Conservative or non-conservative strategy to advance breeding generation? A case study in *Eucalyptus benthamii* using spatial variation and competition model

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Abstract

The greatest challenge faced when breeding populations of forest species is to achieve the right equilibrium among genetic gain and no loss of the effective population size. Thus this study aims to define the best thinning strategy to compose a seed orchard of *Eucalyptus benthamii* to obtain genetic gain maintaining the effective population size. The population of *E. benthamii* studied consisted of 28 open-pollinated progenies. The diameter at breast height (DBH) and height (H) parameters were determined three years after planting. Measurement data were analyzed and compared using four different mathematical models (with and without competition effect and spatial variation). Strategies considering genetic gain and effective population size were simulated considering the number of families, the number of individuals between families, and the total number of individuals. The mathematical model accounting for the competition effect had the best fit for DBH whereas the model accounting for the environmental variation effect presented the best fit for H. The ranking of BLUPs grouped the families into three clusters (best, intermediate/average, worst/poor families). The strategy that maintains 40 % of the individuals, generates a genetic gain of 13 % in DBH and 8 % in total height while maintaining an effective population size greater than 92 for booth traits.

Keywords: *Eucalypt; Recurrent Selection; Effective Size*

Introduction

Breeding programs to improve populations of forest species takes time because these cultures have long cycles, with a reproductive process (flowering) that can often take more than a decade. However, breeders demand genetic gains for traits of interest in the shortest possible time, which can generate strong selection pressure on individuals with such traits, reducing the effective number of individuals required to maintain the genetic variability of the original population while generating a "forgetfulness" of the population breeding for more generations and also of the non-evaluated traits (Resende and Alves, 2021).

Thus, in addition to advancing the breeding generation, an effective population size that allows for recurrent selection cycles must be maintained, otherwise genetic variability tends to decrease with advancing breeding generations (Resende and Vencovsky, 1990). Also, genetic variability is important to face the challenges that may arise (climate changes, pests, diseases, and the quality of the raw material) and maintain genetic gains over the advancing breeding generations (Kitzmiller, 1990).

For crops, such as eucalypts, that allow cloning, two strategies can be used simultaneously, population improvement, which may have lower gains, but maintains the genetic variability (effective population size) and the selection of individuals for cloning. The advancing of breeding generations occurs through progeny tests, as it allows the adequate evaluation and selection of individuals to compose the next generation, in

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addition to predicting the population response to selection. In perennial or long-cycle cultures, selected individuals are kept in the field, often being able to be cloned (grafting or cuttings).

Eucalyptus benthamii Maiden et Cambage belongs to the subgenus Symphyomyrtus, section Maidenaria, and occurs in subtropical and temperate regions with Cfb and Cfa climate classifications (Flores et al., 2016). The species is endemic to the state of New South Wales, occurring restricted to a few populations near Sydney (lat 33° 51'S), between 60 and 230 m altitude (Boland et al., 2006; Brooker; Kleinig, 2006). Despite being from regions with moderate frost, *E. benthamii* tolerates this abiotic stress better than most commercial eucalypts species (Paludzyszyn Filho; Santos; Ferreira, 2006). In Brazil and other countries, this species is especially indicated for regions where severe frosts occur. In the case of Brazil, the species is indicated for the southern region, where frost restricts using the species more widespread in the rest of the country.

This aims was define thinning strategies to compose a seed orchard of the *Eucalyptus benthamii* population, considering competition effects and incorporation of environmental heterogeneity in the studied models; and diverse thinning strategies to obtain an equilibrium among effective population size and genetic gains.

Materials and Methods

Genetic material and experimental description

In November 2017, open pollination progenies (F1) were implanted in the municipality of Otacílio Costa, SC (27°29′ S and 50°7′ W; 852 m, Cfb climate), 26 were collected in an APS (F0), in Jaguariaíva (PR), Brazil (24º15′ S and 49º42′ W; 850 m, Cfb climate). The Seeds Production Area (F0) was implanted with seeds from Kedumba Valley (NSW) (33º49' S and 150º32' E; and 140 m, Cfb climate). Two progenies, obtained by Dendro Seeds, were provided by the Klabin company and also inserted. The experiment with 28 progenies was set up in the randomized block design with linear plots of five plants and ten replications. The implementation followed the commercial pattern of the region, with soil preparation (subsoiling); ant and weed control (pre- and post-emergent herbicides); mineral fertilization with NPK and micronutrients; and post-planting irrigation as well. Three years after planting, the height (H) and diameter at breast height (DBH) were measured.

Analysis

The analysis of this work followed the procedures described by (Araujo *et al.,* 2021). Briefly, the evaluation and model can be given as follows.

Phenotypic evaluation

The growth traits Diameter at Breast Height (DBH, cm) and Height (H, m) of trees were obtained at three years of age. The phenotypic data were analyzed by the four mathematical models below:

1. Standard Mixed Model (std): individual additive linear model:

$$y_i = X\beta + Za + e$$

Where y_i : individual trees for the *i*-th trait; β: fixed effects for block, α: vector of random effect of the families (additive genetic effects), and *e*: residuals (random). *X*, and *Z* are the incidence matrices correlating observations and the model effects in β, and α, respectively.

