



## Intra-genotypic competition of *Eucalyptus* clones generated by environmental heterogeneity can optimize productivity in forest stands



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### ARTICLE INFO

#### Article history:

Received 10 June 2016

Received in revised form 27 July 2016

Accepted 24 August 2016

Available online 28 August 2016

#### Keywords:

Clonal competition  
Mixed models  
Forest breeding  
Plant spacing  
Stand productivity

### 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.

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### 1. Introduction

Studies of genotype  $\times$  environment interactions ( $G \times E$ ) 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 et al., 2015; Schwinning and 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 et al., 2008; Donnelly et al., 2016) and the

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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 et al., 2008; Costa e Silva and 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 competition 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 and 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 et al., 2013).

In the final stages of a forest recurrent selection program, it is common to conduct specific experiments called expanded clonal tests (ECT) (Resende et al., 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 and Foster, 1993; Wendling et al., 2014). Moreover, there may naturally be a mismatch in the common clonal growth, possibly leading to future competition 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.

## 2. Materials and methods

### 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). All experiments were designed in randomized complete blocks with three replications. Of the eight tests, three were implemented with plant spacing of 10 m<sup>2</sup>/plant (3 × 3.33 m) and the others with 6 m<sup>2</sup>/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 (VOL) in cubic meters of trees was calculated by Eq. (1) (Schumacher and Hall, 1934), where DBH is the diameter at breast height in cm, H is the tree height in meters, f is the taper factor (assumed to be 0.43), and π is the ratio between the circumference and diameter of a circle.

$$\text{VOL} = \text{DBH}^2 \frac{\pi}{40,000} \text{H f} \quad (1)$$

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

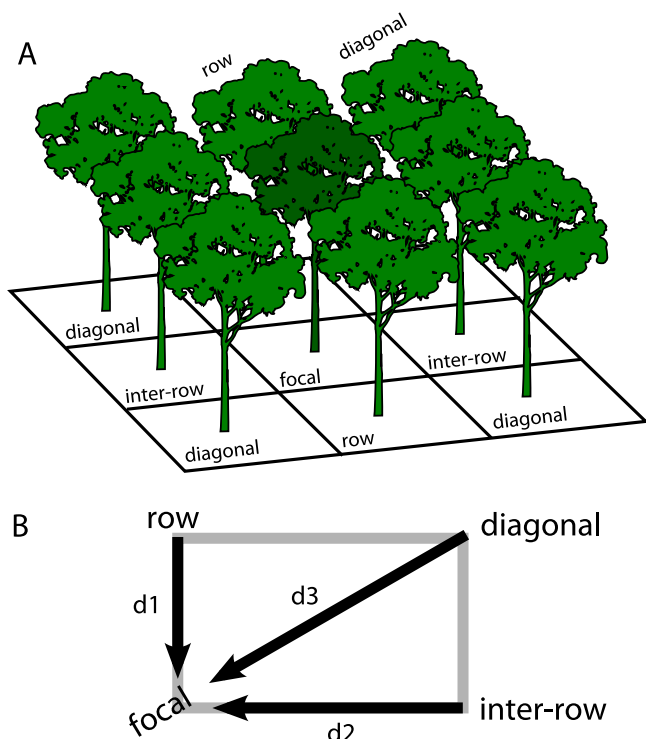
For all experiments comprising 10 × 10 plants per plot, the trees on the border were disregarded, and the remaining 8 × 8 were used to identify neighbors. Thus, the trees of the plot core (6 × 6) were defined as a focal tree (in the center) with 8 surrounding trees identified as neighborhood standardized covariates (2 in the planting row, 2 in the spacing interrow, and 4 on the diagonal) (Fig. 1A). All experiments totaled 306 plots, with 30,600 trees in total, and 11,016 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 **y** is the phenotypic data vector of MAI for focal trees within the plot; **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); ξ is the spatial error of the plot, assuming autoregressive covariance; and **F** is the incidence matrix of fixed effects. The residual variance is given by  $\text{var}(\xi) = \sigma_{\xi}^2 [\sum_r \Phi_r \otimes \sum_c \Phi_c]$ , 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 Φ<sub>r</sub> and Φ<sub>c</sub>, and order equal to the number of rows and columns of the plot, respectively (Resende, 2007). The parameters Φ<sub>r</sub> and Φ<sub>c</sub>, 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.

$$\mathbf{y} = \mathbf{F}\mathbf{n} + \xi \quad (2)$$

**Table 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 (m <sup>3</sup> /ha/year)	Annual Mean Temp. (°C)	Annual Precipitation (mm)	Planting Spacing (m <sup>2</sup> /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.



