Special Supplement: *Cerrado* **[Brazilian Savanna]**

Genetic variability of the initial growth of *Eugenia dysenterica* DC.: implications for conservation and breeding[1]

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ABSTRACT

Eugenia dysenterica DC. is a native tree from the Brazilian Savanna known as a genetic resource for its fruits and culinary potential. The knowledge on the genetic variability of agronomic traits is important to support studies on its conservation and domestication. This study aimed to estimate the quantitative genetic parameters of initial growth traits among and within *E. dysenterica* subpopulations, in provenance and progeny testing, and establish a germplasm collection representative of the species distribution. For that, 25 natural subpopulations were sampled and, within each subpopulation, six mother trees. The progenies were sown in a nursery, in a randomized complete blocks design consisting of 150 progenies, four replications and five plants per plot. The analysis of variance of the initial development traits revealed a greater variability among the progenies within the subpopulation than that observed among the subpopulations. The aboveground biomass represented only 15 % of the total biomass, a recurrent characteristic in Brazilian Savanna species. The estimated heritability and coefficients of genetic variation presented selection potential for the initial development traits, which are important for commercial seedlings production. An *in vivo ex situ* germplasm collection was established for conservation and breeding purposes, using a sample of four plants from each progeny.

KEYWORDS: Cagaita, progeny test, Brazilian Savanna, genetic resources.

RESUMO

Variabilidade genética do crescimento inicial de *Eugenia dysenterica* DC.: implicações para conservação e melhoramento genético

Eugenia dysenterica DC. é uma árvore nativa do Cerrado conhecida como recurso genético por seus frutos e potencial culinário. O conhecimento da variabilidade genética de características agronômicas é importante para subsidiar pesquisas sobre a sua conservação e domesticação. Objetivou-se estimar os parâmetros genéticos quantitativos das características iniciais de crescimento entre e dentro de subpopulações de *E. dysenterica*, em teste de procedências e progênies, e estabelecer uma coleção de germoplasma representativa da distribuição da espécie. Para isso, 25 subpopulações naturais foram amostradas e, dentro de cada subpopulação, 6 árvores matrizes. As progênies foram semeadas em viveiro, em delineamento de blocos ao acaso constituído de 150 progênies, quatro repetições e cinco plantas por parcela. A análise de variância de caracteres do desenvolvimento inicial revelou maior variabilidade entre progênies dentro da subpopulação do que a observada entre as subpopulações. A biomassa acima do solo representou apenas 15 % da biomassa total, característica recorrente em espécies do Cerrado. A herdabilidade estimada e os coeficientes de variação genética apresentaram potencial de seleção para os caracteres de desenvolvimento inicial, importantes para a produção comercial de mudas. Uma coleção de germoplasma *in vivo ex situ* foi estabelecida para fins de conservação e melhoramento, utilizando-se uma amostra de quatro plantas de cada progênie.

PALAVRAS-CHAVE: Cagaita, teste de progênies, Cerrado, recursos genéticos.

INTRODUCTION

Eugenia dysenterica DC., Myrtaceae, is a fruit tree species with potential for commercial exploitation as processed or fresh food (Araújo et al. 2019), as well as a source of bioactive components (Justino et al. 2020). Its fruit, known as cagaita, is harvested by local collectors in the *Cerrado* biome (Brazilian Savanna) (Guéneau et al. 2020), a global conservation hotspot (Myers et al. 2000).

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There is a growing market demand for native socio-biodiverse products such as cagaita. However, the expansion of the production chain is limited by problems such as obtaining raw material in a sustainable manner (Guéneau et al. 2020). Conservation and domestication strategies are essential to avoid the predatory extraction and encourage the commercial exploitation of the species. Due to its high genetic variability and fruit yield, *E. dysenterica* is a good target for breeding programs (Aguiar et al. 2009).

Although the species is allogamous (Rodrigues et al. 2016), it also exhibits self-compatibility, with the self-fertilization of some seeds confirmed by manual pollination (Proença & Gibbs 1994). Its flowering strategy is synchronous and abundant, with pollination performed mainly by bees (Proença & Gibbs 1994).

