimates and best linear unbiased predictors (BLUP), which penalizes the adjusted mean by the amount of available information, increasing the correlation between the true and predicted genotypic values.

Linear mixed models are also fitted to deal with spatially correlated data. Dependence between plots can be caused by external sources of variation, such as soil heterogeneity, disease or pest outbreaks, and inappropriate crop management or experimental designs (Burgueño et al. 2018). The first approaches proposed to deal with spatial trends consisted of adjusting plot results for spatial variability using information from neighboring plots (Wilkinson et al. 1983). Later, statistical models were proposed to sequentially fit a class of autoregressive

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integrated moving averages to the plot errors in row or column directions (Gleeson and Cullis 1987). This model was further extended to two directions, assuming that rows and columns in the field are regularly spaced (Cullins and Gleeson 1991). Currently, one of the most used models to account for spatial trends is the first-order separable autoregressive model for rows and columns, which models the residual variance-covariance matrix in a two-dimensional process and decomposes the residual variation into correlated and uncorrelated residuals (Gilmour et al. 1997).

Controlling external sources of variation by modeling the residual term in single- and multi-environment trials can increase the reliability of selection and genetic gains (Lado et al. 2013, Gogel et al. 2018). Nevertheless, this is often overlooked in tropical wheat breeding programs. In this study, the objective was to show how residual modeling in single- and multi-environment trials can be beneficial for wheat breeding. For that purpose, we compared the goodness-of-fit of the model and the genotype ranking through different residual modeling approaches, and selected the best performing tropical wheat genotypes for grain yield based on the best-fitting model.

MATERIAL AND METHODS

Genotypes and field trials

We evaluated 42 wheat lines from the UFV wheat breeding program and eight commercial checks for grain yield (kg ha^{-1}) in three field trials (FT1, FT2, and FT3) in the Professor "Diogo Alves de Mello" experimental field (lat 20º 45' 14" S, long 42º 52' 55" W, and alt 648 m asl) at the Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil. The soil is classified as an *Oxisol* (Santos et al. 2018), and the climate of the region is a monsoon-influenced humid subtropical climate with wet winters and hot summers, average annual rainfall between 1300 and 1600 mm, and average annual temperature of 21 ºC (Alvares et al. 2013).

FT1 was conducted during the summer of 2020, and FT2 and FT3 were conducted during the winter of 2020 and 2021, respectively. We laid out the trials in a randomized complete block design with three replications. Plots consisted of five 5-m rows spaced at 0.20 m and had a population density of 350 seeds m^{-2}. We performed agronomic practices according to the technical recommendations for wheat growing in the Brazilian South Central region.

Genetic and statistical analyses

We estimated the variance components through the restricted maximum likelihood (REML) method and predicted the genotypic values through best linear unbiased prediction (BLUP) (Patterson and Thompson 1971, Henderson 1975).

Single-environment trial analysis

We considered the following model for the individual analysis of each trial:

$$y = Xb + Zg + e$$

where y is the $n \times 1$ vector of phenotypic observations; b is the $r \times 1$ vector of fixed effects of blocks added to the overall mean; g is the $m \times 1$ vector of random effects of genotypes, $g \sim N(0; I\sigma_g^2)$, where σ_A^2 is the genotypic variance; and e is the $n \times 1$ vector of random residual effects, $e \sim N(0; I\sigma_e^2)$, where σ_e^2 is the residual variance. X and Z are the incidence matrices for those effects.

We fitted four residual covariance structures for modeling the residual effects: the first model (NSPM) did not account for correlations among the rows or columns, i.e., $e \sim N(0, \sigma_\xi^2 I_r \otimes I_c)$, where σ_e^2 is the residual variance, and I_r and I_c are identity matrices representing spatial independence in the row and column directions, respectively. The second model (SPM1) accounted for spatial correlations among rows, i.e., $e \sim N[0, \sigma_\xi^2 \Sigma_r(\rho_r) \otimes I_c]$, where σ_ξ^2 is the variance of spatially correlated residuals, $\Sigma_r(\rho_r)$ is the first-order autoregressive correlation matrix for rows, and $\otimes$ is the Kronecker product. The third model (SPM2) accounted for spatial correlations among columns, i.e., $e \sim N[0, \sigma_\xi^2 I_r \otimes \Sigma_c(\rho_c)]$, where $\Sigma_c(\rho_c)$ is the first-order autoregressive correlation matrix for columns. Finally, the fourth model (SPM3) accounted for correlations in both directions (rows and columns), i.e., $e \sim N[0, \sigma_\xi^2 \Sigma_r(\rho_r) \otimes \Sigma_c(\rho_c)]$.

