https://doi.org/10.1590/1678-4499.20200463

PLANT BREEDING
Article

Estimates of genetic parameters for juvenile traits in macaw palm

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Received: Dec. 2, 2020 | **Accepted:** Mar. 3, 2021
Section Editor: Gabriel Constantino Blain
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How to cite: Lustri, P. A., Siqueira, W. J., Azevedo Filho, J. A., Vianna, S. A. and Colombo, C. A. (2021). Estimates of genetic parameters for juvenile traits in macaw palm. Bragantia, 80, e2821. https://doi.org/10.1590/1678-4499.20200463

ABSTRACT: *Acrocomia aculeata* (Jacq.) Lodd. ex. Mart. (Arecaceae) is a neotropical oil palm of widespread occurrence in the American continent and with great economic potential for the energy and food sectors. Genetic breeding studies for the species are very recent, with a need for basic knowledge from the genetic diversity in agronomic traits. Thus, the aim of this work was to estimate genetic variance, heritability, and genetic gain as well as to propose strategies of selection. Two-year evaluations of eight agromorphological characteristics were carried out in two experimental fields composed of 50 open-pollinated progenies. The results revealed moderate heritability for progeny average to thorn density in the abaxial side ($\hat{h}^2_{mp} = 0.402$ in Pindorama) and relative chlorophyll index ($\hat{h}^2_{mp} = 0.458$ in Presidente Prudente). The selective accuracy was 0.634 and 0.677 for the same traits, respectively. In the combined analysis, the higher values of heritability were obtained to thorn density on the abaxial region of leaves and relative chlorophyll index (0.616 and 0.666, respectively). Moderate to high magnitude values of genetic gain was reached for traits with greatest agronomic interest, as plant height G_s (%) = 19.64, number of leaves G_s (%) = 26.43, stipe diameter at breast height G_s (%) = 12.51, and relative chlorophyll index G_s (%) = 38.12. In conclusion, the results indicate considerable genetic variability for the evaluated traits and suggest that their most effective use for the purpose of genetic gains would be based on the combined selection between and within progenies.

Key words: oleaginous species, Arecaceae, heritability, REML/BLUP, plant breeding.

INTRODUCTION

The global production of vegetable oil is growing, with an estimation of 209 million tons for 2020/2021 according to the USDA-FSA, of which 40% (83.9 million tons) are provided by palm and palm kernel, and 28.5% (59.8 million tons) by soybean (USDA 2020). In addition to representing an important market, there is a concern that only these two species represent 68.5% of all vegetable oil production in the world. Among the forest species that could produce vegetable oil, native and exotic palms have wide potential use. The macaw palm, *Acrocomia aculeata* (Jacq) Lodd. ex. Mart. (Arecaceae), locally known as *macaúba*, is a neotropical species native to Brazil and widely distributed in the tropical and subtropical Americas (Henderson et al. 1995; Lorenzi et al. 2010).

Acrocomia aculeata grows in the dry areas of the New World, from Mexico and the Caribbean Islands to northern Argentina (Morcote-Rios and Bernal 2001). It is a perennial heliophilous palm of 4–15 m height, with a glabrous, fusiform cylindrical stipe that is densely ringed, containing numerous spines. The species is monoicous and protogenic, with an annual seasonal flowering. In most of the Brazilian territory, the flowering season happens from September to February, with a peak in November and December (Berton 2013; Lorenzi 2006; Scariot et al. 1995). The economic interest in *A. aculeata* is growing due to the potential production of pulp and almond oils and to by-products of high added value and great demand in the food, cosmetics, and energy industries. The species is able to produce 4,000 L of oil·ha^{-1}, largely surpassing soybeans, which produce just 400 L, and equaling palm oil (Colombo et al. 2018).

Although with great potential for cultivation, *A. aculeata* is an incipiently domesticated species, that is, there was only human selection in a small sample of the entire wild population, causing a reduction in its genotypic diversity and its phenotypic diversity, in which only one varies little of the ancestral wild population (Clement et al. 2010). Therefore, a breeding program for the species is required to form more homogeneous and productive plantations, with agromorphological traits to facilitate its management. The exploration of the genetic basis of *A. aculeata* presupposes knowing how its genetic diversity is structured. In tree species with a low degree of domestication, it is common to observe higher genetic variability, with greater variation within populations (Sant'Ana et al. 2013; Senna et al. 2012).

Studies analyzing variance components are essential for the efficient exploitation of genetic diversity in the traits of commercial interest (Furlani et al. 2005), mainly because it is a perennial species with a long juvenile period, which can reach six years (Manfio et al. 2012). The reproductive system of *A. aculeata* remain controversial being considered mixed or preferentially allogamous (Abreu et al. 2012; Coelho et al. 2018), with high genetic variability within and among natural populations, especially for morphoagronomic traits (Berton 2013; Lorenzi et al. 2010; Nucci et al. 2008; Oliveira et al. 2012; Vianna et al. 2017).

Due to its high genetic variability, one strategy for genetic improvement of this species would be the selection and recombination of genotypes with the best agronomic traits (Oraguzie et al. 2001). On the other hand, experiments with progenies can also be adopted, once it is possible to evaluate the potential of the parents through the agronomic evaluation of their respective offspring. In addition, the progeny tests enable the estimation of population parameters, like trait heritability and the additive and nonadditive genetic variances, which are obtained by the decomposition of the mean squares into its components in the analysis of variance based on their expected values (Resende 2002). The estimation of genetic parameters, the prediction of possible gains in candidate genotypes for selection, and the knowledge of the genetic control in traits of interest during the progeny life cycle are essential steps for the definition of more efficient breeding strategies (Farias Neto et al. 2013).

