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Artigos

Genetic variability and *ex situ* conservation strategies for the neotropical tree *Parkia platycephala* Benth.

Variabilidade genética e estratégias de conservação *ex situ* para a espécie neotropical *Parkia platycephala* Benth.

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ABSTRACT

Parkia platycephala, known commonly as faveira, is a native species that occurs widely throughout Brazil and has high nutritional value and ecological potential. The objective of this study was to estimate the genetic variability in a *P. platycephala* provenance and progeny test. The test was established using a randomized block design, with 45 progenies from three provenances. The evaluated quantitative traits included height (HEI), diameter at ground level (DGL), and diameter below the first bifurcation (DFB). The data were submitted to Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) analysis, from which estimates of genetic parameters, genetic correlations, BLUPs, genetic gains, and effective population size were obtained. Estimates of individual narrow sense heritability (h_a^2) and within progeny heritability (h_w^2) ranged from low to moderate (0.01 a 0.39), with the highest values observed for DGL (0.32 and 0.39, respectively). The coefficient of individual variation ($CV_{gi(\%)}$) and between progeny genetic variation ($CV_{gp(\%)}$) indicate the existence of genetic variability between and within provenances. The F_{ST} vaues demonstrate low to moderate genetic differentiation among the three populations, and genetic correlations between traits were all positive and significant. The results obtained show that there is genetic variability between the studied provenances and progenies. This ensures not only the *ex situ* conservation of the species, but it can also be exploited in breeding programs.

Keywords: Genetic resources; Faveira; Forest resources; Genetic parameters

RESUMO

Parkia platycephala, popularmente conhecida como faveiro, é uma espécie nativa que ocorre amplamente em todo o Brasil e possui alto valor nutricional e potencial ecológico. Objetivou-se com o trabalho estimar a variabilidade genética em teste de procedências e progênies de *P. platycephala*. O teste foi instalado em blocos casualizados, com 45 progênies de três procedências. Os caracteres quantitativos avaliados foram: altura (ALT), diâmetro a nível do solo (DNS) e diâmetro a altura da primeira bifurcação (DAB) das plantas. Os dados foram submetidos à análise de REML/BLUP, a partir da qual foram obtidas as estimativas de parâmetros genéticos, correlações genéticas, os BLUP's, ganhos genéticos e tamanho efetivo populacional. As estimativas de herdabilidade individual no sentido restrito (h_a^2) e dentro progênies (h_w^2) variaram de baixa a moderada (0,01 a 0,39), sendo os maiores valores observados para o caractere DNS (0,32 e 0,39, respectivamente). Os valores de coeficiente de variação genética individual ($CV_{gi(\%)}$) e entre progênies ($CV_{gp(\%)}$) indicam existência de variabilidade genética entre e dentro de população. Os valores de F_{ST} demonstraram baixa a moderada diferenciação genética entre as três populações. As correlações genéticas entre os caracteres foram todas positivas e significativas. Os resultados obtidos mostram que há variabilidade genética entre as procedências e progênies estudadas. Isso garante não só a conservação *ex situ* da espécie, como também pode ser explorada em programas de melhoramento.

Palavras-chave: Recursos genéticos; Faveira; Recursos florestais; Parâmetros genéticos

1 INTRODUCTION

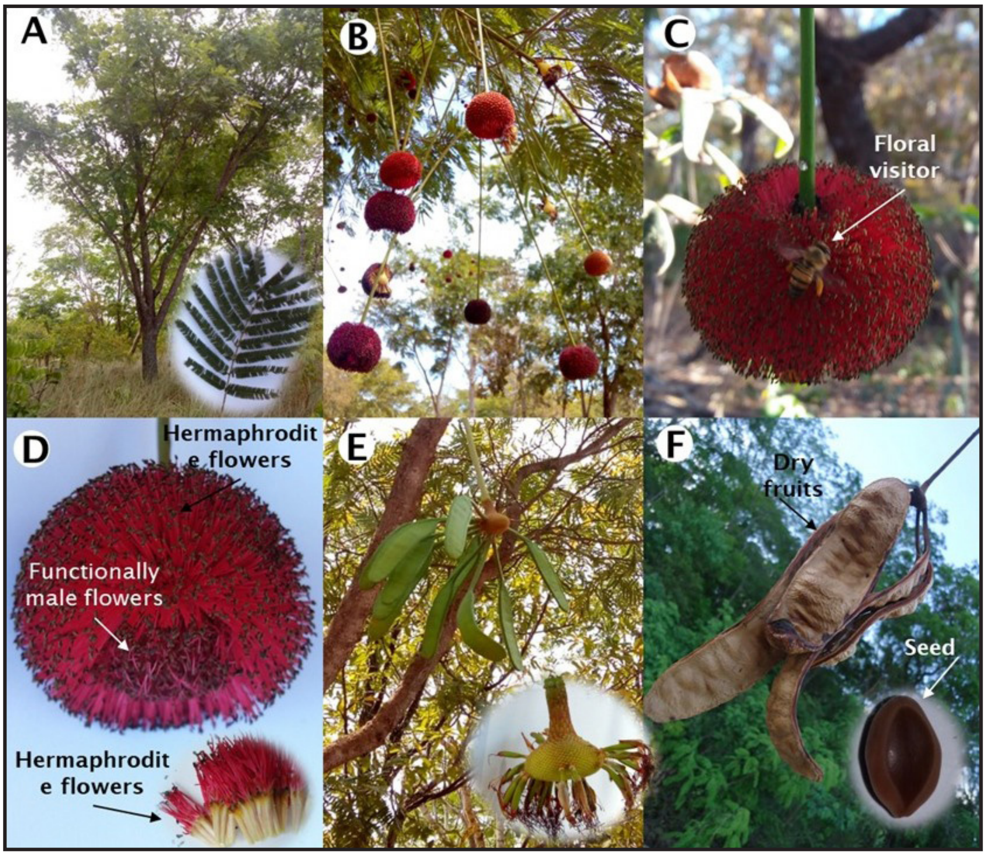
Parkia platycephala Benth., popularly known as faveira, acorn bean or visgueiro, (RNC: registration 24555), is a native forest species that is widely distributed in the North and Northeast regions of Brazil (LORENZI, 2013) (Figure 1). The species has multiple uses, and its ecological, medicinal, and economic potential has attracted the attention of many researchers. *P. platycephala* is a key species for forest restoration programs due to its ecophysiological characteristics as a pioneer and nitrogen fixer, as well as its role facilitating the development of other species (LORENZI, 2013; CARVALHO, 2014). The nutritional potential of its fruits has become an object of study, particularly in terms of animal nutrition. However, there are still no studies on the diversity and genetic structure of *P. platycephala* populations, which can provide indispensable information for conservation strategies and the design of genetic breeding programs.

