RAFAEL TASSINARI RESENDE

# MICRO- AND MACRO-SITE VARIANTS ON GENOTYPE BY ENVIRONMENT INTERACTION IN *Eucalyptus* spp.

Thesis presented to the Universidade Federal de Viçosa, in partial fulfillment of the requirements of Forest Science Program for degree of *Doctor Scientiae*.

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APPROVED: February 5nd, 2019.

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*A Deus,*

**OFEREÇO**

*Aos meus pais Cezar e Auxiliadora,*
*Minha tia Adélia e*
*Minha noiva Úrsula,*
*Por todo amor envolvido.*

**DEDICO**

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**A todos vocês, e eventualmente alguém que por descuido, não tenha sido lembrado:**
**O meu muito obrigado!**

Coragem sim
Força sim
Persistência sim
Vontade sim

Tudo acontecerá
Tudo será
Tudo valerá

Diante de seu existir
Mesmo que as dificuldades batam em sua porta
Seja otimista e seja você mesmo
A razão de seu viver

Pelo ontem
Pelo hoje
E pelo amanhã
Deus sabe.

**(Chiquinho da Floresta, Viçosa-MG, 05/02/2019)**

# SUMMARY

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# OVERALL ABSTRACT

RESENDE, Rafael Tassinari, D.Sc., Universidade Federal de Viçosa, February, 2019. **Micro- and macro-site variants on genotype by environment interaction in *Eucalyptus* spp.** Advisor: Marcos Deon Vilela de Resende. Co-advisor: Helio Garcia Leite.

This thesis is the combination of three scientific papers addressing the same theme: The genotype by environment interaction (GE) between *Eucalyptus spp.* clones. The publications are also online in the journal *Forest Ecology and Management*, and can be accessed through the *Digital Object Identifier* (DOI) (indicated at the beginning of each chapter). The GE interaction is an extremely important aspect of any breeding program. Without it, little effort would be needed to identify the ideal genotypes for certain planting sites. In addition, a small number of cultivars would be fully recommended for the full range of available environments. This work aimed to bring both theoretical and observational features that causes GA, as well as propose an accurate method of recommending genotypes in continuous environments. Therefore, the first chapter demonstrates that competition between identical clones can be triggered by local environmental variants, and those clones with the highest competitive potential tend to be the most stand productives. This study refers to the understanding that natural forest features are also present in monocultures, indicating that competition, when properly managed, either by modeling or silvicultural formations, may contribute to increased forest productivity. The second chapter quantifies in terms of competition; site quality; and environmental heterogeneity, which of these factors lead to greater genetic differentiation, as well as higher yields. This chapter also addresses, in an original way, the interaction between these components within commercial stands and their relationships with forest productivity. Finally, in the third chapter, an elegant way of making genotypic recommendations with a high level of environmental detail is proposed, combining forest genetic improvement with Geographic Information Systems (GIS). Science is in a transition moment, in which countless modern tools are increasingly available. Silviculture and forest management provide scope for such innovations, both in the study of the complex biological interactions present in a growing forest, and in the optimization of resources aiming to increase the yield and quality of the timber products generated.

# RESUMO GERAL

RESENDE, Rafael Tassinari, D.Sc., Universidade Federal de Viçosa, fevereiro de 2019. **Micro e macro variantes locais sobre a interação genótipo por ambiente em *Eucalyptus* spp.** Orientador: Marcos Deon Vilela de Resende. Coorientador: Helio Garcia Leite.

Esta obra é o combinado de três artigos científicos que endereçam um mesmo tema: A interação genótipo por ambiente (GA) entre clones de *Eucalyptus spp*. As publicações também estão online na revista *Forest Ecology and Management*, e podem ser acessadas por meio do *Digital Object Identifier* – DOI (indicado no início de cada capítulo). A interação GA é um aspecto de suma importância em qualquer programa de melhoramento genético. Sem ela, poucos esforços careceriam ser feitos para identificar os genótipos ideais para certos locais de plantio. Além disso, um pequeno número de cultivares seriam totalmente recomendáveis para toda gama de ambientes disponíveis. Esse trabalho visou trazer tanto características teóricas e/ou observacionais causadoras de GA, bem como propor uma método acurado de recomendação de genótipos em ambientes contínuos. Em suma, o primeiro capítulo demonstra que a competição entre clones idênticos pode ser desencadeada por variantes ambientais locais, e àqueles clones com maior potencial competicional tendem a ser os mais produtivos do talhão. Este estudo remete à compreensão de que características de florestas naturais estão também presentes em monocultivos, indicando que a competição, quando manejada corretamente, seja por modelos ou por formatações silviculturais, podem contribuir no aumento da produtividade florestal. O segundo capítulo quantifica em termos de competição; qualidade; e heterogeneidade ambiental, quais destes fatores acarretam maior diferenciação genética, bem como as maiores produtividades. Este capítulo também aborda, de forma original, a interação entre tais componentes dentro do talhão comercial e suas relações com a produtividade florestal. Finalmente, no terceiro capítulo, é proposto uma maneira elegante de realizar recomendações genotípicas com altíssimo nível de detalhamento ambiental, conjugando-se o melhoramento genético florestal com Sistemas de Informações Geográficas (SIG). A ciência encontra-se num momento de transição, em que inúmeras ferramentas modernas estão cada vez mais disponíveis. A silvicultura e o manejo florestal dão margem para aplicação de tais inovações, tanto no estudo das interações biológicas complexas presentes em uma floresta em crescimento, como na otimização de recursos visando aumentos no rendimento e qualidade dos produtos madeireiros gerados.

**CHAPTER I.** Intra-genotypic competition of *Eucalyptus* clones generated by environmental heterogeneity can optimize productivity in forest stands. DOI: 10.1016/j.foreco.2016.08.041

## Abstract

The growth structure of *Eucalyptus* plantations is the result of site environment, genetic material, and different types of interaction between neighboring plants. It is well known that sites that are more homogeneous result in greater forest productivity. However, additional factors inherent in the micro-environment or the quality of cuttings can lead to heterogeneous clonal biomass at the end of the rotation cycle. This study of the growth patterns in commercial stands of *Eucalyptus* clones had two aims: i) to determine whether environmental heterogeneity causes competition among genetically identical individuals and ii) to validate the occurrence of intra-genotypic competition, revealing the potential relationship with forest productivity. The present study was developed based on two linear mixed models: a non-genetic model, which accounts for spatial autocorrelation and is used to estimate the effects of competition between neighboring trees into the single clone plots; and a genetic model to infer the nature of the clonal competition. Three hundred and six square plots containing one hundred plants from eight experiments using a randomized block design, with three replications, were evaluated. The experiments were positioned in different environmental conditions by combining two different plant spacings and two altitude elevations. Using the path analysis procedure, we verified that there were significant direct effects of competition according to the proximity of the trees in the plot. In addition, trees that were more distant caused indirect effects of competition through nearby trees. Stands with uniform growth conditions (measured by residual autocorrelation parameters) actually caused higher productivity. The results from the genetic correlations of intra-genotypic competition and productivity showed that the less competitive clones were always less productive, regardless of the experimental condition. The more competitively aggressive clones could optimize their productivity when planted in sites with high residual levels, reaching productivities similar to those of homogeneous stands. This suggests that the implementation of certain silviculture techniques, seeking to increase site uniformity, is less relevant to these clones. The selection and use of these clones might be useful for large companies, because they offer the opportunity to achieve high productivity, and for smaller producers who do not have access to the silvicultural quality used by large companies.

**Keywords:** Clonal competition; Mixed models; Forest breeding; Plant spacing; Stand productivity

## 1.1. Introduction

Studies of genotype × environment interactions (G × E) generate knowledge of particular genotype features that helps to determine recommendations of superior clones that are more adapted to different local conditions (OGUT et al., 2014). Even when located at a single site, plants may be subject to different micro-environmental stresses, such as different light radiation rates, shading by surrounding trees, water availability, soil fertility, and interaction with soil microorganisms (KIM; BULLOCK; STAPE, 2015; SCHWINNING; WEINER, 1998; STAPE et al., 2010). In this context, some interactions between plants can be observed naturally, owing to competition over optimum growing conditions. In natural forests, a better physiological capacity in the utilization of available resources (BOYDEN; BINKLEY; STAPE, 2008; DONNELLY et al., 2016) and the optimal positioning of the crown and roots in the restricted space where the tree is confined might provide adaptive advantages over neighboring trees, with such placement providing advantages including competition potential between plants. Thus, in the same manner that genotypes may have genetic differences in growth, disease resistance, and wood properties, they are expected to have different patterns of interactions with their neighbors (BOYDEN; BINKLEY; STAPE, 2008; COSTA E SILVA; KERR, 2013). From this, we can deduce that different *Eucalyptus* clones may have diverse levels of competition in plantations.

Within experimental plots, plants display various forms of genetic behavior and express these differences in their intra- and inter-specific interactions, depending on the genetic relationship (or kinship) with their neighbors (GUREVITCH et al., 2010). Thus, tree performance can be stimulated or suppressed owing to a greater or lesser degree of competition with its neighbor, which can directly influence how the genetic clonal selection is made. Many authors have proposed methods and theoretical models to quantify competition between plants. Cappa and Cantet (2008), Cappa et al. (2015), Costa e Silva and Kerr (2013) and Resende et al. (2005) exploit the spatial correlation contained in the experimental gradient combined with competitional interactions between plants. First order autoregressive models (AR1) have been proposed, both to infer the competition as a dominant cause of variation and to correct the trend of the environmental gradient effects (COSTA E SILVA; KERR, 2013; RESENDE et al., 2005). Oda-Souza et al. (2008) and Vanclay (2006) used systematic design to infer competition; however, their studies do not provide adequate randomization and have high plant mortality levels that cause severe problems in data balancing, and the experiments are very different from stands used in commercial forest plantations, as mentioned by the original authors. In addition, the intra-genotypic potential of competition between trees has not been extensively studied, especially in association with *Eucalyptus* clones (LUU; BINKLEY; STAPE, 2013).

In the final stages of a forest recurrent selection program, it is common to conduct specific experiments called expanded clonal tests (ECT) (REZENDE; DE RESENDE; DE ASSIS, 2014). These are large experiments designed to be similar to the actual conditions of planting, and it is based on these tests that superior clones are selected for use in commercial stands. The ECTs contain large square plots filled with single clone replication, which have an appearance similar to commercial stands. Any growth variance observed in these tests, as well as the potential of competition, is theoretically assumed to be of a random nature (RESENDE, 2007).

In forest plantations, productivity is usually greater in uniform sites, which is caused by either natural homogeneity or achieved through the implementation of silvicultural techniques (ALMEIDA et al., 2007; CAMPOE et al., 2013). Thus, it is accepted that any site residual variability sources entail lower productivities. This means that the paradigm stating that the interaction among clones is a negative factor in stand productivity optimization needs to be re-thought. When considering the equilibrium of homogeneity of clonal growth, extra events may be additional factors causing residual variance in the plot, such as cloning procedures, *ontogenetical ageing of clones,* cutting quality, uniform implementation in the field, and mortality rate (CAMPOE et al., 2013; FRAMPTON-JR; FOSTER, 1993; WENDLING; TRUEMAN; XAVIER, 2014). Moreover, there may naturally be a mismatch in the common clonal growth, possibly leading to future competitional interactions.

Based on the hypothesis that environmental heterogeneity can generate dominant trees within the stand and this might trigger intra-genotypic competition among trees, the present study aimed to verify the influence of this competition in forest stand productivity, as well as evaluate the genetic nature of clonal competition.

## 1.2. Materials and Methods

### 1.2.1. Description of experiments and calculation of mean annual increment

Eight ECTs were selected from the CENIBRA S.A. company database, in order to obtain 100 replications of a single clone in square plots of 10 × 10 plants (Table 1.1). All experiments were designed in randomized complete blocks with three replications. Of the eight tests, three were implemented with plant spacing of 10 m²/plant (3 × 3.33 m) and the others with 6 m²/plant (2 × 3 m), and four tests were implanted in a high-altitude area and four in a low-altitude area. Fifty-four clones of *Eucalyptus grandis* × *E. urophylla* hybrids were distributed among the eight tests, of which thirty-one were present in more than one experiment. The eight experiments were implanted between the municipalities of Belo Oriente (19°13'12" S, 42°29'01" W, 400 m above sea level [ASL]), Sabinópolis (18°39'57" S, 43°05'02" W, 670 m ASL), and Barão de Cocais (19°56'45" S, 43°29'13" W, 1425 m ASL) in the state of Minas Gerais, Brazil. All experiments were implanted with 90 g/plant of NPK (6-30-6) and 400 kg/ha of reactive phosphate in the subsoil.

The mean annual increment (MAI) was calculated by extrapolating the volume of individual trees for one hectare divided by age. The volume value ($\mathbf{VOL}$) in cubic meters of trees was calculated by equation [1] (SCHUMACHER; HALL, 1934), where $\mathbf{DBH}$ is the diameter at breast height in cm, $\mathbf{H}$ is the tree height in meters, $\mathbf{f}$ is the taper factor (assumed to be 0.43), and π is the ratio between the circumference and diameter of a circle.

$$\mathbf{VOL} = \mathbf{DBH}^2 \frac{\pi}{\mathbf{40000}} \mathbf{H}\,\mathbf{f} \qquad [1]$$

1.2.2. Autoregressive model (AR1) of intra-genotypic competition effects

For all experiments comprising 10 × 10 plants per plot, the trees on the border were disregarded, and the remaining 8 × 8 were used to identify neighbors. Thus, the trees of the plot core (6 × 6) were defined as a focal tree (in the center) with 8 surrounding trees identified as neighborhood standardized covariates (2 in the planting row, 2 in the spacing interrow, and 4 on the diagonal) (Figure 1.1-A). All experiments totaled 306 plots, with 30600 trees in total, and 11016 focal trees. Each plot represents eight competition effects (one for each of the eight neighbor trees) and these values were obtained using the non-genetic model [2], where $\mathbf{y}$ is the phenotypic data vector of MAI for focal trees within the plot; $\mathbf{n}$ is the fixed effects (i.e., intercept, focal dead tree covariate, covariate of area available owing to dead nearby tree, and the eight neighborhood covariates); $\boldsymbol{\xi}$ is the spatial error of the plot, assuming autoregressive covariance; and $\mathbf{F}$ is the incidence matrix of fixed effects. The residual variance is given by $var(\boldsymbol{\xi}) = \sigma_\xi^2[\sum_r \Phi_r \otimes \sum_c \Phi_c]$, wherein $\sigma_\xi^2$ is the variance owing to spatial trend. The terms $\sum_r \Phi_r$ and $\sum_c \Phi_c$ refer to autoregressive correlation matrix of the first order (AR1⊗AR1) with parameters of autocorrelation $\Phi_r$ and $\Phi_c$, and order equal to the number of rows and columns of the plot, respectively (RESENDE, 2007). The parameters $\Phi_r$ and $\Phi_c$, ranging between –1 and 1, were assigned as a measure of homogeneity and heterogeneity of the plots (i.e., the higher these parameters are, the greater the spatial autocorrelation of the plot residuals, thus these plots are assumed as having more micro-environmental uniformity than others). The fixed effects of the covariates 'focal dead tree' and 'area available owing to nearby dead tree' were included to avoid the confounding effect of growth owing to local causes, and thus only capture plant-to-plant competition between living trees.

$$\mathbf{y} = \mathbf{Fn} + \boldsymbol{\xi} \qquad [2]$$

Due to computational run issues, model [2] was applied for each of the 306 plots, and for this reason, the MAI values in each plot were rescaled to 0–1 to remove the scale effect of plot productivity on competition effects (i.e., the highest MAI value was given as 1, dead trees as 0, and the remaining values were located between these two values).

To verify the direct and indirect effects of neighboring trees and plot spatial homogeneity on the focal tree, the path analysis procedure was performed using canonical correlations (BAGOZZI; FORNELL; LARCKER, 1981). The canonical correlations were obtained from 306 × 8 observations of competition effects (grouped into 2 in the planting row, 2 in the spacing interrow, and 4 on the diagonal), row and column autocorrelations, and productivity. Path analysis was then performed by utilizing the groups of neighboring trees and spatial autocorrelations as the exogenous variables, and plot productivity as the endogenous variable.

### 1.2.3. Bivariate model for evaluating MAI and intra-genotypic competition

We used a bivariate linear mixed model to estimate the genetic variances and covariances between competition and productivity traits as MAI of the *Eucalyptus* clones and to obtain the estimated genotypic values (EGV) for both traits under different experimental conditions (Table 1). The two phenotypes were the sum of the competition values of the four neighboring trees closest to the focal tree ($i = 1$) and the MAI of the plot ($i = 2$). The linear mixed model can be seen in equation [3], where $\mathbf{y_i}$ is the phenotype vector of the two traits; $\mathbf{b_i}$ is the fixed effects vector (i.e., intercept for each trait and effects of experiments and blocks within trials for each trait); $\mathbf{g_i}$ is the vector of genotypes (i.e., clones) nested within the four evaluated experimental conditions (6 and 10 m²/plant × low and high altitudes); and $\mathbf{e_i}$ is the vector of residuals of the two traits. Random effects ($\mathbf{g_i}$ and $\mathbf{e_i}$) are assumed to be normally distributed, with zero mean. $\mathbf{X_i}$ and $\mathbf{Z_i}$ are the incidence matrices of fixed and random effects, respectively.

$$\mathbf{y_i} = \mathbf{X_i b_i} + \mathbf{Z_i g_i} + \mathbf{e_i} \qquad [3]$$

The matrix of variance and covariance can be written as equation [4], where $\mathbf{A}$ is the kinship matrix via pedigree (WRIGHT, 1922) and $\mathbf{I}$ is an identity matrix. The terms $\sigma^2_{g_1}$ and $\sigma^2_{e_1}$ denote the genetic and residual variance of traits competition and MAI, respectively, and the terms $\sigma_{g_{1,2}}$ and $\sigma_{e_{1,2}}$ indicate genetic and residual covariances between the two traits, respectively. The narrow-sense heritability and genetic correlations between the two traits were calculated with $\mathbf{h^2} = \sigma^2_{g_i}/\sigma^2_{f_i}$, where $\sigma^2_{f_i} = \sigma^2_{g_i} + \sigma^2_{e_i}$ , and $\mathbf{r_g} = \sigma_{g_{1,2}}/\left(\sigma^2_{g_1}\sigma^2_{g_2}\right)^{1/2}$, respectively, and $i = \{1, 2\}$. The phenotypic correlations ($\mathbf{r_f}$) were obtained by Pearson correlation through the phenotypic averages of clones traits.

$$\mathbf{V} = \mathrm{var}(\mathbf{y_i}) = \begin{bmatrix} \mathbf{Z_1 A}\sigma^2_{g_1}\mathbf{Z'_1} + \mathbf{I}\sigma^2_{e_1} & \mathbf{Z_1 A}\sigma_{g_{1,2}}\mathbf{Z'_2} + \mathbf{I}\sigma_{e_{1,2}} \\ \mathbf{Z_1 A}\sigma_{g_{1,2}}\mathbf{Z'_2} + \mathbf{I}\sigma_{e_{1,2}} & \mathbf{Z_2 A}\sigma^2_{g_2}\mathbf{Z'_2} + \mathbf{I}\sigma^2_{e_2} \end{bmatrix} \qquad [4]$$

The success of inclusion of the effects of competition in the bivariate model was evaluated using the multivariate heritability ($\mathbf{h^2_m}$) and the effective efficiency ($\mathbf{EE}$) (equations [5] and [6], respectively). These equations can be seen in the study by Resende (2007). The parameter $\mathbf{h^2_m}$ corresponds to the new heritability of MAI, when assessed by the bivariate model, and the parameter $\mathbf{EE}$ represents the gain in selection accuracy provided by the use of the bivariate model.

$$\mathbf{h^2_m} = \mathbf{h^2_y}\left[\mathbf{1} + \frac{(\mathbf{h_x r_g/h_y - r_f})^2}{\mathbf{1 - r_f^2}}\right] \qquad [5]$$

$$\mathbf{EE}(\%) = \left[\frac{\mathbf{h_m}}{\mathbf{h_y}} - \mathbf{1}\right]\mathbf{100} \qquad [6]$$

To evaluate the phenotypic plasticity of the clones in the four experimental conditions, principal component analysis using the EGVs of trait MAI was carried out. The four EGV vectors suffered dimensionality reduction resulting in two principal components (PC1 and PC2). The principal components were then arranged in a graph stratified into four quadrants: QI–clones adapted to all four experimental conditions, QII and QIII–clones adapted to between one and three conditions, and QIV–clones did not adapt to any experimental condition (MURAKAMI; CRUZ, 2004).

### 1.2.4. Computational tools

Data processing and development of computer functions were completed using R software (TEAM R, 2015). For the adjustment of linear mixed models, the *ASReml-R* package was used (BUTLER et al., 2009). All graphics were prepared using the *ggplot2* R package (WICKHAM, 2011). The path analysis model was obtained by the *sem* R package (FOX, 2006). The principal component analysis was performed using the *princomp* R function of *base* package.

## 1.3. Results

### 1.3.1. Competition effects and path analysis

We were able to estimate 2448 effects of competition (306 plots × 8 covariate neighboring trees), with 99.14% having negative effects. The spatial autocorrelation in the direction of rows and columns ($\Phi_r$ and $\Phi_c$, respectively) within the plots showed 100% positive values, with $\Phi_r \times \Phi_c$ equal to 0.04, 0.78, and 0.58, being the minimum, maximum, and median values, respectively.

Figure 1.2 shows a descriptive graphical analysis of the competition values grouped by position of neighboring trees in relation to focal trees. A clear trend of increased competition related to the neighboring position relative to the focal tree can be seen, meaning that the trees from the row and interrow spacing tend to have greater absolute magnitude values, while trees from diagonals presented values closer to zero. Figure 1.2 also shows the confidence intervals (95% probability) between the effects of competition, and from these it can be seen that, in all experiments, the effects of trees on the diagonals are different from those in the row and interrow trees. Between the trees of row and interrow plantings, the difference is almost imperceptible, with this behavior similar for all eight experiments.

