CROP BREEDING AND
APPLIED BIOTECHNOLOGY

ARTICLE

Genotype by environment interaction and clonal recommendation of eucalypts under varying altitudes

Crop Breeding and Applied Biotechnology
25(1): e505925114, 2025
Brazilian Society of Plant Breeding.
Printed in Brazil
http://dx.doi.org/10.1590/1984-70332025v25n1a14

Marcio de Souza Reis[1], Leonardo Oliveira Silva da Costa[2], Joao Edésio de Sousa[1], Elizabete Keiko Takahashi[1] and Evandro Novaes[2*]

Abstract: *The genotype × environment (G × E) interaction is a prevalent phenomenon that can challenge breeding and cultivar recommendation but offers opportunities for gains when the best genotypes are identified and recommended for each site. In this study, conducted in eastern Minas Gerais, Brazil, 46 eucalypt hybrid clones had their wood volume evaluated at contrasting altitudes. The experiments were planted at four different locations, two at high altitudes (> 1000 m asl) and two at low altitudes (<350 m asl), with a complete randomized block design. The high-altitude regions showed superior productivity and a prevalent manifestation of simple G × E interactions, allowing their grouping in a mega environment. Conversely, within the low-altitude environments, we observed a moderate level of G × E interaction, with complex interactions prevailing. Overall, our results highlight that altitude is a major driver of G×E interaction, affecting the selection and recommendation of eucalypt clones.*

Keywords: *Adaptability, stability, mega environments, GGE-biplot*

INTRODUCTION

The Brazilian forestry sector grew by approximately 3.2% annually in the last ten years, representing about 4.2% of Brazil's agriculture, which demonstrates its importance in the country's agribusiness (IBÁ 2024). This good performance is related to the increase in productivity achieved by the Brazilian planted forests. This higher efficiency was made possible by the development of management techniques suited to the conditions of each location, breeding, and vegetative propagation techniques (Assis et al. 2015, Assis and Mafia 2016, Castro et al. 2021, Sá and Tambarussi 2023). In order to maintain the competitiveness of Brazilian forestry, companies need to continue investing in research and innovation in partnership with universities and research centers to increase forest productivity.

With the expansion of eucalypt planting areas to new regions of the country with different edaphoclimatic conditions, it is necessary to reassess the strategy for selecting genetic materials (Resende et al. 2019, Oliveira et al. 2020, Romão et al. 2023). Early clone selection and indirect selection between locations emerge as promising strategies for the forestry industry (Massaro et al. 2010, Pinto et al. 2014, Queiroz et al. 2019). These approaches gain relevance because recommending eucalypt clones requires many years of evaluation and high costs

***Corresponding author:**
E-mail: evandro.novaes@ufla.br
ORCID: 0000-0003-3803-0339

Received: 12 September 2024
Accepted: 21 January 2025
Published: 14 March 2025

[1] CENIBRA, Rodovia BR 381, km 172, 35196-000, Belo Oriente, MG, Brazil
[2] Universidade Federal de Lavras, Trevo Rotatório Professor Edmir Sá Santos, 37203-202, Lavras, MG, Brazil

to establish an experimental network representative of the target planting regions (Queiroz et al. 2019, Grattapaglia 2022). However, for the adoption of these strategies to be successful, it is necessary to evaluate the genetic correlation between locations, which depends on the genotype-by-environment (G × E) interaction.

As eucalypt cultivation advances to new frontiers in the country, the G × E interaction becomes a significant challenge for the safe recommendation of clones in these new environments. The problem is exacerbated in the context of climate change, as the environments where the clones were tested in clonal trials will hardly be replicated in the coming years when the genotype will be planted on a commercial scale (Binkley et al. 2020, Hubbard et al. 2020). Thus, with the low repeatability of climatic conditions between years, it is necessary to select genetic materials with greater stability and tolerance to adverse growth conditions (Silva et al. 2019, Campoe et al. 2020, Lim et al. 2020, Oliveira et al. 2020).

Biplot tools enable the joint identification of stable genotypes and genetically correlated environments, which can therefore be grouped. The most used techniques (i.e., AMMI and GGE-biplot) employ the combination of analysis of variance (ANOVA) and principal component analysis (PCA) to represent genetic effects (G) and G × E interaction effects (Gauch and Zobel 1997, Yan et al. 2000, Agahi et al. 2020, Gonçalves et al. 2020). At the end of the analysis, with the partition of the singular value decomposition (SVD), G + GE is jointly represented graphically using the first two components.

The GGE-biplot method stands out for enabling the evaluation of "who-wins-where" as well as the delimitation of so-called mega environments, i.e., regions with more homogeneous environments where G × E interactions are minimized (Gonçalves et al. 2020, Yan et al. 2000). These definitions can aid breeding programs, as there is a predominance of simple interaction (i.e., no genotype ranking change) among environments within a mega environment.

The objective of this work is to study the implications of altitude on the genotype × environment interaction and the recommendation of eucalypt clones considering their productivity. To this end, we evaluated the stability of 46 eucalypt hybrid clones belonging to the company Cenibra in four locations in the region known as Vale do Rio Doce in the state of Minas Gerais. The experiments were installed in two low-altitude (< 350 m asl) and two high-altitude (> 1000 m asl) environments. Based on genetic parameters, it was also possible to evaluate the gains from selection and the behavior of clones in different environments and at two ages (three and six years after planting).

