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Quantitative genetic characterization of an *in vivo* germplasm collection of *Hymenaea stigonocarpa* Mart. ex Hayne

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Abstract: *Hymenaea stigonocarpa ("jatobá-do-cerrado") is a fruit species native to the Brazilian Cerrado indicated as a priority for research and sustainable exploitation. The present study aimed to characterize the accessions and evaluate the magnitude and distribution of the genetic variability of an in vivo germplasm collection of this species. The experimental material consisted of 336 accessions, from 119 maternal progenies, from 24 subpopulations, sampled over a wide area in the Cerrado. The traits plant height, stem diameter, number of branches and number of leaves were evaluated based on 11 measurements, over 28 months. The growth dynamics varied over time, with greater development in the rainy season. There was a significant difference among subpopulations for all growth traits, showing the potential for selection among provenances in a breeding program. The structuring of quantitative genetic differentiation among subpopulations is compatible with the variation expected by genetic drift, with no sign of divergent selection.*

Keywords: *Fabaceae, genetic resource, native fruit, jatobá, genetic structure*

INTRODUCTION

The advance of agricultural production in the Brazilian Cerrado has resulted in the continued suppression of extensive areas of native vegetation (Jepson 2005, Diniz-Filho et al. 2009). In this scenario, there is a risk of definitive loss of genetic material present in the remnants, which justifies studies of natural variability as a basis for conservation and breeding strategies. Studies with fruit species from the Cerrado have shown high genetic variability with structuring among populations, which can be used as support in actions of collection, management and exploitation of genetic resources (Diniz-Filho et al. 2009, Ganga et al. 2009, Moura et al. 2013, Almeida Junior et al. 2014, Collevatti et al. 2018, Almeida et al. 2019, Chaves et al. 2020).

The great biodiversity of plant resources in the Cerrado biome is exploited in different ways, especially as a source of food. Native fruits are consumed fresh or processed, with potential for exploitation in integrated agricultural, livestock and forestry production systems, feeding livestock and fauna (Silva et al. 2001, Chaves 2006). *Hymenaea stigonocarpa* Mart. ex Hayne, known as "jatobá-do-cerrado", is a tree species of the Fabaceae family with potential for exploitation for fruit production, in addition to medicinal properties (Sano et al. 2016). The

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species list of the Flora do Brasil 2020 project recognizes two botanical varieties within the species: *H. stigonocarpa* var. *stigonocarpa* and *H. stigonocarpa* var. *brevipetiolata* (Pinto et al. 2020). A more recent study recognizes *H. brevipetiolata* as a distinct species from *H. stigonocarpa*, both as monophyletic taxa (Pinto et al. 2023). Some studies for the genetic characterization of accessions and subpopulations of *H. stigonocarpa* have already been carried out, using molecular markers or morphological traits of fruits and seedlings (Braga et al. 2019, Gonçalves et al. 2019, Castro et al. 2021). One of these works resulted in the implementation of an *in vivo* germplasm collection with maternal progenies from 24 subpopulations (local populations) covering a large part of the Brazilian Cerrado (Castro et al. 2021). This collection has an effective population size considered satisfactory for use in breeding programs, being representative of the genetic variability of the species (Gonçalves et al. 2019).

For the sustainable exploitation and conservation of plant genetic resources, decision-making must be guided based on knowledge about the evolutionary process of the species and the structure of genetic diversity among and within subpopulations, as they provide information about the levels of genetic variability available for breeding and conservation programs (Telles et al. 2001, Moura et al. 2013, Lima et al. 2017, Boaventura-Novaes et al. 2018). The present work aimed at the characterization of the quantitative genetic variation of initial growth traits in a germplasm collection of *H. stigonocarpa*, as a support to the conservation and genetic improvement of the species.