Initially, any potential relationship between productivity and the effects of competition between neighboring trees was determined using canonical correlation analyses. For this purpose, the trees in similar positions to the focal tree were placed into groups (i.e., row, interrow, and diagonal trees), and the spatial autocorrelations placed in a fourth group. The canonical correlation between MAI and the competitive effects of the groups was equal to 0.03, 0.13, and 0.22, for plants from row, interrow and diagonal, respectively. Similarly, a canonical correlation of 0.39 between the autocorrelation parameters and MAI was obtained. In the canonical correlations between neighboring groups, it was observed that the shorter the distance between these groups, the greater the correlation between them (Figure 1.1). The trees in interrows and diagonals had smaller distances between them, with a canonical correlation of 0.83; the trees in the rows and diagonals had the second shortest distance, showing correlation equal to 0.81; and the trees of the interrows and rows had the greatest distances, with correlations equal to 0.69. The canonical correlation between the effects of neighboring competitors (rows, interrows, and diagonals) and autocorrelation parameters was equal to 0.29, 0.36, 0.30, and 0.39, respectively.

Table 1.2 shows the direct and indirect path coefficients. The spatial autocorrelation demonstrated a direct effect on the productivity (0.41), indicating that the greater the homogeneity within plots, the greater the MAI. The trees of the rows and interrows showed direct effects equal to –0.49 and –0.28, respectively, indicating significant competition. However, the four diagonal trees showed a positive direct effect of 0.72. All direct effects were significant at 99% probability. The error (*e*) presented a $R^2$ of 0.73, indicating that other causes were also influential in the plot productivities.

Figure 1.3 shows the separation of the 306 plots into 50% more homogeneous (so-called homogeneous plots) and 50% less homogeneous (so-called heterogeneous plots) based on the median of autocorrelation parameters of rows and columns in each plot (i.e., the 153 plots with $\Phi_r \times \Phi_c$ values greater or equal to 0.58 and the 153 plots smaller than 0.58). From this analysis, we found that in homogeneous plots the relationship between intra-genotypic competition and MAI productivity is practically zero. On the other hand, when evaluating heterogeneous plots, the plots with the fiercest competition effects had higher MAI. In general, homogeneous plots showed productivity mean of 42.15, and the heterogeneous plots showed a mean of 35.88 m$^3$/ha/year.

### 1.3.2. Genetic nature of the relationship of competition versus productivity

Only the trees from the row and interrow plantings exhibited direct effects of competition that were reflected in greater plot productivity (Table 1.2). For this reason, the values of competition considered in model [3] were the sum of the effects of the closest four surrounding trees to the focal tree (Figure 1.1-A). Table 1.3 shows results concerning the use of the joint model, as well as four marginal models for each of the experimental conditions. A single model accounting for variance components for each experimental condition did not converge. The average of the effects of competition ranged between –0.38 and –0.41, and the average of MAI ranged between 35.26 and 49.89. Corroborating the results obtained by (JESUS et al., 2015), the results from the present study showed that the experiments in the high altitude regions produced more, on average, than the experiments at low altitude for both plant spacings of 6 m²/plant and 10 m²/plant. The narrow-sense heritability of competition ranged from 0.18 to 0.38, and was 0.22 in the joint model. The MAI narrow-sense heritability ranged from 0.82 to 0.87, and was 0.87 in the joint model under all experimental conditions. Genotypic and phenotypic correlations between competition and MAI were always negative, both in the marginal models and in the joint model, indicating the presence of competition in all experimental conditions evaluated. The joint genotypic and phenotypic correlations were equal to –0.52 and –0.25, respectively. The heritability of MAI updated by adding the competition model ($\mathrm{h}_{\mathrm{m}}^{2}$) was always higher than those of the MAI for $h^2$, and the effective efficiency (EE) of this addition is presented in Table 1.3. The experimental conditions with higher productivity, i.e., high altitudes, were also more effectively efficient. When compared within each altitude, the experiments with greater density of plants (6 m²/plant) also showed higher EE.

Figure 1.4 presents a linear relationship between competition and MAI. In all four experimental conditions, higher competing (or aggressive) clones have higher productivity. Comparing the regression lines, for the 6 m²/plant (both high and low altitudes), the two regression lines are parallel, and for the 10 m²/plant, similar behavior is observed.

Figure 1.5 shows the five best and the five worst clones for each experimental condition, showing both competition and MAI traits. The bars of the five best clones are highlighted in blue and the bars of the five worst in gray. The colored codes of clones with blue and gray are matching (i.e., the coincident clones) between competition and MAI for each experimental condition evaluated, and it can be seen that in all conditions, the less competitive clone was also the least productive. For the four experimental conditions (6 m²/plant-Low, 6 m²/plant-High, 10 m²/plant-Low, 10 m²/plant-High), the coincidence between the 5 best clones was equal to 2/5, 2/5, 1/5 and 3/5 between competition and MAI, and the coincidence between those 5 worst clones was equal to 4/5, 4/5, 2/5 and 4/5, respectively. Note that the lowest coincidence occurred in the 10 m²/plant-Low condition, and highest at 10 m²/plant-High condition (see Figure 1.4).

To evaluate the phenotypic plasticity of clones in all four experimental conditions principal component analysis was performed. The first principal component (PC1) explained 48% of the total variance of the four conditions, and the second principal component (PC2) 22.8%, totaling 70.1%. QI, QII, QIII, and QIV clones can be observed in Figure 1.6 using the quadrants. The five best clones shown in Figure 1.5 are highlighted in blue in Figure 1.6.

## 1.4. Discussion

### 1.4.1. Heterogeneous environments cause competition between clones

Many authors in the literature have shown that clonal stands of greater homogeneity or uniformity also have higher productivity (BOYDEN; BINKLEY; STAPE, 2008; LUU; BINKLEY; STAPE, 2013; SOARES et al., 2016; STAPE et al., 2010). The homogeneity of plant growth in clonal stands is highly dependent on environmental factors (LUU; BINKLEY; STAPE, 2013), since the clonal genetic variability within the plots is theoretically zero (RESENDE, 2007; STAPE et al., 2010). However, to achieve the desired homogeneity of stands requires investigation of silvicultural techniques aimed at maximizing site uniformity (ASPINWALL et al., 2011). In the present study, plots with more homogeneous environments had higher average productivity than did the heterogeneous plots (42.15 versus 35.88 m³/ha/year, respectively) (Figure 1.3), corroborating the aforementioned authors. However, heterogeneous plots with greater effects of competition (negative effects) reached MAI values similar to homogeneous plots. This result leads to the hypothesis that micro-environmental variations within the heterogeneous plots generate a local disturbance event that, over time, triggers competition among neighboring trees (KIM; BULLOCK; STAPE, 2015; MAGNUSSEN, 1994). Campoe et al. (2013) highlighted factors that assist with the emergence of dominant trees in the plot, i.e., i) plant quality of the implanted material, ii) soil fertility differences in micro-sites (either natural or resulting from silviculture operations), and iii) inherent characteristics of the genetic material. A priori, according to the linear relationship between competition and productivity (Figure 1.3), the evaluated hypothesis was that different genetic materials differed in their response (better or worse) to heterogeneous conditions, meaning that in addition to silvicultural techniques, some clones might actively contribute in achieving similar productivities in a uniform environment.

In the present study, 306 square plots containing 100 plants from 4 experimental plantation conditions were evaluated (Table 1.1), and from these we were able to account for the independent effects of competing neighboring trees. Thus, it was seen that in relation to the focal tree (Figure 1.1-A), diagonal trees contributed smaller competition effects than the row and interrow trees (Figure 1.2). These results are easily understood, since distance is a predominant factor in the effects of competition between trees (THORPE et al., 2010), wherein, the diagonal of trees account for the Pythagorean relationship with the distance of the row and interrow trees (Figure 1.1-B). Besides the effect of competition from the eight neighboring trees, model [2] also provided the homogeneity parameters (spatial autocorrelation $\Phi_r$ and $\Phi_c$) of the plots. Thus, with the effects of competition, uniformity, and productivity of the plot, we performed canonical correlation and path analysis (Table 1.2) to verify the direct effects of competition and environment on the MAI, and the indirect effects that competition and plot homogeneity share. The canonical correlation of competition effects between neighboring tree groups and the plot MAI were proportional to the distance between them. These results were anticipated, since the micro-environmental disturbance events are more likely to occur between trees in close proximity (FOX; BI; ADES, 2007), resulting in competition with similar effects.

Taking into account the three possible positions where the neighbor tree is found in relation to the focal tree, only four trees (trees from rows and interrows) showed significant direct effects of competition on plot productivity (values equal to –0.49 for rows and –0.28 for interrows, Table 1.2). The high direct effect of the diagonal trees (0.72) suggests that these trees behave as the average of the plot, not causing direct competition effects on the focal tree, but causing stimulation of growth effects. Furthermore, this result strengthens the use of first order autoregressive models (AR1) for the study of competition between trees (RESENDE, 2007; RESENDE et al., 2005), where a structure of second order (AR2) would not fit. The trees in all positions, including focal trees, belong to a larger network of influences, as seen by the indirect effects (Table 1.2) that all trees mutually perform effects among them, resulting in greater or lesser plot productivity. Two indirect effects were the diagonal trees plot productivity via the row trees (–0.40) and via interrow trees (–0.23), which show that competition occurs in all directions on the plot. In this case, the row tree behaves as the focal tree and the diagonal trees as the interrow trees, demonstrating a perfect network of interactions. Moreover, we can observe that these values are similar to the direct effects of the neighboring row and interrow (both approximately 20% lower). The direct effects of the homogeneity on plot MAI was positive and significant (0.41), reinforcing results shown in Figure 1.3 and confirming the conclusions made by Almeida et al. (2007), Luu et al. (2013), Stape et al. (2010).

### 1.4.2. Genetic nature of clonal competition and phenotypic plasticity under different experimental conditions

Competition ability between trees is also a genetic trait, which may be expressed (COSTA E SILVA; KERR, 2013). However, the separation of effects caused by genetic competition from those attributed to environmental effects is difficult to achieve (DONNELLY et al., 2016). To attempt to filter out the clonal competition of environmental trends, we estimated the particular effects competition in each of the square plots (Figure 1.2), but these effects are only phenotypic values, and may merely be caused by the greater or lesser site heterogeneity (Figure 1.3).

Costa e Silva et al. (2013) estimated the heritable variation of competition between *Eucalyptus globulus* clones using single tree plots and found values of 0.37 ± 0.05 for plants after 4 years. Using square plots and hybrids of *E. grandis* × *E. urophylla*, we found very similar values to these authors (Table 1.3). The heritabilities altered according to the experimental condition, ranging from 0.18 (6 m²/plant-Low) to 0.38 (10 m²/plant-High). The genetic variances ($\sigma_g^2$) in these two conditions were $1.4 \times 10^{-3} \pm 1.1 \times 10^{-3}$ and $5.5 \times 10^{-3} \pm 2.6 \times 10^{-3}$, respectively, and these two values did not overlap when considering the standard error ranges. Under the same two conditions, the variances of the residuals were $6.1 \times 10^{-3} \pm 1.0 \times 10^{-3}$ and $9.1 \times 10^{-3} \pm 1 \times 10^{-3}$, respectively, showing that the maximum and minimum values also did not overlap. These results indicate that different site residual variances triggered genetic competition behaviors that were also statistically different, but directly proportional to the residual variance.

Depending on the weather, and the availability of natural resources in native forests (in both tropical and temperate climates), it is recognized that species and genotypes with strong competitive features are prominent, and become more evolutionarily adapted (BOYDEN; BINKLEY; STAPE, 2008; MCINTOSH, 1970). From the present study, it was observed that the traits MAI and competition had quite relevant $\mathbf{r_g}$ values (Table 1.3). In autogamous crops, the Bulk selection method is based on the competitive potential of genotypes, under the premise that these are more adaptive materials and are therefore more productive (SUNESON, 1956). From the present study, looking at the four conditions evaluated, clones with greater genetic competition potential also excelled in productivity (Figure 1.4). Phenotypic correlations were all negative (i.e., the most aggressive were the most productive), with a mean at low magnitudes (–0.25 to –0.52; Table 1.3), while genetic correlations demonstrate the adaptive relationship more clearly, ranging from –0.41 to –0.73.

Competition is most pronounced with distance between plants (THORPE et al., 2010). In the dense planting condition (6 m²/plant), we observed a stronger relationship between productivity and competition (Figure 1.4) than for the 10 m²/plant condition, demonstrating that in conditions of greater competitive stress, the environment is more rigorous in stimulating competition and may trigger the stimulatory pathway genes that regulate individual growth, thus offsetting development of the neighboring clone (JAENISCH; BIRD, 2003). The veracity of this assumption can be seen by comparing the slope of the straight line in Figure 1.4, wherein both the higher and lower altitudes have straight lines that are parallel in the 6 m²/plant condition. A similar result was seen between the two altitudes spaced at 10 m²/plant, where the slope of the straight lines is less steep, but is approximately parallel.

The higher productivity of *Eucalyptus* clones is strictly related to environmental quality (BOYDEN; BINKLEY; STAPE, 2008; KIM; BULLOCK; STAPE, 2015; STAPE et al., 2010). In high altitude environments, productivity was considerably higher, being approximately 20% greater than in low altitudes (Table 1.1 and Table 1.3). This typically occurs owing to *Eucalyptus* shoot-blight disease in lower altitudes (ALMEIDA; RIBEIRO; LEITE, 2013), and a more conducive climate for *Eucalyptus* growth in higher altitudes of the studied Brazilian region. The accounting of competition in model [3] is particularly suitable in experiments at higher altitudes, making improvements in the accuracy selection or effective efficiency (EE) by 6.51% (at spacing of 6 m²/plant) and 5.09% (at spacing of 10 m²/plant). Our results suggest that in addition to appropriate silvicultural treatments, some genetic material is able to regulate site resource distributions and optimize stand productivity, thus bypassing problems of environmental heterogeneity. Dominant trees can use site resources more efficiently (BINKLEY et al., 2010), thus ensuring these resources are less available to the weaker neighboring trees. This phenomenon creates an impression that since a number of trees are being harmed, the overall stand productivity will reduce, when in fact weakened trees on an equal footing with dominant trees in nature would not take advantage of site resources. Possibly, the *Eucalyptus* planting tends to naturally thin the surrounding trees that are in poor development (ZEIDE, 2001), seeking the optimal accommodation of the trees into the stand. This process might maximize the stand productivity, since the resources are allocated to trees that have the greatest potential to take advantage of them (BINKLEY, 2004). There is quite a coincidence between productive and aggressive clones (Figure 1.5), with the present study highlighting the five best and worst clones with respect to productivity and competitiveness for the four experimental conditions. From this it can be seen that the less competitive clones were always less productive, regardless of the experimental condition. These clones are specified non-regulatory of plot productivity, and are less productive.

Clone selection is a very important step for forestry companies, given that large areas are occupied by a single clone (LUU; BINKLEY; STAPE, 2013). For this reason, the recommendation of superior materials must be sufficiently accurate to not cause future problems. To achieve this, assessment at various locations would be necessary, and should be performed with accuracy to ensure phenotypic stability of the clones (OGUT et al., 2014). To verify stable clones in all the evaluated conditions, we performed principal component analysis, reducing information from the four conditions into two components. Therefore, by means of Figure 1.6, we identified stable clones that are well-suited to any condition. As with the inclusion of competition, the productivity model has increased the accuracy of selection (between 2 and 6%) (Table 1.3), and the following clones are the most productive and have the greatest competitive potential. The clones **1196**, **1213**, **1063**, **1857**, **C7074**, **1856**, **1857**, and **1281** are present at QI, and were ranked among the top five in one or more experimental conditions (Figure 1.5). Among these, **1281** had good performance at lower altitudes for all of the plant spacings, and **1213** had good performance at higher altitudes for all of the plant spacings tested. Thus, besides being stable clones, they showed great phenotypic plasticity to deal with heterogeneous sites, performing noticeable productivity optimization, regardless of the plant spacing used. Some clones were highly specific to some experimental conditions (QII and QIV). However, no clone of QIII was ranked among the top five in any condition (Figure 1.5 and Figure 1.6). Furthermore, the results demonstrate that the entire selection process of the clones (clonal preliminary tests and ECTs) was adequate to select the best genotypes in intra-genotypic competition.

## 1.5. Conclusions

A given clone replicated in the stand, even though it might theoretically be of identical genetic material, demonstrated the potential for differential competition when compared to other clones. It is believed that the stimulatory mechanism of intra-genotypic competition is owing to local micro-environmental disturbances on a single tree that trigger plant-to-plant interactions. Therefore, some genotypes are able to benefit more or less from these micro-events.

The presented results indicate that there exists a genetic relationship between the clone competitive potential and its MAI, and this relationship can be affected by the plant spacing of trees and by specific environmental features. Some clones can optimize their stand productivity, thus mitigating expenses with the application of silvicultural techniques to homogenize growth factors of the plots.

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**Table 1.1.** Information on the experiments and silviculture conditions considered in the genetic model of productivity and competition.

| Test | Location | Age | Mortality Rate (%) | Soil order | Calcareous (kg/ha) | Number of clones | Average of MAI (m³/ha/year) | Annual Mean Temp. (ºC) | Annual Precipitation (mm) | Planting Spacing (m²/plant) | Altitude (m ASL) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ECT05 | BO | 5.92 | 3.93 | Dystrophic Red Oxisol | 1500 | 20 | 30.989 | 23.4 | 1179.9 | 6 | 400 (Low) |
| ECT06 | BO | 6.00 | 3.23 | Dystrophic Yellow-Red Oxisol | 1500 | 10 | 40.144 | 23.4 | 1179.9 | 6 | 400 (Low) |
| ECT01B | SAB | 6.00 | 3.12 | Acric Red Oxisol | 2000 | 6 | 58.817 | 20.1 | 1490.0 | 6 | 670 (High) |
| ECT7A1 | COC | 6.15 | 4.58 | Acric Yellow Oxisol | 2000 | 10 | 45.715 | 20.0 | 1445.1 | 6 | 1425 (High) |
| ECT7A2 | COC | 6.15 | 3.39 | Acric Yellow Oxisol | 2000 | 8 | 42.630 | 20.0 | 1445.1 | 6 | 1425 (High) |
| ECT01A | BO | 5.88 | 24.09 | Dystrophic Fluvisol | 1000 | 8 | 29.299 | 23.4 | 1179.9 | 10 | 400 (Low) |
| ECT02 | BO | 6.02 | 4.37 | Dystrophic Fluvisol | 1000 | 28 | 36.067 | 23.4 | 1179.9 | 10 | 400 (Low) |
| ECT04 | SAB | 6.01 | 4.30 | Dystrophic Yellow-Red Oxisol + Dystrophic Red Oxisol | 2000 | 12 | 46.888 | 20.1 | 1490.0 | 10 | 670 (High) |

**ECT**: Expanded clonal test; **Location**: BO = Belo Oriente, SAB = Sabinópolis, COC = Barão de Cocais; m ASL = meters above sea level

**Table 1.2.** Path coefficients using information from 306 plots in 8 experiments. Values in bold are the direct effects and coefficient of determination of residuals, and the remaining values are the indirect effects. Statistical significances are presented for the direct effects.

| Direct Effect | Indirect effect | Values |
|---|---|---|
| **Spatial autocorrelation of rows and columns** | – | **0.41***** |
| | Row | -0.14 |
| | Inter-row | -0.10 |
| | Diagonal | 0.22 |
| **Neighbors of Row** | – | **-0.49***** |
| | Spatial AR1 | 0.12 |
| | Inter-row | -0.19 |
| | Diagonal | 0.59 |
| **Neighbors of Inter-row** | – | **-0.28**** |
| | Spatial AR1 | 0.15 |
| | Row | -0.34 |
| | Diagonal | 0.59 |
| **Neighbors of Diagonal** | – | **0.72***** |
| | Spatial AR1 | 0.12 |
| | Row | -0.40 |
| | Inter-row | -0.23 |
| **Error (*e*)** | | **0.73***** |

P-values for the direct effects: $\Phi_r$, $\Phi_c$ < 0.001; row < 0.001; interrow = 0.002; extremity < 0.001; *e* < 0.001. *** indicates significance at 99.9%, ** is 99%, and * is 95% probability.