MATERIAL AND METHODS

The trials were planted in December 2002 in four distinct locations in the municipalities of Belo Oriente, Pingo d'Água, Ferros (Cocais), and Sabinópolis, all in the state of Minas Gerais, in the Vale do Rio Doce region (Figure 1). The

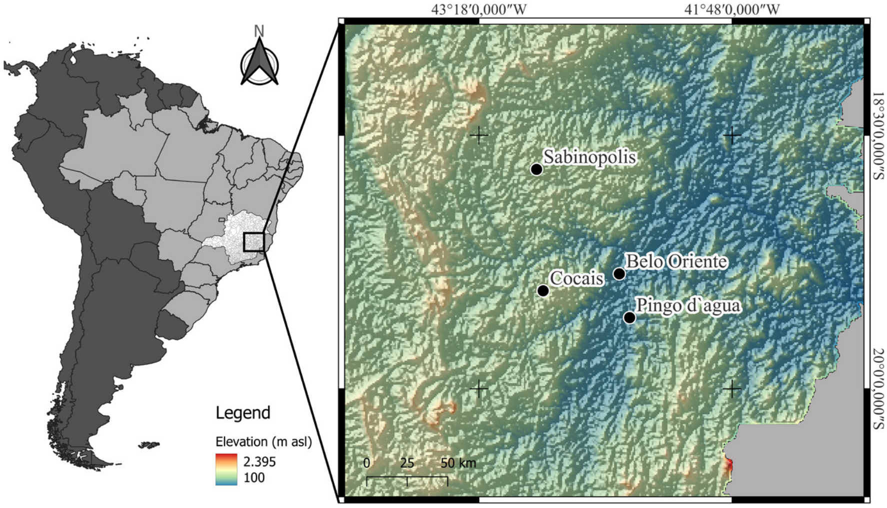


Figure 1. Location of the four trials for the evaluation of 46 eucalypt hybrid clones at contrasting altitudes.

edaphoclimatic conditions of these locations, where 46 clones were evaluated, are presented in Table 1.A (Supplementary material). These genotypes originate from a mass selection of open-pollinated hybrids of *Eucalyptus urophylla* × *Eucalyptus grandis*. Each trial was conducted using a randomized block design with five repetitions in a linear plot of five plants, at a spacing of 3 × 2 m.

The clones were evaluated in two low-altitude and therefore warmer sites (Belo Oriente and Pingo d'Água) and two higher-altitude sites (Cocais and Sabinópolis). The company has used these two conditions as a basis for stratifying environments for cultivar recommendations. The clones were evaluated at 36 and 72 months (three and six years after planting) for diameter at breast height (DBH, measured at 1.3 meters above ground, in cm) and total height (H, m). Based on these variables, the commercial volume with bark (V, m³) was estimated using the model proposed by Leite et al. (1995), based on Schumacher and Hall (1933). The coefficients of the formulas for estimating the volume of individual trees (i = 1, 2, 3, …, n) were adjusted according to the characteristics of the trees at each location, as per the equations below:

$$V_{iBelo\ Oriente} = e^{[-10.2924 + 1.7653(DBH_i) + 1.2206\ ln\ (H_i)]}$$

$$V_{iPingo\ d'Água} = e^{[-10.1646 + 1.8638(DBH_i) + 1.0913\ ln\ (H_i)]}$$

$$V_{iCocais} = e^{[-10.3545 + 1.7359(DBH_i) + 1.2683\ ln\ (H_i)]}$$

$$V_{iSabinópolis} = e^{[-10.1237 + 1.8636(DBH_i) + 1.0980\ ln\ (H_i)]}$$

Mean annual increment (MAI) was calculated by multiplying individual volume by the total number of trees per ha (1667) and dividing by the number of years after planting (three or six years). Statistical analyses were performed with the average value of MAI for each plot.

From the structure of the randomized complete block design employed in the clonal tests, the genotypic values of the clones were estimated separately for each age (three and six years) and location using the REML (Restricted Maximum Likelihood) and BLUP (Best Linear Unbiased Prediction) approaches according to the following statistical model:

$$y = 1\mu + X\beta + Zu_c + \epsilon$$

Where, y: vector of wood productivity (MAI - Mean Annual Increment) values at three or six years, 1μ: intercept; β: vector of the fixed effects of blocks; $u_c \sim N(0, I\sigma^2_c)$: vector of random effects of clones; X and Z: incidence matrices for the fixed and random effects, respectively; ϵ: vector of residuals.

After verifying the significant genetic effects and the selection accuracy within each location, a joint analysis was performed for each age using the following statistical model:

$$y = 1\mu + X\beta + Zu_c + Zu_{ce} + \epsilon$$

Where, y: vector of MAI values at three or six years, 1μ: intercept; β: vector of fixed effects of blocks within locations; $u_c \sim N(0, I_c\sigma^2_c)$: vector of random effects of clones; I_c: identity matrix of order equal to the number of clones; σ^2_c: variance of clones; $u_{ce} \sim N(0, I_{ce}\sigma^2_{ce})$: vector of random effects of clone by environment interactions; I_{ce}: identity matrix of order equal to the number of clones × number of environments; σ^2_{ce}: variance of clones × environment interaction; X and Z: incidence matrices for the fixed and random effects, respectively; ϵ: vector of residuals. The verification of the most appropriate model, regarding the homoscedasticity or heteroscedasticity of the residual variance, was defined using the BIC criterion (Schwarz 2007). For joint analyses across the two ages, the heteroscedastic residual variance structure (BIC3 = 6.33 and BIC6 = -79.45) yielded lower BIC values compared to the homoscedastic structure (BIC3 = 64.69 and BIC6 = 22.61), indicating a better model fit for the heteroscedastic structure. Therefore, the heteroscedastic model was selected for subsequent analyses.