Multi-environment trial analysis

For the multi-environment trial analyses, we used the following model:

$$y = X_1 t + X_2 b + Z_1 g + Z_2 i + e$$

where y is the $n \times 1$ vector of phenotypic observations; t is the $s \times 1$ vector of fixed effects of trials added to the overall mean; b is the $r \times 1$ vector of fixed effects of replicates nested within trials; g is the $m \times 1$ vector of random effects of genotypes, $g \sim N(0; I\sigma_g^2)$; i is the $ms \times 1$ vector of the random effects of the genotype-by-environment interactions, $i \sim N(0; I\sigma_i^2)$, where σ_i^2 is the genotype-by-environment interaction variance; and e is the $n \times 1$ vector of random effects of the residuals $e \sim N(0; I\sigma_e^2)$. X_1, X_2, Z_1, and Z_2 are the incidence matrices for those effects.

We modeled the residuals in the joint analyses using three covariance structures. The first approach (SSM1) assumed a homogeneous residual variance across the trials, i.e., $e \sim N(0, \sigma_e^2 I_m \otimes [I_r \otimes I_c])$, where σ_e^2 is the residual variance and I_m is an identity matrix whose dimension is the number of trials. The second approach (SSM2) assumed heterogeneous residual variances, i.e., $e \sim N(0, \sigma_e^2 D_m \otimes [I_r \otimes I_c])$, where D_m is a diagonal matrix containing the residual variance of each trial. Given the results of the single-environment trial analyses, where the best-fitting model for each field trial considered spatial correlations among columns, i.e., SPM2, the third approach for the multi-environment trial analysis (SSM3) considered heterogeneous residual variances and the spatial correlation in column directions in each field trial, i.e., $e \sim N(0, \sigma_e^2 D_m \otimes [\sigma_\xi^2 I_r \otimes \Sigma_c(\rho_c)])$.

Model selection

We selected the best-fitting model using the Akaike Information Criterion (AIC) (Akaike 1974):

$$AIC = -2logL + 2p$$

where $logL$ is the logarithm of the maximum of the restricted likelihood function; p is the number of parameters estimated; and n is the number of observations. The best-fitting model is the one with the lowest AIC value.

Likelihood ratio test

We tested the significances of the genotype and the genotype-by-environment interaction effects using the likelihood ratio test (LRT) (Wilks 1938), given by:

$$LRT = -2(LogL_F - LogL_R)$$

where $LogL_F$ is the logarithm of the restricted likelihood function of the full model, and $LogL_R$ is the logarithm of the restricted likelihood function of the reduced model. The significance of the random effects was tested using the chi-square distribution, considering 5% and 1% probabilities.

Genetic parameters

We estimated broad sense heritability as follows (Cullis et al. 2006):

$$h^2 = 1 - \frac{\overline{v}_{BLUP}}{2\sigma_g^2}$$

where $\overline{v}_{BLUP}$ is the mean variance of a difference of two BLUPs; and σ_g^2 is the genotypic variance.

We estimated accuracy as follows:

$$\hat{r}_{gg} = \sqrt{1 - \frac{PEV}{\sigma_g^2}}$$

where PEV is the prediction error variance; and σ_g^2 is the genotypic variance.

Selection gain

For selection of the top performers across the trials, we considered a 20% selection proportion. The predicted genetic gain from selection was calculated as follows:

$$SG_{\%} = \frac{\mu_s - \mu_o}{\mu_o} \times 100$$

where μ_s is the mean of the selected genotypes; and μ_o is the original mean.

Linear regression and Kappa coefficient

To investigate the degree of dissimilarity among the outcomes of each model, we fitted a linear regression model using the BLUPs of the SSM1, SSM2, and SSM3 as follows:

$$\hat{y}_j = \hat{\beta}_0 + \hat{\beta}_1 x_i + e$$

where $\hat{y}_j$ is the BLUP of the j^{th} model; $\hat{\beta}_0$ is the intercept; $\hat{\beta}_1$ is the angular coefficient of the regression; x_i is the BLUP of the i^{th} model; and e is the error. We also computed the Kappa coefficient (K) (Cohen 1960) to evaluate the agreement among models in the ranking of the 20% best selected genotypes:

$$K = \frac{p_o - p_c}{1 - p_c}$$

where p_o is the proportion of matching selected genotypes; and p_c is the proportion of matching selected genotypes expected by chance.