MATERIAL AND METHODS

The work was carried out in the *in vivo H. stigonocarpa* germplasm collection of the Federal University of Goiás, located at Goiânia, Goiás, Brazil (lat 16º 35’ 58.19’’ S, long 49º 16’ 57.10’’ W, alt 719 m asl). The climate of the region is Aw, according to Köppen’s classification, typical of the Brazilian Cerrado region, with a rainy season from October to April and a dry season from May to September (Lobato 2016). The soil at the site is a *Latossolo vermelho escuro distrófico* (Oxisol) (Embrapa 1999).

The germplasm collection was implemented in 2013, in a complete randomized block design, with 120 progenies (treatments), with one plant per plot spaced 2.5 m x 3.0 m and four replications (blocks), totaling 480 plants (Castro et al. 2021). Mother plants were sampled in 24 provenances, with six mother plants per subpopulation, in a wide area of the Cerrado biome in the states of Goiás, Mato Grosso do Sul, Mato Grosso, Tocantins, Bahia and Minas Gerais (Table 1). Due to germination failures and seedling losses in the nursery, only 120 progenies out of 144 collected were transplanted to the field, with an unbalanced number of progenies per subpopulation. At each collection site, mother plants were selected according to the aspect of fruit production, and at least ten fruits per plant were collected.

Experimental data were collected in the initial development phase, in 336 individual remaining accessions, from 119 maternal progenies, assumed to be half-siblings. Eleven measurements were carried out, seven from January to July 2015, four in the months of September, November 2015, February and April 2016. In each individual accession, the following growth traits were evaluated: plant height, stem diameter at 10 centimeters from the soil level (mm), number of primary branches and total number of leaves. From the plant height and stem diameter data, the height growth rate (HGR – cm/30 days) and the stem diameter growth rate (DGR – mm/30 days) were estimated by the slope of the regression line as a function of time. The values obtained, together with the data of the trait final plant height (FPH) and final stem diameter (FSD), obtained in the eleventh reading, were used for analysis. The average data by measuring date were used for the graphic representation of plant growth dynamics.

The estimates of variance components and derived genetic parameters were obtained by the restricted maximum likelihood procedure (REML). The analyses were performed using the free software R (R Core Team 2022), with the “lmer” function of the “lme4” package, considering all variable effects as random. Two analysis models were used, the first with the total effect of progenies according to a randomized complete block design and, sequentially, the effect of progenies was hierarchically decomposed into the effects of subpopulations and progenies within subpopulations. The significance of the estimates of the variance components of each effect was checked using the Likelihood Ratio Test (LRT).

The estimates of the genetic parameters were obtained using the estimators: $\hat{\sigma}^2_{f_{prog}} = \hat{\sigma}^2_{p/s} + \hat{\sigma}^2_{s} + \frac{\hat{\sigma}^2_{e}}{k_1}$; $\hat{\sigma}^2_{f_{ind}} = \hat{\sigma}^2_{p/s} + \hat{\sigma}^2_{s} + \hat{\sigma}^2_{e}$; $\hat{h}^2_{prog} = \frac{\hat{\sigma}^2_{p/s} + \hat{\sigma}^2_{s}}{\hat{\sigma}^2_{f_{prog}}}$; $\hat{h}^2_{ind} = \frac{4\hat{\sigma}^2_{p/s} + \hat{\sigma}^2_{s}}{\hat{\sigma}^2_{f_{ind}}}$, where: $\hat{\sigma}^2_{prog}$: phenotypic variance among progeny means; $\hat{\sigma}^2_{f_{ind}}$: phenotypic variance at the individual level; $\hat{h}^2_{prog}$: heritability coefficient at the progeny means level; $\hat{h}^2_{ind}$: heritability coefficient at the individual

Table 1. Collection locations (provenances) of *Hymenaea stigonocarpa* populations in the Brazilian Cerrado and mean values of the traits height growth rate (HGR – cm/30 days), stem diameter growth rate (DGR – mm/30 days), final plant height (FPH – cm) and final stem diameter (FSD – mm)