For genetic breeding of perennial plants with unbalanced data, it is usual to estimate parameters and to predict genetic values using mixed linear models, especially with the Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) methodologies (Araujo et al. 2019; Bergo et al. 2019). In this way, it is possible to obtain more precise estimates of genetic parameters by allowing the comparison of individuals across time (years or generations) and space (locations or blocks), while simultaneously using a large number of data and correcting environmental effects in test progenies (Assis and Resende 2011). The use of this analysis methodology has been well applied in different forest species, such as *Euterpe oleracea* (Farias Neto et al. 2012; Navegantes et al. 2018), *Elaeis guineensis* (Cedillo et al. 2018), *Eucalyptus urophylla* (Rosado et al. 2009), and *A. aculeata* (Coser 2016; Costa et al. 2018; Rosado et al. 2019).

The efficiency of a breeding program for genetic improvement may be expressed by the genetic gain per unit time. For a perennial species like *A. aculeata*, the number of years to complete a selection cycle constitutes the primary obstacle to species improvement using recurrent selection. Thus, the time interval between generations in the selection cycles should be reduced as much as possible to maximize the gains per unit time (Borralho et al. 1992). For A. aculeata, early selection plays an important role.

Therefore, the present study was conducted to obtain genetic parameters of agronomic traits in open-pollinated progenies of *A. aculeata*, in an experiment installed in two locations with two-year data collection. This is the first study ever carried out with these particularities for *A. aculeata*, being a promising way to obtain more competitive genetic materials.

MATERIAL AND METHODS

Study material and characterization of experimental areas

The study was carried out with 50 open-pollinated progenies of 4 to 5-year-old obtained from selected plants in 24 native populations of the Brazilian states of São Paulo and Minas Gerais. The choice of mother trees (one to six per population) for fruit collection was based on the criteria of low size, higher fruit production, and the high oil content in fruits. After germination and seedling formation, they were transplanted in 2013 to two experimental fields of the Agência Paulista de Tecnologia dos Agronegócios (APTA). The first one was the Regional Center – North Pole, located in the municipality of Pindorama at 530 m altitude, presenting the Aw climatic type (Köppen-Geiger classification), with average annual precipitation of 1284 mm, the average annual temperature of 22.3 °C, and a Podzolic Red-Yellow Tb eutrophic soil with a medium texture. The second one was the Alta Sorocabana Regional Pole, located in the municipality of Presidente Prudente at 472 m altitude, presenting climatic type Cfa (Köppen-Geiger classification), with average annual precipitation of 1207 mm, average annual temperature of 21.6 °C, and a sandy Argisol type soil with sandy texture (CLIMATE-DATA.ORG 2020a,b; Oliveira et al. 1999).

The experimental design adopted was a randomized block with three replications, with the plots represented by progenies containing from three to nine plants per repetition, in the spacing of 5 × 4 m. Twenty-eight progenies (403 genotypes) were planted in Pindorama and 41 progenies (475 genotypes) in Presidente Prudente, with 19 progenies being common to both experiments.

Agromorphological evaluated traits

The progenies with four and five years of age were evaluated in July of 2017 and 2018 regarding (i) plant height (cm) measured with the aid of a telescopic ruler; (ii) diameter of the stipe at the base (cm) and (iii) diameter of the stipe at chest height (cm) measured with a tree caliper; (iv) number of expanded leaves; (v) total leaf length (m) considering the sheath, petiole, and leaf blade, and (vi) length of the pinnate region (m) considering the insertion point of the first pinna from the base to the apex, measured with the aid of a metric tape; (vii) thorn density by counting in a delimited area of 10 × 10 cm on the abaxial face of the pinna; (viii) relative chlorophyll index determined using the SPAD-502 Plus equipment through an average of six readings (two pinnas of three leaves in the middle of the treetop).

Statistical analyzes and estimates of genetic parameters

The measured traits were analyzed statistically by calculating position measurements (minimum value, first quartile, median, third quartile, and maximum value) represented by boxplot graphs. Additionally, the data were subjected to the calculation of Pearson's correlation coefficient (r) using the software Genes (Cruz 2013).

The difference between the progenies regarding the measured traits was obtained from the analysis of deviance using the software Selegen – Statistical System of Computerized Genetic Selection (Resende 2016), which provides the values of deviance from models with and without the effects to be tested, by obtaining the likelihood ratio. With the application of the chi-square test ($p \leq 0.05$, 1 GL), the significance was tested via likelihood ratio test (LRT).

The estimates of variance components and genetic parameters for each location were obtained with the mixed model approach (maximum restricted likelihood/best unbiased linear prediction), using the Selegen software – restricted estimation maximum likelihood/best linear unbiased predictor (REML/BLUP), considering half-sibling progenies, complete block design with several plants per plot, a single location, and a single population, following the Eq. 1:

$$y=X_r+Z_g+W_p+e \tag{1}$$

where: y represents data vectors, r is the effect of blocks (fixed), g is the additive genetic effect (random), p is the effect of plots (random effects of the common environment of the plots), and e the effect of random errors, respectively, and X, Z and W are the matrices of incidence for r, g and p, respectively (Resende 2016).