Software

We performed all analysis in the R version 4.2.2 software (R Core Team 2022). Mixed-model analyses were fitted using the asreml package, version 4.2 (Butler 2023), and plots were prepared with the ggplot2 package (Wickham 2016).

RESULTS AND DISCUSSION

The genotype effects were significant at 1% probability by the Chi-square test in all three field trials considering all four mixed models fitted (Table 1). In FT1, heritability estimates ranged from 0.62 (NSPM) to 0.68 (SPM3) and accuracy estimates from 0.78 (NSPM) to 0.82 (SPM3). The autocorrelation coefficient estimates for rows were -0.13 (SMP1) and -0.15 (SPM3), and the autocorrelation coefficient estimates for columns were 0.23 (SPM2) and 0.25 (SPM3). In FT2, heritability estimates ranged from 0.65 (NSPM) to 0.68 (SPM3) and accuracy estimates from 0.81 (NSPM) to 0.82 (SPM3).

Table 1. Summary of the single- and multi-environment analyses.

Single-environment analyses								
Trial	Model	σ^2_g	σ^2_r	p_r	p_c	h^2	Ac	AIC
FT1	NSPM	193778.00**	342250.90	-	-	0.62	0.78	1436.41
	SPM1	193396.80**	341808.20	-0.13	-	0.63	0.78	1437.75
	SMP2	**209833.80****	**342199.30**	**-**	**0.23**	**0.66**	**0.80**	**1435.79**
	SPM3	215433.00**	341589.20	-0.15	0.25	0.68	0.82	1436.94
FT2	NSPM	130158.30**	198332.50	-	-	0.65	0.81	1371.20
	SPM1	127232.50**	198513.50	-0.24	-	0.67	0.81	1370.51
	SPM2	**120592.70****	**210281.70**	**-**	**0.4**	**0.67**	**0.81**	**1363.66**
	SPM3	120293.60**	205084.20	-0.16	0.38	0.68	0.82	1364.34
FT3	NSPM	341879.20**	757516.80	-	-	0.57	0.74	1422.96
	SPM1	340942.50**	759049.70	0.03	-	0.57	0.75	1424.86
	SPM2	**320041.80****	**801839.60**	**-**	**0.30**	**0.58**	**0.74**	**1421.09**
	SPM3	320077.20**	801980.00	0.01	0.30	0.57	0.74	1423.08

Multi-environment analyses						
Model	σ^2_g	σ^2_{ge}	h^2	Ac	GS%	AIC
SSM1	188338.85**	48012.57	0.66	0.81	15.25%	4251.75
SSM2	164764.95**	1848.40	0.67	0.82	12.11%	4210.93
SSM3	**147657.80****	**20642.48**	**0.65**	**0.79**	**11.21%**	**4200.86**

FT1, field trial 1; FT2, field trial 2; FT3, field trial 3; NSPM, non-spatial model; SPM1, spatial model 1; SMP2, spatial model 2; SPM3, spatial model 3; σ^2_g, genotypic variance component; σ^2_r, residual variance component; p_r, auto-correlation coefficient for rows; p_c, auto-correlation coefficient for columns; h^2, heritability; Ac, accuracy; AIC, Akaike Information Criterion; SSM1, single-stage model 1; SSM2, single-stage model 2; SSM3, single-stage model 3; σ^2_{ge}, genotype-by-environment variance component; GS%, percentage predicted genetic gain. Bold values indicate the best-fitting model; ** significant genotype effects at 1% probability by the Chi-square test.

The autocorrelation coefficient estimates for rows were -0.24 (SPM1) and -0.16 (SPM3), and the autocorrelation coefficient estimates for columns were 0.40 (SPM2) and 0.38 (SPM3). Lastly, in FT3, heritability estimates ranged from 0.57 (NSPM) to 0.58 (SPM2) and accuracy estimates from 0.74 (NSPM) to 0.75 (SPM1). The autocorrelation coefficient estimates for rows were 0.03 (SPM1) and 0.01 (SPM3), and the autocorrelation coefficient estimate for columns considering models SPM2 and SPM3 was 0.30.