The α vector was assumed distributed as $a \sim N\,(0, A\hat{\sigma}_a^2)$, $\hat{\sigma}_a^2$ is the additive genetic variance estimated; *A* is the relationship matrix from the pedigree information (considering as half-siblings). The vector *e* is distributed as $e \sim N\,(0, I\hat{\sigma}_e^2)$, where *I* is the identity matrix and $\hat{\sigma}_e^2$ is the estimate of the residual variance.

2. Spatial Mixed Model: First-order autoregressive (ar1), as the residual covariance for rows and columns (ar (1) x ar (1)), described in Dutkowski *et al.* (2002):

$$y_i = X\beta + Za + \xi + \eta$$

The difference to model std was the vector of spatial dependence residual (ξ), first-order autoregressive structure in rows and columns; η vector of independent residuals.

Residual covariance structure: $\boldsymbol{R} = \hat{\sigma}_\xi^2[ar1(\rho_{col}) \otimes ar1(\rho_{row})] + \boldsymbol{I}\hat{\sigma}_\eta^2$, where $\hat{\sigma}_\xi^2$ is the spatially dependent residual variance estimated; ρ_{col} and ρ_{row}: autocorrelation parameters, and $\hat{\sigma}_\eta^2$**:** estimate of the independent residual variance, that is associated with the identity matrix ***I*****.** Spatial autocorrelation coefficient in rows (ρ_{row}) and columns (ρ_{col}).

3. Competition Mixed Model (Comp): linear model of the additive competition, fitted following Cappa and Cantet (2008):

$$yi = X\beta + Z_d a_d + Z_c a_c + Z_p p + e$$

The a_d and a_c are the breeding values (direct additive genetic effects) and compection (indirect). The additive genetic effects distributed as $a_d \sim N\,(0, A\hat{\sigma}_{a_d}^2)$ and $a_c \sim N\,(0, A\hat{\sigma}_{a_c}^2)$, where $\hat{\sigma}_{a_d}^2$ and $\hat{\sigma}_{a_c}^2$ are the estimates of the variances. The incidence matrices Z_d and Z_c are the associated with the effects a_d and a_c. The *p* is the environmental competition's permanent effect, considered as random vector associated with the Z_p incidence matrix. Z_c are the factor of Competition Intensity (CI) f_{ij}, that is the competition intensity of the *j*-th neighbor on the *i*-th tree. The average f_{ij} in the directions of rows, columns, and diagonals ($f_{ijR}, f_{ijC}, f_{ijD}$, respectively):

$$f_{ijR} = f_{ijC} = \sqrt{\frac{2}{n_{iR} + n_{iC} + n_{iD}}}, f_{ijD} = \frac{1}{\sqrt{n_{iR} + n_{iC} + n_{iD}}}$$

Where n_{iR}, n_{iC}, n_{iD} are respectively competitors in the rows, columns and diagonals. The genetic competition effects were evaluated from the correlation of direct and competition effects ($\hat{r}_{a_d a_c}$).

4. Spatial+Competition Mixed Model (ar1Comp): Additive mixed linear model that was fitted as Cappa *et al.* (2015):

$$yi = X\beta + Z_d a_d + Z_c a_c + Z_p p + \xi + \eta$$

Models Comparison

Given the estimates of variance components, narrow sense heritability (h^2_a), were obtained:

$$h^2_a = \frac{\sigma^2_a}{\sigma^2_p}$$

Where: $\hat{\sigma}^2_a$: additive genetic variance; σ^2_p : phenotypic variance

The comparation were perfomed by the Akaike Information Criterion (AIC), as described in Akaike (1998) and the Likelihood Ratio Test (LRT) (Neyman and Pearson, 1928b, a). Was calculated the predicted breeding values accuracy ($\hat{r}_{aa}$) as:

$$\hat{r}_{aa} = \sqrt{1 - \frac{PEV}{\hat{\sigma}^2_{genetic}}}$$

Where: $\hat{\sigma}^2_{genetic}$ - are $\hat{\sigma}^2_a$ when obtained by the std and ar1 models and $\hat{\sigma}^2_{a_d}$ when estimated by the Comp and ar1Comp models. The predicted breeding values are the variances of the errors in the mixed model equations. The fit of the described models was carried out using the breedR package of the software R (Muñoz and Sanchez, 2020; R Core Team 2022).

