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Age trends in genetic parameters for growth performance across country-wide provenances of the iconic conifer tree *Araucaria angustifolia* show strong prospects for systematic breeding and early selection

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ABSTRACT

Understanding the growth patterns of long-lived conifer tree species is important to devise breeding and early selection strategies, predict future biomass productivity and assess adaptive tree fitness for long term conservation efforts. We investigated the genetic variation for growth traits of *Araucaria angustifolia,* the grandiose renowned "Paraná pine" tree, in a trial involving 122 families across 15 provenances covering the entire natural range of the species in Brazil. Measurements at ages 7, 24, 32, 33 and 35 were used to adjust continuous growth curves based on nonlinear mixed-effect models for all 2158 trees, providing annual estimates for unmeasured ages in the 7-to-35-year interval. Estimated values closely matched observed ones and a reduction of the coefficient of residual variation was observed in the estimated data, possibly due to removal of random error in the observed measurements, making the estimated curves more reliable to predict growth patterns. Genetic variation for growth within provenances was greater than between, with a trend of increasing heritabilities over time for most provenances. Substantial genetic variation found both within and between families could drive efficient early selection at both levels. All provenances included individual trees and families with good potential to be selected for shorter rotations. Growth curves show that trees invest first in height and later in diameter growth. Considerable variation was observed across provenances for the optimal age and optimal tree volume at which annual growth increment peaks, a tipping point that could be used as a predictor of the optimal rotation age and expected tree volume. The data clearly indicate potential for early selection for growth at age 7–10 with an 85% prediction accuracy of growth at age 35. Additionally, growth data indicate potential of shortening harvest age from 30–35 to 15–20 years by selecting the best individuals and families. These results underscore the potential of expanding investments in breeding and plantation forestry of *A. angustifolia,* which in parallel could contribute to enhancing conservation efforts of this iconic subtropical conifer.

1. Introduction

Paraná pine [*Araucaria angustifolia* (Bertol.) O. Kuntze.] is an iconic long-lived subtropical conifer distributed exclusively in South America, with most of its populations concentrated in southern and southeastern Brazil (Reis et al., 2014), and some populations also found in Argentina and Paraguay. Other 19 species in the genus are found in Australasia and one in South America, such as *Araucaria araucana* (Molina) K. Koch in Chile and Argentina, *Araucaria bidwillii* Hooker and *Araucaria cunninghamii* Aiton ex D.Don in eastern Australia and New Guinea, and *Araucaria hunsteinii* Schumann in New Guinea (Zonneveld, 2012). In Brazil, since the last century the original extension of the *A. angustifolia* forest, estimated at approximately 200,000 km^2 has declined by more than 97% (Medina-Macedo et al., 2014). The interest in its very high-quality

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timber and the expansion of agricultural frontiers in high fertility lands in the southern regions are the main causes of this severe reduction. Despite its status of ‘Critically Endangered’ according to IUCN Red List of Threatened Species (Thomas, 2013), and a specific law in Brazil (BRASIL, 2001) aiming at the conservation of *A. angustifolia* by strictly limiting cutting and fostering the exploration of its edible seeds and other products, some small farmers still insist on clandestine thinning of trees and removal of seedling regenerants.

Species and ecosystem conservation in Brazil has advanced by the creation and management of Conservation Units throughout the country (Montagna et al., 2012). Additionally, *ex situ* conservation strategies have played a key role for the maintenance of biological and genetic resources (Ferreira et al., 2012). In the case of highly valuable forest trees such as *A. angustifolia*, forest plantations could serve as supplementary important storehouses of genetic diversity, by ensuring genetic composition mirroring natural populations (Stefenon et al., 2008). The investment in breeding programs of the species could therefore have a positive effect both on the conservation of genetic diversity in germplasm banks paired with the utilitarian purpose of producing highly valuable wood. Genetic improvement strategies that also include conservation efforts have been a reality for conifers in countries with temperate climates. In addition, the slow tree growth compels the forest growers to adopt sustainable exploitation plans (Farjon and Page, 1999). In Brazil, while exotic *Eucalyptus* and *Pinus* species have received great attention from the germplasm conservation and breeding efforts given their exceptional silvicultural performance and economic value (IBA, 2020), advances in conservation allied to breeding for native forest trees is still timid. *A. angustifolia*, has been somewhat of an exception given its keystone ecological role and valuable wood, with some efforts throughout the years with the establishment and evaluation of provenance and progeny trials (Kageyama and Jacob, 1979; Shimizu, 1999; Sebbenn et al., 2003; da Silva et al., 2018). In an previous study, considerable variation was reported for growth and stem form at early ages between different populations of *A. angustifolia*, and also between individual trees within populations (Sebbenn et al., 2003). Opportunities, therefore, exist to improve the silvicultural value of the species by identifying the best wild seed sources and selecting individuals within them to develop varieties that are considerably better than the wild material. Additionally, understanding the geographical distribution of ecologically relevant genetic variation and the environmental factors driving adaptive divergence within species will help ensuring appropriate sourcing of material not only for the structuring of tree breeding programs but also for ecological restoration and conservation prioritization (Lu et al., 2016).

Provenance trials combined with progeny (family) tests provide a rich foundation to inform breeding and serve as valuable repositories to source material for conservation and restoration (O’Brien et al., 2007; White et al., 2007). These kinds of studies have been important drivers of breeding for a large number of economically important forest trees including species of *Pinus* (Dieters et al., 1995; Haapanen, 2001; Hodge and Dvorak, 2001; Kroon et al., 2011), *Cryptomeria* (Hiraoka et al., 2019) and *Eucalyptus* (Stackpole et al., 2010) to name a few. To date while much is known about patterns of geographic variation for temperate and subtropical forest trees, fewer are studies with tropical species. Noteworthy is the important effort of gene conservation and breeding through provenance/progeny trials carried out by CAMCORE for tropical pines (Hodge and Dvorak, 2001) and more recently with tropical *Eucalyptus* (Hodge and Dvorak, 2015). Following provenance and progeny trials, tree breeding involves sequential steps of mating, testing and selection to increase the frequency of useful alleles for several traits concurrently in a target population. Quantitative data are used for estimating genetic variances, types of genetic action, heritabilities and genetic correlations for the key traits, and results used to predict and estimate gain with successive selection cycles (Lynch and Walsh, 1998). In practice, however, there is strong economic pressure to reduce the time needed to complete a breeding cycle (White et al., 2007) and to shorten the rotation cycle of a production forest (Haapanen et al., 2016). Especially in slow growing species, early indirect selection is key and has been widely investigated for conifer species such as those in genera *Pinus* (Lambeth, 1980; Foster, 1986; Carter et al., 1990; Gwaze et al., 2002; Weng et al., 2007; Chauhan et al., 2013), *Picea* (Newton, 2003) and *Larix* (Dong et al., 2019) as examples.

Besides quantitative genetic parameters, knowledge of the growth behavior of a forest tree species is a key element, be it for early genetic selection, prediction of future biomass production, or to understand patterns of adaptive fitness (Bowman et al., 2013). Hess and Schneider (2009), evaluating three sites in southern Brazil, described *A. angustifolia* height growth as a sigmoid form, with higher rates of increase between 15 and 20 years, and a trend of stagnation after 30 years. These same authors demonstrated that the Araucaria diameter presents a sigmoid growth form in the three environments evaluated, with higher rates of increase between 20 and 33 years, depending on the region (Hess et al., 2009). Similarly, height growth of Scots Pine, between ages four and 18 years, was described as approximately linear by Haapanen (2001), but suggesting a moment of inflection after these earlier ages. In forestry, it is common to use nonlinear functions such as Weibull, Chapman-Richards and Logistics, to describe tree growth, and in particular, random-effect models are interesting for tree-to-tree growth estimates (Subedi and Sharma, 2011), allowing for greater flexibility of the model for growth projections taking into account the particular effects of the site on individual development or even its genetic features.

In this study, we investigated the genetic variation for growth traits in a *A. angustifolia* provenance and progeny (family) trial during a 35-year growth period involving 122 open pollinated families from 15 provenances collected across four Brazilian states. Our objectives were: i) to present an efficient methodology to estimate growth in *A. angustifolia* for unmeasured ages; ii) to assess the variation in genetic parameters for growth traits across provenances and ages; and iii) to evaluate the efficacy of early genetic selection within and between families and provenances. The underlying goal of the study was to provide an update on the long-term growth patterns and age trends in genetic parameters of the most comprehensive genetic trial of *Araucaria angustifolia* currently running in Brazil to potentially foster initiatives toward more systematic breeding and plantation of this iconic Brazilian conifer.

