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## Genetic variation in populations and progênies of Aroeira (*Astronium urundeuva* (M. Allemão) Engl.) from Cerrado (Savanna) Biome

### Variação genética em populações e progênies de Aroeira (*Astronium urundeuva* (M. Allemão) Engl.) no Bioma Cerrado

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#### RESUMO

Conservar a diversidade genética mantém a variabilidade, necessária à adaptação das espécies. *Astronium urundeuva* (M. Allemão) Engl. (Anacardiaceae) é conhecida e explorada em função de sua madeira, mas avanços nas fronteiras agrícolas também afetou a sua distribuição. Os objetivos deste estudo foram caracterizar progênies de *A. urundeuva*, distribuídas em diferentes regiões geográficas e idades. Parâmetros genéticos de três testes de progênies e procedências, dois de origem de áreas de Cerrado, e uma de área de transição de Mata Atlântica/Cerrado foram estimados para caracteres de crescimento, padronizados pela estatística Z, e caracteres reprodutivos, medidos em 2019, em Selvíria-MS. Os dados também foram avaliados quanto à eficiência, a partir de covariável índice de falhas quanto à competição entre indivíduos. A sexagem foi determinada pelo florescimento individual. A partir dos resultados iniciais, a seleção das melhores progênies foi feita com avaliação da sobreposição de gerações (com inclusão das mães) e com correlações de Spearman entre efeitos aditivos (a) e de dominância (d). Os resultados mostraram que modelos com covariáveis foram ineficientes ( $-26.18\% > EF\% > 2.34\%$ ). As populações estão em desequilíbrio sexual (1♀:2♂), relacionada à distribuição espacial da espécie e características ecológicas. Com poucas mães superiores (2-9 por população), há indicação de que os cruzamentos podem ser aparentados. Uma correlação significativa entre a e d ( $S=0.7415$ ,  $p < 0.01$ , em média) mostrou que tanto as sementes como os propágulos podem ser utilizados e, ainda assim, haverão ganhos genéticos. A espécie mostrou ser longeva, de crescimento lento, sem interferência competitiva, em função do espaçamento de plantio, um comportamento típico de espécies do Cerrado.

**Palavras-chave:** Conservação; Desbaste; Desequilíbrio; Diversidade; Ex Situ; Germoplasma.

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#### ABSTRACT

Conserving genetic diversity keeps variability, necessary to species adaptation. *Astronium urundeuva* (M. Allemão) Engl. (Anacardiaceae) is known and logged for its wood, but advances in agricultural frontiers also affected its distribution. The aims of this research were to characterize *A. urundeuva* progenies, distributed from different geographic regions and ages. Genetic parameters from three progeny and provenance tests, two originated in Cerrado areas and one in Atlantic Forest/Cerrado transition, were estimated for growth characters, standardized by Z statistics, and reproductive traits, measured in 2019, in Selvíria-MS. Data were also evaluated for efficiency in failure rate covariate use for competition between

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individuals. Sexing was determined by individual flowering. From initial results, best progenies selection was made through generations (including mothers) overlapping and Spearman's correlation between additive (a) and dominance (d) effects. Results showed that models with covariates were inefficient ( $-26.18\% > EF\% > 2.34\%$ ). Populations are in sexual imbalance ( $1♀:2♂$ ), related to species spatial distribution and ecological characteristics. With few superior mothers (2-9 per population), indicated that crosses may have been targeted. A significant correlation between a and d ( $S = 0.7415$ ,  $p < 0.01$ , on average) showed that both seeds and propagules can be used, even so, there will be genetic gains. The species proved to be long-lived, with slow growth, without competition interference, as a function of planting spacing, a typical behavior of Cerrado plants.

**Keywords:** Conservation; Diversity; Ex Situ; Germplasm; Harvesting.

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## INTRODUCTION

Formed by a complex vegetation composition, Cerrado biome constitutes the second largest phytogeographic domain in South America (IBGE, 2004; Coutinho, 2006; MMA, 2014) and its biodiversity is threatened by agriculture advance (Strassburg et al., 2017; Vacchiano et al., 2019; Gonçalves et al., 2019). Even so, Cerrado ensures water quality, soil integrity and is home to diverse organisms communities (Mendonça et al., 1998; Rodrigues et al., 2021). Due to these factors, this biome is considered a biodiversity hotspot in our planet (Jenkins and Pimm, 2006; INPE, 2018).

Among the species that occur in Cerrado, “aroeira” (*Astronium urundeuva* (M. Allemão) Engl., Anacardiaceae) is a tropical tree species, dioecious and native to Brazil (Silva-Luz et al., 2020), with high wood density (1.19 g cm<sup>-3</sup>) (Paes et al., 2009), late secondary or anthropogenic pioneer (Ferretti et al., 1995), pollinated by bees and dispersed by wind (Carvalho, 1994). Although it doesn't belong to the current list of threatened species by Brazilian Environmental Ministry (Silva-Luz et al., 2020), it was and still is a widely logged species, due to its multiple uses for wood (the hardest wood in Brazil) and non-timber (broad medicinal use) (Lucena et al., 2008; Oliveira et al., 2010). Despite efforts to manage and conserve the species, its ability to survive is compromised (Freitas et al., 2006).