Parkia platycephala presents self-incompatibility, which favours crossbreeding (CHAVES; SANTOS; SILVA, 2020). As it is a physiological mechanism that supports allogamy and genetic diversity, it has been the target of study, including by plant breeders and geneticists (IWANO; TAKAYAMA, 2012). Besides being allogamous, *P. platycephala* is monoecious, with male and hermaphrodite flowers in the same inflorescence (see flower structure in Figure 1D) (CHAVES; SANTOS; SILVA, 2020). The pollination syndrome of the species is chiropterophilous and entomophilous, and primary seed dispersal is through autochory (*Apis mellifera* floral visitors are shown in Figure 1C) (PILON; UDULUTSCH; DURIGAN, 2015). The conservation of *P. platycephala* across its natural range may be compromised due to recent increases in deforestation. Meanwhile, the factors effecting these ecosystems, such as fragmentation (KUBOTA *et al*., 2015), climate change, reduction in the number of individuals, and the spatial isolation of populations (SEBBENN *et al*., 2011), directly interfere in basic and essential evolutionary processes, including gene flow, genetic drift, reproductive isolation, inbreeding, mutation, and natural selection (VENCOVSKY; NASS; CORDEIRO, 2007).

As such, the implementation of provenance and progeny tests that provide *ex situ* conservation of native forest species germplasm offers an important strategy to guarantee the maintenance of genetic variability outside a species' natural environment. These tests may also serve as foundational populations for forest improvement and genetic conservation programs (e.g., seed orchards) (SEBBENN *et al*., 2011; AGUIAR *et al*., 2019).

Based on the premise that the species' gene flow via pollen is long distance (pollination through chiropterophily) and seed dispersal is restricted (autochory), higher levels of genetic divergence and significant structuring of families within populations are expected. Understanding the genetic variability in provenance and progeny tests is essential for developing conservation and genetic breeding programs (AGUIAR *et al*., 2019), thus the aims of the study were to: a) verify the distribution of genetic variability among and within populations; b) estimate Best Linear Unbiased Prediction values (BLUPs); c) estimate the effective population size of the *P. platycephala* provenance and progeny test; and d) evaluate selection strategies to inform conservation programs, genetic breeding, and the formation of a seedling seed orchard (SSO).

Figure 1– Morphological characteristics of the *Parkia platycephala* Benth.



Source: Authors (2017)

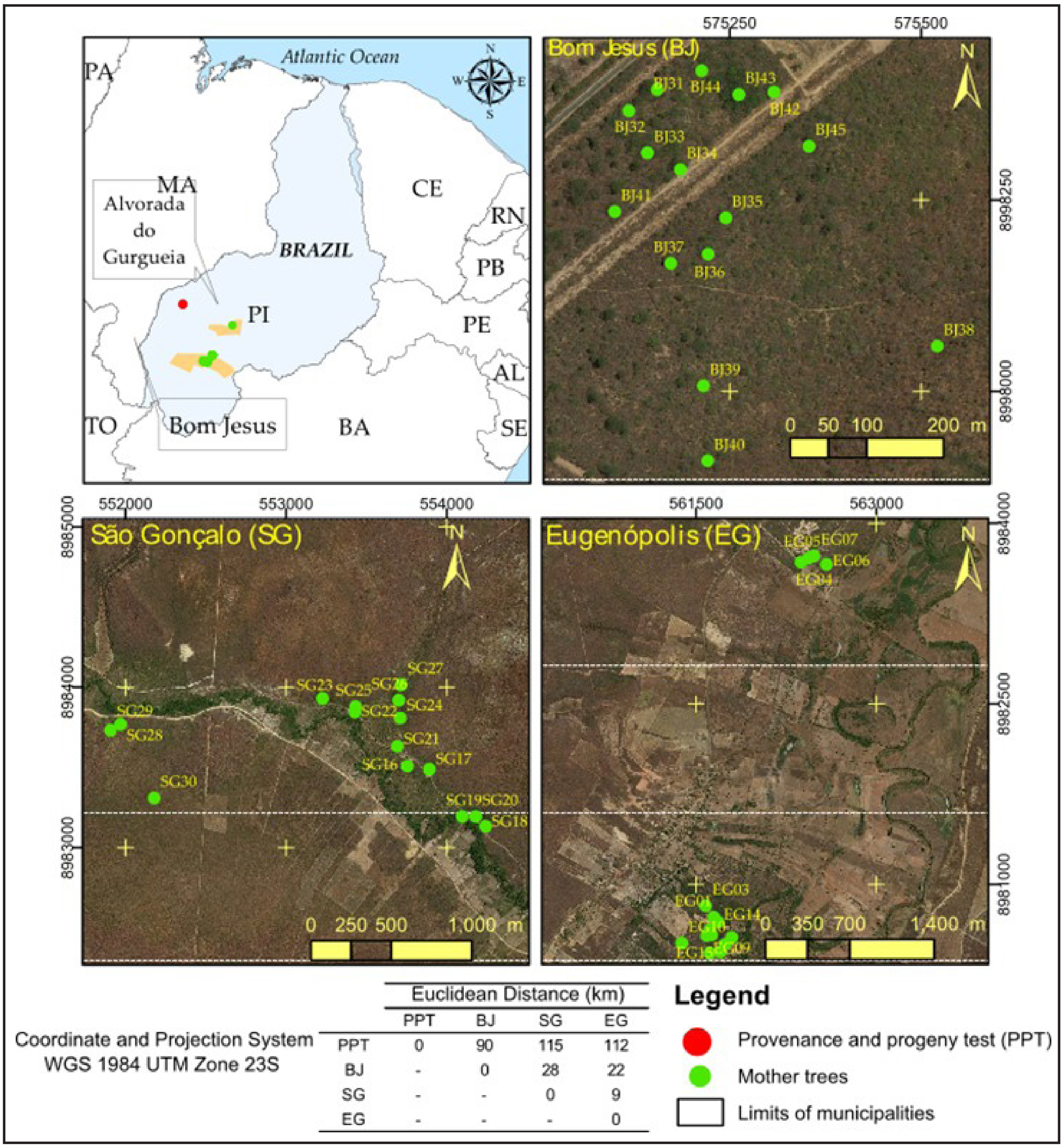
In where: Tree. A) common stem shape (adult individual) and leaf phyllotaxis; B) flowering; C) floral visitors (*Apis mellifera*); D) flowers of the inflorescence; E) development of fruits from the same inflorescence; F) dry indehiscent fruits and seed.

