# Genetic control of silvicultural traits in *Balfouro-dendron riedelianum* (ENGL.) ENGL.

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## Abstract

The Atlantic Forest has very high levels of biodiversity and is considered one of the most important and threatened biomes in the world. *Balfourodendron riedelianum* is one of the forest's characteristic tree species that is currently under considered endangered due to timber extraction and forest fragmentation. With the goal of generating information that may contribute to the genetic conservation of *B. riedelianum*, genetic parameters are estimated for quantitative traits important for silviculture in a provenance and progeny test located in the Experimental Station of Luiz Antônio, São Paulo State, Brazil. The test was established in 1986 and consists of three provenances, from which open-pollinated seeds from 19 seed trees were collected. The following traits were evaluated at 32 years of age: diameter at breast height (DBH), total height (H), stem height (SH), stem straightness (SS), and forking (FOR). The estimates were carried out using the REML/BLUP method. Significant genetic variation among progenies was detected for all traits (except SH) and between provenances for DBH. The coefficient of individual genetic variation ($CV_{gi}$) ranged from 2.5 to 9.5 %. The mean heritability among progeny ($h_f^2$) was substantial for DBH (0.44) and FOR (0.36), enabling the selection of families with the highest DBH and lowest FOR for population improvement. Genotypic and phenotypic correlations among traits were also found. We conclude that there is genetic variability in the population that can be exploited in future breeding programs and for the genetic conservation of the species.

Keywords: : *Genetic variation, genetic enhancement, pau-marfim, provenance and progeny test, tree improvement*

## Introduction

Natural forests around the world have been devastated extensively due to the expansion of agriculture, livestock, and urban development (Lander et al., 2010). Combined with the current pattern of consumption, this has resulted in increasing pressure on natural resources and severe alterations to ecosystems (Kareiva et al., 2007). Consequently, the native forest cover in most tropical regions has become highly fragmented (Ribeiro et al., 2009).

Fragmentation isolates populations spatially and reproductively due to changes in the breeding system resulting

from the alteration of individual tree density and pollinator behaviour (Aguilar et al., 2008). This process results in a loss of alleles, reduced heterozygosity and gene flow, and increased inbreeding and genetic differentiation among populations (Tambarussi et al., 2017). The main consequence of inbreeding is the phenomenon known as inbreeding depression, which occurs due to the expression of deleterious recessive alleles, which leads to reduced productivity, fertility, and seed viability, subjecting fragmented populations to even greater risk of extinction (Tambarussi et al., 2015). In this sense, *ex situ* conservation programs are of increasing importance as recent studies on tropical tree species have found signs of declining genetic diversity and increased inbreeding in fragmented populations; however, such changes may take generations to manifest as remaining adult individuals still represent the pre-fragmentation population (Manoel et al., 2012; Tambarussi et al., 2015).

The *ex situ* conservation of species carried out in the form of provenance and progeny tests serve as a source of genetic material (e.g., seedling seed orchards) for forest restoration, while also enabling the assessment of genetic parameters for quantitative traits, the effectiveness of the sampling strategy used, and the maintenance of genetic variability levels (Sebbenn et al., 2007). In addition, they provide relevant information on the silvicultural behaviour of tree species. Thus, it is possible to conserve representative samples of populations that, after being assessed and multiplied, can be used in research on genetic improvement, conservation, and species management (Hayward and Hamilton, 1997).

The demand for seeds of native forest species has increased in recent years (Carmo et al., 2017). An effective alternative to supply improved seeds for grow traits and that are genetically variable is the transformation of provenance and progeny tests into seed orchards (Rocha et al., 2009; Canuto et al., 2016). This can be done through the thinning of undesirable individuals (Rocha et al., 2009). When compared to other types of seed sources, seed orchards present greater genetic gains in shorter periods of time and improved large-scale seed production (Selvik and Topaçoglu, 2015).