Regional studies have assessed the genetic variability of *E. dysenterica* for initial growth (plant height and stem diameter) (Trindade & Chaves 2005, Aguiar et al. 2009), with others investigating breeding purposes (Chaves et al. 2011, Silva et al. 2017, Novaes et al. 2018). However, there are no large-scale studies on initial growth traits with extensive sampling in the Brazilian Savanna.

Knowledge on the species' genetic variability for different growth traits is important for domestication purposes, to select economically beneficial genotypes, and for conservation, to visualize the diversity among families and access its genetic vulnerability. Genetic variability is essential to ensure the species' resistance to environmental changes. Genetic uniformity causes vulnerability in both cultivated and natural populations because it increases the chance of inbreeding depression and loss of alleles in each generation, and reduces the alternatives for natural or artificial selection. As such, studies on phenotypic traits in progeny tests are important for future predictions of genetic differentiation. Genetic variability is relevant, and the climate changes predicted for the coming decades highlight the importance of genetic resources conservation (Swarup et al. 2021).

Establishing native fruit germplasms of species threatened by anthropic pressure is the foundation for exploring genetic diversity and necessary for domestication and conservation (Diniz-Filho et al. 2020). The Universidade Federal de Goiás (UFG) (Goiânia, Goiás state, Brazil) has an *in vivo E. dysenterica* collection, sampled from 23 subpopulations in southeastern, northern and northeastern Goiás state (Trindade & Chaves 2005, Aguiar et al. 2009, Chaves & Telles 2010). Despite its importance, the collection contains no germplasm from other regions of the species' natural distribution.

This study aimed to assess the quantitative genetic variability for initial growth stages within and among *E. dysenterica* subpopulations, and compile a germplasm collection to support breeding and conservation programs for the species.

MATERIAL AND METHODS

Provenance and progeny tests were conducted using seeds sampled from 25 subpopulations across the species' distribution in the *Cerrado* biome (Figure 1). Six mother trees were sampled for each subpopulation, generating 150 open-pollinated progenies (maternal families). The collected fruits were transported from the field in a cooler box filled with ice chips and refrigerated for 5 to 15 days, until physical characterization of fruit and seed traits (Novaes et al. 2018). The seeds were then sown for a nursery experiment.

A completely randomized blocks design was used, with 150 treatments (maternal families). Four replicates and five seeds per plot were used for each treatment, resulting in 20 plants per progeny, totaling 3,000 planted seeds. Seeds were individually sown in 1 L plastic bags filled with a mixture of soil, sand and manure (1:1:1). The experiment was carried out from November 2011 to November 2013, in a nursery of the Universidade Federal de Goiás, in Goiânia, Goiás state, Brazil (16º36'S, 49º17'W and altitude of 736 m). The climate in the region is classified as Aw, according to the Köppen-Geiger system (Alvares et al. 2013), hot and semi-humid, with a well-defined dry season from May to September, with average annual temperature of 22.1 ºC, average minimum and maximum temperatures of 15.2 ºC and 30.4 ºC, respectively, and average annual rainfall of 1,495 mm (Casaroli et al. 2018). In the absence of rainfall, manual irrigation was performed. Weeds were removed manually when present.

The following traits were evaluated between 1 and 20 months after sowing (Table 1): emergence percentage, days to emergence, emergence speed, initial and final plant height, initial and final stem diameter, leaf length and width, and number of