2 MATERIAL AND METHODS

2.1 Experimental trial and plant material

The collection of open-pollinated *P. platycephala* seeds to produce the seedlings was carried out in three populations (Eugenópolis [9°11’38”S and 44°25’49,2”W], São Gonçalo [9°11’32,4”S and 44°30’49,2”W], and Bom Jesus [9°41’00”S and 44°18’57,0”W]) located in areas of transition between Cerrado and Caatinga, in the southwest region of the state of Piauí, Brazil. Seeds were collected from 45 seed trees (15 trees/ population), with at least 100 meters distance between them (Figure 2).

Figure 2 – Location of Parkia platycephala Benth. source populations used in the provenance and progeny test installed at the Alvorada do Gurgueia Experimental Farm, Alvorada do Gurgueia, Piauí, Brazil, and spatial distribution of the 45 seed trees



Euclidean Distance (km)

	PPT	BJ	SG	EG
PPT	0	90	115	112
BJ	-	0	28	22
SG	-	-	0	9
EG	-	-	-	0

Source: Authors (2020)

Seedlings were germinated and planted in the field at six months of age, at which point the average values for seedling height and diameter were 28.5 cm and 6.43 mm, respectively. The provenance and progeny test were installed in February 2017 at the

Alvorada do Gurgueia Experimental Farm (FEAG), of the Federal University of Piauí (UFPI), located in the municipality of Alvorada do Gurgueia, southwest Piauí, Brazil (8°22’23.34”S and 43°51’24.31” W). The experiment was established with a randomized block design, 13 repetitions and one plant per plot, for a total of 585 plants from 45 *P. platycephala* progenies and three provenance/populations (Eugenópolis (POP1), São Gonçalo (POP2), and Bom Jesus (POP3)) (Figure 2). The climate of the region where the test was established is hot semi-arid and categorized as BSh according to the Köppen-Geiger classification (KÖPPEN; GEIGER, 1928). The elevation is 281 m, and the soil of the experimental area was predominantly sandy, with flat relief.

To evaluate the growth and early establishment of plants in the field, an assessment of the experiment was carried out at 34 months. As such, quantitative silvicultural traits were measured, such as tree height (HEI, m), diameter at ground level (DGL, mm), and diameter below the first bifurcation (DFB, mm). Measurements were performed with a measuring tape (HEI) and digital callipers (DGL and DFB) to two decimal places. To evaluate the adaptation of the plants at the test site, the survival rate was also evaluated by provenance, and the statistical difference between the means ($p<0.05$) was verified (FERREIRA *et al*., 2021).

2.2 Modelling procedures and parametric computation

For the analysed traits, to verify the existence of genetic variability, the components of variances and genetic parameters were estimated using the Restricted Maximum Likelihood/Best Linear Unbiased Prediction method (REML/BLUP). For this, two mixed linear models (Models 1 and 2) were adjusted using the sommer statistical package (PAZARAN, 2016) in the R software environment (R CORE TEAM, 2018). For the adjusted mixed linear models, it was assumed that the evaluated progenies are from open pollination and the degree of relatedness between them is half sibs. For statistical model [1], the analyses were performed considering the population as a random effect, and for statistical model [2] the population was considered a fixed effect. Both models were used to assess the genetic variances between and within populations. Model [1] allowed us to estimate the genetic variance between populations, and thus calculate (genetic differentiation between populations). With model [2] it was possible to statistically differentiate the means of the studied traits between populations, and assess genetic variances within each population.

$$y = Xf + Za + Wb + Ts + e\,[1], \qquad y = Xf + Za + Wb + e\,[2]$$

where: y is the phenotypic vector of the trait under analysis; f is the vector of effects assumed to be fixed (general average) [1] or the vector of population effects (fixed) plus the general average [2]; a is the vector of individual additive genetic effects (assumed to be random) [1 and 2]; b is the vector of block effects (assumed to be random) [1 and 2]; s is the vector of population effects (assumed to be random) [1]; e is the vector of residuals (random) [1 and 2]. The capital letters X, Z, W, and T represent the incidence matrices of the said effects.