Conserving species genetic diversity is important not only for their survival, but also for gene pool maintenance, with sufficient variability, necessary for the species to adapt to environmental changes (Lande, 1995; Ayala, 1997; Meffe and Carroll, 1997). With agricultural advances, habitat fragmentation increases, as well as spatial distance between remnants and it also isolates populations. These changes have a direct influence on population genetic composition, by altering dispersal patterns, and can ultimately cause extinction (Fahrig, 2003; Ghazoul, 2005; Avise, 2010; Caballero et al., 2010). Studies to understand the genotype distribution patterns in the landscape become important not only for natural resources conservation, but also for genetic improvement, as they help to keep species genetic variability and develop strategies for threatened species (Melo et al., 2015). With the growing need for quality raw materials, use of improved materials also guarantees genetic quality for commercial and environmental purposes (Pinto-Júnior et al., 2013; Freitas et al., 2018). Therefore, this research aimed to genetically characterize *A. urundeuva* populations progenies, distributed from different geographic regions (Atlantic Forest and Cerrado biomes) and ages.

## MATERIALS AND METHODS

### Progenies Test Populations

There are three areas whose materials originated to the three progeny and provenance tests: CUIA (Cuiabá-MT, typical conserved Cerrado, homogeneous plantation), GO (Itarumã-GO, typical anthropized Cerrado, intercropped with *Cordia trichotoma* (Vell.) Arr. ex Steud., Boraginaceae), PF (Paulo de Faria-SP, Cerrado-Atlantic Forest transition area, intercropped with *Corymbia citriodora* (Hook.) K.D. Hill & L.A.S. Johnson, Myrtaceae (already logged) and *Hymenaea stigonocarpa* Mart. ex Hayne, Fabaceae). Seeds from 30 mothers of each population were collected, in an open pollination system, on different dates.

Tests installation took place at different periods, with different plots (Table 1), installed in Teaching, Research and Extension Farm (FEPE: Fazenda de Ensino, Pesquisa e Extensão), Ilha Solteira Engineering Faculty (FEIS: Faculdade de Engenharia de Ilha Solteira), at São Paulo State University (UNESP: Universidade Estadual Paulista), located at Paraná River right bank, in Selvíria-MS, at 22° 22' 02' south latitude and 51° 25' 08' west longitude and 335 meters above sea level.

**Table 1 – General characterization in three populations of *Astronium urundeuva* installed in Selvíria-MS.**

PT	Prov.	P/P	Prog.	N	Spc. (m)	Rep.	Installation	Age (in Years) (2019)
<b>CUIA</b>	Cuiabá/MT	1	29	615	4 x 3	24	07/01/2010	9
<b>GO</b>	Itarumã/GO	3	30	1080	2 x 6	12	28/06/2004	15
<b>PF</b>	Paulo de Faria/SP	6	30	540	3 x 6	3	12/05/1997	22

PT = progeny tests; Prov. = provenance; P/P = number of plants per plot; Prog. = number of progenies; N = number of individuals; Spc.= spacing; Rep.= Repetitions

Source: the authors (2022).

Local climate is tropical humid, with a rainy season in summer and a dry season in winter (Aw) (Köppen, 1948), an average annual temperature of 24.5 °C, an average annual precipitation of 1350 mm and an average annual relative humidity of 66% (Santos and Hernandez, 2012). Moderately flat to wavy relief, formed by a dystrophic Red Latosol (dRL) typical, compacted, very deep and moderately acidic (Santos et al., 2018).

### Silvicultural data collection

Silvicultural variables measured in three populations were i) height (HT, m); ii) diameter at breast height (DBH, cm); iii) average crown diameter (ACD, m), where:  $ACD = (L_1 + L_2)/2$ ,  $L_1$  = measure in the line and  $L_2$  = measure between lines; iv) survival (SV, %), where 1 = present plant and 0 = absent plant; v) sexing, evaluated based on flowering: 1 = male flowers ( $\sigma$ ), 2 = female flowers ( $\rho$ ), 3 = female and male flowers (monoecious plants), 4 = no flowers and 5 = presence of flowers, no sex determination; vi) tree trunk quality up to 2.20 m height, given by:  $TTQ = (B + S)/2$ , where  $B$  = bifurcation (1 = below 1.30 m, with a diameter equal to the main tree trunk; 2 = bifurcation above 1.30 m, with diameter equal to the main tree trunk; 3 = bifurcation below 1.30 m, with a diameter smaller than the main tree trunk; 4 = bifurcation above 1.30 m, with diameter smaller than the main tree trunk and 5 = no bifurcation) e  $S$  = tree trunk straightness (1 = accentuated tortuosity along the entire length; 2 = accentuated tortuosity below 1.30 m; 3 = accentuated tortuosity above 1.30 m; 4 = slight tortuosity along the entire extension and 5 = without tortuosity) (OTSUBO et al., 2015); vii) failure index covariate, composed of the equation:  $FI = (P_1 \cdot NF_L) + (P_2 \cdot NF_C) + (P_3 \cdot NF_D)$ , where:  $P_1 = E_L/E_L$ ,  $P_2 = E_L/E_C$ ,  $P_3 = E_L/\sqrt{(E_C)^2 + (E_L)^2}$ ,  $E_L$  = spacing in the line of progeny test in field,  $E_C$  = spacing in the column (or spacing) of progeny test in field,  $NF_L$  = number of failures in lines,  $NF_C$  = number of failures in columns (spacing) and  $NF_D$  = number of failures in diagonal lines.

Indirectly, volume was also evaluated, according to Smalian equation, adapted to the species:  $Veq = -0,0002 + (0,376 \cdot DBH^2 \cdot HT.)$  (J. Cambuim, personal communication).

### Silvicultural data analysis

The REML/BLUP (Restricted Maximum Likelihood/Best Unbiased Linear Prediction) procedure, through mixed linear models, was used in individual and joint analyses to estimate variance components and genetic parameters of each characters evaluated in progeny tests. These estimates were obtained using SELEGEN software (Resende, 2016). Different models were used, depended on desired analysis (depending on number of plants per plot and covariate inclusion or exclusion), in addition to a cluster analysis for each progenies test at SELEGEN software (Model 104: genotypic divergence

measures – Mahalanobis statistical distance and Tocher grouping) (Resende, 2016) (Table 2).