It is important to emphasize that *ex situ* conservation is not sufficient to conserve species, as natural disasters can result in the loss of gene banks. Therefore, it is fundamental to reconfigure this conservation strategy and expand it through reforestation (Sebbenn et al., 2007). In addition, it is essential to provide subsidies for the sustainable use and management of timber and non-timber resources of these species.

Experiments based on progenies from different provenances enable a better understanding of the genetic variability of populations of a species, and promote the selection of genotypes that are better adapted to the environmental conditions of a reforestation site (Menegatti et al., 2016). Meanwhile, the information obtained complements future breeding programs and *ex situ* genetic conservation of the species.

*Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae) is an endangered species (IUCN, 2015). The species is a late secondary, deciduous, hermaphrodite tree, with zoophilic pollination (Carvalho, 2004). The samara-type fruits are dispersed via anemochory. The tree can reach 35 m in height and 1 m in diameter at breast height (DBH); it has a straight and cylindrical trunk with a shaft height of up to 15 m. Its wood is dense (0.84 g cm$^{-3}$, Lorenzi, 2008), poorly resistant, and subject to decay due to the attack of xylophages, most of which belong to the *Brentidae* family (Carvalho, 2004). The wood has high economic value and is used in civil construction and carpentry (Lorenzi, 2008).

The aim of this study was to quantify the genetic variation and genetic control of quantitative and qualitative traits in a *B. riedelianum* provenance and progeny test, to make a thinning and to convert the already established field trial into a seedling seed orchard. This information will also be useful for the management of the population in the plantation and for fragmented natural populations of the species, contributing to breeding and genetic conservation programs for environmental recovery.

## Materials and Methods

### Study site and sampling

The study was developed using a *B. riedelianum* provenance and progeny test established in 1986 at the Luiz Antônio Experimental Station of the Instituto Florestal de São Paulo, Brazil (21° 40′ S, 47° 49′ W). The trial was established with open-pollinated seeds collected from 19 seed trees in each of three provenances: Alvorada do Sul, Paraná State (22º 46′ 49″ S, 51º 13′ 52″ W); Gália (22º 20′ 0″ S, 49º 40′ 0″ W) and Bauru (22º 19′ 0″ S, 49º 04′ 0″ W), São Paulo State. A compact family block design (Wright 1978) was used to establish the trial, with provenances allocated in plots and progeny within provenance in sub-plots, using six block replicates, five plants per sub-plot spaced 3 x 3 m, and a double row surrounding the experiment. The total area of the trial is 1.86 ha. Originally, the trial consisted of 1710 planted individuals (Sebbenn et al., 2007), but due to mortality (16.8 %), the test has a final total of 1422 individuals. The following traits were measured at 32 years of age: diameter at breast height (DBH); total height (H); stem height (SH); stem straightness (SS); and forking (FOR). The traits H and SH were measured with the aid of a Hypsometer (*Häglof, Hypometer Vertex III*). DBH was estimated by measuring the circumference at breast height with a tape measure. Stem straightness and forking were categorized following Sant'Ana et al. (2013), based on a scale of grades, varying from 1 to 5. For SS, the scale of grades was: 1- strong tortuosity along the whole trunk; 2- tortuosity below DBH; 3- tortuosity above DBH; 4- weak tortuosity along the whole trunk; 5- rectilinear trunk. Grading scale for forking was determined in relation to the main trunk, with values ranging from 1 to 5: 1- forking with diameter similar to main trunk and below the DBH; 2- forking with diameter similar to main trunk and above the DBH; 3- forking with diameter lower than main trunk and below the DBH; 4- forking with diameter lower to main trunk and above the DBH; 5- without forking.

