

genetics &amp; tree improvement

# Improving Genetic Analysis of *Corymbia citriodora* subsp. *variegata* with Single- and Multiple-Trait Spatial-Competition Models

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Environmental heterogeneity and/or genetic and environmental competition were quantified on two growth traits, diameter at breast height and total height, and wood density in a progeny trial of *Corymbia citriodora* subsp. *variegata*. Three single-trait mixed models with random spatial and/or competition effects were compared to a standard analysis by analyzing fit, dispersion parameters, accuracy of breeding values, genetic gains, and ranking of trees. In addition, a multiple-trait spatial-competition model was fitted to estimate correlations among direct and indirect additive genetic effects, and to explore relations between traits. Single-trait analyses with spatial and/or competition effects outperformed the standard model. However, the performance of these models depended on the sensitivity of each trait to detect each effect. Direct–indirect genetic correlations from the multiple-trait spatial-competition model showed inverse and strong relations among growth traits and wood density, suggesting that growth traits can be affected by competition and environmental heterogeneity, but also wood density might be influenced by these effects. The approach proposed was useful to improve the genetic analysis of the species as well as to gain an understanding of the genetic relations between traits under the influence of environmental heterogeneity and competition.

**Keywords:** Argentina, genetic correlation, indirect genetic effects, two-dimensional surface, wood density

The genus *Corymbia* has traditionally been planted as wind-break and shade tree in some rural areas in northeastern Argentina. It is widespread in the province of Corrientes, where frosts are milder than in the surrounding departments (Golfari 1985). Despite the fact that the genus is not currently planted for timber in Argentina, it is gaining popularity because of its particular features, such as high growth, drought resistance, and excellent solid wood. Although some previous field trials have shown the potential of this genus in the country, it was only in 2000 that the first species and provenance trials were introduced by Instituto Nacional de Tecnología Agropecuaria (INTA). The introduction of *Corymbia* was aimed at developing a genetic source for two purposes: to produce high-quality timber from a fast-growing species and to replace the consumption of similar woods from natural forests in order to decrease the depletion of native hardwoods. The analysis of these first trials showed that *Corymbia citriodora*

subsp. *variegata* (F.Muell.) A.R. Bean & M.W. McDonald (hereafter *C. citriodora*) was the taxon with the highest growth in the area, surpassing other species of the genus (López et al. 2009).

INTA's *C. citriodora* breeding program has used the well-known best linear unbiased prediction (BLUP) of breeding values for selecting trees by means of the single-trait mixed-model approach (Henderson 1984). However, this approach has not accounted for the effects of environmental heterogeneity and competition between individuals on tree selection. Since the inclusion of spatial and/or competition effects can improve estimation of variances, accuracies of breeding values (BVs), and gain responses (Dutkowski et al. 2002, Resende et al. 2005, Costa e Silva and Kerr 2013), their addition to data analysis should be considered in order to improve the accuracy of predictions. Variables included in INTA's *Corymbia* breeding program (e.g., growth traits and wood density [WD]) might be predicted more accurately by adding the effect

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of environmental heterogeneity, the effect of competition, or both effects together.

A wide variety of spatial analyses have been used to quantify environmental heterogeneity in forest genetic trials. Such variety includes the kriging method (Hamann et al. 2002), autoregressive residual structures (Dutkowski et al. 2006), and nearest neighbor (Gezan et al. 2010), to name just a few. The use of the tensor product of cubic B-spline basis (Eilers and Marx 2003) has also been proposed to account for spatial patterns in the progeny test. B-splines are piecewise polynomial functions from segments of low degree polynomials, whose segment joints are called knots. These functions use a covariance structure of random knot effects to capture most of the variation without requiring a regular arrangement (Cappa and Cantet 2007).

In regard to competition, Muir (2005), Cappa and Cantet (2008), and Costa e Silva and Kerr (2013) applied a mixed linear model that included direct and indirect (i.e., competition) additive genetic effects. Whereas the former effects refer to the focal-tree genotype, the latter are the effects of the surrounding tree genotype on the focal tree phenotype (Griffing 1967, Moore et al. 1997). In addition, an environmental competition effect was also included in order to quantify the nongenetic competition exerted on the focal tree by its neighbors. Cappa and Cantet (2008) quantify competition by using the “intensity of competition” elements (ICs), which are covariates with nonzero elements of the incidence matrix of competition effects. The ICs allow the model to account for different numbers of neighbors in rows, columns, and diagonal directions when mortality and borders are present.

Joint analyses of environmental heterogeneity and competition have been conducted in agronomic crops (Stringer et al. 2011, Hunt et al. 2013, Elias et al. 2018) and forest genetic trials (Magnussen 1994, Resende et al. 2005, Cappa et al. 2015) by using a univariate analysis without taking advantage of multitrait evaluation. Costa e Silva et al. (2017) developed the first bivariate analysis of forest genetic trials with a spatial-competition model. They extended a previous single-trait model to a multitrait level in order to estimate trait–trait correlations between direct and indirect additive genetic effects. Because tree selection involves several correlated traits, accounting for covariances among traits for direct and indirect genetic effects led to a better understanding of their relations and their genetic response. Nevertheless, the study was confined to the traits diameter at breast height (DBH) and disease severity index, without exploring relations between other traits or variables. Studies with different aims will require measurement of other traits. A multivariate approach that explores the relation between growth and wood properties under the influence of competition and environmental heterogeneity may increase our understanding of the interaction among trees within forest genetic trials. This approach may be especially useful for INTA’s *C. citriodora* breeding program, which is aimed at improving growth traits and WD (López et al. 2009).