Vectors containing the random effects for model [2] assumed multivariate normal distribution, centred at zero, with the following structures of variance and covariance: $Cov(a, a') = G_0 \otimes A$, $e \sim \text{NID}\,(0, \text{I}\sigma_e^2)$ (Normal and Independent Distribution) and $Cov(a, \varepsilon')$, where G_0 is a diagonal matrix of order 3; σ_{a1}^2, σ_{a2}^2, and σ_{a3}^2 in the diagonals with additive genetic variances of each of the three populations and covariance (values outside the diagonal) equal to zero; is the matrix formed by the denominator of additive coefficients of $g \times g$ order, where g is the total number of individuals; and $\otimes$ denotes the *Kronecker* product between matrices.

The appropriateness of the models was verified using the lmerTest package (KUZNETSOVA *et al*., 2017), in which the random and fixed effects of the models were extracted and tested. For random effects their respective significance was verified by the Chi-square test (χ^2) using the likelihood ratio test (LRT), and for fixed effects the significance was verified by the F test.

The variance components obtained were: genetic variance between populations/ provenances (σ_{pop}^2) [model 1]; additive genetic variance between and within each population (σ_a^2); variance between blocks (σ_{bloc}^2); environmental variance (σ_e^2); and phenotypic variance (σ_f^2). After obtaining the variances, the following genetic parameters were estimated:

a) individual narrow sense heritability ($h_a^2 = \frac{\sigma_a^2}{\sigma_f^2}$) (LUSH, 1936), with the standard deviation obtained using the 'pin' function in the sommer package;

b) heritability within progenies ($h_w^2 = \frac{0{,}75\sigma_a^2}{\sigma_e^2}$);

c) coefficient of individual additive genetic variation ($CV_{gp(\%)} = \sqrt{0{,}25\sigma_a^2}/m \cdot 100$), where *m* corresponds to the average of the evaluated trait);

d) coefficient of genotypic variation between progenies ($CV_{gp(\%)} = \sqrt{0{,}25\sigma_a^2}/m \cdot 100$);

e) coefficient of environmental variation ($CV_{e(\%)} = \sqrt{\sigma_e^2}/m \cdot 100$) (NAMKOONG, 1979);

f) relative coefficient of variation ($\hat{b} = CV_{gp(\%)}/CV_{e(\%)}$) (VENCOVSKY; BARRIGA, 1992);

g) accuracy in selecting the best progenies ($\hat{r}_{aa} = \sqrt{h_m^2}$, where $h_m^2 = (0{,}25\sigma_a^2)/(0{,}25\sigma_a^2 + \sigma_e^2/nb)$), where *b* corresponds to the number of blocks and *n* to the number of individuals per plot) (RESENDE, 2002).

The measure of genetic differentiation between populations (F_{st}) was estimated according to the formula proposed by Resende (2015) ($F_{st} = \sigma_{pop}^2/(\sigma_p^2 + 2\sigma_a^2)$) for which we used the variances between (σ_{pop}^2) and within populations (σ_a^2) obtained from the adjusted mixed model [1].

The genetic correlations ($\hat{r}_g$) were estimated from the BLUPs of all evaluated individuals, and phenotypic correlations ($\hat{r}_f$) were estimated from the phenotypic data. We used Pearson's rank correlation coefficient in R to estimate correlations, and significance was verified with the *t* test. The predicted genetic values (BLUPs) for the evaluated traits were obtained using the 'randef' function in the sommer package. As one of the objectives is to transform the *P. platycephala* provenance and progeny test into a seedling seed orchard, we simulated scenarios with different selection intensities. According to Sebbenn and Ettori (2001), managing (thinning) at low intensities (selected proportion) ensures a greater value for effective size of the test population (N_e). Sebbenn *et al*. (2007) also recommend thinning at low intensities and argue that if a selection is made within provenances (populations) and progenies, the genetic variability existing in the test will be maintained and recombined in the reproductive period. Thus, selection intensities were tested based on such recommendations with the goal of identifying efficient selection strategies that meet the needs for both conservation and genetic improvement programs of the species.

Among the genetic parameters assessed herein, the effective population size (N_e) is one of the most appropriate to provide a basis for artificial selection, since high values of N_e ensure the continuation of existing genetic variability (SEBBENN; ETTORI, 2001; AGUIAR *et al*., 2019). Thus, the effective population size (N_e) of the *P. platycephala* provenance and progeny test was estimated using the formula proposed by Resende and Bertolucci (1995): $N_e = (4N_f\bar{k}_f)/(\bar{k}_f + 3 + (\sigma^2_{kf}/\bar{k}_f))$; where, $\bar{k}_f$ is the average number of individuals selected per family; σ^2_{kf} is the variance of the number of individuals selected per family; and N_f is the number of selected families.

Considering the potential use of the test in both conservation and breeding programs, we estimated the minimum viable population (MVP), or the minimum number of individuals necessary to guarantee short and long-term genetic conservation. According to Nunney and Campbell (1993), to meet these requirements, the effective reference population size (N_f) required is 150 and 1,500, respectively. The MVP was estimated using the formula proposed by Nunney and Campbell (1993): $MVP = \hat{N}_{ef}/\hat{N}_e/n$; where, $\hat{N}_{ef}$ corresponds to the effective reference population size (150 and 1,500); $\hat{N}_e$ is the estimated effective population size; and *n* is the number of individuals in the population.

3 RESULTS AND DISCUSSION

3.1 Initial development and survival of *P. platycephala* progenies

The *P. platycephala* progenies presented an average height (HEI) of 3.11 m, average DGL of 64.09 mm, and average DFB of 56.62 mm. The survival rate of the progenies in the test was significantly different ($p < 0.05$) and ranged between populations (POP1=72.82% (a), POP2= 63.59% (b), and POP3=74.35% (a), where different letters indicate statistical difference). Progenies from Bom Jesus (POP3) showed the best performance for height (HEI=3.20 m) and diameter (DGL=67.72 mm; DFB=60.61 mm), as well as the highest survival rate (74.35%).