2. Material and methods

2.1. Sampling and experimental design

The field experiment was originally described in Sebbenn et al. (2003). In brief, seeds from open-pollinated families were collected from trees sampled in 15 natural populations of *A. angustifolia* henceforth called provenances, in four Brazilian States - Minas Gerais (MG) São Paulo (SP), Paraná (PR) e Santa Catarina (SC) (Fig. 1). A total of 122 families were sampled, with the number of families per provenance varying from four to 14 (Table 1). The experiment was set up in the Itapeva Experimental Station of the São Paulo State Forest Institute (24°17′ S, 48°54′ W and 930 m altitude). The trial was established in a compact-family design, with 15 provenances (plots), with four to 14 families per provenance (subplots), 10 individuals per subplot and three replicates in a 3 m × 2 m spacing and borders consisting of two rows. Seeds were collected in May 1979 and seedlings planted in March 1980. The trial was measured after four, seven, 24, 32 and 35 years for total tree height (HEI) in meters and after seven, 24, 32, 33 and 35 years for diameter at breast height (DBH) (1.3 m from the ground) in centimeters. All measurements were used to adjust the individual growth curves for all 2,158 surviving trees but for standardization and better quality of the adjusted values only data from measurements conducted between ages seven and 35 were used in the genetic models analyzed.

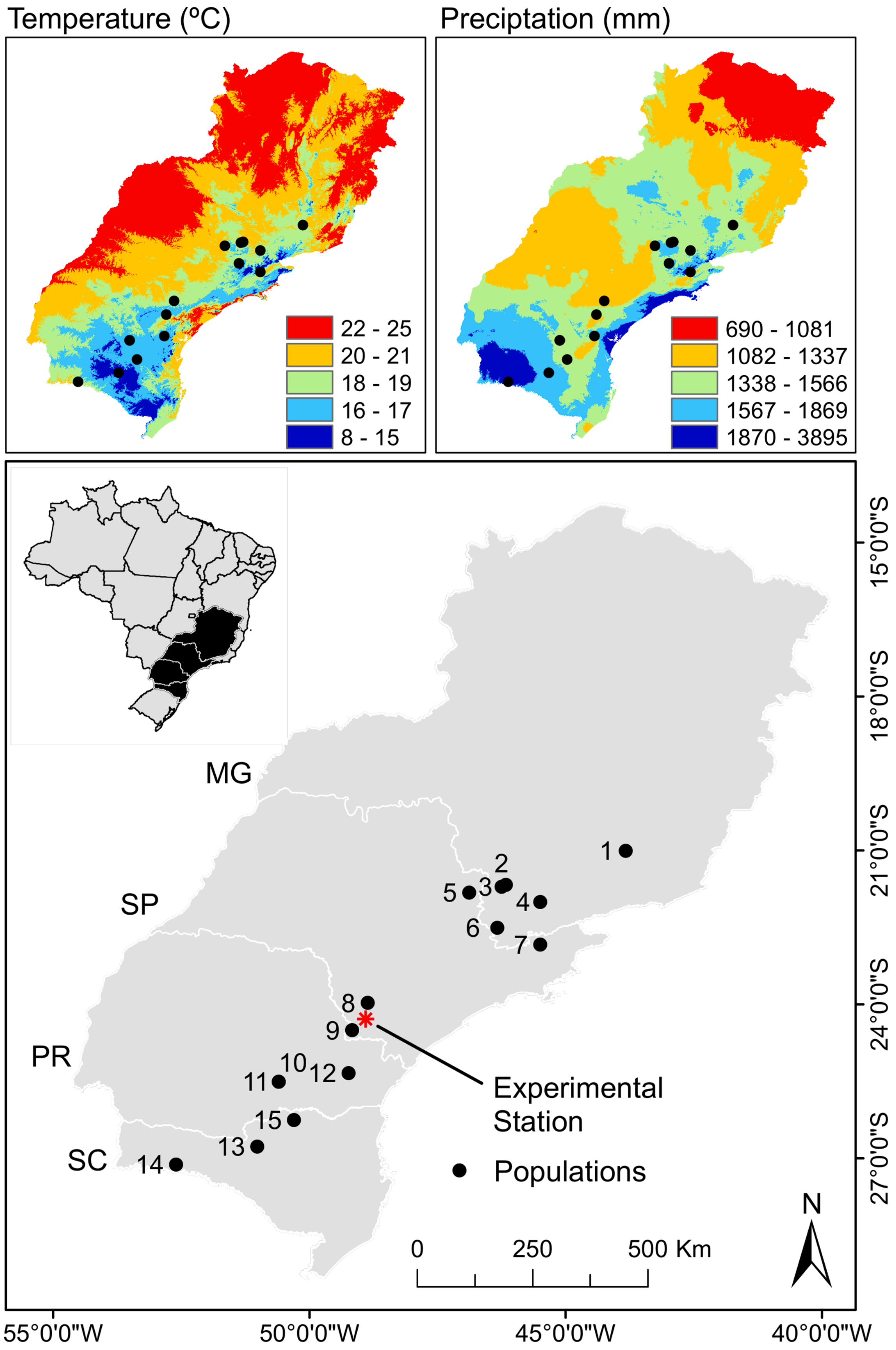

Fig. 1. Top panels: temperature and precipitations distributions charts in the sampled region. Bottom panel: geographic location of the 15 *Araucaria angustifolia* provenances studied: 1. Barbacena – MG; 2. Ipiúna de Calda, MG; 3. Congonhal, MG; 4. Lambarí, MG; 5. Vargem Grande do Sul, SP; 6. Camanducaia, MG; 7. Campos do Jordão, SP; 8. Itapeva, SP; 9. Itararé, SP; 10. Iratí, PR; 11. Iratí (Tardio), PR; 12. Quatro Barras, PR; 13. Caçador, SC; 14. Chapecó, SC; 15. Três Barras, SC. Indicated also the experimental station where the provenance/family field trial was located. Locations of provenances 10 and 11 overlap showing as a single dot in the chart.

Table 1
Descriptive statistics of the *Araucaria angustifolia* provenance and family trial studied and evaluated trait means at age 35 years adopted as a benchmark.

Provenance	No. of Trees	No. of living Trees	Surviving rate (%)	Families count	Average number of individuals within family	Trait average (at age 35 yr)		
						HEI (m)	DBH (cm)	VOL (m^3)
1	270	154	57.04	9	17.11	18.86 ± 0.31	21.92 ± 0.57	0.49 ± 0.03
2	430	238	55.35	14	17.00	18.37 ± 0.27	21.64 ± 0.51	0.50 ± 0.03
3	180	112	62.22	6	18.67	18.93 ± 0.40	21.46 ± 0.73	0.49 ± 0.04
4	150	84	56.00	5	16.80	19.58 ± 0.41	24.28 ± 0.97	0.64 ± 0.05
5	150	110	73.33	5	22.00	19.27 ± 0.32	20.65 ± 0.65	0.45 ± 0.03
6	210	113	53.81	7	16.14	17.70 ± 0.35	20.01 ± 0.75	0.42 ± 0.04
7	270	186	68.89	9	20.67	15.74 ± 0.30	18.25 ± 0.51	0.32 ± 0.02
8	270	134	49.63	9	14.89	17.46 ± 0.34	19.98 ± 0.62	0.40 ± 0.03
9	300	146	48.67	10	14.60	16.94 ± 0.34	19.04 ± 0.60	0.36 ± 0.02
10	210	117	55.71	7	16.71	17.91 ± 0.32	20.45 ± 0.62	0.41 ± 0.03
11	300	189	63.00	10	18.90	17.28 ± 0.26	18.37 ± 0.46	0.33 ± 0.02
12	270	180	66.67	9	20.00	15.14 ± 0.29	17.25 ± 0.48	0.27 ± 0.02
13	120	67	55.83	4	16.75	14.18 ± 0.46	16.07 ± 0.81	0.23 ± 0.03
14	270	159	58.89	9	17.67	17.31 ± 0.32	19.29 ± 0.53	0.37 ± 0.02
15	270	169	62.59	9	18.78	16.54 ± 0.27	17.45 ± 0.44	0.28 ± 0.02
All	3670	2,158	59.18	122	17.78	17.37 ± 0.09	19.65 ± 0.16	0.39 ± 0.01

2.2. Extrapolation modeling of HEI and DBH to the entire 7-to-35-year growth range

Modeling was applied to provide a full range of year-to-year estimates of growth in DBH and HEI for individual trees. To that end an adjustment was carried out using adequate growth functions and individual plant growth modeling (Burkhart and Tomé, 2012). Random nonlinear models were applied using the function ‘nlme’ in R (Pinheiro et al., 2016).