**Table 1.3.** Marginal and joint model results. The mean and variance components, narrow-sense heritability, genetic and phenotypic correlation, and effective efficiency of the bi-trait model on productivity accuracy selection are presented. These parameters were calculated for competition and mean annual increment at 6 years (MAI) traits.

| | | **Experimental conditions** | | | | |
|---|---|---|---|---|---|---|
| | | **6 m²/plant, Low altitude** | **6 m²/plant, High altitude** | **10 m²/plant, Low altitude** | **10 m²/plant, High altitude** | **multi-conditions** |
| **Number of clones** | **Total** | 27 | 21 | 33 | 12 | 54 |
| | **Shared** | 16 | 17 | 29 | 8 | 31 |
| **Average** | **Comp** | –0.39 | –0.41 | –0.40 | –0.38 | –0.40 |
| | **MAI** | 35.26 | 49.89 | 38.12 | 49.12 | 41.34 |
| $\boldsymbol{\sigma_g^2}$ | **Comp** | 1.36±1.13 | 3.28±2.30 | 5.50±2.60 | 4.86±3.80 | 2.22±0.90 |
| | **MAI** | 33.60±9.01 | 118.75±65.31 | 118.24±31.17 | 52.95±24.07 | 106.50±17.01 |
| $\boldsymbol{\sigma_p^2}$ | **Comp** | 7.50±2.16 | 9.25±3.50 | 14.60±4.10 | 14.66±6.70 | 10.09±1.68 |
| | **MAI** | 39.11±10.04 | 136.89±68.46 | 129.14±33.02 | 59.05±25.92 | 116.77±18.06 |
| **h²** | **Comp** | 0.18±0.11 | 0.36±0.09 | 0.38±0.08 | 0.33±0.07 | 0.22±0.05 |
| | **MAI** | 0.82±0.01 | 0.87±0.04 | 0.87±0.01 | 0.85±0.02 | 0.87±0.01 |
| **Correlations** | $\mathbf{r_g}$ | –0.64±0.05 | –0.73±0.04 | –0.41±0.07 | –0.69±0.04 | –0.52±0.06 |
| | $\mathbf{r_p}$ | –0.36±0.07 | –0.32±0.07 | –0.25±0.07 | –0.52±0.06 | –0.25±0.07 |
| $\mathbf{h_m^2}$ | **MAI$_{\mathbf{\vert Comp}}$** | 0.86±0.02 | 0.98±0.06 | 0.91±0.02 | 0.94±0.04 | 0.91±0.03 |
| **EE** | | 2.62% | 6.51% | 2.12% | 5.09% | 2.28% |

The values after ± are standard errors; $\boldsymbol{\sigma_g^2}$ are the additive genetic variance; $\boldsymbol{\sigma_p^2}$ are the phenotypic variance; **h²** are the narrow-sense heritability; $\mathbf{r_g}$ and $\mathbf{r_p}$ are the genotypic and phenotypic correlation, respectively, between competition and MAI; $\mathbf{h_m^2}$ are the updated narrow-sense heritability of MAI, including competition on the model. **EE** is the effective efficiency or selection accuracy gain, including competition on the model. The variance components and the standard errors of competition traits are multiplied by 1000.

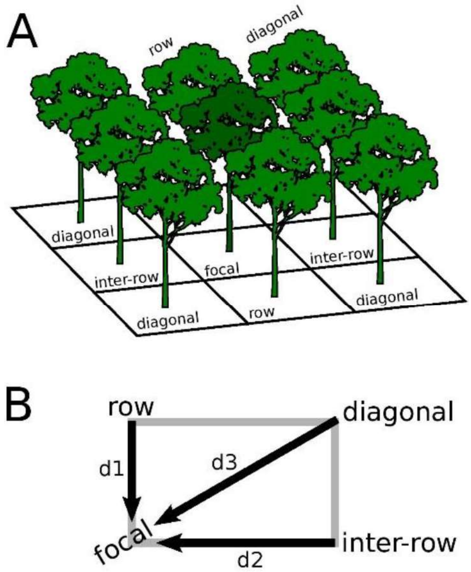

**Figure 1.1.** (A) Schematic diagram showing the positions of the eight neighboring trees in relation to the focal tree (central dark green). Two neighboring trees are in the *row* planting, two are in the *interrow* planting, and four are *diagonally* in reference to the focal tree. (B) Distances between the three possible positions of neighboring trees and the focal tree, $\mathbf{d1} < \mathbf{d2} < \mathbf{d3}$ and $\mathbf{d3} = \sqrt{\mathbf{d1}^2 + \mathbf{d2}^2}$.

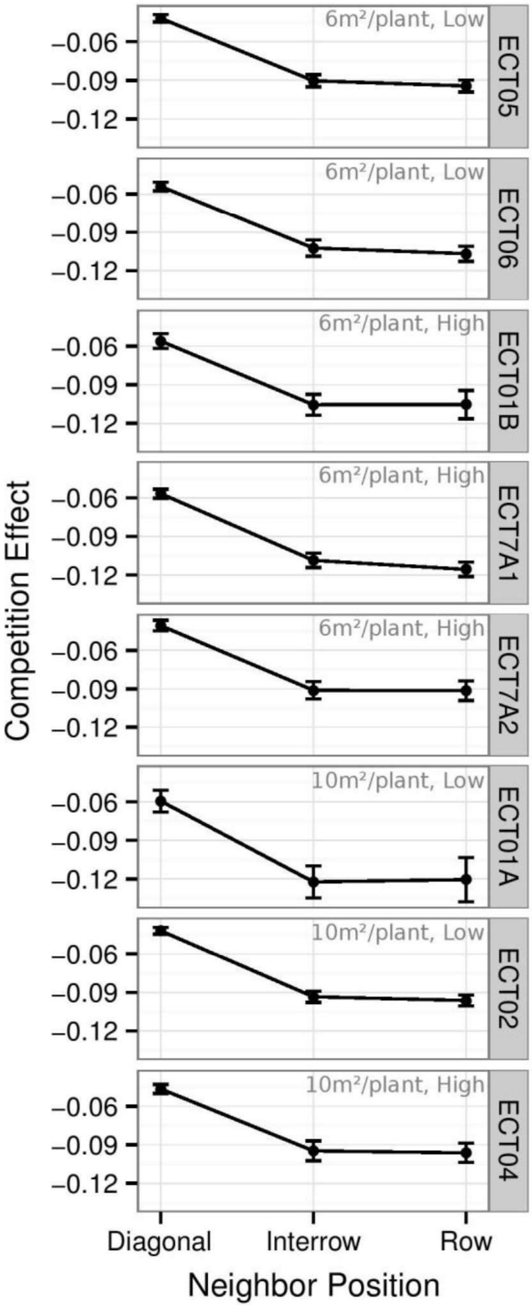

**Figure 1.2.** Means and confidence intervals (95% probability) of the effects of neighboring trees on focal trees. The effects are grouped according to the neighboring tree position from the focal tree (two trees in the planting row, two in the spacing interrow, and four on the diagonal). Each horizontal box represents an evaluated expanded clonal test (ECT).

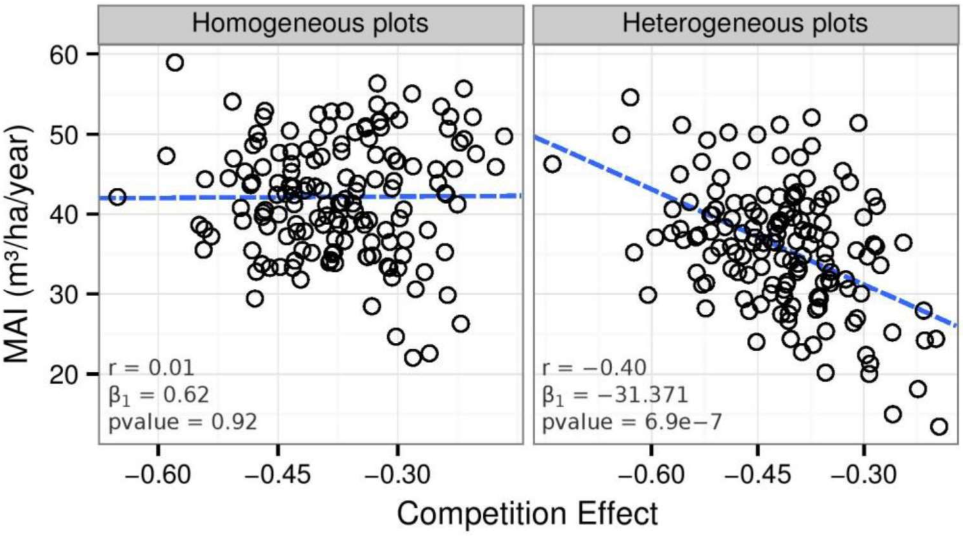

**Figure 1.3.** Linear relationship between competition/aggressiveness (sum of the effects of the row and interrow trees on the focal tree) and productivity (measured in mean annual increment at 6 years – MAI). The 306 evaluated plots were divided by 50% more homogeneous (so-called 50% heterogeneous plots), by the median autocorrelations parameters. r is the correlation coefficient between competition and MAI; $\boldsymbol{\beta_1}$ is the slope regression coefficient; and p-value is the associated significance with $\boldsymbol{\beta_1}$.

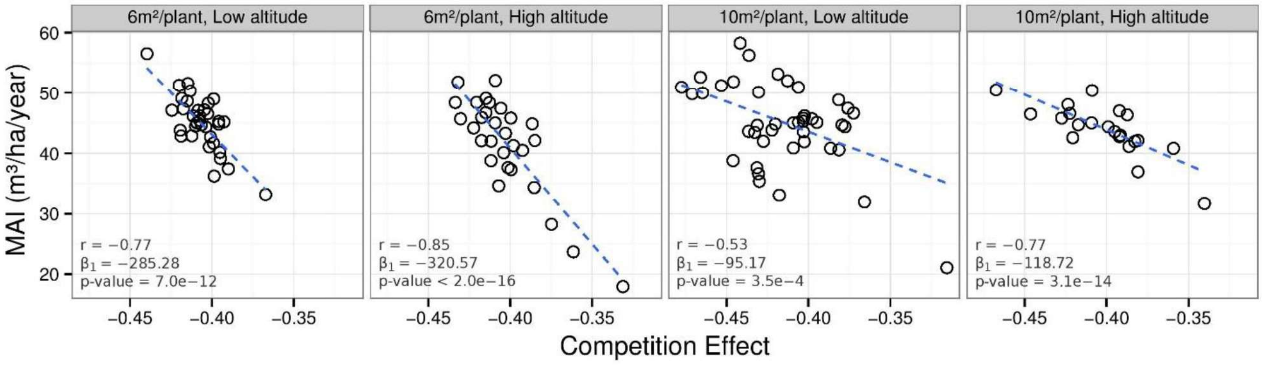

**Figure 1.4.** Linear relationships between estimated genetic values (EGV) of competition/aggressiveness versus mean annual increment at 6 years (MAI) for each experimental condition. All experiments demonstrate a negative linear relationship, hence the greater the potential for competition (in the negative values), the greater productivity in MAI. r is the correlation coefficient between competition and MAI; $\boldsymbol{\beta_1}$ is the slope regression coefficient; and p-value is the associated significance with $\boldsymbol{\beta_1}$.

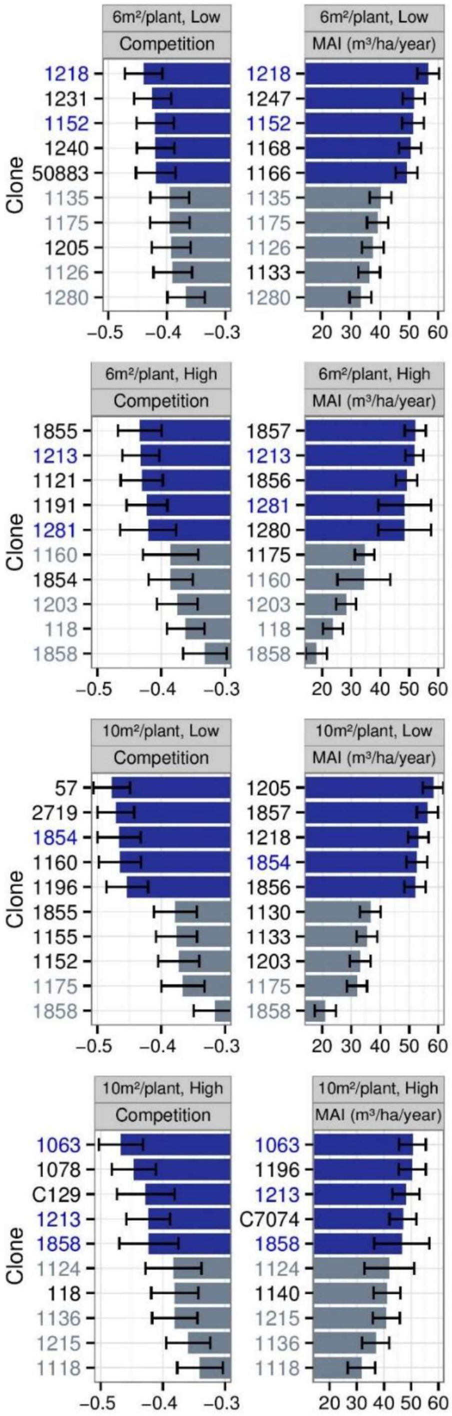

**Figure 1.5.** Ranking of estimated genetic values (EGV) showing the five best clones (blue bars) and five worst clones (gray bars) separated by experimental condition, traits competition and mean annual increment at 6 years (MAI). The ranges (upper and lower) of each bar are the standard error. The codes of clones colored in blue and gray represent coincidences between competition and MAI.

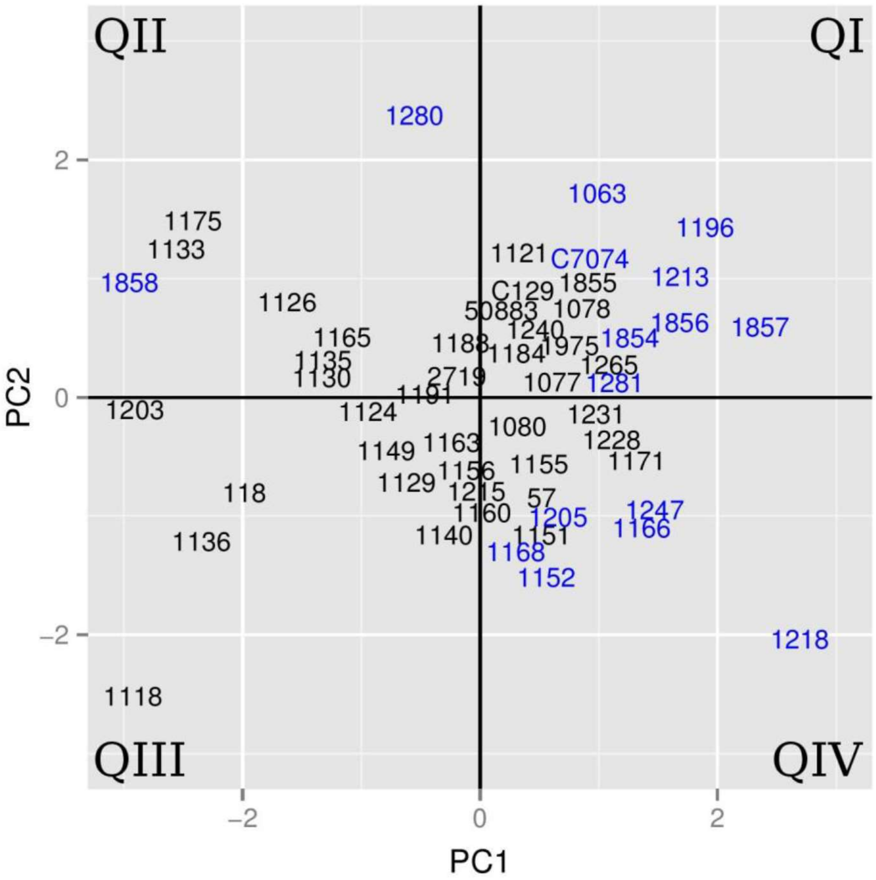

**Figure 1.6.** Principal components arranged in four quadrants (QI, QII, QIII, and QIV). PC1 explains 48.0% of the experimental conditions and PC2 explains 22.8%, totaling 70.8%. The codes distributed between the ordinate and abscissa are the identifiers of the clones. Clones highlighted in dark blue are the five best of each condition shown in Figure 1.5.

## **CHAPTER II.** Environmental uniformity, site quality and tree competition interact to determine stand productivity of clonal Eucalyptus. DOI: 10.1016/j.foreco.2017.12.038

## Abstract

The major determinants of productivity in *Eucalyptus* plantations include the site productive capacity, local environmental uniformity, and the tree genetics, which impact their growth potential and competitiveness. While these factors have received a lot of attention individually, less attention has been given to the relative importance of these factors and the interactions between them. We examined these factors and their interactions using eight experiments located along a gradient in site productivity, consisting of 54 clonal genotypes (*Eucalyptus urophylla* × *E. grandis* hybrids) at two plant spacings (3 × 3.33 and 3 × 2 m). Stand productivity was quantified as the mean annual increment at age 6 years ($m^3$ $ha^{-1}$ $year^{-1}$). Site productive capacity was represented using a site index based on mean dominant height at age 6 years. Environmental uniformity was calculated from within-plot variability in growth of very young stands using residual spatial autocorrelation. The competitive ability of a given phenotype was calculated as the percent loss in potential growth due to neighbor competition. Productivity increased with all variables but site quality had the greatest effect, followed by environmental uniformity and then competitive ability, with corresponding changes in productivity of about 30, 20 and 10 $m^3$ $ha^{-1}$ $year^{-1}$, respectively, across the range of the given variable. With higher environmental heterogeneity, competition among genotypes increased, especially at dense spacing, showing that in such situations, highly competitive genotypes may display productivities similar to the less competitive genotypes in uniform environments. Experimental plots distributed across site quality and uniformity gradients provide opportunity for greater genetic differentiation than plots covering more homogeneous environments, reinforcing the recommendation of establishing genetic tests in locations with extreme site qualities. Our work suggests that the G × E interaction is linked to site quality and, to a lesser degree, to the local environmental uniformity. This work shows the value of adopting environmental gradient-based approaches in tree genetic testing and clone recommendation as a way to more accurately match genotypes to specific sites.

**Keywords:** Clonal forest; Breeding; *Eucalyptus sp.*; Forest management; Mixed models; Random regression; Plant based Indexes; Structural diversity; Phenotypic plasticity

## 2.1. Introduction

The impacts of the structural heterogeneity of a forest stand on its overall functioning or productivity performance have often been studied in terms of tree-species diversity, with many studies showing positive relationships (FORRESTER; BAUHUS, 2016; GAMFELDT et al., 2013; LIANG et al., 2016; ZHANG; CHEN; REICH, 2012). However, tree-species diversity is only one component of structural heterogeneity. Far less attention has been given to other components, such as the diversity of tree sizes (diameter or height) (LEI; WANG; PENG, 2009; LIANG et al., 2007); the local environmental heterogeneity in terms of spatial distributions of resources within stands (BOYDEN et al., 2012); the intraspecific genetic diversity (BOYDEN; BINKLEY; STAPE, 2008); and the relationship between individual tree size and growth, resource uptake or use efficiency (BINKLEY et al., 2010). These structural components can have similar or even greater effects on stand productivity than species-diversity.

When isolated from species diversity, such as in the case of monocultures, structural diversity can have the opposite effect to what might be expected from species mixtures. For example, the mean increase in productivity due to tree-species mixing in a meta-analysis was about 24% (ZHANG; CHEN; REICH, 2012). However, studies with planted experiments or using large inventory data sets, have shown that increasing structural heterogeneity in monocultures in terms of individual tree sizes or growth rates can decrease stand productivity by 10 to 20% for different species and across wide ranges in site productivity (BOURDIER et al., 2016; SOARES et al., 2016; STAPE et al., 2010).

Genetic diversity, in the absence of species diversity, also modulates the effects of structural heterogeneity on tree growth. For example, neighbor size was found to be more important in determining individual tree growth in clonal stands than in seed-origin stands (BOYDEN; BINKLEY; STAPE, 2008).

There can also be significant differences between genotypes of a given species in terms of how much a given increase in structural heterogeneity reduces productivity (ASPINWALL et al., 2011; BINKLEY et al., 2010; RESENDE et al., 2016; SOARES et al., 2016). Studies using monoclonal stands have enabled analyses that exclude or account for the effects of genetic diversity compared with other aspects of structural heterogeneity.

Heterogeneity within plantations is likely to result from at least three factors. One is the heterogeneity of environmental conditions within the plantation (e.g. Schume *et al.*, 2004; Boyden *et al.*, 2012). A second is the competitiveness of individuals towards their neighbors, in terms of the strength of the relationships between individual tree growth and neighboring tree growth (RESENDE et al., 2016). If there is a very weak relationship between the growth of an individual tree and that of its neighbors, then stand productivity may be lowered because the larger trees are not effective enough at outcompeting the smaller trees. On the one hand, this may be important because the larger trees often tend to grow faster, acquire more resources and use them more efficiently (BINKLEY et al., 2010). So, at the stand level, it could be advantageous if stronger individuals are very efficient at developing a competitive advantage. But on the other hand, if large trees do not rapidly outcompete smaller trees, the stand uniformity may decrease very slowly and not impact as greatly on stand productivity. A third potential factor leading to structural heterogeneity is any initial variability in the size and health of the cuttings or seedlings from the nursery (e.g. number of leaves, height, root mass, nutrition), although this is not considered further in this study. While all three factors have been extensively studied, the relative importance of environmental uniformity and competitive ability has received little attention, nor has their interaction with climatic and edaphic conditions (RESENDE et al., 2016).

The effects of environmental uniformity, competitive ability and initial variability in seedling size or health, also have clear practical applications because they can be directly influenced by forest management via the selection of genetic material, changing microsite heterogeneity via site preparation practices or altering current and previous tree positions (BOYDEN; BINKLEY; STAPE, 2008), influencing tree size heterogeneity (e.g. by thinning) and site productivity (e.g. fertilizer application or irrigation). Even disregarding any interactions between structural diversity and genotype, the performance of different genotypes is difficult to predict due to phenotypic differences in the response to climatic and edaphic variation (DES MARAIS; HERNANDEZ; JUENGER, 2013). This interaction between genotypes and environments, known as G × E, is one of the major challenges faced by tree breeders and many methods have been developed to facilitate the matching of sites and genotypes (ELIAS et al., 2016).

Understanding the interaction between site quality, local environmental heterogeneity, tree competition and genotype responses, could enable foresters to improve the efficiency with which site resources are used and hence to improve productivity. The aim of this study was to test the hypotheses that (i) stand productivity increases with environmental uniformity and (ii) the positive effects of environmental uniformity and the competitive ability of different genotypes on productivity interact with site quality, thereby causing a G × E interaction.