The average of the two-year evaluation was used to obtain the estimates of genetic parameters in grouped analysis with the same software, also applied to half-sib progenies in the randomized block design, with several locations and a single harvest, using from the Eq. 2:

$$y=X_r+Z_a+W_p+T_i+e \tag{2}$$

where: *y* represents the data vector, *r* is the vector of the repetition effects (fixed) added to the general average, *a* is the vector of the individual additive genetic effects (random); *p* represents the vector of the plot effects (random), *i* represents the vector of the effects of the genotype × environment interaction (random), *e* is the vector of errors or residues (random), and *X*, *Z*, *W* and *T* are the incidence matrices for *r*, *a*, *p* and *i*, respectively.

To evaluate the selection response of the progenies in both experimental fields considering the selection intensity of 10%, the average values predicted for each genotype were used based on the analysis models, with the calculation performed using the ranking of the 10%, in which the selection gain G_s (%) = average of the additive genetic values of the selected individuals/*m*) × 100, where *m* corresponds to the general average of the experiment for a given trait.

RESULTS

Phenotypic variation for both sites

The values shown in the boxplot graphs indicate the presence of variation in the experimental fields, with higher maximums for the progenies located in Pindorama, except for the chlorophyll relative index trait, which obtained a maximum value of 67.9 in Presidente Prudente and 65.9 in Pindorama (Fig. 1). The median value for height and diameter of the stipe, both at the base and at the chest height, revealed taller plants with a greater circumference of the stipe in the progenies of Pindorama (3.5 and 3.0 m) when compared to Presidente Prudente (18 and 6 cm). The number of expanded leaves, total leaf length, and leaf blade length traits showed the closest median and variation values in the two evaluated sites, with an advantage for Pindorama, especially for the higher variation in the total leaf length and leaf blade length (6.50 and 2.60 m to 2.10 m, respectively), while for Presidente Prudente this same variation was to 7 and 2.23 m to 1.80 m, respectively. Regarding the thorn density on the abaxial face of the pinna, the median values obtained in the progenies of Pindorama and Presidente Prudente were also very close (15 and 16, respectively), although with higher variation in the progenies of Pindorama.

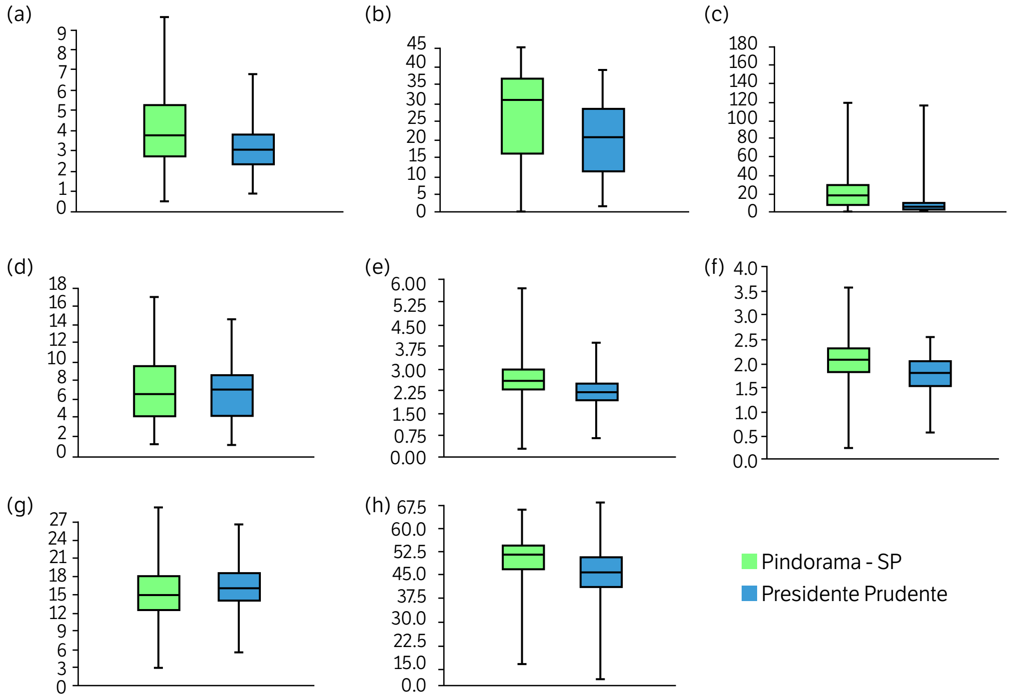

Figure 1. *Box-plot*: a) plant height (m); b) diameter at the base of the stipe (cm); c) diameter of the stipe at chest height; d) (iv) number of expanded leaves; (v); e) total leaf length; f) length of the pinnate region; g) thorn density on the abaxial face of the pinna; h) relative chlorophyll index; of 5-year-old macaw palm progenies in the São Paulo municipalities of Pindorama and Presidente Prudente.

Genetic parameters by location

The ikehood ratio test (LRT) values obtained for the evaluated descriptors did not reveal significant differences for any character in both experimental location (Table 1).

Table 1. Deviance values of morphological traits in open-pollinated progenies of the palm *A. aculeata* obtained in two-year evaluation (2017 and 2018) from experimental fields installed in 2013 in the municipalities of Pindorama and Presidente Prudente.

