Genetic Variation in Provenance-Progeny Test of *Araucaria angustifolia* (Bert.) O. Ktze. in São Paulo, Brazil

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Abstract

A combined provenance-progeny test of *Araucaria angustifolia* (Araucariaceae) was established in Itapeva Experimental Station, São Paulo State, Brazil, in a compact family design with 15 provenances, 4 to 14 families per provenance, 10 individuals per subplot and 3 replications. Variation among and within regions, provenances and families and genetic parameters for DBH, height and volume were investigated, about 21 years after planting. Analysis of variation for DBH, height and volume revealed significant differences among regions, provenances, provenances within regions and families within provenances. Significant differences among provenances and provenances within regions were also found for survival. The evaluation of components of variation showed that provenance/region effects (ranging from 2.7% to 6.2%) contribute more to total variance than family/provenance effects (ranging from 1.3 to 1.7%). Growth performance of South provenances is generally better than other regions. Heritabilities were low for all traits (< 0.15) and genetic gain within families were not superior to 4.9%. A combination of seed production and conservation strategies for *A. angustifolia* provenance-progeny test is suggested.

Key words: Araucaria angustifolia, provenance-progeny test, genetic variation, genetic parameters, quantitative traits.

Introduction

Araucaria angustifolia (Paraná Pine) is an economically important tree in southern Brazil. It is dioecious, wind-pollinated and it produces a valuable construction timber, being also a source of raw material for pulp and paper industry. It can be found in Brazil between latitudes 19°15'S and 31º39'S and from longitude 41°00 W to 54°30 W, and being is also found in small patches in Argentina and Paraguay. The species grows exclusively in the Tropical Wet Mixed Forest (Araucaria Forest) in the Alluvial (gallery), Sub-Montane, Montane and High-Montane formation, between altitudes of 500 and 2,300 m (CARVALHO, 1994). The area originally occupied by this species was 73,778 km2 in the State of Paraná (36.7%), 56,693 km^2 in the State of Santa Catarina (60.1%), 46,482 km^2 in the State of Rio Grande do Sul (17.4%), and 5,340 km^2 in the State of São Paulo (2.2%). Today there are left only 3,166 km^2 (4,2%) of *A. angustifolia* forest in the State of Paraná, 1,800 km^2 (3,2%) in the State of Santa Catarina, 657 km^2 (1,4%) in State of Rio Grande do Sul, where most areas are second growth A. angustifolia forests (MACHADO and SIQUEIRA, 1980).

A. angustifolia is a Brazilian indigenous tree mostly used in breeding and genetic conservation studies (CARVALHO, 1994), and is listed in the Brazilian threatened flora under the vulnerable category (FAO, 1996). Genetic variations have been detected among provenances of *A. angustifolia* for quantitative traits (GURGEL and GURGEL FO, 1965; BALDANZI et al., 1973; AHLER and LUCCA, 1980; KAGEYAMA and JACOB, 1980; MONTEIRO and SPELTZ, 1980; SHIMIZU and HIGA, 1980; GIANNOTTI et al., 1983; SHIMIZU, 1999), as well as among natural populations to allozyme loci (SOUSA, 2000; AULER et al, 2002). The genetic variation detected among regions and provenances within regions has been interpreted as an evidence of geographical races (GURGEL and GURGEL FO, 1973).

Traditionally, forest genetic tests have been conducted sequentially with successive species, provenance and progeny trials. In practice, however, there is strong economic pressure to reduce the testing interval between these stages in a traditional tree improvement programme. The use of combined provenance-progeny test has been advocated to reduce the testing interval between provenance and progeny stages (ZHENG et al., 1994). It may be extended to combine provenance testing, progeny testing, seed production (ZHENG et al., 1994) and *ex situ* conservation, in a single trial.

