RESEARCH ARTICLE

Longitudinal analysis of *Pinus caribaea* var. *hondurensis* full-sibling progenies based on multivariate analysis

Vanessa Ishibashi[1], Paulo C. Flores-Junior[2], Diego T. Martinez[1], Alexandre S. G. Coelho[3], and Antonio R. Higa[1]

[1]*Federal University of Paraná. Av. Lothário Meissner 632, 80210-170 Curitiba, PR, Brazil.* [2]*Federal Rural University of the Amazon. Estr. Principal da Ufra 2150, 66077-830 Belém, PA, Brazil.* [3]*Federal University of Goiás. Av. Esperança s/n, 74690-900 Goiânia, GO, Brazil.*

Abstract

Aim of study: To define an early selection strategy based on tests applied to full-sibling progenies of *Pinus caribaea* var. hondurensis grown in the *Cerrado* Biome.

Area of study: Prata region (MG), Brazil.

Materials and methods: Progeny tests were cultivated in 2006; the study followed a completely randomized design, with 79 families of full-siblings and 15 repetitions, with one plant per plot. Thinning was carried out at the age of 6 and 8 years; 615 individuals and 44 families were included in the test. The following quantitative variables were used in the statistical analysis of data on the remaining individuals: diameter at breast height (DBH) in cm, total height (H) in m, and volume in dm³ at the age of 3, 4, 5, 6, 7, 8 and 11 years. BLUP multi-trait multivariate model, with non-structured covariance structure matrix, was adopted for calculations.

Main results: There were strong additive genetic correlations (above 90%) between variables DBH and H, in all analyzed ages. Strong volume correlations were estimated based on the age group over four years; volume selection efficiency reached its peak at the age of five years. Selection based on volume at the age of 5 years leads to genetic gains in this variable; selection intensity values can range from 7.8% to 6.4% and 5.4%, and from 10% to 20% and 30%.

Research highlights: The best strategy lies on carrying out the selections at the age of five years, based on 30% selection intensity.

Additional key words: early selection; multi-trait BLUP; unstructured matrices

Abbreviations used: BLUP (best linear unbiased prediction); DBH (diameter at breast height); H (total height); REML (restricted maximum likelihood); VOL (volume).

Introduction

One of the main targets of genetic enhancement programs lies on making genetic gain estimates as soon as possible, since early selection processes are important to maximize gains per time unit to get fast capture of gains and reproductive cycle reduction (Belaber *et al.,* 2018; Hayatgheibi *et al.,* 2019).

Early *Pinus* selection allows identifying commercial features of interest in juvenile trees, since its rotation cycles can range from 15 to 22 years, in Brazil (Aguiar *et al.,* 2015; Coutinho *et al.,* 2017; Flores Jr *et al.,* 2021). Genetic gain at rotation age can be predicted through age-age correlation to mean genetic gain in earlier age (Luo & Thomas, 2021). Therefore, it is essential knowing correlation magnitudes among different age groups (Belaber *et al.,* 2018). Correlation is high when genotypic classifications are stable, overtime; it is low when it changes significantly (Rweyongeza, 2016). Any trait must be recurrently assessed overtime in order to collect longitudinal data to model heritability

changes and genetic/age correlations (Apiolaza & Garrick, 2001). Longitudinal data can be taken as multivariate data, since their analysis also shows some peculiarities; it is so, because several measurements are correlated to each other and because there may be variance and covariance heterogeneity among them (Mariguele *et al.,* 2011).

The multivariate model, also known as unstructured covariance matrix, is recommended to analyze data sets, such as the herein assessed ones (Mariguele *et al.,* 2011). Best unbiased linear multi-trace prediction (BLUP) is a quite efficient alternative, since it simultaneously uses all information and deals with repeated measurements - as if they were different and correlated features - by taking into consideration their heritability and genetic correlations (Alves *et al.,* 2019). This model was used in the longitudinal data analysis applied to *Jatropha curcas* (Alves *et al.,* 2019).