Traits	Pindorama			Prudente		
	Progenies	Complete model	LRT[1]	Progenies	Complete model	LRT[1]
PH	90.72	90.19	0.53^{ns}	–319.30	–320.12	0.82^{ns}
DBS	1320.61	1320.01	0.60^{ns}	1387.64	1387.32	0.32^{ns}
NEL	1386.22	1386.21	0.01^{ns}	896.00	896.02	0.02^{ns}
DCH	486.11	485.92	0.19^{ns}	402.83	402.28	0.55^{ns}
TLL	–263.50	–263.67	0.17^{ns}	–648.94	–649.89	0.95^{ns}
LPR	–505.07	–505.25	0.18^{ns}	–941.88	–942.71	0.83^{ns}
CLF	962.81	960.92	1.89^{ns}	1175.49	1173.97	1.52^{ns}
TDAP	1648.26	1647.77	0.49^{ns}	2025.05	2022.73	2.32^{ns}

Note. PH: plant height, DBS: diameter at the base of the stipe, DCH: diameter of the stipe at chest height, NEL: number of expanded leaves, TLL: total leaf length, LPR: length of the pinnate region, TDAP: thorn density on the abaxial face of the pinna, RCI: relative chlorophyll index. [1]Chi-square tabulated: ns = not significant; 3.84 (*) e 6.63 (**) for levels of significance 5% e 1%, respectively.

The value of the heritability of the additive effects within progenies of the analyzed traits in the experimental field of Pindorama varied from $\hat{h}^2_{ad} = 0.018$ (diameter at breast height) to $\hat{h}^2_{ad} = 0.188$ (relative chlorophyll index), while the mean heritability varied from $\hat{h}^2_{mp} = 0.015$ (the number of leaves expanded) to $\hat{h}^2_{mp} = 0.458$ (relative chlorophyll index) (Table 2). Comparing the individual genetic variation coefficients CV_{gi} (%) analyzed in both experiments, it is possible to notice that most of the traits presented greater results in Presidente Prudente. In this location, the traits with the highest values were: the number of expanded leaves, with $CV_{gi} = 14.55$ in Presidente Prudente and $CV_{gi} = 13.80$ in Pindorama, the total leaf length, with CV_{gi} (%) 8.31 in Presidente Prudente and CV_{gi} (%) = 7.03 in Pindorama, the thorn density in the abaxial region, with CV_{gi} (%)= 16.55 in Pindorama and CV_{gi} (%) = 22.43 in Presidente Prudente, and the relative chlorophyll index, with CV_{gi} (%) = 21.01 in Pindorama and CV_{gi} (%) = 36.57 in Presidente Prudente (Table 2).

Predicted genetic gains can be considered of moderate to high magnitudes, with emphasis on the diameter characteristics at the base of the stipe, with $G_s = 19.53\%$ in Pindorama, thorn density on the abaxial face of the pinna, with $G_s = 34.47\%$ in Presidente Prudente, and relative chlorophyll index, with $G_s = 47.18\%$ in Presidente Prudente.

Table 2. Estimation of genetic parameters for vegetative morphological traits in open-pollinated progenies of *A. aculeata*, based on the average two-year evaluation (2017 and 2018) of 4 and 5-years-old, respectively, from experimental fields installed in 2013 in the municipalities of Pindorama and Presidente Prudente.

Parameters	Local	PH	DBS	DCH	NEL	TLL	LPR	TDAP	RCI
$\hat{\sigma}^2_a$	A	0.049	0.497	0.110	0.065	0.009	0.006	0.292	0.607
	B	0.022	0.181	0.025	0.059	0.011	0.009	0.346	1.343
$\hat{\sigma}^2_e$	A	0.369	3.975	4.736	0.820	0.205	0.128	2.006	7.931
	B	0.203	2.564	1.286	0.588	0.127	0.081	1.675	5.752
$\hat{\sigma}^2_f$	A	0.438	4.645	5.393	0.937	0.217	0.137	2.305	8.602
	B	0.227	2.781	1.356	0.658	0.140	0.091	2.063	7.138
$\hat{h}^2_{ad}$	A	0.112 ± 0.083	0.107 ± 0.081	0.020 ± 0.035	0.069 ± 0.065	0.045 ± 0.052	0.048 ± 0.054	0.126 ± 0.088	0.070 ± 0.0650
	B	0.100 ± 0.068	0.065 ± 0.055	0.018 ± 0.029	0.089 ± 0.064	0.084 ± 0.062	0.103 ± 0.069	0.167 ± 0.088	0.188 ± 0.093
$\hat{h}^2_{mp}$	A	0.274	0.275	0.048	0.181	0.158	0.161	0.365	0.233
	B	0.303	0.212	0.063	0.015	0.273	0.308	0.402	0.458
$\hat{r}_{aa}$	A	0.524	0.524	0.220	0.425	0.398	0.402	0.604	0.483
	B	0.551	0.460	0.251	0.518	0.523	0.555	0.634	0.677

continue...

Table 2. Continuation...