For the evaluation of the trials, selection accuracy was calculated based on the predictive error variance (PEV): $r_{gg} = \sqrt{1 - \frac{PEV}{\sigma^2_c}}$ (Resende and Duarte 2007) and generalized heritability based on the average variance of pairwise BLUP comparisons ($\underline{v}^{BLUP}_{\Delta..}$): $h^2_g = 1 - \frac{\underline{v}^{BLUP}_{\Delta..}}{2\sigma^2_c}$ proposed by Cullis et al. (2006). The coefficients of determination of G × E interaction for each age (a = 3 and 6) were calculated by $c^2_{ce_a} = c^2_{ce_a} / (c^2_{c_a} + c^2_{ce_a} + \overline{c^2_{e_a}})$, were $\overline{c^2_{e_a}}$ is the mean residual variance obtained from the average of four residual variances, calculated for each environment. Given the unbalanced nature of the dataset, generalized heritability is preferable as it provides a more accurate measure of heritability in designs with incomplete or unevenly distributed data, by incorporating the average variance of pairwise BLUP comparisons.

To evaluate the G × E interaction, the variance component of the interaction was decomposed into simple and complex parts using the method of Cruz and Castoldi (1991). Through this method, $\frac{1}{2}(\sqrt{\sigma^2_{c_j}} - \sqrt{\sigma^2_{c_{j'}}})^2$ corresponds to the simple part, and $(1 - r_{g_{jj'}})\sqrt{\sigma^2_{c_j}\sigma^2_{c_{j'}}}$ corresponds to the complex part of the interaction, where $\sigma^2_{c_j}$ is the genetic variance of location j; $\sigma^2_{c_{j'}}$ is the genetic variance of location j'; and $r_{g_{jj'}}$ is the genetic correlation between environments j and j' calculated using the following expression $r_{g_{jj'}} = \sigma^2_{c_{jj'}}/(\sigma^2_{c_{jj'}} + \sigma^2_{ce_{jj'}})$.

The interaction was also evaluated through the prediction of gains with indirect selection in another environment. When there is a strong G × E interaction, it is expected that the clones selected in one environment will not perform well in other environments. Therefore, the gain with indirect selection in another environment should be reduced. This gain of indirect selection was estimated with the following equation: $GS_{j(j')} = h^2_{j'} DS_{j(j')}$. Where: $GS_{j(j')}$: Gain in environment j' from selection in environment j; $h^2_{j'}$: Heritability in environment j'; $DS_{j(j')}$: Selection differential in environment j', where the selected individuals are those with the best performance in environment j.

For the study of genotypic stability, the GGE-biplot method (Yan et al. 2000) was performed using the contingency table with the genotypic value of each clone in each site. The model for GGE-biplot analysis using two principal components is given by:

$$y_{ij} - y_j = \lambda_1 \varepsilon_{i1} \rho_{j1} + \lambda_2 \varepsilon_{i2} \rho_{j2} + \epsilon_{ij}$$

Where, λ_1 and λ_2 are the maximum eigenvalues for principal components 1 (PC1) and 2 (PC2); ε_{i1} and ε_{i2} are the eigenvalues of genotype i for PC1 and PC2; ρ_{j1} and ρ_{j2} are the eigenvalues of environment j for PC1 and PC2; and ϵ_{ij} is the random error. The biplots were produced with standardized data using the tester-centered model (G + GE) and the decomposition of singular values was done by the symmetric method. Statistical analyses were conducted in R software (R Core Team 2023), using the sommer package (Covarrubias-Pazaran 2016) and GGEBiplots package (Dumble 2022).

RESULTS AND DISCUSSION

At six years old, the high-altitude region showed the highest productivity, with 43.94 $m^3\ ha^{-1}\ year^{-1}$ in Sabinópolis and 29.63 $m^3\ ha^{-1}\ year^{-1}$ in Cocais. In the lowland region, Pingo d'Água showed 28.01 $m^3\ ha^{-1}\ year^{-1}$ and Belo Oriente 24.88 $m^3\ ha^{-1}\ year^{-1}$. Among all the sites, only Sabinópolis exceeds the national average of 33.70 $m^3\ ha^{-1}\ year^{-1}$ in productivity (IBÁ 2024). Unlike the results at six years, Pingo d'Água showed better performance compared to Cocais at three years of age. Sabinópolis is the most productive environment of the company at both ages.

These results highlight the edaphoclimatic differences of each environment and their influence on production (Binkley et al. 2020, Campoe et al. 2020, Ryan et al. 2020). Despite having the lowest water deficit, Cocais also had lower active photosynthetic radiation than the other environments (Table 1A - Supplementary material). This may explain, at least in part, a lower average productivity compared to Sabinópolis (both from the high-altitude region). Furthermore, altitude is strongly associated with critical factors for eucalypt growth, such as temperature and soil water availability (Fick and Hijmans 2017, Ryan et al. 2020). As a result, higher-altitude environments often provide more favorable edaphoclimatic conditions for plant growth. In this context, the Cocais and Sabinópolis regions exhibit temperatures close to the optimal range for eucalypt development (20–22 °C) (Binkley et al. 2020) and experience lower soil water deficits.