The main motivation for using non-linear random models was the ability to predict data outside the sampled range (Calegario et al., 2005), especially for trees that have missing data for early or late ages. In addition, modeling presents the opportunity to correct unreliable data, such as non-sampling errors, or trees that oddly seem to have shrunk over time. We used the methodology described by Calegario et al. (2005) and Lindstrom and Bates (1990) to adjust the continuous growth of the trees based on nonlinear mixed-effect models. The variable considered x_{ij} represents the i-th tree on j-th measurement time, being $i = [1, 2, \cdots, 2158]$ trees and $j = \{4, 7, 24, 32, 35\}$ for HEI and $j = \{7, 24, 32, 33, 35\}$ for DBH, in years. All ages contain approximately the same number of trees, except for missing data.

The non-linear function $x_{ij} = F(\theta_{ij}, v_{ij}) + \int_{ij}$ could be applied to represent the relationship between the response variable and the covariates within the ith tree, where F is a general function of a group-specific parameter vector θ_{ij} and a covariate vector v_{ij}, and ϵ_{ij} is a normally distributed within-group error term. The parameter vector θ_{ij} has the form:

$$\theta_{ij} = L_{ij}\beta_i + K_{ij}r_i \tag{1}$$

$$r_i\ N(0, \varphi)$$

where β is a vector of fixed effects; r_i is a vector of random effects associated with the ith tree; and L_{ij} and K_{ij} are incidence matrices of random and fixed effects, respectively. In the basic assumptions, the within group errors are independently distributed with mean zero and variance σ^2 and independent of the random effects.

The Chapman-Richards (Eq. [2]), function was chosen to estimate plant height over time following the instructions described earlier (Hess and Schneider, 2009). The function chosen to estimate DBH over time was the Logistic function (Eq. [3]) based on the comparison to other non-linear functions which proved to be precise and flexible in this case (results not shown).

Chapman-Richards model for estimating HEI:

$$HEI_{ij} = \theta_{1i}\left[1 - exp^{\left(-\theta_{2i}t_{ij}\right)}\right]^{\theta_{3i}} + \varepsilon_{ij} \tag{2}$$

Logistic model for estimating DBH:

$$DAP_{ij} = \frac{\theta_{1i}}{1 + exp^{\left(\theta_{2i} - t_{ij}\right)/\theta_{3i}}} + \varepsilon_{ij} \tag{3}$$

where, HEI_{ij} and DAP_{ij} are respectively plant height and diameter at breast height for the i-th tree on the j-th age; t_{ij} is the age (time) in j years of the tree i; ε_{ij} is the random error.

$$\theta_i = \begin{bmatrix} \theta_{1i} \\ \theta_{2i} \\ \theta_{3i} \end{bmatrix} = \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} r_{1i} \\ r_{2i} \\ r_{3i} \end{bmatrix} = \beta + r_i \tag{4}$$

$$r_i\ N(0, \varphi), \varepsilon_{ij}\ N\left(0, \sigma^2\right)$$

Here, β is a vector of fixed effects and r_i represents the vector of random effects. ε_{ij} and r_i are independents.

The individual volume estimate of the tree (VOL) in m^3 was obtained according to Sanquetta et al. (2016), using a Spurr Log model, as follows:

$$lnVOL = -9,6687 + 0,9650\left[ln\left(DBH^2 HEI\right)\right] \tag{5}$$

2.3. Genetic modeling

For modeling the phenotypic growth values (HEI, DBH and VOL), the mixed model of Eq. [6] was used. The execution of the model was done in R by using the function ’regress’ (Clifford et al., 2014). However, to speed up simultaneous adjustments for each of the ages, its configuration was inspired by model #5 of the free software SELEGEN REML-BLUP (Resende, 2016): complete blocks, several provenances, half-sib families tested in one location (Fig. 1):

$$y = Xb + Za + Wp + Ts + e \tag{6}$$

where y is the data vector (HEI, DBH or VOL); b is the blocking effect vector (presumed as fixed effects) summed to overall average; a is the vector of individual additive genetic effects (presumed as random effects); p is the plot effect vector (presumed as random effects); A is the Half-sib relationship matrix between all 2,158 individuals; s is the provenance effect vector (random) and e is the error or residuals vector (random). The capital letters X, Z, W, and T represent the incidence matrices for these effects. The variance structure of the model was as follows:

$$a|A, \sigma_a^2\ N\left(0, A\sigma_a^2\right)$$

$$p|\sigma_{plot}^2\ N\left(0, I\sigma_{plot}^2\right)$$

$$s|\sigma^2_{prov}\ N\left(0, I\sigma^2_{pop}\right)$$

$$e|\sigma^2_e\ N\left(0, I\sigma^2_e\right)$$

Narrow-sense heritability was obtained by: $h^2_a = \sigma^2_a / \left(\sigma^2_a + \sigma^2_{prov} + \sigma^2_{plot} + \sigma^2_e\right)$; the coefficient of provenance determination was obtained by: $c^2_{prov} = \sigma^2_{prov} / \left(\sigma^2_a + \sigma^2_{prov} + \sigma^2_{plot} + \sigma^2_e\right)$. It should be noted that $\sigma^2_a + \sigma^2_{prov} + \sigma^2_{plot} + \sigma^2_e$ correspond to the component of the phenotypic variance of the model. To adjust the parameters for each provenance k, being $k = [1, 2, \cdots, 15]$, the reduced form of the model from Eq. [6] was adopted:

$$y_k = X_k b_k + Z_k a_k + T_k s_k + e_k \tag{7}$$

where, y, the effects b, a, s, e, the incidence matrices X, Z and T and the variance structures are corresponding to those of Eq. [6]. Heritability in the narrow sense for each k provenance was obtained by: $h^2_a k = \sigma^2_a k / \left(\sigma^2_a k + \sigma^2_{plot} k + \sigma^2_e k\right)$. It is important to note that the models of equations [6] and [7] were repeated individually for each of the ages (7–35 years).

Genetic correlations (r_{gg}) within families were estimated based on Pearson correlations between predicted genetic values for each year ($\hat{a}$, from Eq. [6]). This strategy was adopted to generate inferences about early selection, since when measuring data at a given time j, i.e., data at $j+1$ is unknown. It was also for this same reason that the models were adjusted individually for each year, so that the data increment of other years did not provide an unrealistically better fit than expected.

The calculation of the genetic correlations between families was done in a manner analogous to the genetic correlation between individuals (within families), replacing the additive component of Eq. [6] with the family index vector making $y = Xb + Qf + Wp + Ts + e$, where f is the random effects of the 122 families and Q is their respective incidence matrix. The other components are described in Eq. [6]. Genetic correlations between families were finally obtained through Pearson's correlation between the random effects of families between each of the evaluated years. Models of equations [6] and [7] are reciprocal given that $\sigma^2_a = 4\sigma^2_f$. To provide an initial assessment of the potential of the trial for directional early selection, three selection intensities were simulated on the 2,158 trees evaluated, namely, high: 1% (22 individuals), intermediate: 5% (108 individuals) and low: 10% (216 individuals). For each trait separately, these selection intensities (1%, 5% and 10%) were applied on the estimated data at each age independently, yearly from 7 to 35 years. All trees and their respective family and provenance that were selected in at least one age were recorded to constitute the final number of selected trees.

3. Results

3.1. Random regression estimates

Annual growth was estimated from age seven to 35 years for 2,158 *A. angustifolia* trees (Fig. 2). Parts 'a' and 'b' show the relationship between the observed and model estimated values. Points scattered below the dashed line (45°) correspond to trees that have "shrunk" over time. In other words, measurement or annotation errors that occurred during data collection, causing the data to differ from the true values, suggesting greater reliability in the estimated values than in the observed ones. Scattered points above this line are likely recording errors super estimating the actual measurements. Graphs in 'c' and 'd' show that the residues concentrate strongly around zero, indicating some rare observed values with deviation between 10% and 20%. Parts 'e' and 'f' show the behavior of the adjusted growth data over time for a randomly taken sample of 25 trees. It is noted that for HEI, growth stagnation generally starts around age 30 years, while for DBH the growth is still in full swing at that same age for most trees. The relationship between DBH and HEI for different time scales is shown in Supplementary Figure S1. Even at age 35 *A. angustifolia* does not show biomass growth stagnation, but a deceleration in height increments can already be noticed. The red curves corresponding to the relationship for the sequential ages show that the trees invest slightly more in height growth early on and as time passes this trend shifts to diameter growth. To validate the estimated data, the parameter estimates were compared for both the observed data and the estimated data (Table 2). For comparison, only ages seven, 24, 32 and 35 were used when coincident measurement for HEI and DBH were taken.