Genetic gain ($\hat{G}_s$) and effective population size (N_e)

With the best-fit model for DBH and H traits, several thinning strategies and intensities of selection were simulated while the genetic gain ($\hat{G}_s$) and the number of effective population sizes (N_e) were calculated as:

$$N_e = \frac{4N_f\bar{K}_f}{\bar{K}_f+3+\left(\frac{\sigma^2_{Kf}}{\bar{K}_f}\right)} \text{ (Resende 2002)}$$

$$\hat{G}_s = \frac{\overline{BV}}{\mu} - 1$$

Where N_f: selected families; K_f: average of individuals per family; σ^2_{Kf}: variance of the individuals selected per family; $\overline{BV}$: mean of the breeding values; μ: phenotypic mean of the trait under consideration.

Regarding thinning strategies, a total of 33 were simulated (Table 1). In this process, the families, individuals within families, and selected individuals varied between the strategies devised. Based on the predicted breeding values ($\widehat{BV}$), the families were ranked and grouped into three clusters: Group/Cluster 1 (G1) had the 10 best families; Group/Cluster 2 (G2) had families that ranked between 11th and 19th; Group/Cluster 3 (G3) had the lower-ranked families, 20th to 28th. To form the clusters, the families were grouped based on analysis of the curve of the BLUP (genetic effects), function of the families' ranking. The strategies were performed based on the selection between and within families (BW-type strategies) – strategies numbers from 1 to 19 – and the selection of the best individuals (BI-type) – strategies numbers from 20 to 33.

Table 1
Selection simulated strategies with and within families (1 to 19) and selection of the individuals (20 to 33) of *Eucalyptus benthamii*.

Strategy Number	Maximum trees per family			Total trees	Selection
	Group 1	Group 2	Group 3		
1	30	30	30	840	60.0%
2	30	30	20	740	52.9%
3	30	30	10	640	45.7%
4	30	30	0	1040	74.3%
5	30	20	20	660	47.1%
6	30	20	10	560	40.0%
7	30	20	0	960	68.6%
8	30	10	10	480	34.3%
9	30	10	0	880	62.9%
10	30	0	0	1200	85.7%
11	20	20	20	560	40.0%
12	20	20	10	460	32.9%
13	20	20	0	860	61.4%
14	20	10	10	380	27.1%
15	20	10	0	780	55.7%
16	20	0	0	1100	78.6%
17	10	10	10	280	20.0%
18	10	10	0	680	48.6%
19	10	0	0	1000	71.4%
20				14	1.0%
21				42	3.0%
22				70	5.0%
23				98	7.0%
24				126	9.0%
25				154	11.0%
26				182	13.0%
27				210	15.0%
28				238	17.0%
29				266	19.0%
30				294	21.0%
31				420	30.0%
32				560	40.0%
33				700	50.0%

$\hat{G}_s - \widehat{BV}$ – *curve*

The Taylor regression procedure was applied to obtain the inflection point of the $\hat{G}_s - \widehat{BV}$ curve (Christopoulos, 2017). The $\hat{G}_s - \widehat{BV}$ curve was obtained as the relationships among estimate genetic gain with selection and the simulated thinning strategies ranked by the $\widehat{BV}$. Similar to Araujo et al. (2021), the inflection point, the strategies were classified as conservative and non-conservative. The characterization of the simulated thinning strategies considered the N_e, $\hat{G}_s$ and the number of trees to be kept. All analysis and graphs were obtained using the R software (R Core Team 2022) and RStudio IDE (RStudio Team 2022).

Results

In this experiment, the survival and Mean Annual Increment (MAI) were 84 % and 35 m^2 ha^{-1} y^{-1}, respectively. The best-fit models to describe the DBH and H traits were the competition (Comp) and autoregressive (ar1) models, respectively, based on the AIC criterion and Likelihood Ratio Test – LRT (table 2). Furthermore, the correlation between the additive direct and competitive genetic effect ($\hat{r}_{a_d a_c}$) was higher for DBH (0.88) and lower for H (0.34) trait; the autocorrelation coefficients were the same (0.2) for DBH and H (ρ_{row}) in the rows but opposite 0.8 for H and -0.8 for DBH (ρ_{col}) in the columns. For the DBH trait, the Comp model increased the narrow sense heritability (h_a^2) and accuracy ($\hat{r}_{aa}$) (Figure 1).

To initialize the thinning strategies, the additive genetic effects (BLUPs) for DBH and H traits of families were plotted as a function of ranking (Figure 2). Three clusters were obtained: Cluster 1 (G1) with the best families; Cluster 2 (G2) with the intermediate families; and Cluster 3 (G3) grouped the worst families. G1 and G2 were empirically divided according to the inflection point (blue dashed line – Figure 2) and the limit of G3 are the families with negative genetic effects (red dashed line – Figure 2).

The Taylor polynomial regression (degree 3) was used to obtain the $\hat{G}_s$ (dependent variable) inflection point of the curve, as a function of strategies ranked by $\hat{G}_s$ (categorical independent variable). The inflection points to strategy 32 for both DBH (Figure 3a; position 20 on the graph) and H traits (Figure 3b; position 20 on the graph).

From the inflection point, the strategies were divided into conservative and non-conservative (red dashed line in Figure 4). As it moves from the red dashed line to the left, the strategies became less conservative such that the genetic gain increased.