The results of the single-environment trial analyses obtained in this study demonstrate that accounting for spatial trends in column directions (SPM2) provide better outcomes than the compound symmetry model (NSPM) does. This is confirmed by the low AIC estimates obtained by SPM2 in all field trials. Additionally, modeling the spatial trends also had positive impacts on the heritability and accuracy estimates. Although those parameters can be considered moderate to high by NSPM (Resende and Alves 2022), fitting SPM2 allowed for a slight increase in the heritability and accuracy estimates, indicating that accounting for residual correlations might increase the accuracy and, consequently, leverage genetic gains from selection. Those results are consistent with previous reports aiming to evaluate the suitability of spatial analysis for genetic evaluation of soybean, maize, and common bean field trials (Bernardeli et al. 2021, Salvador et al. 2022).

The variograms of the best-fitting model (SPM2) for the three field trials showed peaks of field spatial dependencies along columns for most of the trials (Figure 1). These results are consistent with the autocorrelation coefficient estimates for the three field trials fitting SPM2 and SPM3, i.e., there is a certain correlation among residuals in the column direction. The results obtained from the variograms and the moderate autocorrelation coefficient estimates in the single-environment trial analyses indicate the presence of heterogeneity patterns of adjacent plots in the column direction (Burgueño et al. 2018). Additionally, the positive autocorrelation estimates mean that the plots were under the same environmental conditions (Bernardeli et al. 2021). The low magnitude of the autocorrelation coefficient estimates for row direction shows the presence of undefined patterns of spatial variability and, because those coefficients were negative, it indicates a certain competition among plots (Andrade et al. 2020).

Examining the presence of spatial dependencies through variogram inspection and estimation of autocorrelation coefficients by single-environment trial analyses might be useful for further modeling of the residual effects, i.e., including the row and column effects in the fixed and random parts of a global model. This approach has been adopted as part of a two-stage strategy in common bean and elephant grass; and it is able to enhance prediction of the genotypic values (Salvador et al. 2022, Ferreira et al. 2022).

Traditionally, single-stage analysis is considered the gold-standard approach (Smith et al. 2001), since it provides best linear unbiased estimators (BLUE) of all fixed effects and BLUP of all random effects under the assumed single-stage model (Piepho et al. 2012). Nevertheless, a two-stage approach might be suitable, especially when a large number of environments need to be analyzed. This strategy can leverage speed, simplicity, and computational efficiency (Möhring and Piepho 2009). Commonly, in the two-stage approach, the BLUE and the weights obtained in the first stage are used in the second stage for the predictions. However, if a two-stage analysis needs to be implemented, it is reasonable to

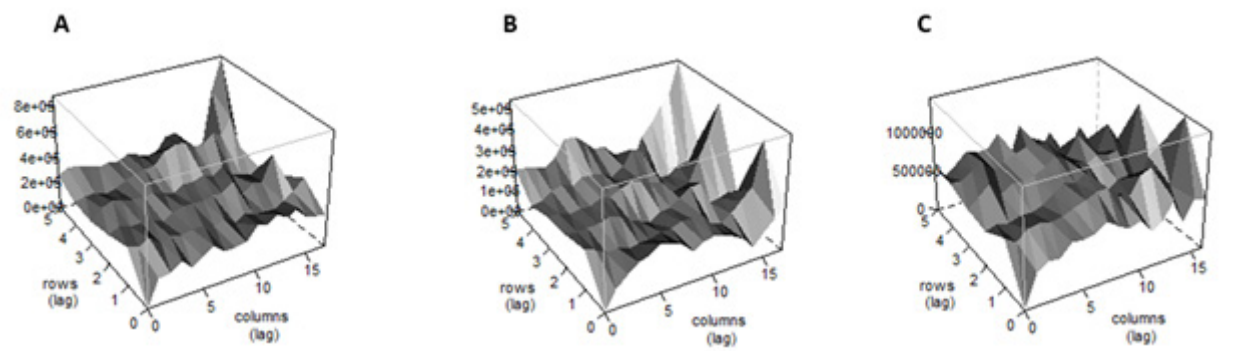

Figure 1. Variograms obtained from the best-fitting model (SPM2) used for analysis of field trial 1 (A), field trial 2 (B), and field trial 3 (C).

consider the genetic effects as random in the first stage (Verbyla 2023). After that, the estimates obtained in the first stage need to be de-regressed and used in the second stage, along with a full weight matrix.