3.2. Genetic parameters from observed and modeled data

The modeling approach used to provide estimates of growth data for the entire time span showed good agreement between the observed and estimated data at the four ages for which coincidental measurements were taken for HEI and DBH. A coefficient of determination R^2 above 0.9 was already observed for both traits at age 7, increasing above 0.98 at age 35 with a concurrent reduction of Root Mean Square Error (RMSE) down to the 3–5% range (Table 2). This result is also illustrated by the overall small differences between the estimates of genetic parameters (heritability and variance components) obtained with observed and estimated data for essentially all genetic parameters. The good agreement observed between the observed and estimated data support the growth data modeling employed for the unsampled ages (Fig. 2). This agreement might be explained by an improved capture of the genetic variance in the estimated data due to the absence of non-sampling errors. This is also shown by a reduction of the coefficient of residual variation CV_e in practically all the ages for both traits. The coefficients of determination of provenances (c^2_{pop}) were constant across the four measured ages and greater than the heritability in the narrow sense (h^2_a) only at age seven years. By performing a naïve Chi-square test of observed against estimated data among the four variances of the models, *p-values* obtained were 0.63–0.99 for HEI and 0.83–0.99 for DBH, indicating no significant difference between the parameters for the two traits.

The additive genetic variance showed an exponential increase from age 7 to age 24 for both traits but while for HEI it practically leveled off at age 24, for DBH it had a further increase from age 24 to 35 (Table 2). This increase in genetic variance is mirrored by an equivalent increase in heritabilities from age 7 to 24 and the same pattern of leveling off after that age (Table 2). Provenance specific estimates of individual narrow sense heritabilities (colored lines) were obtained across all ages showing considerable variation across provenances, although generally increasing with age, as also shown by the overall estimate (dashed black line) (Fig. 3). Note that the overall heritability within provenances (black dashed line) is greater than the heritability between provenances (red dotted line) as expected (Vencovsky et al. (2012), while most individual-provenance heritabilities (colored lines) are substantially higher. Provenances 8, 2, 6, 10 (for HEI); 6, 10, 8, 13, 11, 9, 2 (for DBH); and 6, 10, 8, 2, 11, 13 (for VOL) are the ones with greater genetic variability and probably those that will allow greater gains from directional selection while provenances 1, 3, 12, and 15 conversely are the ones displaying the lowest genetic variance in the trial site.

Estimates of average growth traits for the 15 provenances show the same overall ranking across ages, with southeastern region provenances 1–5 showing considerably higher growth rates for all traits when compared to the remaining provenances, and provenance 4 from the municipality of Lambarí, state of Minas Gerais, showing the most outstanding average performance (Fig. 4). Southern provenances 12, 13 and 15 had the worst overall performances and provenances 8 and 9, located closest to the experimental site showed an average performance.

Age-age genetic correlations between all ages and age 35 for the

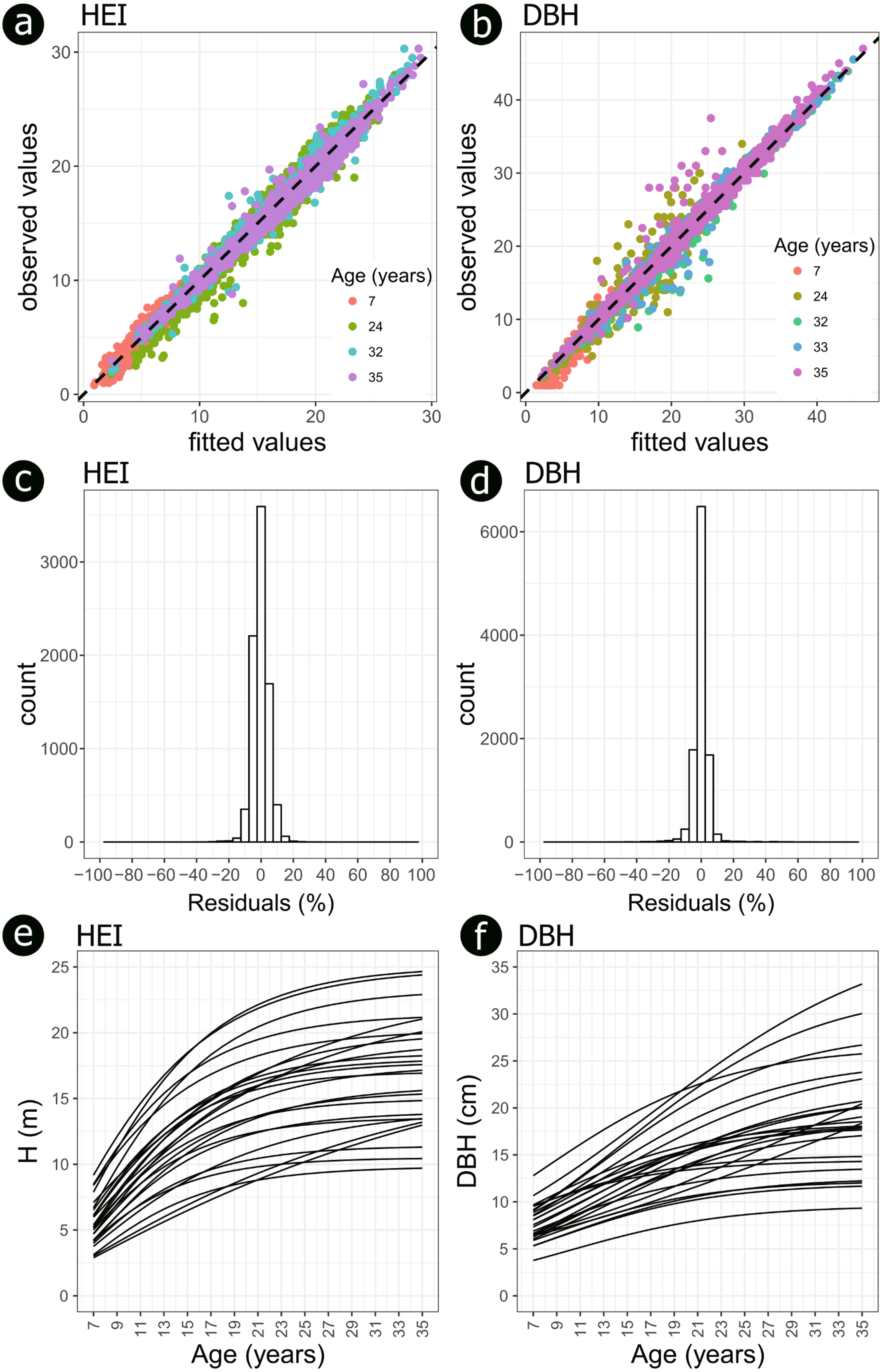

Fig. 2. Annual estimates of Tree Height (HEI) and Diameter at Breast Height (DBH) of 2,158 *Araucaria angustifolia* trees in the trial. Panels “a” and “b”: dispersions of observed versus model fitted estimated values for the two traits. Panels “c” and “d”: residuals histogram in percentage. Panels “e and “f”: growth curves of 25-tree samples across ages 7–35-years.

Table 2
Summary of the quantitative genetics parameters for height (HEI) and diameter at breast height (DBH) from observed data and estimated data with the non-linear random regression adjustments.

Parameter	HEI			
	07 yr	**24 yr**	**32 yr**	**35 yr**
R^2	0.914	0.962	0.982	0.984
RMSE (%)	9.984	5.819	3.159	3.502
$\bar{y}$**(m)**	5.48 / 5.66	16.47 / 16.14	17.14 / 17.17	17.22 / 17.52
h_a^2	0.004 / 0.009	0.157 / 0.153	0.190 / 0.176	0.177 / 0.181
c_{prov}^2	0.114 / 0.110	0.076 / 0.118	0.121 / 0.121	0.133 / 0.122
σ_a^2	0.011 / 0.021	2.774 / 2.070	2.973 / 2.701	2.727 / 2.860
σ_{prov}^2	0.317 / 0.243	1.343 / 1.601	1.894 / 1.863	2.049 / 1.922
σ_{plot}^2	0.339 / 0.304	1.362 / 1.022	1.133 / 1.118	1.921 / 1.148
σ_e^2	2.107 / 1.641	12.242 / 8.834	9.620 / 9.664	9.369 / 9.848
CV$_e$ (%)	13.597 / 11.975	10.330 / 8.841	8.821 / 8.746	8.993 / 8.759
	DBH			
	07 yr	**24 yr**	**32 yr**	**35 yr**
R^2	0.967	0.971	0.991	0.985
RMSE (%)	8.206	5.785	3.676	4.738
$\bar{y}$**(cm)**	8.13 / 8.31	17.28 / 17.25	19.04 / 19.21	20.03 / 20.08
h_a^2	0.005 / 0.007	0.218 / 0.206	0.250 / 0.256	0.233 / 0.266
c_{prov}^2	0.087 / 0.087	0.052 / 0.068	0.060 / 0.062	0.062 / 0.061
σ_a^2	0.052 / 0.052	7.284 / 6.537	11.884 / 11.931	12.464 / 13.638
σ_{prov}^2	0.824 / 0.611	1.740 / 2.161	2.835 / 2.895	3.294 / 3.112
σ_{plot}^2	0.834 / 0.753	1.197 / 1.265	1.059 / 1.321	1.830 / 1.341
σ_e^2	7.773 / 5.633	23.220 / 21.745	31.697 / 30.507	35.970 / 33.185
CV$_e$ (%)	15.926 / 13.705	11.991 / 11.404	11.785 / 11.851	12.474 / 12.033