**Fig. 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,  $d1 < d2 < d3$  and  $d3 = \sqrt{d1^2 + d2^2}$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 et al., 1981). The canonical correlations were obtained from  $306 \times 8$  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.

### 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 Eq. (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  $10$  m<sup>2</sup>/plant  $\times$  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.

$$\mathbf{y}_i = \mathbf{X}_i \mathbf{b}_i + \mathbf{Z}_i \mathbf{g}_i + \mathbf{e}_i \quad (3)$$

The matrix of variance and covariance can be written as Eq. (4), where  $\mathbf{A}$  is the kinship matrix via pedigree (Wright, 1922) and  $\mathbf{I}$  is an identity matrix. The terms  $\sigma_{g_1}^2$  and  $\sigma_{e_1}^2$  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  $\mathbf{h}^2 = \sigma_{g_i}^2 / \sigma_{f_i}^2$ , where  $\sigma_{f_i}^2 = \sigma_{g_i}^2 + \sigma_{e_i}^2$ , and  $\mathbf{r}_g = \sigma_{g_{1,2}} / (\sigma_{g_1}^2 \sigma_{g_2}^2)^{1/2}$ , respectively, and  $i = \{1, 2\}$ . The phenotypic correlations ( $\mathbf{r}_f$ ) were obtained by Pearson correlation through the phenotypic averages of clones traits.

$$\mathbf{V} = \text{var}(\mathbf{y}_i) = \begin{bmatrix} \mathbf{Z}_1 \mathbf{A} \sigma_{g_1}^2 \mathbf{Z}_1' + \mathbf{I} \sigma_{e_1}^2 & \mathbf{Z}_1 \mathbf{A} \sigma_{g_{1,2}} \mathbf{Z}_2' + \mathbf{I} \sigma_{e_{1,2}} \\ \mathbf{Z}_1 \mathbf{A} \sigma_{g_{1,2}} \mathbf{Z}_2' + \mathbf{I} \sigma_{e_{1,2}} & \mathbf{Z}_2 \mathbf{A} \sigma_{g_2}^2 \mathbf{Z}_2' + \mathbf{I} \sigma_{e_2}^2 \end{bmatrix} \quad (4)$$

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

MAI, when assessed by the bivariate model, and the parameter **EE** represents the gain in selection accuracy provided by the use of the bivariate model.

$$h_m^2 = h_y^2 \left[ 1 + \frac{(h_x r_g / h_y - r_f)^2}{1 - r_f^2} \right] \quad (5)$$

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

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 and Cruz, 2004).

### 2.4. Computational tools

Data processing and development of computer functions were completed using R software (Team, 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.

## 3. Results

### 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.

Fig. 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. Fig. 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 (Fig. 1). The trees in interrows and diagonals had smaller distances between them, with a canonical

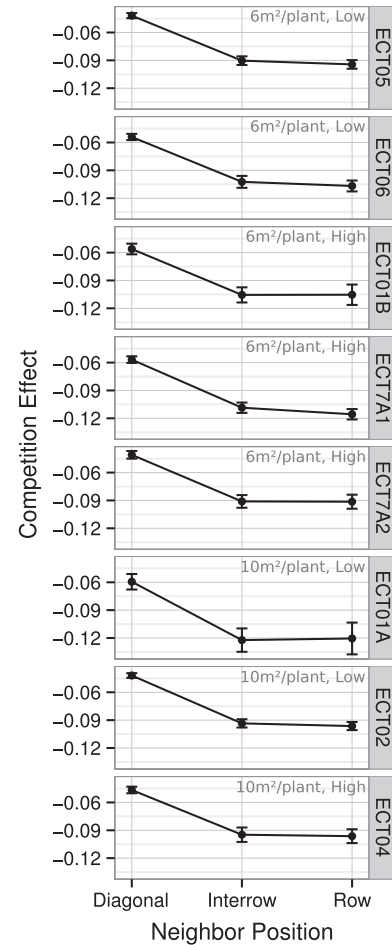


Fig. 2. Means and confidence intervals (95% probability) of the effects of neighboring trees on focal trees. The effects are grouped according to the neighboring tree position from the focal tree (two trees in the planting row, two in the spacing interrow, and four on the diagonal). Each horizontal box represents an evaluated expanded clonal test (ECT).

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 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.