Studies conducted with different species belonging to the herein investigated genus have pointed towards the feasibility of early selection processes based on using diameter at breast height (DBH) as selection criterion. Belaber *et al.* (2018) conducted a study with the *Pinus caribaea* var. *hondurensis × Pinus elliottii* hybrid and recorded high age-age correlations to growth traits; thus, the selection process can be carried out when plants are three years old. Tambarussi *et al.* (2018) conducted a study with this very same hybrid and found genetic correlations ranging from 0.96 to 0.99 between growth variables evaluated at the age of four and eight years. Based on the study conducted by Flores Jr *et al.* (2021) with *Pinus taeda*, high age-age genetic correlations were recorded for DBH between the age of 10 and 20 years (0.64), whereas low and non-significant age-age genetic correlations were recorded between the age of 6 and 20 years (0.39). Coutinho *et al.* (2017) showed family ordering correlation higher than 0.80 between the age of 8 and 15 years. Kurt & Isik (2021) conducted a study with *Pinus brutia* and recorded positive and high age-age genetic correlations for DBH, whose values ranged from 0.72 to 0.99.

Based on the hypothesis that it is likely finding correlation among ages to achieve early selection, the aim of the present study was to draw an early selection strategy in progeny tests of *P. caribaea* var. *hondurensis* full-siblings cultivated in a *Cerrado* region based on multi-trait BLUP.

Material and methods

Genetic materials and experiment description

The study was carried out in Prata region (MG), Southeastern Brazil (19°30' S, 43º92' W, altitude 630 m), where one mainly finds the prevalence of tropical climate with dry season in Winter (Aw). Mean temperature in the site reaches 22 °C, and mean annual rainfall is 1,500 mm. Overall, soil in the region is acidic and has low fertility (Alvares *et al.,* 2013).

Base population was formed by commercial plantations resulting from seeds provided by the Seed Production Area, Agudos County (SP), Poptún, Guatemala. The phenotypic selection of matrices was carried out in 1993, when trees were at the age of four years, at selection intensity of 1:5000. Selection criteria were volume, stem straightness, smallest number of branches, branch thickness, longest distance between internodes and regularity between internodes.

Controlled crossing between selected mother trees was carried out in 1998, 1999 and 2000. Progeny tests were implemented, in 2006, with 79 families of full-siblings, based on completely randomized experimental design, with 15 repetitions and one plant per plot (3 m × 2 m spacing). Families comprised 25 mothers and 43 fathers; they did not follow pre-established crossing designs.

The following quantitative variables were used in the statistical analysis: DBH in cm, total height (H) in m, and volume (VOL) in dm3 at the age of 3, 4, 5, 6, 7, 8 and 11 years. Volume was calculated through Eq. (1):

$$VOL = [(\pi DBH^2/40)] \times H \times 0.42 \qquad (1)$$

Thinning was performed at the age of six years; all individuals belonging to 20 families (that have assumingly presented the lowest performance) were excluded from the experiment. Other 14 families were eliminated at the age of eight years; thus, 44 families and 615 individuals remained for the test (Table 1). Thus, 615 common individuals, at all ages, were used in the analysis. Thinning was carried out because experiment managers wanted to gradually reduce the number of families used in the experiment; families presenting the lowest volumetric growth at the age of 6 and 8 years were thinned.

Statistical analysis

The multi-feature statistical model was given by Eq. (2):

$$y = Xb + Za + Wf + \xi + \eta \qquad (2)$$

wherein, y is the vector of phenotypic data, b is the vector of fixed blocks added to the general average, a is the vector of individual (randomized) additive genetic effects, and f is the full-sibling's (random) vector of random genetic effects. X, Z and W represent the matrices associating fixed and random effects with y (Hernández *et al.,* 2019). An autoregressive spatial component was added, and the residual vector e was partitioned into spatially dependent (ξ) and independent (η) residues. Spatially dependent residues (ξ) were modeled by using a covariance structure that embodies a first-order autoregressive process separable into lines *(ρ_{col})* and columns *(ρ_{row}),* whose R matrix is $R = (\sigma_\xi^2[AR1(\rho_{col}) \otimes AR1(\rho_{row})] + \sigma_\eta^2 I)$; wherein, σ_ξ^2 is the dependent spatially residual variance between column and line, σ_η^2 is the independent residual variance, $\otimes$ is the