OBS / EST: Estimated parameters using the Observed data (left of the slash) and those estimated by the random regression models (right of the slash); h_a^2: heritability in the narrow sense (i.e. additive); c_{prov}^2: provenance coefficient of determination; σ_a^2: additive genetic variance; σ_{prov}^2: variance between provenances; σ_{plot}^2: variance between experimental plots; σ_e^2: variance within experimental plots.

three traits are shown in Fig. 5a. Both correlations for individual trees within families and among families followed the same trend, although slightly higher values were seen for among family's correlations. Correlations were high and increased over time and approached unity at age 35. Correlations ranged from 0.83 to 1.00 for HEI, 0.81 to 1.00 for DBH and from 0.75 to 1.00 for VOL. The strongest age-age correlations at both levels were seen for HEI. Expected genetic gains for growth at age 35 following early selection at different ages were estimated based on breeding values (Fig. 5-b). Consistent with the age-age correlations graphs, expected gains from early selection increased when approaching the target age without showing any plateauing, indicating that the maximal gain will likely be made only at age 35. In each age independently (annually from 7 to 35 years) three selection intensities were applied on the estimated data for all 2,158 trees evaluated, namely, high: 1% (target number of 22 individuals), intermediate: 5% (target number of 108 individuals) and low: 10% (target number of 216 individuals) for each trait. All trees and their respective family and provenance that were selected in at least one age were recorded to constitute the final number of selected trees (nID) (Table 3) that met the selection plan described above. For example, for the 1% selection intensity for HEI, not necessarily the same 22 trees were selected in all ages, but a total of 46 were eventually selected, as age-age genetic correlations, although high, were not equal to 1. In other words, the selection intensities specified above were applied in each age separately and because the age-age genetic correlations are not equal to 1, the final number of selected trees in this assessment is numerically higher than the target number of individuals with the age-specific selection intensity applied. Percent gains were 5 to 10X higher when selecting for VOL when compared to HEI and DBH and, as expected, increased with increasing selection intensity (lower percent selected). Despite the large performance differences among the provenances, superior trees for growth were observed in all fifteen provenances, especially when performing selection with intermediate (5%) and low intensities (10%) (Table 3), consistent with the large amount of within-provenance genetic variation observed in the species.

4. Discussion

We have presented a comprehensive picture of age trends in genetic parameters and growth curves of the most genetically inclusive provenance and family trial of *A. araucaria* available to date. Using a modeling approach that allowed generating data for unsampled ages, a set of high-quality year-to-year growth and genetic parameter estimates were obtained for diameter at breast height (DBH), total tree height (HEI) and individual volume (VOL) for 2,158 individuals, corresponding to about 59% of the trees that survived the originally planted experiment. This unique long-term provenance, family and individual level growth dataset, encompassing a countrywide representation of *A. araucaria* natural populations, represents a valuable asset, together with the actual trial, for genetic improvement, germplasm conservation and restoration efforts of this highly valuable species, still largely unexploited from the point of view of sustainable forest plantation.

4.1. Patterns of heritability change with age

Genetic variation for growth traits in *A. angustifolia*, namely DBH, HEI and VOL, tends to increase over time as shown by an increase in narrow-sense heritability (h_a^2) (Fig. 3). Such an increase is expected following the differentiation of biomass accumulation of some individual trees compared to others over time. While in early ages trees tend to have a smaller difference in biomass, over time this difference becomes increasingly pronounced. The individual narrow sense heritability for HEI and DBH in *A. angustifolia* reached values in the range of ~0.2 to 0.25 at age 35. These values are lower than some of the estimates reported in earlier studies where values between 0.03 and 0.6 were observed (Kageyama and Jacob, 1979; da Silva et al., 2018). This difference could be explained by the significantly broader country-wide sampling in this trial in comparison to previous ones, by including provenances from a much wider geographical range and correspondingly variable sampling of genetic variation and heritability behavior (Fig. 3).

An increase in narrow sense heritability for growth with age has been reported in a number of studies of different conifer species, particularly of genus *Pinus* (McKeand, 1988; Hodge and White, 1992; Balocchi et al., 1993; Dieters et al., 1995; Costa and Durel, 1996; Li et al., 1996; Jansson et al., 2003; Weng et al., 2007), although other reports have shown either non-linear (Gwaze et al., 2002) or constant (Haapanen, 2001) heritabilities with age. When individual *Araucaria angustifolia* provenances are considered, narrow-sense heritabilities for growth traits showed quite variable patterns across the 15 provenances of *A. angustifolia* and along the ages evaluated (Fig. 3), in line with the fact that the expression of genetic and residual variances may depend on the provenance and also on the age of the individuals (Jansson et al., 2003). A decrease in heritability for DBH was observed in provenances 9, 13 and 14 while in provenances 1, 14, 9 and 10 the decrease was in heritability for HEI (Fig. 3).

Our results highlight the fact that using an average estimate of heritability for all provenances irrespectively of age, would lead to significant inaccuracies in the selection of the best individuals within families. For example, for provenance 6, using an average heritability would be

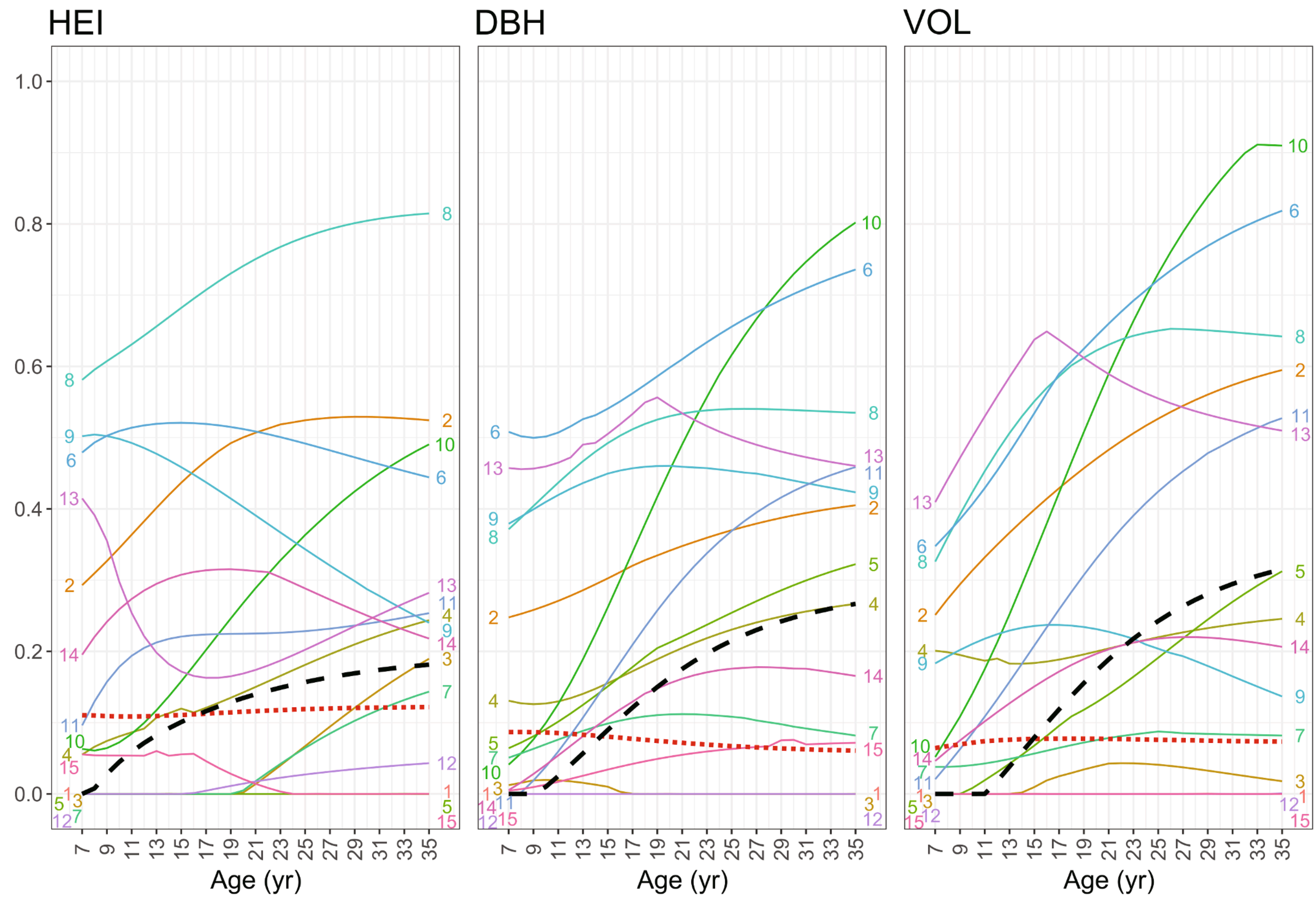

Fig. 3. Narrow-sense heritabilities (h_a^2) (Y axis) across ages for traits HEI (tree height), DBH (diameter at breast height) and VOL (individual tree volume). The charts present h_a^2 estimates for a model with all 15 provenances (dashed black lines) and for each individual provenance (colored lines). The red dotted lines are coefficient of provenance determination (c_{prov}^2) for the complete model with all 15 provenances.