## 2.2. Material and Methods

### 2.2.1. Experiments description

We used eight so called “expanded clonal tests” (ECT), installed by the company Celulose Nipo Brasileira-CENIBRA S. A. in the midwest region of the state of Minas Gerais, southeastern Brazil (Figure 2.1). The study areas are located between three municipalities, namely Belo Oriente (19°13'12"S

42º29'01W), Sabinópolis (18°39'57"S 43°05'02"W) and Barão de Cocais (19°56'45"S 43°29'13"W). This area includes a range of climatic and edaphic conditions.

The predominant Köppen climate classes (according to Alvares *et al.*, 2013) are: Aw, Cwa and Cwb, respectively. During the study period, the mean annual temperature varied between 19.7 ºC and 23.8 ºC and the annual rainfall ranged between 1144 mm and 1506 mm. The altitude ranges from 247 m up to 884 m above the sea level (Table 2.1).

All of the ECT were installed in a complete randomized block design with three replicates and experimental units of 100 trees (10 rows × 10 trees). Among the experiments, three ECT had a planting spacing of 3 m × 3.33 m (10 m²/plant), while the other five were planted at 3 m × 2 m (6 m²/plant) (Table 2.1). In total, 54 different genotypes (*E. grandis* × *E. urograndis* hybrids) were tested, among which 33 were present in more than one ECT.

### 2.2.2. Tree and stand variables

The growth variables used in this study were the mean and periodic annual volume increment (MAI and PAI, respectively) during the periods from 0 to 6 ($MAI_{0\text{-}6}$, or simply MAI), 0 to 3 ($PAI_{0\text{-}3}$) and 3 to 6 years ($PAI_{3\text{-}6}$). The PAI and MAI were calculated at the individual tree and stand levels. Tree volume in cubic meters (**V**) was estimated as a function of the diameter, in centimeters, at 1.30 height (**DBH**) and total tree height in meters (**Ht**), in the form of Schumacher & Hall (1933)'s equivalent equation (Eq. [1]), wherein **f** is the taper factor (assumed to be 0.43). Tree MAI and PAI were calculated as the volume increment during the given period divided by the length of the period (i.e. 3 or 6 years).

$$\mathbf{V} = \mathbf{DBH}^2 \frac{\pi}{40{,}000} \mathbf{Ht}\,\mathbf{f}, \qquad [1]$$

To account for the G × E interaction and plant competition within plots, we used three indices: (i) site quality (i.e. the traditional site index), measured as the dominant height at age 6 years; (ii) site uniformity, measured with an autoregressive correlation function, as the autoregressive residual correlation between trees within a plot; and (iii) competition among plants, measured as the degree of growth reduction caused by neighbors. These components are thoroughly described as follows:

**(i) Computation of site index based on the dominant height.** Dominant height was calculated as the mean height of the largest (by diameter) 10% of trees in each plot at age 6 years (CAMPOS; LEITE, 2013). To remove the effects of genotype and planting spacing, mean dominant height was computed as

$\hat{\mathbf{e}} + \overline{\mathbf{Hd}}$, in which $\hat{\mathbf{e}}$ is the residual in the fitted equation Eq. [2] and $\overline{\mathbf{Hd}}$ is the overall mean of dominant tree height.

$$\mathbf{Hd} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e}, \qquad [2]$$

where, **Hd** is the observed mean dominant height; **b** is the fixed effect (mean of all 305 $\mathbf{Hd}$; and planting spacing); **g** is the random effect of genotypes; **X** and **Z** are the incidence matrices on the fixed and random effects respectively, and **e** is the random error.

**(ii) Autoregressive AR1 model of environmental uniformity and (iii) tree competitive ability.** These growth components were obtained by means of spatial modeling of the autocorrelated residuals of Eq. 3 and through the effects of neighborhood covariates, as described by Resende et al. (2016). The environmental uniformity was obtained using $PAI_{0\text{-}3}$, which was assumed to represent the growth increment before the onset of competition, when tree growth is mostly affected by the environment (REZENDE; DE RESENDE; DE ASSIS, 2014; WENDLING; TRUEMAN; XAVIER, 2014). Therefore, the differences in growth during this period would be mostly explained by local environmental effects. On the other hand, competition was obtained using tree $PAI_{3\text{-}6}$, assuming that differences in increments during this period are predominantly due to competition effects in a fully closed canopy environment (BINKLEY, 2004).

In each 10 × 10-tree plot, a border comprising the two outermost rows were disregarded and the remaining 8 × 8 trees were used in the identification of neighbors. The innermost 6 × 6 trees were each considered as target-trees, and each target-tree had eight immediate neighbors, which were identified as neighbor covariates. The total number of target-trees was 10,980 out of 30,500 trees from the 305 plots. Each tree had eight effects of competition (one for each surrounding neighbor). These values were obtained through model [3].

$$\boldsymbol{\gamma} = \mathbf{Fn} + \boldsymbol{\xi}, \qquad [3]$$

where $\boldsymbol{\gamma}$ is the vector of observations of the target-trees' PAI; $\mathbf{F}$ is the incidence matrix on the fixed effects, as in Resende *et al.* (2016); **n** is the fixed effect (i.e: intercept, dead target-tree; covariate of available area associated with dead neighbors; and the eight live neighbor covariates, quantified in terms of their PAI); $\boldsymbol{\xi}$ is the plot spatial error assuming autoregressive covariance. The residual variance is given by $var(\boldsymbol{\xi}) = \sigma_{\xi}^{2}\left[\sum_{\rho_r} \otimes\right]$, where $\sigma_{\xi}^{2}$ is the variance given to the spatial trend. The terms $\sum_{\rho_r}$ and $\sum_{\rho_r}$

refer to the first-order correlation matrices (AR1⊗AR1) with autocorrelation parameters $\rho_r$ and $\rho_c$ and order equal to the number of rows and columns of the plots, respectively (Eq.'s 4 and 5). The fixed effects of "dead target-tree" and "area associated with dead neighbors" were included to better account for the target-tree response to neighbor competition when one or more surrounding trees died. Without accounting for this effect, the faster growth of a tree that results from an increase in available area where neighbors have died would constitute a confounding effect, which could seriously jeopardize the analysis.

$$\Sigma_{\rho_r} = \begin{bmatrix} 1 & \rho_r & \rho_r^2 & \rho_r^3 & \rho_r^4 & \rho_r^5 \\ \rho_r & 1 & \rho_r & \rho_r^2 & \rho_r^3 & \rho_r^4 \\ \rho_r^2 & \rho_r & 1 & \rho_r & \rho_r^2 & \rho_r^3 \\ \rho_r^3 & \rho_r^2 & \rho_r & 1 & \rho_r & \rho_r^2 \\ \rho_r^4 & \rho_r^3 & \rho_r^2 & \rho_r & 1 & \rho_r \\ \rho_r^5 & \rho_r^4 & \rho_r^3 & \rho_r^2 & \rho_r & 1 \end{bmatrix}, \qquad [4]$$

$$\Sigma_{\rho_c} = \begin{bmatrix} 1 & \rho_c & \rho_c^2 & \rho_c^3 & \rho_c^4 & \rho_c^5 \\ \rho_c & 1 & \rho_c & \rho_c^2 & \rho_c^3 & \rho_c^4 \\ \rho_c^2 & \rho_c & 1 & \rho_c & \rho_c^2 & \rho_c^3 \\ \rho_c^3 & \rho_c^2 & \rho_c & 1 & \rho_c & \rho_c^2 \\ \rho_c^4 & \rho_c^3 & \rho_c^2 & \rho_c & 1 & \rho_c \\ \rho_c^5 & \rho_c^4 & \rho_c^3 & \rho_c^2 & \rho_c & 1 \end{bmatrix}, \qquad [5]$$

Due to non-convergence during model fitting, the model of Eq. [3] was applied to each one of the 305 plots. For that reason, the PAI values of all trees within each plot were scaled to values between 0 and 100 in order to remove the effects of differences in plot productivity.

Hence, the effects of competitive ability could be quantified using the slope of the relationship between the target-tree' $\text{PAI}_{3\text{-}6}$ and the $\text{PAI}_{3\text{-}6}$ of the eight neighbors. Similar to the approach shown in Boyden et al. (2008), greater percentage reductions in $\text{PAI}_{3\text{-}6}$ would occur for genotypes that are more sensitive to competition from their neighbors. The environmental uniformity was then quantified as $\rho_r \times \rho_c$ using the modeling with $\mathbf{y}$: $\text{PAI}_{0\text{-}3}$.

### 2.2.3. Random regression mixed-effects models (Genetic model)

The effects of environmental uniformity, competitive ability and site index on stand productivity were examined using the linear mixed effect model [6].

$$\mathbf{y} = \Lambda\boldsymbol{\delta} + \Gamma\mathbf{g} + \varepsilon, \qquad [6]$$

where $\mathbf{y}$ is stand productivity (MAI); $\boldsymbol{\delta}$ represents the fixed effects (intercept and the effects of the aggressiveness, environmental uniformity and site index nested in experiments with planting spacing of 6 m² and 10 m² per plant); and their respective incidence matrix $\Lambda$; $\Gamma$ is the incidence matrix on the random effects **g**, in which $\mathbf{g}' = \{\mathbf{g}_{\beta_0 ik} \vdots \mathbf{g}_{\beta_1 ik}\}$, for the $i$th genotype and its respective $\beta_{0_k}$ and $\beta_{1_k}$ coefficients of random regression. It was assumed that $\mathrm{g} \sim \mathrm{N}(0, \Sigma_\mathrm{g} \otimes \mathrm{A})$, where $\Sigma_\mathrm{g}$ is a block-diagonal covariance matrix, $\mathrm{A}$ is the pedigree-based matrix, and $k = \{1, 2, 3, 4\}$ the four environment conditions (site index and uniformity *versus* 10 and 6 m²/plant spacing), as follows:

$$\Sigma_\mathrm{g} =$$

$$\begin{bmatrix} \sigma^2_{g_{\beta_{0_1}}} & \sigma_{g_{\beta_{0_1}\beta_{1_1}}} & & & & & & \\ \sigma_{g_{\beta_{0_1}\beta_{1_1}}} & \sigma^2_{g_{\beta_{1_1}}} & & & & & 0 & \\ & & \sigma^2_{g_{\beta_{0_2}}} & \sigma_{g_{\beta_{0_2}\beta_{1_2}}} & & & & \\ & & \sigma_{g_{\beta_{0_2}\beta_{1_2}}} & \sigma^2_{g_{\beta_{1_2}}} & & & & \\ & & & & \sigma^2_{g_{\beta_{0_3}}} & \sigma_{g_{\beta_{0_1}\beta_{1_3}}} & & \\ & 0 & & & \sigma_{g_{\beta_{0_3}\beta_{1_3}}} & \sigma^2_{g_{\beta_{1_3}}} & & \\ & & & & & & \sigma^2_{g_{\beta_{0_4}}} & \sigma_{g_{\beta_{0_1}\beta_{1_4}}} \\ & & & & & & \sigma_{g_{\beta_{0_4}\beta_{1_4}}} & \sigma^2_{g_{\beta_{1_4}}} \end{bmatrix}, \qquad [7]$$

The residual vector is distributed as $\varepsilon \sim \mathrm{N}(0, \Sigma_\varepsilon \otimes \mathrm{I})$, $\sigma^2_{c_k}$, where

$$\Sigma_\varepsilon = \begin{bmatrix} \sigma^2_{c_1} & 0 & 0 & 0 \\ 0 & \sigma^2_{c_2} & 0 & 0 \\ 0 & 0 & \sigma^2_{c_3} & 0 \\ 0 & 0 & 0 & \sigma^2_{c_4} \end{bmatrix}, \qquad [8]$$

To examine how much of the variability in stand productivity (MAI) and competitive ability was related to differences in genotypes as opposed to site quality and environmental uniformity, the heritabilities ($\mathrm{h}^2$) and the genetic correlations ($\mathrm{r_g}$) across the gradients of site quality and environmental uniformity were obtained using equations [9] and [10] respectively:

$$\mathrm{h}^2_{\mathrm{j_k}} = \frac{\sigma^2_{\mathrm{g}_{\mathrm{j_k}}}}{\sigma^2_{\mathrm{g}_{\mathrm{j_k}}} + \sigma^2_{\varepsilon_{\mathrm{j_k}}}}, \qquad [9]$$

$$\mathrm{r}_{\mathrm{g}_{\mathrm{jj}'}} = \frac{\sigma_{g_{\beta_{0_k}\beta_{1_k}}}}{\sqrt{\sigma^2_{\mathrm{g}_{\mathrm{j}_\mathrm{k}}}\sigma^2_{\mathrm{g}'_{\mathrm{j}_\mathrm{k}}}}}, \qquad [10]$$

where $\sigma^2_{\mathrm{g}_{\mathrm{j}_\mathrm{k}}}$ is a vector of genetic variance for a given interval j of site quality or environmental uniformity defined between the parametric space of both variables; $\sigma^2_{\varepsilon_{\mathrm{j}_\mathrm{k}}}$ is the residual variance for each $\mathrm{k}$ experimental condition; $\sigma_{g_{\beta_{0_k}\beta_{1_k}}}$ is the genetic covariance between $\beta_{0_k}$ e $\beta_{1_k}$.

### 2.2.4. Computational tools

All analyses were performed in R 3.4.0 (R Core Team, 2017). The *ASReml-R* package (BUTLER et al., 2009) was used to fit the linear mixed effect models. Plots were built with *ggplot2* (WICKHAM, 2011) and *lattice* (SARKAR, 2008) R packages.

## 2.3. Results

Mortality was very low, around 3% to 4% in all ECT except in ECT01A in Belo Oriente in which the mortality reached 24%. The full-period mean annual increment (MAI) ranged from 29.3 $m^3$ $ha^{-1}$ $year^{-1}$ to 58.8 $m^3$ $ha^{-1}$ $year^{-1}$. The 6-$m^2$ planting density treatments presented altogether a higher MAI (40.2 $m^3$ $ha^{-1}$ $year^{-1}$) than the 10-$m^2$ treatments (36.9 $m^3$ $ha^{-1}$ $year^{-1}$). The periodic annual increment after the third year ($PAI_{3-6}$) was greater than the early period ($PAI_{0-3}$) for six of the eight ECT. These results are summarized in Table 2.1.

The MAI was positively correlated with site index and environmental uniformity, and negatively correlated with tree competitive ability (Figure 2.2). The negative values of tree competitive ability reflect a loss in production of the focal tree caused by its neighbors. That is, the more negative the value, the greater the competitive ability. As competitive ability increases (more negative), the stand MAI increases.

Site index had a much greater influence on MAI than environmental uniformity and competitive ability as indicated by the almost vertical level curves in the plots with site index in the $x$ axis (Figure 2.2). Nevertheless, with increasing site index, a marginal effect of the other two variables can also be noted in Figure 2.2 (A, C, D, and G).

Both environmental uniformity and site index were highly significant in both planting spacings (refer to the fixed effects in Table 2.2). All *p*-values were smaller than 0.001, except for environmental uniformity in the 6 $m^2$/plant spacing, which had a *p*-value of 0.023. The reaction norms of the effect of increasing environmental uniformity and site index for each clone and both planting spacings are presented in Figure 2.3. The variances and covariances of the fixed parameters ($\beta_0$ and $\beta_1$) of the random regression for the effects of environmental uniformity and site quality on focal tree production for both spacings, as well as their respective error variances, are shown in Table 2.2.

The heritability ($h^2$) in denser plots (6 m²/plant) was significantly greater than in the 10 m²/plant plots, that is, 0.90 ±0.041 *versus* 0.73 ±0.039. In accordance with Resende (2007), the genetic correlation between these two types of experiments is considered medium to high (0.62), indicating that there is moderate modification in the genotypic ranking between these two densities.

There was a minor variation in $h^2$ across the environmental uniformity gradient, and $h^2$ was always greater than 0.90 in the 6 m²/plant plots and between 0.88 and 0.92 in the 10 m²/plant plots. However, regarding site quality, there was considerable variation in $h^2$, ranging between 0.74 and 0.96 at 6 m²/plant and 0.65 and 0.98 at 10 m²/plant plots (Figure 2.4).

The genetic correlation ($r_g$) along the environmental variations (uniformity and site), which can be interpreted as a measure of genotype × environment interaction (G × E), varied little in relation to environmental uniformity for both planting spacings and only reached values below 0.5 at extreme values of uniformity. On the other hand, the genetic correlation had a much wider variation along the gradient of site quality, reaching values below -0.5 towards the extremes of site quality (Figure 2.4).

## 2.4. Discussion

Productivity was influenced by all variables, with site quality having the largest effect, environmental uniformity having an intermediate effect and competitive ability having the smallest effect, where the effect size is indicated by the change in MAI (Figure 2.2). This study shows that the negative effects of structural heterogeneity on productivity are actually a combination of several different structural attributes, all of which interact with each other.

There are two basic ways to quantify site quality in forests, i.e., via Earth based indices, in which environmental data (climate, topographical, and soil conditions) are used to characterize site and productive capacity; or via plant-based indices in which productive capacity is described using stand growth measures (SKOVSGAARD; VANCLAY, 2008). Site index based on the mean dominant height at a reference age is a commonly used proxy for site productive capacity (BURKHART; TOMÉ, 2012; CAMPOS; LEITE, 2013; VAN LAAR; AKÇA, 2007).

A plant-based site index was used in this study because the high number of plots measured enabled a local (plot-level) characterization of productive capacity. This could not be appropriately achieved using environmental variables due to the much coarser resolution on which they are recorded. Although edaphic and climatic variables are a good indicator of productivity (STAPE et al., 2010), the information was only available at a regional level and not at the experimental plot level for this study (Table 2.1). The plant-based site index used in this study was found to be positively correlated with productivity (r = 0.71) and with the climatic variables of rainfall (r = 0.66) and altitude (r = 0.74), while negatively so with temperature (r = -0.68).

Productivity was positively correlated with site index, but for a given site index and genotype, productivity increased with increasing environmental uniformity and increasing (more negative values) competitive ability. Therefore, our results suggest that stands of a given genotype or on the same site class may differ in productivity due to the effects of local heterogeneity and the competitive ability of the genotype (Figure 2.2).

Different genotypes responded differently to local environmental heterogeneity and competition. The mechanisms underlying this variability may be driven, for instance, by different rates of nutrient and water uptake and use efficiency (e.g. Li *et al.*, 1991), different biomass partitioning (e.g. Almeida *et al.*, 2004; Ryan *et al.*, 2010; Donnelly *et al.*, 2016) or differences in tree architecture or morphological and physiological plasticity (FERNÁNDEZ et al., 2011; GARCÍA, 2014).

When these mechanisms change with tree size in contrasting ways for each genotype, the competition can differ considerably, enhancing differences in total stand productivity. For example, the competitive ability of the dominant trees, i.e. their ability to grow faster and to constrain the growth of surrounding trees, was more pronounced for some genotypes than others. Prior to this study, it was unclear whether a low competitive ability would reduce productivity (e.g., by impeding trees from becoming more dominant and efficient) or increase productivity (e.g., by slowing the increase in stand heterogeneity). The higher competitive ability was found to increase stand productivity, suggesting that a stronger competitive ability of large trees may have had a larger positive effect on stand productivity than any increase in heterogeneity caused by this competitive ability. Differences in environmental heterogeneity and competitive ability may not always be large enough to jeopardize the guide-curve site classification on an operational scale (BURKHART; TOMÉ, 2012), but this study indicates that they may be responsible for different productivities of stands with the same site index.

Even though environmental uniformity was positively correlated with productivity, the interaction with competitive ability may result in situations in which less uniform environments are as productive as more uniform environments. This may occur if the genotype deployed in the less uniform environment has a greater competitive ability than the genotype in the more uniform environment, as also shown by Resende et al. (2016). That is, the positive relationship between environmental uniformity and productivity was modulated by the competitive ability of the genotypes.

In addition, the interaction between environmental uniformity, competitive ability and site index is likely to change with time. As the stand ages, the onset of competition intensifies the effect that environmental heterogeneity had on size differentiation because in addition to the spatial variability in resources, the larger trees now have an advantage related to their larger resource capturing organs (i.e. root system and crown).

The constrained access to resources and the lower efficiency in their use have been identified as a cause for the lower productivity of heterogeneous tree monocultures compared with more uniform stands (BINKLEY et al., 2010; BOURDIER et al., 2016; LUU; BINKLEY; STAPE, 2013; RESENDE et al., 2016; SOARES et al., 2016; STAPE et al., 2010). This study shows that the effect of heterogeneity found in these studies can actually be divided into the effects of environmental heterogeneity and competitive ability. Furthermore, competitive ability can differ between genotypes (RESENDE et al., 2016), between stands of different genetic diversity (Boyden et al. 2008), species composition (BOYDEN; BINKLEY; SENOCK, 2005; FORRESTER et al., 2013) and between stands with different diameter distributions, ages and site quality (FORRESTER; ELMS; BAKER, 2013).

Stand density, in terms of the initial planting spacing significantly influenced the effect that competitive ability had on productivity. In the densest plots, the highest productivity (area above 50 $m^3$/ha/year in Figure 2.2) tended to concentrate in the zone with high competitive ability (below -10 units), whereas in the widest spacing, the high productivity also occurred at low values of competitive ability (greater than -5 units). Stand density has also been found to influence the effects of structural or species diversity in other studies. For example, higher densities have been found to increase heterogeneity in plantations (Aspinwall et al. 2011, Soares et al 2016) and increases in stand density have been found to increase or decrease the positive effects of species interactions on productivity (FORRESTER et al., 2013). Therefore, the management of stand density at planting or by thinning could reduce the effect of structural heterogeneity on productivity.