Parameters	Local	PH	DBS	DCH	NEL	TLL	LPR	TDAP	RCI
CV_{gi} %	A	13.977	23.839	14.349	13.807	7.037	6.076	22.719	21.014
	B	10.804	17.943	10.151	14.553	8.313	7.741	27.059	36.579
CV_{gp} %	A	6.988	11.917	7.174	6.903	3.518	3.038	11.359	10.507
	B	5.402	8.971	5.075	7.276	4.156	3.870	13.529	18.289
CV_e %	A	16.055	27.362	44.970	20.741	11.458	9.785	21.167	26.888
	B	11.566	24.425	27.677	16.976	9.579	8.203	23.314	28.112
CV_r %	A	0.435	0.435	0.159	0.332	0.307	0.310	0.536	0.390
	B	0.467	0.367	0.183	0.428	0.433	0.471	0.580	0.650
G_s	A	12.16	19.53	6.88	9.58	4.06	3.47	21.31	14.2
	B	10.88	15.29	5.27	14.24	7.8	7.66	34.47	47.18
$\bar{x}$	A	4.16	26.85	27.58	7.09	2.58	2.05	15.19	15.27
	B	3.11	20.02	9.47	6.44	2.19	1.75	16.10	16.10

Note. A: Pindorama, B: Presidente Prudente. PH: plant height, DBS: diameter at the base of the stipe, DCH: diameter of the stipe at chest height, NEL: number of expanded leaves, TLL: total leaf length, LPR: length of the pinnate region, TDAP: thorn density on the abaxial face of the pinna, RCI: relative chlorophyll index. $\hat{\sigma}^2_a$ = individual additive genetic variance; $\hat{\sigma}^2_e$ = residual variance; $\hat{\sigma}^2_f$ = phenotypic variance; $\hat{h}^2_{ad}$ = additive heritability within progenies; $\hat{h}^2_{mp}$ = heritability of the average of progenies, assuming complete survival; $\hat{r}_{aa}$ = accuracy of progeny selection, assuming complete survival; CV_{gi} % = coefficient of genotypic variation; CV_{g9}% = coefficient of genotypic variation between progenies; CV_e= residual coefficient of variation; $CV_r = CV_g/CV_e$ coefficient of relative variation; G_s = predicted gain with selection; $\bar{x}$ = overall average of the experiment.

Joint genetic analyzes

A joint analysis was carried out considering the two-year average of the two experimental fields to obtain genetic parameters. For this purpose, only data from the common progenies in both experimental fields were considered. In other words, data from 19 progenies present in both Presidente Prudente and Pindorama were used for this analysis. Only 19 common progenies were used in the joint analysis in both experiments because the Selegen software requires the balance of progenies to obtain the desired genetic parameters.

Unlike the analyzes carried out for each location separately (Table 1), the LRT^1 values of the combined analysis revealed significant differences for progenies differentiation of the traits, except for the total length of the leaf, whose LRT^1 was 2.28 (Table 3).

Table 3. Deviance values of the joint analysis of 19 open pollination progenies of *A. aculeata* calculated from the average of morphological traits evaluated over two years (2017 and 2018), of 4 and 5-years-old, respectively. The experimental fields were installed in 2013 in the municipalities of Pindorama and Presidente Prudente, state of Sao Paulo.

Traits	Progeny	Complete model	LTR1
PH	–21.33	–28.30	6.97**
DBS	1637.33	1632.35	4.98*
NEL	–265.88	–272.96	7.08**
DCH	593.54	587.73	5.81*
TLL	–486.13	–491.41	2.28^{ns}
LPR	–721.04	–726.27	5.23*
CLF	1301.17	1293.53	7.64**
TDAP	2177.69	2171.35	6.34*

Note. PH: plant height, DBS: diameter at the base of the stipe, DCH: diameter of the stipe at chest height, NEL: number of expanded leaves, TLL: total leaf length, LPR: length of the pinnate region, TDAP: thorn density on the abaxial face of the pinna, RCI: relative chlorophyll index. ^{1}Chi-square tabulated: ns = not significant; 3.84 (*) e 6.63 (**) for levels of significance 5 and 1%, respectively.

The diameter at breast height revealed the lowest value of heritability in the narrow sense ($\hat{h}^2_a$ = 0.057), and also was the variable with the lowest values estimated in the individual analyses. The thorn density on the abaxial region was the trait with the highest value ($\hat{h}^2_a$ = 0.216). For the coefficient of determination for the plot effects (C^2parc), relatively low values were found, ranging from 0.001 for leaf blade length, up to 0.002 for the diameter at breast height (Table 4).

Table 4. Estimation of genetic parameters for vegetative morphological traits of 19 open pollination progenies of *A. aculeata* cultivated in experimental fields implanted in 2013 in the municipalities of Pindorama and Presidente Prudente (state of Sao Paulo), obtained in 2017 and 2018.

Parameters	PH	DBS	DCH	NEL	TLL	LPR	TDAP	RCI
$\hat{\sigma}_a^2$	0.073	0.672	0.081	0.152	0.026	0.018	0.532	1.565
$\hat{\sigma}_e^2$	0.273	3.279	11.716	0.700	0.1490	0.105	1.916	7.274
$\hat{\sigma}_f^2$	0.352	4.025	11.797	0.867	0.176	0.124	2.458	8.876
$\hat{h}_a^2$	0.209 ± 0.098	0.167± 0.088	0.057± 0.051	0.1757 ± 0.090	0.147 ± 0.083	0.144 ± 0.082	0.216± 0.100	0.176 ± 0.090
C^2parc	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.001
C^2int	0.015	0.0168	0.111	0.015	0.005	0.005	0.002	0.003
$\hat{h}_{mp}^2$	0.635	0.576	0.215	0.593	0.567	0.562	0.666	0.616
$\hat{r}_{aa}$	0.797	0.759	0.463	0.770	0.753	0.750	0.8161	0.784
$\hat{h}_{ad}^2$	0.168	0.133	0.049	0.140	0.115	0.113	0.172	0.138
rg_{loc}	0.774	0.712	0.114	0.745	0.874	0.876	0.949	0.931
G_s	19.64	35.19	12.01	26.43	12.51	11.11	37.27	38.12
$\bar{x}$	3.49	22.43	9.05	6.62	2.35	1.88	15.81	47.84