Municipality (State)	**Latitude** (S)	**Longitude** (W)	**HGR**	**DGR**	**FPH**	**FSD**	**Sum of ranks**
Cuiabá (MT)	05° 23′ 40″	55° 59′ 18″	2.17	0.54	78.13	16.25	43
General Carneiro (MT)	15° 34′ 45″	53° 01′ 11″	2.27	0.53	69.98	14.15	64
Jussara (GO)	15° 56′ 04″	51° 12′ 54″	2.66	0.49	74.68	13.43	67
Jaraguá (GO)	15° 38′ 19″	49° 18′ 03″	2.38	0.49	70.93	13.43	80
Porangatu (GO)	13° 16′ 18″	49° 07′ 52″	2.43	0.47	73.21	13.29	80
S. M. do Araguaia (GO)	13° 05′ 56″	50° 13′ 24″	2.75	0.54	78.42	14.24	35
Mozarlândia (GO)	14° 46′ 26″	50° 32′ 20″	2.58	0.51	77.91	13.95	58
Bom Jardim (GO)	16° 07′ 49″	52° 10′ 04″	2.25	0.49	68.66	12.96	89
Água Boa (MT)	14° 24′ 49″	52° 13′ 36″	2.38	0.49	68.79	13.03	82
Pedro Gomes (MS)	17° 44′ 31″	54° 44′ 44″	2.74	0.54	76.07	13.80	47
Bandeirantes (MS)	19° 52′ 38″	54° 22′ 17″	3.03	0.54	81.47	14.28	22
Ribas do R. Pardo (MS)	20° 27′ 36″	52° 55′ 42″	2.58	0.53	74.75	14.99	47
Selvíria (MS)	20° 27′ 07″	51° 30′ 05″	2.75	0.59	79.33	15.65	23
Aporé (GO)	18° 45′ 26″	52° 04′ 24″	3.05	0.58	79.96	15.34	18
Urutaí (GO)	17° 25′ 30″	48° 04′ 27″	2.93	0.53	81.14	14.19	37
Paracatu (MG)	17° 08′ 37″	46° 57′ 15″	2.93	0.55	82.72	14.66	22
Buritizeiro (MG)	17° 24′ 32″	45° 05′ 23″	3.02	0.53	83.05	14.16	31
Bonfinópolis (MG)	16° 23′ 50″	45° 59′ 05″	3.22	0.52	84.86	13.74	34
São Desidério (BA)	12° 35′ 44″	45° 54′ 04″	2.96	0.53	78.01	13.57	45
Monte Alegre (GO)	13° 16′ 00″	46° 54′ 50″	2.14	0.43	64.72	12.34	96
Planaltina (GO)	15° 10′ 19″	47° 37′ 11″	2.60	0.49	75.42	13.64	65
Araguari (MG)	18° 38′ 55″	47° 59′ 02″	2.67	0.53	72.32	13.93	59
Bambuí (MG)	20° 05′ 31″	45° 58′ 21″	2.88	0.48	83.83	13.65	50
Perdizes (MG)	19° 23′ 29″	47° 20′ 06″	3.35	0.60	87.11	15.47	6

level: $\hat{\sigma}^2_{p/s}$: genetic variance among progenies within subpopulations; $\hat{\sigma}^2_s$: genetic variance among subpopulations; $\hat{\sigma}^2_e$: residual variance; k_1: number of replications approximated by the harmonic average of the number of replications of each progeny.

From the components of variance the following statistics were calculated: Coefficient of genotypic variation ($CV_g = \frac{\hat{\sigma}^2_{p/s}}{\hat{m}} \cdot 100$), with m being the overall mean of the experiment; residual coefficient of variation ($CV_e = \frac{\hat{\sigma}^2_e}{\hat{m}} \cdot 100$), where $\hat{\sigma}^2_e$ is the residual standard error; selective accuracy [$SA = (1 - 1/F)^{1/2}$], where the Snedecor F is the variance ratio for the effects of treatments (progenies) (Resende and Duarte 2007).