**Table 2 – Models and equations for *Astronium urundeuva* evaluation tests through Selegen-REML/BLUP software.**

PT	P/P	Model with covariate	Model without covariate
CUIA	1	135 ( $y = Xr + \beta Cov + Za + e$ )	95 ( $y = Xr + Za + e$ )
GO	3	131 ( $y = Xr + \beta Cov + Za + Wp + e$ )	93 ( $y = Xr + Za + Wp + e$ )
PF	6	131 ( $y = Xr + \beta Cov + Za + Wp + e$ )	93 ( $y = Xr + Za + Wp + e$ )

PT = progeny tests; P/P = number of plants per plot; y = data vector; r = repetition effects (fixed) vector, added to the overall average; a = individual additive (random) genetic effects vector; p = plot effects vector (random); e = errors or residuals vector (random);  $\beta$  = regression coefficient associated with covariable. Capital letters are the incidence matrices for these effects (as in Resende, 2016).

Source: the authors (2022).

From the models, the following parameters were estimated: 1. Variances: additive genetics ( $\hat{\sigma}_a^2$ ), environmental between plots ( $\hat{\sigma}_c^2$ ), genetics between progenies ( $\hat{\sigma}_p^2$ ), residual (environmental + non-additive) ( $\hat{\sigma}_e^2$ ), individual phenotypic ( $\hat{\sigma}_f^2$ ), from genotypic values prediction error, assuming complete survival (PEV), predicted genotypic value deviation pattern, assuming complete survival (SEP). 2. Heritability: individual for additive effects:  $\hat{h}_a^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_p^2 + \sigma_e^2)$ , individual adjusted for plot effects ( $\hat{h}_{aj}^2$ ), based on progeny means:  $\hat{h}_m^2 = ((\frac{1}{4})\sigma_a^2) / ((\frac{1}{4})\sigma_a^2 + \frac{\sigma_c^2}{r} + \frac{(0,75\sigma_a^2 + \sigma_e^2)}{nr})$ , additive within plots ( $\hat{h}_{ad}^2$ ); approximate accuracy:  $r_{aa} = \sqrt{\hat{h}_m^2}$ . 3. Coefficients of variation: individual additive genetics:  $CV_{gi} = 100 (\sqrt{\sigma_a^2} / m)$ , genotypic between progenies:  $CV_{gp} = 100 (\sqrt{0,25(\sigma_a^2) / m})$ , relative:  $CV_r = CV_g / CV_e$  and residual:  $CV_e = 100 (\sqrt{[(0,75\sigma_a^2 + \sigma_e^2) / n] + \sigma_c^2} / m)$ . 4. Coefficient of determination of plot effects:  $c_{parc}^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_p^2 + \sigma_e^2)$ ,  $\hat{m}$  general means; LRT (Likelihood Ratio Test); and  $\chi^2$  (Chi-square of deviance). Mathematical expressions of these parameters can be found in Vencovsky and Barriga (1992); Resende (2002) and Martins et al.

### Covariate index data analysis

Since  $CV_e$  is also given by  $CV_e = (\sqrt{QM_e} \cdot 100) / \hat{m}$ , where  $QM_e$  is the error mean square and  $\hat{m}$  the general mean, each model efficiency (EF, %) was proportional calculated, in which it was considered as more efficient ( $EF_{\%} = 100$ ) the model with covariate (because it is more complete), through the equation  $EF_{\%} =$

$[(QM_{ec} \cdot 100)/QM_{es}] - 100$ , in which  $QM_{ec}$  is the covariate-included model variable error mean square while  $QM_{es}$  is the covariate-excluded model variable error mean square, with result given in percentage (%).

### **Mother-progenies selection**

Best progenies selection, in comparison with their mothers, was made from data resulted from each model evaluation. In other words, each variable analyzed in models showed a topic with progenies genetic values sorted in descending order, called "Selection with overlapping generations" ( $S_{up}(\%)$ ), where mothers are represented by number zero and progenies with their corresponding numbers.

With the variable classification results, a new spreadsheet is organized, in which each column is composed of a variable, the number of progenies best placed in this classification is counted, related to the mothers, this value is, then, divided by the total, and multiplied by 100:  $S_{up}(\%) = [N_p/N] \cdot 100$ , where  $N_p$  = absolute number of progenies superior to the mother for analyzed variable and  $N$  = total number of progenies for analyzed variable.

### **Additive x dominance effects analysis**

In order to compare additive genetic effects ( $a$ ) with dominance effects ( $d$ , sexual propagation), a Spearman correlation was used. As it is a non-parametric correlation coefficient, it evaluates relationships between ordinal variables, which uses only ranks, without assumptions, since variables results are in ordinal format. As a function of  $a$ , it is necessary to order data from  $a$  and  $d$  depending on progenies, and then carry out the correlation analysis. It is also necessary to remember that, in the software, average dominance degree equals 1 and, therefore, it considers complete dominance, in which it is not possible to distinguish heterozygotes from dominant homozygotes (Resende, 2016).

### **Population comparison data**

For comparison purposes between populations, when necessary, original data were subjected to standardization through  $Z$  statistic,  $Z_{ij} = (y_{ij} - y_{-j})/s_j$ , in which  $Z_{ij}$  is the standardized variable value in population  $i$  ( $i = 1, 2, 3$ ) in repetition  $j$  ( $j = 1, 2, 3, \dots$ );  $y_{ij}$  is the population variable observation  $i$  in repetition  $j$ ;  $y_{-j}$  is the three tests variable general mean in repetition  $j$

and  $s_j$  is the three tests variable general mean in repetition  $j$  (Mendes et al., 2009; Reis et al., 2011), which consists of standardizing results in pure numbers, similar to normal distribution, however, with always positive values between 0 and 3, which allows comparing populations at different ages for the same variable. The variables then underwent a new evaluation in proposed models (Table 2).