## Estimates of genetic parameters

To verify the significant differences among provenances and progenies for the traits studied the deviance analysis was used. The data were analyzed using the lme4 package (Bates et al., 2015) in the R statistical environment (R Core Team 2017), which uses the Restricted Maximum Likelihood procedure (REML) based on the mixed model $y = Xb + Up + Zt + Wbt + e$ where: $y$ is the data vector; $b$ is the fixed effect associated with block; $p$ is the random effect associated with provenances; $t$ is the random effect associated with progenies; $bt$ is the random effect associated with the interaction between block and progeny (sub-plot); and $e$ is the residual error. Capital letters represent the incidence matrices for these effects. From analysis of variance, the following variance components were estimated: variance associated with the effect of provenance ($\sigma_p^2$); genetic variance among progenies ($\sigma_{pt}^2$); variance associated with the interaction between block and progeny ($\sigma_{bt}^2$); phenotypic variance within plots ($\sigma_w^2$); and total phenotypic variance ($\sigma_F^2 = \sigma_{pt}^2 + \sigma_{bt}^2 + \sigma_w^2$). The additive genetic variance ($\sigma_A^2 = \sigma_{pt}^2 / \rho$, where $\rho = 2\Theta$, and $\rho$ and $\Theta$ are the coefficients of relatedness and coancestry within progeny, respectively) was estimated assuming open-pollinated progenies as half-sibs originating from either random mating ($\Theta = 0.125$) or from non-random mating ($\Theta = 0.138$; Aguiar, 2018). Heritability in the individual narrow sense ($h_i^2$), mean heritability among progenies ($h_f^2$) and heritability within progeny ($h_w^2$), were estimated respectively by:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_F^2} ;$$

$$h_f^2 = \frac{\sigma_{pt}^2}{\sigma_{pt}^2 + \dfrac{\sigma_{bt}^2}{b} + \dfrac{\sigma_w^2}{nb}} ; \text{ and}$$

$$h_w^2 = \frac{(1-\rho)\sigma_A^2}{\sigma_w^2} ,$$

where $b$ is the number of blocks and $n$ is the mean number of trees within sub-plots. We also calculated the coefficients of genetic variation among progenies ($CV_{pt} = 100(\sqrt{\sigma_{pt}^2 / x})$, individual addictive genetic variation ($CV_{gi} = 100(\sqrt{\sigma_A^2 / x})$), environmental variation ($CV_e = 100(\sqrt{\sigma_{bt}^2 / x})$ and variation among provenances ($CV_p = 100(\sqrt{\sigma_p^2 / x})$, where is the mean of the traits. The coefficient of relative variation was estimated as $CV_r = CV_g / CV_e$ (Vencovsky and Barriga, 1992). The effective population size ($N_e$) was estimated for DBH according to the expression proposed by Resende (2002):

$$N_e = \frac{4 N_p \overline{k}_f}{3 + \overline{k}_f (\sigma_{kf}^2 / \overline{k}_f)} ,$$

where $N_p$ is the number of selected progenies; $\overline{k}_f$ is the average number of individuals selected within progenies; and $\sigma_{kf}^2$ is the variance of the number of individuals selected within progenies.

## Results

The likelihood ratio test (LRT) detected significant differences among provenances for diameter at breast height (DBH) and among progeny for all traits except stem height (SH). These results suggest the presence of genetic variability that can be exploited through selection (Table 1).

Table 1
 Likelihood ratio test (LRT) for provenance and progeny as the source of variation and mean (*x*) for the traits diameter at breast height (DBH), total height (H), stem height (SH), stem straightness (SS), and forking (FOR).

| Source of variation | DBH | H | SH | SS | FOR |
|---|---|---|---|---|---|
| Provenance | 4.38[*] | 0.03 | 0 | 1.31 | 0.10 |
| Progeny | 34.61[**] | 9.46[**] | 3.30 | 13.76[**] | 8.09[**] |
| Mean: $x$ | 16.01 cm | 15.99 m | 7.52 m | 4.05 | 3.13 |

[*]P< 0.05; [**]P< 0.01.