In light of these considerations, the aims of this study were (1) to identify and quantify the effects of environmental heterogeneity and competition on two growth traits (DBH and total height [TH]) and WD in a single progeny test of *C. citriodora*; (2) to compare the fit and dispersion parameters of the following single-trait mixed models: a standard model with only block and additive genetic effects (no competition and spatial effects), a spatial model

with spatial effects of B-splines, a competition model that includes competition effects by using ICs, and a model that fits jointly competition and spatial effects; (3) to compare the degree of improvement that the inclusion of spatial and/or competition effects have on accuracy of predicted BVs, genetic gains, and ranking of trees; and (4) to extend the single-trait spatial-competition model to a multiple-trait level in order to estimate direct and indirect genetic correlations and explore relations between these traits under the influence of environmental heterogeneity and competition.

## Materials and Methods

### Trial Description, Genetic Material, and Quantitative Traits Evaluated

Growth and WD were measured on a single 6-year-old progeny trial largely composed of *Corymbia citriodora* subsp. *variegata*. This trial is located in the province of Corrientes, Argentina (latitude and longitude coordinates 28°26′34.6″S and 58°58′51.8″W) at 65 m a.s.l., where climate is humid and mesothermal, and it can be described as belonging to the group C2 B<sub>4</sub> ra’ of Thornthwaite’s classification (Castro et al. 1991). According to records of a weather station located near the trial, the mean annual rainfall is 1,260 mm, whereas the mean annual temperature is 20.9° C, with an annual minimum and maximum of 15.7° C and 26.2° C, respectively. The length of the frost-free season has been recorded as 330 days per year, and records of wind speed have shown a mean of 5 km h<sup>-1</sup>. The site has a sandy loam paleudalf soil, which is deep and well drained, but poor in fertility, organic matter, cation-exchange capacity, and retention of humidity. The site was previously used as an orange farm before becoming a forest plantation.

The trial was designed as a randomized complete block with 15 replications in single-tree plots, where every single tree was identified by its specific position on a grid composed of 39 rows and 21 columns. The spacing between trees was 4 m for rows and 2.5 m for columns. Mechanical and chemical control of weeds was carried out periodically during the first 2 years after afforestation. Additionally, all trees were pruned to 2 m height at age 2. The survival rate was 67 percent at the time of assessment.

The genetic materials tested were obtained from open-pollinated seedlots of 50 families: 20 originated in Woondum (Queensland) collected by CSIRO Australian Tree Seed Centre, and 30 derived from trees phenotypically selected for growth and form from three species/provenance trials previously established in northeast Argentina in 2000. The number of families sampled (i.e., seedlots) from the Argentinian trials varied from one to seven in seven groups, corresponding to seven Australian provenances selected in the three species/provenance Argentinian trials. Therefore, eight genetic groups

### Management and Policy Implications

Including spatial and competition effects in genetic analyses of trees improves estimation of dispersion parameters, accuracy of breeding values, genetic gains, and ranking. This approach is useful to avoid bias on selection and enhance genetic parameters, but it might also enable the forester to increase productivity of woods by the planting of noncompetitive genotypes. In this scenario, trees with a high potential for growth might have a tendency to exert less competition, which would result in an increased yield per unit area.

were formed according to provenances. A generalized linear mixed model with a logistic link function was used to analyze survival of families and genetic groups at the time of assessment. No statistically significant differences were found for either genetic groups or families

The properties evaluated on trees at 6 years of age included DBH (1.3 m), total tree height (TH), and basic WD. Units of measurement were centimeters (cm), meters (m), and kilogram per cubic meter ( $\text{kg m}^{-3}$ ) for DBH, TH, and basic WD, correspondingly. Growth traits DBH and TH were measured on the 503 trees of the trial. Basic WD was measured on 490 trees, excluding 13 small trees from the total in order not to damage them during the wood sample. Whereas DBH and TH were measured using a forest caliper and a hypsometer, respectively, 5-mm-diameter cores were taken with a Pressler increment borer to evaluate basic WD from the North exposure of trees at 1.3 m height. To obtain a single measurement of basic WD from pith to cambium for each tree, the maximum moisture content method was followed (Smith 1954). The overall means (and standard deviations) were 15.2 ( $\pm 4.9$ ) cm, 13.9 ( $\pm 4.2$ ) m, and 581 ( $\pm 54$ )  $\text{kg m}^{-3}$  for DBH, TH, and WD, respectively.

### Diagnosis of Environmental Variability and Competition Effects

To identify and quantify the effect of environmental heterogeneity and competition, a series of diagnostic analyses were carried out. For each trait, a basic single-trait individual-tree mixed model with fixed genetic group and random breeding values was fitted. By using this model, the following two analyses were made. First, since positive correlations may reflect tendencies associated with environmental variability, and negative correlation structures are assigned to detect interplant competition (Magnussen 1994), residuals of the model were used to show these trends. Therefore, Pearson correlations ( $r$ ) between residuals of each focal tree from the basic mixed model and phenotypic means of focal tree neighbors were calculated, as proposed by Durban et al. (2001). These correlations were computed for four different configurations of adjacent trees: the maximum eight first-order focal tree neighbors, the maximum two focal tree neighbors in a row direction, the maximum two focal tree neighbors in a column direction, and the maximum four focal tree neighbors in a diagonal direction. Second, an isotropic empirical semivariogram of residuals from the basic mixed model mentioned above was plotted. The isotropic semivariogram represents the half-average variation in pairwise residual differences as a function of distance. Finally, additive genetic correlations between direct and indirect effects ( $r_{dc}$ ) from the single-trait competition model were examined to study competition effects at genetic level (see competition mixed model below, Equation 3). The rationale is based on the fact that a high and negative correlation between both types of genetic effects (higher than  $-.3$ ) suggests strong genetic competition (Resende et al. 2005).