## Flowering data analysis

### Population sex ratio and effective size

As for flowering, individuals identification was performed by separating male and female individuals and, thus, sex ratio was calculated:  $r = N_f / (N_f + N_m)$ , effective population size:  $N_e = 4 \cdot t / D_5$ ,  $t = N_f + N_m$ ,  $D_5 = (1/r \cdot (1 - r)) + ((1 - u)(t - 1)/F) + ((1 - v)(t - 1)/M)$ ,  $u = F/N_f$ ,  $v = M/N_m$ , ( $0 < u, v \leq 1$ ), effective population size:  $N'_e = N_e / (1 + F)$ , proposed to dioecious species by Vencovsky et al. (2012), where  $F, M$  = number of plants with female flowering ( $F$ ) and male ( $M$ ) which, effectively participated in the reproductive event and  $N_f, N_m$  = total of plants with female and male flowering of the population, respectively. Plants that did not flower in the observation period were not considered in the sex ratio assessment.

### Actual effective size and siblings analysis

Percentages of  $N_e$  and  $N'_e$ , regarding the total number of individuals:  $N_e\% = (N_e \cdot 100) / N$ ,  $N'_e\% = (N'_e \cdot 100) / N$ , and means for the effective size per progenies:  $\overline{N_e} = N_e / P_g$ ,  $\overline{N'_e} = N'_e / P_g$ , where  $P_g$  = number of progenies per provenance.

Data about half sibs (HS), full sibs (FS) and SFS were calculated...

## RESULTS

### Covariate index and genetic parameters for each population

Models with a covariate were not more efficient than models without it (Table 3). Failure index covariate inefficiency may be related not only to progeny number of individuals within the plot, but also to the fact that tests in consortium with other species (PF and GO) have shown less or no significance, in relation to homogeneous assay (CUIA). Beta ( $\beta$ ) values found in models with covariates were between -0.11 and 0.39,



without transforming data into Z; while, with transformation, values were between -0.22 and 0.09 (Table 4). All these values indicate survival in these progeny tests are high (CUIA = 82.60%, GO = 86.76%, PF = 85.74%). Only DBH (CUIA = 17,87, GO = 49,00, PF = 11,22,  $\alpha = 0,05$ ) and Veq (CUIA = 14,21, GO = 43,73, PF = 5,14<sup>ns</sup>,  $\alpha = 0,05$ , ns = not significant) could be used to compare the genetic parameters estimates in other experiments with this species, within the corresponding regions, since they were variables with significant differences for progenies in the three tests (Table 4).

**Table 3 – Model efficiency estimates for silvicultural characters in three *Astronium urundeuva* tests, installed in Selvíria/MS, measured in 2019, with data transformation in Z.**

PT	Variable	$QM_{es}$	$QM_{ec}$	EF	$EF_{\%}$	Efficiency
CUIA	HT	0,732687	0,732153	99,92701	-0,07299	N/C
	DBH	0,743906	0,740619	99,55811	-0,44189	N/C
	ACD	0,721729	0,721374	99,95078	-0,04922	N/C
	TTQ	0,831720	0,821949	98,82517	-1,17483	N/C
	SV	0,661811	0,652321	98,56596	-1,43404	N/C
	Veq	0,915367	0,914228	99,87565	-0,12435	N/C
GO	HT	0,281468	0,276894	98,37492	-1,62508	N/C
	DBH	0,293650	0,281563	95,88391	-4,11609	N/C
	ACD	0,305818	0,305750	99,97783	-0,02217	N/C
	TTQ	0,321770	0,305142	94,83231	-5,16769	N/C
	SV	0,338790	0,320931	94,72835	-5,27165	N/C
	Veq	0,313808	0,313560	99,92102	-0,07898	N/C
PF	HT	0,314830	0,266611	84,68422	-15,3158	N/C
	DBH	0,229487	0,217214	94,65176	-5,34824	N/C
	ACD	0,242456	0,214456	88,45136	-11,5486	N/C
	TTQ	0,366230	0,309420	84,48778	-15,5122	N/C
	SV	0,318025	0,234740	73,81172	-26,1883	N/C
	Veq	0,227193	0,232509	102,3400	2,339952	W/C

PT = progeny tests, HT = height, DBH = diameter at breast height (1.30 m above ground), ACD = average crown diameter, TTQ = tree trunk quality, SV = survival, Veq = estimated volume,  $QM_{es}$  = mean square error for model without covariate,  $QM_{ec}$  = mean square error for model with covariate, EF = efficiency of complete model (with covariates)  $EF_{\%}$  = percentage efficiency of complete model (with covariates) N/C =, no covariate W/C = with covariate.

Source: the authors (2022).