Assuming progenies as half-sibs (HS), the estimates of individual narrow sense ($h_i^2$) and within progeny ($h_w^2$) heritability decreased 9.4 and 12.6 %, respectively, when corrected using the within progeny coancestry coefficient (NR) estimated from the mating system index (Table 2). The corrected values indicate low levels of genetic control for all traits at the individual ($h_i^2$: 0.030–0.133) and family levels ($h_w^2$: 0.024–0.112). However, the mean heritability among progeny ($h_f^2$) showed higher genetic control for the studied traits ($h_f^2$: 0.14–0.44), especially for DBH and FOR. The coefficient of genetic variation among progenies ($CV_{pt}$) was low for traits (1.3–5 %), and lower than the individual additive genetic variation ($CV_{gi}$: (2.5–9.5 %). The coefficient of provenance variation was low ($CV_p$: 1.3–4.4 %) and was lower than the $CV_{pt}$ for DBH, SH and FOR, higher for H and similar for SS. The coefficient of environmental variation ($CV_e$) ranged from low (12 %) to moderate (48.2 %), consistent with the low $CV_{pt}$. The coefficient of relative variation ($CV_r$) was low for traits (0.10–0.20), indicating low potential to obtain genetic gains by selection.

The selection of the best individuals was simulated for DBH and based on the effective population size ($N_e$). The effective size of the total population (57 progenies) was 200.6. When selecting for a smaller $N_e$, the number of remaining individuals is decreased and as expected, the gains with selection increase (Table 3).

The coefficient of phenotypic correlation ($r_p$) was significantly higher than zero for DBH vs H, H vs SH, H vs SS, SH vs SS, SH vs FOR, and SS vs FOR and significantly lower than zero for DBH vs FOR (Table 4). The coefficient of genotypic correlation ($r_g$) was significantly higher than zero between DBH vs H, DBH vs SH, H vs SS, and SH vs FOR.

Table 2

Estimates of genetic parameters for diameter at breast height (DBH), total height (H), stem height (SH), stem straightness (SS), and forking (FOR) assuming progenies originated from either random mating (HS) or non-random mating (NR).

| Parameter | DBH (cm) | H (m) | SH (m) | SS | FOR |
|---|---|---|---|---|---|
| $h_i^2$ (HS) | 0.146 | 0.050 | 0.034 | 0.041 | 0.083 |
| $h_i^2$ (NR) | 0.133 | 0.045 | 0.030 | 0.037 | 0.075 |
| Overestimate | 9.4% | | | | |
| $h_w^2$ (HS) | 0.128 | 0.042 | 0.027 | 0.038 | 0.066 |
| $h_w^2$ (NR) | 0.112 | 0.037 | 0.024 | 0.033 | 0.058 |
| Overestimate | 12.6% | | | | |
| $h_f^2$ | 0.44 | 0.21 | 0.17 | 0.14 | 0.36 |
| $CV_{pi}$ (%) | 5.0 | 2.9 | 4.6 | 1.3 | 5.0 |
| $CV_{gi}$ (%) | 9.5 | 5.6 | 8.6 | 2.5 | 9.3 |
| $CV_p$ (%) | 4.1 | 4.4 | 1.3 | 1.3 | 2.0 |
| $CV_e$ (%) | 24.5 | 24.8 | 48.2 | 12.0 | 33.3 |
| $CV_r$ | 0.20 | 0.12 | 0.10 | 0.11 | 0.15 |

$h_i^2$ is the individual narrow sense heritability; $h_w^2$ is the heritability within progeny; $h_f^2$ is the mean heritability among progeny; $CV_{pi}$ is the genetic variation coefficient among progeny; $CV_{gi}$ is the individual genetic variation coefficient; $CV_p$ is the provenance variation coefficient; $CV_e$ is the experimental variation coefficient; $CV_r$ is the coefficient of relative variation ($CV_r = CV_{pi}/CV_e$).

Table 3

Estimates of effective population size ($N_e$), absolute genetic gain (GG), and mean diameter at breast high (DBH) for number of remaining progenies (MSP).

| $N_p$ | $N_e$ | MSP | GG | GG % |
|---|---|---|---|---|
| 57 (Total) | 200.6 | 16.01 cm | - | - |
| 54 | 150 | 18.37 cm | 0.35 cm | 2.2 |
| 31 | 50 | 22.29 cm | 0.93 cm | 5.8 |

$N_p$ is the number of remaining progenies; GG % is the percentage of genetic gain.

