SOIL RESISTANCE AND MULTIVARIATE ANALYSIS AS AN AUXILIARY METHOD FOR SELECTING *Calophyllum brasiliense* PROGENIES

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ABSTRACT – Precision silviculture is being developed to manage and improve *Calophyllum brasiliense*, a tree species associated with wet and swampy soils. This study estimated genetic parameters for growth traits in response to soil resistance as an auxiliary tool for identifying and selecting progenies adapted to water-saturated soils. This was undertaken in a progeny test of *C. brasiliense* in which 1,200 seedlings grown from seeds collected from a natural population were planted in a randomized complete block design for single-tree plots. Genetic statistical analysis was conducted using the REML/BLUP method. Significant differences ($p<0.01$) in diameter at breast height were observed among the progenies. The coefficients of genetic variation and heritability at the individual and progeny levels were low for diameter at breast height and height, indicating low genetic control for these traits, while high positive and significant genetic and phenotypic correlations were detected between diameter at breast height and height. Theoretical genetic gains and multivariate statistical analysis indicated three groups of progenies with different degrees of tolerance and adaptability to flooded soils, which could be useful in future breeding programs for this species, although further analysis at advanced ages is still required. The mean heights of tolerant and sensitive progenies were 12 and 58%, respectively, lower than the theoretical values, indicating that constant soil flooding is harmful to this species.

Keywords: Precision silviculture; Progeny tests; REML/BLUP.

RESISTÊNCIA DO SOLO E ANÁLISES MULTIVARIADAS COMO UM MÉTODO AUXILIAR PARA A SELEÇÃO DE PROGÊNIES DE Calophyllum brasiliense

RESUMO – Metodologias de silvicultura de precisão vêm sendo desenvolvidas visando ao manejo e melhoramento genético de ***Calophyllum brasiliense****, uma espécie naturalmente associada a solos brejosos. O presente estudo estimou parâmetros genéticos para caracteres de crescimento em resposta à resistência do solo como uma ferramenta auxiliar para a identificação e seleção de progênies mais tolerantes a solos alagados. O trabalho foi conduzido em um teste de progênies de* ***C. brasiliense****, no qual 1200 mudas produzidas a partir de sementes coletadas de uma população natural foram plantadas em blocos casualizados completos, em arranjo single-tree plot. As análises estatísticas dos componentes genéticos foram realizadas com auxílio do método REML/BLUP. Foram observadas diferenças significativas (***p*** < 0,01) entre progênies para diâmetro à altura do peito (DAP). Os coeficientes de variação genética e herdabilidade em nível individual e entre progênies foram baixos para o DAP e altura (H), indicando baixo controle genético para os caracteres, ao mesmo tempo em que foram observadas correlações genéticas e fenotípicas entre DAP e H. A interação de ganhos genéticos preditos com os modelos matemáticos indicou a existência de três grupos de progênies com diferentes graus de tolerância a solos com drenagem deficiente, revelando o potencial de uso dessas ferramentas em programas de melhoramento da espécie, mesmo que novas avaliações sejam necessárias em idades mais avançadas de plantio. A altura média das progênies sensíveis e tolerantes foi 58 e 12%, respectivamente, inferior aos valores máximos teóricos, indicando o efeito nocivo do alagamento para essa espécie.*

Palavras-Chave: REML/BLUP; Silvicultura de precisão; Teste de progênies.

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1. INTRODUCTION

Forest breeding programs present specific challenges resulting from the perennial, cross-pollinated, and long-lived nature of tree species and their genetic variability in response to environmental effects. Precision forestry has emerged to assist in forest management with geospatial information and specific deployments for individual production sites to develop forest products with greater embedded technology and aggregated value (Kovácsová and Antalová, 2010).

Despite species diversity and economic potential, native tree breeding programs in Brazil are limited to a few species such as Araucaria angustifolia (Silva et al., 2018a), *Bactris gasipaes* (Borges et al., 2017), *Dipteryx alata* (Rocha et al., 2015), *Euterpe oleraceae* (Farias Neto et al., 2008), *Hevea brasiliensis* (Dourado et al., 2018), *Ilex paraguariensis* (Costa et al., 2009), *Myracrodruon urundeuva* (Canuto et al., 2017), *Schizolobium parahyba* var. *amazonicum* (Baldoni et al., 2020), and *Theobroma cacao* (Duval et al., 2017). Another species under study is *Calophyllum brasiliense* Cambess (Schühli et al., 2013).

Calophyllum brasiliense (also known as guanandi) is a monoecious/hermaphrodite open-pollinated (mainly by bees and small insects) neotropical Calophyllaceae species that naturally occurs from Central to South America, in areas from sea level to 1,200 m with mean annual rainfall of 1,100–3,000 mm and temperatures from 18 to 27 ºC (Carvalho, 2003; Wrege et al., 2017). The species is often distributed in watersheds (Oliveira-Filho and Ratter, 1995; Mendonça et al., 2014), and seeds and plants remain viable and tolerant to flooding even if submerged (Marques and Joly, 2000). Although it occurs in riparian zones, *C. brasiliense* exhibits good development in well-drained soils (Silva et al., 2018b; Devide et al., 2019), and is sensitive to drought (Campelo et al., 2015; Rocha et al., 2016).

Calophyllum brasiliense is a valuable hardwood species (Rosa et al., 2017) because of its moderately dense pinkish wood, which is comparable to *Swietenia macrophylla* (Shupe et al., 2005) or *Eucalyptus* sp. (Wrege et al., 2017). Furthermore, its roots, flowers, and fruits present pharmacological activity against diabetes, liver disorders, hypertension, and rheumatism (Isaias et al., 2004; Goméz-Verjan et al., 2015; Carvalho et al., 2016; Klein-Júnior et al., 2017). Environmentally, the symbiotic microbes living in the rhizosphere of this species have been recognized for practical applications as an agricultural inoculant (Souza et al., 2019).