Table 1. Description of progeny tests applied to full-siblings of *Pinus caribaea* var. *hondurensis,* overtime

Year	Age	# Families	# Fathers	# Mothers	# Individuals	Remaining trees
2009	3	79	43	24	1147	94.4%
2013	7	59	38	21	847	69.7%
2017	11	44	33	16	615	50.6%

sense of Kronocker product; and AR1(ρ) represents the first-order product of the autoregressive correlation matrix heading towards the column and the line, respectively. The values of ρ_{col} and ρ_{row} were defined based on the lowest values recorded for the Akaike information criterion (Akaike, 1974).

Assumingly, vector a is distributed as follows: $a\sim N\,(0, \Sigma_a \otimes A)$; wherein, Σ_a is the covariance matrix of random additive genetic effects and A is the mean relative numerator of the relationship matrix based on pedigree information, vector f is distributed as $f\sim N\,(0, \Sigma_f \otimes I)$; wherein, Σ_f is the covariance matrix of the family's random genetic effects, vector ξ is distributed as $f\sim N\,(0, \Sigma_\xi \otimes I)$; wherein, Σ_ξ is the covariance matrix of spatially dependent residues' random genetic effects and vector η is distributed as $f\sim N\,(0, \Sigma_\eta \otimes I)$; wherein, Σ_η is a covariance matrix of spatially independent residues' random effects and I is an identity matrix of an order appropriate to the respective random effect. Furthermore, Σ_a, Σ_f, Σ_ξ and Σ_η are non-structured covariance structures (Gilmor *et al.,* 2015; Alves *et al.,* 2018)

Genetic parameter estimates

Variance components were estimated based on the Restricted Maximum Likelihood Method (REML). These components were found by using the expectation maximization algorithm (EM), in the R software (R Core Team, 2021), at function reml90 of the breedR package (Muñoz & Sanchez, 2019).

Heritability itself, $(\hat{h}_a^2)$, was estimated through Eq. (3):

$$\hat{h}_a^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_f^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{es}^2} \quad (3)$$

wherein, $\hat{\sigma}_a^2$ is additive genetic variance, $\hat{\sigma}_f^2$ is family variance, $\hat{\sigma}_e^2$ is residual variance and $\hat{\sigma}_{es}^2$ is spatial variance.

Genetic correlation (*cor*) among ages was estimated through Eq. (4):

$$cor = COV_{x,y} \Big/ \sqrt{\hat{\sigma}_x^2 \times \hat{\sigma}_y^2} \quad (4)$$

wherein, $\hat{\sigma}_e^2$ is additive genetic variance of age x, $\hat{\sigma}_e^2$ is additive genetic variance of age y, and $COV_{x,y}$ is covariance among ages.

Selection efficiency (*SE*) was calculated through equation Eq. (5), described by Hayatgheibi *et al.* (2019):

$$SE = \big(i_E h_E cor_a\big) \Big/ \big(i_A h_A\big) \quad (5)$$

wherein, i_E is selection intensity at early age, h_E is heritability root at early age, cor_a additive genetic correlation among ages, i_A selection intensity at reference age and h_A is heritability root at reference age. The same selection intensities, at early age and at reference age, were used for the calculations.

Compliance among selected individuals was calculated based on the Cohen coefficient (Kappa) (Cohen, 1960), through Eq. (6) described by Resende (2015):

$$Kappa = NO\text{-}NA \,/\, NP\text{-}NA \quad (6)$$

wherein, *NO* is the number of coincident individuals/families among different ages, NP is the number of data pairs and *NA* is the random number of coincident individuals/families *(NA = NP × selection intensity).*

Selection gains (*GS*) recorded for each feature were predicted by taking into consideration selection intensities equal to 10%, 20% and 30% at the age of 5 years, based on the following Eq. (7):

$$GS = \sum_n VG \,/\, n \quad (7)$$

wherein, *VG* is the predicted genetic value and n is the number of selected individuals.