In the multi-environment trial analyses, the genotype effects were significant at 1% probability and the genotype-by-environment interaction effects were not significant by the Chi-square test (Table 1). Those results indicate suitable genetic variability and a consistent response of the genotypes across the environments. The absence of the genotype-by-environment interaction might be explained by the fact that the trials were conducted in the same location. Increasing the number of environments (locations, years, and seasons) could potentially lead to differential responses of the genotypes. Consequently, robust biometric approaches would be required to quantify the genotype-by-environment interaction and recommend the genotypes according to their overall performance and stability (Chaves et al. 2023).

The heritability estimates were 0.66, 0.67, and 0.65 for the models SSM1, SSM2, and SSM3, respectively. The accuracy estimates were 0.81, 0.82, and 0.79 for the models SSM1, SSM2, and SSM3, respectively. The predicted genetic gain from selection of the 20% best performing genotypes were 15.25%, 12.11%, and 11.21% for the models SSM1, SSM2, and SSM3, respectively. The highest predicted genetic gain was observed for SSM1, which is the compound symmetry model. Nevertheless, the AIC obtained for both SSM2 and SSM3 shows that modeling the residual variance across environments and accounting for spatial trends might be better options for multi-environment trial analyses. The AIC has been used as a standard criterion for selection of non-nested models (Verbyla 2019), and in this case in particular, SSM3 had the lowest AIC, exhibiting the most reliable results. Thus, the predicted genetic gains observed for SSM1 and SSM2 might be overestimated and might not be achieved in practice.

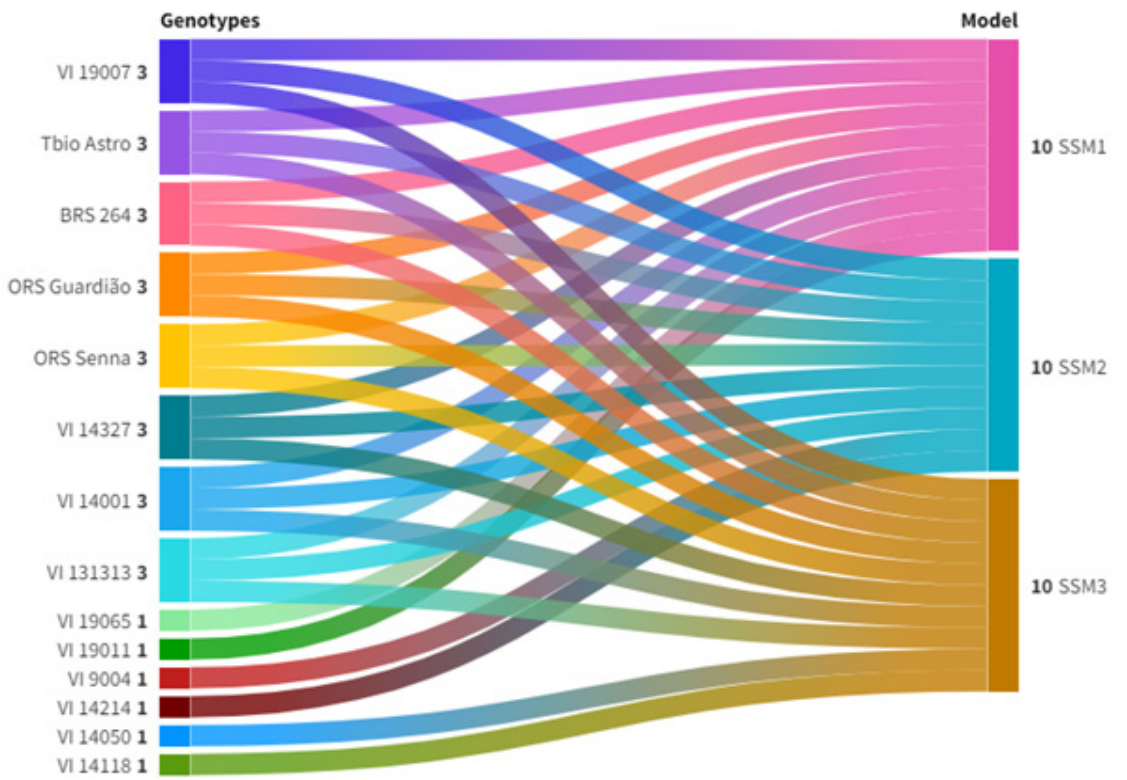

Figure 2. Genotypes selected by joint analysis of three field trials using three residual modeling strategies: A, homogeneous residual variance across the trials (SSM1); B, heterogeneous residual variances across the trials (SSM2); C, heterogeneous residual variances with spatial column adjustment (SSM3). The number beside the genotype represents the number of criteria for which this genotype appears in the top ten.