When evaluating the same species at four years of age, Alves *et al*. (2016) obtained a similar survival rate (80%) but lower values for height and diameter (2.0 m and 38.47 mm, respectively). The survival rate obtained herein is consistent with those found for other forest species in the same ecosystem (70%) (PILON; DURIGAN, 2013). Factors such as adaptability to the environment, competition between plants (CANUTO *et al*., 2015), and the level of inbreeding in the source populations (TAMBARUSSI *et al*., 2017), may have contributed to the increased mortality of the progenies. Endogamous forest species have greater difficulty in adapting to extreme environmental conditions, which results in mortality and poor performance during early stages of development (SOUZA JÚNIOR, 2001).

3.2 Deviance analysis, correlation, and estimates of genetic parameters

Deviance analysis showed only significant effects of provenance for DGL and DFB ($p < 0.05$ and $p \leq 0.01$, respectively) and significant effects of block for height (HEI) and DGL ($p \leq 0.01$) in the two adjusted models (Table 1).

Effects of progenies and populations for tree height can be verified when the test is re-evaluated at subsequent stages of development. In later stages, growth (HEI, DGL, and DFB) and other traits (including productivity, fruit protein content, and wood volume) tend to show minimized effects of the environment and increased genetic values. Continuous studies carried out on *Balfourodendron riedelianum* Engl. (SEBBENN *et al*., 2007; KUBOTA *et al*., 2015; AGUIAR *et al*., 2019) demonstrate that these effects can be verified, thus emphasizing the importance of performing consecutive analyses in provenance and progeny tests until maturity.

Table 1 – Deviance analysis, significance of random and fixed effects of the adjusted mixed models, for height (HEI), diameter at ground level (DGL), and diameter below the first bifurcation (DFB), in a provenance and progeny test of *Parkia platycephala* Benth. at 34 months, based on likelihood ratio test (LRT) using the Chi-square (χ^2)

Pop. as random effect	**LRT (χ^2)**		
	HEI	**DGL**	**DFB**
Population	1.55^{ns}	6.41*	7.87**
Progeny	0.25^{ns}	0.43^{ns}	0.00^{ns}
Block	35.75***	17.08***	1.58^{ns}
Pop. as fixed effect			
Population	2.96^{ns}	7.14**	7.11**
Progeny	0.24^{ns}	0.42^{ns}	0.00^{ns}
Block	35.83***	17.10***	1.58^{ns}

Source: Authors (2020)

In where: Pop. - Population; Tabulated chi-square - 3.84, 6.63, and 10.83 for significance levels of 5%, 1%, and 0.1%, respectively; significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; “ns” not significant.

According to Ettori *et al*. (2006), until a plant reaches full development in the field, the environmental influence on growth traits can vary widely. Similarly, Resende (2015) reports that the phenotypic values for perennial plants are the result of varying environmental conditions and instabilities throughout the life cycle.

When observing the results for additive genetic variance (σ_a^2) between populations (model [1]) and for each population (model [2]), it appears that the additive genetic variance (σ_a^2) of the Eugenopolis population (POP1) was practically reset to zero for DGL (σ_a^2= 2.0 10^{-3}). The populations that presented low additive genetic variance (σ_a^2) (Table 2, model [2]), were responsible for the reduction in the total additive genetic variance (σ_a^2) between populations (Table 2, model [1]). For these populations, null values of σ_a^2 imply genetic estimates of low magnitude.

Table 2 – Genetic parameters, genetic correlations (upper diagonal), and phenotypic correlations (lower diagonal) of the traits evaluated in a provenance and progeny test of *Parkia platycephala* Benth. at 34 months

Population assumed to be a random effect	**HEI (m)**	**DGL (mm)**	**DFB (mm)**
σ^2_{pop}	59.70	9.46	11.45
σ^2_a	620.01	32.10	47.63
σ^2_{bloc}	551.82	15.53	4.87
σ^2_e	3040.29	154.55	221.04
σ^2_f	4271.82	211.64	284.99
h^2_a	0.14 ± 0.021	0.15 ± 0.021	0.17 ± 0.021
h^2_d	0.15	0.16	0.16
$CV_{gi(\%)}$	8.01	8.84	12.18
$CV_{gp(\%)}$	4.00	4.42	6.09
$CV_{e(\%)}$	17.75	19.40	26.25
$\hat{b}$	0.22	0.23	0.23
$\hat{r}_{aa}$	0.63	0.63	0.64
F_{st}	0.05	0.13	0.11
Average	3.11	64.09	56.65

Population assumed to be fixed effect	**Population**								
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
σ^2_a	578.44	1244.99	28.13	0.002	69.42	74.67	5.26	92.75	84.35
σ^2_{bloc}		503.32			17.19			5.50	
σ^2_e		3075.03			142.81			211.69	
σ^2_f	4156.79	4823.34	3606.48	160.00	229.42	234.67	222.46	309.95	301.54
h^2_r	0.14± 0.099	0.26± 0.082	0.01± 0.121	0.00001± 0.133	0.30 ± 0.079	0.32± 0.074	0.02± 0.138	0.30± 0.084	0.28 ± 0.085
h^2_w	0.14	0.30	0.01	0.00001	0.36	0.39	0.02	0.33	0.30
$CV_{gi(\%)}$	7.74	11.36	1.71	0.07	13.00	13.48	4.05	17.00	16.21
$CV_{gp(\%)}$	3.87	5.68	0.85	0.03	6.50	6.74	2.02	8.50	8.10
$CV_{e(\%)}$	17.89	18.41	17.36	19.36	19.09	17.65	27.17	26.15	24.00
$\hat{b}$	0.22	0.32	0.01	0.02	0.35	0.36	0.08	0.33	0.31
$\hat{r}_{aa}$	0.61	0.75	0.17	0.01	0.78	0.79	0.27	0.77	0.75
Average	3. 10	3.01	3.19	61.71	62.59	67.72	53.54	55.63	60.61

To be continued ...