The following Eq. (8) was used to calculate the effective population size (*Ne*) (Resende, 2015):

$$Ne = \big(2 \times N_f \times K_f\big) / \big(K_f + 1 + (\sigma_{Kf}^2 / K_f)\big) \quad (8)$$

wherein, N_f is the number of selected families, K_f is the mean number of selected individuals per family and σ_{Kf}^2 is the variance recorded for the number of selected individuals, per family.

Results

Variance components

Overall, variance estimates recorded for DBH and VOL have increased until the test model reached the age of 8 years. The reversed outcome was observed for variable H, since additive genetic variance $\hat{\sigma}_a^2$ and residual variance $\hat{\sigma}_e^2$ estimates decreased, overtime. The greatest contribution to total variance was attributed to residual and spatial residues, in all variables and at all ages (Table 2).

Table 2. Estimates of variance components and genetic parameters recorded for diameter at breast height (DBH), volume and total height, assessed through progeny tests applied to full-siblings of *Pinus caribaea* var. *hondurensis* at seven different ages

Age	$\hat{\sigma}_a^2$	$\hat{\sigma}_f^2$	$\hat{\sigma}_{es}^2$	$\hat{\sigma}_e^2$	$\hat{h}_a^2$
DBH					
3	0.174	0.258	0.946	1.478	0.06
4	0.386	0.367	2.230	1.652	0.08
5	0.707	0.478	4.129	1.606	0.10
6	0.745	0.629	6.482	1.269	0.08
7	0.757	0.789	8.456	1.597	0.07
8	0.853	0.944	10.240	1.800	0.06
11	0.746	1.157	13.810	2.462	0.04
5^{full}	0.862	1.507	5.787	0.421	0.10
Volume					
3	6.498	42.200	83.490	219.600	0.02
4	18.600	92.600	396.900	520.000	0.02
5	94.590	226.800	1806.000	787.800	0.03
6	188.500	447.000	3980.000	1269.000	0.03
7	328.600	831.000	8180.000	1813.000	0.03
8	447.300	1333.000	13140.00	2308.000	0.03
11	675.800	2484.000	27630.00	3782.000	0.02
5^{full}	97.30	297.00	1853.00	524.000	0.04
Total height					
3	0.201	0.165	0.413	1.362	0.09
4	0.103	0.0731	0.272	1.567	0.05
5	0.132	0.0746	1.025	1.824	0.04
6	0.106	0.0812	1.367	1.251	0.04
7	0.112	0.0706	1.960	1.186	0.03
8	0.101	0.114	3.032	1.377	0.02
11	0.081	0.138	5.369	1.114	0.01
5^{full}	0.139	0.543	0.558	3.289	0.03

$\hat{\sigma}_a^2$ is additive genetic variance. $\hat{\sigma}_f^2$ is family variance. $\hat{\sigma}_e^2$ is residual variance. $\hat{\sigma}_{es}^2$ is spatial variance. $(\hat{h}_a^2)$ is heritability, itself. 5^{full} is the analysis performed at the age of 5 years, composed of all individuals in the test.

Heritability $(\hat{h}_a^2)$ was low in all variables and at all ages; it increased between the age of 3 and 5 years, for DBH and VOL; but it decreased again, at older ages. The highest value recorded for $(\hat{h}_a^2)$ predicted for DBH was observed at the age of 5 years (0.10), at the age of 5 to 8 years for VOL (0.03), and at the age of three years for H (0.09) (Table 2).

Genetic correlation between age and selection efficiency

Genetic correlations recorded for DBH and H were high and significant. This finding points out that early selection, at the age of 3 years, can lead to positive gains at the age of 11 years. Low VOL correlations were observed between the age of 3 years and the other assessed ages. However, correlations between ages were high and significant in the age over 4 years (Fig. 1).

Selection efficiency takes into consideration $(\hat{h}_a^2)$ and cor$_a$ estimates. Early selection reached its peak at the age of 5 years for DBH, at the age of 5 and/or 6 years for VOL, and at the age of 3 years for H (Fig. 2).