problematic as low values of h_a^2 were estimated at advanced ages and high values at early ages, with the highest estimate of h_a^2 observed for VOL at age 35. On the other hand, for provenance 4 a more stable behavior is observed across ages, while provenance 13 has a variable behavior and provenance 1 results are practically null throughout the evaluation period. There are some possible explanations for this observed variability in heritability time-trend across provenances: i) a fluctuating growth interaction between individuals over time; ii) variable interaction of provenances and families with the environmental variation in the testing site with time; iii) differential expression of inbreeding depression across provenances and families within provenances as the magnitude of inbreeding depression can be expressed at different life stages (Tambarussi et al., 2017); iv) patchy mortality rates over time across provenances, which reduces genetic variance and / or increases residual variance (Kroon et al., 2011).

4.2. Age-age genetic correlation and early selection gains

While heritabilities are measures of the degree to which trait variances are governed by genetic rather than environmental factors, genetic correlations describe the extent to which breeding values (i.e., measures of the additive ‘genetic worth’ of individuals for a specific trait, age and environment) co-vary. Genetic correlations between all ages and age 35 were high both for individual trees within families and among families. For DBH and HEI, regardless of the growth period, genetic correlations were always greater than 0.85, and for volume, greater than 0.70. Selecting for HEI and DBH individually is slightly better than on VOL, as there is a tendency to achieve higher correlations with age 35 faster (Fig. 5-a). When the seventh year of growth is reached, genetic correlations with age 35 years are already above 0.80, except for selection within families for variable VOL, which is approximately 0.75. To reach genetic correlations higher than 0.90, selection needs to be carried out beyond age 12 years for all three traits HEI, DBH and VOL. From age 30 onward the parametric estimates demonstrate a genetic correlation approximately equal to 1.0 with age 35 years. Our age-age correlations estimates are equivalent or higher than those reported for other conifers. While this could be an intrinsic biological property of *A. angustofolia*, the modeling approach used to improve data quality might have also contributed to this result. Reported results for other conifers vary. Age-age genetic correlations in conifers have shown variable trends. In loblolly pine correlations of early height with 8-year volume reached values above 0.8 (Xiang et al., 2003), and were also high between juvenile and mature ages HEI and DBH in Larix (Dong et al., 2019). Conversely, modest genetic correlations of 0.468 for HEI and 0.531 for DBH between ages 5 and 30 years were reported for *Cryptomeria japonica* (Hiraoka et al., 2019) and 0.51 for HEI between ages 7 and 24 years for *Pinus contorta* (Xie and Ying, 1996).

The high genetic correlations observed in *A. angustifolia* represent an exciting result, opening promising opportunities for carrying out efficient early selection. A commonly cited limitation to increase investment in *A. angustifolia* plantation forestry in Brazil is the slow growth and consequently the long investment timeframe necessary to capture returns and the long breeding cycles needed to improve populations. This becomes even more evident when comparisons with fast growing

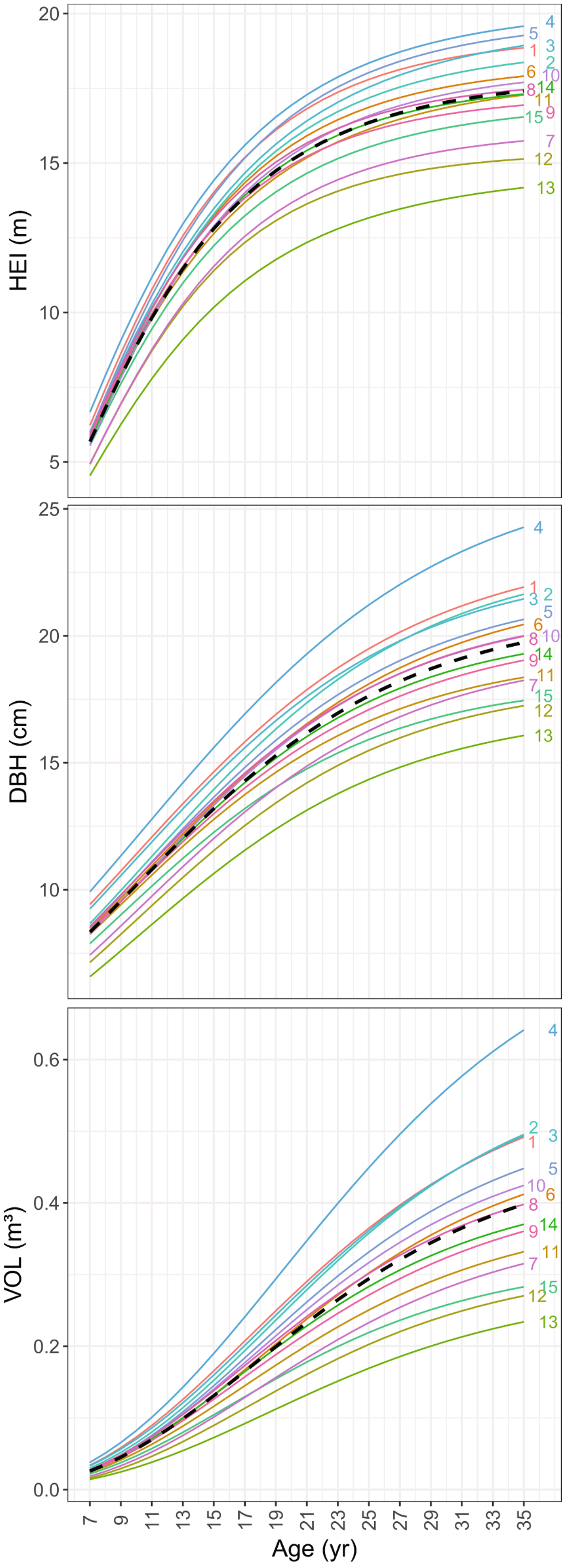

Fig. 4. Growth trait averages for HEI (tree height), DBH (diameter at breast height) and VOL (individual tree volume) for the 15 *Araucaria angustifolia* provenances across the 35-year time span. The dashed line is the average across all fifteen provenances.

Pinus taeda or *Eucalyptus* sp. are made, although such comparisons are not legitimate given the significant differences in the final wood product and market price. *A. angustifolia* wood is fine in texture, uniform in color, with fiber length around 5 mm, much higher than *Eucalyptus* (1 mm), and pines (3–4 mm), superior mechanical strength and flexibility when compared to other commercial conifers (Santini et al., 2000), basic density between 400 and 500 kg/m^3 (Trevisan et al., 2016) and cellulose content up to 60%. Currently there are no ongoing systematic efforts to attempt to reduce the breeding cycles of *A. angustifolia,* mostly due to the still limited interest in extensive plantation forestry of the species.

Our study indicates that correlations between ages 7 and 35 would already allow efficient early selection (Fig. 5a). Nevertheless recombination of selected *A. angustifolia* trees depends on emission of strobilus which generally takes place only around age 10–15 years in isolated trees and from 20 years of age onward in homogeneous plantations (Sousa and Hattemer, 2003). Unless some early flowering techniques commonly used in conifers are optimized for *A. angustifolia,* such as induction of grafted scions with gibberellin (Greenwood, 1982) or top grafting on reproductively older trees (Perez et al., 2007), a considerable time lag will be necessary to complete a breeding cycle despite early selection. To date no attempts of early flower induction by top grafting young seedling on reproductively older trees have been reported in *A. angustifolia*, an area of research that should merit attention as an important tool to accelerate breeding, reminding that the species is dioecious therefore requiring flower induction in individuals of both sexes.