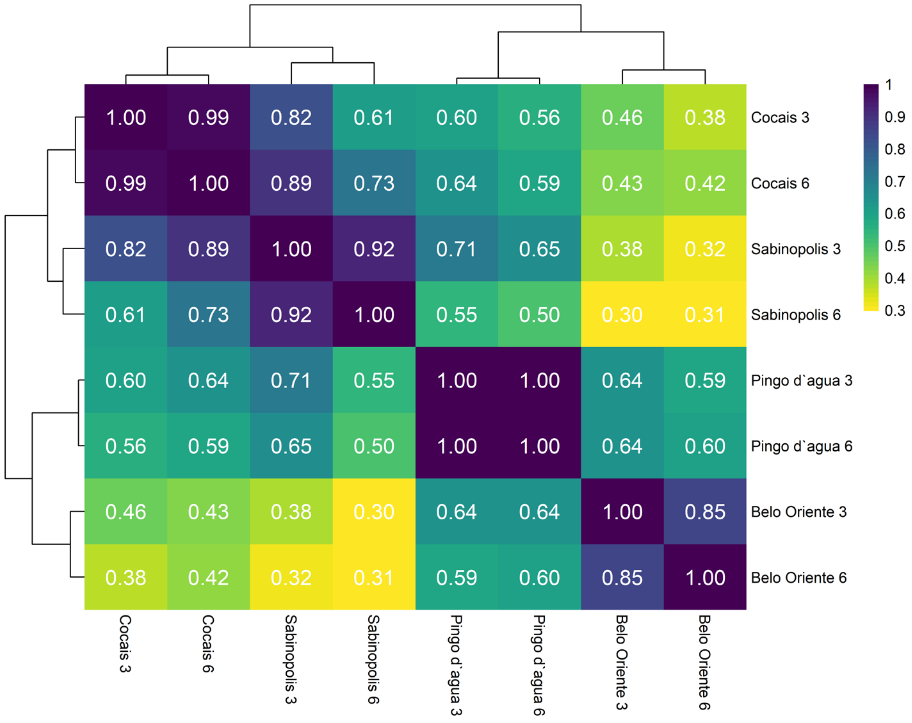
The components of genetic variance and G × E interaction estimated were significant (p-value < 0.001) by the likelihood ratio test (Table 1B - Supplementary material). The experiments showed high quality, as expressed by the values of selection accuracy ranging from 0.95 to 0.97 at three years and from 0.94 to 0.97 at six years. These heritability estimates indicate the possibility of success in the selection of genetically superior clones (Resende and Duarte 2007, Resende and Alves 2022, Ziegler and Tambarussi 2022).

The mean annual increment (MAI) at three years of age for plantations in the lowland region is higher compared to six years (Figure 1C - Supplementary material). In practice, the growth rate of these plantations is not constant until the harvest age of 6-7 years. This result can be explained by higher temperatures and consequently higher water deficit limiting forest growth in lower regions, especially when trees start to compete for natural resources (Table 1A - Supplementary material). Studies conducted in the northeast region of Bahia showed that forest growth rate varies according to average precipitation and age (Miranda et al. 2015). These results corroborate the behavior of the clones evaluated in this study.

When using the heteroscedastic model, the estimated genetic variances at all locations and ages were significant (p-value < 0.001) by the likelihood ratio test (Table 2B - Supplementary material). Regarding the coefficient of determination of G × E interaction (Table 2B - Supplementary material), the G × E contribution to phenotypic variation was 0.29 at 3 years and 0.36 at a later age. This increase indicates that the G × E effect becomes more pronounced as eucalypt plantations mature.

Regarding the performance of clones at six years of age within each environment, the standout clones are C33, C35, C24, C38, and C81 with above-average performance in all environments (Figure 3). Due to the G × E interaction, it is possible to observe that different clones show superior performance in different locations. For example, clone C90 shows above-average performance in low-altitude environments (Belo Oriente and Pingo d'Água), but below-average performance in high-altitude environments. The same trend is observed for this clone at three years of age (Figure 2C - Supplementary material).

The genetic correlations for productivity in the experiments analyzed at three and six years demonstrate high consistency in clones' performance among ages (Figure 2). When comparing the same environments at three and six years after planting, the genetic correlations were 0.85 for Belo Oriente, 0.99 for Cocais, 1.00 for Pingo d'Água, and 0.99 for Sabinópolis. The high genetic correlation between different ages within each location is indicative that early selection can be performed at three years of age. Early selection reduces cycles and increases genetic gain per breeding time (Massaro et al. 2010, Pinto et al. 2014, Queiroz et al. 2019). The use of the approach for selecting *Eucalyptus urophylla* clones at three years in Guanhães, a neighboring municipality to Sabinópolis, showed an efficacy of 97.94% for DBH and 95.73% for height (Pinto et al. 2014). In other evaluations, efficiencies of 87.95%, 71.51%, and 88.80% were found in selection practiced at 25 months for DBH, height, and volume, respectively, compared to selection practiced at 72