For the DBH and H traits, the 20 non-conservative strategies obtained leave between 14 (strategy 20; 1 % of trees or 16 trees ha^{-1}) and 560 (strategy 32; 40 % of trees or 640 trees ha^{-1}) trees in the field while the thirteen conservative strategies obtained leave between 280 (strategy 17; 20 % of trees or 320 trees ha^{-1}) and 840 (strategy 1; 60 % of trees or 960 trees ha^{-1}) trees in the field. The expected genetic gain from selection ($\hat{G}_s$) and effective population size (N_e) for non-conservative strategies and the DBH trait ranged from 12.8 % to 31 % and from 11.2 to 95.7, respectively. Concerning conservative strategies, the $\hat{G}_s$ and N_e ranged from 6.3 % to 14.1 % and from 56.4 to 101.8, respectively. For the H trait, the $\hat{G}_s$ and N_e ranged from 7.8 % to 16.6 % and from 10.6 to 92.3. In turn, for the conservative strategies, the $\hat{G}_s$ and N_e ranged from 3.4 % to 7.8 % and the H trait from 57.2 to 101.8, respectively.

Table 2
Akaike criterion (AIC), and Likelihood Ratio Test (LRT) for model comparison in the trial with *Eucalyptus benthamii*.

Model	AIC	-2 Loglik	Df	LRT_value	LRT_p.value
DBH					
standard model	6232.01	6228.01	2	0	1
spatial mode (ar1)	6230.06	6224.06	3	3.95	0.05
competition model	6228.81	6218.81	5	9.20	0.03
competition-spatial model	6230.19	6218.19	6	9.82	0.04
Total Height (TH)					
standard model	5724.60	5720.60	2	0	1
spatial model (ar1)	5722.23	5716.23	3	4.37	0.04
competition model	5727.89	5717.89	5	2.71	0.44
competition-spatial model	5726.23	5714.23	6	6.36	0.17

Df: Degree of freedom of the parameters in each specific model; LRT_value: -2 Loglik difference of the standard model; LRT_p.value: p-value of the chi-square test of the LRT_value.

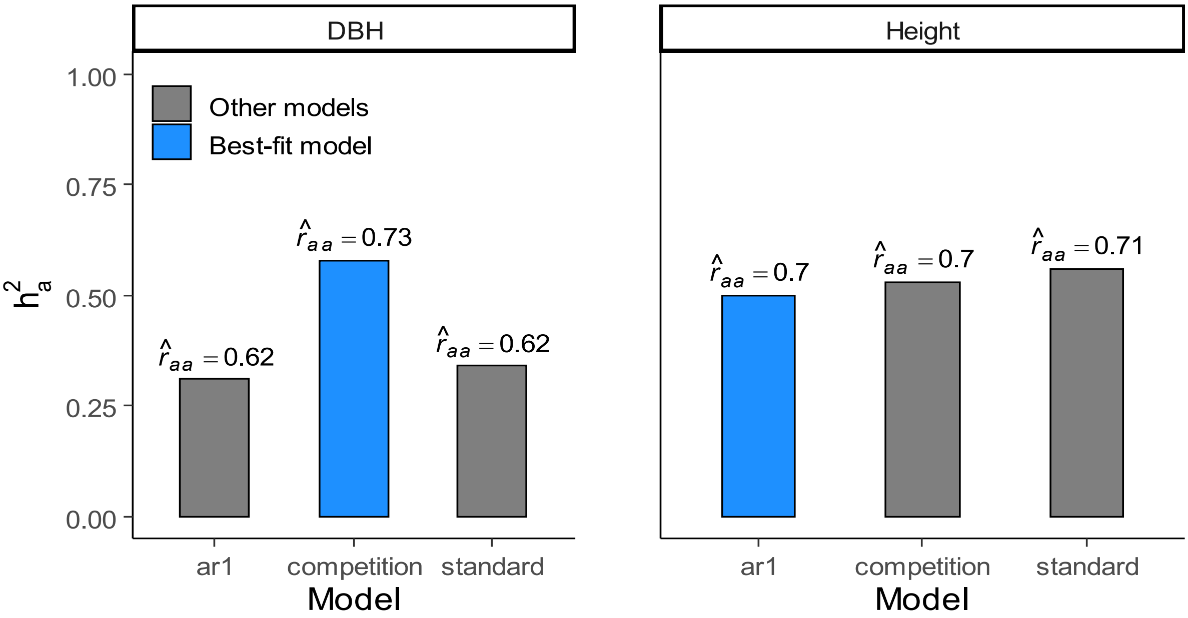
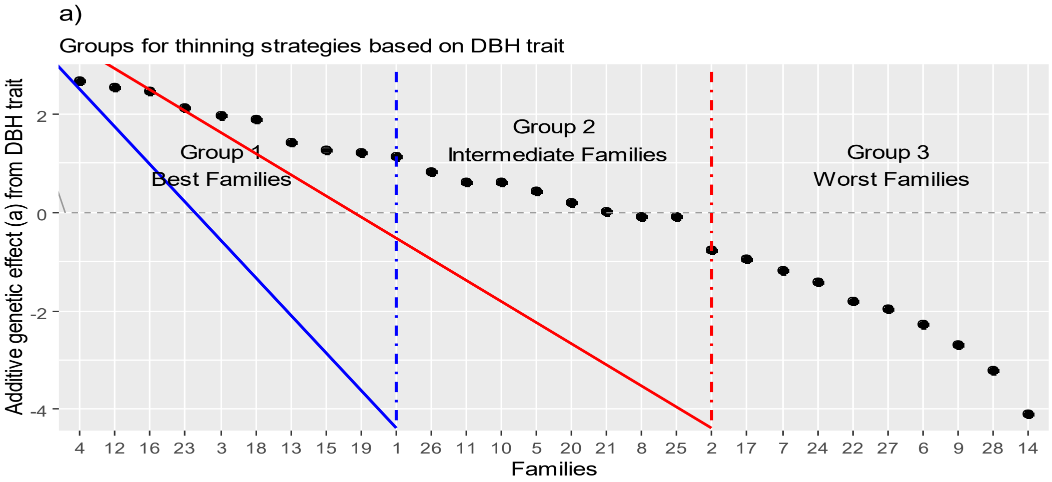