The gain from selection, as a percentage of the overall mean of the traits was estimated assuming selection intensities of 20% (selection differential equivalent to 1.4 standard deviations), half-sib progenies and maternal selection. The selection gains at individual level (GS_{ind}) and at progeny mean level (GS_{prog}) were obtained by the following estimators: $GS_{ind} = \frac{1.4\,\frac{(4\hat{\sigma}^2_{p/s} + \hat{\sigma}^2_s)/2}{\hat{\sigma}^2_{find}}}{\hat{m}} \cdot 100$ and $GS_{prog} = \frac{1.4\,\frac{(\hat{\sigma}^2_{p/s} + \hat{\sigma}^2_s)/2}{\hat{\sigma}^2_{prog}}}{\hat{m}} \cdot 100$. When assuming the maternal families as half-sib progenies, it is assumed that all the genetic variance among them is additive or epistatic additive x additive. This is an approximation, as the variance among means of subpopulations may contain some dominance effect associated with inbreeding due to structuring (Chaves et al. 2011).

The quantitative genetic differentiation among subpopulations, assuming reproduction by allogamy, was measured by the Q_{ST} parameter, which is an analogue of Wright's F_{ST}, estimated for each quantitative trait, using the estimator: $\hat{Q}_{ST} = \frac{\hat{\sigma}^2_s}{\hat{\sigma}^2_s + 2\hat{\sigma}^2_A}$, where: σ^2_s is the genetic variance among subpopulations and σ^2_A is the additive genetic variance within subpopulations estimated by $\hat{\sigma}^2_A = 4\hat{\sigma}^2_{p/s}$ (Spitze 1993, Chaves et al. 2020).

RESULTS AND DISCUSSION

At the time of the last data collection, 25 months after planting, 344 plants with aerial parts were observed, 71.6% of the 480 initial accessions. The observed reduction was due to accidental loss and death of the aerial part. Subsequently, regrowth of some plants was observed, with a survival rate of 73.5% four years after planting (Gonçalves et al. 2019). The observed regrowth can be attributed to root reserves, an adaptation for deep water absorption in the dry period and survival to recurrent fires (Hoffmann and Franco 2003). The germplasm collection can be considered representative of natural populations, which was confirmed in a study using microsatellite markers in the same collection, in which an effective population size of 54.9 and an allelic representativeness of 79.9% was estimated in relation to a study with a broad sampling in 32 natural populations (Braga et al. 2019, Gonçalves et al. 2019).

Great variations among accessions were observed in the traits of initial development of *H. stigonocarpa*, with coefficients of phenotypic variation greater than 30% for all traits and means of 76.7 cm in height and 14.0 mm in diameter in the last evaluation (Table 2). Some negative values were observed for plant height (HGR) and stem diameter (DGR) growth rates. This occurred in some accessions due to the death of the aerial part and the emergence of new shoots, which reduces plant height and stem diameter. This behavior is common in Brazilian Cerrado species, as a strategy for plant recovery after stresses due to fire, mechanical damage, predation or pest attack.

Table 2. Descriptive statistics at the individual level for the traits height growth rate (HGR – cm/30 days), stem diameter growth rate (DGR – mm/30 days), final plant height (FPH – cm) and final stem diameter (FSD – mm), at the *Hymenaea stigonocarpa* germplasm collection of Federal University of Goiás

Statistics	HGR	DGR	FPH	FSD
Minimum	-0.79	-0.37	11.80	2.06
Maximum	8.22	1.26	168.60	28.62
Mean	2.71	0.52	76.71	13.97
Standard deviation	1.46	0.25	30.48	4.66
Coefficient of variation (%)	53.65	47.75	39.74	33.32

The graph of the average height and stem diameter of the accessions over the 11 measurements (Figure 1) shows that the dynamics of plant growth is different, in the dry and rainy seasons, as expected. The initial growth of this