	Cocais 3	Cocais 6	Sabinopolis 3	Sabinopolis 6	Pingo d`agua 3	Pingo d`agua 6	Belo Oriente 3	Belo Oriente 6
Cocais 3	1.00	0.99	0.82	0.61	0.60	0.56	0.46	0.38
Cocais 6	0.99	1.00	0.89	0.73	0.64	0.59	0.43	0.42
Sabinopolis 3	0.82	0.89	1.00	0.92	0.71	0.65	0.38	0.32
Sabinopolis 6	0.61	0.73	0.92	1.00	0.55	0.50	0.30	0.31
Pingo d`agua 3	0.60	0.64	0.71	0.55	1.00	1.00	0.64	0.59
Pingo d`agua 6	0.56	0.59	0.65	0.50	1.00	1.00	0.64	0.60
Belo Oriente 3	0.46	0.43	0.38	0.30	0.64	0.64	1.00	0.85
Belo Oriente 6	0.38	0.42	0.32	0.31	0.59	0.60	0.85	1.00

Figure 2. Genetic correlation across four environments at varying growth ages.

months of age (Massaro et al. 2010). These findings highlight that effective selection can be achieved as early as three years of age with strong accuracy for eucalypt. In fact, this is the age that most companies use for selection. Moreover, our results suggest that age is much less important than locations for the G × E interaction.

In this study, most of the interaction was estimated to be of complex origin, with proportions ranging from 61.54% to 99.99%, except between the Cocais and Sabinópolis locations, where simple interaction was greater than complex, with 50.84% and 49.16%, respectively (Table 3.B - Supplementary material). Overall, these results demonstrate that the classification (ranking) of clones varies between locations.

Nunes et al. (2002), evaluating clonal eucalypt test experiments planted in southern Bahia and Espírito Santo, identified percentages close to 50% for both simple and complex interactions. For the environments evaluated in this study, the pair of environments Cocais-Sabinópolis had values close to 50% for each type of interaction (simple and complex). When the simple part is predominant, selection is facilitated because the genotypic classification in different environments does not change significantly. Conversely, when the complex part is more expressive, improvement becomes more difficult,

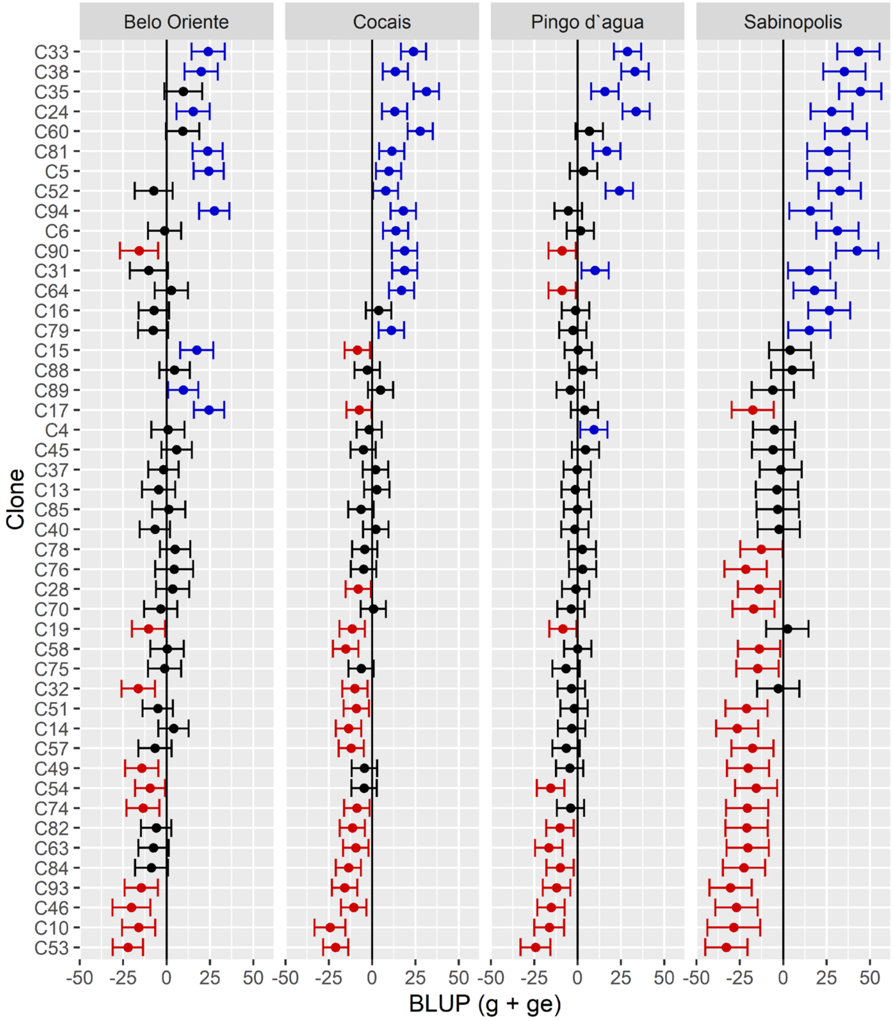


Figure 3. BLUP (g+ge) of the mean annual increment (MAI) evaluated for 46 eucalypt clones assessed at six years of age in four locations. Blue points and bars represent values above the overall mean; black points and bars represent values that do not differ from the mean; and red points and bars represent values below the mean. The bars represent 95% confidence intervals of the predicted values, calculated based on the prediction error variance (PEV).

as in this case, some genotypes are more adapted to specific environments (Ramalho et al. 2012).