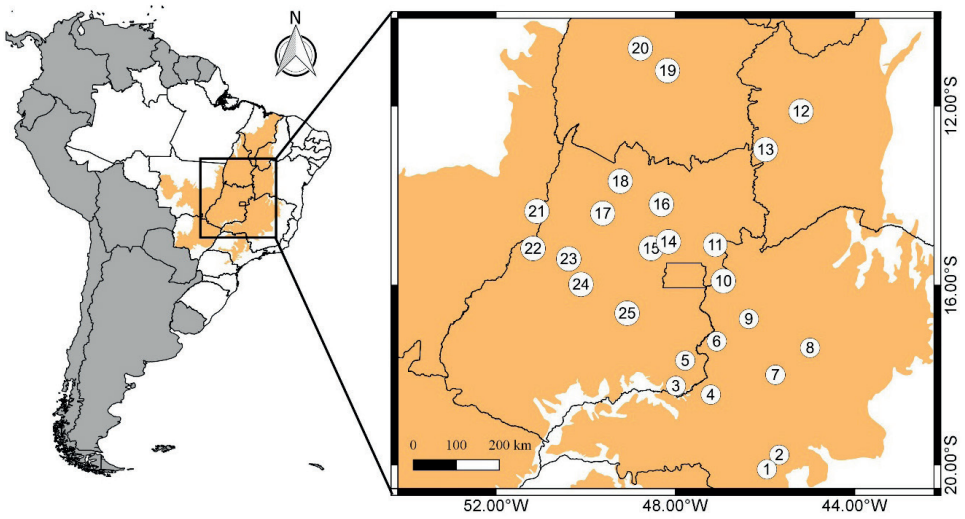

Figure 1. Location of 25 *Eugenia dysenterica* DC. subpopulations used in provenance and progeny testing. The lines indicate Brazilian states borders. The *Cerrado* biome (Brazilian Savanna) is highlighted in orange.

Table 1. Date of quantitative traits assessments in a progeny test of *Eugenia dysenterica* DC.

Trait	Date	Number of evaluations
Emergence percentage	15 Nov. 2011 to 15 Apr. 2012	3,000
Days to emergence	15 Nov. 2011 to 15 Apr. 2012	2,461
Initial plant height (cm)	01 Feb. 2012	2,419
Plant height (cm)	15 Feb. 2012	2,438
Plant height (cm)	29 Feb. 2012	2,451
Plant height (cm)	29 Mar. 2012	2,451
Plant height (cm)	02 May 2012	2,475
Plant height (cm)	18 June 2012	2,475
Plant height (cm)	30 Aug. 2012	2,464
Final plant height (cm)	30 Oct. 2012	2,476
Initial stem diameter (mm)	02 Feb. 2012	1,824
Stem diameter (mm)	16 Feb. 2012	2,387
Stem diameter (mm)	01 Mar. 2012	2,415
Stem diameter (mm)	30 Mar. 2012	2,452
Stem diameter (mm)	02 May 2012	2,470
Stem diameter (mm)	11 June 2013	2,475
Stem diameter (mm)	30 Aug. 2012	2,477
Final stem diameter (mm)	31 Oct. 2012	2,475
Leaf length (cm)	18 June 2012	4,862
Leaf width (cm)	18 June 2012	4,862
Number of leaves	18 June 2012	2,462
Root fresh mass (g)	22 Nov. 2012	566
Root dry mass (g)	24 Nov. 2012	562
Aboveground fresh mass (g)	22 Nov. 2012	566
Aboveground dry mass (g)	24 Nov. 2012	563
Root length (cm)	22 Nov. 2012	566
Shoot length (cm)	22 Nov. 2012	566

leaves. Diameter was determined using a digital caliper. Leaf and root height and length were obtained with a millimeter ruler and expressed in cm. The growth rates for plant height and stem diameter were estimated using the linear regression coefficient of the data obtained from eight measurements during the seedling development. At 12 months, the root fresh and dry mass, aboveground fresh and dry

mass, and root and shoot length were measured for each progeny, in four plants randomly chosen from different blocks. Next, assessments were carried out with 4 plants per plot. The leaf area was calculated according to Oga & Fonseca (1994) for *E. dysenterica*. The relationships among the traits were determined by the Spearman's correlation, with significance assessed using the Student's *t* test, including some fruit and seed traits from a previous study (Novaes et al. 2018).

The genetic parameters were estimated by analysis of variance, using the hierarchical model: $Y_{ijk} = \mu + s_i + f_{j(i)} + b_k + e_{k(ij)}$, where Y_{ijk} is the value of the variable *Y* from progeny *j*, within subpopulation *i* in block *k*; μ the general mean; s_i the random effect of subpopulation *i*, *i* = 1, 2, ..., S; $f_{j(i)}$ the random effect of progeny *j* within subpopulation *i*, *j* = 1, 2, ..., F_i; b_k the random effect of block *k*, *k* = 1, 2,..., B; and $e_{k(ij)}$ the experimental error. The coefficients of genetic variation and heritability were estimated for progenies within subpopulations. All the analyses were performed with scripts developed for the R software (R Core Team 2013).