Large swaths of the Brazilian coast (along stretches of the BR-277 highway from Morretes to Paranaguá, for example, as well as in the municipality of Antonina, all in the state of Paraná) are subject to periodic flooding, with negative effects on plant development. Although *C. brasiliense* is known to be tolerant to up to 120 days of flooding (Oliveira and Joly 2010), persistent hydromorphic conditions can cause growth damage even in this species.

Measuring soil resistance (SR) can identify compaction layers and/or microspatial flooding in soils, and together with geospatial techniques can be useful to avoid damage and ensure plant survival and development. Moreover, when combined with assessment of genetic parameters, SR is an innovative tool for identifying and selecting progenies of flood-tolerant species like *C. brasiliense* that are better adapted to saturated soils.

2. MATERIALS AND METHODS

Seeds were collected from 30 open-pollinated trees from a natural but highly disturbed remnant population of *C. brasiliense* in Pontal do Paraná, Brazil (Figure 1) in areas naturally subjected to seasonal elevation of the water table, and the seedlings were produced at the Embrapa Forestry greenhouse in Colombo, Paraná. The progeny test was conducted at the Embrapa Forestry Experiment Station in Morretes, on the coast of Paraná state (25°26'59" S, 48°52'07" W, 21 m). The experimental plot had previously been used for decades in irrigated rice trials, making it the perfect setting to test flood tolerance.

The progenies were planted in July 2014 in a 2.5 x 2.0 m randomized complete single-tree plot design (40 blocks x 30 progenies) totaling 1,200 plants over 0.6 ha. The plot is located on silt-loam-clay soil with medium fertility (37% clay, 15% sand, 48% silt, 6.2 pH SMP, 0.39 cmol$_c$.dm^{-3} Al, 2.89 cmol$_c$.dm^{-3} Ca, 1.66 cmol$_c$.dm^{-3} Mg, 0.12 cmol$_c$.dm^{-3} K, 32.91 mg.dm^{-3} P, 5.05 cmol$_c$.dm^{-3} CEC, and 7.68 m% at the 0–20 cm soil layer).

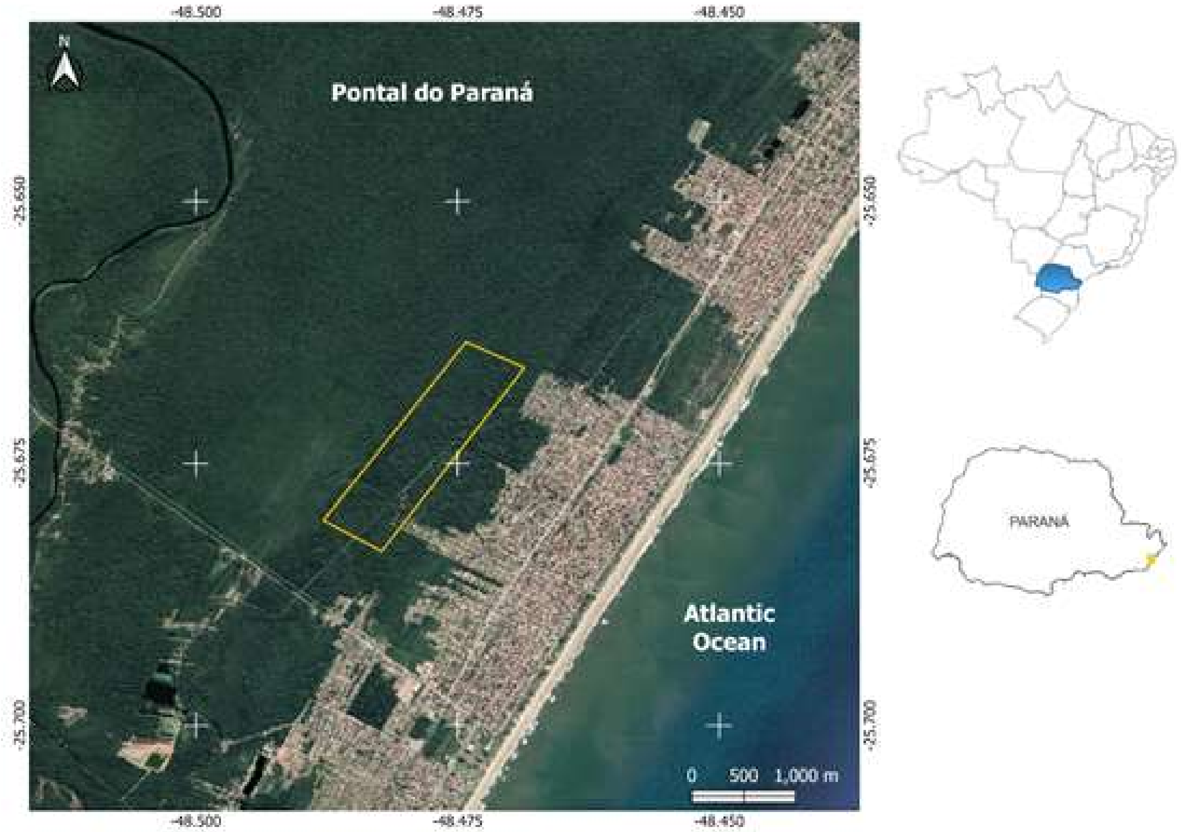

Figure 1 – Natural strongly remnant area of *C. brasiliense* (yellow rectangle) in Pontal do Paraná, Brazil, where seeds were collected. Source: Google Satellite (2022).