### Statistical Analysis

Each trait was analyzed by using the following single-trait individual-tree mixed models:

#### Standard Mixed Model (TM)

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_b\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (1)$$

where the vector  $\mathbf{y}$  contains the phenotype data; the vector  $\boldsymbol{\beta}$  includes the fixed effects of genetic group to account for the means of different origins of parents;  $\mathbf{b}$  is the vector of random block effects;  $\mathbf{a}$  is the vector of random additive genetic effects with distribution  $\mathbf{a} \sim N(0, \mathbf{A}\sigma_a^2)$ , where  $\mathbf{A}$  is the relation matrix from the pedigree information, and  $\sigma_a^2$  is the additive genetic variance;  $\mathbf{e}$  is the vector of random residual effects with distribution  $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$ , where  $\mathbf{I}$  is the identity matrix, and  $\sigma_e^2$  is the residual variance; and  $\mathbf{X}$ ,  $\mathbf{Z}_b$ , and  $\mathbf{Z}_a$  are incidence matrices that relate the phenotype  $\mathbf{y}$  to the effects  $\boldsymbol{\beta}$ ,  $\mathbf{b}$ , and  $\mathbf{a}$ , respectively.

#### Spatial Mixed Model (SM)

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{S}\mathbf{s} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (2)$$

where the elements  $\mathbf{X}$ ,  $\boldsymbol{\beta}$ ,  $\mathbf{Z}_a$ ,  $\mathbf{a}$ , and  $\mathbf{e}$  were as defined above. In Equation 2, the matrix  $\mathbf{S}$  contains the two-dimensional B-splines basis evaluated in the corresponding row and column for each tree, whereas the vector of coefficients of the tensor product of B-spline basis  $\mathbf{s}$  is normally distributed with mean zero and covariance matrix  $\mathbf{U}\sigma_s^2$ , where  $\mathbf{U}$  is a fixed spatial structure, and  $\sigma_s^2$  is the spatial variance parameter. A more detailed explanation of the two-dimensional surface and the covariance structure used in this work can be found in Cappa and Cantet (2007). To fine-tune the smoothness of the spatial surface, an increasing number of knots were tested individually for rows and columns. The optimal number of knots was defined by the lowest value of the Akaike information criterion (AIC, Akaike 1974).

#### Competition Mixed Model (CM)

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_b\mathbf{b} + \mathbf{Z}_d\mathbf{d} + \mathbf{Z}_c\mathbf{c} + \mathbf{Z}_p\mathbf{p} + \mathbf{e} \quad (3)$$

where the elements  $\mathbf{X}$ ,  $\boldsymbol{\beta}$ ,  $\mathbf{Z}_b$ ,  $\mathbf{b}$ , and  $\mathbf{e}$  were as defined above. The study by Cappa and Cantet (2008) was closely followed to describe the competition mixed model. The vectors  $\mathbf{d}$  and  $\mathbf{c}$  are the direct and indirect (i.e., competition) additive genetic effects (i.e., breeding values), respectively, which are distributed one to one as  $\mathbf{d} \sim N(0, \mathbf{A}\sigma_d^2)$  and  $\mathbf{c} \sim N(0, \mathbf{A}\sigma_c^2)$ , where  $\sigma_d^2$  and  $\sigma_c^2$  are the variances of direct and indirect additive genetic effects, respectively. The  $\mathbf{A}$  matrix allows the link between direct and indirect genetic effects, since  $\text{cov}(\mathbf{d}, \mathbf{c}) = \mathbf{A}\sigma_{dc}$ , where  $\sigma_{dc}$  is the covariance between direct and indirect breeding values. The vector  $\mathbf{p}$  includes the environmental competition effects (or permanent environmental competition effects) distributed as  $\mathbf{p} \sim N(0, \mathbf{I}\sigma_p^2)$ , where  $\mathbf{I}$  is the identity matrix, and  $\sigma_p^2$  is the variance of environmental competition effects.  $\mathbf{Z}_d$ ,  $\mathbf{Z}_c$ ,  $\mathbf{Z}_p$  are incidence matrices that relate the phenotype  $\mathbf{y}$  to the random effects  $\mathbf{d}$ ,  $\mathbf{c}$ , and  $\mathbf{p}$ , respectively. Every row of  $\mathbf{Z}_d$  has all elements equal to zero except for 1 in the column belonging to  $\mathbf{d}$ . Similarly, each row of matrices  $\mathbf{Z}_c$  and  $\mathbf{Z}_p$  has all elements equal to zero except in the positions of the  $n_p$  neighbors of the tree  $p$ , with values  $f_{pq}$  ( $q = 1, \dots, n_p$ ). These positive coefficients can be interpreted as the IC that each neighbor exerts over the phenotype of each tree. Assuming that the intensity of competition is related to the inverse of the distance between the tree  $p$  and the neighbor  $q$ , the IC for competitors that lie in the same row or column of the tree  $p$  ( $f_{p\text{Row-Col}}$ ) and for competitors lying in the diagonal positions with respect to tree  $p$  ( $f_{p\text{Dia}}$ ) are

$$f_{p\text{Row-Col}} = \sqrt{\frac{2}{2n_{p\text{Row-Col}} + n_{p\text{Dia}}}}; f_{p\text{Dia}} = \frac{1}{\sqrt{2n_{p\text{Row-Col}} + n_{p\text{Dia}}}}$$

where  $n_{pRow-Col}$  are the respective numbers of competitors laying in rows or columns, and  $n_{pDia}$  are the respective numbers of competitors laying in diagonals. Further details can be found in [Cappa and Cantet \(2008\)](#).

### Spatial-Competition Mixed Model (SCM)

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{S}\mathbf{s} + \mathbf{Z}_d\mathbf{d} + \mathbf{Z}_c\mathbf{c} + \mathbf{Z}_p\mathbf{p} + \mathbf{e} \quad (4)$$

All vectors of fixed and random effects and matrices of Equation 4 were described above. The SCM was defined according to [Cappa et al. \(2015\)](#). Like the SM, the number of knots was also adjusted independently for rows and columns (see SM, Equation 2).

Finally, the single-trait SCM (Equation 4) was extended to the following multiple-trait model in order to study genetic correlations between direct and indirect additive genetic effects for the analyzed traits.