The *in vivo* germplasm collection was compiled 24 months after sowing, with three plants from each progeny randomly selected from different blocks in the nursery. The experimental area consists of 3 x 2 m spacing in three completely randomized blocks, with one plant per block and 150 treatments. The soil is classified as a Red Latosol (Santos et al. 2018) or Typic Hapludox (USDA 2014), and the coordinates and climate are the same as those of the nursery. The representativeness of the germplasm collection was determined based on the effective population size, calculated using the appropriate model for the provenance and progeny design (Vencovsky et al. 2007) $N_e = 2D$, in which:

$$D = \theta_P \left[\left(\frac{1 + C_S^2}{S} \right) \left(\frac{S^*}{S^* - 1} \right) - \frac{1}{S^* - 1} - \frac{1 + C_m^2}{M} \right] + \theta_M \left(\frac{1 + C_m^2}{M} - \frac{1}{N} \right) + \frac{1 + F}{2N}$$

where θ_P is the genetic divergence among subpopulations, equivalent to the Wright's F_{ST}; θ_M the remote coancestry coefficient of individuals within progenies and subpopulations, calculated as $\theta_M = \theta'_M + \theta_P (1 - \theta'_M)$; θ'_M the recent coancestry coefficient among individuals within families; *N*, *M* and *S* the total number of plants, families and subpopulations, respectively; *F* the total fixation index equivalent to the Wright's F_{IT}; C_S and C_m the number of plants and coefficients of variation per subpopulation and family, respectively; S^* the supposed number of subpopulations in nature, considered $S^* \approx \infty$ for *E. dysenterica*, making $[S^*/(S^* - 1)] = 1$ and $1/(S^* - 1) = 0$. The molecular genetic parameters for the Wright´s equivalents were estimated in a previous study ($F = 0.3215$; $\theta_p = 0.198$; $\theta_{m'} = 0.153$), with a sample of the same seedlings (Boaventura-Novaes et al. 2018).

RESULTS AND DISCUSSION

The sources of variation differed significantly for emergence percentage, days to emergence and emergence speed (Table 2). The average germination percentage was 82 %. The literature reports several values for the emergence percentage of *E. dysenterica*, some of which were homogeneous among treatments (Oga et al. 1992, Mota et al. 2018) and others heterogeneous within a single subpopulation (Duarte et al. 2006), varying from

Table 2. Analysis of variance, coefficients of experimental variation (*CVe*), genetic variation (*CVg*) and heritability on a mean basis (h^2_m) for phenotypic growth traits of 25 subpopulations of *Eugenia dysenterica* DC. provenance and progeny testing.

Source of variation	DF	Mean square								
		EP	DE	ES	IH	FH	HR	ID	FD	DR
Blocks	3	306.91*	78.12^{ns}	0.003**	0.25^{ns}	18.01***	0.19***	0.046***	0.528***	0.007***
Subpopulations	24	455.14*	375.11*	0.012***	3.27***	13.42***	0.04***	0.052***	0.143***	0.001***
Progenies/subpopulations	123	256.02***	214.61***	0.006***	0.71***	2.33***	0.01*	0.016***	0.042***	0.0003**
Error	427	89.21	54.43	0.001	0.14	0.76	0.01	0.004	0.014	0.0002
Mean		82.03	32.13	2.93	2.29	4.53	0.25	0.89	1.13	0.01
CVe		4.75	3.44	18.15	40.28	40.63	39.81	16.20	20.57	110.66
CVg		21.16	17.35	1.22	21.29	14.16	9.26	6.20	7.55	26.56
h^2_m		0.82	0.65	0.86	0.80	0.68	0.23	0.75	0.66	0.36

*, **, *** and ^{ns}: p-value < 5 %, 1 % and 0.1 % and non-significant, respectively, by the F test. EP: emergence percentage; DE: days to emergence; ES: emergence speed; IH: initial height (cm); FH: final height (cm); HR: height growth rate; ID: initial diameter (cm); FD: final diameter (cm); DR: diameter growth rate.