Selection strategies

Selection based on volume at the age of 5 years leads to genetic gains in this variable; selection intensity values can range from 7.8% to 6.4% and 5.4%, and from 10% to 20% and 30%. The highest gains were recorded under the
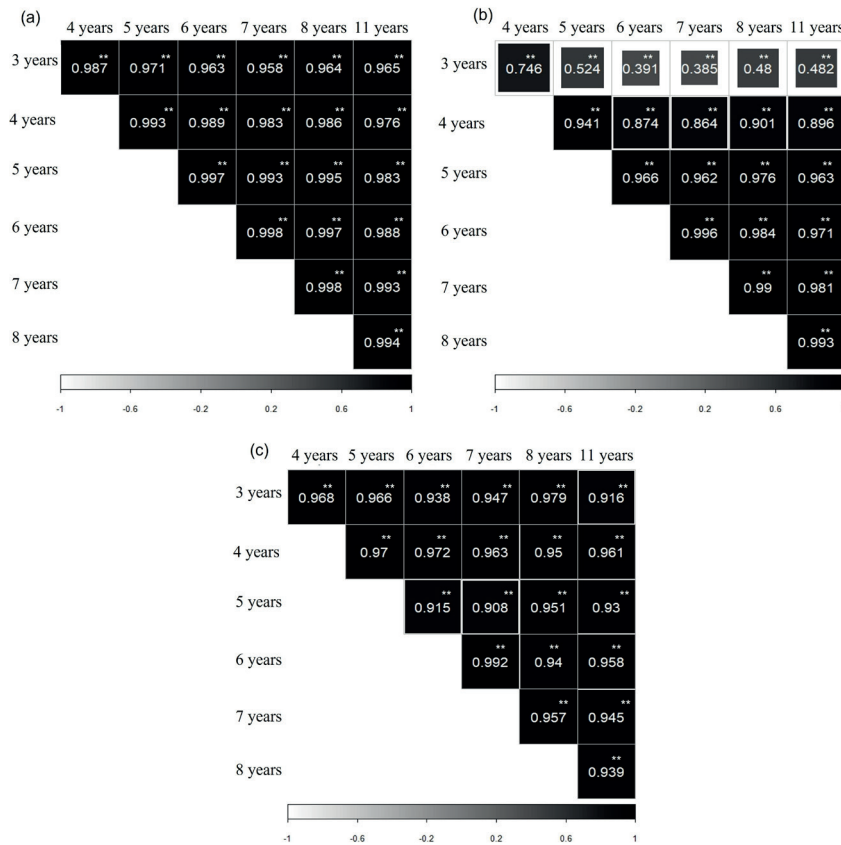
Figure 1. Additive genetic correlations among ages assessed in progeny tests applied to full-siblings of *Pinus caribaea* var. *hondurensis*. (a) DBH, (b) Volume and (c) Height. **: significant at 1% probability.

highest selection intensities, but it also accounted for decrease in effective population size. Indirect positive gains were also observed in the other variables (Table 3).

Effective population sizes ranged from 16 to 35.5 (Table 3). Kappa coefficient between selected individuals

reached 65%, at most, at 30% selection intensity (Table 3). Accordingly, the strategy balancing genetic gains, effective population size and coincidence of individuals lies on selections carried out at the age of 5 years, based on 30% selection intensity.
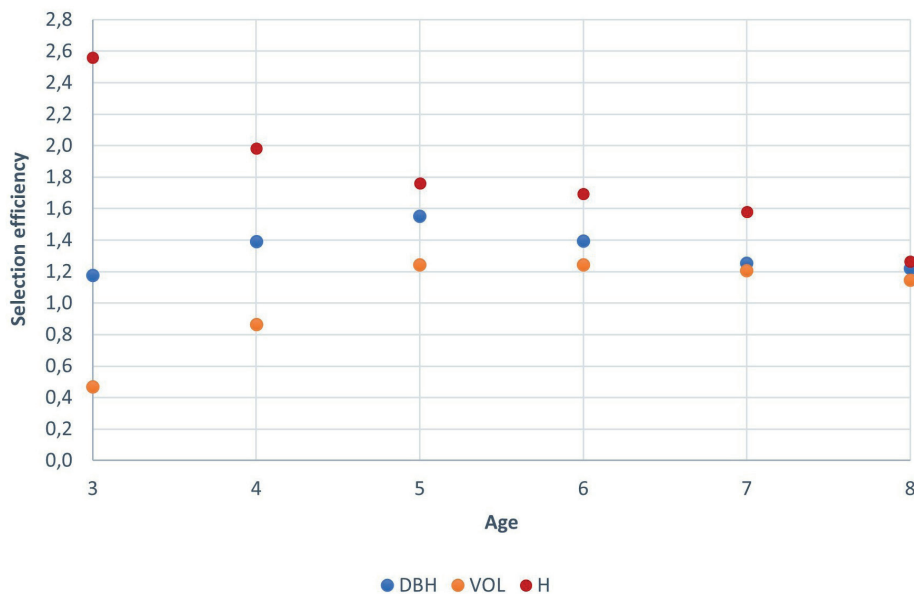