Genetic material of *Eucalyptus* species available in Brazil and Latin America in general, in the form of elite clones of single genotypes or improved seed sources covers a wide variability of species and hybrids (FLORES et al., 2016). This study shows that prior knowledge and caution are highly recommended when deploying genotypes matching their expected response to environmental characteristics. Different genotype responses, in terms of productivity, in relation to the environment is a recurring topic in the literature and long standing challenge to forest tree breeders (DES MARAIS; HERNANDEZ; JUENGER, 2013; ELIAS et al., 2016; RESENDE et al., 2017). This interaction was shown to play an important role even at the scale of local climate (MARCATTI et al., 2017).

Our results show that a denser spacing was more advantageous when selecting for the best individuals. This is supported by the results of selection accuracy (Table 2.2), i.e., around 10% greater for 6 $m^2$/plant plots. Furthermore, at a density of 6 $m^2$/plant, heritability was higher and genetic response was better than the 10 $m^2$/plant treatment in terms of environmental uniformity and site quality.

The heritabilities ($h^2$) were generally constant (0.90 to 0.92) across the gradient of environmental uniformity for both planting densities. On the other hand, site quality had a greater influence on the estimate of heritability, especially at wider spacings ($h^2$ was as low as 0.65 for mean site quality). At both spacings, the heritability values increased towards the highest and lowest values of site index. This indicates that genetic selection will be more efficient in either poor or very productive sites than in intermediate ones.

Selected genotypes from genetic trials can be deployed to sites other than those where the experiments are located. This is because companies assign some areas for experimental purposes and others for operational scale plantations, which, naturally, share similarity in the environmental characteristics (REZENDE; DE RESENDE; DE ASSIS, 2014). The plantation area assessed in this study includes two somewhat distinct environmental conditions, i.e., regions at higher altitudes (the most productive) and regions in at lower altitudes (less productive) (refer to Table 2.1). These two conditions are typically adopted as breeding zones by the company that installed the experiments of this study, that is, there is a specific breeding program for each of these two zones.

The plateaus in Figure 2.4 represent a maintenance of the genotypes productivity rank in gradually distinct environments. For site quality, the plateaus were observed for extreme sites (poor *vs* very productive sites), but not for intermediate sites. This indicates that a genotype may present similar behavior when deployed in slightly different sites in relation to the site under evaluation. However, the deployment of a genotype in a more distinct site from the testing site is likely to drastically jeopardize its performance (Figure 2.4).

It is worth highlighting that the environmental indices used in this paper are indirect representations of the effects of site quality, competitive ability and local uniformity, and only explain a fraction of such variations. There are likely to be temporal and spatial changes in above and belowground growth responses to competition for different resources (light, water and nutrients), which will also differ between individuals within a stand. Soil-plant-atmosphere studies about the uptake and use of nutrients, water and light by individual trees (BINKLEY et al., 2010; COMERFORD; SMETHURST; ESCAMILLA, 1994; FORRESTER, 2015; KIM; BULLOCK; STAPE, 2015; SMETHURST; COMERFORD, 1993) are likely to be an important next step to develop a process-based understanding of stand heterogeneity effects. Similarly, genetic interactions with above- and below-ground factors also vary temporally and spatially. The complexity of the G × E interaction has been the focus of other studies i.e. Binkley et al. (2017), which investigated the G × E interaction of a collection of genotypes and showed a large inter- and intra-genotype variability in productivity across Brazil and Uruguay. The G × E interaction has also been observed at finer scales in a restricted Brazilian area of approximately 7300 km² (Marcatti et al., 2017). In this sense, joint efforts to isolate and understand the factors that cause the G × E interaction are quite important, and will contribute to the understanding of the complex interactions that culminate in the phenotypic variations of a given genotype in different environments.

## 2.5. Conclusions

Productivity was most strongly influenced by site quality (MAI range of about 30 $m^3$ $ha^{-1}$ $year^{-1}$), moderately by environmental uniformity (MAI range of about 20 $m^3$ $ha^{-1}$ $year^{-1}$), and to a lesser extent by competitive ability (MAI range of about 10 $m^3$ $ha^{-1}$ $year^{-1}$). All of these variables also interacted to influence productivity and the phenotypic plasticity.

The highest genetic variability in growth response was found for site quality, so careful genotype selection at the highest and lowest quality sites is probably particularly important in order to maintain stable genotypes in terms of growth rank. In addition, densely spaced plots ($6m^2$/plant) promoted greater genetic differentiation than widely spaced plots (10 $m^2$/plant).

Due to the interaction between environmental heterogeneity and competitive ability, a more aggressive genotype in a heterogeneous environment may achieve productivities similar to less aggressive genotypes in more uniform environments.

Despite the great advancements in tree breeding and clonal silviculture, it is still possible to increase the productivity of *Eucalyptus spp.* stands with a more accurate selection of genotypes, while taking into account the site quality, the effect of environmental heterogeneity and the competitive ability of the genotype.

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**Table 2.1.** Information on the experiments and growth conditions.

| **Test Code** | | **ECT01B** | **ECT05** | **ECT06** | **ECT7A1** | **ECT7A2** | **ECT01A** | **ECT02** | **ECT04** |
|---|---|---|---|---|---|---|---|---|---|
| Location | | SAB | BO | BO | COC | COC | BO | BO | SAB |
| Planting Spacing ($m^2$/plant) | | 3 × 2 (6) | 3 × 2 (6) | 3 × 2 (6) | 3 × 2 (6) | 3 × 2 (6) | 3 × 3.33 (10) | 3 × 3.33 (10) | 3 × 3.33 (10) |
| Age Measurement | 1th | 2.92 | 3.02 | 2.91 | 2.95 | 2.95 | 3.00 | 3.10 | 3.02 |
| | 2th | 6.00 | 5.92 | 6.00 | 6.15 | 6.15 | 5.88 | 6.02 | 6.01 |
| Mortality Rate (%) | | 3.12 | 3.93 | 3.23 | 4.58 | 3.39 | 24.09 | 4.37 | 4.3 |
| Soil order | | Acric Red Oxisol | Dystrophic Red Oxisol | Dystrophic Yellow-Red Oxisol | Acric Yellow Oxisol | Acric Yellow Oxisol | Dystrophic Fluvisol | Dystrophic Fluvisol | Dystrophic Yellow-Red Oxisol + Dystrophic Red Oxisol |
| Number of clones | | 6 | 20 | 10 | 10 | 8 | 8 | 28 | 12 |
| Average of PAI and MAI ($m^3$/ha/yr) | 0-3yr | 53.03 | 33.76 | 44.76 | 34.88 | 37.99 | 22.76 | 32.09 | 38.95 |
| | 3-6yr | 64.83 | 28.92 | 36.46 | 56.05 | 47.12 | 32.63 | 40.18 | 55.24 |
| | 0-6yr | 58.82 | 30.99 | 40.14 | 45.72 | 42.63 | 29.30 | 36.07 | 46.89 |
| Annual Mean Temp. (°C) | | 19.8 | 23.8 | 23.6 | 20.9 | 21.1 | 23.7 | 23.8 | 19.7 |
| Annual Preciptation (mm) | | 1506 | 1156 | 1161 | 1386 | 1389 | 1158 | 1144 | 1487 |
| Altitude (m ASL) | | 778 | 256 | 255 | 726 | 692 | 274 | 247 | 884 |

**ECT**: Expanded clonal test; **Location**: BO = Belo Oriente, SAB = Sabinópolis, COC = Barão de Cocais; m ASL = meters above sea level.

**Table 2.2.** Overall mean and clonal sharing between planting spacing conditions, and random regression model coefficients of Environmental Uniformity and Site Index accounting for both planting spacing conditions.

| | | 6 $m^2$/plant | 10 $m^2$/plant | Joint |
|---|---|---|---|---|
| MAI ± sd | | 40.20<br>±11.58 | 36.92<br>±10.34 | 38.66<br>±11.12 |
| Clones | Total | 44 (81.5%) | 39 (72.2%) | 54 (100%) |
| | Shared | 29 (65.9%) | 29 (74.4%) | |

| Stand feature | Plant Spacing | Fixed effect$^*$ | $Var(\beta_0)$ ±se | $Var(\beta_1)$ ±se | $Cov(\beta_0, \beta_1)$ ±se | $\sigma^2$ ±se |
|---|---|---|---|---|---|---|
| Env. Uniformity | 6 $m^2$/plant | 0.0231 | 148.58<br>±35.00 | 56.91<br>±34.81 | 0.12<br>±29.08 | 17.08<br>±2.51 |
| | 10 $m^2$/plant | <0.001 | 76.75<br>±22.46 | 58.65<br>±34.75 | 6.29<br>±24.54 | 10.30<br>±1.55 |
| Site Quality | 6 $m^2$/plant | <0.001 | 198.81<br>±49.50 | 450.29<br>±169.81 | 210.27<br>±78.66 | 34.94<br>±5.26 |
| | 10 $m^2$/plant | <0.001 | 60.91<br>±20.22 | 677.63<br>±247.19 | −18.48<br>±56.55 | 21.24<br>±3.29 |

$^*$*p*-values of Wald test; sd: standard deviation; se: standard error; $\sigma^2$: model error variance. Environmental Uniformity was measured by means of residual spatial autocorrelation over each experimental plot. Site Quality was measured by means of the dominant tree heights within plots.

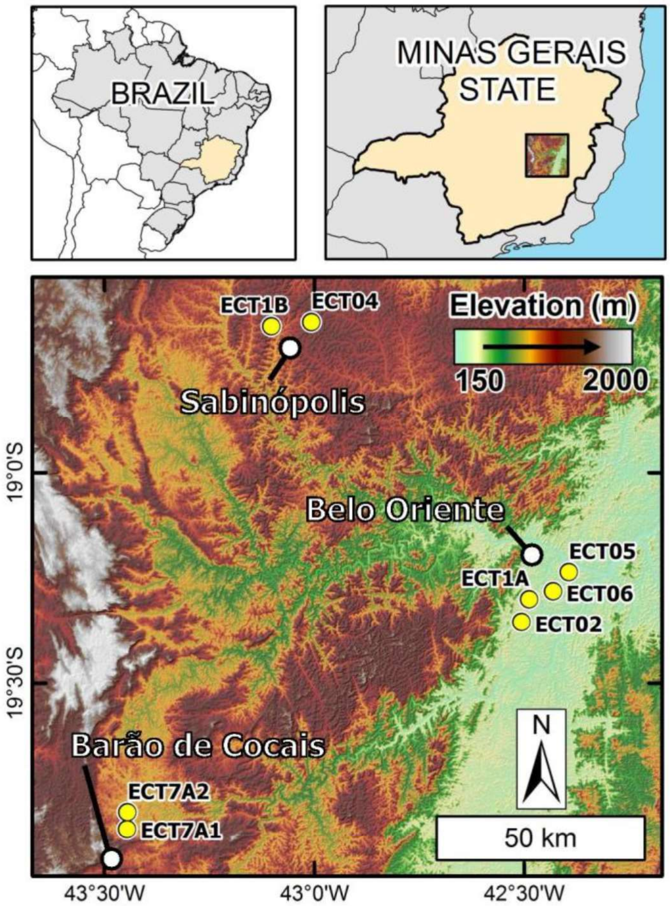

**Figure 2.1.** Map of the site locations within Minas Gerais state of Brazil. The yellow points describe the location of the 8 clonal tests evaluated. The municipalities of Sabinópolis, Belo Oriente and Barão de Cocais are also displayed (white points).

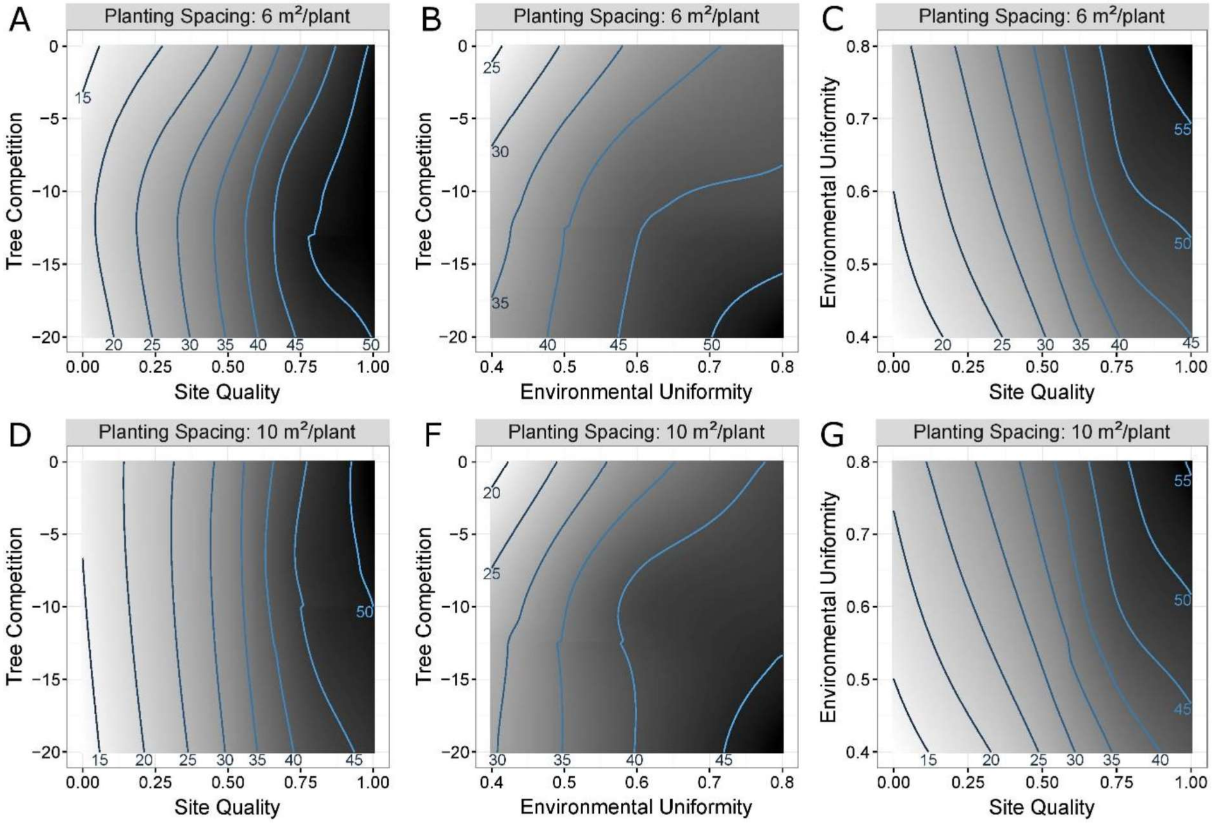

**Figure 2.2.** Relationship between stand productivity (MAI, measured in wood m³/ha/year), competitive ability (% reduction in MAI due to competition from neighbors), environmental uniformity (residual autocorrelation coefficient) and site index (based on stand dominant height) at two initial tree densities. The blue level curves refer to the MAI as affected by the variables on the two axes, presented as: (A) and (B) for the effect of tree competitive ability and site index; (C) and (D) for tree competitive ability and site uniformity; (D) and (E) for environmental uniformity and site index. Plots in the upper row (A to C) correspond to a density of 6 m²/plant and the plots in the lower row refer to the density of 10 m²/plant.

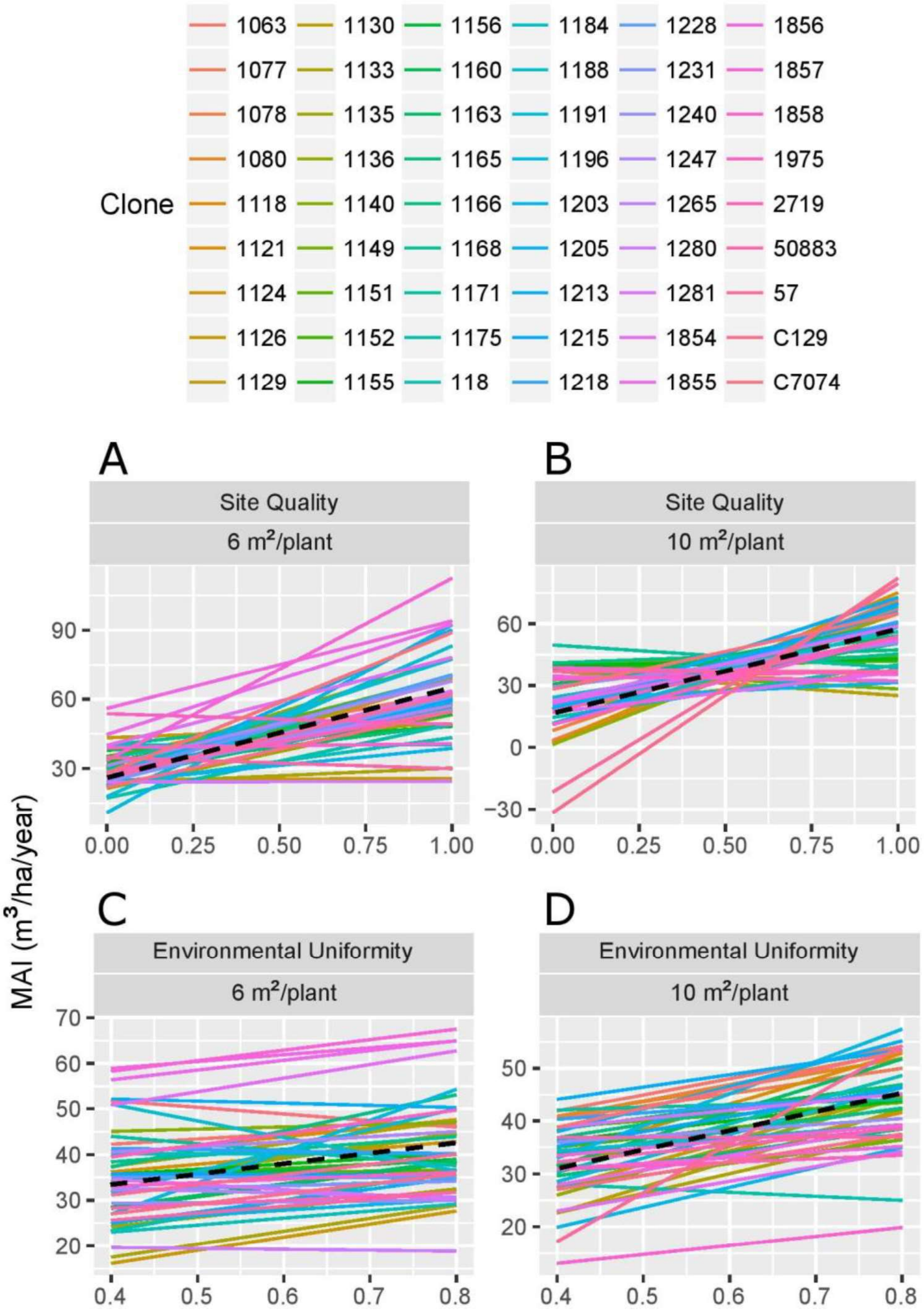

**Figure 2.3.** Reaction norm for the 54 random regression slopes (β0, β1) of genotypes (clones) over the stand productivity components: site quality (based on dominant height of stand) and environmental uniformity (residual autocorrelation coefficient). Clones are identified by the colored lines.

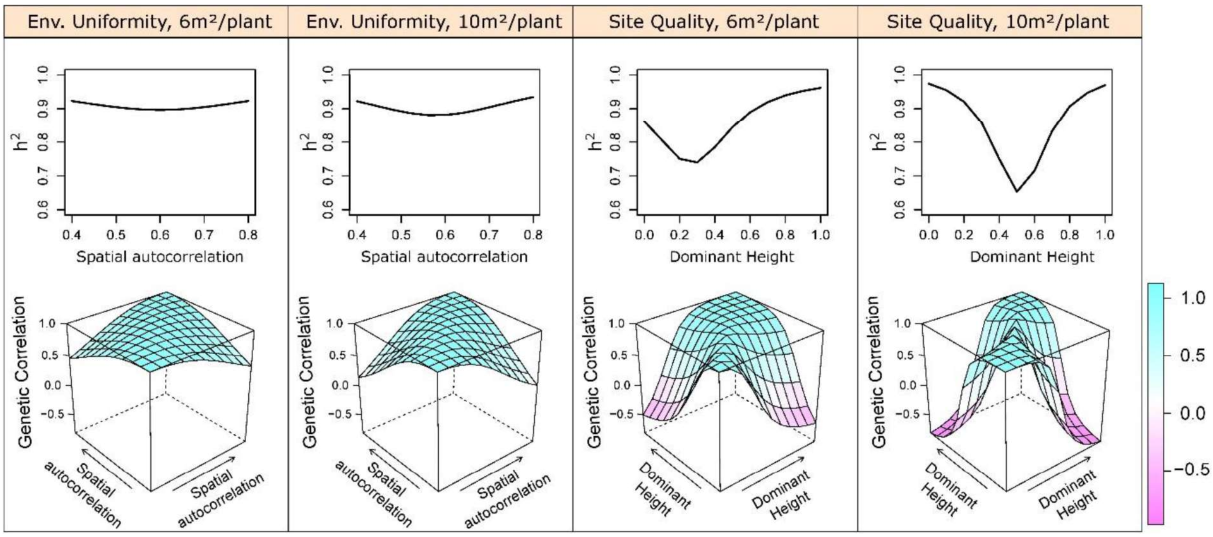

**Figure 2.4.** Top bivariate charts: Relationship between heritability and the environmental conditions (environmental uniformity and site quality). Bottom surface charts: genetic correlation against environmental uniformity and site quality. The genetic correlation charts represent the clonal rank change across the different environment conditions, i.e., the greater the distance from the unit, the greater the Genotype by Environment (G × E) interaction.