80.6 (Souza et al. 2001) to 99 % (Mota et al. 2018). As shown in these articles, emergence percentages and number of days to emergence are homogeneous among the studies, even for different populations and environmental sowing conditions.

The seedling emergence began at 19 days after sowing. The latest emergence was observed at 198 days after sowing in the subpopulation 3 (Catalão, GO). In 42 days, 75 % of all the seedlings had emerged. Similar estimates have been reported for this trait in assessments conducted under different environments (Souza et al. 2001, Martinotto et al. 2007, Nunes et al. 2020). Studies testing different substrates (Souza et al. 2001, Nunes et al. 2020), presence of light and seed teguments *in vitro* (Martinotto et al. 2007) reported results comparable to those obtained here. The recalcitrant seeds and short period of favorable environmental conditions before the end of the rainy season resulted in an evolutionary investment in rapid seedling establishment. The fruits ripened between October and November, coinciding with the rainy season. Seedlings must be established by mid-April, when the dry season begins in the *Cerrado* biome. A previous study demonstrated that the uniform selection may be the cause of the homogeneity observed (Boaventura-Novaes et al. 2018).

The subpopulation sampling chronology was not related to germination percentage, confirmed by non-significant correlations with seed storage time (data not shown). Thus, the fruit storage conditions were adequate to preserve the seeds for 40 days without loss of viability. A low storage temperature was previously recommended by Farias Neto et al. (1991). Andrade et al. (2003) detected a complete loss of viability in *E. dysenterica* seeds at moisture levels between 18 and 22 %. Seed recalcitrance is a characteristic of several fruit species from the *Cerrado* biome, such as *Hancornia speciosa*, *Campomanesia adamantium*, *Eugenia klotzschiana*, *Mauritia flexuosa* and *Brosimum gaudichaudii* (Brasil 2016). As such, the storage methodology used here can be applied to seeds that are sensitive to desiccation, such as *E. dysenterica*.

The emergence speed, which reflects the germination vigor, is positively correlated with seed mass and longitudinal and transverse diameters (Figure 2). Larger seeds also exhibit a greater germination vigor. Since the seedling growth is slow and irregular in the field (Souza et al. 2002), an indirect selection of seeds with a greater mass may result in a faster seedling development. The heritability for emergence percentage (0.82) and days to emergence (0.65) (Table 2) suggest the possibility of selecting for genetic gains.

The coefficients of genetic variation (*CVg*) for emergence time and percentage were relatively high, when compared to the values obtained in cultivated species (Table 2). Fruit ripeness may also explain the variability observed in early seedling development. The fruits were harvested at different maturation stages, characterizing a maternal effect. This characteristic influenced the dormancy and initial development of another fruit from the same genus, namely *Eugenia uniflora* L. (Antunes et al. 2012).

For seedling height and stem diameter, there was a significant variability among the subpopulations and progenies within subpopulations (Table 2). On average, the subpopulation 23 (Britânia, GO) had the smallest seedlings, and the subpopulations 1, 2 and 21 (Bambuí, MG; Luz, MG; and Cocalinho, MT, respectively) the largest ones. The coefficient of genetic variation was higher for diameter than for height growth rate (Table 2). The higher the *CVg*, the better the traits' selection response. Thus, the initial height and stem diameter growth rates are more favorable for early selection. Trees typically take several years to complete a selection cycle, making it difficult for breeders. However, in the event of significant correlations between initial growth traits and yield, these indirect traits may be combined into an index that enables early selection (Padi et al 2012).

Maternal effects may have a considerable influence on estimating initial genetic variability, since both the seedling height and stem diameter were significantly and positively correlated with fruit and seed size and mass (Figure 2). Considering maternal effects, the accuracy of the genetic effects for fruit and seed traits may be lower, even in studies resulting from a progeny test (Roach & Wulff 1987), because the maternal genotype or phenotype may exert a causal influence on phenotypic variability in offspring. Given that the timing and amount of fruit production vary among *E. dysenterica* trees (Souza et al. 2013), it would be relevant to determine whether early plant growth and development are associated with fruit production, when they reach reproductive maturity.