### Multiple-Trait Spatial-Competition Mixed Model (MSCM)

$$\begin{aligned} \begin{bmatrix} \mathbf{y}_{DBH} \\ \mathbf{y}_{TH} \\ \mathbf{y}_{WD} \end{bmatrix} &= \begin{bmatrix} \mathbf{X}_{DBH} & 0 & 0 \\ 0 & \mathbf{X}_{TH} & 0 \\ 0 & 0 & \mathbf{X}_{WD} \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_{DBH} \\ \boldsymbol{\beta}_{TH} \\ \boldsymbol{\beta}_{WD} \end{bmatrix} \\ &+ \begin{bmatrix} \mathbf{S}_{DBH} & 0 & 0 \\ 0 & \mathbf{S}_{TH} & 0 \\ 0 & 0 & \mathbf{S}_{WD} \end{bmatrix} \begin{bmatrix} \mathbf{s}_{DBH} \\ \mathbf{s}_{TH} \\ \mathbf{s}_{WD} \end{bmatrix} \\ &+ \begin{bmatrix} \mathbf{Z}_{d,DBH} & 0 & 0 \\ 0 & \mathbf{Z}_{d,TH} & 0 \\ 0 & 0 & \mathbf{Z}_{d,WD} \end{bmatrix} \begin{bmatrix} \mathbf{d}_{DBH} \\ \mathbf{d}_{TH} \\ \mathbf{d}_{WD} \end{bmatrix} \\ &+ \begin{bmatrix} \mathbf{Z}_{c,DBH} & 0 & 0 \\ 0 & \mathbf{Z}_{c,TH} & 0 \\ 0 & 0 & \mathbf{Z}_{c,WD} \end{bmatrix} \begin{bmatrix} \mathbf{c}_{DBH} \\ \mathbf{c}_{TH} \\ \mathbf{c}_{WD} \end{bmatrix} \\ &+ \begin{bmatrix} \mathbf{Z}_{p,DBH} & 0 & 0 \\ 0 & \mathbf{Z}_{p,TH} & 0 \\ 0 & 0 & \mathbf{Z}_{p,WD} \end{bmatrix} \begin{bmatrix} \mathbf{p}_{DBH} \\ \mathbf{p}_{TH} \\ \mathbf{p}_{WD} \end{bmatrix} \\ &+ \begin{bmatrix} \mathbf{e}_{DBH} \\ \mathbf{e}_{TH} \\ \mathbf{e}_{WD} \end{bmatrix} \end{aligned} \quad (5)$$

where  $\mathbf{y}_{DBH}$ ,  $\mathbf{y}_{TH}$ , and  $\mathbf{y}_{WD}$  are the vectors of individual-tree observation for the traits dbh, TH, and WD. The matrices  $\mathbf{X}_{DBH} \oplus \mathbf{X}_{TH} \oplus \mathbf{X}_{WD}$ ,  $\mathbf{S}_{DBH} \oplus \mathbf{S}_{TH} \oplus \mathbf{S}_{WD}$ ,  $\mathbf{Z}_{d,DBH} \oplus \mathbf{Z}_{d,TH} \oplus \mathbf{Z}_{d,WD}$ ,  $\mathbf{Z}_{c,DBH} \oplus \mathbf{Z}_{c,TH} \oplus \mathbf{Z}_{c,WD}$ , and  $\mathbf{Z}_{p,DBH} \oplus \mathbf{Z}_{p,TH} \oplus \mathbf{Z}_{p,WD}$  relate the observation to the means of the genetic groups in  $[\boldsymbol{\beta}'_{DBH} \boldsymbol{\beta}'_{TH} \boldsymbol{\beta}'_{WD}]$ , the vector of coefficients of the tensor products of B-spline basis in  $[\mathbf{s}'_{DBH} \mathbf{s}'_{TH} \mathbf{s}'_{WD}]$ , the direct additive genetic effects in  $[\mathbf{d}'_{DBH} \mathbf{d}'_{TH} \mathbf{d}'_{WD}]$ , the indirect additive genetic effects in  $[\mathbf{c}'_{DBH} \mathbf{c}'_{TH} \mathbf{c}'_{WD}]$ , and the environmental competition effects in  $[\mathbf{p}'_{DBH} \mathbf{p}'_{TH} \mathbf{p}'_{WD}]$ , for the traits dbh, TH, and WD. The vector  $[\mathbf{e}'_{DBH} \mathbf{e}'_{TH} \mathbf{e}'_{WD}]$  is the residual vector. The symbols  $\oplus$  and  $'$  indicate the direct sum of matrices and the transpose operation, respectively. The covariance matrix of the stacked vector of individual additive genetic effects is as follows:

$$\text{var} \begin{bmatrix} \mathbf{d}_{DBH} \\ \mathbf{d}_{TH} \\ \mathbf{d}_{WD} \\ \mathbf{c}_{DBH} \\ \mathbf{c}_{TH} \\ \mathbf{c}_{WD} \end{bmatrix} = \begin{bmatrix} \sigma_{d,DBH}^2 & \sigma_{d,DBH,d_{TH}} & \sigma_{d,DBH,d_{WD}} & \sigma_{d,DBH,c_{DBH}} & \sigma_{d,DBH,c_{TH}} & \sigma_{d,DBH,c_{WD}} \\ \sigma_{d,TH}^2 & \sigma_{d,TH,d_{WD}} & \sigma_{d,TH,c_{DBH}} & \sigma_{d,TH,c_{TH}} & \sigma_{d,TH,c_{WD}} \\ \sigma_{d,WD}^2 & \sigma_{d,WD,c_{DBH}} & \sigma_{d,WD,c_{TH}} & \sigma_{d,WD,c_{WD}} \\ \sigma_{c,DBH}^2 & \sigma_{c,DBH,c_{TH}} & \sigma_{c,DBH,c_{WD}} \\ \sigma_{c,TH}^2 & \sigma_{c,TH,c_{WD}} \\ \sigma_{c,WD}^2 \end{bmatrix} \otimes \mathbf{A}$$