In this study, we investigated genetic variation for growth traits in 123 families from 15 *A. angustifolia* provenances originated from three Brazilian regions. Our objectives were: *i*) to examine the distribution of genetic variation among and within regions, provenances and families within provenances, *ii*) to determine the extent of genetic control for growth traits, and, *iii*) to estimate genetic gains of selection within families.

Material and Methods

Sampling and Experimental Design

Seeds from open-pollination were collected from trees distributed in 15 natural *A. angustifolia* provenances in four Brazilian States which, in turn, were divided into three regions (*Table 1; Figure 1*). Progeny identity was kept during collection. A total of 123 families were sampled, with the number of family per provenance varying from 4 to 14 (*Table 1*).

The experiment was set up in a single site at the Itapeva Experimental Station of São Paulo State Forest Institute. The site's latitude, longitude and altitude are, respectively, 24°17' S, 48°54' W and 930 m. The winter is dry and lasts from June to September and the mean annual rainfall (approximately 1,300 mm) falls mostly during summer months. The mean annual temperature is approximately 18.6 °C. The trial was established in a compact-family design, with 15 provenances (plots), 4 to 14 families per provenance (subplots), 10 individuals per subplot and 3 replicates. Three by two meter spacing was used and borders consisted of two rows. Seeds were collected in May 1979 and seedlings planted in March 1980. Trial was measured in May 2001 (21 years after planting) for survival, DBH (1.3 m), total height and volume/tree. Survival data were transformed by logarithm arc-sin $(\sqrt{(\%Survival/100)}+0.5)$ for the analysis of variance, which was carried out at the subplot mean level.

Variance Components Estimates

The analyses of variance were those used by ZHENG et al. 1994. Since the experiment was unbalanced due to unequal

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Table 1. – Details of the provenances and number of family sampled per provenance.

	Provenances	Families	Lat. (° S)	Long. (° W)	Alt. (m)
	Region A				
1	Barbacena -MG	9	21°00'	43°50'	1,206
2	Ipiúna de Calda - MG	14	21°40'	46°10'	1,300
3	Congonhal - MG	6	21°42'	46°15'	854
4	Lambarí - MG	5	22°00'	45°30'	878
5	Vargem Grande do Sul - SP	5	21°30'	46°30'	800
6	Camanducaia - MG	7	22°30'	46°20'	1,600
7	Campos do Jordão – SP	9	22°50'	45°30'	1,800
	Region B				
8	Itapeva – SP	9	24°17'	48°54'	930
9	Itararé –SP	10	24°30'	49°10'	930
12	Quatro Barras – PR	9	25°20'	49°14'	915
	Region C				
10	Iratí - PR	7	25°30'	50°36'	880
11	Iratí (Tardio) – PR	10	25°30'	50°36'	880
13	Caçador – SC	4	26°46'	51°01'	960
14	Chapecó - SC	9	27°07'	52°36'	675
15	Três Barras - SC	10	25°15'	50°18'	760

number of surviving trees in the subplots and unequal number of families per provenance, the Restricted Maximum Likelihood (REML) method was used to estimate the variance components. REML and VARCOMP procedures from SAS statistical program (SAS, 1999) were used in combination.

A linear random model was used to estimate the components of variance. The model used was:

$$Y_{ijkl} = \mu + b_i + t_j + f_{j:k} + e_{ijkl} \quad (1)$$

where: Y_{ijkl} is the phenotypic value of the lth individual of the kth family of the jth provenance in the ith replication; μ is the fixed overall mean; b_i is the random effect of the ith replication; t_j is the random effect of the jth provenance; $f_{j:k}$ is the random effect of the kth family in the jth provenance; e_{ijkl} is the effect of the lth tree within the kth family of the jth provenance in the ith replication. The latter component includes error effects; i = l,..., b (b is the number of replications); j = 1,..., t (t is the number of provenances); k = l,..., f (f is the number of families within provenances); l = l,..., n (n is the number of trees per family).