Table 2 – Conclusion

Correlations			
Trait	HEI	DGL	DFB
HEI	-	0.66**	0.49**
DGL	0.64**	-	0.80**
DFB	0.48**	0.78**	-

Source: Authors (2020)

In where: HEI - total plant height (m); DGL - diameter at ground level (mm); DFB - diameter below the first bifurcation (mm); σ^2_{pop} - variance between populations; σ^2_a - additive variance; σ^2_e - residual variance; σ^2_f - phenotypic variance; h^2_a - narrow sense individual heritability; h^2_w - heritability within progenies; $CV_{gi(\%)}$ - individual additive genetic variation coefficient; $CV_{gp(\%)}$ - coefficient of genotypic variation between progenies; $CV_{e(\%)}$ - coefficient of environmental variation; $\hat{r}_{aa}$ - selection accuracy; $\hat{b}$ - relative coefficient of variation; F_{st} - quantitative genetic differentiation between origins.

Based on the values obtained for F_{st} (≤ 0.13), the genetic differentiation between the three studied populations varies from low (HEI, $F_{st} = 0.05$) to moderate (DGL and DFB, $F_{st} = 0.13$ and 0.11, respectively) (Table 2). Low levels of genetic differentiation between *P. platycephala* populations was expected given the species' pollination syndrome and reproductive system, as discussed above. Moderate levels of genetic differentiation between populations, and a greater degree of kinship within populations, are expected for species with gene flow via long-distance pollen dispersal and restricted seed dispersal (SEBBENN *et al*., 2011), such as *P. platycephala*. By interpreting the estimated values for F_{st}, we can confirm this hypothesis.

Factors such as geographical distance (see Figure 2), reproductive system, pollinating agents (Figure 1 C and D), and seed dispersal mechanisms may explain and contribute to the low and moderate genetic variability observed between the provenances. In the case of *P. platycephala*, if we consider the geographical distances between populations (Figure 2), its chiropterophilic pollination (CHAVES; SANTOS; SILVA, 2020) may have favoured gene flow between the three populations, as bats can fly long distances, reaching a flight radius of up to 18 km (GRIBEL *et al*., 1999). However, these inferences should be confirmed through more advanced studies, for example using molecular markers.

According to Rossi *et al*. (2014), tropical tree species populations often present higher levels of genetic variability within than among populations. Hamrick and Loveless (1989) argue that the genetic similarity observed between populations is mainly the result of pollination and seed dispersal vectors, which are often animals that can travel long distances, favouring gene flow between populations.

The species' reproductive system was also a determining factor in genetic differentiation between populations. *P. platycephala* is allogamous, and in order to support crossbreeding, it has self-incompatibility mechanisms (CHAVES; SANTOS; SILVA, 2020). According to Kageyama *et al*. (2003), allogamous species tend to exhibit high levels of genetic diversity within and relatively low levels of divergence between populations. This result may also be related to a reduction in heterozygosity due to genetic drift that may be occurring in these populations as a result of fragmentation.

The low values for environmental variation coefficients ($CV_{e(\%)}$) demonstrate precision in the estimates of the genetic parameters and the adequacy of the experimental design. These values varied from 17.75 to 26.25% when estimated using model [1], which assumes populations as a random effect, and from 17.36 to 27.17% when estimated within each population using model [2] (Table 2). According to the classification of Mora and Arriagada (2016), the results for the coefficient of environmental variation range from moderate (DGL) to high (HEI and DBF). $CV_{e(\%)}$ values of this magnitude or even higher are common when evaluating provenance and progeny tests of forest species (CANUTO *et al*., 2015; KUBOTA *et al*., 2015; AGUIAR *et al*., 2019).

The estimates of individual narrow sense heritability and heritability within progenies (h_a^2 and h_w^2, respectively) ranged from 0.14 to 0.17, when the three populations were analysed together, and from 0.00 to 0.39 when estimated separately for each population (Table 2). The best estimates of heritability were obtained when populations were evaluated separately, with the highest values h_a^2 of h_w^2 and obtained for DGL (0.32 and 0.39, respectively) for progenies from Bom Jesus (POP3; Table 2). Higher values of additive genetic variance (σ_a^2) resulted in higher estimates of heritability and coefficients of genetic variation (Table 2).

The evaluated traits do not present high levels of genetic control. However, such results are expected for quantitative traits, since they are controlled by several genes and are significantly influenced by the environment (RESENDE, 2015). Heritability values may vary according to the population studied, the trait evaluated, estimation methods, population diversity, sample size, inbreeding level, precision in conducting the experiment, data collection, species, age of assessment, and environmental conditions (RESENDE, 2002).

For the coefficients of individual additive genetic variation ($CV_{gi(\%)}$) and genotypic variation between progenies ($CV_{gp(\%)}$), the values ranged from 0.07 to 17% and 0.03 to 8.50%, respectively (Table 2). Regardless of the statistical model used, the trait DFB showed the highest values for $CV_{gi(\%)}$ and $CV_{gp(\%)}$ ($CV_{gi(\%)}$=12.18 [1] and 17% [2]; $CV_{gp(\%)}$= 6.09 [1] and 8.50% [2]). In general, the values for coefficients of individual additive genetic variation ($CV_{gi(\%)}$>7%) were high (SEBBENN *et al*., 1998). The higher the value obtained for $CV_{gi(\%)}$, the greater the genetic variability that exists between the evaluated progenies (CANUTO *et al*., 2015).