Figura 1 *– Remanescente natural altamente antropizado (retângulo amarelo), localizado no Pontal do Paraná, de onde foram coletadas as sementes de* ***Calophyllum brasiliense****. Google Satélite (2022).*

Uneven plant development was observed throughout the blocks; this had previously been attributed to the presence of some physically restrictive layer in the soil resulting from sedimentary origins, construction rubble deposited from neighboring roads, or topsoil removal when used for irrigated rice trials. Soil samples were collected from different depths to evaluate compaction layers, but varying drainage conditions during rainy periods revealed significant excess humidity in the soil (evidenced by a gleying process) that could be correlated with low development in some plots. Soil resistance was subsequently measured with a penetrograph device (PenetroLog, Falker) from 0 to 60 cm to investigate the effects of soil resistance and soil water saturation on plant development.

Five years after the trial began (2019), the surviving trees were georeferenced (Garmin GPSmap 76CSx) and their circumference at breast height (CBH) and height (H) were recorded. The CBH value (cm) and height (m) were obtained using a graduated tape measure; CBH was transformed into diameter at breast height (DBH).

Values for variance components and genetic parameters were estimated according to the REML/BLUP method, using unbalanced H and DBH data and Selegen-REML/BLUP genetic statistical software (Resende, 2006; 2016). The linear mixed model that considers half-sibling progenies in one site ($y = Xr + Za + e$) was used, where y: data vector; r: repetition effect vector (assumed as a fixed value) added to the overall average; a: vector of individual additive genetic effects (assumed as a random value); and e: residual vector (also assumed as random). Capital letters represent the incidence matrix for these effects (Resende, 2016).

Analysis of deviance was implemented to test differences among progenies using the likelihood ratio test (LRT), obtained by determining the difference between deviance for models with and without the effect to be tested (progenies) using chi-square values to test the significance of the models.

The phenotypic and genetic correlations between DBH and H were also estimated using Selegen-REML/BLUP software (Resende, 2006; 2016), while standard errors and significance for genetic and phenotypic correlations were estimated with GENES software (Cruz, 2006). Data expression by plotting associations between DBH and H and mean values for these traits was obtained with R scripts (R Core Team, 2019).

The effects of soil resistance on plant growth in proposed soil layers were determined by Pearson correlation for each of all 30 progenies, and multiple linear regression curves were fitted, when possible. Because soil drainage is inversely related to soil

Table 1 – Mean values, standard deviations (sd) and estimated genetic gains (u + a and Gain) for height (H) and diameter at breast height (DBH) in progenies of *Calyphyllum brasiliense* at five years of age.

Tabela 1 *– Média, desvio padrão (sd) e estimativas de ganhos genéticos (u+a e Gain) para altura (H) e diâmetro à altura do peito (DBH) de progênies de* ***Calophyllum brasiliense*** *aos cinco anos de idade.*

Progeny	**N**	**Survival**	**H (m)**				**DBH (cm)**			
		(%)	**Mean**	**(± sd)**	**u + a**	**Gain**	**Mean**	**(± sd)**	**u + a**	**Gain**
1	38	95.0	2.71	1.01	2.7590	0.1280	2.74	1.54	2.7575	0.1480
2	38	95.0	2.54	0.96	2.6614	0.0405	2.58	1.76	2.7342	0.1225
3	37	92.5	2.42	1.05	2.6656	0.0441	2.42	1.59	2.6870	0.0696
4	38	95.0	2.65	0.94	2.7334	0.1001	2.59	1.39	2.6936	0.0755
7	35	87.5	2.59	1.05	2.7218	0.0930	2.47	1.59	2.7198	0.1029
8	38	95.0	2.43	0.78	2.5271	0.0066	2.32	1.52	2.5505	0.0074
9	37	92.5	2.58	0.87	2.6462	0.0302	2.69	1.65	2.7439	0.1343
10	38	95.0	2.54	0.79	2.5833	0.0178	2.46	1.44	2.6278	0.0212
11	40	100.0	2.94	0.94	2.8288	0.1522	3.06	1.71	2.8504	0.1803
15	35	87.5	2.56	1.06	2.6485	0.0335	2.41	1.87	2.6618	0.0577
16	40	100.0	2.71	0.81	2.6956	0.0679	2.53	1.39	2.6229	0.0174
17	36	90.0	2.60	1.04	2.6987	0.0785	2.38	1.75	2.6597	0.0522
20	40	100.0	2.91	0.96	2.8393	0.1602	3.19	1.91	2.9370	0.2314
21	37	92.5	2.87	1.19	2.8663	0.1738	2.97	1.99	2.9007	0.2132
22	40	100.0	2.71	0.91	2.6991	0.0851	2.58	1.66	2.6403	0.0335
23	38	95.0	2.60	1.12	2.6939	0.0635	2.84	1.88	2.7879	0.1640
24	36	90.0	2.24	0.89	2.5005	0.0000	2.03	1.43	2.4924	0.0000
26	39	97.5	2.59	0.82	2.6269	0.0263	2.59	1.58	2.6581	0.0472
27	38	95.0	2.64	1.08	2.7433	0.1169	2.61	1.61	2.7195	0.0955
29	34	85.0	2.56	1.08	2.7337	0.1075	2.47	1.56	2.7139	0.0887
30	37	92.5	2.60	0.98	2.6740	0.0516	2.44	1.54	2.6049	0.0132
31	39	97.5	2.61	1.02	2.6939	0.0596	2.45	1.66	2.6332	0.0252
32	36	90.0	2.29	1.08	2.5688	0.0128	2.44	1.55	2.6502	0.0380
33	38	95.0	2.56	1.07	2.6977	0.0729	2.45	1.71	2.6527	0.0424
34	38	95.0	2.62	0.93	2.6863	0.0557	2.66	1.66	2.7203	0.1117
35	40	100.0	2.91	0.85	2.8264	0.1476	3.03	1.80	2.8585	0.1892
36	39	97.5	2.63	0.86	2.6723	0.0478	2.645	1.60	2.6737	0.0636
37	36	90.0	2.49	0.90	2.6249	0.0227	2.30	1.48	2.6370	0.0292
38	37	92.5	2.84	1.02	2.8033	0.1403	2.87	1.91	2.8833	0.2014
39	35	87.5	2.42	1.08	2.6566	0.0370	2.39	1.67	2.6961	0.0817
Min.	34	85.0	1.00				0.30			
Mean	38	93.9	2.73	0.85			2.75	1.57		
Max.	40	100.0	5.80				8.53			