Fig. 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



**Table 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	–	<b>0.41</b> ***
	Row	–0.14
	Inter-row	–0.10
	Diagonal	0.22
Neighbors of Row	–	<b>–0.49</b> ***
	Spatial AR1	0.12
	Inter-row	–0.19
	Diagonal	0.59
Neighbors of Inter-row	–	<b>–0.28</b> **
	Spatial AR1	0.15
	Row	–0.34
	Diagonal	0.59
Neighbors of Diagonal	–	<b>0.72</b> ***
	Spatial AR1	0.12
	Row	–0.40
	Inter-row	–0.23
Error (e)		<b>0.73</b> ***

P-values for the direct effects:  $\Phi$ ,  $\Phi_c < 0.001$ ; row  $< 0.001$ ; interrow = 0.002; extremity  $< 0.001$ ;  $e < 0.001$ .

\* Significance at 95% probability.

\*\* Significance at 99% probability.

\*\*\* Significance at 99.9% probability.

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<sup>3</sup>/ha/year.

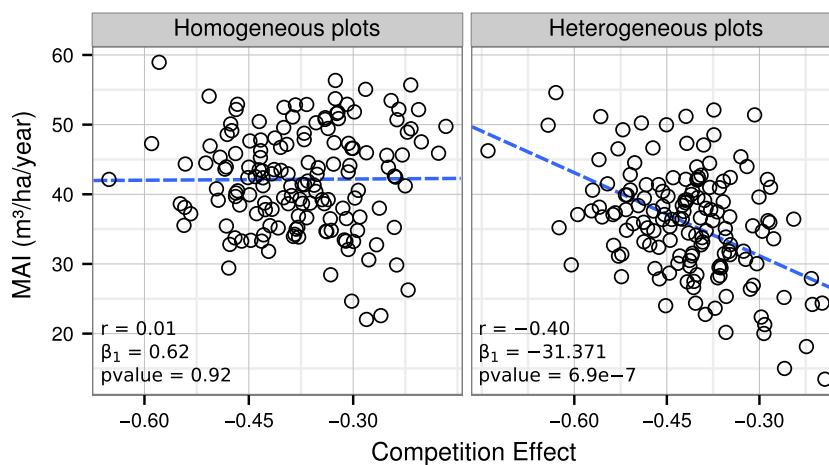
### 3.2. Genetic nature of the relationship of competition versus productivity

Only the trees from the row and interrow plantings exhibited direct effects of competition that were reflected in greater plot productivity (Table 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 (Fig. 1A). Table 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 m<sup>2</sup>/plant and 10 m<sup>2</sup>/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 ( $h_m^2$ ) was always higher than those of the MAI for  $h^2$ , and the effective efficiency (EE) of this addition is presented in Table 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 m<sup>2</sup>/plant) also showed higher EE.

Fig. 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 m<sup>2</sup>/plant (both high and low altitudes), the two regression lines are parallel, and for the 10 m<sup>2</sup>/plant, similar behavior is observed.

Fig. 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 m<sup>2</sup>/plant-Low, 6 m<sup>2</sup>/plant-High, 10 m<sup>2</sup>/plant-Low, 10 m<sup>2</sup>/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



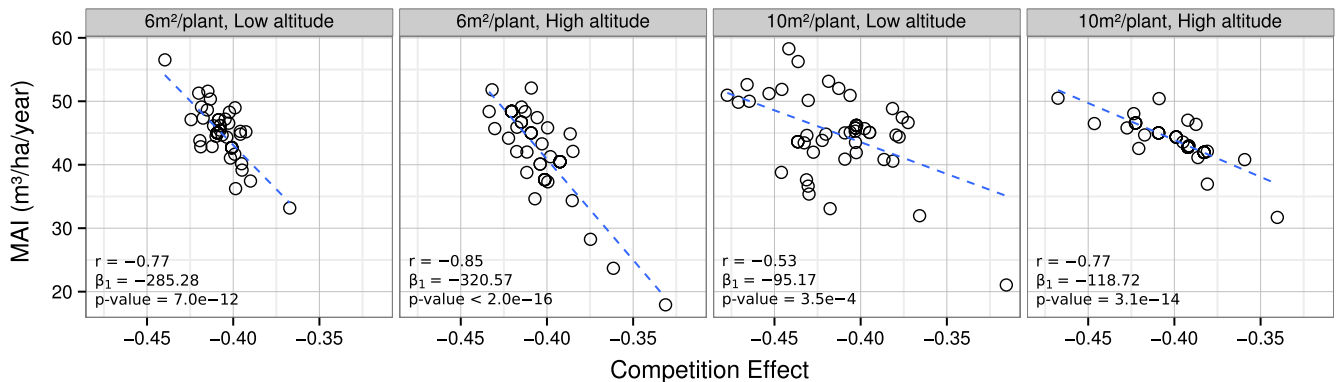
**Fig. 3.** Linear relationship between competition/aggressiveness (sum of the effects of the row and interrow trees on the focal tree) and productivity (measured in mean annual increment – MAI). The 306 evaluated plots were divided by 50% more homogeneous (so-called homogeneous plots) and 50% less homogeneous (so-called 50% heterogeneous plots), by the median autocorrelations parameters.  $r$  is the correlation coefficient between competition and MAI;  $\beta_1$  is the slope regression coefficient; and **p-value** is the associated significance with  $\beta_1$ .