**Table 4 – Estimates of variance components and genetic parameters for significant silvicultural variables of *Astronium urundeuva* in three progeny tests installed in Selvíria/MS, measured in 2019, with data transformation to Z.**

	CUIA (p=29, n=508)						GO (p=30, n=948)						PF (p=30, n=463)					
	N/C (95)			W/C (135)			N/C (93)			W/C (131)			N/C (93)			W/C (131)		
	HT (m)	DBH (m)	Ve <sub>q</sub> (m <sup>3</sup> )	HT (m)	DBH (m)	Ve <sub>q</sub> (m <sup>3</sup> )	HT (m)	DBH (m)	Ve <sub>q</sub> (m <sup>3</sup> )	HT (m)	DBH (m)	Ve <sub>q</sub> (m <sup>3</sup> )	HT (m)	DBH (m)	Ve <sub>q</sub> (m <sup>3</sup> )	HT (m)	DNH (m)	Ve <sub>q</sub> (m <sup>3</sup> )
$\hat{\sigma}_a^2$	0,98	0,93	0,64	1,00	0,93	0,64	0,31	0,36	0,46	0,31	0,37	0,47	0,12	0,27	0,26	0,13	0,27	0,26
$\hat{h}_m^2$	0,89	0,88	0,80	0,89	0,88	0,80	0,76	0,79	0,81	0,76	0,80	0,82	0,22	0,47	0,46	0,26	0,48	0,46
$\hat{h}_{aj}^2$	-	-	-	-	-	-	0,35	0,39	0,44	0,34	0,40	0,46	0,14	0,29	0,28	0,15	0,29	0,28
$\hat{h}_{ad}^2$	1,01	0,94	0,53	1,03	0,95	0,53	0,28	0,33	0,37	0,28	0,33	0,39	0,11	0,24	0,23	0,12	0,23	0,23
$r_{aa}$	0,94	0,94	0,90	0,94	0,94	0,90	0,87	0,89	0,90	0,87	0,89	0,91	0,47	0,68	0,68	0,51	0,69	0,68
$CV_{gp}$	19,34	18,38	14,99	19,55	19,92	14,98	10,37	10,74	11,66	10,28	10,81	11,84	6,55	9,66	9,05	6,72	9,61	9,08
$CV_e$	33,38	32,86	35,74	33,39	35,47	35,70	20,15	18,95	19,28	19,94	18,95	19,28	21,06	17,83	16,95	19,61	17,34	17,15
$\hat{m}$	2,56	2,63	2,68	2,56	2,43	2,68	2,69	2,80	2,91	2,69	2,80	2,91	2,63	2,69	2,81	2,63	2,69	2,81
$\beta$	-	-	-	-0,09	-0,04	-0,03	-	-	-	-0,03	0,02	0,09	-	-	-	-0,14	-0,06	0,05
LRT ( $\chi^2$ )	124,60*	112,34*	55,04*	224,23*	164,80*	68,14*	41,22*	59,33*	66,67*	138,95*	9,78*	57,13*	0,65 <sup>ns</sup>	4,09**	3,91**	3,93**	11,82*	7,27*

p = number of progenies; n = number of individuals in progeny test; N/C = no covariate; W/C = with covariate; HT = height (m); DBH = diameter at 1.30 m from the ground (at breast height, m); Ve<sub>q</sub> = volume (m<sup>3</sup>); \* = significance at 1% probability; \*\* = significance at 5% probability; ns = not significant.

Source: the authors (2022).

In general, heritability based on progeny means decreased with tests increasing age, although the estimates obtained in this research were higher than those found in previous literature, regardless of origin region or trial installation arrangement. Furthermore, heritability based on average progenies was greater than that of individual within plots, as in Sebbenn and Etori (2001) and Canuto et al. (2016), which indicates selection among progenies possibility. Data collected can be considered accurate ( $47\% > r_{\hat{a}a} > 94\%$ ). Between 70 and 90%, they are quite precise regarding access to genetic variation, based on phenotypes observed for the studied characters (Resende and Duarte, 2007). Considering most of the growth variables, there was environmental interference on the tests conditions, with ( $16.95\% < CV_e < 35.74\%$ ), reasonable values, for being relatively low, for experiments installed in the field (Pimentel-Gomes and Garcia, 2002).

Cluster analysis and Tocher grouping, showed that, while CUIA formed two groups, GO formed nine and PF only one, when considering all variables, there was no interference from failure index covariate regarding genetic diversity of populations distribution.

### Sex ratio and effective size

Sex ratio is in equilibrium only in GO ( $1\text{♀}:1\text{♂}$ ), while in the others it is  $1\text{♀}:2\text{♂}$ , that is, males number is twice females (Table 6).

**Table 6 - Sex ratio (r), effective size ( $N_e$ ), average effective size per progeny ( $\bar{N}_e$ ), percentage of effective size in relation to population ( $N_e(\%)$ ), corrected effective size ( $N'_e(\%)$ ) size of progenies of half siblings, (HS), full siblings (FS) and self-fertilization siblings (SFS) of *Astronium urundeuva* for three tests in a Cerrado area, in Selvíria/MS, measured in 2019.**

PT	R	$N_{\text{♂}}$	$N_{\text{♀}}$	MN	NFI	N	$N_e$	$N_e(\%)$	$N'_e$	$N'_e(\%)$	HS	FS	SFS
CUIA	$1\text{♀}:2\text{♂}$	246	121	1	140	508	327	64,2	286	56,3	72	143	286
GO	$1\text{♀}:1\text{♂}$	405	368	17	130	948	790	83,3	689	72,7	173	345	689
PF	$1\text{♀}:2\text{♂}$	147	71	1	246	463	194	41,7	171	36,9	43	86	171

PT = progeny tests (populations), R = sex ratio,  $N_{\text{♂}}$  = total males in population,  $N_{\text{♀}}$  = total females in population, MN = monoecious individuals in population, NFI = non-flowering individuals in population, N = total surviving individuals in population.

Source: the authors (2022).

When considering a total of 89 progenies, distributed in three populations, finding half-sib progenies with similar values ( $HS_{\text{CUIA}} = 72$ ,  $HS_{\text{GO}} = 173$ ,  $HS_{\text{PF}} = 43$ ) are possible indications of segregation between males and females. Shading of individuals of A.