Figure 1
Comparison of narrow sense heritability and accuracy among models



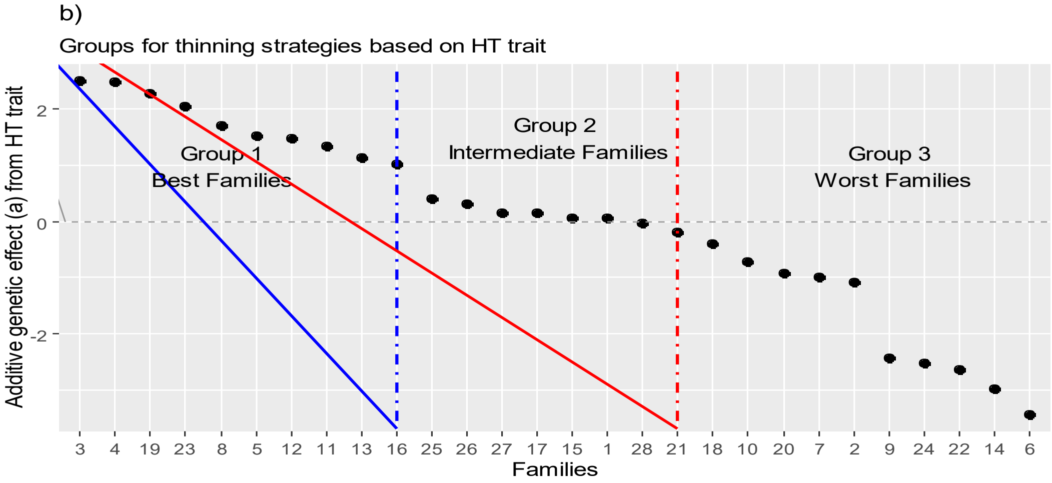


Figure 2
Groups by additive genetic effects, function of the ranked of the families: a) Competition Model for Diameter at Breast Height (DBH); b) First-order autoregressive Model for Total Height (H) in *Eucalyptus benthamii.*