An extra term (region effect) was added to the model to investigate the significance of the difference among regions. Provenance grouping in regions followed the principle of proximity (*Figure 1*). The interaction terms were ignored to simplify the analyses, conducted at the level of individual plants. Therefore, model 1 becomes:

$$Y_{ijkl} = \mu + b_i + r_z + t_{j:z} + f_{j:k} + e_{ijkl} \quad (2)$$

where r_z is the random effect of the zth region.

The variance component estimates were,

$\hat{\sigma}^2_r$ = variance among regions;

$\hat{\sigma}^2_p$ = variance among provenances within regions;

$\hat{\sigma}^2_f$ = variance among families within provenances;

$\hat{\sigma}^2_e$ = interaction variance among families within provenances;

$\hat{\sigma}^2_w$ = phenotypic variance within families.

Genetic Parameter Estimate

The genetic and phenotypic variation, heritability, genetic and phenotypic correlations and expected selection gains were calculated according to NAMKOONG (1979) and to FALCONER and MACKAY (1998). Progeny was assumed to be half sibs and additive genetic variance ($\hat{\sigma}^2_A$) was estimated as $\hat{\sigma}^2_A = 4\hat{\sigma}^2_f$, where $\hat{\sigma}^2_f$ is the genetic variance among families within provenances.

Narrow sense individual ($\hat{h}^2_i$), family ($\hat{h}^2_f$) and within family ($\hat{h}^2_w$) heritability were estimated by:

$$\hat{h}^2_i = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_F} \; (3), \qquad \hat{h}^2_f = \frac{\hat{\sigma}^2_f}{\frac{\hat{\sigma}^2_w}{nb} + \frac{\hat{\sigma}^2_e}{b} + \hat{\sigma}^2_f} \; (4), \qquad \hat{h}^2_w = \frac{(3/4)\hat{\sigma}^2_A}{\hat{\sigma}^2_w} \; (5)$$

where, $\hat{\sigma}^2_F$ is the total phenotypic variance estimated by $\hat{\sigma}^2_F = \hat{\sigma}^2_w + \hat{\sigma}^2_e + \hat{\sigma}^2_f$. (6)

Phenotypic and genetic correlations among traits were estimated for individual trees according to the equations:

$$\hat{r}_{P_{XY}} = \frac{\hat{\sigma}_{P_X P_Y}}{\sqrt{\hat{\sigma}^2_{P_X} \hat{\sigma}^2_{P_Y}}} \quad (7) \qquad \hat{r}_{g_{XY}} = \frac{\hat{\sigma}_{f_X f_Y}}{\sqrt{\hat{\sigma}^2_{f_X} \hat{\sigma}^2_{f_Y}}} \quad (8)$$

where $\hat{r}_{P_{XY}}$ and $\hat{r}_{g_{XY}}$ are the phenotypic and genetic correlation coefficients; $\sigma_{P_X P_Y}$ and $\sigma_{f_X f_Y}$ are the phenotypic and genotypic products of x and y traits; $\hat{\sigma}^2_{P_X}$, $\hat{\sigma}^2_{f_X}$ and $\hat{\sigma}^2_{P_Y}$, $\hat{\sigma}^2_{f_Y}$ are the phenotypic and genetic variances among families within provenances of x and y traits, respectively.

The response to selection ($\hat{R}$) was estimated by: $\hat{R} = i\hat{\sigma}_w \hat{h}^2_w$ (9), where i is the selection intensity in standard deviation unities and $\hat{\sigma}_w$ is the standard deviation of the phenotypic variance within families. One quarter of trees within families were selected resulting in the standardized selection intensity i = 1.2711 (HALLAUER and MIRANDA, FO. 1988, p. 166). The genetic gain in percentage [$\hat{R}$ (%)] was estimated by:

$$\hat{R}(\%) = \frac{\hat{R}}{\overline{X}} x100 \quad (10)$$

where $\overline{X}$ is the overall mean trait.