**CHAPTER III.** GIS-based approach applied to optimizing recommendations of Eucalyptus genotypes.

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## Abstract

The study of the genotype × environment interaction is a prominent issue, requiring care for recommending improved superior genotypes to certain areas. Experimentally, it is possible to infer that the puzzle of genotype recommendations relies on edaphic and climatic changes over different terrain latitudes and longitudes, and further fluctuates in microenvironments as a result of site variations. Different gene expression is activated or suppressed in accordance with environmental requirements, resulting in phenotypic plasticity of cultivars. The goal of this study was to generate an optimal recommendation of eucalyptus genotypes in a 6846.0 $km^2$ using climatic and geographical information. For this purpose, we used 24 clones unevenly distributed in 988 plots over the area, with planting ages between 2.5 and 6.5 years. The evaluated trait was production, measured in cubic meters of wood per hectare. Our study area typically has a mid-to-high altitude range (0-390 m), rainfall between 599-1749 mm, temperature from 22 to 25 °C, and a series of other bioclimatic variables. For statistical analysis, we used the random regression via mixed-effects models (REML/BLUP) combined with logistic growth models. Among the total number of clones, six proved to be the most suitable to maximize volumetric production in the work area. In addition, a change in the recommendation was verified for clones between 2.5 to 6.5 years of age. This study presents an alternate concept of environmental stratification, which to date has been made categorically by evaluating a number of locations. Our study proposes a way to perform quantitative stratum over an entire area, according to the environmental gradient. The optimal selection of genotypes promotes increased wood production without necessarily increasing the planting area, which is extremely desirable because land is a resource that is becoming increasingly scarce. Furthermore, eucalyptus productivity represents an important part of the costs and revenues of the forest enterprise, such that minimal improvements can significantly affect profit margins. The proposed method is easily adapted for use for other crops and domestic animal production.

**Keywords:** Breeding; Non-linear Mixed Model; Climatic Variables; Growth Curve; Reaction Norm; Adaptability; Stability; Resilience.

## 3.1. Introduction

Plant breeding has been conducted through many ages, from Mendel and Fisher up to the current application of molecular markers in the selection of the most reliable genotypes (BRADSHAW, 2016). Nonetheless, the study of the genotype × environment interaction (G × E) is a prominent issue with respect to improved materials recommendations (BRAWNER et al., 2013; OGUT et al., 2014). It is possible to infer that the decision regarding the indication of genotypes can vary because of the macro-environmental, edaphic, and climatic changes over different latitudes, longitudes, and times (BOURRET et al., 2015; GRAY et al., 2016) and can vary further with respect to micro-environmental changes at a particular site (RESENDE et al., 2016; SOARES et al., 2016). Different gene expressions are activated or suppressed in accordance with the environmental requirements, resulting in phenotypic plasticity to cultivars (EL-SODA et al., 2014). This phenomenon is pivotal to governing the G × E interaction. Thus, especially when dealing with traits with mid-to-low heritability, such as the productivity of *Eucalyptus* sp. (CASTRO et al., 2016), the environmental interference is even more problematic in the trait expression (LYNCH; WALSH, 1998) and requires carefully detailed recommendations according to changes in the environmental profile (OGUT et al., 2014; TAÏBI et al., 2015).

Certain genotypes are more stable in different environments. In most cases, these genetic materials are selected because they do not present unwanted yield surprises, being more resilient to local climate change (EBERHART; RUSSELL, 1966; NUNES et al., 2002). Moreover, some genotypes are more adaptive, responding positively to improvements in environmental growth conditions (BRAWNER et al., 2014; SANTOS et al., 2015). The recommendation of cultivars for different environments is effective when the cultivar contains certain alleles that are compatible to the site growth response, in other words, genotypes that can maximize the conversion of the available resources to biomass or productivity (EL-SODA et al., 2014).

Eucalyptus is a culture of great economic importance in Brazil. For this reason, many researchers and companies investing in research are seeking to better understand the environmental factors that increase its productivity. The country has continental proportions. It is estimated that there are currently 5.1 million hectares of eucalyptus plantations distributed throughout Brazil (ABRAF, 2014). It is known that gender responds in a very peculiar way to environmental changes. Several studies (DA SILVA et al., 2016; RYAN et al., 2010; STAPE et al., 2010; STAPE; BINKLEY; RYAN, 2004) have demonstrated productivity gains according to the availability of light, water, and nutrients in southeast and northeast Brazil. Almeida et al. (2010) and Calegario et al. (2005) mapped eucalyptus productivity according to spatial and temporal variations and recommend the practice of genetic selection to increase productivity. In this sense, Pérez-Cruzado et al. (2011) performed productivity prediction of *E. nitens* using a similar methodology to previous authors. Although the aforementioned authors address the use of different genetic material, there are no studies in the literature that examine, at a breeding level, a clonal recommendation according to continuous environmental change in the area.

Commonly environmental variables are assigned as discrete phenomena, generating groups with similar environmental features – called the stratum – such that environments are treated as categorical variable levels (BURDON, 1977). In a geographic information system (GIS), the environmental information may be represented by a *raster*, a continuous spatial variable (LI; ZHU; GOLD, 2004). Considering the environment categorically means losing the ability to diagnose smooth and gradual changes of the environment. Thus, GIS can be considered a useful tool in edaphic and climatic characterization of region, allowing the recommendation of genotypes to areas with environmental features similar to those in which certain genotypes performed well.

The number of planted clones is also something broadly discussed in the forestry sector (IVETIĆ et al., 2016; ROBERDS; BISHIR, 1997). The recommendation of a few genotypes (e.g., the most stable ones) becomes attractive from an economic point of view because of a reduction of productivity losses risks and nursery costs (REZENDE; DE RESENDE; DE ASSIS, 2014). However, to maintain genetic variability and to prevent unmanageable disease incidence problems (CASTRO et al., 2016), a suitable number of clones should be maintained and planted recurrently.

In animal and plant science, is quite common to use mixed-effects regression and reaction norms for studies of biological behavior and ecological interactions (CALEGARIO et al., 2005; NOTHDURFT; KUBLIN; LAPPI, 2006). This method also has several applications in breeding and G × E studies (PÉREZ-RODRÍGUEZ et al., 2015; RAIDAN et al., 2015; VAN DE POL, 2012). The mixed effects regression is typical for calculating regression coefficients for each random effect, such as genotypes in genetic selection studies (RESENDE, 2007).

In this context, the aim of this study was to propose a method to optimize genotype recommendations in accordance with environmental gradients, and thus determine the optimal number of eucalyptus clones that will maximize the productivity of the available area.

## 3.2. Material and Methods

### 3.2.1. Data and work area description

We used continuous forest inventory data from forest stands of eucalyptus clones, including 988 plots, that had been measured four or five times (4197 observations in total). In addition to the variables commonly derived from inventories (such as age, height, dominant height, and volume), genotype provenance (total of 24 clones distributed unevenly throughout the work area) and geographical location (coordinates X, Y on Figure 3.1) were also noted for each plot. The classical site index (i.e., based on the dominant height of the stand) was computed for validation of the proposed environmental index (based on climatic variables). Climatic information was obtained using the WorldClim dataset (HIJMANS et al., 2005), which includes 19 bioclimatic variables (see Table 3.1). Bioclimatic variables represent annual trends, seasonality, and extreme and limiting environmental factors, such as precipitation during the driest quarter. This database is available in *raster* format, with a spatial resolution of approximately 0.9 km², and corresponds to a historical series from 1950 to 2000. These variables are derived from monthly values of temperature and precipitation. The study area consisted of 8132 pixels, distributed in 76 lines and 107 columns.

The area was delimited from a rectangular buffer extending 5 km beyond the geographic extent of the spatial feature points (the location of inventory plots), covering 19 municipalities in the northeastern Bahia state of Brazil (Fig. 1). The region is characterized by high variation in precipitation, with high rainfall near the coast (bathed by the Atlantic Ocean) that gradually decreases further inland. Similar behavior is observed for the temperature, but the decrease is more related to increasing elevation.

### 3.2.2. Methodology

#### *3.2.2.1. Step 1: Environmental Index (EI)*

The first step of the methodology is to obtain variables representing the environmental gradient of the study area. In order to summarize the climatic variables, while maintaining simplicity of interpretation and developing parsimonious models, we created a single environmental indicator called the environmental index (EI). There are several statistical methods for generating indices (JOHNSON; WICHERN, 2014; SKOVSGAARD; VANCLAY, 2008). In this study, the index was created using the principal components analysis procedure (PCA).

The EI must represent the productive capacity of the site. In forest science, there are two basic approaches to express productive capacity through local indexes: (1) Plant-based, that is based on the development of the plant itself (usually dominant stand height at a reference age) and (2) earth-based, based on site characteristics such as topography, climate, and soils (SKOVSGAARD; VANCLAY, 2008).

The EI used was derived only from climatic variables (earth-based type), specifically the 19 bioclimatic variables obtained from WorldClim, is represented as *raster* data, with a length, pixel size, and alignment equal to the bioclimatic variables. The application of PCA was performed using the *prcomp* function of the package R *stats* (TEAM R, 2015). The EI was the first component (PCA1) normalized to values between 0 and 1 (Eq. [1]) (Figure 3.2 - Step 1). To assess the quality of the EI, we evaluated its correlation with the decision variable (i.e., the stand volume). In the case of forest species, we also evaluated the correlation between EI and the site index (derived from the dominant height of the stand).

$$EI = \frac{\mathrm{PCA1} - \mathrm{PCA1}_{\mathrm{min}}}{\mathrm{PCA1}_{\mathrm{max}} - \mathrm{PCA1}_{\mathrm{min}}}, \tag{1}$$

where, $EI$ is the environmental index after the normalization of the first principal component (PCA1); $\mathrm{PCA1}_{\mathrm{min}}$ is the minimum value of PCA1, and $\mathrm{PCA1}_{\mathrm{max}}$ is its maximum value.

### *3.2.2.2. Step 2: Model*

The prediction model volume was constructed based on mixed-effects models, a modeling strategy that enables the coefficients to change according to the level of interest, such as genotype level for the present study. After testing some types of models with linear and nonlinear functions (results not shown), the logistic nonlinear model of Eq. [2] presented the best fit, with parameterization by Pinheiro and Bates (2006).

$$VOL = \frac{a_1}{\left[1+e^{(a_2 - Age)/a_3}\right]} + \varepsilon, \tag{2}$$

where, $VOL$ is stand volume (m³/ha), $Age$ is in years; $\alpha_1$, $\alpha_2$ and $\alpha_3$ are model coefficients; and $\varepsilon$ is the residual. The non-linear mixed effects model considering the volumetric production is presented in Eqs. [3], [4], and both are combined in Eq. [5] (NOTHDURFT; KUBLIN; LAPPI, 2006). This model is intended to represent the relationship between the production volume of the response and the covariates of age and the environmental index (EI) for the $i^{\text{th}}$ clone in the $j^{\text{th}}$ observation on time and $k^{\text{th}}$ model coefficient.

$$a_{ijk} = X_{ij}\boldsymbol{\beta} + Z_{ij}\boldsymbol{g}_i, \tag{3}$$

where, $\boldsymbol{\beta}$ corresponds to the fixed effect (i.e., overall average); $\boldsymbol{g}_i$ is the random effects vector of genotypes, with the covariance structure $\boldsymbol{g} \sim N(0, \boldsymbol{I}\sigma_g^2)$, associated with the $i^{\text{th}}$ clone; and $X_{ij}$ and $Z_{ij}$ are the incidence matrices of fixed and random effects, respectively. Thus, the clones were assumed to be nonrelated genotypes. In basic assumptions, the error is independently distributed with a mean of zero and a variance of $\sigma^2$ independent of the random effects.

The model of Eq. [4] represents an expansion of the model of Eq. [2], which allows the estimation of stand volume depending on the age and EI. The EI and its corresponding coefficient $\alpha_4$, were associated with the model through a sum to the asymptotic coefficient $\alpha_1$. A more detailed description of physical/biological interpretability of these four parameters can be followed in the discussion topic.

$$y_{ij} = \frac{\alpha_{1i}+\alpha_{4i}\,EI}{\left[1+e^{(\alpha_{2i}-Age)/\alpha_{3i}}\right]} + \varepsilon_{ij}, \qquad [4]$$

where, $y_{ij}$ is the volumetric production (m³/ha) of the $i$th clone in time $j = \{1, \dots, n_i\}$ (CALEGARIO et al., 2005); $\varepsilon_{ij}$ is the random error of the logistic model; EI is the covariate of environmental index, and Age is a covariate in years.

$$\boldsymbol{\alpha}_i = \begin{bmatrix} \alpha_{1i} \\ \alpha_{2i} \\ \alpha_{3i} \\ \alpha_{4i} \end{bmatrix} = \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \\ \beta_4 \end{bmatrix} + \begin{bmatrix} g_{1i} \\ g_{2i} \\ g_{3i} \\ g_{4i} \end{bmatrix} = \boldsymbol{\beta} + \boldsymbol{g}_i, \qquad [5]$$

Eqs. [4] and [5] are combined in Eq. [6], as follows:

$$y_{ij} = \frac{(\beta_1+g_{1i})+[(\beta_4+g_{4i})\,EI]}{\left[1+e^{\frac{(\beta_2+g_{2i}-Age)}{\beta_3+g_{3i}}}\right]} + \varepsilon_{ij}, \qquad [6]$$

with corresponding terms of Eq. [3]:

$$\boldsymbol{\beta}_k = (X_{ij}\beta)_k;$$
$$\boldsymbol{g}_i = (Z_{ij}g)_i;$$
$$\boldsymbol{g} \sim \mathrm{N}(0, \boldsymbol{I}\sigma_g^2);$$
$$\varepsilon_{ij} \sim \mathrm{N}(0, \sigma^2),$$

wherein, $\boldsymbol{\beta}$ is a fixed effect as described above; and $g_{ki}$, where $k = \{1, \dots, 4\}$, is the random effect of the $i$th genotype associated with the $k$th behavioral coefficient.

We constructed and evaluated three models: (i) non-linear logistic model with only fixed effects, i.e., volume according to age [$VOL = f(Age)$]; (ii) non-linear logistic model adopting the random effect of genotypes [$VOL = f(Age, G)$]; and (iii) adjustment of the non-linear logistic model adopting the random effect of genotypes and including the covariate environmental index [$VOL = f(Age, G, EI)$]. This evaluation is important because the methodology is based on the hypothesis that there is difference among genotypes in production volume and that the local quality (environmental index) affects the volume of production. These hypotheses were tested using the maximum likelihood ratio test (LRT). The models were also evaluated using quality indicators, such as a scatterplot of observed and predicted values, residual histograms, and quality statistics (AIC – Akaike Information Criterion, RMSE – Root Mean Square Error, $R^2$ – Coefficient of Determination).

For the adjustment of the models, we used tabular data from the forest inventory; specifically for $VOL = f(Age, G, EI)$, an additional field was generated in the corresponding data to the EI. The field was created as follows: (1) converting the tabular data in a spatial feature vector of point-type using the coordinates (X, Y) as spatial information; (2) extraction of the EI information (stored in raster format) corresponding to each plot using the feature points as a reference; and (3) finally, the conversion was carried out by assigning table spatial feature points (with the already included EI) to the tabular data. The adjustment was made using the *lme* function (Nonlinear Mixed-Effects Models) of the *nlme* R package (PINHEIRO et al., 2016) (Figure 3.2 - Step 2).

#### *3.2.2.3. Step 3: Production prediction and optimum genotypes recommendation*

The prediction of the production was performed only for the selected model [$VOL = f(Age, G, EI)$]. The model was applied for all combinations of the following variables: Genotypes ranging from 1 to 24 (total: 24); fixed ages of 2.5, 3.5, 4.5, 5.5, and 6.5 (total: 5); EI (total: 1), generating a total of 120 prediction scenarios. All prediction scenarios were represented as *raster* data, with extensions, pixel sizes, and alignments equal to the EI. An optimum recommendation was determined for each age (2.5, ..., 6.5), and was made as follows: all genotype prediction *rasters* were overlaid, and the surface genotype (i.e., which are responsible for higher production in each pixel) was the elected clone for the particular region (Figure 3.2 - Step 3). In this study, the procedures for predicting production and recommendation were automated using basic functions of the software R (TEAM R, 2015). Consistency was evaluated by the accuracy of selection ($h$) (RESENDE, 2007).

## 3.3. Results

### 3.3.1. Environment Index (EI)

The first three principal components explained about 95% (72% for the PCA1, 19% for the PCA2, and 4% for PCA3) of the variation in climatic data. PCA1, responsible for explaining of the major fraction of total variance, was attributed to the environmental index (EI) after normalization from 0-1 (Figure 3.3A). Three aspects were considered for this decision: (1) to explain the dominance of PCA1 in relation to other components; (2) a high and significant correlation (with p-value <0.001) between PCA1 and the site index (SI) (0.7742 – Figure 3.3B) and the stand volume (0.7088 – Figure 3.3C). The same correlation levels were not found for the other components (volume correlations with PCA2 and PCA3 were equal to -0.1336, -0.0416 respectively); and (3) the relationship between SI and EI was approximately linear (Figure 3.3B). Furthermore, the relationship between volume and EI was slightly exponential (Figure 3.3C). Relationships in (3) were found using a local regression adjustment (LOESS).

Because the association between volume and EI is positive, we can infer that as the EI value increases, the local quality also increases (i.e., values closer to 1 indicate better environmental conditions for eucalyptus productivity). Thus, the EI can also be interpreted as a site quality measure. However, for purposes of nomenclature simplification, environmental index (EI) is maintained throughout the manuscript.

### 3.3.2. Longitudinal and geo-modeling

The non-linear model adopting the random effect on genotypes [$VOL = f(Age, G)$] was more likely than that composed only of fixed effects [$VOL = f(Age)$], as determined by the LRT (p-value <0.001); the test indicates a significant effect of genotype on the production volume. Among the three evaluated models, the $VOL = f(Age, G, EI)$ was chosen for recommending genotypes because of its predictive properties. These properties were investigated using the scatter plot between observed and predicted values, the residual histogram, and fit quality statistics (Figure 3.4). In addition, the LRT between the two models was significant (p-value <0.001), indicating that the model $VOL = f(Age, G, EI)$ was most likely related to its competitor model. In addition, the results also indicate that an environmental effect on the production volume actually exists in the study area.

The reaction norms of each model were also generated. They indicate the phenotypic responses of each genotype to environmental variations. The model $VOL = f(Age)$ shows the relationship of age to volume production, and the model $VOL = f\ (Age, G)$ is useful for evaluating the effect of age on the volume of each genotype production (Figure 3.5B). The model $VOL = f\ (Age, G, EI)$, besides age (Figure 3.5C), also allows the evaluation of environmental effect with respect to volume production (Figure 3.5D).

### 3.3.3. Production prediction and optimum genotype recommendation

Figure 3.6 shows the recommendation of genotypes for ages 2.5, 3.5, 4.5, 5.5, and 6.5 for each location (represented by pixel) of the study area. The trait heritability of productivity (measured as m³/ha/year) was equal to 0.38 ± 0.03. The predicted genetic values (PGV) varied between 24.74 ± 1.44 and 42.41 ± 1.64 for clones **21** and **22**, respectively (Table 3.2). Even with the unevenness in the distribution of clones throughout the study area (Figure 3.1) and different numbers of plots and measurements for each clone, all genotypes showed high predictive accuracy values ($h$), varying between 0.85 and 0.98 – to reference values see Resende (2007). The clone with $h$ = 0.85 is **16**, which shows only one plot and 5 measurements over time.

The prediction of stand volume production (Figure 3.7) was presented for each genotype (**1**, **3**, **7**, **13**, **17**, **22**) that was featured on the recommendation map (Figure 3.6). The prediction of an ideal scenario (optimum) was also computed, that is, implantation of the indicated genotypes for each specific location (pixel) of the study area.

## 3.4. Discussion

### 3.4.1. The environmental index can explain the volume production of clones

Out of the two main approaches employed in the forestry sector for generating local indices (earth-based and plant-based), with some exceptions, the plant-based is the most widely used (SKOVSGAARD; VANCLAY, 2008). The indices generated can be used as inputs for growth and yield models in land classification procedures and the generation of strata (CAMPOS; LEITE, 2006). The main feature of this approach is that it uses the plant's own development information (usually dominant height) to infer the site quality and is considered a direct method of index generation (SKOVSGAARD; VANCLAY, 2008). Despite the use advantages, this approach has some limitations that restricts its use as a basis for the methodology presented here, among which include: (1) a need for the existence of the culture in the local area of interest, which would restrict the application of the methodology to sites that already deployed the culture, making it not applicable in areas of plantation expansion, newly acquired land, new potential fomented producers, etc.; (2) in the case of selecting genotypes, the plant-based method can introduce a bias in the generation of the index because sites of similar quality can show growth differences in height due to the genetic influence of genotype (REHFELDT et al., 2014). Given these limitations of the plant-based approach, the earth-based approach was used as base method for generating EI, because it is easily applicable throughout the study area and is able to generate a general index for the entire area.

The earth-based approach is based on local properties, such as climate, topographical, and soil conditions (CORONA; SCOTTI; TARCHIANI, 1998). The EI comprised only climatic factors. Factors related to soil class were not included in the index because of the lack of accurate data for the site. Topographic factors were included at first but later discarded. These reasons for this were many, such as a high correlation with climatic variables, especially temperature (the main case of elevation, which was used as input in the interpolation process of the temperature of WordClim data); a low correlation with stand volume (e.g., aspect and radiation solar potential); and a lack of accuracy due to the digital elevation model limitations (e.g., the terrain slope and topographic index of moisture).

Some issues should be considered for the selection of environmental information that will comprise the environmental index, such as: a previous study or literature review to determine which variables can affect the development of the culture of interest; and the availability of quality data associated with the trait of interest of the intended culture. Moreover, the issue of high correlations among environmental variables is not a limitation; it can be circumvented by using the PCA technique, which transforms the set of environmental observations in uncorrelated vectors (JOHNSON; WICHERN, 2014). Although it comprises only climatic variables, the EI was sufficient to represent the environmental gradient of the area, being governed mainly by the variation in precipitation (correlation between precipitation and EI was equal to 0.96). Several studies have also highlighted the importance of climate variables in the productivity quality of the site in the context of forest species (ANTÓN-FERNÁNDEZ et al., 2016; BRAWNER et al., 2014; JIANG et al., 2014; YUE et al., 2016).