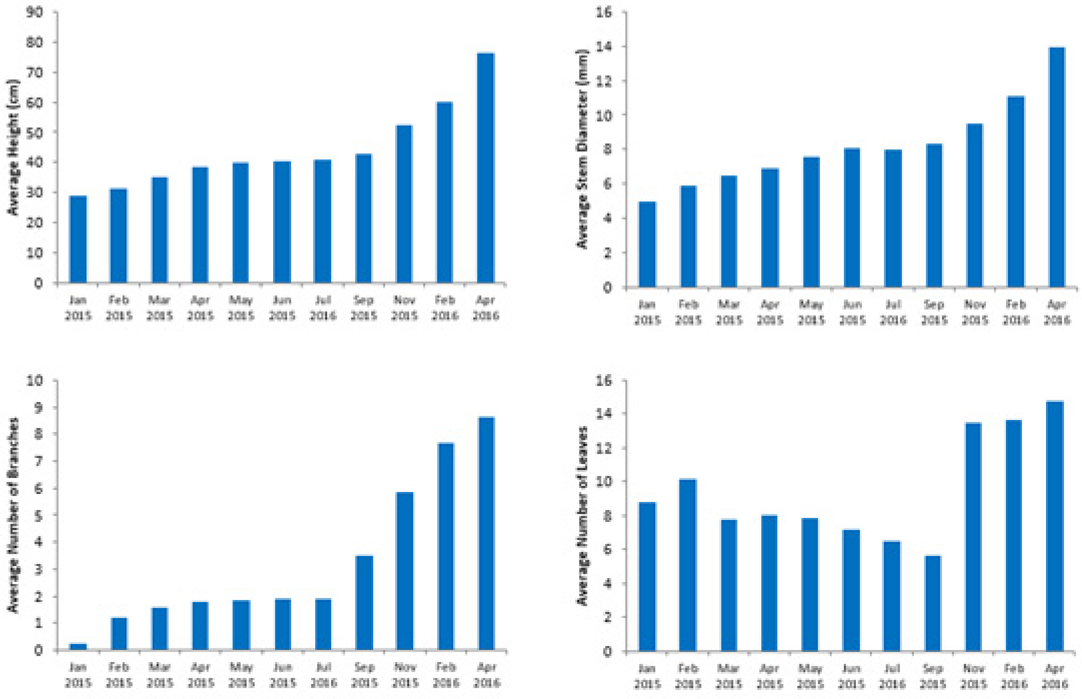

Figure 1. Growth in plant height, stem diameter, number of branches and number of leaves per plant. Means over the total accessions of the *Hymenaea stigonocarpa* germplasm collection of Federal University of Goiás.

species favors the formation of the root system to the detriment of the shoot, which also occurs with other species of the Brazilian Cerrado (Hoffmann and Franco 2003, Oliveira et al. 2006). This strategy of allocating a greater volume of photoassimilates to the root system, in the initial phase, is essential for the establishment of seedlings. The growth in height and diameter at the beginning of the second year of evaluation was greater than in the first year, as evidenced by the linear regression coefficient of the two periods (data not shown), even considering that the intervals between measurements were different.

The graphical analysis of the average number of branches (Figure 1) shows that the accumulation of branches was not linear during the evaluation period, with the emergence of new branches stopped between the months of April and September, which correspond to the dry season. The average number of leaves remained relatively constant from March to May, with a noticeable drop from June to September. At the beginning of the subsequent rainy season, the average number of leaves increased abruptly, remaining stable until February of the following year, followed by a perceptible growth until April 2016. The evident non-similarity between the number of leaves and the number of ramifications is indicative that *H. stigonocarpa* plants favor the emergence of new leaves at the beginning of the rainy season. During the evaluations, the constant emergence of new leaves at the end of the main stem was noticeable.

The diagnosis of the residual normality assumption, for purposes of deviance analysis and estimation of genetic parameters, indicated outlier values in all traits. For the number of branches and number of leaves the analysis was unfeasible. For the other traits, few discordant values were observed. In this analysis, the removal of outliers was followed by the continued emergence of new outliers. This fact can be attributed to the high dispersion of the values of the traits, which is frequent in plants native to the Cerrado biome. Removing these values could compromise the characterization of the subpopulations represented in the collection. For this reason, it was decided not to eliminate discordant observations.