u + a = beeding value.

u + a: valor genético.

resistance (Silva et al., 2016), and most soil resistance values were found up to 2,000 kPa, which is the upper limit for desirable root development (Taylor et al., 1966; Tormena et al., 1998), lower soil resistance values indicate elevated water table and/or flooded soils for practically the entire year in the study area, while higher values indicate soils with a deeper water table and/or better-drained soils during the 5-year period.

3. RESULTS

3.1. *Initial plant growth and genetic parameters in the progenies*

At the first evaluation at 5 years of age, only 73 individuals had died (93.9% survival), indicating the progenies' good tolerance of the environmental conditions. Major losses were observed in progeny 29 (-15%), while 5 progenies (11, 16, 20, 22, and 35) showed 100% survival (Table 1). Height varied from 2.24 to 2.94 m, while DBH varied from 2.03 to 3.19 cm (Table 1). Deviance analysis found strong significant differences in DBH among progenies according to the LRT test (Table 2).

Table 2 – Genetic parameters for height (H) and diameter at breast height (DBH) of *Calophyllum brasiliense* progenies at five years of age.

Tabela 2 *– Parâmetros genéticos para altura (H) e diâmetro à altura do peito (DBH) de* ***Calophyllum brasiliense*** *aos cinco anos de idade.*

Parameter	H	DBH
h^2_a	0.11 (± 0.06)	0.06 (± 0.04)
h^2_{mp}	0.53	0.37
Ac_{prog}	0.73	0.61
h^2_{ad}	0.09	0.04
$CV_{gi}\%$	7.68	10.09
$CV_{gp}\%$	3.84	5.04
$CV_e\%$	22.80	41.67
CV_r	0.17	0.12
General mean	2.69	2.71
DEV_{prog}	193.04	1,500.68
DEV_{model}	183.05	1,497.49
LRT	9.99**	3.19^{ns}

Values between parentheses show standard deviation. h^2_a: individual narrow sense heritability; h^2_{mp}: heritability on average of progeny; Acprog: progeny accuracy; h^2_{ad}: additive heritability; $CV_{gi}\%$: coefficient of individual genetic variation; $CV_{gp}\%$: coefficient of genetic variation among progenies; $CV_e\%$: residual variation coefficient; CV_r: coefficient of relative variation, calculated as CV_g/CV_e; DEV_{prog}: standard deviance for progeny; DEV_{model}: deviance for model; LRT: likelihood ratio test. Values followed by ** indicate significance at 1% according to the chi-square test; ns: not significant.

Valores entre parênteses: desvio padrão. h^2_a *: herdabilidade individual no sentido restrito;* h^2_{mp} *: herdabilidade da média de progênies; Acprog: acurácia da seleção de progênies;* h^2_{ad} *: herdabilidade aditiva;* CV_{gi}*: coeficiente de variação genotípica aditiva individual;* CV_{gp}*: coeficiente de variação genotípica entre progênies;* CV_e*: coeficiente de variação residual;* CV_r*: coeficiente de variação relativa, calculado como* CV_{gp}/CV_e*;* DEV_{prog}*: deviância média entre progênies;* DEV_{model}*: deviância do modelo; LRT: teste de razão de verossimilhança. Valores seguidos de ** indicam significância a 1% pelo teste Qui-quadrado; ns: não significância.*

Because of the large number of surviving plants (1,127), accuracy varied from 61% (DBH) to 73% (H). A higher accuracy value indicates more trustworthy estimates for genetic parameters and BLUP. However, individual narrow sense heritability (h^2_a) and heritability within progeny (h^2_{ad}) were low (0.04–0.11), while the mean value for progeny heritability (h^2_{mp}) was substantial (0.37–0.53), indicating that genetic control of growth traits was very low at the individual level and moderate and high at the progeny level, and coefficient of relative variation (CV_r) values were also moderate and high at the progeny level (Table 2). Because h^2_a and h^2_{ad} were low, expected genetic gains may be capitalized by mass selection in the trial and within the progeny.

Higher additive genetic values were estimated for 15 progenies (1, 4, 7, 9, 11, 16, 20, 21, 22, 23, 27, 29, 34, 35, and 38) (Table 1). However, the low values for genetic parameters indicate that the environment significantly influenced these traits. The phenotypic correlation between H and DBH was higher (0.91) than the genetic correlation (0.85), indicating that selecting one of the traits (H or DBH), based on visual observation of the trees (phenotypes) in the trial, can result in the indirect selection of trees that are genetically superior for the other trait (H or DBH).

3.2. *Plant growth in response to soil resistance*

Most of the values for soil resistance (SR) in the 1,198 collection points were between 100 and 2,000 KPa (539.9 KPa at 0–10 cm, 1554.7 at 10–20 cm, 1453.6 at 20–40 cm, and 1124.5 at the 40–60 cm soil layer). Lower SR values (<100 KPa) were found in the 0–10 cm soil layer (mainly in blocks 30–33, which were the most affected by flooding), while the higher values (>2,000 KPa) were found in the 10–20 cm soil layer, randomly distributed throughout the experimental plot.