### 3.4.2. Coefficients of genetic behavior over age and environmental gradient

Random effects models are widely used in breeding studies; they allow the coefficients to vary between individuals, which makes it possible to generate predictions and test specific hypotheses for each genotype (PÉREZ-RODRÍGUEZ et al., 2015; RAIDAN et al., 2015; VAN DE POL, 2012). For these reasons, this modeling approach was used as the basis for building the predictive model.

The growth pattern of many species, including eucalyptus, can be described by a sigmoidal model characterized by rapid early growth, tending towards stability over time (asymptotic) (CAMPOS; LEITE, 2006). In this study we used the sigmoid logistic model parameterization presented in Pinheiro and Bates (2006). The logistic model belongs to the class of non-linear models. Although it is more complex and more difficult to adjust (more computationally intensive) and requires an approximate procedure for estimating coefficients, this model has the noteworthy advantage of being biologically consistent (SCHOOLFIELD; SHARPE; MAGNUSON, 1981). Adopting a linear model would be unwise because they do not ensure the consideration of the development of forest species characteristics, such as asymptotic and monotonic growth (PINHEIRO; BATES, 2006).

Another advantage of using a logistic model (Eq. (2); Figure 3.5A and 3.5B) is that each of the coefficients has a physical/biological interpretation: $\alpha_1$ is the horizontal asymptote, the volume value when age extends to infinity, and represents the theoretical maximum amount (Maximum Volume - MV); $\alpha_2$ is the age at which the stand reaches half the theoretical maximum amount ($\alpha_1/2$) and represents the inflection point of the curve, also known as half-life (HL); $\alpha_3$ is the elapsed time between the half-life ($\alpha_1/2$) and approximately 3/4 of the theoretical maximum volume ($3/4\alpha_1$) and can be interpreted as the inverse of the growth rate (Inverse Growth Rate - IGR), for which a lower value means that the population reaches the theoretical maximum volume ($\alpha_1$) faster.

The logistic model adjusted for the inclusion of EI also presents the possibility of interpreting the coefficients (Eq. (4); Figure 3.5C e 3.5D). The coefficients $\alpha_2$ and $\alpha_3$ (Table 3.2) have the same physical/biological interpretation as Eq. (2), while the $\alpha_1$ represents the theoretical maximum only in situations where EI is zero, in other words worst ambient conditions for favorable development. In the model of Eq. (4), $\alpha_1$ can be interpreted as a measure of resistance or tolerance, such that a higher the $\alpha_1$ value means the individual (i.e., genotype) is hindered by unfavorable environmental conditions. Thus, individuals with higher $\alpha_1$ are the best for volume production in less favorable environments. The coefficient $\alpha_1$ was called endurance (EN). The coefficient $\alpha_4$ indicates the gain in individual volume (genotype) as EI increases. The higher the coefficient $\alpha_4$, the more the individual is favored by environmental improvement and the possibility of being one of the best in the more favorable environments increases. Genotypes with larger $\alpha_4$ values tend to be more specialized, i.e., exhibit far superior performance in favorable sites than in unfavorable environments. The coefficient $\alpha_4$ was called specificity (SP). Table 3.2 presents the coefficients EN, HL, IGR, and SP for each one of the 24 evaluated genotypes.

The ideal scenario for any breeding program would generate a genotype with high values of EN and SP, for instance, a genotype that presents the best performance in the harshest environments and has a positive response to the improvement of the environment. But this scenario is overly optimistic; in practice a genotype is rarely the best in both situations. Usually, the best genotypes are site specific, which reinforces the importance of a better system of genotype recommendation (OGUT et al., 2014). In general, genotypes with higher SP values are indicated for more favorable environments, such as clone **22**, which had the second highest value of SP (567.75) and was recommended for the entire coastal region (Figure 3.6), which is the region considered more favorable for production volume according to the EI (Figure 3.3). Moreover, genotypes with higher values of EN are indicated for less favorable environments. Clone **17** showed an EN value of 197.69 (the higher of all) and was recommended for the entire farther region from the coast (Figure 3.6), which is the least favorable region (Figure 3.3). Some genotypes have very low values of EN, or even negative values, which means that these genotypes tend to have very poor performance in the harshest environments. In order to draw this conclusion, however, this genotype should be examined in more representative samples in the worst environmental conditions.

Interestingly, with the inclusion of EI in the model, the age effect on production was minimized. This can be seen by the lower spread of age reactions in volume production in Figures 3.5B and 3.5C. The environment reaction norm is characterized by complex interactions (YUE et al., 2016), i.e., changing the ranking of best genotypes according to the change in environment. This suggests that no genotype is sovereign in all sites. In fact, in practice, it tends to occur in the opposite manner (justified by the high negative correlation between EN and SP equal to -0.90). There are also those genotypes with intermediate behavior, which have satisfactory production in all environments along the gradient; these are the more stable genotypes (Eberhart and Russell, 1966).

### 3.4.3. Maximizing productivity through optimum genotypes allocation on area

Genotype recommendations should be based on the culture information (usually production) near the rotation age. In the case of eucalyptus in Brazil, this is somewhere around 5 to 7 years (REZENDE; DE RESENDE; DE ASSIS, 2014). However, for greater reliability in the decision, it is interesting to evaluate production over time, since the timber can be used for various purposes when harvested in early or late stages (CASTRO et al., 2016). From 4.5 years on there was no drastic change in the clonal recommendation, only minor local changes in stratum border regions. Basically we stratified three distinct regions of recommendation: coastal region (high growth quality); more distant coastal regions towards the interior of the continent (low growth quality); and intermediate region (average growth quality) (Figure 3.6).

Forest enterprises often work with more than one genotype recommendation alternative for the same region. This provides greater security with regard to pest/disease attack and/or other problems not initially known (CASTRO et al., 2016). To risk minimization and ensure the selection of the optimal number of genotypes for a particular location (IVETIĆ et al., 2016; ROBERDS; BISHIR, 1997), this methodology can be easily adapted by simply eliminating the previously selected genotype database and adjusting the prediction model. Consequently, the second genotype most appropriate for the site will be selected. This procedure can also be useful in situations where the selected genotype has low representation in the sampling, i.e., the company does that not use the genotype at many locations yet, and in this case the choice deserves careful attention. The choice of alternative genotypes can progressively continue to select the number of genotypes considered safe for the site (IVETIĆ et al., 2016). Furthermore, this methodology itself tends to select more than one genotype for the total area of deployment immediately, while maximizing productivity at a location; this adds to the number of genetic variability genetic materials. However, the application of few genotypes is also critical because of the loss of genetic accuracy ($h$), so it should also be done carefully (RESENDE, 2007).

The refinement level of the proposed methodology can be increased without necessarily increasing its complexity. The decision variable used in the recommendation was the volume of timber production; it is widely used to derive costs and revenues of the forest enterprise, and is the basis for planning in general, both at an operational and strategic level (FROMBO et al., 2016). Nonetheless, the recommendation may be based on more than one genetic trait. An example is the genotype susceptibility information regarding some stress, such as that caused by drought, frost, pest attack, disease, etc. (GONÇALVES et al., 2013). In this case, a map indicating the locations most likely to experience an event that causes stress would be required, and the recommendation of genotypes for those places should restrict susceptible cones. Furthermore, to increase the level of refinement, a second EI may be generated as well as a second model for new genetic traits of interest. At the end, the recommendation will be based on more than one trait, combined in a multi-criteria analysis procedure, such as a weighted linear combination, so that the decision traits may have different weights (in importance scale) or be combined into a single multivariate model containing traits of economic interest (RESENDE, 2007).

The incorporation of the methodology in a GIS environment presents a number of advantages, meeting the needs of agricultural or forestry industries regarding area productivity information (PÉREZ-CRUZADO et al., 2011; YUE et al., 2016). Another aspect is the possibility of working with different levels of detail (chose of pixel size) (LI; ZHU; GOLD, 2004). In the present study, the pixel size was 0.9 km², limited only by the weather database WorldClim, which was used to generate the EI. However, the methodology could be applied to finer databases with pixel sizes in metric units and even sub metrics. The limitation would be the database used to generate the indexes. Regarding the disadvantages, we note the increasing complexity to generate the recommendation models; for example, for large pixel areas and reduced sizes, the processing time can be high. However, it has to be pointed out that there is a general trend in all sectors of society to spatialize data and information. The spatial component forms part of the new conception of information and is important for making decisions (MIGHTY, 2015).

Competition in the agricultural and forestry sectors is increasingly fierce, resulting in reduced profit margins, forcing companies to embark on a continuous search for process improvement and increased efficiency (FROMBO et al., 2016). Any improvement in forest yield is attractive, but increased productivity is particularly noteworthy. After all, it has a strong influence on the cash flow of the company and makes it possible to increase production without necessarily increasing the planting area. This is extremely desirable because the land is a scarce resource (GARNETT et al., 2013), especially in these times when the arable land is under pressure from urbanization due to population increase, there is a growing increase in unproductive areas, and there is a gradual reduction of land productivity due to soil degradation (TILMAN et al., 2002).

The progress of genetic breeding generally promotes specialized genotypes, i.e., the creation of genotypes adapted to specific conditions (BRAWNER et al., 2013; IVETIĆ et al., 2016). Therefore, the proposed methodology can be used to increase productivity in agricultural and forestry enterprises; it tries to optimize the recommendation of genotypes in order to select (allocate) indicated genotypes (adjusted) for a specified location.

## 3.5. Conclusions

The incorporation of new methodologies into a GIS environment follows a current trend in science by assigning a geographic location to data and information. It has become increasingly evident that the spatial component is crucial to information context and has consequent importance in result interpreting and decision making. The approach presented here allows the genotypic recommendation to be processed pixel by pixel for a given area and is limited only by the level of detail of the initial database.

In the current context of high competition in the agricultural and forestry enterprises, companies must invest in initiatives that improve the efficiency of their activities. Crop productivity has a significant role in the production process; thus improvements in this operation can directly trigger significant cost reductions. In addition, increased productivity makes possible increase revenue, without necessarily expanding the planting area, which is highly desirable because land is a resource that is becoming increasingly scarce.

Therefore, the proposed methodology can optimize the recommendation of specific and suitable genotypes along an implantation area, contributing to raising the productivity of agricultural and forestry crops. Although our approach has been made to optimize the recommendation of eucalyptus genotypes, it could be easily adapted and used for other forest species, agricultural crops, or domestic animal production.

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**Table 3.1.** Descriptive statistics of the age and growth variables measured in the stands and bioclimatic variables used in the study.

| Variable | Mean | SD* | Min | Max |
|---|---|---|---|---|
| Stand | | | | |
| Stand age (years) | 3.97 | 1.11 | 2.15 | 6.55 |
| Dominant height (m) | 19.88 | 4.37 | 9.76 | 38.06 |
| Index site (m) | 23.46 | 3.96 | 14.00 | 37.80 |
| Stand volume (m³/ha) | 123.88 | 65.19 | 35.56 | 499.98 |
| Bioclimatic | | | | |
| BIO1 (˚C) Annual mean temperature | 23.6 | 0.5 | 22.2 | 24.9 |
| BIO2 (˚C) Mean diurnal range | 8.6 | 0.4 | 7.9 | 9.4 |
| BIO3 Isothermality (BIO2/BIO7) (*100) | 67.2 | 1.0 | 64.0 | 70.0 |
| BIO4 (˚C) Temperature seasonality (the standard deviation of monthly temperature averages) | 147.9 | 3.4 | 133.6 | 157.0 |
| BIO5 (˚C) Max temperature of the warmest month | 30.2 | 0.6 | 28.3 | 31.8 |
| BIO6 (˚C) Min temperature of the coldest month | 17.4 | 0.6 | 16.3 | 19.1 |
| BIO7 (˚C) Annual temperature range (BIO5–BIO6) | 12.7 | 0.4 | 11.8 | 13.8 |
| BIO8 (˚C) Mean temperature of the wettest quarter | 23.3 | 0.6 | 21.3 | 24.6 |
| BIO9 (˚C) Mean temperature of the driest quarter | 23.8 | 1.2 | 21.2 | 26.0 |
| BIO10 (˚C) Mean temperature of the warmest quarter | 25.2 | 0.5 | 23.7 | 26.5 |
| BIO11 (˚C) Mean temperature of the coldest quarter | 21.5 | 0.6 | 20.0 | 22.9 |
| BIO12 (mm) Annual precipitation | 1189.5 | 296.7 | 599.0 | 1749.0 |
| BIO13 (mm) Precipitation of the wettest month | 179.6 | 55.1 | 80.0 | 303.0 |
| BIO14 (mm) Precipitation of the driest month | 51.4 | 12.2 | 21.0 | 70.0 |
| BIO15 Precipitation seasonality (the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation) | 39.4 | 5.2 | 29.0 | 49.0 |
| BIO16 (mm) Precipitation of the wettest quarter | 469.1 | 138.6 | 227.0 | 749.0 |
| BIO17 (mm) Precipitation of the driest quarter | 184.0 | 41.1 | 85.0 | 249.0 |
| BIO18 (mm) Precipitation of the warmest quarter | 239.3 | 36.3 | 183.0 | 322.0 |
| BIO19 (mm) Precipitation of the coldest quarter | 367.5 | 111.6 | 147.0 | 575.0 |

*SD: Standard deviation. The Site Index (SI) is based on stand dominant height

**Table 3.2.** Information on used genotypes/clones and estimated genetic parameters.

| Clone ID | Number of plots | Total measures | Range of values (Amplitude) | | PV (m$^3$/ha/yr) | PGV (m$^3$/ha/yr) | $h$ | Genetic behavior coefficients | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Age (years) | EI | | | | EN ($\alpha_1$) | HL ($\alpha_2$) | IGR ($\alpha_3$) | SP ($\alpha_4$) |
| 1 | 70 | 291 | 2.22 – 6.25 | 0.17 – 0.61 | 32.20 | 33.53 ± 0.39 | 0.98 | 133.46 | 3.24 | 1.86 | 242.32 |
| 2 | 5 | 20 | 2.39 – 5.25 | 0.64 – 0.67 | 45.20 | 32.75 ± 1.44 | 0.94 | -8.08 | 3.27 | 1.21 | 466.06 |
| 3 | 21 | 105 | 2.71 – 6.42 | 0.73 – 0.80 | 58.29 | 39.76 ± 0.65 | 0.97 | -17.71 | 3.26 | 1.28 | 526.58 |
| 4 | 14 | 56 | 2.51 – 5.42 | 0.59 – 0.82 | 49.68 | 33.57 ± 0.88 | 0.96 | -31.65 | 3.25 | 1.41 | 471.89 |
| 5 | 3 | 12 | 2.35 – 5.17 | 0.17 – 0.66 | 24.8 | 26.91 ± 1.82 | 0.92 | 61.70 | 3.24 | 1.86 | 313.68 |
| 6 | 72 | 303 | 2.30 – 6.55 | 0.17 – 0.78 | 28.92 | 28.49 ± 0.38 | 0.98 | 120.96 | 3.25 | 1.71 | 182.67 |
| 7 | 36 | 178 | 2.42 – 6.17 | 0.22 – 0.54 | 22.55 | 26.92 ± 0.50 | 0.97 | 40.30 | 3.23 | 1.95 | 429.38 |
| 8 | 50 | 236 | 2.40 – 6.00 | 0.16 – 0.33 | 21.93 | 26.49 ± 0.43 | 0.97 | 116.95 | 3.21 | 2.34 | 126.27 |
| 9 | 34 | 156 | 2.50 – 6.08 | 0.21 – 0.59 | 24.27 | 26.91 ± 0.53 | 0.97 | 93.62 | 3.23 | 2.04 | 219.36 |
| 10 | 22 | 91 | 2.23 – 5.75 | 0.13 – 0.28 | 27.98 | 36.15 ± 0.70 | 0.97 | 178.54 | 3.22 | 2.31 | 47.65 |
| 11 | 26 | 110 | 2.70 – 6.00 | 0.18 – 0.57 | 31.62 | 30.32 ± 0.63 | 0.97 | 114.76 | 3.23 | 1.98 | 237.44 |
| 12 | 32 | 139 | 2.67 – 6.25 | 0.21 – 0.65 | 29.23 | 28.69 ± 0.56 | 0.97 | 76.72 | 3.23 | 1.92 | 296.77 |
| 13 | 35 | 144 | 2.50 – 5.92 | 0.23 – 0.56 | 35.27 | 32.94 ± 0.56 | 0.97 | 174.74 | 3.22 | 2.21 | 145.78 |
| 14 | 397 | 1626 | 2.15 – 6.33 | 0.11 – 0.85 | 26.60 | 30.33 ± 0.17 | 0.98 | 106.36 | 3.24 | 1.89 | 272.79 |
| 15 | 3 | 15 | 2.50 – 5.92 | 0.22 – 0.24 | 29.57 | 36.39 ± 1.64 | 0.93 | 174.17 | 3.23 | 2.16 | 119.56 |
| 16 | 1 | 5 | 2.36 – 5.83 | 0.23 – 0.23 | 30.02 | 36.95 ± 2.60 | 0.85 | 146.35 | 3.24 | 1.90 | 191.13 |
| 17 | 4 | 16 | 2.68 – 5.17 | 0.14 – 0.15 | 31.60 | 41.15 ± 1.60 | 0.93 | 197.69 | 3.23 | 2.21 | 81.56 |
| 18 | 2 | 10 | 2.61 – 6.17 | 0.29 – 0.29 | 21.35 | 26.01 ± 1.96 | 0.91 | 51.78 | 3.24 | 1.79 | 326.95 |
| 19 | 2 | 8 | 2.59 – 5.00 | 0.17 – 0.19 | 30.98 | 37.75 ± 2.16 | 0.89 | 178.90 | 3.23 | 2.09 | 119.42 |
| 20 | 112 | 469 | 2.51 – 6.42 | 0.57 – 0.82 | 48.93 | 34.52 ± 0.31 | 0.97 | -175.90 | 3.25 | 1.21 | 685.77 |
| 21 | 5 | 20 | 2.66 – 5.48 | 0.70 – 0.75 | 36.57 | 24.74 ± 1.44 | 0.94 | 99.80 | 3.24 | 1.85 | 204.77 |
| 22 | 3 | 15 | 2.67 – 6.25 | 0.77 – 0.78 | 61.37 | 42.41 ± 1.64 | 0.93 | -40.54 | 3.26 | 1.23 | 567.75 |
| 23 | 36 | 157 | 2.26 – 6.08 | 0.11 – 0.31 | 29.40 | 34.62 ± 0.53 | 0.97 | 157.73 | 3.24 | 1.90 | 155.81 |
| 24 | 3 | 15 | 2.71 – 6.33 | 0.74 – 0.78 | 52.92 | 34.89 ± 1.64 | 0.93 | -7.66 | 3.26 | 1.32 | 464.91 |
| All | 988 | 4197 | 2.15 – 6.55 | 0.11 – 0.85 | 34.64 | 32.63 ± 1.05 | 0.95 | 80.96 | 3.24 | 1.82 | 287.34 |

EI = Environmental Index also described as the first Principal Component (PC1); PV = Phenotypic Values (Average of Clone productivity in all stands); PGV = Predicted Genetic Values (BLUP + overall mean); $h$ = accuracy of selection; EN = Endurence; HL = Half-Life; IGR = Inverse Growth Rate; SP = Specificity.

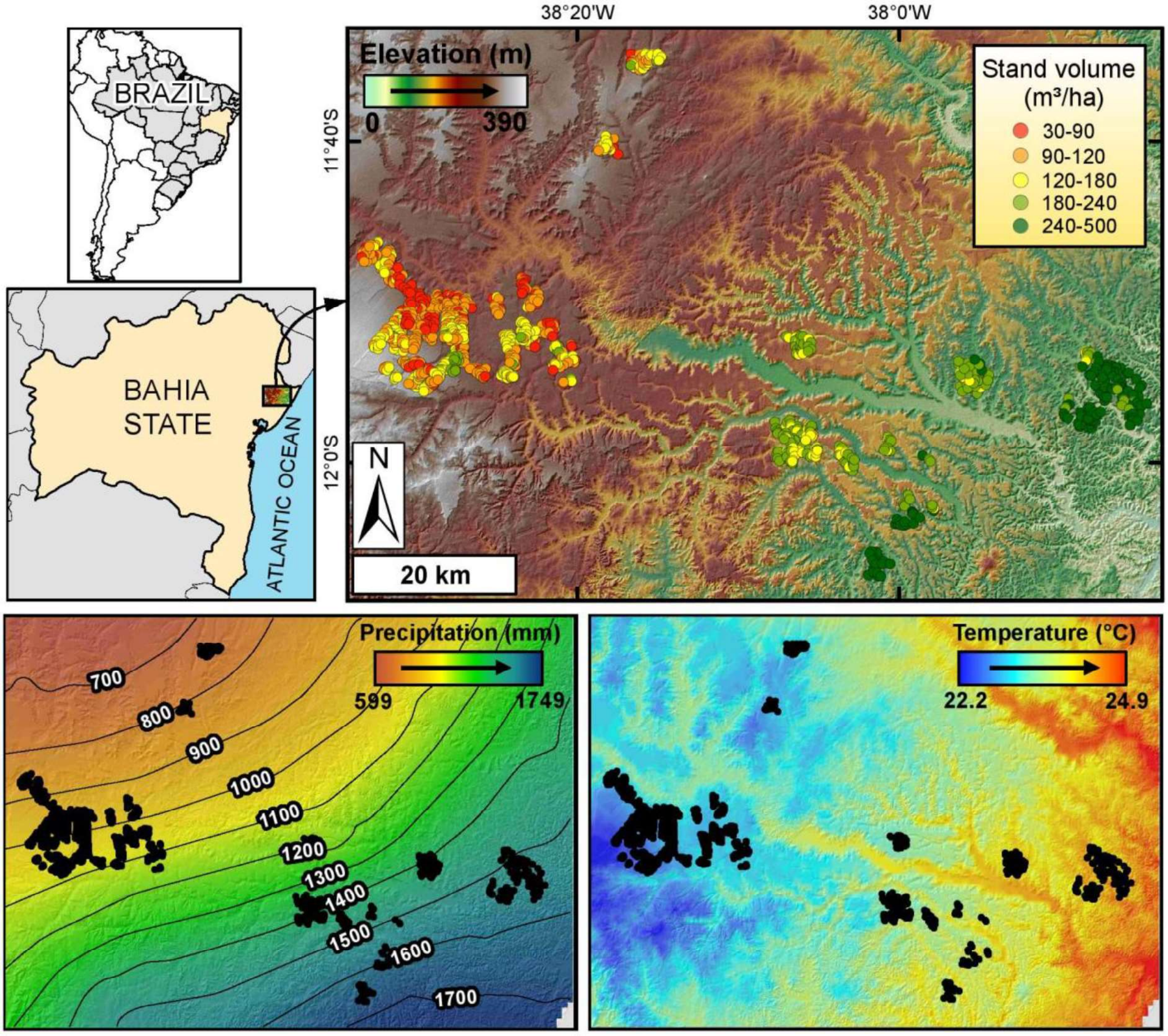

**Figure 3.1.** Location and characterization of the work area. The points highlighted in the images refer to the 988 plots.