*urundeuva* by other species, observed in field in PF, for example, may also have influenced flowering parameters estimates, either by advancing or delaying start and end time of reproductive events. The three progeny tests had a good effective size, either when considering minimum viable number ( $N_e = 50$  (Resende, 2002); CUIA = 326, GO = 789, PF = 193), or by progenies average, when assuming panmictic populations ( $N_e = 4$ ; Viegas et al., 2011), although deviations in sex ratio were detected. Even so, there is a possibility of maintaining genetic variability, to avoid inbreeding depression, which allows keeping them as banks for an *ex-situ* species conservation.

### Mother-progenies selection

Regarding mothers' superiority, in the three tests, there were one to three superior trees, compared to all individuals (30 progenies per test) (Table 7).

**Table 7 – Mothers superior to *Astronium urundeuva* progenies for three progeny tests in a Cerrado area, in Selvíria/MS, measured in 2019, with data transformed into Z. Variables in bold are those found for all mothers.**

TP	Model	Superior Mothers	Variables
CUIA	95 (n/c)	1	HT, <b>DBH</b> , ACD, <b>TTQ</b> , SV, <b>Ve<sub>q</sub></b>
		2	<b>DBH</b> , <b>TTQ</b> , <b>Ve<sub>q</sub></b>
		3	HT, <b>DBH</b> , ACD, <b>TTQ</b>
	135 (w/c)	1	HT, <b>DBH</b> , ACD, <b>TTQ</b> , SV, <b>Ve<sub>q</sub></b>
		2	<b>DBH</b> , <b>TTQ</b> , <b>Ve<sub>q</sub></b>
		3	<b>DBH</b> , ACD, <b>TTQ</b> , <b>Ve<sub>q</sub></b>
GO	93 (n/c)	5, 13	SV
		8, 9, 14, 15	<b>Ve<sub>q</sub></b>
		10	HT, DBH
		16	HT, DBH, <b>TTQ</b> , <b>Ve<sub>q</sub></b>
		21	<b>TTQ</b>
	131 (w/c)	5, 13	SV
		8, 14, 15	<b>Ve<sub>q</sub></b>
		10	HT, DBH, SV, <b>Ve<sub>q</sub></b>
		16	HT, DBH, <b>TTQ</b> , <b>Ve<sub>q</sub></b>
PF	93 (n/c)	14	HT, DBH, <b>TTQ</b> , SV, <b>Ve<sub>q</sub></b>
		22	<b>Ve<sub>q</sub></b>
	131 (w/c)	14	HT, DBH, <b>TTQ</b> , SV, <b>Ve<sub>q</sub></b>
		22	<b>Ve<sub>q</sub></b>

PT = progeny tests; n/c = no covariate; w/c = with covariate; HT = height, DBH = diameter at breast height (1.30 m above ground), ACD = average crown diameter, TTQ = tree trunk quality, SV = survival, Ve<sub>q</sub> = estimated volume.

Source: the authors (2022).

### Additive x dominance effects

Survival was the character that showed no significant difference in terms of additive and dominance effects for half-sib progenies in GO (Table 8). This means that, except for SV, selection of individuals based on evaluated characters can be made, either by additive variation or by variation in dominance, that is, material can be harvested both by seed production and by vegetative propagation.

**Table 8 - Significance of correlation between additive and dominance effects, in half-sib progenies, evaluated in *Astronium urundeuva*, in three progeny tests installed in a Cerrado area, in Selvíria/MS, measured in 2019, with data transformed into Z. Values in bold were not significant.**

PT	Variable	n/c		w/c	
		S	<i>p-value</i>	S	<i>p-value</i>
CUIA	HT	0,8709	< 2,2 *10 <sup>-16</sup>	0,8778	< 2,2 *10 <sup>-16</sup>
	DBH	0,8832	< 2,2 *10 <sup>-16</sup>	0,8869	< 2,2 *10 <sup>-16</sup>
	ACD	0,8772	< 2,2 *10 <sup>-16</sup>	0,8781	< 2,2 *10 <sup>-16</sup>
	TTQ	0,8479	< 2,2 *10 <sup>-16</sup>	0,8577	< 2,2 *10 <sup>-16</sup>
	SV	0,7434	< 2,2 *10 <sup>-16</sup>	0,7919	< 2,2 *10 <sup>-16</sup>
	Ve <sub>q</sub>	0,7202	< 2,2 *10 <sup>-16</sup>	0,7195	< 2,2 *10 <sup>-16</sup>
GO	HT	0,6230	< 2,2 *10 <sup>-16</sup>	0,6239	< 2,2 *10 <sup>-16</sup>
	DBH	0,7203	< 2,2 *10 <sup>-16</sup>	0,7211	< 2,2 *10 <sup>-16</sup>
	ACD	0,6333	< 2,2 *10 <sup>-16</sup>	0,6332	< 2,2 *10 <sup>-16</sup>
	TTQ	0,5719	< 2,2 *10 <sup>-16</sup>	0,5569	< 2,2 *10 <sup>-16</sup>
	<b>SV</b>	<b>0,0241</b>	<b>0,4285</b>	<b>0,0700</b>	<b>0,02141</b>
	Ve <sub>q</sub>	0,6680	< 2,2 *10 <sup>-16</sup>	0,6750	< 2,2 *10 <sup>-16</sup>
PF	HT	0,7794	< 2,2 *10 <sup>-16</sup>	0,7956	< 2,2 *10 <sup>-16</sup>
	DBH	0,8137	< 2,2 *10 <sup>-16</sup>	0,8169	< 2,2 *10 <sup>-16</sup>
	ACD	0,7242	< 2,2 *10 <sup>-16</sup>	0,7370	< 2,2 *10 <sup>-16</sup>
	TTQ	0,8399	< 2,2 *10 <sup>-16</sup>	0,8316	< 2,2 *10 <sup>-16</sup>
	SV	0,5188	< 2,2 *10 <sup>-16</sup>	0,4203	< 2,2 *10 <sup>-16</sup>
	Ve <sub>q</sub>	0,7726	< 2,2 *10 <sup>-16</sup>	0,7800	< 2,2 *10 <sup>-16</sup>

PT = progeny tests; n/c =no covariate; w/c = with covariate.