where  $\sigma_{d_i}^2$ ,  $\sigma_{c_i}^2$  for trait  $i$ , and  $\mathbf{A}$  were defined above for the competition mixed model;  $\sigma_{d_i,d_j}$  is the covariance between direct additive genetic effects of traits  $i$  and  $j$ ,  $\sigma_{c_i,c_j}$  is the covariance between the indirect additive genetic effects of traits  $i$  and  $j$ ,  $\sigma_{d_i,c_j}$  is the covariance between the direct additive genetic effects of trait  $i$  and the indirect additive genetic effects of trait  $j$ , and  $\otimes$  denotes the Kronecker product. The covariance matrix for the vector of coefficients of the tensor products of B-spline basis is as follows:

$$\text{var} \begin{bmatrix} \mathbf{s}_{DBH} \\ \mathbf{s}_{TH} \\ \mathbf{s}_{WD} \end{bmatrix} = \begin{bmatrix} \sigma_{s,DBH}^2 & \sigma_{s,DBH,TH} & \sigma_{s,DBH,WD} \\ \sigma_{s,TH}^2 & \sigma_{s,TH,WD} \\ \sigma_{s,WD}^2 \end{bmatrix}$$

where  $\sigma_{s_i}^2$  for the trait  $i$  was defined above, and  $\sigma_{s_i,s_j}$  is the covariance between coefficients of traits  $i$  and  $j$ . The environmental competition effects as symmetric covariance matrix are as follows:

$$\text{var} \begin{bmatrix} \mathbf{p}_{DBH} \\ \mathbf{p}_{TH} \\ \mathbf{p}_{WD} \end{bmatrix} = \begin{bmatrix} \sigma_{p,DBH}^2 & \sigma_{p,DBH,TH} & \sigma_{p,DBH,WD} \\ \sigma_{p,TH}^2 & \sigma_{p,TH,WD} \\ \sigma_{p,WD}^2 \end{bmatrix}$$

where  $\sigma_{p_i}^2$  for the trait  $i$  was defined above, and  $\sigma_{p_i,p_j}$  is the covariance between environmental competition effects of traits  $i$  and  $j$ . Finally, the covariance matrix for residual vector is as follows:

$$\text{var} \begin{bmatrix} \mathbf{e}_{DBH} \\ \mathbf{e}_{TH} \\ \mathbf{e}_{WD} \end{bmatrix} = \begin{bmatrix} \sigma_{e,DBH}^2 & \sigma_{e,DBH,TH} & \sigma_{e,DBH,WD} \\ \sigma_{e,TH}^2 & \sigma_{e,TH,WD} \\ \sigma_{e,WD}^2 \end{bmatrix}$$

where  $\sigma_{e_i}^2$  for the trait  $i$  was defined above, and  $\sigma_{e_i,e_j}$  is the covariance between residuals of traits  $i$  and  $j$ .

### Single-Trait Model Comparison

The AIC ([Akaike 1974](#)) was computed to compare the fit of each of the four single-trait models. The lower the AIC, the better the model, as this outcome indicates a better fit and a lower degree of model complexity. Variance components were compared for the four single-trait models. In addition, the narrow-sense individual heritability was estimated as  $h^2 = \sigma_a^2 / \sigma_{PH}^2$  for the three traits, where the numerator  $\sigma_a^2$  was the estimated additive genetic variance, and the denominator  $\sigma_{PH}^2$  was the estimated phenotypic variance. The phenotypic variance was computed as  $\sigma_{PH}^2 = \sigma_a^2 + \sigma_c^2$  for the standard mixed model and the SM. Regarding the competition mixed model and the SCM, the phenotypic variance was computed as  $\sigma_{PH}^2 = \sigma_d^2 + \sigma_c^2 + \sigma_p^2 + \sigma_e^2$ . The permanent environmental competition effect  $\sigma_p^2$  was included in the phenotypic variance of the competition and the SCM according to previous studies ([Chen et al. 2008](#), [Sartori and Montavani 2013](#), [Bennewitz et al. 2014](#)). For the numerator of the heritability formula in the competition

mixed model and the SCM, the additive genetic variance  $\sigma_a^2$  was replaced with the estimated total additive genetic variance, which was equal to  $\sigma_d^2 + \sigma_c^2$  (Cappa and Cantet 2008, Cappa et al. 2017). This definition of heritability does not adhere to the standard quantitative genetics assumptions for the spatial and SCMs (Cullis et al. 2006), and it should only be interpreted as a descriptive measure of precision (or ability) to detect additive genetic differences among the models.

To study changes in the ranking of offspring trees between models, the proportion of common individuals (PCI%) within the top 5 percent (i.e., 25 trees) was calculated. This variable expresses the ratio between the number of common individuals of two models and the total number of individuals selected by either model (Costa e Silva and Kerr 2013). A further single-trait model comparison was provided by the average accuracy of prediction of BVs and the additive genetic gain for one generation of improvement. To obtain the former value, individual accuracies were calculated using the following equation:

$$r = \sqrt{\frac{1 - PEV}{\sigma^2}} \quad (6)$$

where  $r$  is the accuracy of prediction for each tree, PEV is the prediction error variance of BVs, and  $\sigma^2$  is the additive genetic variance (i.e.,  $\hat{\sigma}_a^2$  or  $\hat{\sigma}_d^2$  depending on the model). The additive genetic gain (G%) was computed as a percentage of the ratio between the response to selection ( $\Delta G$ ) and the phenotypic mean of each trait, using the following expression (Resende 2002):

$$\Delta G = i r \hat{\sigma} \quad (7)$$

where  $\Delta G$  is the additive genetic response to selection,  $i$  is the selection intensity value of 5 percent of the population,  $r$  is the average accuracy of prediction for the population, and  $\sigma$  is the additive genetic standard deviation (i.e.,  $\sigma_a$  or  $\sigma_d$  depending on the model).