Results and Discussion

Genetic Variation and Growth Rate

Significant differences were found in the analysis of variance among regions, provenances, provenances within regions and families within provenances for all the traits, except for the survival trait of regions and families within provenances (*Table 2*). These results showed that trial has potential for selection. Genetic variations among *A. angustifolia* provenances were also observed in other studies. In Ribeirão Branco (Itapeva region) SHIMIZU and HIGA (1980) detected genetic differences for survival and height if 2, 4 and 6-year-olds in 18 provenances in the south of Brazil (Paraná, Santa Catarina and Rio Grande do Sul States), as well as in the southeast (São Paulo State). GIANNOTTI et al. (1983) who studied the behavior of 15 *A. angustifolia* provenances, during 2 years-old, in Itapeva, SP, detected genetic variations for height. In Monte Alegre, Paraná

Table 2. – Mean squares for traits at 21 years of age in provenance-progeny test of *A. angustifolia* in Itapeva, Brazil.

Source of variation	D.F.	Mean squares			
		Survival	DBH (cm)	Height (m)	Volume/tree (m³)
Blocks	2	0.00657	110.0824 **	72.7532 **	0.00243 **
Region	2	0.00484	79.7653 **	25.4736 **	0.00287 **
Provenance	14	0.00343 *	62.7410 **	31.7358 **	0.00131 **
Provenance/Region	12	0.00423 *	62.8238 **	32.3126 **	0.00116 **
Family/Provenance	122	0.001862	25.4143 **	7.4168 **	0.00037 **
Error	202	0.002321	19.7343	7.0497	0.00028

*: $P \leq 0.05$; **: $P \leq 0.01$.

State, Monteiro and Speltz (1980), studied 24 *A. angustifolia* provenances derived from the States of São Paulo, Santa Catarina, Paraná and Rio Grande do Sul, observing genetic variations for volume during 11 years. Furthermore, studies based on allozyme loci have also detected genetic differences among *A. angustifolia* natural populations. Auler et al. (2002) reported low F_{ST}-value, 0.044 for nine populations from Santa Catarina State and Sousa (2000) reported low F_{ST}-values among populations in the regions of Campos do Jordão, SP (0.004), Irati, PR (0.043) and Caçador, SC (0.048) and reasonable values among these mentioned regions (0.098).

Table 3. – Components of variance and relative contribution (numbers in parentheses) of region, provenance/region, family/provenance and within family to total variance in provenance-progeny test of *A. angustifolia* in Itapeva, Brazil.

Components of variance	DBH (cm)	Height (m)	Volume/tree (m^3)
Variance among regions - $\hat{\sigma}_r^2$	0.0352 (0.4%)	0.0060 (0.2%)	0.000002 (1.3%)
Variance among provenances/region - $\hat{\sigma}_p^2$	0.2519 (2.7%)	0.1478 (6.2%)	0.000005 (3.2%)
Variance among families/provenance - $\hat{\sigma}_f^2$	0.1608 (1.7%)	0.0409 (1.7%)	0.000002 (1.3%)
Phenotypic variance within family - $\hat{\sigma}_w^2$	8.7904 (95.2%)	2.1954 (91.9%)	0.000143 (94.2%)

The components of variance and their relative contributions toward total variance are shown in *Table 3*. Regarding total variance, regions accounted for less than 2%, provenance within regions accounted for 2.7% to 6.2%, families within provenances accounted nearly 1.7% and trees within families 91.9% to 95.2%. The higher value toward variance among provenances within regions in relation to families within provenances suggested that provenances within regions are isolated or gene flow is insufficient to overlap the effects of selection and/or genetic drift. Larger genetic variance among provenances within regions than genetic variance among families within provenances were also observed in provenance-progeny test by Li et al. (1993) on *Picea glauca*, in Canada, Zeng et al. (1994) for *Pinus caribaea* var *bahamensis* in China and Baliuckas et al. (1999) for *Acer platanoides, Alnus glutinosa, Fagus sylvatica* and *Fraxinus excelsios* in Sweden.