Note. A: Pindorama, B: Presidente Prudente. PH: plant height, DBS: diameter at the base of the stipe, DCH: diameter of the stipe at chest height, NEL: number of expanded leaves, TLL: total leaf length, LPR: length of the pinnate region, TDAP: thorn density on the abaxial face of the pinna, RCI: relative chlorophyll index. $\hat{\sigma}_a^2$= individual additive genetic variance; $\hat{\sigma}_e^2$ = residual variance; $\hat{\sigma}_f^2$ = phenotypic variance; $\hat{h}_a^2$ = heritability at the level of individual plants in the narrow sense; C^2parc= coefficient for determining the effects of the parcel; C^2int =*coefficient of determination of the effects of genotype × environment interaction* $\hat{h}_{mp}^2$= heritability of the average of progenies, assuming complete survival; $\hat{r}_{aa}$ = accuracy of progeny selection, assuming complete survival; $\hat{h}_{ad}^2$ = additive heritability within progenies; rg_{loc} = genotypic correlation between progeny performance in different environments; G_s = predicted gain with selection; $\bar{x}$ = overall average of the experiment.

Moderate values of the estimates of average heritability ($\hat{h}_{mp}^2$), selective accuracy ($\hat{r}_{aa}$), and genotypic correlation (*rgloc*) were found for the diameter at breast height (0.215, 0.463, and 0.114, respectively), while the thorn density on the abaxial face of the pinna was the trait with the higher values for the same estimates (0.666, 0.8161, and 0.949, respectively). The genetic gain with the predicted selection (G_s%) considering the selection of the 10% best genotypes in both locations, ranged from 11.11% (leaf blade length) to 38.12% (relative chlorophyll index) (Table 4).

The highest values of correlation between variables were estimated for leaf blade length × total leaf length (r = 0.95), plant height × number of expanded leaves (r = 0.80), and plant height × diameter at the base of the stipe (r = 0.73), meaningfulness at 5 and 1% probability by t test. The traits of the number of expanded leaves × diameter at the base of the stipe (r = 0.66), plant height × total leaf length (r = 0.54), and diameter at the base of the stipe × total leaf length (r = 0.50) showed moderated correlation values, while the other analyzed traits showed weak correlations (Table 5).

Table 5. Estimates of the phenotypic correlation coefficient between morphological traits of 19 open pollination progenies of *A. aculeata* cultivated in experimental fields implanted in 2013 in the municipalities of Pindorama and Presidente Prudente (state of Sao Paulo). Average data from two years of evaluation, 2017 and 2018.

Traits	DBE	DAP	NFE	CTF	CLF	DEAB	IRC
PH	0.73^{**}	0.60^{**}	0.80^{**}	0.54^{**}	0.49^{**}	-0.05^{ns}	-0.04^{ns}
DBS	**1.00**	0.52^{**}	0.66^{**}	0.50^{**}	0.47^{**}	-0.03^{ns}	0.06^{ns}
NEL		**1.00**	0.46^{**}	0.38^{**}	0.34^{**}	-0.19^{**}	-0.28^{**}
DCH			**1.00**	0.36^{**}	0.34^{**}	0.00^{ns}	-0.03^{ns}
TLL				**1.00**	0.95^{**}	-0.16^{**}	-0.00^{ns}
LPR					**1.00**	-0.16^{**}	0.01^{ns}
CLF						**1.00**	0.09^{ns}

Note. * and ** Significant at 5 and 1% probability by t test, respectively. PH: plant height, DBS: diameter at the base of the stipe, DCH: diameter of the stipe at chest height, NEL: number of expanded leaves, TLL: total leaf length, LPR: length of the pinnate region, TDAP: thorn density on the abaxial face of the pinna, RCI: relative chlorophyll index.

DISCUSSION

Analysis of the observed phenotypic variation

High phenotypic variation was observed for all descriptors analyzed, both within and between progeny averages (Fig. 1), which allows us to suppose that the selection for the most important agronomic traits can be conducted. This type of response is expected in open-pollinated tree species with a low degree of domestication (Aguiar et al. 2019), like *A. aculeata*. Expressive variation for morphological traits in *A. aculeata* was also observed by several authors (Coelho et al. 2019; Domiciano et al. 2015).

The breeding program conducted with the *Acrocomia* palm at Campinas Agronomic Institute (IAC) considers fruit traits, like mass per plant and oil content, the main characteristics targeted for genetic selection and breeding, exploring the variation of other botanical traits can be very useful for crop management. However, other characteristics such as height and number of thorns are also important, especially for the management of plants in the field, facilitating the harvest when lower and avoiding work accidents when with low thorns.