### Estimating Genetic Correlations

For the analysis from the multiple-trait SCM, the direct–direct genetic correlation between traits  $i$  and  $j$  was calculated as:  $\sigma_{d_i, d_j}$ , where  $r_{d_i, d_j} = \hat{\sigma}_{d_i, d_j} / \sqrt{\hat{\sigma}_{d_i}^2 \hat{\sigma}_{d_j}^2}$  is the estimated covariance between the direct additive genetic effects of traits  $i$  and  $j$ , and  $\hat{\sigma}_{d_i}^2$  and  $\hat{\sigma}_{d_j}^2$  are the estimated variances of direct additive genetic effects for traits  $i$  and  $j$ , respectively. The indirect–indirect genetic correlation between traits  $i$  and  $j$  was computed as:  $r_{c_i, c_j} = \hat{\sigma}_{c_i, c_j} / \sqrt{\hat{\sigma}_{c_i}^2 \hat{\sigma}_{c_j}^2}$ , where  $\hat{\sigma}_{c_{ij}}$  is the estimated covariance of indirect additive genetic effects for traits  $i$  and  $j$ , and  $\hat{\sigma}_{c_i}^2$  and  $\hat{\sigma}_{c_j}^2$  are the estimated variances of indirect additive genetic effects for traits  $i$  and  $j$ , respectively. The genetic correlation between direct and indirect additive genetic effects was estimated as:  $r_{d_i, c_i} = \hat{\sigma}_{d_i, c_i} / \sqrt{\hat{\sigma}_{d_i}^2 \hat{\sigma}_{c_i}^2}$  and  $r_{d_i, c_j} = \hat{\sigma}_{d_i, c_j} / \sqrt{\hat{\sigma}_{d_i}^2 \hat{\sigma}_{c_j}^2}$  for the same trait  $i$  and different traits  $i$  and  $j$ , respectively, where  $\hat{\sigma}_{d_i, c_i}$  is the estimated covariance between direct and indirect additive genetic effects for trait  $i$ ,  $\hat{\sigma}_{d_i, c_j}$  is the estimated covariance between the direct additive genetic effects of trait  $i$  and the indirect additive genetic effects of trait  $j$ , and  $\hat{\sigma}_{d_i}^2$ ,  $\hat{\sigma}_{c_i}^2$ , and  $\hat{\sigma}_{c_j}^2$  were defined above.

Restricted maximum likelihood (Patterson and Thompson 1971) was used to estimate the variance components of random

effects in the single- and multiple-trait mixed models described above. The statistical analyses were performed with the software R version 3.3.3 (R core team 2017) and the R-package `breedR` (Muñoz and Sanchez 2015) using the function `remlf90`, which is based on the programs `REMLF90` and `AIREMLF90` of the `BLUPF90` library (Miszta 1999). Whereas `REML90` uses the expectation maximization algorithm for estimating variance components, `AIREMLF90` is based on the average information approach. The former is slower but is more robust to any initial value than the latter. The R codes used in this research are available as [Supplementary Material \(see R code S1\)](#).

## Results

### Identification and Quantification of Environmental Heterogeneity and Competition

Table 1 (see also [Supplementary Figure S1](#)) lists the Pearson correlations between residuals of the basic single-trait mixed model and phenotypic means of focal tree neighbors, as well as the correlations between direct and indirect additive genetic effects from the competition mixed model (Equation 3). To begin with, DBH had relatively small and negative coefficients of correlation between residuals and phenotypic means, ranging from  $-.02$  to  $-.13$ . In addition, the genetic correlation between direct and indirect additive genetic effects was high ( $r_{dc} = -.90$ ). These results are consistent with the isotropic empirical semivariogram of residuals from the basic model ([Figure 1a](#)), with no general trend but a decreasing variation at very short range (i.e., a sudden initial drop), a typical pattern of competition.

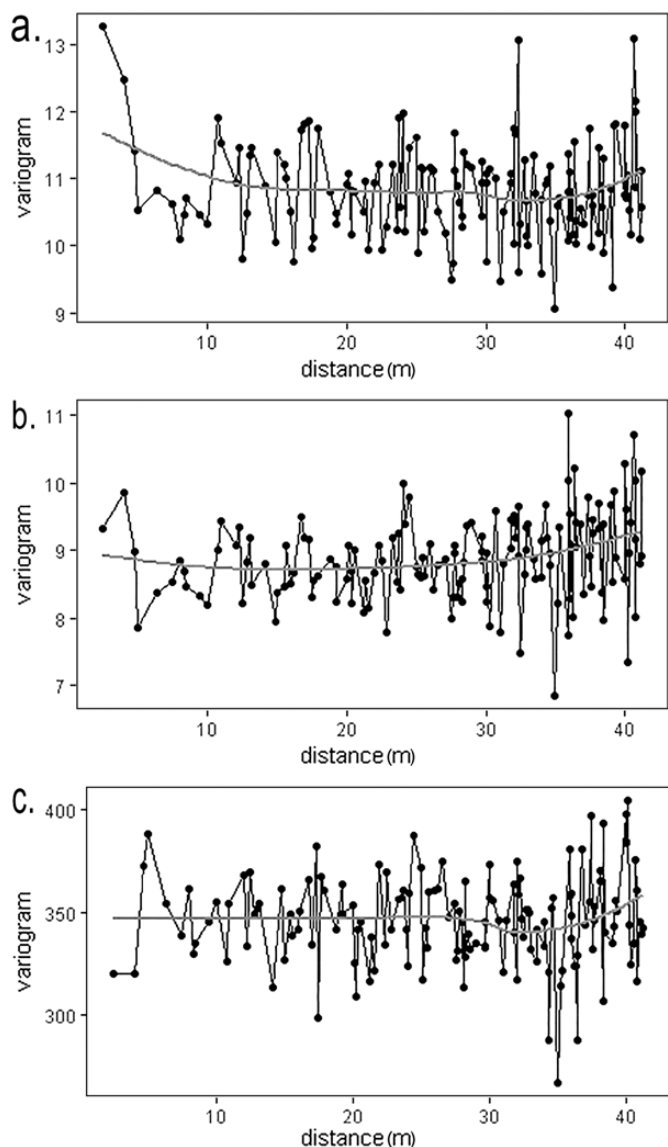
As regards TH, small positive coefficients of correlation between residuals and phenotypic means were found, ranging from  $.02$  to  $.13$ . The genetic correlation between direct and indirect additive genetic effects was negative and moderate ( $r_{dc} = -.39$ ). The residual semivariogram showed a tendency toward increasing variation at very short range with an increment of distance with no general trend ([Figure 1b](#)).