Interestingly, the stem diameter growth rate was negative for 16.38 % of the progenies,

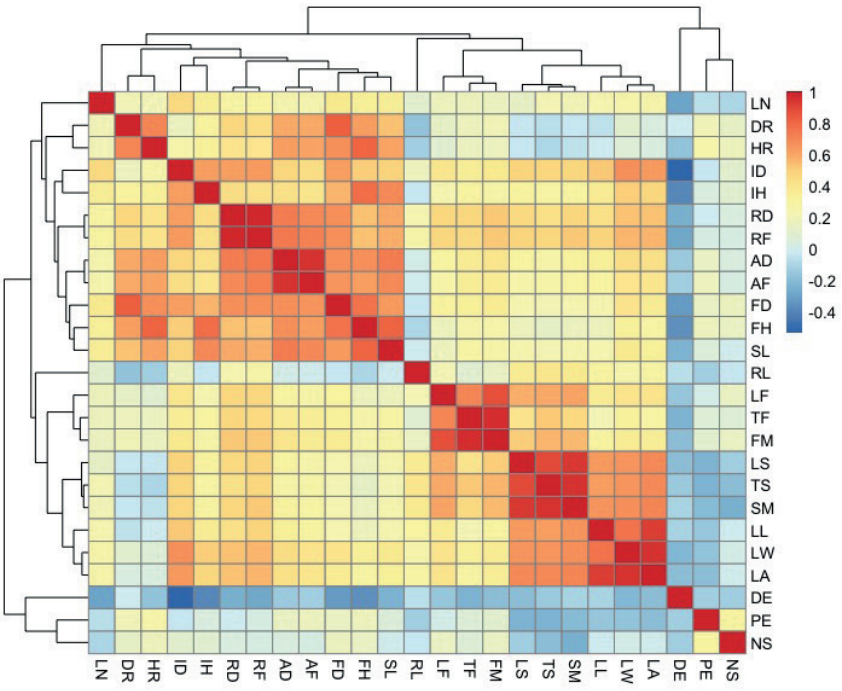

Figure 2. Fruit, seed and seedling traits correlations heatmap of *Eugenia dysenterica* DC. DR: diameter growth rate; HR: height growth rate; ID: initial diameter; IH: initial height; RD: root dry mass; RF: root fresh mass; AD: aboveground dry mass; AF: aboveground fresh mass; FD: final diameter; FH: final height; SL: shoot length; LF: fruit longitudinal length; TF: fruit transverse diameter; FM: fruit mass; LS: seed longitudinal diameter; TS: seed transverse diameter; SM: seed mass; LL: leaf length; LW: leaf width; LA: leaf area; RL: root length; LN: leaf number; DE: days to emergence; PE: emergence percentage; NS: number of seeds per fruit.

considering the measurements taken between February and October, i.e., 3 to 11 months after planting. The last two measurements (August and October), at the peak of the dry season, contributed to the negative growth rate in these progenies. Stem diameter is sensitive to water levels, which can be modulated by turgor pressure, osmotic potential and mainly by xylem water potential (Génard et al. 2001). Diameter may vary according to the stem water content, even over a one-day period (Schepper et al. 2012). Low air humidity causes leaf water loss, creating a negative pressure that can shrink the plant stem. Although the *E. dysenterica* seedlings were irrigated daily, the dry weather and low humidity between May and September, typical of the *Cerrado* biome, may have caused the decline in stem diameter observed in some progenies.

There were significant differences among progenies and subpopulations for number of leaves and leaf area (Table 3). The results demonstrate a high heterogeneity for most of the evaluated traits. The highest *CVg* was recorded for fresh and dry mass and the lowest one for leaf-related traits. Heritability ranged from 0.04 for root length to 0.78 for leaf width (Table 3).

During the first dry season, before the plants lost their leaves, the number of leaves ranged from 1 to 10, with most seedlings displaying 2. The leaf area ranged from small (0.04 cm^2) to large (19.40 cm^2). The subpopulations 8 and 10 (Pirapora, MG; and Brasilândia de Minas, MG) had a higher average number of leaves and, consequently, a larger leaf area. The subpopulation 21 (Cocalinho, MT) obtained the lowest average values for aboveground mass, leaf length, number of leaves and leaf area.