Figure 2. Selection efficiency for DBH, volume and total height in progeny tests applied to full-siblings of *Pinus caribaea* var. *hondurensis*.

Table 3. Genetic gain, effective population size, new mean and Kappa coefficient recorded for different selection intensities carried out in progeny tests applied to full-siblings of *Pinus caribaea* var. *hondurensis,* at the age of 5 years.

	Selection intensity		
	10%	**20%**	**30%**
Selected individuals	62	123	185
Effective size	16.2	29.0	35.6
Kappa5^{-11}	21%	15%	65%
GS$_{VOL}$	7.8%	6.4%	5.4%
New mean VOL (dm³)	169.21	166.92	165.35
GS$_{DBH}$	5.6%	4.5%	3.8%
New mean DBH (cm)	19.23	19.04	18.91
GS$_H$	1.5%	0.3%	0.0%
New mean H (m)	13.40	13.49	13.55

Kappa$_{5-11}$ is Kappa coefficient at the ages of 5 and 11 years. GS$_{VOL}$ is genetic gain in volume. GS$_{DBH}$ is genetic gain in DBH. GSH is genetic gain in total height.

Discussion

Variance and heritability components feature the trait variation-related genetic control degree; they follow different trends throughout tree-growth time (Dong *et al.,* 2019). Additive genetic variation and $(\hat{h}_a^2)$ estimates were herein considered low, and it must imply small gains due to selection (Souza *et al.,* 2017). These values were lower than those recorded by Sampaio *et al.* (2000) in progeny tests applied to *P. caribaea* var. *hondurensis* from Isla de Guanaja (Honduras) and Poptún (Guatemala), which were assessed at the age of 5 years – $(\hat{h}_a^2)$ estimates recorded for Isla de Guanaja were higher than those recorded for specimens coming from Poptún. Souza *et al.* (2017) also found the highest $(\hat{h}_a^2)$ values in a combined provenance/progeny test carried out at the age of 5 years to assess variables H and VOL. These authors recorded $(\hat{h}_a^2)$ estimates of 0.23 for height, 0.06 for DBH and 0.08 for VOL through joint analysis; it took into consideration the five provenances in the test. On the other hand, individual analysis based on provenance showed significant variation in this parameter; however, overall, they followed the same trend.

Low $(\hat{h}_a^2)$ was hypothesized because thinning decreased population's genetic variability, since the analysis was only applied to individuals that had remained after the second thinning, at all ages. The thinning procedure reduced by 55% the number of individuals and families. The analysis comprising all individuals (n=1138) showed the highest family variance estimates and reduced residual and/or spatial variance, whereas additive genetic variance and $(\hat{h}_a^2)$ recorded rough estimates (Table 2). This outcome indicated that low genetic variability featured the investigated population, rather than resulted from thinning.