Pearson correlations between H and DBH were significantly positive for all progenies (0.87 to 0.95, p<0.001), with phenotypic correlation (0.91) higher than genetic correlation (0.85). A significant phenotypic variation in plant development was also

Table 3 – Pearson correlation coefficient among height (H) and diameter at breast height (DBH), multiple linear regression coefficients, and theoretical and real minimum and maximum height values for progenies of Guanandi, according to soil resistance values at different soil layers.

Tabela 3 – *Correlação de Pearson entre altura (H) e diâmetro à altura do peito (DBH), coeficientes da regressão linear múltipla, e valores mínimos e máximos teóricos e reais de altura para cada uma das progênies de guanandi, em resposta à resistência do solo em diferentes profundidades do solo.*

Prog	DBH	Soil layer (cm)				Multiple linear coefficient					r^2	*F prob*	TH_{min}	TH_{max}	RH_{min}	RH_{max}
		0–10	10-20	20–40	40–60	A	B1	B2	B3	B4			---------- m ----------			
1	0.90**	0.55**	0.59**	0.59**		0.561	0.0017	0.0002	0.0011		0.50	0.0000	1.70	4.65	1.50	4.57
2	0.88**	0.67**	0.65**	0.47**		-0.726	0.0011	0.0005	0.0010	0.0006	0.67	0.0000	0.59	4.42	1.50	4.44
3	0.92**		0.57*	0.58**	0.38*	-0.643	0.0002	0.0006	0.0008	0.0009	0.59	0.0000	0.47	3.24	1.50	3.96
4	0.94**	0.33*	0.49**	0.49**		0.179	0.0003	0.0005	0.0006	0.0007	0.42	0.0014	1.06	3.41	1.80	4.35
7	0.92**	0.52**		0.40**		1.408	0.0009				0.20	0.0091	1.51	2.45	1.50	4.28
8	0.94**	0.39*		0.55**		0.572	0.0008	-0.001	0.0012		0.37	0.0014	1.53	3.90	1.40	4.24
9	0.91**	0.51**	0.54**			0.464	0.0008	0.0007	-0.001	0.0011	0.45	0.0008	0.71	2.37	1.70	4.44
15	0.93**	0.40*	0.62**	0.33*		0.234	0.0007	0.0010			0.46	0.0001	1.02	3.85	1.40	4.95
16	0.88**	0.56**	0.61**	0.52**		1.526	0.0009	0.0004	0.0005	-0.001	0.43	0.0005	2.33	4.93	1.59	4.51
17	0.89**		0.47**	0.38*		1.543	0.0008				0.22	0.0044	1.64	2.47	1.50	4.64
20	0.94**		0.40*	0.51**		1.158	0.0012				0.26	0.0009	1.30	2.55	1.49	5.33
21	0.93**	0.58**	0.67**	0.54**	0.31*	0.537	0.0012	0.0005	0.0007		0.59	0.0000	1.61	5.06	1.68	4.98
22	0.95**	0.55**	0.48**	0.38*		0.876	0.0015	0.0002	0.0005		0.35	0.0017	1.61	4.41	1.50	5.80
23	0.93**	0.58**	0.57**	0.62**	0.51**	0.194	0.0007	0.0004	0.0006	0.0005	0.55	0.0000	1.06	3.61	1.50	4.64
24	0.87**	0.35*	0.47**	0.50**		0.638	0.0004	0.0007			0.37	0.0006	1.17	3.07	1.00	4.00
27	0.92**	0.35*		0.55**		1.586	0.0017	-0.001	0.0012		0.39	0.0008	2.16	4.00	1.58	4.75
29	0.93**			0.32*		0.836	0.0008	0.0009			0.36	0.0011	1.56	4.29	1.84	4.82
30	0.90**		0.37*	0.60**		0.546	0.0015				0.37	0.0001	0.72	2.29	1.20	4.48
31	0.88**	0.54**	0.35*		-0.36*	0.763	0.0009	0.0003	0.0012	-0.001	0.53	0.0000	2.08	5.61	1.50	4.32
32	0.91**	0.38*	0.66**	0.46**		0.366	-0.001	0.0012	0.0005		0.43	0.0004	1.51	3.91	1.06	4.50
34	0.91**	0.33*	0.55**	0.68**		0.355	0.0006	0.0009			0.56	0.0000	1.06	3.58	1.59	4.75
35	0.95**			0.50**	0.44**	1.486	0.0009				0.25	0.0010	1.59	2.53	1.82	4.65
36	0.89**		0.33*	0.48**	0.34*	0.863	0.0004	-0.001	0.0007	0.0009	0.38	0.0020	1.35	2.49	1.00	4.64
37	0.95**		0.47**	0.55**		1.121	-0.001	0.0001	0.0015	-0.001	0.40	0.0030	2.39	4.63	1.54	4.45
38	0.94**	0.55**	0.51**	0.68**	0.54**	-1.015	0.0007	0.0006	0.0006	0.0014	0.59	0.0000	-0.01	2.96	1.00	4.79
39	0.90**	0.43**	0.48**			0.936	0.0005	0.0007			0.30	0.0036	1.48	3.48	1.68	4.74

Prog. (progeny). Values followed by ** (significance at $p<0.001$); Values followed by * (significance at $0.001 \leq p < 0.005$); missing values (not significantly correlation). A–B4: regression coefficients (A: linear coefficient; B1-B4: angular coefficients according to linear-to-4th degree regressions; B1: 0–10 or 10-20 or 20-40 cm; B2: 10–20 cm; B3: 20–40 cm; B4: 40–60 cm); missing values for progenies 10, 11, 26, and 33: no significant curves fitted. Prog.: progeny; TH_{min}: theoretical minimum height, calculated at SR=0 kPa; TH_{max}: theoretical maximum height, calculated at SR=2,000 kPa; RH_{min}: real minimum height; RH_{max}: real maximum height.