Despite the low values of (0.36), and the test consisting of juveniles (34 months), the effectiveness of the phenotypic selection of the best *P. platycephala* progenies and the genetic gains to be obtained from selection for the evaluated traits, are supported by good accuracy values ($\hat{r}_{aa}$ ≤ 0.64). The good accuracy values obtained suggest effectiveness in phenotypic selection of the best *P. platycephala* progenies and the genetic gains to be obtained with selection (RESENDE, 2002). The higher the observed accuracy value, the greater the expected genetic gains with selection (RESENDE, 2015).

Aiming at a future breeding program for *P. platycephala*, and taking into consideration the multiple uses of the species, to obtain gains in volume, a good selection strategy would be based on diameter at ground level (DGL), since this trait presented good values for heritability (h_r^2 and h_w^2), coefficients of genetic variation

($CV_{gi(\%)}$ and $CV_{gp(\%)}$), accuracy ($\hat{r}_{aa}$), and genetic ($\hat{r}_g$) and phenotypic ($\hat{r}_f$) correlations with height. The quantitative traits evaluated showed positive and significant genetic (upper diagonal) and phenotypic (lower diagonal) correlations, which ranged from moderate (0.48 to 0.66) to strong (0.78 to 0.80) (Table 2).

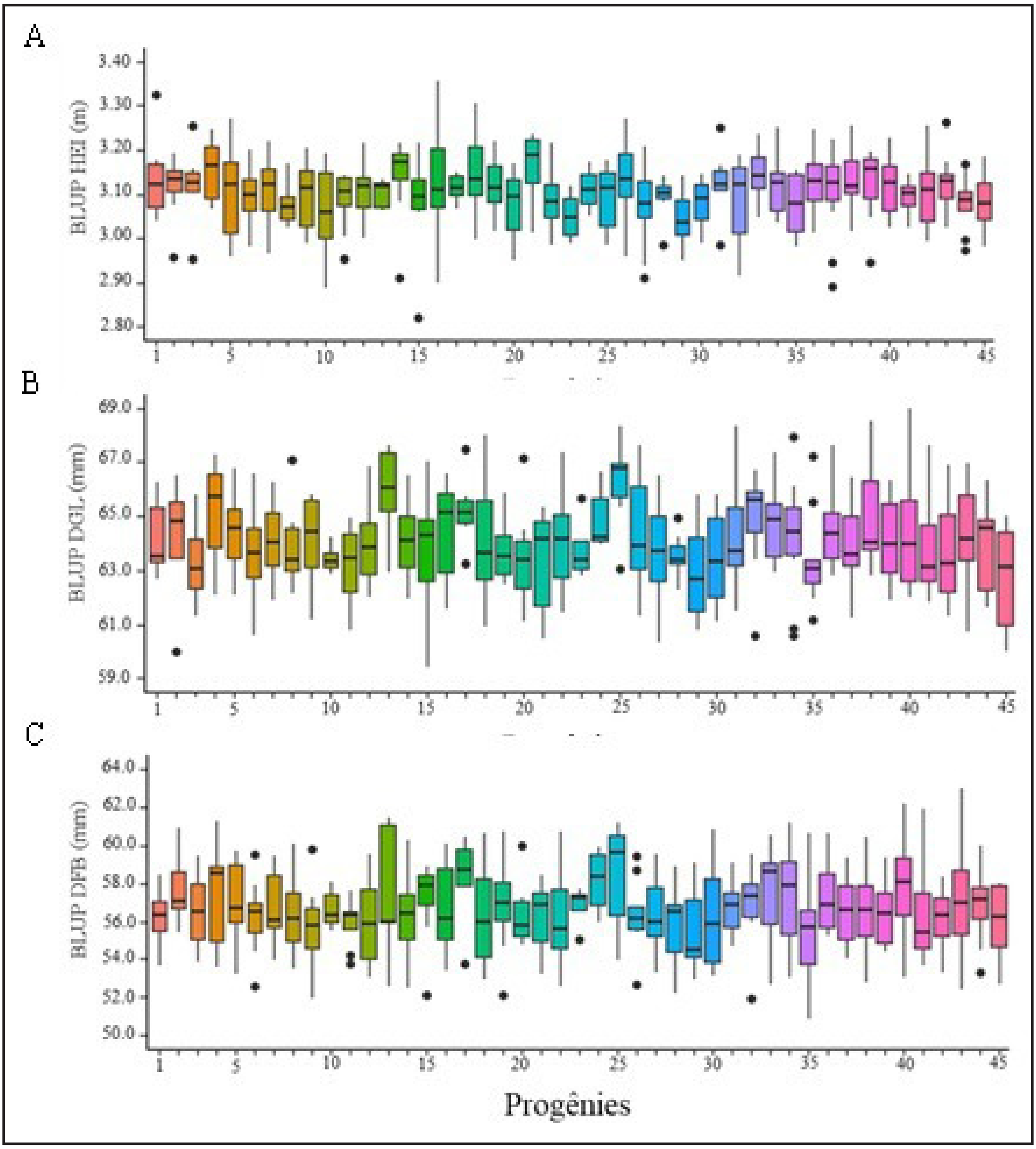
The moderate to strong, positive genetic correlation ($\hat{r}_g$) observed for the evaluated quantitative traits may be due to pleiotropy between the genes responsible for these traits (RESENDE, 2015). The values for genetic and phenotypic correlation are essential to determine the selection strategy to be used, since the choice of a given trait to establish an improvement program will result in indirect gains of the correlated traits (RESENDE, 2015).