Our data show that the abundant genetic variation found both within and between families could drive efficient early selection at both levels. In theory family selection is expected to provide greater genetic gains at any selection intensity (Kageyama and Jacob, 1979; Diao et al., 2016). However, our analyses indicate that early individual or family selection would provide similar efficiencies (Fig. 5a), suggesting that, operationally, in an initial stage of improvement it may be more advantageous to select the best individuals within the best families. Additionally, it might also be recommended to consider selecting the best individuals within families in more geographically distinct provenances. Although the southeastern provenances displayed a considerably higher average growth performance at least in the trial site (Fig. 4), fast growing trees can also be found in southern provenances (Table 3). Recently, genome-wide single nucleotide polymorphism data have shown a considerably higher genetic divergence between southeastern and southern populations of *A. angustifolia* challenging previous microsatellite based estimates (Silva et al., 2020). Selecting top trees in genetically divergent provenances might allow exploiting inter-provenance heterotic effects as demonstrated in other conifers such as *Picea* and *Pinus* (Kaya and Lindgren, 1992; Harfouche et al., 2000; de la Mata et al., 2014), a breeding strategy still generally underappreciated in conifer breeding. Finally, although scalable sustainable conifer cloning still represents a technical challenge, unless somatic embryogenesis is developed (Park, 2002), vegetative propagation of elite Araucaria trees could be considered by rooted cutting for the establishment of clonal plantations, clonal seed orchards or for conservation purposes (Wendling et al., 2016).

Our results provide useful information to identify the growth patterns of individual provenances, families or individuals to allow selection at these different levels to shorten the final rotation age. The few existing commercial *A. angustifolia* plantations are grown in pure stands and harvested at a rotation age of approximately 30 years. Wood products include pulp for paper and cardboard, timber for construction, and veneer (Nutto et al., 2005). In this study, the Mean Annual Increment (MAI) was estimated for each provenance, with the maximum volume observed around ages 26–28 years for most provenances (Fig. 6), which indicates that this could be an ideal rotation age as far as volume growth. However, observing the individual trees growth curves, a total of 239 trees reached the maximum growth increment before age 20 years, and 17 trees at age 15 years (Supplementary Figure S2).

Overall, in the trial site at Itapeva, provenances 1–5 originated from

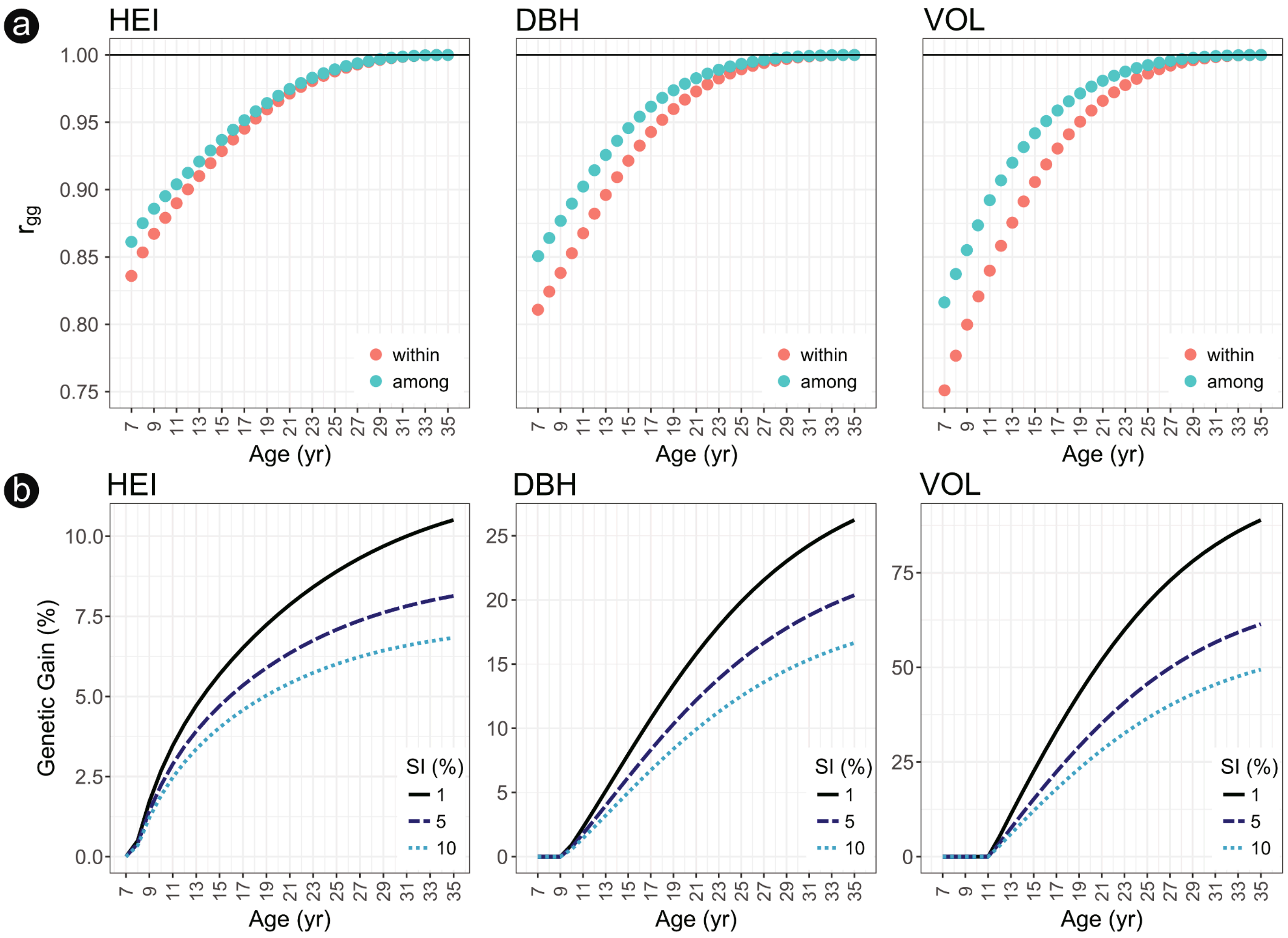

Fig. 5. **a**) Genetic correlation (r_{gg}) between ages and the final age 35 year are presented both as genetic correlations of within (individual tree level) and among families to illustrate early selection expectations. **b**) Expected genetic gain following individual tree selection for different selection intensities (SI) (1% (22 individuals), 5% (108 individuals) and 10% (216 individuals).

Table 3
Number of individuals (nID) and families (nFam) (in parentheses) ultimately selected for each trait (columns) and provenance (rows) in the trial with 2,158 trees. Three selection intensities were carried out on the estimated data at each age independently (yearly from 7 to 35 years) (1%: 22 individuals; 5%: 108 individuals; and 10%: 216 individuals) but all individual trees that were selected in at least one of the ages were retained in the total final selected set.

	HEI			**DBH**			**VOL**		
Provenance	1%	5%	10%	1%	5%	10%	1%	5%	10%
1	0 (0)	3 (3)	15 (6)	0 (0)	12 (5)	26 (7)	5 (4)	16 (5)	27 (7)
2	6 (2)	21 (5)	49 (9)	10 (2)	25 (5)	49 (8)	8 (3)	31 (8)	58 (9)
3	8 (1)	15 (2)	20 (4)	1 (1)	10 (4)	16 (5)	3 (3)	10 (4)	18 (5)
4	1 (1)	10 (3)	18 (3)	5 (2)	17 (3)	27 (4)	5 (3)	17 (4)	26 (4)
5	0 (0)	6 (2)	13 (3)	0 (0)	9 (3)	17 (4)	1 (1)	12 (4)	16 (4)
6	3 (1)	12 (2)	22 (4)	7 (2)	13 (4)	24 (5)	5 (2)	15 (5)	25 (5)
7	0 (0)	5 (1)	13 (4)	1 (1)	7 (3)	16 (5)	1 (1)	7 (4)	14 (7)
8	5 (3)	26 (4)	39 (4)	7 (3)	17 (3)	30 (6)	2 (2)	17 (6)	26 (7)
9	3 (3)	15 (5)	29 (6)	0 (0)	8 (4)	27 (6)	2 (2)	5 (4)	14 (6)
10	11 (1)	18 (1)	20 (1)	7 (1)	19 (1)	25 (2)	3 (1)	14 (2)	23 (4)
11	2 (2)	15 (3)	26 (5)	1 (1)	12 (3)	25 (5)	0 (0)	11 (5)	23 (7)
12	1 (1)	4 (3)	9 (4)	0 (0)	2 (2)	8 (4)	0 (0)	5 (4)	8 (5)
13	0 (0)	5 (1)	8 (1)	0 (0)	6 (1)	7 (1)	0 (0)	3 (1)	7 (1)
14	5 (1)	18 (5)	29 (6)	3 (1)	14 (5)	26 (5)	5 (3)	16 (6)	25 (7)
15	1 (1)	3 (2)	17 (7)	0 (0)	2 (2)	10 (4)	1 (1)	3 (3)	12 (7)
Total nID	46	176	327	42	173	333	41	182	322
Total nFam	17	42	67	14	48	71	26	65	85
Total nProv	11	15	15	9	15	15	12	15	15

nID: total number of individual trees selected (max = 2,158); **nFam**: number of families (max = 122); **nProv**: number of provenances (max = 15).