Under conditions of significant interaction, where companies cultivate vast areas with different site qualities, it may be necessary to identify specific clones for each environment. This strategy is costly, requiring large experimental networks, numerous clones in nurseries, and strict quality control. Without this, the focus shifts to identifying clones with good adaptation and high phenotypic stability. Stability is also important because future climatic conditions to be faced in commercial plantations cannot be precisely predicted (Silva et al. 2019, Oliveira et al. 2020). Normally, the conditions under which clones were evaluated for selection are unlikely to be the same in future plantations. In this context, the GGEbiplot method was used to define mega-environments as well as identifying clones with greater stability at six years.

From the "which-won-where" graph, the red vectors divide the plane into different sectors, where environments located in the same sector are grouped into a mega-environment. Thus, it was possible to identify a mega-environment containing the high-altitude locations of Sabinópolis and Cocais (Figure 4). Environments grouped into a mega-environment show a high genetic correlation (Figure 2), and a higher predominance of simple interaction (Table 3.B - Supplementary material). Genotypes positioned in sectors without environments exhibit the worst performance for all tested environments and, therefore, should not be recommended.

The biplots presented in Figure 4 facilitate the identification of clones that align more closely with an ideotype that merges stability and productivity. The closer a clone is to the arrow on the blue central axis (average environment), the closer it is to the ideotype (Yan and Tinker 2006). In this study, clone C33 is the genotype closest to the ideotype for the environments used. Other notable materials are C38 and C24. These clones combine high productivity and phenotypic stability across locations. Completing the top eight most productive genotypes are C35, C81, C60, C5, and C94, showing strong performance across the average environment.

For the overall top eight clones identified using the GGE biplot, the coincidence with the best location-specific clones ranged from 50.00% (Cocais) to 75.00% (Sabinópolis) (Tables 3 and 4.C - Supplementary Material). Recommending these clones across all regions results in selection gain losses ranging from 22.62% in Pingo D'Água to 12.32% in Sabinópolis, compared to selecting clones specific to each environment. Despite these losses, this strategy simplifies the logistics of clone recommendation and facilitates their progression to expanded clonal testing.

The two environments in the higher region (Sabinópolis and Cocais) exhibit similar soil and climatic characteristics. Therefore, the relative productivity of clones should remain stable between these two locations (Table 1.A - Supplementary material). Thus, the joint results of the correlations of genotypic values and the interpretation of GGEbiplot graphs

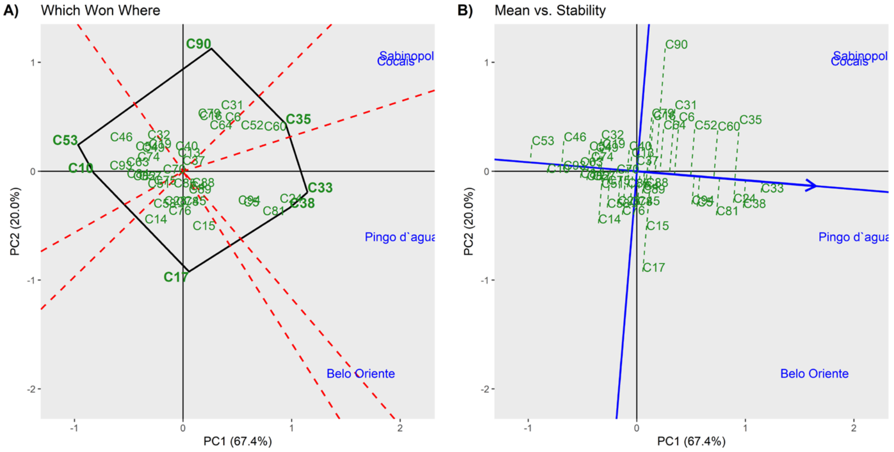


Figure 4. Adaptability and stability analysis via GGE-Biplot of 46 eucalypt hybrid clones evaluated in four locations: two at high altitude (Sabinópolis and Cocais) and two at low altitude (Pingo d'Água and Belo Oriente). 1) "Which-Won-Where" graph, indicating C35 as the most productive in high altitude locations and clones C24, C33, and C38 as the most productive in Pingo d'Água and Belo Oriente. 2) Ranking and classification of genotypes in relation to an ideal type for the average environment. Clones closer to the central line, pointing towards the ideal type (arrow), have higher stability.

Table 1. Wood productivity gains achieved by direct (diagonal in bold) and indirect selection (off diagonal) of the top ten clones from each environment at 6 years after planting. The table is not symmetrical because the indirect selection gain depends on where the top 10 clones were selected. For example, the ten best clones from Belo Oriente had a predicted productivity of 10.84 m^3 ha^{-1} $year^{-1}$ in Pingo d'Água, while the ten best clones from Pingo d'Água had a productivity of 7.36 m^3 ha^{-1} $year^{-1}$ in Belo Oriente

Selection in environment	**h²**	**Selection gain in environment** (m^3 ha^{-1} $year^{-1}$)			
		Belo Oriente	**Pingo d'Água**	**Cocais**	**Sabinópolis**
Belo Oriente	0.902	**18.72**	10.84	9.96	20.15
Pingo d'Água	0.933	7.36	**17.39**	13.41	27.20
Cocais	0.954	6.28	9.61	**18.96**	34.54
Sabinópolis	0.95	5.13	12.66	15.61	**38.97**

corroborate that these environments can receive a single recommendation of clones for commercial plantations and be grouped for allocation of a single representative experimental unit for the region. Conversely, in the two environments in the lowland region (Belo Oriente and Pingo d'Água), a single recommendation seems unfeasible.