Finally, the correlations between residuals and phenotypic means were around zero for WD ( $-.01$  to  $.05$ ). The genetic correlation between direct and indirect additive genetic effects from the competition mixed model was positive for this trait ( $r_{dc} = .47$ ). As regards the residual semivariogram of WD, the degree of spatial dependence remained constant, showing no general trend ([Figure 1c](#)).

**Table 1. Pearson correlation coefficients ( $r$ ) between residual and phenotypic mean of the  $m$  (maximum 8) first-order neighboring trees (All), and the first-order neighboring trees for the three spatial directions: row (Row), column (Col), and diagonal (Dia); and correlations between direct and competition additive genetic effects from the competition model ( $r_{dc}$ ), for DBH, TH, and WD.**

	DBH (cm)	TH (m)	WD (kg m <sup>-3</sup> )
$r_{All}$	-.11	.13	.03
$r_{Row}$	-.10	.02	.01
$r_{Col}$	-.13	.10	-.01
$r_{Dia}$	-.02	.13	.05
$r_{dc}$	-.90	-.39	.47

*Note:* DBH, diameter at breast height; TH, total height; WD, wood density.



**Figure 1.** Isotropic empirical semivariograms for the analyzed traits: (a) diameter at breast height (DBH, cm), (b) total height (TH, m), and (c) wood density (WD, kg m<sup>-3</sup>).

### Assessment of Statistical Single-Trait Models

Table 2 lists the AIC and estimated dispersion parameters for each trait and all the single-trait models fitted. The performance of the analytical models differed for the different traits, as shown by the values of AIC. In addition, the standard mixed model yielded the highest residual variance for all analyzed characters. As regards the trait diameter, the SM was slightly better than the standard mixed model, because of the addition of a random effect of B-splines with a grid of 9 × 8 knots (change in AIC of 0.24). The inclusion of random effects of genetic and environmental competition decreased the AIC even further for the competition mixed model in comparison with the standard mixed model (change in AIC of 4.09). However, the best performance was found by simultaneously fitting spatial effects (with a grid of 9 × 10 knots) and competition effects (SCM, change in AIC of 4.97). The  $\sigma_d^2$  from the SCM was higher than  $\sigma_a^2$  from the standard mixed model (75.03 percent), whereas  $\sigma_c^2$  from the SCM was lower than the corresponding value from the standard

**Table 2.** Statistics and parameters of the compared models.

Model		DBH (cm)	TH (m)	WD (kg m <sup>-3</sup> )
TM	AIC	3,461.54	3,288.98	5,652.62
	$\sigma_a^2$	8.41	5.40	1,757
	$\sigma_b^2$	0.01	1.18	9.01
	$\sigma_c^2$	15.83	11.07	929.70
	$h^2$	0.35	0.33	0.65
SM	AIC	3,461.30	<b>3,267.42</b>	<b>5,649.14</b>
	$\sigma_a^2$	8.49	5.51	1,730
	$\sigma_s^2$	0.14	2.75	115.50
	$\sigma_c^2$	15.73	10.54	919.70
	$h^2$	0.35	0.34	0.65
CM	AIC	3,457.45	3,290.22	5,656.81
	$\sigma_d^2$	14.60	6.89	1,754
	$\sigma_c^2$	1.33	2.17	40.42
	$\sigma_p^2$	0.22	0.20	52.56
	$\sigma_b^2$	0.15	1.12	0.77
	$\sigma_c^2$	9.08	7.56	855
	$h^2$	0.63	0.54	0.66
SCM	AIC	<b>3,456.57</b>	3,269.45	5,654.62
	$\sigma_d^2$	14.72	7.65	1,720
	$\sigma_c^2$	1.37	1.49	35.44
	$\sigma_p^2$	0.21	0.14	35.93
	$\sigma_s^2$	0.31	2.88	97.53
	$\sigma_c^2$	8.95	7.17	868.90
	$h^2$	0.64	0.56	0.66

*Note:* The lowest AIC values are shown in bold. AIC, Akaike information criterion; CM, competition mixed model;  $\sigma_a^2$ , Estimates of additive genetic variance;  $\sigma_c^2$ , additive indirect genetic variance of competition;  $\sigma_d^2$ , additive direct genetic variance;  $\sigma_p^2$ , variance of environmental competition effects;  $\sigma_b^2$ , variance of block effects;  $\sigma_s^2$ , variance of knots;  $\sigma_c^2$ , residual variance; DBH, diameter at breast height;  $h^2$ , narrow-sense individual heritability; SCM, spatial-competition mixed model; SM, spatial mixed model; TH, total height; TM, standard mixed model; WD, wood density.

mixed model (43.46 percent). Non-negligible indirect additive genetic variances were accounted for in the competition mixed model and the SCM. Heritability values ranged from 0.35 to 0.64 for different models of diameter.

Regarding TH, comparisons to the standard mixed model show that the SCM had a good performance (change in AIC of 19.53), but the fit of the SM was even better, having the lowest AIC with a grid of 10 × 8 knots (change in AIC of 21.56). However, the SCM had a higher reduction in  $\sigma_c^2$  (35.23 percent) than the SM (4.79 percent). Variances of focal tree genotype were similar between the standard mixed model ( $\sigma_a^2 = 5.40$ ) and the SM ( $\sigma_a^2 = 5.51$ ); however, they were higher in the SCM ( $\sigma_d^2 = 7.65$ ). Values of heritability varied from 0.33 to 0.56.