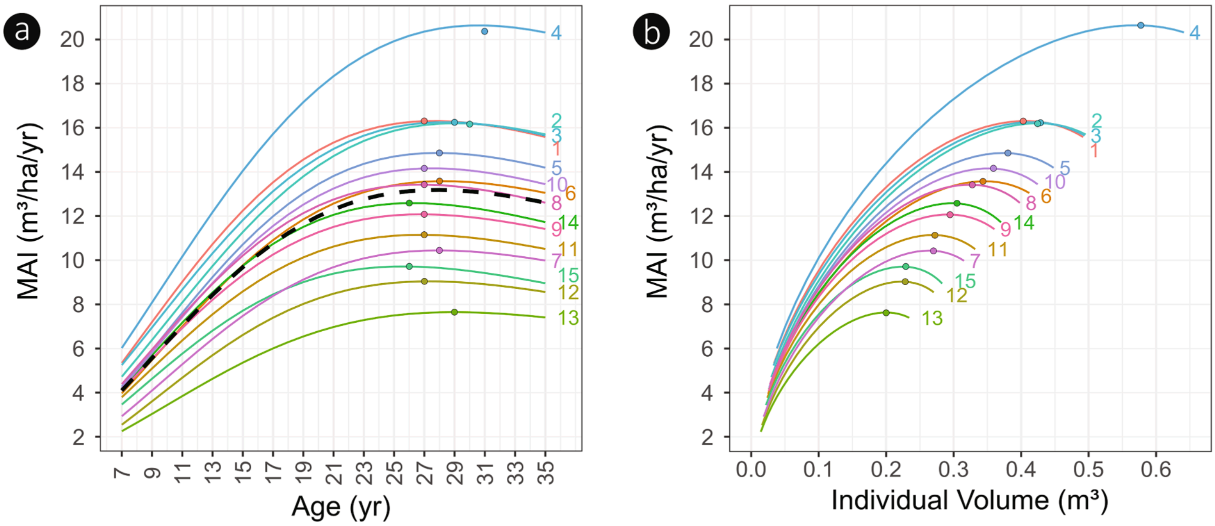

Fig. 6. **a)** Relationship of the average tree mean annual increment (MAI) in volume with increasing age; **b)** Relationship of the average tree mean annual increment (MAI) in volume with the average volume per tree suggesting appropriate moments for rotation age termination (indicated by dots) for the 15 provenances (colored lines).

the southeastern region showed an increasingly better growth performance as the trees aged than provenances 11 to 15 from the most southern regions and, interestingly, even better than provenances 8 and 9 from essentially the same region as the one of the trial site (Fig. 6a and 6b). This behavior is consistent with the marked environmental differences, especially in elevation and average temperature, between those in the southernmost provenances and those of the trial site. Nevertheless, all provenances included individual trees with good potential to be selected for shorter rotations with considerable variation across provenances for the optimal age (Fig. 6a) and optimal tree volume (Fig. 6b) at which annual growth increment peaks, a tipping point that could be used as a predictor of the optimal rotation age and expected tree volume. For example, provenance 4 from Lambari, showed a remarkably higher growth rate when compared to all others, with a peak of average growth rate at 0.56 m^3 per tree. On the other hand, other provenances, such as the southern and higher elevation provenance 13 from Caçador, peaks its average growth rate at just 0.2 m^3 per tree. It is important to mention that increasing growth rates may reduce the longevity of conifers. Rapid and large growth rates may mean reduced investment in defenses, lower wood density and mechanical resistance, greater hydraulic resistance, as well as problems with negative growth regulation during periods of stress (Bigler and Veblen, 2009). Data from individual growth curves therefore represent valuable information to be integrated into selection decision to potentially reduce the rotation cycle of *A. angustifolia*, although considerations regarding optimal age for wood properties traits need to be taken into account as well (Nutto et al., 2005).

4.3. Araucaria as a viable tropical commercial conifer option

A. angustifolia is currently considered an endangered species at the international level and protected by a 20-year-old law in Brazil (BRASIL, 2001). Although the management of naturally forested areas of this species is mostly forbidden, recent initiatives have proposed that Mixed Ombrophilous Araucaria forests in Southern Brazil can be managed as sustainable sources of environmental, social and economic benefits (Longhi et al., 2018; Arnoni Costa et al., 2020). Clearly, however, much research is still needed to develop solid scientific data to support truly sustainable management strategies for such complex mixed stands subtropical forests, as models for low species diversity, temperate conifer stands, do not necessarily apply (Hess et al., 2018).

A. angustifolia plantation, however, is fully legal and increasingly seen as a viable alternative that has recently attracted renewed interest, especially by small and medium size farmers that have to restore forested areas in their properties to abide to the new Brazilian forest code (E. Schaitza, EMBRAPA, pers. comm.). Nevertheless, the common question posed by both small- and large-scale forest enterprises is the economic viability of *A. angustifolia* versus exotic conifer species of *Pinus*. A recent economic analysis based on formal economic metrics such as NPV (Net Present Value), IRR (Internal Rate of Return) and ROI (Return on Investment), concluded that Araucaria plantations only become competitive with pines on average quality sites that would support an MAI of 23 m^3/ha/year for a 1,111 tree pure species stand at age 15 (Eisfeld et al., 2018). Although our experimental trial data does not provide direct estimates of MAI for stands established with genetically improved material, provisional estimates were calculated using the top 50 and 100 individual trees in the trial (Supplementary Figure S3). Data show that such MAI could be potentially reached in the Itapeva trial site by several individual trees from specific families in the top performing provenances.

Clearly a systematic breeding effort based on the data and germplasm provided in this study, together with further improvements in silvicultural practices specifically tailored to the species, could represent an important move toward economic viability of extensive *A. angustifolia* commercial forest plantation. Advanced genomic-based breeding approaches exploiting the power of DNA marker data would be particularly useful to accelerate *A. angustifolia* breeding in the same way as it is currently happening with mainstream conifers and hardwoods (Grattapaglia et al., 2018). The recently developed high-throughput genotyping chip for *A. angustifolia* with 3,000 SNPs (single nucleotide polymorphisms) markers (Silva et al., 2020) opens the prospects of adopting genomic selection to accelerate breeding cycles, increase selection intensity, improve the accuracy of breeding values and innovate in genetic parameters' estimation and breeding approaches. Due to its country-wide distribution, studies involving multiple environmental variables could also be explored for site-specific recommendation of the best genotypes using enviromics approaches (Resende et al., 2020). Finally, given the iconic relevance of the species, breeding programs should also value genetic diversity and the establishment of forests with high environmental adaptive value (Marcatti et al., 2017).

5. Concluding remarks

Although *A. angustifolia* has a long and somewhat unfortunate history of over-exploitation, high levels of genetic diversity are still found in the remnant natural populations in Brazil, both at the DNA sequence level (Stefenon et al., 2007; Stefenon et al., 2019; Silva et al., 2020; Sousa et al., 2020) and at the phenotypic level for growth, as shown in our study. The overall growth data surveyed in this work match the DNA sequence data described previously as far as pointing to a major separation of the existing provenances into two major ecogeographical and genetic groups with the southeastern provenances (1–7) showing, on average, a better growth performance than the more southern (8–15) provenances (Fig. 6) although the genetic variation within provenances is greater than the variation found between provenances. Our data also underscore the potential for early selection for growth with high prediction accuracy of later ages, and the possibility of shortening the harvest cycle by selecting the best individuals and families. Taken together, all the data presented provide significant opportunities for directional selection toward systematic breeding of the species which could in turn foster greater interest and investment in sampling, characterizing and ultimately conserving a wider germplasm base of this valuable keystone Brazilian conifer.

CRediT authorship contribution statement

Rafael T. Resende: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Pedro Italo T. Silva:** Conceptualization, Data curation, Formal analysis, Writing – original draft. **Orzenil B. Silva-Junior:** Data curation, Formal analysis, Writing – review & editing. **Miguel L. Menezes Freitas:** Validation, Project administration, Funding acquisition, Resources. **Alexandre Sebbenn:** Validation, Project administration, Funding acquisition, Resources. **Valderês A. Sousa:** Validation, Writing – review & editing, Project administration, Funding acquisition, Resources. **Ananda V. de Aguiar:** Validation, Writing – review & editing, Project administration, Funding acquisition, Resources. **Dario Grattapaglia:** Conceptualization, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119671.

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