The estimates of gains from direct selection are derived from the top ten clones in each location (Table 1). Sabinópolis showed the highest estimated gain from selection at 89.54%, whereas Pingo d'Água recorded the lowest estimated gain at 62.44%. Also, Table 1 shows estimates of gains from indirect selection, i.e., an increase in average productivity with clones selected in another location. Because of the expression used for calculating selective gains, the direct selection response, values on the diagonal, will always be superior to the indirect response. The Sabinópolis environment, followed by Cocais and Pingo d'Água, maximizes gains in all considered environments. On the other hand, clones selected in Belo Oriente generated the lowest gains when tested in other environments.

In the experiments evaluated in the southern Bahia and Espírito Santo, across nine environments, gains obtained from indirect selection ranged from 23.80% to 49.98% between pairs of environments, while in direct selection, gains ranged from 43.27% to 87.18% (Nunes et al. 2002). In this context, evaluating clones selected in one environment and planted in other environments is a strategy to reduce the amount of experimentation and clones to manage. Therefore, indirect selection can be a good option as long as the G × E interaction is not pronounced enough for the gains to be satisfactory indirectly.

This study confirms that altitude influences eucalypt productivity, both directly and indirectly, such as through its impact on other environmental factors like temperature. Variations in altitude also amplify the genotype × environment (G × E) interactions across different locations. Thus, recommendation of eucalypt clones in locations with different altitudes needs to consider this strong G × E interaction, by selecting either the most adapted clones in each location or those that are more stable and have good productivity in different environments. The latter strategy, although more conservative, may even generate higher productivity given the climatic instabilities and increasing incidence of biotic and abiotic stress in eucalypt cultivation.

ACKNOWLEDGMENTS

LOSC is grateful for the research funding by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) - Finance Code 001. EN receives a research productivity grant (314269/2023-1) from the National Council for Scientific and Technological Development – CNPq, which he gratefully acknowledges. Productivity data was provided by Ceniba S.A.

DATA AVAILABILITY

The datasets generated and/or analyzed in this study are available from the corresponding author upon reasonable request.

REFERENCES

Agahi K, Ahmadi J, Oghan HA, Fotokian MH and Orang SF (2020) Analysis of genotype × environment interaction for seed yield in spring oilseed rape using the AMMI model. **Crop Breeding and Applied Biotechnology 20**: e26502012.

Assis TF and Mafia RG (2016) Hibridação e clonagem. In Borém A (ed)

Biotecnologia florestal. Editora UFV, Viçosa, p. 93-121.

Assis TF, Abad JIM and Aguiar AM (2015) Melhoramento genético do eucalipto. In Shumacher MV and Vieira M (eds) **Silvicultura do eucalipto no Brasil**. Editora UFSM, Santa Maria, p. 217-244.

Binkley D, Campoe OC, Alvares CA, Carneiro RL and Stape JL (2020) Variation in whole-rotation yield among *Eucalyptus* genotypes in response to water and heat stresses: The TECHS project. **Forest Ecology and Management 462**: 117953.

Campoe OC, Alvares CA, Carneiro RL, Binkley D, Ryan MG, Hubbard RM, Stahl J, Moreira G, Moraes LF and Stape JL (2020) Climate and genotype influences on carbon fluxes and partitioning in *Eucalyptus* plantations. **Forest Ecology and Management 475**: 118445.

Castro CAO, Santos GA, Takahashi EK, Nunes ACP, Souza GA and Resende MDV (2021) Accelerating *Eucalyptus* breeding strategies through top grafting applied to young seedlings. **Industrial Crops and Products 171**: 113906.

Covarrubias-Pazaran G (2016) Genome-assisted prediction of quantitative traits using the r package sommer. **PLoS ONE 11**: e0156744.

Cruz CD and Castoldi FL (1991) Decomposição da interação genótipos x ambientes em partes simples e complexa. **Revista Ceres 38**: 422-430.

Cullis BR, Smith AB and Coombes NE (2006) On the design of early generation variety trials with correlated data. **Journal of Agricultural, Biological, and Environmental Statistics 11**: 381-393.

Dumble S (2022) GGEBiplots: GGE Biplots with "ggplot2.". Available at <https://cran.r-project.org/web/packages/GGEBiplots/GGEBiplots.pdf.>. Accessed on March 12, 2024.

Fick SE and Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. **International Journal of Climatology 37**: 4302-4315.

Gauch HG and Zobel RW (1997) Identifying mega-environments and targeting genotypes. **Crop Science 37**: 311-326.

Gonçalves GMC, Ferreira-Gomes RL, Lopes ÂCA and Vieira PFMJ (2020) Adaptability and yield stability of soybean genotypes by REML/BLUP and gge biplot. **Crop Breeding and Applied Biotechnology 20**: e282920217.