Genetic parameters by location

Our study did not identify significant differences for any of the evaluated traits between the progenies when considering each location separately, indicating low variability present in individual analyzes (Table 1). The lack of significance for progenies with morphological data in the juvenile stage is reported in other palm tree species. In an experiment with open pollination progeny of açaí (*E. oleracea*) in the juvenile stage, Farias Neto et al. (2012) and Navegantes et al. (2018) did not identify significant differences between progenies for the number and total leaf length, plant height, and stipple circumference traits. According to Dransfield et al. (2008), palm trees have short internodes at the beginning of development, and, as they get age, the differences between the length of these internodes become more evident. This effect occurs due to the fact that many palm tree species carry out the complete development of their root system in the juvenile phase, followed by the growth of the aerial part afterward.

Another important genetic variability indicator to be explored for breeding purposes is the coefficient of genetic variation for the trait. According to Farias Neto et al. (2013), this coefficient is directly proportional to the genetic variance and should be equal to or greater than the coefficient of the environmental or residual variation in the analysis of variance. Results show higher values of the residual variation coefficient compared with the genetic variation coefficient, indicating that the estimated average values were highly influenced by the environment. In this study, it was observed moderate values of the estimated genetic variation coefficient for plant height and stipe diameter traits in Presidente Prudente (CV_{gi}%= 13.97 and CV_{gp}%= 6.988) and in Pindorama (CV_{gi} %= 10.151 and CV_{gp} =5.075) (Table 3). These values were close when compared to the research with *A. aculeata* performed by Rosado et al. (2019), who obtained CV_{gi}%= 15.27 and CV_{gp}%= 7.08 for plant height, and CV_{gi}%= 10.15 and CV_{gp}%=5.07 for the stipe diameter.

It was observed that the values of the individual genetic variation coefficient for the evaluated traits was higher than the same coefficient when calculated for the average of progenies (Table 2). When Martins et al. (2001) analyzed the variables plant height and diameter at breast height for *Eucalyptus grandis*, and Sampaio et al. (2000) studied data on volume and shape of the top tree shaft and the survival of *Pinus caribaea*, they verified higher gain estimates with the selection between and within progenies, thus exploring individual genetic variation through CV_{gi} and genetic variation of progenies through CV_{gp}.

Genetic parameters based on joint analysis

The joint analysis was performed with average data from 19 progenies common to both sites and considering the two-year evaluation. With the exception of the total leaf length, a significant contrast for all other evaluated traits was observed, as shown in the deviance (LRT^1) values in Table 2, which demonstrates the possibility of selection for the analyzed traits. Significant deviance values of the joint analysis as opposed to nonsignificant values for the individual analyzes in both locations (Presidente Prudente and Pindorama) is explained by the greater expression of the genetic variance in the joint analysis, validated by the superior values of average and individual heritability of progenies in the joint analysis (Table 4).

The experimental quality in mixed models is indicated by the coefficient of determination of the plot effects, which also measures the environmental variation between plots within blocks. High C^2parc values mean high variability between plots within the blocks and high environmental correlation between observations within the plot. The results obtained from the joint analysis demonstrate the low environmental variation between the plots, which indicates the correct choice of the experimental model adopted in the present study (Resende 2002).

The most expressive values of heritability in the restricted sense at the individual level were found for thorn density on the abaxial face of the pinnas ($\hat{h}_a^2$ = 0.216), plant height ($\hat{h}_a^2$ = 0.209), relative chlorophyll index ($\hat{h}_a^2$ = 0.176), number of expanded leaves ($\hat{h}_a^2$ = 0.176), and diameter at the base of the stipe ($\hat{h}_a^2$ = 0.167), which can be considered promising for obtaining genetic gains (Table 4). Values of moderate to low magnitude for heritability ($\hat{h}_{mp}^2$) are expected for quantitative traits, usually controlled by a large number of genes with reduced individual effects and with strong environmental interference (Borem 1997).

Heritability in the strict sense corresponds to the proportion of the additive genetic variability in relation to the total phenotypic variation observed in the investigated traits. According to Assis and Resende (2011), heritability values below 0.15 are classified as "low", values from 0.15 to 0.50 are considered as "moderate", and above 0.50 are classified as "high". This parameter is of great relevance for selection because the alleles and their effects fully advance to the following generations (Carvalho et al. 2001). In a study conducted with *A. aculeata*, Domiciano et al. (2015) found the heritability value of 0.50 for total plant height; Table 4 shows the results of the present study (0.635). Evaluating the same species, Manfio et al. (2012) estimated heritability values of 0.87 for the plant growth and 0.48 for the number of leaves emitted, both considered of high and moderate magnitude, respectively. The difference between the heritability estimated here with the other authors is due to the number of genotypes analyzed and their origin from different locations.

According to Falconer and Mackay (1995), the values of the genetic parameters can vary according to the populations, environments, and the estimation methods used. Studying different palm trees species of Arecaceae, Carvalho et al. (2008) and Farias Neto et al. (2007) obtained heritability values of 0.90 and 0.24, respectively, for the leaf number trait in *E. oleracea*. Bovi et al. (2004) found a lower value of 0.10 for the same trait in *Bactris gasipaes*. In *E. oleracea*, the average heritability of progenies for plant height obtained by Farias Neto et al. (2012) was 0.64, close to the findings of this study ($\hat{h}_{mp}^2$ = 0.63) (Table 4). In contrast, Yokomizo et al. (2016) found a lower value of heritability ($\hat{h}_{mp}^2$ = 0.23) for plant height also in E. oleracea. These results indicate that there is a great variation in heritability for agromorphological traits within the Arecaceae family. Specifically, for the plant height, the heritability values of are very dependent on the plant vegetative stage (Rochon et al. 2007).