Considering that the residual variances are heterogeneous across the environments is a strong assumption since the trials might experience different environmental conditions (Araújo et al. 2023). This is true even in experiments carried out in the same site across the years or seasons. Additionally, it is reasonable that plots located close to each other are more likely to be under similar environmental conditions, leading to spatial dependence (Resende and Sturion 2003). These facts reinforce the need to model residual variances in multi-environment trial analyses.

Eight genotypes (VI 19007, Tbio Astro, BRS 264, ORS Guardião, ORS Senna, VI 14327, VI 14001, and VI 131313) were simultaneously selected by the three models fitted in the multi-environment trial analyses (Figure 2). Nevertheless, the main practical consequence of fitting different models is modification in the rankings provided by each model. This reinforces the need to use a criterion for selection of the best-fitting model, which will allow for accurate selection and recommendation of superior genotypes. Since the AIC indicated SSM3 as the best-fitting model, the 20% best performing

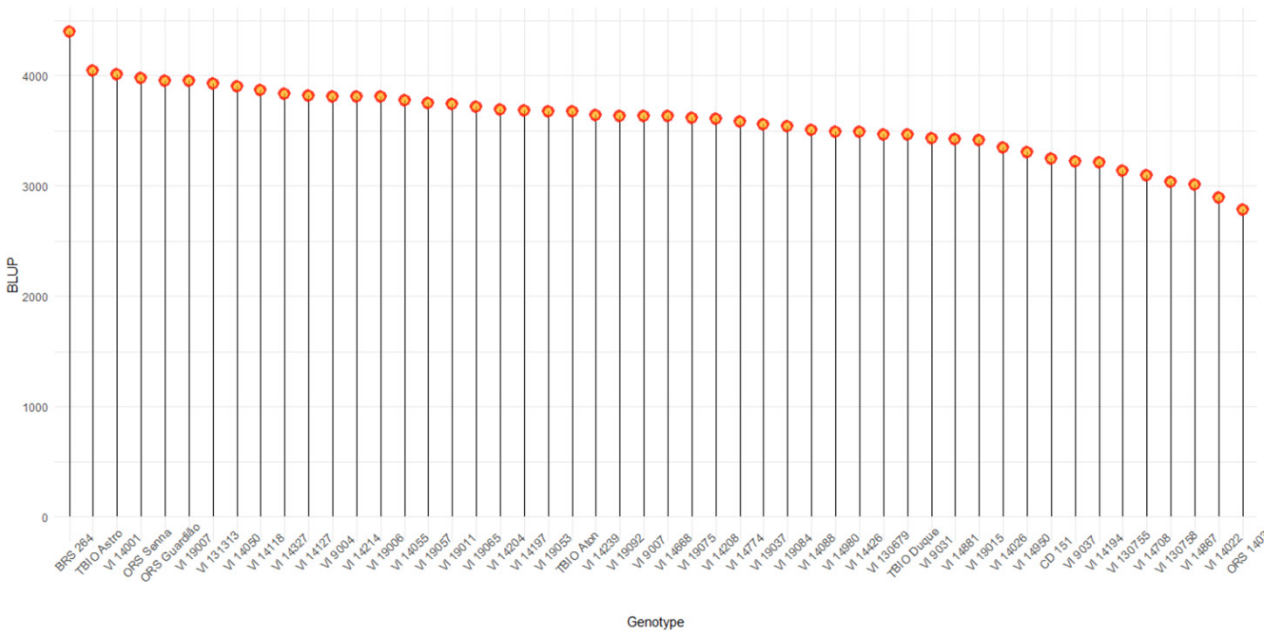

Figure 3. Genotype ranking of the best-fitting model (SSM3) in the multi-environment trial analysis.