Table 3. Estimates of variance components for the traits height growth rate (HGR – cm/30 days), diameter growth rate (DGR – mm/30 days), final plant height (FPH – cm) and final stem diameter (FSD – mm), at the *Hymenaea stigonocarpa* germplasm collection of Federal University of Goiás

Sources of variation	**Variance components**			
	HGR	**DGR**	**FPH**	**FSD**
Blocks	0.0878^{*}	0.0028^{**}	31.06^{*}	0.6770
Progenies	0.5656^{***}	0.0119^{**}	218.74^{***}	4.6680^{**}
Subpopulations	0.2861^{***}	0.0056^{*}	118.52^{**}	2.4351^{**}
Progenies/Subpop	0.2550^{*}	0.0060	86.20	2.0452
Error	1.5028	0.0470	696.12	17.1930

*, **, ***: significant at the 0.05, 0.01 and 0.001 levels, respectively, by the likelihood ratio test (LRT).

Table 4. Estimates of statistical genetic parameter for the traits height growth rate (HGR), stem diameter growth rate (DGR), final plant height (FPH) and final stem diameter (FSD), at the *Hymenaea stigonocarpa* germplasm collection of Federal University of Goiás

Parameter	**HGR**	**DGR**	**FPH**	**FSD**
CV_e (%)	45.18	41.97	34.40	29.68
CV_g (%)	27.11	20.86	18.65	15.15
h^2_{ind}	0.26	0.20	0.23	0.21
h^2_{prog}	0.45	0.36	0.39	0.36
SA	0.71	0.64	0.69	0.66
GS_{ind} (%)	23.57	16.55	14.09	11.43
GS_{prog} (%)	12.66	8.74	8.10	6.37
Q_{ST}	0.12	0.11	0.15	0.13

h^2_{ind}: heritability coefficient at the individual level; h^2_{prog}: heritability coefficient at the progenies level; CV_e: residual coefficient of variation; CV_g: genetic coefficient of variation among progenies; SA: selective accuracy; GS_{ind}: gain from selection at the individual level (20% selected individuals); GS_{prog}: gain from selection at the progeny level (20% selected progenies); Q_{ST}: quantitative divergence among subpopulations.

The deviance analysis and the likelihood ratio test (LRT) showed significant effects ($p < 0.05$ or $p < 0.01$) of the variance components for the set of progenies for all growth traits (Table 3). The hierarchical partition of the progeny effect showed significant variation among subpopulations for all traits. The means of the growth traits at the subpopulation level confirm this remarkable variation (Table 1). The variance among progenies within subpopulations was significant only for the height growth rate (HGR), showing a not significant additive genetic variance for the other traits. Of the total variance among progenies, about 50% is among subpopulations, which indicates a great structuring of quantitative genetic variability. This is indicative that the selection among subpopulations (provenances) must be effective for the improvement of *H. stigonocarpa* focusing on growth traits. The provenances that reached the lowest sum of ranks for the four growth traits were Perdizes – MG, followed by Aporé – GO, Paracatu – MG, Bandeirantes – MS and Selvíria – MS, in that order (Table 1).

Estimates of statistical genetic parameters showed a not discrepant pattern among the different traits (Table 4). The residual coefficients of variation (CV_e) were relatively high, ranging from 29.7% (FSD) to 45.2% (HGR). This behavior is common in tree species native to the Brazilian Cerrado (Trindade and Chaves 2005, Aguiar et al. 2009, Ganga et al. 2009, Almeida et al. 2019, Moura et al. 2013, Mota et al. 2020), increased by the use of single plant plots. The coefficients of genetic variation (CV_g) showed lower values than CV_e, even so, showing enough variability for selection.

The estimates of the heritability coefficient at the individual level ($\hat{h}^2_{ind}$) ranged from 0.20 (DGR) to 0.26 (HGR) (Table 4), values considered moderate (Ziegler and Tambarussi 2022). The heritability coefficients at the progeny means level ($\hat{h}^2_{prog}$) were about 1.7 times higher than the individual heritability for the four traits. The suitability of the set of accessions for selection is confirmed by the selective accuracy (*SA*) values, which ranged from 0.64 to 0.71. Selective accuracy is considered the best indicator of the quality of experiments for selection purposes, with the values found here in the limit between moderate ($0.50 \leq SA < 0.70$) and high ($0.70 \leq SA < 0.90$) classes (Resende and Duarte 2007).