Selective accuracy ($\hat{r}_{aa}$) is indicative of the quality of information and procedures adopted to predict genetic values. This measure considers the correlation between predicted genetic values and individuals' real genetic values (Resende 2002). The greater is the selective accuracy of a trait, the greater is the evaluation reliability and the value predicted for the individual. In the range from 0.1 to 0.4, the selective accuracy is considered low; from 0.4 to 0.7 is median, and higher than 0.7 is considered high (Assis and Resende 2011). Selective precision values higher than 0.7 for all evaluated traits, except for diameter at breast height, with a value of 0.463 were observed (Table 4).

The values of selective accuracy indicate a favorable condition for obtaining genetic gains from agronomic interest traits studied. The possibility of gathering these agronomically favorable traits through genetic recombination in individuals with complementary traits leads the idea of obtaining more competitive ideotypes for the species. Due to the variations found and the promising values of heritability, the attainment of small-size plants (below 5 m), with leafy canopy (above 27 leaves), thick stipe (above 116 cm), and a lower density of thorns, among other characteristics that will be analyzed in the future, such as fruit production and oil content, can be idealized.

The predicted genetic gain was significant for the following variables: relative chlorophyll index (G_s% = 38.12), diameter at the base of the stipe (G_s% = 35.19), and the number of expanded leaves (G_s% = 26.43), as a result of the joint analysis. The relative chlorophyll index, an important trait for representing the greatest expected gain, can be used for the selection of progenies that present a better response to nitrogen fertilization, since it provides quick diagnosis of the nutritional status in relation to the nitrogen content (Argenta et al. 2004).

The highest correlation values were found for traits associated with plant vigor, such as leaf blade length × total leaf length ($r = 0.95$), total plant height × number of expanded leaves ($r = 0.80$), and total plant height × diameter at the base of the stipe ($r = 0.73$). In *E. oleracea*, a high magnitude correlation between plant vigor traits was detected over a three-year evaluation, suggesting the possibility of adopting early selection (Farias Neto et al. 2012). Also, in *E. oleracea*, Oliveira et al. (2000) found that the stipe diameter and the number of live leaves were correlated with production traits, enabling early selection for the species. In *Archontophoenix alexandrae*, significant positive correlations were found between vegetative traits, such as stipe diameter, plant height, number of leaves, and the fourth sheet length, with direct components of palm heart production (Uzzo et al. 2002). In addition, it was found that these correlations are valid since the beginning of cultivation, indicating the possibility of early selection of superior plants for the fruit production on the stipe diameter, the height, and the number of tillers (Bovi et al. 1990).

For the oil palm (*E. guineensis*), it was not found a correlation between plant height and higher fruit production (Rafii et al. 2013). On the other hand, there is still no literature showing a genetic association between plant vigor and fruit production in macaúba palm. The existence of a correlation between vegetative traits and fruit production is very desirable, especially for those with higher heritability. As a rule, later traits with measurement difficulties, like fruit production and/or with low heritability, can be considered in the selection activities based on high heritability traits and with a high correlation among them (Souza et al. 1998). This strategy allows the breeder to make progress with the use of indirect selection, saving time, effort, and money. In this study, the relative chlorophyll index was the trait with the highest heritability; however, with a low correlation with the other evaluated traits. Domiciano et al. (2015) observed that macaw palm accessions of lower height fix atmospheric CO_2 with the same efficiency as tall plants, corroborating these results.

CONCLUSION

Most of the evaluated traits have considerable genetic variability, revealing a favorable situation for the breeding of *A. aculeata*.

Combined selection between and within progenies is indicated to obtain superior genetic gains by selection.

High estimates of accuracy and high genetic gains predicted in both experimental fields indicate the formation of seed orchards through the negative selection of plants with undesirable characteristics for the composition of an ideotype for the species.

AUTHORS' CONTRIBUTION

Conceptualization: Lustri E. A., Colombo C. A., Siqueira W. J. and Azevedo Filho J. A.; **Methodology:** Lustri E. A., Colombo C. A. and Siqueira W. J. **Formal analysis:** Lustri E. A., Colombo C. A., Siqueira W. J. and Viana S. A.; **Investigation:** Lustri E. A., Colombo C. A. and Siqueira W. J.; **Project administration:** Colombo C. A.; **Resource:** Colombo C. A.; **Writing – original draft:** Lustri E. A., Colombo C. A., Siqueira W. J. and Azevedo Filho J. A.; **Writing – review editing:** Lustri E. A.; Siqueira W. J., Azevedo Filho J. A. and Viana S. A.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

FUNDING

Fundação de Amparo à Pesquisa do Estado de São Paulo
[https://doi.org/10.13039/501100001807]
Grants No. 2014/23591-7; 2017/20381-0

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
[https://doi.org/10.13039/501100002322]
Finance Code 43415985890

ACKNOWLEDGMENTS

We thanks to Dr. Antonio Lúcio Mello Martins (Regional Center North Center in Pindorama) and Dr. Nobuyoshi Narita (Polo Regional Alta Sorocabana in Presidente Prudente) for the maintenance of the respective experimental fields.

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