*Prog (proênie). Valores seguidos de ** (significância a $p<0,001$); valores seguidos de * (significância a $0,001 \leq p<0,05$); valores ausentes (correlação não significativa). A-B4: coeficientes da regressão (A: coeficiente linear; B1-B4: coeficientes angulares, de acordo com modelos simples até 4a ordem; B1: 0-10, 10-20 ou 20-40 cm; B2: 10-20 cm; B3: 20-40 cm; B4: 40-60 cm); valores ausentes para as progênies 10, 11, 26 e 33: impossibilidade de ajuste de modelo significativo para essas progênies. TH_{min}: altura mínima teórica, calculada em SR=0kPa; $TH_{máx}$: altura máxima teórica, calculada em SR=2000kPa; RH_{min} e $RH_{máx}$: alturas reais, mínima e máxima, observadas.*

observed in response to soil drainage in different layers until 60 cm deep. Correlations between H and soil resistance (0–10 and 10–20 layers: 0.32 to 0.67; 20–40: 0.32 to 0.68; 40–60: -0.36 to 0.54; $p<0.001$) and DBH and soil resistance (0–10: 0.32 to 0.72; 10–20: 0.32 to 0.76; 20–40: 0.34 to 0.72; 40–60: 0.33 to 0.58; $p<0.001$) varied among the progenies (Table 3).

Soil resistance values throughout the soil layers showed a similar but non-significant pattern for all progenies, but plant growth was mainly affected in layers up to 40 cm deep. Multiple linear regression models were fitted for H growth in response to SR values at different depths (Table 3), according to the correlation matrix values shown in Table 5, and as single models of SR values in the 1–10, 11–20, or 21–40 cm soil layers, double (11–20 and 21–40 cm), triple (1–10, 11–20 and 21–40 cm), and quadruple models (1–10, 11–20, 21–40, and 41–60 cm).

Height development of 10 progenies (2, 3, 4, 9, 16, 23, 31, 36, 37, 38) was affected by all 60 cm layers of soil, while 6 progenies (1, 8, 21, 22, 27, 32) did not respond to SR values in the 40–60 cm layer, 5 progenies (15, 24, 29, 34, 39) were only affected by SR values in the 11–20 and 21–40 cm layers, and another 5 progenies (7, 17, 20, 30, 35) were affected by only the 1–40 cm soil layer. Furthermore, no curves fit four progenies (10, 11, 26, 33). All linear and multiple regressions were plotted for all progenies, and curves were chosen according to their r^2 and significant F probability values, after testing all models (Table 3).

All single and/or multiple linear regression coefficients were then used for an initial assessment of potential growth of progenies in extreme drainage conditions, for flooding risk (TH_{min} at SR=0 kPa) as well as in well-drained soils (TH_{max} at SR=2,000 kPa). (Table 3) This yielded three sets of flood-