**Table 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 (MAI) traits.

		Experimental conditions				Multi-conditions
		6 m <sup>2</sup> /plant, Low altitude	6 m <sup>2</sup> /plant, High altitude	10 m <sup>2</sup> /plant, Low altitude	10 m <sup>2</sup> /plant, High altitude	
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
$\sigma_g^2$	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
$\sigma_p^2$	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
$h^2$	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	$r_g$	-0.64 ± 0.05	-0.73 ± 0.04	-0.41 ± 0.07	-0.69 ± 0.04	-0.52 ± 0.06
	$r_p$	-0.36 ± 0.07	-0.32 ± 0.07	-0.25 ± 0.07	-0.52 ± 0.06	-0.25 ± 0.07
$h_m^2$	MAI <sub>Comp</sub>	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;  $\sigma_g^2$  are the additive genetic variance;  $\sigma_p^2$  are the phenotypic variance;  $h^2$  are the narrow-sense heritability;  $r_g$  and  $r_p$  are the genotypic and phenotypic correlation, respectively, between competition and MAI;  $h_m^2$  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.



**Fig. 4.** Linear relationships between estimated genetic values (EGV) of competition/aggressiveness versus mean annual increment (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;  $\beta_1$  is the slope regression coefficient; and **p-value** is the associated significance with  $\beta_1$ .

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 m<sup>2</sup>/plant-Low condition, and highest at 10 m<sup>2</sup>/plant-High condition (see Fig. 4).

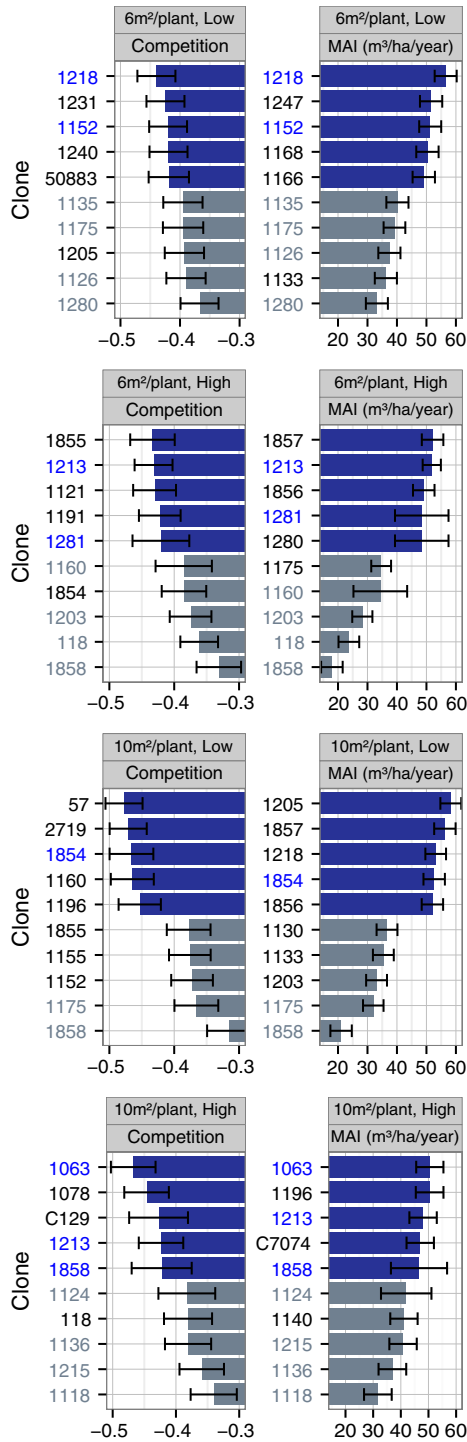
To evaluate the phenotypic plasticity of clones in all four experimental conditions principal component analysis was performed. The first principal component (PC1) explained 48% of the total variance of the four conditions, and the second principal component (PC2) 22.8%, totaling 70.1%. QI, QII, QIII, and QIV clones can be observed in Fig. 6 using the quadrants. The five best clones shown in Fig. 5 are highlighted in blue in Fig. 6.