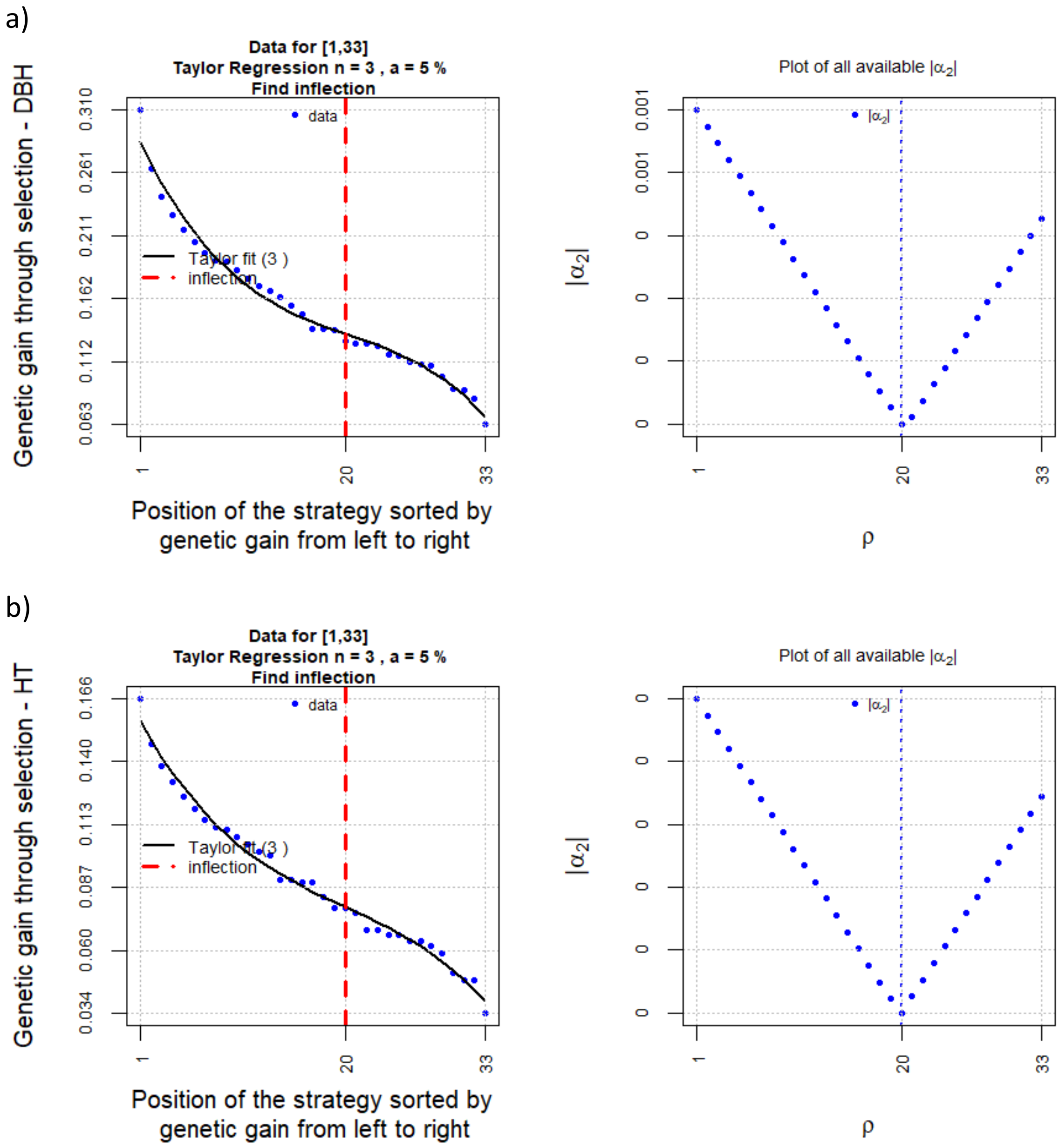


Figure 3

Curve point inflection from Gˆ_s as a function of differents strategies.