The south region's (C region) growth rate was superior to other regions (*Figure 1; Table 4*). Provenances from faster growing regions are about 4% larger for both DBH and height and 15% higher for volume than those from slowest growing regions (A region). However, when considering standard error, differences among regions and provenance means are not statistically significant. Chapecó had the highest growth and presented approximately 18% higher DBH and height and 40% greater volume than the least growth provenance, Lambarí. Barbacena provenance seemed to also be the second best in survival and growth for DBH and height. DBH and height differences between first and second provenances were about 5% and 4%, respectively. The differences observed here in traits growth are possibly associated to climatic characteristics. Regions A and B are drier than region C.

Figure 1. – Location of the provenances seed collection sites (●) and site trial (▲) of *Araucaria angustifolia*.

Table 4. – Survival and growth date (mean ± standard error) for each provenance at 21 years after planting in provenance-progeny test of *Araucaria angustifolia* in Itapeva, Brazil (number in parentheses are ranks).

Rerion/Provenence	Survival (%)	DBH (cm)	Height (m)	Volume/tree (m^3)
Region A				
1	93.3 (2)	10.77±3.01 (2)	7.55±1.81 (2)	0.013±0.010 (4)
2	90.4 (5)	9.96±3.12 (10)	6.71±1.53 (10)	0.009±0.008 (10)
3	88.3 (9)	9.79±3.20 (12)	6.59±1.71 (12)	0.010±0.008 (11)
4	96.0 (1)	9.32±2.87 (15)	6.41±1.57 (15)	0.009±0.006 (14)
5	86.2 (12)	10.62±3.57 (4)	6.92±1.83 (8)	0.012±0.010 (5)
6	89.3 (6)	9.61±3.26 (13)	6.47±1.68 (14)	0.011±0.009 (13)
7	93.0 (4)	10.26±3.44 (7)	6.98±1.71 (6)	0.011±0.009 (8)
Mean	89.2±1.26	9.95±1.19	6.77±0.63	0.011±0.004
Region B				
8	88.7 (7)	10.53±3.38 (6)	7.07±1.71 (4)	0.012±0.016 (6)
9	87.8 (11)	9.38±3.34 (14)	6.49±1.88 (13)	0.009±0.008 (15)
12	86.1 (11)	10.56±3.73 (5)	7.37±6.52 (3)	0.013±0.016 (3)
Mean	87.5±1.65	10.35±1.88	6.93±0.96	0.011±0.007
Region C				
10	88.6 (8)	9.74±2.80 (11)	6.62±1.51 (11)	0.010±0.006 (12)
11	93.3 (3)	10.20±3.07 (9)	6.94±1.53 (7)	0.011±0.008 (9)
13	84.2 (15)	10.64±4.43 (3)	6.90±6.65 (9)	0.016±0.024 (1)
14	85.2 (14)	11.31±3.31 (1)	7.88±1.62 (1)	0.015±0.012 (2)
15	88.1 (10)	10.24±3.35 (8)	7.06±2.15 (5)	0.012±0.011 (7)
Mean	87.9±1.7	10.37±1.59	7.06±0.85	0.013±0.007
General mean ($\bar{x}$)	89.2±9.8	10.20±0.56	6.93±0.42	0.010±0.003

Preliminary studies in Itapeva region, south of São Paulo State, suggest that natural species distribution provenances originated in the north of Brazil grow more in height than in the south. Shimizu and Higa (1980) studying 2, 4 and 6 year-old *A. angustifolia* provenances, observed that north provenances (from Parque Nacional do Itatiaia and Parque Estadual da Bocaina) grow more in height than local and south provenances. Giannotti et al. (1983) in preliminary studied of the present test, detected in two years-old, that provenances from Lambari, Quatro Barras and Ipuiúna grow more on height than other provenances. The Chapecó provenance studied here showed the best performance in DBH and height and second best for volume. Shimizu and Higa (1980) showed it ranked eleventh in height growth, Giannotti et al. (1983) showed it ranked nine in height growth and Shimizu (1999) showed it ranked third in height, fifth in DBH and sixth in volume growth. These results show caution is necessary when extrapolation data from juvenile to adult phases.