## 4. Discussion

### 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 et al., 2008; Luu et al., 2013; Soares et al., 2016; Stape et al., 2010). The homogeneity of plant growth in clonal stands is highly dependent on environmental factors (Luu et al., 2013), since

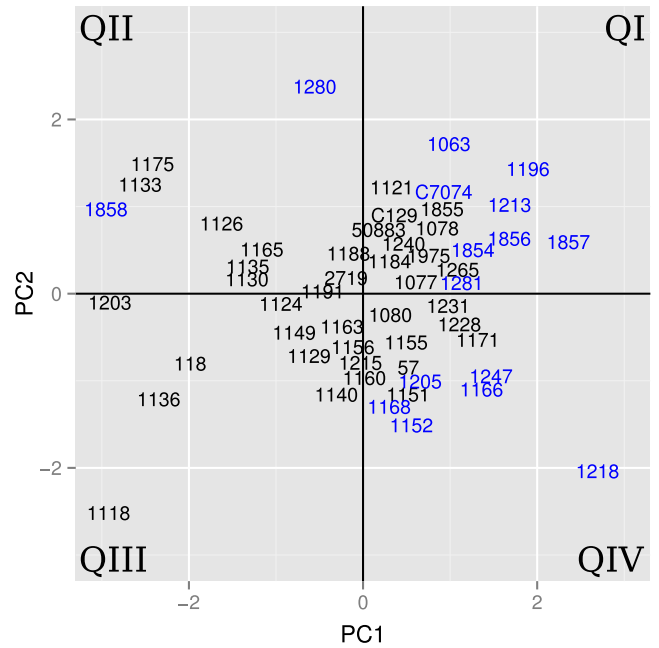
the clonal genetic variability within the plots is theoretically zero (Resende, 2007; Stape et al., 2010). However, to achieve the desired homogeneity of stands requires investigation of silvicultural techniques aimed at maximizing site uniformity (Aspinwall et al., 2011). In the present study, plots with more homogeneous environments had higher average productivity than did the heterogeneous plots (42.15 versus 35.88 m<sup>3</sup>/ha/year, respectively) (Fig. 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 et al., 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 (Fig. 3), the evaluated hypothesis was that different genetic materials differed in their response (better or worse) to



**Fig. 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 (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.

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), and from these we were able to account for the independent effects of competing neighboring trees. Thus, it was seen that



**Fig. 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 Fig. 5.

in relation to the focal tree (Fig. 1A), diagonal trees contributed smaller competition effects than the row and interrow trees (Fig. 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 (Fig. 1B). 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 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 et al., 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 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 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 Fig. 3 and confirming the conclusions made by Almeida et al. (2007), Luu et al. (2013), and Stape et al. (2010).

#### 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 and 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 (Fig. 2), but these effects are only phenotypic values, and may merely be caused by the greater or lesser site heterogeneity (Fig. 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  $0.37 \pm 0.05$  for plants after 4 years. Using square plots and hybrids of *E. grandis*  $\times$  *E. urophylla*, we found very similar values to these authors (Table 3). The heritabilities altered according to the experimental condition, ranging from 0.18 (6 m<sup>2</sup>/plant-Low) to 0.38 (10 m<sup>2</sup>/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 et al., 2008; McIntosh, 1970). From the present study, it was observed that the traits MAI and competition had quite relevant  $r_g$  values (Table 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 (Fig. 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 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 m<sup>2</sup>/plant), we observed a stronger relationship between productivity and competition (Fig. 4) than for the 10 m<sup>2</sup>/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 and Bird, 2003). The veracity of this assumption can be seen by comparing the slope of the straight line in Fig. 4, wherein

both the higher and lower altitudes have straight lines that are parallel in the 6 m<sup>2</sup>/plant condition. A similar result was seen between the two altitudes spaced at 10 m<sup>2</sup>/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 et al., 2008; Kim et al., 2015; Stape et al., 2010). In high altitude environments, productivity was considerably higher, being approximately 20% greater than in low altitudes (Tables 1 and 3). This typically occurs owing to *Eucalyptus* shoot-blight disease in lower altitudes (Almeida et al., 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 m<sup>2</sup>/plant) and 5.09% (at spacing of 10 m<sup>2</sup>/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 (Fig. 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 et al., 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 Fig. 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 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 (Fig. 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 (Figs. 5 and 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.



## 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.

## Acknowledgements

The forest breeder Antonio Marcos Rosado for important initial ideas. CENIBRA S.A. company for the financial support and availability of data, and their employees João Edésio Sousa, Everton Souza, Fernando Palha Leite, and Maria Nascimento S. de Assis for all assistance. The first author thanks National Counsel of Technological and Scientific Development (CNPq) for the PhD scholarship.

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