Grattapaglia D (2022) Twelve years into genomic selection in forest trees: Climbing the slope of enlightenment of marker assisted tree breeding. **Forests 13**: 1554.

Hubbard RM, Carneiro RL, Campoe O, Alvares CA, Figura MA and Moreira GG (2020) Contrasting water use of two *Eucalyptus* clones across a precipitation and temperature gradient in Brazil. **Forest Ecology and Management 475**: 118407.

IBÁ - Indústria Brasileira de Árvores (2024) Relatório anual 2024. Available at <https://iba.org/datafiles/publicacoes/relatorios/relatorio2024.pdf >. Accessed on October 20, 2024.

Leite HG, Guimarães DP and Campos JCC (1995) Descrição e emprego de um modelo para estimar múltiplos volumes de árvores. **Revista Ceres 19**: 65-79.

Lim H, Alvares CA, Ryan MG and Binkley D (2020) Assessing the cross-site and within-site response of potential production to atmospheric demand for water in *Eucalyptus* plantations. **Forest Ecology and Management 464**: 118068.

Massaro RAM, Bonine CAV, Scarpinati EA and Paula RC (2010) Viabilidade de aplicação da seleção precoce em testes clonais de *Eucalyptus* spp. **Ciencia Florestal 20**: 597-609.

Miranda ROV, Dias AN, Filho AF, Soares ID and Cruz JP (2015) Modelagem do crescimento e produção em classes de precipitação pluviométrica para *Eucalyptus* sp. **Floresta 45**: 117-128.

Nunes GHS, Rezende GDSP, Ramalho MAP and Santos JB (2002) Implications of the genotype-environment interaction effects on *Eucalyptus* clone selection. **Cerne 8**: 49-58.

Oliveira RS, Ribeiro CVG, Neres DF, Porto ACM, Ribeiro D, Siqueira L, Zauza EÂV, Coelho ASG, Reis CAF, Alfenas AC and Novaes E (2020) Evaluation of genetic parameters and clonal selection of *Eucalyptus* in the Cerrado region. **Crop Breeding and Applied Biotechnology 20**: e29982031.

Pinto DS, Resende RT, Mesquita AGG, Rosado AM and Cruz CD (2014) Seleção precoce para características de crescimento em testes clonais de *Eucalyptus urophylla*. **Scientia Forestalis 42**: 251-257.

Queiroz MM, Arriel DAA, Tsukamoto Filho AA, Oliveira OE, Moraes PM, Skowronski L and Costa RB (2019) Early selection in *Eucalyptus camaldulensis* Dehnh. progenies in Savanna, Brazil. **African Journal of Biotechnology 18**: 347-351.

R Core Team (2023) A language and environment for statistical computing. Available at <https://www.R-project.org/>. Accessed on December 10, 2023.

Ramalho MAP, Abreu AFB, Santos JB and Nunes JAR (2012) **Aplicações da genética quantitativa no melhoramento de plantas autógamas**. Editora UFLA, Lavras, 522p.

Resende MDV and Alves RS (2022) Statistical significance, selection accuracy, and experimental precision in plant breeding. **Crop Breeding and Applied Biotechnology 22**: e42712238.

Resende MDV and Duarte JB (2007) Precisão e controle de qualidade em experimentos de avaliação de cultivares. **Agricultural Research in the Tropics 37**: 182-194.

Resende RT, Piepho HP, Silva-Junior OB, Silva FF, Resende MDV and Grattapaglia D (2019) Enviromics in breeding: Applications and perspectives on envirotypic-assisted selection. **Theoretical and Applied Genetics 134**: 95-112.

Romão KCS, Nunes ACP, Santos AP, Santos OP and Valente BMRT (2023) Multi-site comparison of clonal arrangements for tropical and subtropical hybrids of *Eucalyptus*. **Industrial Crops and Products 197**: 116536.

Ryan MG, Stape JL, Binkley D and Alvares CA (2020) Cross-site patterns in the response of Eucalyptus plantations to irrigation, climate and intra-annual weather variation. **Forest Ecology and Management 475**: 118444.

Sá LF and Tambarussi EV (2023) Melhoramento genético como estratégia de gestão da produtividade florestal. **Revista do Instituto Florestal 35**: 99-112.

Schumacher FX and Hall FS (1933) Logarithmic expression of timber-tree volume. **Journal of Agricultural Research 47**: 719-734.

Schwarz G (2007) Estimating the dimension of a model. **The Annals of Statistics 6**: 461-464.

Silva PHM, Marco M, Alvares CA, Lee D, Moraes MLT and Paula RC (2019) Selection of *Eucalyptus grandis* families across contrasting environmental conditions. **Crop Breeding and Applied Biotechnology 19**: 47-54.

Yan W and Tinker NA (2006) Biplot analysis of multi-environment trial data: Principles and applications. **Canadian Journal of Plant Science 86**: 623-645.

Yan W, Hunt LA, Sheng Q and Szlavnics Z (2000) Cultivar evaluation and mega-environment investigation based on the GGE biplot. **Crop Science 40**: 597-605.

Ziegler ACF and Tambarussi EV (2022) Classifying coefficients of genetic variation and heritability for *Eucalyptus* spp. **Crop Breeding and Applied Biotechnology 22**: e40372222.