Differences in traits growth were greater among families than among provenances. The best growing family exceeded the least growing family by 65%, 81% and 94% for DBH, height and volume, respectively (data not shown), showing the potential of provenance-progeny test of *A. angustifolia* for selection.

Genetic Parameters

All genetic and phenotypic correlations among traits (*Table 5*) were high (range 0.88 to 1.0) and statistically significant ($P < 0.01$) indicating the possibility of selection in one trait while obtaining gain in another. Genetic correlations were superior to phenotypic correlations. The greatest correlations coefficient was found to be between DBH and volume and the smallest between height and diameter.

Table 5. – Genetic (upper diagonal) and phenotypic (lower diagonal) correlation coefficients among traits in a provenance-progeny test of *A. angustifolia* in Itapave, Brazil.

	DBH	Height	Volume/tree
DBH		0.97 **	1.00 **
Height	0.97 **		0.94 **
Volume	0.96 **	0.88 **	

**: $P \le 0.01$

Narrow sense individual ($\hat{h}_i^2$) and within families ($\hat{h}_w^2$) heritability for traits were lower (close to 0.055) than those reported in other studies on *A. angustifolia* (*Table 6*). PIRES et al. (1983) studied 32 half-sib *A. angustifolia* families and found narrow sense individual heritability of approximately 0.31 for DBH and 0.47 for height. KAGEYAMA and JACOB (1980) observed narrow sense individual heritability varying from 0.12 to 0.56 for height and 0.03 to 0.64 for DBH in three *A. angustifolia* provenances aged 3.5 years. Heritability obtained here was lower, indicating the genetic control of traits is weak and the possibility of genetic gains with selection is limited.

Family heritability ($\hat{h}_m^2$) was higher than *narrow sense* individual ($\hat{h}_i^2$) and within family ($\hat{h}_w^2$) heritability, indicating the possibility of greater gains with selection among families rather than mass selection (*Table 6*). However, since the main objective of this study was ex situ genetic conservation of *A. angustifolia* provenances, but keeping in mind that management should also maintain growth rate and material recombination, selection will be carried out only within families. To achieve this, 25% of the trees will be selected within families. Since *A. angustifolia* is dioecious, it is possible to select trees of the same sex within subplots, therefore reducing the probability of outcrossing among sibs. Two subplots will be kept with female trees and one with male trees for the best performing families, and the opposite (that is, two subplots male trees and one female trees) for the worst performing family. Since there are 123 families, 62 will be kept in two subplots with three female trees and one subplot with three male trees and 61 in two subplots with three male trees and one plot with three female trees. The resulting sex ratio will be close to 1:1, maximizing the effective size (CROW and KIMURA, 1970). This selection scheme creates low genetic gains for DBH (2.03%) and height (1,49%) but reasonable gains for volume per tree (4.96%) with the advantage of maintaining the wide genetic base and maximizing effective provenance size, capitalizing gains and minimizing outcrossing among relatives (*Table 6*).

Table 6. – Estimated heritabilities (± standard error) and responses to selection within family in a provenance-progeny test of *A. angustifolia* in Itapave, Brazil.

Parameters	DBH	Height	Volume/tree
Heritability at individual plant level - $\hat{h}_i^2$	0.059 ± 0.004	0.053 ± 0.006	0.053 ± 0.005
Family heritability - $\hat{h}_f^2$	0.133 ± 0.019	0.103 ± 0.021	0.119 ± 0.020
Heritability within family - $\hat{h}_w^2$	0.055 ± 0.005	0.056 ± 0.005	0.051 ± 0.005
Response to selection within family $\hat{R}$	2.03 %	1.49 %	4.96 %

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