Source: the authors (2022).

## DISCUSSION

### Covariate index and genetic parameters

Tree species with high quality wood tend to grow slowly. Furthermore, environmental conditions, such as presence of other species, belonging or not to the consortia (for example: invasive grasses), can contribute to decrease parameters found values (Pupin et al., 2017). Betas shown that the covariate did not influence results as much, but that it could be important at thinning stage, by opening up more space, as spacing was already large in relation to the species initial establishment, since the individual cut no longer influences around. Still, covariates should not be completely discarded, since adequate choices for the experiment site, reduction of the experimental

error variance are as important or more important than error caused by covariates (Leonardecz-Neto et al., 2003; Pavan et al., 2012; Ishibashi et al., 2017). Including HT in these measurements, along with DBH and  $V_{eq}$  would be useful, despite the results found, since selection of growth characters must also be considered according to management and production needs. Better growth in DBH can occur for mastic trees intercropped with annual crops and with other forest species (Freitas et al., 2006; Moraes et al., 2012), but better results in height are found in homogeneous plantations (Canuto et al., 2016). DBH is usually the most suitable character to apply in breeding programs, as it presents greater variation and genetic control and greater gains with selection. In early years, *A. urundeuva* tends to have better development and adaptation conditions when planted in intercropping, while materials in homogeneous plantations tend to compete (Freitas et al., 2006). Heterogeneous plantations tend to be promising for most variables of interest for plant growth (Oliveira et al., 2000), although homogeneous ones tend to have better trunk quality (Freitas et al., 2006), which may represent, depending on management purposes, better use and selection of genetic material. Other factors, such as test age and environmental conditions, for example, may also have influenced its means, as observed by Otsubo et al. (2015), also working with *A. urundeuva*. Low heritability ( $h^2 < 0,3$ ) usually appears when there is no significant genetic variability, which limits genetic progress and breeding programs (Rocha et al., 2009). The physiological state and expression of growth genes, at a young age, are different from adult trees (Namkoong et al., 1988), which could explain differences in parameters obtained between the tests (Pires et al., 2014). Differences in latitude, climate and precipitation in seed collection areas can give rise to individuals with local adaptation characters (Silva et al., 2018). Ecologically, *A. urundeuva* is classified as late secondary, slow growing, probably caused by progenies non-uniformity within the plots, since there are dominated trees that have lost competition for light (Barros et al., 2010; Recco et al., 2016).

### **Sex ratio and effective size**

Greater diversity was expected in CUIA progenies, due to their origin (Chapada dos Guimarães, Integral Protection Conservation Unit), but greatest diversity was found precisely in GO, which is an extremely anthropized area. The differentiation into so many groups may have happened as a result of the junction of small populations with their

neighbors, by neutralizing genetic erosion, leaving them viable not as populations per se, but as metapopulations (Andrewartha and Birch, 1954; Hanski, 1999).

Although individuals are isolated, by keeping them all, a metapopulation structure may have been maintained, along with gene flow between populations (Sousa et al., 2015). Furthermore, fragmentation directly influences population genetic composition, as it alters pollen and seed dispersal patterns (Ghazoul, 2005).

Variation between and within populations is the result of evolutionary factors (mutation, migration/gene flow, drift and natural selection). In this case, selection may have led individuals to differentiate, causing local adaptation (Sousa et al., 2015). Climate may also have influenced these progenies differentiation, and is generally considered a major factor in species selection, adaptation and differentiation on a large scale (Macel et al., 2007). What can reduce this influence is the creation of collection areas, which would represent a natural area, without so many negative impacts, whose ecological conditions are sufficiently uniform, and allow the assumption of phenotypic or genetic similarity for species quantitative characters (Frankel, 1970; Graudal et al., 1997; Sebbenn, 2002; Van der Mijnsbrugge, Bischoff and Smith, 2010). Outlining these areas means installing experiments with materials from different sources in the same place (Lindgren and Ying, 2000).

When collecting seeds, it is necessary to consider inbreeding depression, drift and the founder effect, linked to heterozygosity degree, common in native species small populations, more than the origin itself (Procaccini and Piazzzi, 2001). In Brazil's native species, it is common to collect at minimum distances of 100 m between parent trees, or twice their height (Sebbenn, 2003). As for the number of individuals collected per population, recommendations are variable: 25 (Sebbenn, 2002; Sebbenn, 2006; Crossa and Vencovsky, 2011), 10-50 for rare species *ex situ* conservation (Falk and Holsinger, 1991; Brown and Briggs, 1991); 10-20 (Fischer and Matthies, 1998; Vergeer et al., 2003). This sampling is also dependent on collection size, effective population size and species' reproductive system.

Since genetic diversity magnitude decreases with the number of seeds harvested per mother increases (Kashimshetty, Pelikan and Rogstad, 2017), it is recommended to collect fewer seeds from more mothers, in order to capture between 82% and 95% of rare alleles in a population, randomly, although lead to greater walking, within 500 m area plots, away from boundaries (Marshall and Brown, 1975; Aitken, 2004).