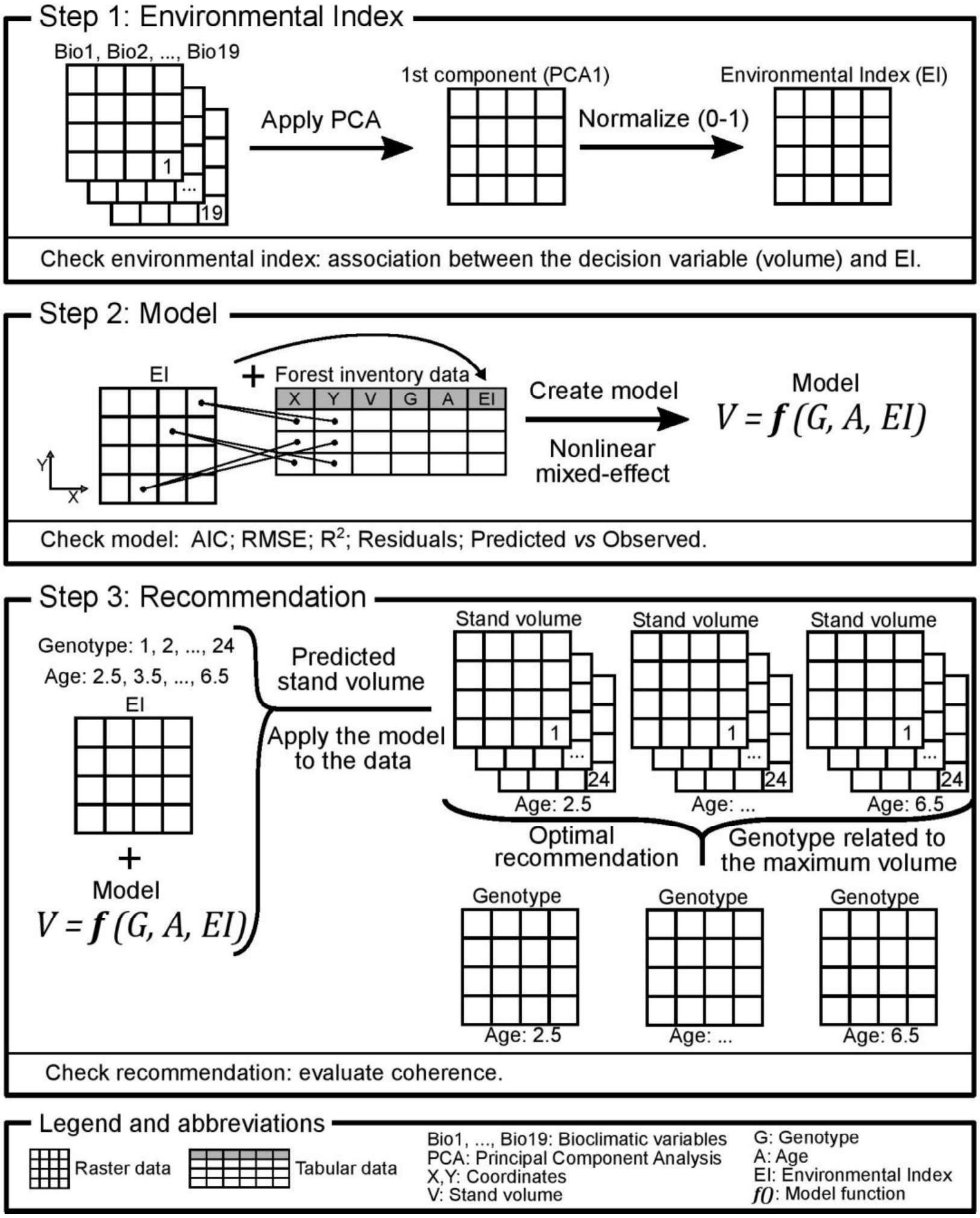

**Figure 3.2.** Flowchart illustrating the three basic steps to optimizing recommendations of Eucalyptus genotypes: Step 1: Determination of the environmental index (EI); Step 2: Construction and fitting of non-linear mixed effects model; Step 3: Production prediction and optimum genotypes recommendation.

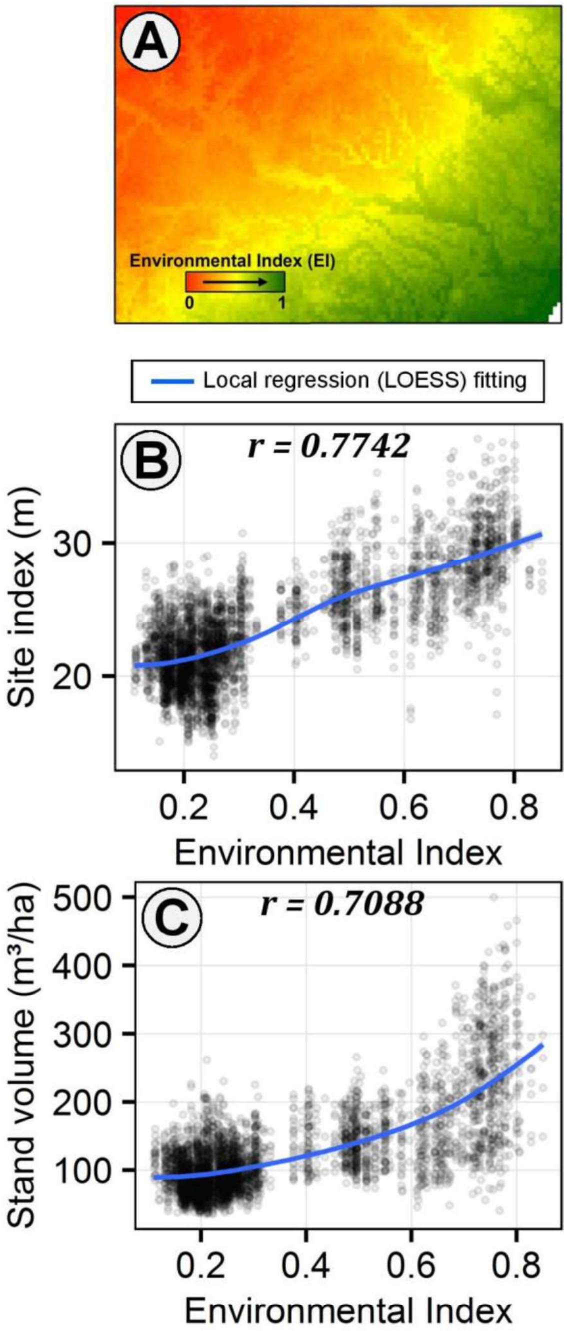

**Figure 3.3.** (A) Environmental Index (EI) based on first principal component analysis (PCA1); (B) relationship between site index (based on stand dominant height) and EI; (C) relationship between stand volume and EI. r is the correlation coefficient.

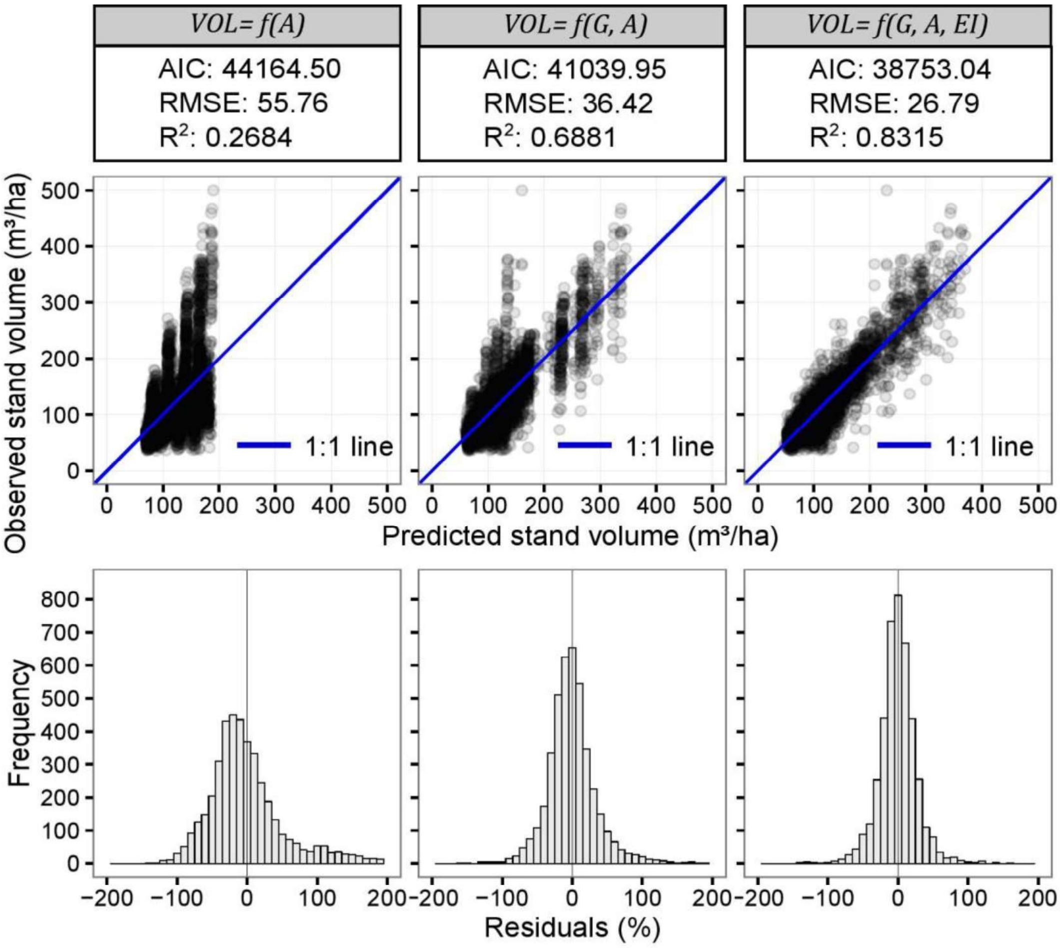

**Figure 3.4.** Model evaluation. $VOL = f\,(Age)$: Stand volume ($VOL$) as a function of Age; $VOL = f\,(Age, G)$: Stand volume as a function of Age, adopting genotypes random effect ($G$); $VOL = f\,(Age, G, EI)$: Stand volume as a function of Age and Environmental Index (EI), adopting random effect on genotypes. AIC: Akaike Information Criteria; RMSE: Root Mean Squared Error; $R^2$: Coefficient of Determination.

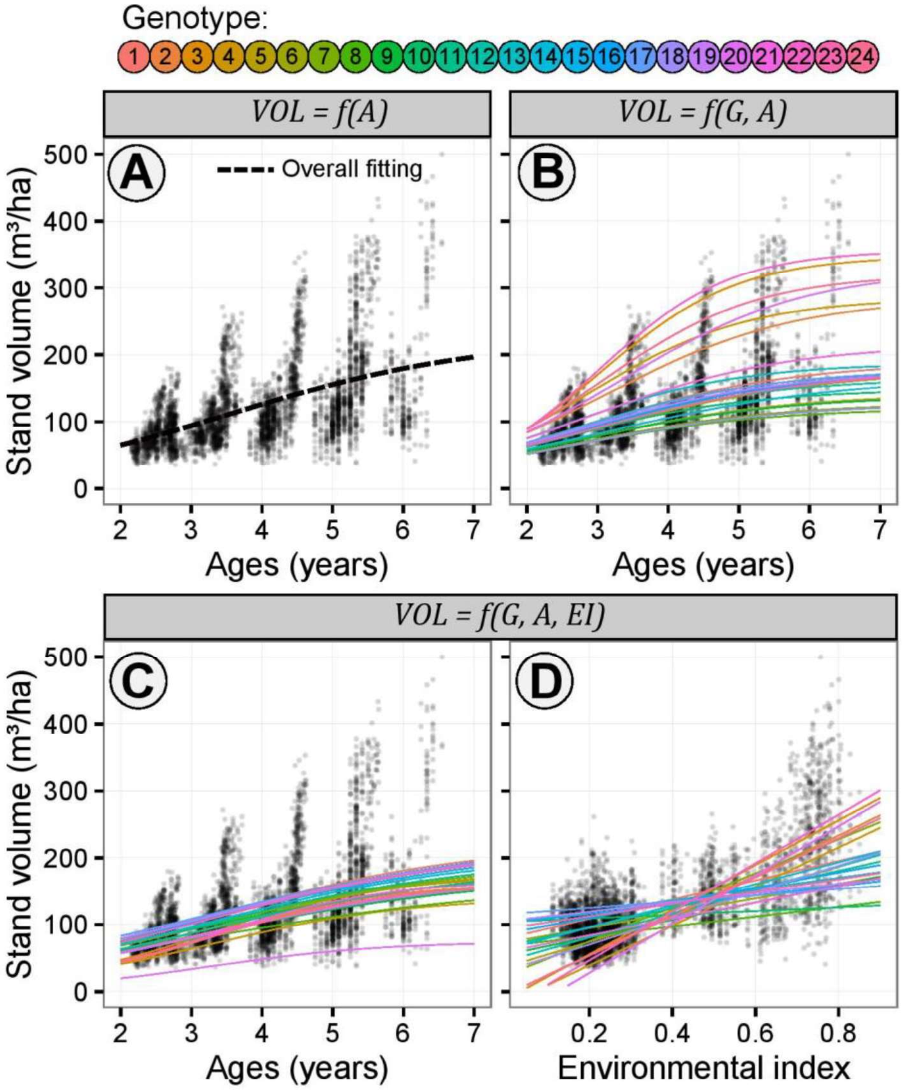

**Figure 3.5.** Reaction Norms. (A) $\boldsymbol{VOL = f\ (Age)}$ model: Stand volume ($\boldsymbol{VOL}$) as a function of Age; (B) $\boldsymbol{VOL = f\ (G, Age)}$ model: Stand volume depending on the Age adopting genotypes as random effect (G); (C) and (D) $\boldsymbol{VOL = f\ (G, Age, EI)}$ model: Stand volume as a function of Age, and Environmental Index (EI), adopting random effect on genotypes.

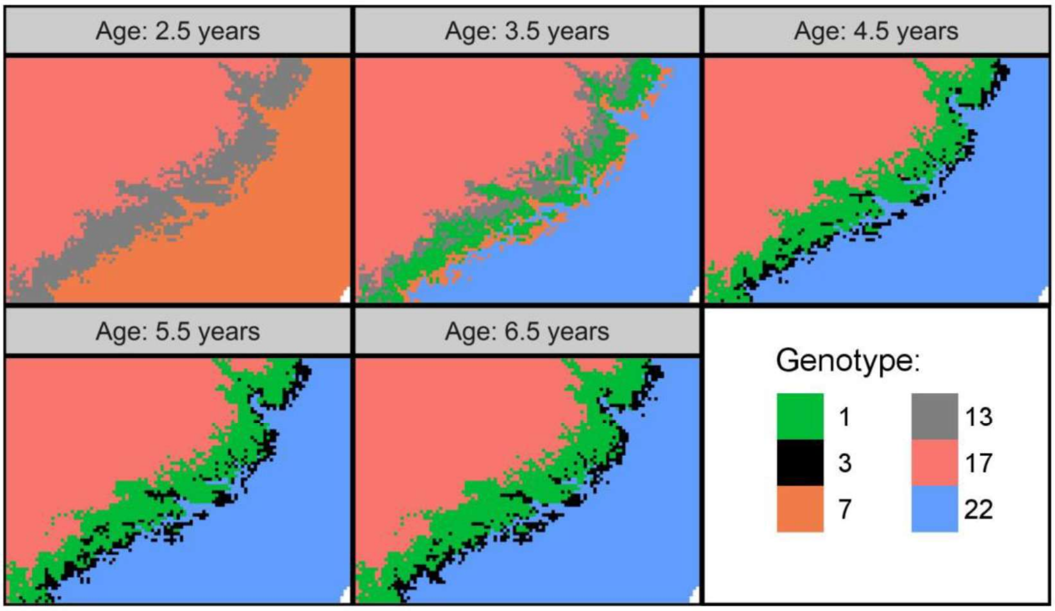

**Figure 3.6.** Recommendation map: Selected genotypes for the work area. Each box is the clonal recommendation at ages 2.5, 3.5, 4.5, 5.5, and 6.5 years. Fill colors are the clones code.

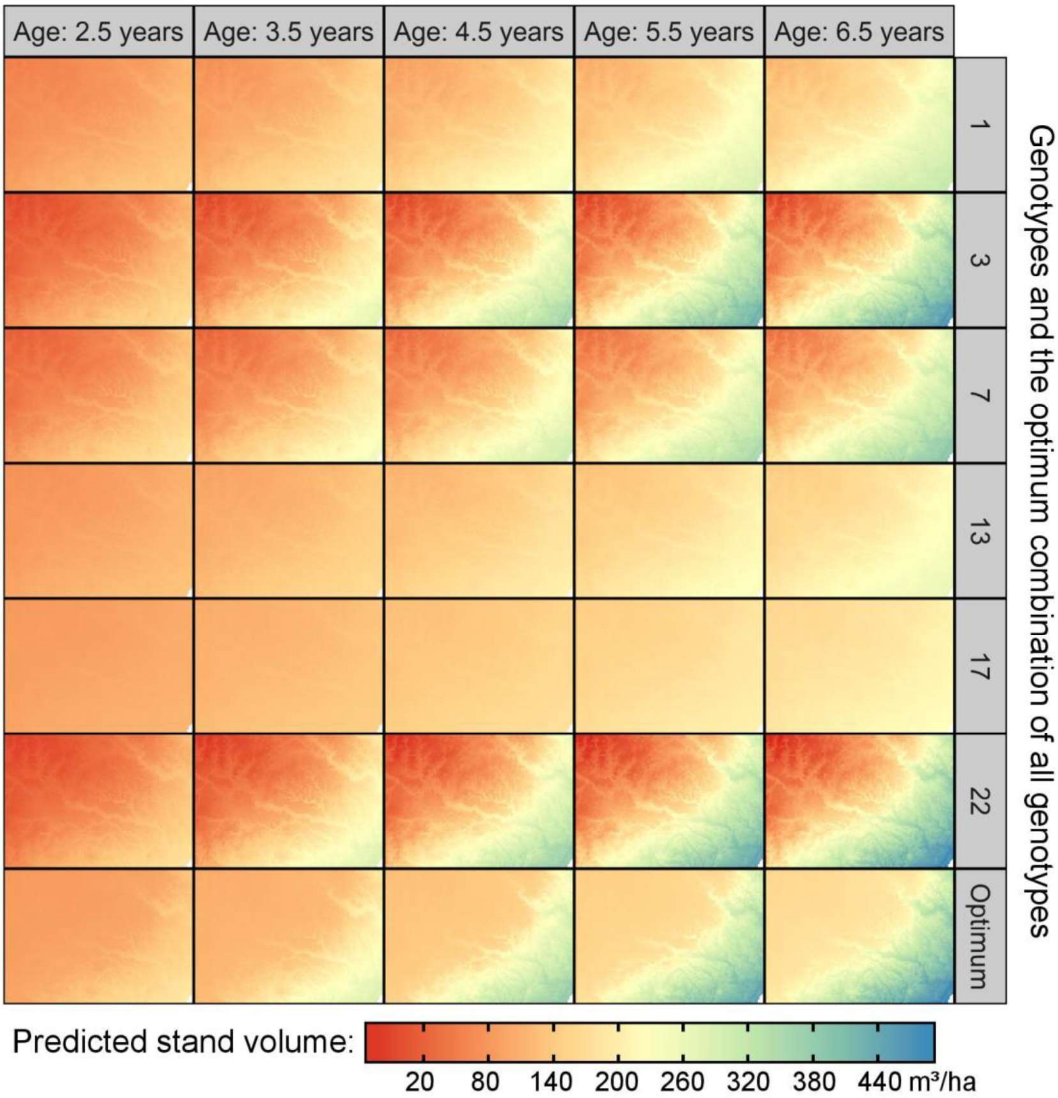

**Figure 3.7.** Stand volume prediction of the selected genotypes (1, 3, 7, 13, 17, and 22) that at some point figured on the Recommendation Map (Figure 6). The ideal combination of genotypes (optimum) to ages 2.5, 3.5, 4.5, 5.5, and 6.5 is also shown.