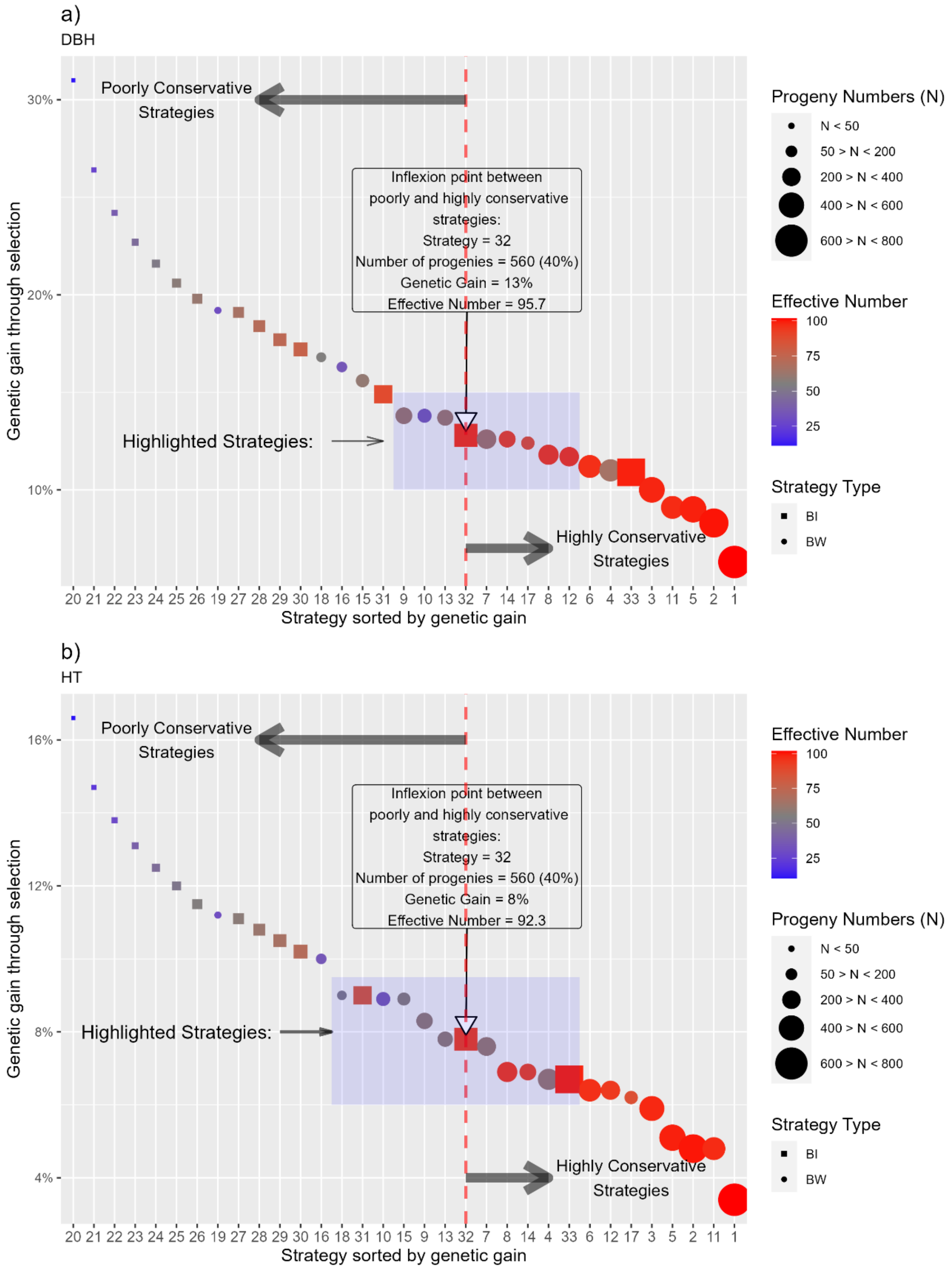


Figure 4
Inflection point strategies in *E. benthamii* trial according to conservation levels. Legend: BW - Selection with and within. BI- Best individual selection.

The most conservative strategy for both traits (strategy 1; Table 1 and Figure 4) leaves 60 % of the trees in the field, consisting of 30 trees from each family in the trial (retained 3 trees per plot). The least conservative strategy (strategy 20) leaves 1 % of the trees in the field, whose selected individuals are the best in the ranking based on BLUPs regardless of the families to which they belong; this strategy retains only individuals of the G1 and G2 groups.

Some strategies described here are separated between non-conservative and conservative around the inflection point (Figure 4). For the DBH trait, the highlighted strategies comprise $\widehat{G}_S$ ranging from 12 % (strategy 12; two remaining plants per plot for Group 1 and Group 2 families – 40 % of the trees in the plot – and one remaining plant per plot for Group 3 families – 20 % of the trees in the plot) to 16.2 % (strategy 10; three remaining plants per plot for Group 1 family – 60 % of the trees in the plot – and zero remaining plants per plot for Group 2 and Group 3 families – thinning all trees in the plot) and N_e from 14.5 (strategy 10; as described earlier) to 95.7 (strategy 32; ranking trees concerning their breeding values and applying selection intensity of 40 %).

For the H trait, the highlighted strategies provided $\widehat{G}_S$ ranging from 6.5 % (strategy 12; two remaining plants per plot for Group 1 and 2 families – 40 % of the trees in the plot – and one remaining plant per plot for Group 3 families – 20 % of the trees in the plot) to 9.3 % (strategy 18; one remaining plant per plot for Group 1 and Group 2 families – 20 % of the trees in the plot – and zero remaining plants per plot for Group 3 families – thinning all trees in the plot). N_e ranged from 32.7 (strategy 10; as described earlier) to 98.6 (strategy 33; ranking trees concerning their breeding values and applying 50 % of selection intensity).

Discussion

The obtained productivity is similar to the yearly average productivity of 36.8 m^3 ha^{-1} reported in Brazil (Ibá, 2021), although the population is a seminal plantation whose genotypes come from different families. Similar volumetric productivity under other environmental conditions in Brazil, with *Eucalyptus grandis* and *E. urophylla* (Silva et al. 2019a,b), the two main species used in Brazilian forestry sector. This result is due to the favorable climate conditions and the good adaptability of the *E. benthamii* to the site (Paludzyszyn Filho; Santos; Ferreira, 2006). Furthermore, alongside the higher narrow sense heritability found, *E. benthamii* shows great potential for advancing the generation with good individuals seeking to increase productivity in the southern region of Brazil.

Two different models provided the best DBH and H traits fit. The model accounting for the competition effect provided the best fit for the DBH trait, while the model accounting for spatial variability provided the best fit for the H trait. Likewise, Araujo *et al*., (2021) reported similar results for a *Eucalyptus dunnii*. The DBH trait is more sensitive to competition effect whereas H is more favorable to detecting environmental heterogeneity, however less sensitive to competition, as previously described in other studies (Magnussen 1989, Hannrup *et al.* 1998, Dutkowski *et al.* 2006, Ye and Jayawickrama 2008, Cappa *et al.* 2016, Hernández *et al.* 2019).