In dioecious species, balance (1:1) in sex ratio distribution is usually observed. But deviations related to an increase in males proportion are linked to differences in energy amount spent on reproduction (Lloyd and Webb, 1977), including influencing variables such as diameter and height. These males tend to be larger in early life years, while females become larger in the long run, differences that can also be influenced by environment (Armstrong and Irvine, 1989). Also, spatial distribution patterns in dioecious species are usually greater than in monoecious, due to evolutionary factors, such as gene flow, which interfere with genetic diversity (Nazareno et al., 2013). Furthermore, gene flow is capable of determining gene dispersion distance (Loiselle et al., 1995).

These patterns may also be related to ecological characters: while monoecious have low distribution (low density/area), and are represented by mothers with asynchronous flowering among individuals with wide crowns, dioecious species tend to have aggregated distribution and synchronous flowering (Harrison and Shanahan, 2005; Nazareno et al., 2013), decreasing pollen dispersion pressures over long distances, increasing correlated crosses.

Another reason for deviations in sex ratio may be gamete selection during fertilization (Correns, 1922; Lloyd, 1974), by genetic mechanisms of sex determination (Westergaard, 1958), apomixis, differences in energy investment in progenies by parents (Fisher, 1930), differential mortality (Lloyd, 1973), different ripening time, difference in vegetative breeding potential, or differences in flower production (Opler and Bawa, 1978). At younger ages and sizes, tendency is for more males than females to appear in populations, and it is believed that, with increasing size, changes in flower production (from males to females) can occur (Queenborough et al., 2007). This exchange is more common in shrub species and poorly documented for tropical and subtropical species (Korpelainen, 1998; Yamashita and Abe, 2002).

In tropical areas, males also experience earlier and more frequent flowering periods (Armstrong and Irvine 1989). Shading can cause delays in flowering onset, prolong flowering time, reduce number of flowers and seeds produced (Hlatshwayo and Wahome, 2010), reduce flower fresh weight, increase flower diameter, and produce more flowers with a weak color (Zhao et al., 2012), or may be associated with higher floral and vegetative biomass production, while late flowering is related to fruit biomass (Cai, 2011).



Sexual characters can also secondarily influence species reproduction, since each sex has a different demand (Korgiopoulou et al., 2019). Also, plants considered invasive also impact native species reproduction directly, through competition for light and other resources (McKinney and Goodell, 2010).

Seed harvesting strategy, population progenies sex ratio, and the proportion of reproductive mothers are parameters that influence the effective size (Martins et al., 2018). If the number of breeding mothers is low (20-50%, as in PF),  $N_e$  decreases, and it is necessary to increase the number of mothers to be sampled (Vencovsky et al, 2012). In addition, it should be remembered that effective size is usually smaller than total number of individuals in progeny tests, as it only considers active sires, sex ratio, and population density fluctuations (Frankel and Soulé, 1981; Vencovsky, 1987; Montalvo et al., 1997).

Although measured indirectly, since it is only possible to measure progenies paternity using molecular techniques, if this concentration of superior characteristics were found in a few progenies of the same family, it can be indicated that, during the phenological year of seed production that gave rise to the planted progenies, crosses were directed to these progenies' mothers. On the other hand, superiority may not necessarily have only maternal origin, that is, superior fathers may have offered pollen in greater amounts, which also keeps crosses targeted.

Concentration on individuals' sexual distribution in certain areas may also have influenced crossbreeding (Armstrong and Irvine, 1989). When mothers are superior to progenies, there are no outside male gametes that can contribute to form superior progenies. On the other hand, when progenies are better than mothers, paternal gametes could contribute to offspring superiority. Identifying parents tells us which progenies are out of the sampling, which allows us to know migration patterns and gene flow within a region (Smouse and Sork, 2004). An increase in gene flow can be caused either by fragmentation (Dick, 2001), information that is not always reasonable for populations, since it modifies effective size and reduces local adaptation.

Additive effects are transmitted between generations, while dominance effects are not explored in the selection, since it is not possible to repeat the genotypes of selected individuals. When the selected individual genotype is passed on to next generation, dominance effects are also explored. Whether usage should be considered as it helps to assess gains, which also optimizes selection age in breeding. There are few studies, even

in species of agronomic importance, related to these effects, mainly due to the difficulty of using controlled pollination, especially in forest species (Bouvet et al., 2008).

In perennial species, additive effects often exceed dominance effects for growth traits. Effects of phenotypic selection on parentals can influence additive and dominance estimates. The nature of the dominance effect also depends on the effect between alleles and its frequency (Gallais, 1991; Lynch and Walsh, 1998). The percentage of mortality can also change variances according to age (Volker et al., 2008).

Furthermore, additive effects tend to be more influential in early years of planting, while dominance effects start to appear more as population gets older (Isik et al., 2003). This information becomes important for selection at older ages for certain characters. Tests with vegetatively propagated individuals must be applied in order to assess dominance effects on the characters of interest.

## CONCLUSION

The three tests, coming from different Cerrado areas, settled in Mato Grosso do Sul state eastern region (Selvíria-MS) presented a behavior similar to results found in literature, either in intercropping or in homogeneous planting, representing typical Cerrado areas, with good genetical diversity. Covariates usage was not as efficient in progenies tests evaluated, due to their longevity, to relatively large spacing established during planting. Populations tend to be unbalanced in terms of sex ratio. Therefore, careful sampling in natural populations, such as harvesting at mothers separated by greater distances, for example, must be carried out while obtaining germplasm. There was a significant correlation between additive effects and dominance effects, for most variables, within the three progenies tests studied. When considering the three tests, both selection by additive and dominance values can be used to obtain good parents.

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*Recebido em: 05/07/2022*

*Aprovado em: 12/08/2022*

*Publicado em: 16/08/2022*