The SM with a grid of 10 × 8 knots was the best model for WD. The competition mixed model and the SCM showed a worse fit (i.e., higher AIC) than the standard mixed model. Estimates of  $\sigma_c^2$  followed the same trend detected on TH, showing that the SCM had a higher reduction in the residual variance (6.54 percent) than the SM in comparison with the standard mixed model. Values of heritability remained constant for the different statistical models.



competition, TH was not so sensitive to them. In a study of three trials of Douglas-fir aged 35 years, [Cappa et al. \(2016\)](#) found that diameter was more sensitive in identifying competition than height, whereas height was more sensitive in detecting environmental heterogeneity than diameter. As reported in the present study, they also noted that the lower the distance between the trees, the higher the competition. Regarding diameter, the same study revealed that the correlation between the phenotypic mean of neighboring trees and residuals of a model without spatial and competition effects was  $-.36$  (higher than that reported in the present study), whereas correlations between direct and indirect genetic effects yielded a maximum value of  $-.84$  (slightly lower than those reported in the present study), showing a strong effect of competition for this trait at residual and genetic levels. It is expected that as the *C. citriodora* trial grows and gets older, competition will increase, resulting in higher negative correlation values than those shown in the present research.

The results showed that single-trait mixed models with spatial and/or competition effects outperformed the standard single-trait model for the three studied traits. The present study also revealed that the performance of the models varied for the different traits ([Table 2](#)). As shown by DBH, the SCM had the best fit when the analyzed trait was more sensitive in detecting competition than environmental heterogeneity. As regards TH, given the relatively slight competition effect at the genetic level ([Table 1](#),  $r_{dc} = -.39$ ), the AIC penalized the additional number of parameters of the SCM. Thus, the SM was a more parsimonious model for this trait, and so the SM was the best model when the analyzed trait was more sensitive in detecting environmental heterogeneity than competition and when the trait did not show sensitivity in detecting either of these effects, as shown by TH and WD, respectively. These results highlight that identifying the ability of a trait to detect environmental heterogeneity and/or competition is an important step for choosing the most suitable statistical model.

### Improvements for Adding Environmental Heterogeneity and Competition

The fit of a smoothed surface reduced the residual variance for the three studied traits ( $\sigma_e^2$ , [Table 2](#)). Despite the fact that this reduction was small, a correct assessment of environmental heterogeneity was achieved by the addition of the more complex structure of B-splines. The reason for this relies on the fact that randomized complete blocks attempt to separate the site's heterogeneity into homogeneous blocks. This notion is idealistic, since two most-distant measurements taken within the same block should in theory share the same variance, whereas two close measurements of the neighboring trees on the border of two blocks are assumed to vary by a different magnitude. Spatial analysis overcomes this issue, accounting for a continuously environmental variation. The fit of the standard mixed model was expectedly abrupt, as block effects are parameters for a categorical variable. On the other hand, the estimated surfaces with spatial and SCMs showed a correct adjustment of continuous spatial variability (see [Supplementary Figure S2](#)). This confirms that there was environmental heterogeneity, which was not adequately accounted for by variances of blocks.

The fit of genetic and environment competition effects induced increases in the additive genetic variance and decreases in the residual variance, according to the sensitivity of each trait in detecting competition. Thus, diameter was the trait with the most significant

changes in values of variance, following by TH. Since WD showed a lack of competition effects, values of additive genetic variance and residual variance did not change significantly with the addition of competition effects. As a result, values of heritability of the competition model and the spatial-competition model increased significantly for diameter and height, whereas they remained stable for WD. On the other hand, heritability values of WD were high for all models, according to registers for this trait in literature ([Zobel and Jett 2012](#)). Since heritability values were obtained from a small population in a single site only, upward bias in additive genetic variance is expected, as the environmental (genotype-by-site) component of variation cannot be quantified. The Argentinian breeding program of *C. citriodora* might take advantage of the effect of competition. Competition exerted by fast-growing trees increases the number of suppressed individuals in the plantation ([Cannell 1983](#)). A breeding strategy based on selecting noncompetitive genotypes of *C. citriodora* might reduce the number of suppressed individuals in forests, increasing yields per unit area of future commercial plantations in Argentina.

In the present study, modeling environmental heterogeneity and competition enabled the analysis to increase accuracies of prediction (both parents and offspring) as well as additive genetic variances, resulting in higher genetic gains ([Table 3](#)). Some comparisons can be made with former studies; however, research about the joint effect of environmental heterogeneity and competition on tree selection is still scarce. Previous studies showed greater improvements than the present research when spatial effects were added to genetic analysis. In studies of DBH in *Eucalyptus globulus*, accuracies of breeding values were improved by 66 percent and 60 percent for parents and offspring, respectively, when B-splines were used in the analysis of a trial with strong spatial trends ([Cappa and Cantet 2007](#)). The current research does not show such pronounced spatial tendencies, which resulted in lower accuracies of breeding values when a spatial structure was added. Also, by including a spatial structure in the analysis of height in *Pinus sylvestris* trials, [Cappa et al. \(2011\)](#) enhanced the accuracy of breeding values by up to 46.03 percent and 44.68 percent for parents and offspring, respectively. Unlike the present work, this previous study was designed as a simple completely random experiment with parcels of 50 plants, thus enabling this analysis to obtain greater improvements than the current study when a spatial structure was added. [Dutkowski et al. \(2006\)](#) used spatial effects to estimate accuracies of breeding values, showing improvements up to 0.2 for WD for some trials, whereas other trials did not show enhancement, such as the present research. The same study found that the maximum genetic gains were around 20 percent for diameter. The present work shows higher genetic gains for this trait. This could be explained by the fact that the genetic gains were increased by the addition of competition effects.

### Genetic Correlations

Direct-direct genetic correlations have been recorded for growth traits and WD in previous research on the genus *Corymbia*. The high and positive genetic correlations between diameter and height found in this research ( $r_{d_{DBH}d_{TH}} = .98$ ) confirmed previous studies in which values varied from .84 to 1 ([Sato et al. 2010](#), [Lan et al. 2011](#), [Hung et al. 2016](#)). Correlations around zero between growth traits and WD agreed with the finding that diffuse-porous hardwoods have





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