The underground biomass represented 85 % of the total biomass, on average. Like other native plants from the *Cerrado* biome, *E. dysenterica* is exposed to extended periods of water deficit, requiring mechanisms to capture water at greater depths. Biomass allocation to the roots may also be an adaptive strategy for the recurring fires in this biome (Tomlinson et al. 2012). A greater biomass allocation to the roots, if compared to shoots, is an adaptive characteristic retained by uniform selection, whereby the selection pressure to maintain plants

Table 3. Leaf and root traits analysis of variance, coefficients of experimental variation (*CVe*), genetic variation (*CVg*) and heritability on a mean basis (h^2_m) for provenance and progeny testing of 25 *Eugenia dysenterica* DC. subpopulations.

Source of variation	DF	Mean squares									
		LA	LL	LW	NL	RD	AD	RF	AF	RL	SL
Blocks	3	10.94***	2.21***	0.27^{ns}	2.29***	2.63***	0.22***	9.08***	0.72***	28.95^{ns}	8.56***
Subpopulations	24	19.66***	3.58***	0.72***	1.74***	1.07***	0.04*	1.73*	0.10^{ns}	185.90***	13.25***
Progenies/subpopulations	123	4.84***	0.72***	0.20^{ns}	0.59***	0.52***	0.02***	1.02***	0.06**	95.04^{ns}	3.49***
Error	425	1.19	0.19	0.45	0.33	0.24	0.01	0.49	0.04	91.37	1.68
Mean		4.76	3.92	1.64	2.77	1.09	0.18	1.58	0.30	27.61	6.32
CVe		19.63	10.12	10.79	9.86	54.82	72.29	52.50	76.46	35.44	25.57
CVg		7.05	9.41	12.17	7.23	24.74	26.88	23.55	24.78	3.54	10.86
h^2_m		0.74	0.74	0.78	0.27	0.53	0.42	0.52	0.34	0.04	0.52

*, **, *** and ^{ns}: p-value < 5 %, 1 % and 0.1 %, and non-significant, respectively, by the F test; LA: leaf area (cm^2); LL: leaf length (cm); LW: leaf width (cm); NL: number of leaves; RD: root dry mass (g); AD: aboveground dry mass (g); RF: root fresh mass (g); AF: aboveground fresh mass (g); RL: main root length (cm); SL: shoot length (cm).

under regrowth conditions allows individuals to survive until conditions in the *Cerrado* biome become favorable again during the rainy season (Boaventura-Novaes et al. 2018).

An *in vivo ex situ* germplasm collection was planted in the experimental area of the Universidade Federal de Goiás, with a sample of three plants from each of the 150 progenies studied here (N = 450 trees). The recalcitrant nature of *E. dysenterica* makes its conservation in seed banks unviable. Thus, *in vivo* conservation has become the standard for *ex situ* germplasms of the species.

The estimated effective size of the germplasm collection was $N_e \cong 56$, with the entire population of *E. dysenterica* as reference. This apparently low value is due to the strong genetic structure observed in the population, which does not meet the conditions of panmixia (Boaventura-Novaes et al. 2018). However, this effective population size is consistent with results from other studies with species from the Brazilian Savanna, such as *Hymenaea stigonocarpa* (Gonçalves et al. 2019) and *Dipteryx alata* (Guimarães et al. 2019). This representativeness is insufficient to ensure long-term genetic conservation (Vencovsky & Crossa 2003), suggesting the importance of complementary *in situ* conservation. On the other hand, this germplasm collection is sufficiently representative to be used as a base population in breeding programs.

CONCLUSIONS

1. The sampled population of *Eugenia dysenterica* exhibits genetic variability among subpopulations and progenies within subpopulations for almost all the assessed traits. This indicates a potential for genetic gain with selection at the two hierarchical levels;
2. The indirect selection of large seeds with greater mass shortens the seedling development time in the nursery;
3. The *in vivo E. dysenterica* germplasm collection of the Universidade Federal de Goiás has sufficient genetic representativeness to support a pre-breeding program for the species.

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