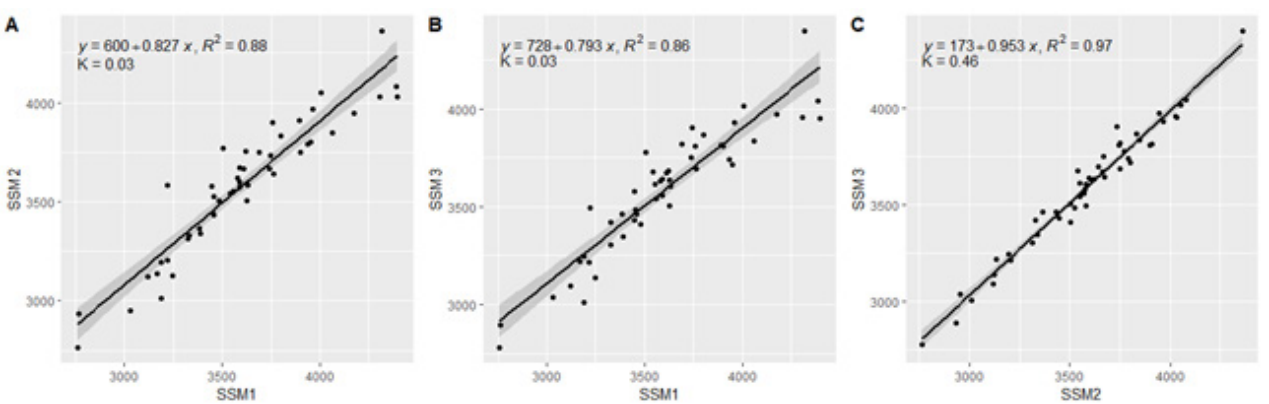

Figure 4. Kappa coefficient (K) and simple linear regression among the predicted genotypic values of the genotypes using three modeling strategies: homogeneous residual variance across the trials (SSM1), heterogeneous residual variances across trials (SSM2), and heterogeneous residual variances with spatial column adjustment (SSM3) in joint analysis of three wheat field trials.

genotypes (top 10 genotypes) should be selected. These genotypes are: BRS 264, TBIO Astro, VI 14001, ORS Senna, ORS Guardião, VI 19007, VI 131313, VI 14060, VI 14118, and VI 14327 (Figure 3). These genotypes had been previously evaluated regarding genetic diversity (Casagrande et al. 2020, Lima et al. 2021) and they showed suitable performance for grain yield and other important agronomic traits, e.g., yield components, disease resistance, short cycle, and plant height.

The coefficient of the linear regression between the BLUP from SSM1 and SSM2 (Figure 4A) was 0.88, and agreement in the ranking of the 20% best performing genotypes was 0.03. The coefficient of the linear regression between the BLUP from SSM1 and SSM3 was 0.86, and agreement in the ranking of the 20% best performing genotypes was also 0.03 (Figure 4B). The coefficient of the linear regression between the BLUP of SSM2 and SSM3 was 0.97, and agreement in the ranking of the 20% best performing genotypes was 0.46 (Figure 4C). SSM3 showed high correlation and good agreement with SSM2 (Figure 4C) in the ranking of the best performing genotypes, indicating that modeling residual effects can lead to better genetic parameter estimation.

Since the first-order separable autoregressive model proposal (Gilmour et al. 1997), several studies have shown the benefits of accounting for spatial trends in different crops, as discussed above. To the best of our knowledge, this study is the first attempt to provide insights on residual modeling under the mixed-model framework in a tropical wheat breeding program in Brazil, and it confirms that using such approaches can provide for better outcomes. The residual modeling approaches presented here might also be combined in different strategies aiming to accurately predict the performance of the genotypes and to reach desired genetic gains. The genotypes selected through SSM3 could be included in future crossing blocks for the development of base populations with enough variability for carrying out selection in the UFV Wheat Breeding Program.

CONCLUSION

Fitting a first-order autoregressive model for columns in the single-environment trial analyses allowed for slight increases in heritability and accuracy estimates in most scenarios compared to the compound symmetry model, and proved to be the best-fitting model. In the multi-environment trail analyses, considering the variances across the trials as heterogenous and fitting a first-order autoregressive model for columns led to better performance than the compound symmetry model did. The best genotypes for grain yield performance were BRS 264, TBIO Astro, VI 14001, ORS Senna, ORS Guardião, VI 19007, VI 131313, VI 14060, VI 14118, and VI 14327.

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