Table 4

Matrix of phenotypic (upper diagonal) and genotypic (lower diagonal) correlations for diameter at breast height (DBH), height (H), stem height (SH), stem straightness (SS), and forking (FOR).

| | DBH | H | SH | SS | FOR |
|---|---|---|---|---|---|
| DBH | - | 0.54[**] | -0.08 | 0.04 | -0.23[**] |
| H | 0.74[**] | - | 0.26[**] | 0.15[**] | 0.04 |
| SH | 0.25[**] | 0.12 | - | 0.30[**] | 0.70[**] |
| SS | 0.10 | 0.28[**] | 0.08 | - | 0.22[**] |
| FOR | 0.12 | -0.08 | 0.98[**] | -0.06 | - |

[*]P< 0.05; [**]P< 0.01.

## Discussion

Our results show that there is significant genetic variability, both among and within provenances for DBH, and among progenies for H, SS, and FOR, that can be exploited through selection. Thus, the provenances do not contribute much for selection to change the mean trait values and pool out all progenies of the three provenances and to continue without the effect of provenance is the best selection strategy for improvement. Similarly, previous analysis on this trial at 21 years of age detected genetic variability among provenances for DBH and SS and among progenies for DBH (Sebbenn et al., 2007). Kubota et al. (2015) studied quantitative traits for the same *B. riedelianum* provenances and progenies in a trial established at Pederneiras Forest, São Paulo State, Brazil, at age 27 and detected significant differences between provenances for DBH, H, and SS; however, no differences were observed among progenies for any of the evaluated traits. Considering that provenances are composed of only 19 progenies and only DBH showed significant differences among provenances, we suggest maintaining all provenances and undertaking selection among progenies irrespective of provenance.

In our study, ignoring the mating system (HS) does not have significant impacts on the results, since *B. riedelianum* has a mixed mating system, the value of the mean coancestry coefficient is very similar to half-sibs. By assuming that the progenies originated from random mating and relatedness within progeny was half-sibs (HS), both coefficients of individual narrow sense ($h_i^2$) and within progeny ($h_w^2$) heritability were overestimated (9.4 and 12.6 %, respectively), in relation to estimates based on the coancestry coefficient ( = 0.138), which were calculated from mating system analysis and using microsatellite markers. Progenies are mainly composed of half-sibs (89–93 %), but some self-sibs, self-half-sibs, and full-sibs also occur (Aguiar 2018). As open-pollinated progenies are always composed of mixtures of different levels of relatedness (Degen and Sebbenn, 2014), it is important to consider the mating system in genetic parameter estimates in studies on the genetic control of traits (Tambarussi et al., 2018). Thus, the following discussion will be based on the results of the NR analysis.

The mean heritability among progeny ($h_f^2$) was always higher than the individual narrow sense ($h_i^2$) and within progeny ($h_w^2$) heritability for all evaluated traits, indicating high levels of genetic control at the progeny level. This value indicates that mass selection within progenies can result in limited changes in mean population traits. However, the $h_f^2$ showed moderate genetic control for the studied traits, especially DBH and FOR (0.36–0.44), indicating that selection among progenies is likely to obtain better genetic gains in the present population. However, our estimates of $h_i^2$ and $h_w^2$ were low and $h_f^2$ was moderate for DBH at 32 years of age. In provenance and progeny tests, the mortality results in inter-tree competition, affecting the growth of traits as DBH (Magnuseen and Yeatman, 1987; Leonardecz-Neto et al., 2003; Pavan et al., 2011) and decreasing the estimates of genetic parameters as heritability (Leonardecz-Neto et al., 2003; Pavan et al., 2011). As the DBH is

a sensitive trait for competition (Magnuseen and Yeatman, 1987; Leonardecz-Neto et al., 2003; Pavan et al., 2011), the individual variation for competition resulted from mortality (16.8 %) can explain the estimated low heritability values. Under this condition is hard to be efficient in the genetic selection because DBH will reflect a large environmental effect due to competition, which affects also the selection of genotypes, favoring grow of trees of the best progenies for grow traits (Pavan et al., 2011).