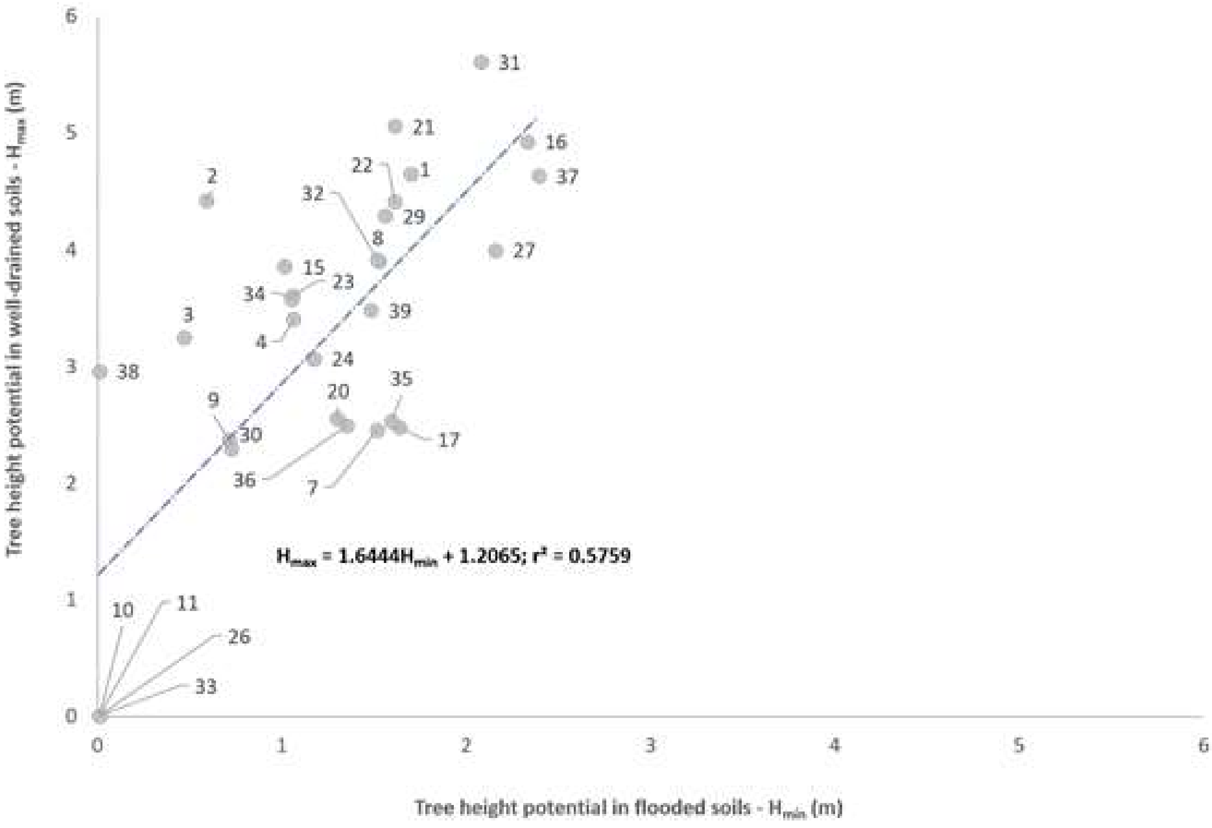

Figure 2 – Tree height growth potential for progenies of *Calophyllum brasiliense* at five years of age in response to flooded and well-drained soils, according to the theoretical multiple linear regression values shown in Table 3.

Figura 2 – *Potencial de crescimento em altura da progênies de* ***Calophyllum brasiliense****, aos cinco anos de idade, em solos alagados e bem drenados, de acordo com os valores teóricos ajustados nos modelos lineares expostos na Tabela 3.*

tolerant progenies with development proportional to environmental effects (9, 16, 24, 30, close to the line), tolerant of these effects (1, 2, 3, 4, 8, 15, 21, 22, 23, 29, 31, 32, 34, 38, above the line), and sensitive to these effects (7, 10, 11, 17, 20, 26, 27, 33, 35, 36, 37, below the line) (Figure 2).

Constant flooding of the soil resulted in 12.2% and 58.6% losses in theoretical maximum growth capacity for tolerant and sensitive progenies, respectively (Table 3). In fact, only a few progenies (1, 16, 21, 31, 37) showed real maximum height values that exceeded the theoretical ones (1.7%, 9.7%, 1.6%, 29.8% and 4.1%, respectively), indicating that even among genetic material that is tolerant, sensitive, or capable of proportional growth, the response to environmental conditions varies significantly.

4. DISCUSSION

4.1. *Initial plant growth and genetic parameters of progenies*

Genetic differences for DBH were observed among the progenies, indicating that superior plants can be selected for breeding purposes. Individual narrow sense heritability (h^2_a) was low for growth traits (0.06–0.11), which means that the additive genetic effects explain only a small proportion of the total variance for these traits (Kvestad et al., 2010). In contrast, mean heritability among progeny was moderate for the traits (0.53 for H, and 0.37 for DBH), indicating that genetic gains can be obtained by selecting the most productive progenies.

Breeding programs for *C. brasiliense* will require the introduction of new germplasm sources to boost genetic variability in future generations, as well as improved environmental control in experimental designs to minimize environmental influences. Among the genetic parameters (and despite our preliminary results at 5 years of age), genotypic variance, heritability, and genotypic and phenotypic correlations demonstrated precise and accurate values. Meanwhile, heritability at the progeny level was moderate to high for growth traits, indicating that genetic gains may be obtained via progeny selection.

Estimates of genetic parameters can shed light on the contribution of genetic and environmental variation to the heritability of traits. Heritability values exceeding 30% indicate that genetic control of a given phenotype can be transferred to the next generation.

Variables of a complex genetic nature are influenced by the environment, and their selection is usually complicated due to the significant stochastic effects involved (Cruz, 2010); however, significance may be found among these variables, permitting indirect selection. Heritability values for H and DBH in both the restricted and broad sense were low because of environmental influences, due to continuous distribution (Baldoni et al., 2020; Braga et al., 2020; Souza et al., 2020).

Genetic and phenotypic correlations between H and DBH in forest species tend to be highly positive, but can change at more advanced ages (Venlovsky and Barriga, 1992; Kien et al., 2009; Sumardi et al., 2016).

Low genetic control of native tropical species is very common in progeny tests, particularly for species that are highly dependent on open pollination. In studies involving REML/BLUP, UPGMA, and PCA, Maia et al. (2016a,b; 2018; 2020) found positive correlations between fruit yield/quality and growth traits in early selection of native Brazilian fruit species such as *Anacardium* spp. (cajuí), *Hancornia speciosa* (mangaba), and *Platonia insignis* (bacuri), all collected from native populations and/or in the first cycle of recurrent selection. But in all cases these authors emphasized the need for new assessments, since the genotypes came from base populations.

However, it should be noted that unlike the species in the aforementioned studies, the most desirable commercial product from *C. brasiliense* is not fruit or seeds. For this reason, genetic interactions across recurrent selections with genotypes also coming from a disturbed native population appear less important than the genotype/environment interaction, which results in better tree development and wood production.

The highly positive genetic correlations we have found suggest a common gene is responsible for phenotypic expression (pleiotropy) of H and DBH (Baltunis et al., 2007; Gapare et al., 2015), and that the indirect selection for DBH could yield indirect gains in H, since genetic correlations remove some components of environmental error.

In a previous study focusing on selecting *C. brasiliense* from commercial stands, also at 5 years of age, Kalil Filho et al. (2012) obtained plants with an average height of 3.69 m and DBH of 18.41 cm, results that exceeded our values (mean H=2.73m, mean DBH=2.75 cm). Although the genotypes came from natural populations, with no breeding stage, they were all planted on well-drained and managed soils.

For this reason, of the environmental error components that can affect plant growth, better management of soil drainage could positively impact progenies of *C. brasiliense* collected from segregating populations, at least at early ages.