The traits have different characteristics (i.e., competition for DBH and spatial variability for TH) that affect the predicted phenotypic and genetic values. For the DBH trait, neglecting the competition effect may mask additive genetic information and reduce the correlation among predicted and true breeding values, i.e., features related to narrow-sense heritability and accuracy respectively. Operationally, compared to H, the DBH is the easiest trait to measure in the field being, therefore, very useful for breeders in the selection strategies, and very recommended for taking into account the competition effect. Otherwise, the ranking of families and individuals may be compromised (Dong *et al.* 2020).

Unlike DBH, the competition effect has little impact on the H trait, however, the environmental heterogeneity must be taken into account if the selection is carried out based on the H trait. Regarding narrow sense heritability and accuracy, these parameters basically did not change among the fitted models, but changes in the ranking were observed at the levels of families and individuals. The H trait is less important than DBH to determine the tree volume once after primary growth decrease or stops the secondary growth in trees continues (Gadow and Gangying Hui, 1999; Hernández *et al.,* 2019). Therefore, similar to *Eucalyptus dunnii* (Araujo *et al.,* 2021), DBH is the best growth field trait, regarding precision and accuracy, in the individuals selection in this trial with *E. benthamii*.

According to the genotypic values, the families were grouped into three clusters, G1 grouped the best families, G2 the intermediate families while selecting individuals from families of the G3 cluster provided the lowest genetic gain. This ranking was used to compose the breeding strategy, considering the balance between genetic gain and Ne while seeking simultaneously the desirable performance improvement concerning growth (i.e., increase favorable alleles - additive effects to growth) and preserving possible alleles related to other traits that are not the target in this stage of the breeding program (improve the adaptation, not considering wood quality for example).

The population of *E. benthamii*, the study target, is an F1 breeding generation, so for the following discussion implications, breeding at the recurrent selection strategy will be considered. Recurrent selection for general combining ability is the most common strategy used by forest breeders (Isik and McKeand, 2019).

Strategy 1 (leaves 60 % of the trees in the field, consisting of 30 trees from each family in the trial) scenario is extremely conservative whereas strategy 20 (leaves 1 % of the trees in the field, whose selected individuals ranked best based on BLUPs regardless of the families to which they belong) retained only individuals of the G1 and G2 groups and represents an extremely non-conservative one. For the DBH trait, the N_e and $\widehat{G}_S$ values are 101.8 and 11.2 % (Strategy 1), and 6.3 and 31 % (Strategy 20), respectively. For the H trait, the values were 101.8 and 10.6 % for the most conservative strategy and 3.4 and 16.6 % for the most non-conservative strategy. This result shows a trade-off between genetic gain and preservation of genetic variability (Kang and Namkoong 1988, Gea 1997, Wei *et al.* 1997), and both have practical consequences in breeding. While extreme non-conservative breeders aim to increase the gain from short-term selection, extreme conservative breeders aim to avoid the loss of alleles seeking to maintain genetic variability to design long-term breeding strategies.

Extreme non-conservative breeders by increasing the short-term genetic gain, supply more wood to the industry in the first years and the business becomes more profitable in this period, but this brings some consequences. By adopting strategy 1, the N_e drops considerably compared to strategy 20 and the inbreeding rate increases thus decreasing potential long-term genetic progress (Robertson,, 1960, Muir, 2000, Isik and McKeand, 2019). This accelerates the inevitable loss of genetic variability due to increasing relatedness in a recurrent breeding program (White, 2001).

Breeders whose profile is between non-conservative and conservative seek to match sustainable genetic gain while maintaining genetic variability. This is no easy feat in population breeding strategies and, there is a direct relationship with selection between and within families. The choice of the number of families and individuals within families affects the progress of selection performed for breeders of all profiles. For a constant number of F_1 individuals, increasing the number of F_1 families leads to lower aggregate genetic gain and less loss of genetic variability. The opposite happens when increasing the number of seeds for a constant number of F1 families (Li et al. 2022). However, some strategies lead to similar genetic gain with different N_e, as the strategies shown in Figure 4, considering the DBH trait. The strategies 9, 10 and 13 have practically the same expected genetic gain, however, the first and third have N_e equal to 52 and 55 respectively, while strategy 10 has only 14 of Ne.

Endemic to a few populations in NSW (Boland et al., 2006; Brooker; Kleinig, 2006), *E. benthamii* is a species with a naturally restricted genetic base so generation advance must be achieved while maintaining a good effective population size. It should be emphasized that the eucalypt genotype can also be fixed through cloning (with a lower or higher level of difficulty, depending on the species and genotype). Therefore, strategy 32 (Figure 4) is recommended for generation advance since it provided a 13 % gain in DBH and an effective population size of 95, thus delivering genetic gain and maintaining a good effective population size while allowing cloning of the best individuals for a short time.

Conclusions

- The DBH adjusted with the model that considered the competition effect exhibited higher precision since H is more susceptible to environmental heterogeneity and has lower measurement accuracy.
- The strategy that allows an adequate balance among effective population size and genetic gains of the *E. benthamii* F1 population consists of maintaining 40 % of the best individuals to compose the orchard.

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