The coefficient of environmental variation ($CV_e$) was generally high for the studied traits (> 20 %). According to Pimentel-Gomes and Garcia (2002), values of $CV_e$ ranging from 10 to 20 % in field experiments with high competition can be classified as low to moderate and above 20 % as relatively high (which includes all traits in the present study except stem straightness). However, this classification does not take into account different genetic and environmental factors, and it is common in field-level tree provenance and progeny tests to have $CV_e$ levels higher than 20 % (Kubota et al., 2015; Lima et al., 2015; Martins et al., 2018).

For all evaluated traits, the estimates of $CV_{pt}$ were higher than $CV_p$. Thus, the results suggest that there is more genetic variability within progeny that can be exploited than among provenances. Furthermore, the coefficient of genetic variation among progeny ($CV_{pt}$) was lower than the individual additive genotypic variation ($CV_{gi}$), indicating that although genetic gains may be obtained by selection within progeny, there is potential for greater genetic gains to be achieved through combined selection involving selection of individuals based on a combination of individual and progeny merit. The higher the value of $CV_{gi}$, the more effective it will be to identify superior individuals that will promote gains with selection (Moreira et al., 2014).

The coefficient of relative variation ($CV_r$) indicates the potential to obtain genetic gains by selection; values close to unity indicate greater genetic control of the traits through selection (Vencovsky and Barriga, 1992). Our $CV_r$ values were lower than 0.21, which can be classified as low to moderate according to Resende (2002).

If the selection seeks the maximum immediate gains, it must be performed considering a $N_e$ of 50; this would leave 31 progenies in the orchard and the gain would reach 5.8 %. Resende and Bertolucci (1995) suggest restricting $N_e$ to a maximum of 50 in order to not compromise selection intensity. However, a $N_e$ of 50 will only retain alleles with a frequency equal to or greater than 6 % (Vencovsky and Barriga, 1992). When considering a $N_e$ of 150 for the selection, which is a common value in the literature and is known as the reference $N_e$, a gain of 2.2 % is obtained due to the removal of the three progenies with inferior performance (maintaining 54 of 57 total progenies). Since our main concern here is genetic conservation, the most appropriate approach is to select for a higher $N_e$, even if it means limited genetic gains. Selection based on the reference $N_e$ (150) can ensure the retention of rare alleles that occur with a frequency equal to or greater than 1 % (Vencovsky and Barriga, 1992).

The coefficient of phenotypic ($r_p$) and genotypic ($r_g$) correlation were positive and high (> 0.5) for DBH vs H and SH vs FOR. Positive and high phenotypic and genetic correlation between two traits indicates that they can be considered as one in the selection process, since they do not cause damage to the correlated traits, nor do they have a negative influence over the other traits in the selection (Vencovsky and Barriga, 1992). Thus, the selection of trees with higher DBH will also result in an increase in H, and an increase in SH will result in an increase in FOR. This facilitates selection, since selecting for one trait can result in indirect gains for another. This strategy enables faster progress, since it provides gains in more than one trait. The high correlation between DBH and H can be explained by taking into account tree growth, which also increases height. This also means that these growth traits are largely influenced by the same pleiotropic genes (Vencovsky and Barriga, 1992).

## Conclusion

In general, the study showed that for *B. riedelianum*, all evaluated traits have low genetic variability. Therefore, in order to obtain significant genetic gains, selection must be directed at the progeny level. The results suggest that for this species, there is limited genetic control of stem height, stem straightness, and forking. If improvements in these traits are desired, control at the local level should be implemented. This study also revealed that, due to positive correlations among some traits, indirect gains can be optimized through selection of one of the correlated traits.

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