4.2. *Plant growth development in response to soil resistance*

Soil resistance was highest in the 20–40 cm layer, which can result from physical changes in the soil structure (Tormena et al., 2002) due to compaction from agricultural machines (Silva et al., 2000; Gülser and Candemir, 2012), root density, water/soil or O_2/CO_2 imbalance, and soil hydric potential across field capacity (100 kPa) and permanent wilting point (1,500 kPa), mediating non-limiting and least limiting water range, and optimal hydric interval of soils (Letey, 1985; Silva et al., 1994; Orellana et al., 1997), which limit plant development at lower or upper values (Silva et al., 1994). A slight linear response to soil resistance was observed in tree height, which may be explained by the large number of observations (N=1,127) as well as the large genetic variability among progenies, environmental characteristics, and the trees' initial response to water/soil stress. However, of all the significant correlation indexes, at least 30% of the variability in height and DBH values result from environmental conditions, which could be potentially related to soil resistance.

4.3. *Integrated plant growth development in response to genetic potential and soil resistance*

Genetic variation is essential for survival and adaptation to environmental changes (Gribel, 2000), and although soil resistance is not an intrinsic factor for cell metabolism or plant physiology, it does affect biochemical relations and aspects of root morphology and has been investigated for its significant correlation with plant development (Gubiani et al., 2013). Water saturation in the soil has various adverse effects on plant development, all related to hypoxia, such as stomatal closure, photosystem-II damage, reduced photosynthesis capacity, and reduction of carbon assimilation mechanisms, including drastic decreases in Rubisco enzyme and ethylene growth regulator concentrations (Koslowski, 1997; Pezeshki, 2001; Herrera et al., 2008).

The most common flooding tolerance mechanisms are linked to foliar senescence and abscission, reduction of new leaves, and changes in growth and stem/root anatomy (increased size, presence of lenticels, development of adventitious and diageotropic roots, formation of aerenchyma) (Davanso-Fabro et al., 1998; Medri et al., 2012; Oliveira and Gualtieri, 2017). Despite its strong adaptative capacity to occupy riparian soils (Kawaguici and Kageyama, 2001; Percuoco et al., 2014), *C. brasiliense* can suffer severe damage if the time of exposure or recurrent stress surpasses 120 days, with height losses reaching 14% (Oliveira and Joly 2010).

For this reason, integrative analysis of estimated genetic gains (Table 1) and development growth potential of progenies in response to soil drainage (Figure 2) could offer useful solutions. All the genetic evaluations performed in this study at 5 years of age indicated significant gains in height for 14 progenies, which should be selected to establish clonal seed or seedling orchards to supply commercial plantations or establish the next generation for breeding, particularly to maintain genetic variability, which is already low in commercial stands. By simulating the effects of soil resistance on tree development, this could lead to advances in establishing different sets of *C. brasiliense* progenies, both confirming genetic estimated gains (progenies 1, 4, 21, 22, 23, 29, and 38), as well as contradicting them (7, 11, 17, 20, 27, 35, 36, 37, and 39).

4.4. Final Considerations

Because of the original nature of this study investigating how low and/or high SR values affect the development of tree species, some questions remain unanswered, and the specific effects of certain SR values on given soil layers and specific progeny still remain unknown. Still, the results were considered in a highly conservative manner to avoid making unreliable extrapolations.

Additional approaches at more advanced ages are needed, including new mathematical and statistical tools such as PCA, geostatistical mapping, and the constant integration of new data. As part of precision silviculture, the results of this study also indicate at least two different approaches for the future: maintain environmental stress in order to assess breeding for flood tolerance over time, or improve soil drainage to increase growth of *C. brasiliense* and boost wood production.

5. CONCLUSIONS

The development of *Calophyllum brasiliense* varied significantly among progenies. Despite high positive genetic and phenotypic correlations between growth traits, which indicate the possibility of an indirect selection strategy for the species, genetic control was low, particularly at the individual level.

Integrated analysis of additive genetic gains and tree growth resulting from soil resistance made it possible to group the experimental progeny according to different degrees of tolerance to water soil saturation. Even tolerant progenies (1, 2, 3, 4, 8, 15, 21, 22, 23, 29, 31, 32, 34, 38) exhibited growth 12% below the expected theoretical value, while for sensitive progenies (7, 10, 11, 17, 20, 26, 27, 33, 35, 36, 37) growth was reduced by as much as 59%. Meanwhile, growth expectations for some tolerant progenies (1, 21, 31) increased from 1.6% to 29.8%, while for proportional (16) and sensitive (37) progenies this increase was 9.7% and 4.1%, respectively.

The innovative combination of mathematical and analytical tools presented in this study demonstrates precision silviculture's potential to determine which genetic materials are best suited for different environmental conditions and also to assist in decision making for forest management to avoid harmful environmental effects.

AUTHOR CONTRIBUTIONS

Conceptualization, Fowler, J. A. P., Kalil Filho, A. N. and Bognola, I. A.; methodology, Bognola, I. A.; formal analysis, Oliveira, E. B., Froufe, L. C. M. and Aguiar, A. V.; investigation, Fowler, J. A. P., Kalil Filho, A. N., Bognola, I. A. and Froufe, L. C. M.; data curation, Fowler, J. A. P. and Froufe, L. C. M.; writing—original draft, Froufe, L. C. M.; resources, Fowler, J. A. P., Bognola, I. A. and Kalil Filho, A. N.; writing—review and editing, all authors; visualization, all authors; project administration, Fowler, J. A. P. and Bognola, I. A.; funding acquisition, Fowler, J. A. P., Bognola, I. A. and Kalil Filho, A. N. All authors have read and agreed to the published version of the manuscript.

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