The expected gains from selection, assuming a selection percentage of the 20% superior individuals or progenies, showed the potential of the germplasm collection as a base population for improvement aiming at initial growth traits (Table 4). The largest predicted gains, as a percentage of the overall mean, occurred for the height growth rate (HGR) both at the individual level (23.57%) and at the level of progeny means (12.66%). The genetic gain at the individual level was superior to the genetic gain at the progeny level for all traits. This is due to the fact that individual selection exploits the additive variance both among and within progenies. In addition, the use of single plant plots reduces the environmental control of genetic variation among plants within progenies that is confounded with variation among blocks. The pairwise genetic correlation coefficients among traits were all positive and of high magnitude, ranging from 0.61 (HGR with FSD) to 0.95 (HGR with FPH) (data not shown). Thus, selection based on the height growth rate, which had the highest expected genetic gain, should result in indirect gains for all traits. This information should be combined in the future with data of production and other agronomic attributes of the accessions for the selection of superior mother plants.

Q_{ST} values ranged from 0.11 (DGR) to 0.15 (FPH) (Table 4). The Q_{ST} parameter is analogous to Wright's F_{ST} and refers to the genetic differentiation among subpopulations as measured by quantitative traits (Spitze 1993). The derivation of the F_{ST} parameter considers a model of selective neutrality, with the differentiation among subpopulations being attributed to the balance between genetic drift and gene flow (Wright 1951). This parameter can be estimated using neutral molecular markers, and microsatellite markers (SSR) are the most used in this kind of study. As quantitative traits can be subject to selection, the comparison between the Q_{ST} parameter of each trait with the F_{ST} estimated with neutral markers provides information about the possible action of natural selection on the traits, which is relevant in evolutionary studies. Thus, $Q_{ST} > F_{ST}$ indicates the occurrence of divergent selection among subpopulations, $Q_{ST} < F_{ST}$ indicates uniform selection and $Q_{ST} \approx F_{ST}$ is compatible with the absence of selection, and the differentiation among subpopulations can be attributed to genetic drift (Spitze 1993, Chaves et al. 2020). Studying the same germplasm collection using nine microsatellite loci, Gonçalves et al. (2019) estimated a value of $\theta_p = 0.152$, θ_p being the F_{ST} version estimated via analysis of variance of allelic frequency (Weir 1996). The values found here for Q_{ST} are close to the F_{ST} value, indicating the absence of divergent selection for the studied traits, and these values are compatible with the differentiation caused by genetic drift only. For another fruit species native to the Brazilian Cerrado (*Eugenia dysenterica* DC), genetic drift was considered the main force shaping the genetic structure among subpopulations (Boaventura-Novaes et al. 2018). Also, for *Hancornia speciosa* Gomes, genetic drift was the main evolutionary force explaining the differentiation among subpopulations within botanical varieties, while the differentiation among botanical varieties was influenced by divergent selection in addition to drift (Chaves et al. 2020).

CONCLUDING REMARKS

The results of the present study attest to the usefulness of the in vivo germplasm collection of *H. stigonocarpa* as a base population for a breeding program for the species. The selection of individual accessions is more effective than the selection among progeny means. This encourages the use of the germplasm collection as a seed orchard, without thinning, to maintain the genetic variability conserved in the collection. Selection among subpopulations was effective for growth traits. It is recommended to carry out new collections in provenances with better average performance, with sampling of a greater number of mother plants, for later progeny testing. The provenances indicated as a priority for new collections are: Perdizes – MG, Aporé – GO, Paracatu – MG, Bandeirantes – MS and Selvíria – MS, in that order. The structuring of quantitative genetic differentiation among subpopulations is compatible with the variation expected by genetic drift, with no sign of divergent selection.

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