Silva *et al.* (2011) and Moraes *et al.* (2007) assessed genetic tests applied to *P. caribaea* var. *hondurensis* before and after pruning and found that $(\hat{h}_a^2)$ values recorded for height decreased two years after thinning, whereas values estimated for DBH and VOL increased. It is important highlighting that values found by Silva *et al.* (2011) were lower than the ones recorded in the present study (Table 2) and higher than values recorded by Moraes *et al.* (2007). These authors did not use mixed model analyses with spatial components, and it opposed what was described by Belaber *et al.* (2018), who emphasized the importance of fitting mixed models capable of identifying and measuring the effects of environmental competition and heterogeneity on the analysis of experiments conducted at more mature ages, which show higher variation levels in trials, as the effect of competition or thinning. Spatial models take into consideration continuous environmental variations, whereas models, such as the autoregressive ones, reflect the existence of correlated errors between individuals and their neighbors, if one takes into account environmental trends and competition effects during the adjustment process (Stringer *et al.,* 2011; Silva & Kerr, 2013; Hernández *et al.,* 2019).

Belaber *et al.* (2018) and Tambarussi *et al.* (2018) have estimated genetic correlations between earlier ages, whereas Coutinho *et al.* (2017), Flores Jr. *et al.* (2021) and Kurt & Isik (2021) have estimated genetic correlations between ages closer to the final age of *Pinus* species' cycle. Similar to the present study, it is possible seeing that the greater the interval between ages, the lower the correlation between them. According to Kurt & Isik (2021), it happens because predicted genetic correlations are mainly found when the observed genes are used. Another interesting factor lies on the study by Coutinho *et al.* (2017), who recorded ordering correlations higher than 0.80 between the age of 8 and 15 years. However, individuals' early selection was only effective in environments whose climate and phytogeography were similar to the ones observed in the place where mother trees were selected.

According to Flores Jr. *et al.* (2021), the selection process shall be carried out when ($\hat{h}_a^2$) presents its maximum value in order to maximize genetic gains. In addition, genetic values recorded at selection age must be highly correlated to those observed at harvest age. Thus, according to recommendations by the aforementioned authors, the selection process shall be carried out at the age of 10 years, since it was the age when the highest genetic gain and ($\hat{h}_a^2$) estimates were identified. The selection efficiency index used in the present study, as well as by Dong *et al.* (2019), who conducted a study with species *Larix principis*, took into consideration ($\hat{h}_a^2$) and *cor$_a$* estimates. Unlike what was found in the present study, Dong *et al.* (2019) reported that variable H reached its selection peak at age older than that observed for DBH, as well as that the selection efficiency index recorded for both traits has quickly increased to its maximum value; subsequently, it decreased back. Variable DBH recorded selection efficiency peak at the age of 6 years, whereas H recorded selection efficiency peak age ranging from 8 to 9 years. Kurt & Isik (2021) calculated selection efficiency as gain:year ratio between early selection and selection in the harvest year. According to the aforementioned authors, the optimal early selection age for species *P. brutia* ranged from 4 to 6 years. The selection efficiency peak herein recorded for variable VOL was observed at the age of 5 years. Early selection based on this variable can be performed at the age of 5 years, since it is the main goal of breeding programs.

Gains recorded for variable DBH were higher than those recorded by Silva *et al.* (2011), but, yet, with smaller effective population sizes. Assumingly, effective population size n=30 is enough to proceed with a long-term genetic enhancement program (Ishibashi *et al.*, 2020). Effective population size n=40 can capture alleles at 6% frequency (Nunes *et al.*, 2021); it leads to 10% probability of losing alleles at 5% frequency in the source population (Ingvarsson & Dahlberg, 2019). Small effective population sizes can account for accumulation of harming alleles, inbreeding, inbreeding depression and reduced population ability to respond to environmental changes. These issues get worse in commercial forests under long rotation times, since the effects of future environmental changes are quite uncertain (Ingvarsson & Dahlberg, 2019). Similar to effective population size, Kappa index plays important role in the continuity of breeding programs and in generation-advancement processes, since it enables new selection and recombination cycles.

Based on the analyses carried out during the progeny tests applied to *P. caribaea var. hondurensis* at different ages, DBH and H recorded strong and significant additive genetic correlations at all analyzed ages. Strong correlations were estimated from the age group over 4 years, for

variable VOL. Selection efficiency recorded for variable VOL reached its peak at the age of 5 years. Selection based on VOL, at the age of 5 years, at 30% selection intensity, was the strategy accounting for balancing genetic gains, effective population size and match between individuals.

Acknowledgement

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