3.3 BLUPs, expected gains with selection, and effective population size (N_e)

The prediction of individual genetic values from BLUPs for height, DGL, and DFB were only estimated with model [1], considering the infeasibility of selection in populations whose additive genetic variance values (σ_a^2) are practically nil. The phenotypic averages predicted from the BLUP for individuals in the *P. platycephala* provenance and progeny test ranged from 2.82 to 3.36 m for HEI, 59.42 to 68.98 mm for DGL, and 50.84 to 63.00 mm for DFB (Figure 3). In addition to the variability between and within progenies (Figure 3), we highlight progenies 1, 2, 4, 7, 16, 17, 18, 24, 26, 31, 33, 36, 38, 40, and 43 as promising for selection, since they present the best genetic values (BLUPs) for HEI and DGL.

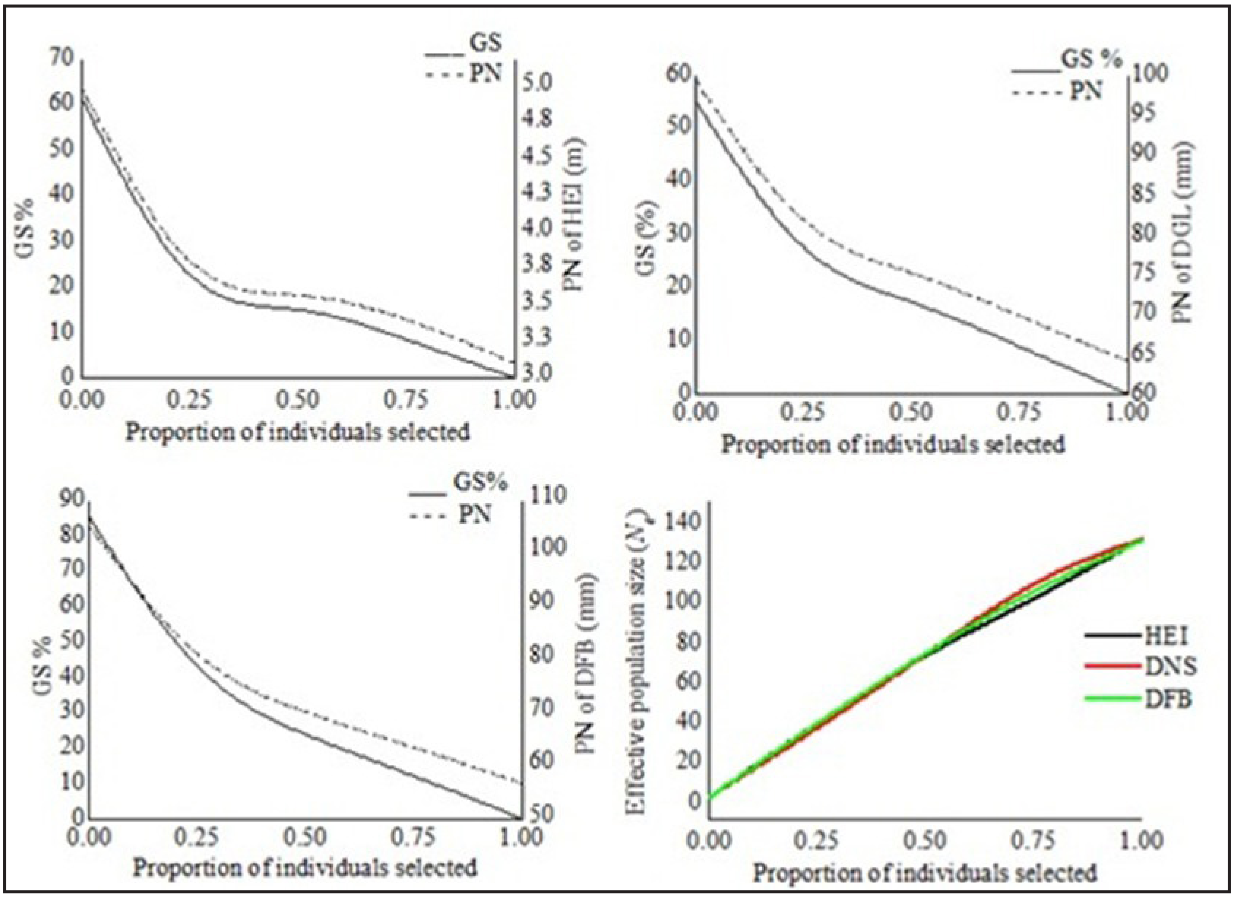
From Figure 4, we can see the estimates of possible genetic gains (GS), phenotypic mean (NP), and effective population size (N_e) that could be obtained with selection. We observed that the estimated genetic gains were very similar among the evaluated traits, which decreased with an increase in the intensity of selection applied to the total provenance and progeny test, resulting in zero gains if 100% of the test individuals are selected (Figure 4).

Figure 3 – Predicted phenotypic averages based on genetic values (BLUPs) for the traits (A) height (HEI), (B) diameter at ground level (DGL), and (C) diameter below the first bifurcation (DFB) for a *Parkia platycephala* Benth. provenance and progeny test at 34 months



Source: Authors (2020)

Figure 4 – Estimates of gains (GS), new phenotypic mean (PN), and effective population size (N_e) calculated in response to different selection intensities for the total population of *Parkia platycephala* Benth. at 34 months



Source: Authors (2020)

Although greater genetic gains could be obtained when applying selection intensities between 10 to 20% for all evaluated traits, the low values for effective population size (N_e = 19 to 30) make this selection strategy unfeasible as it would compromise the genetic variability of subsequent generations. To reach effective population sizes (N_e) of 50 and 100, the best strategy corresponds to selection intensities of at least 0.38 and 0.72, respectively, for the provenance and progeny test. That is, at least 38% of *P. platycephala* individuals from the test should be selected to obtain a N_e of 50, or 72% to obtain an N_e of 100 (Figure 4). The effective population size

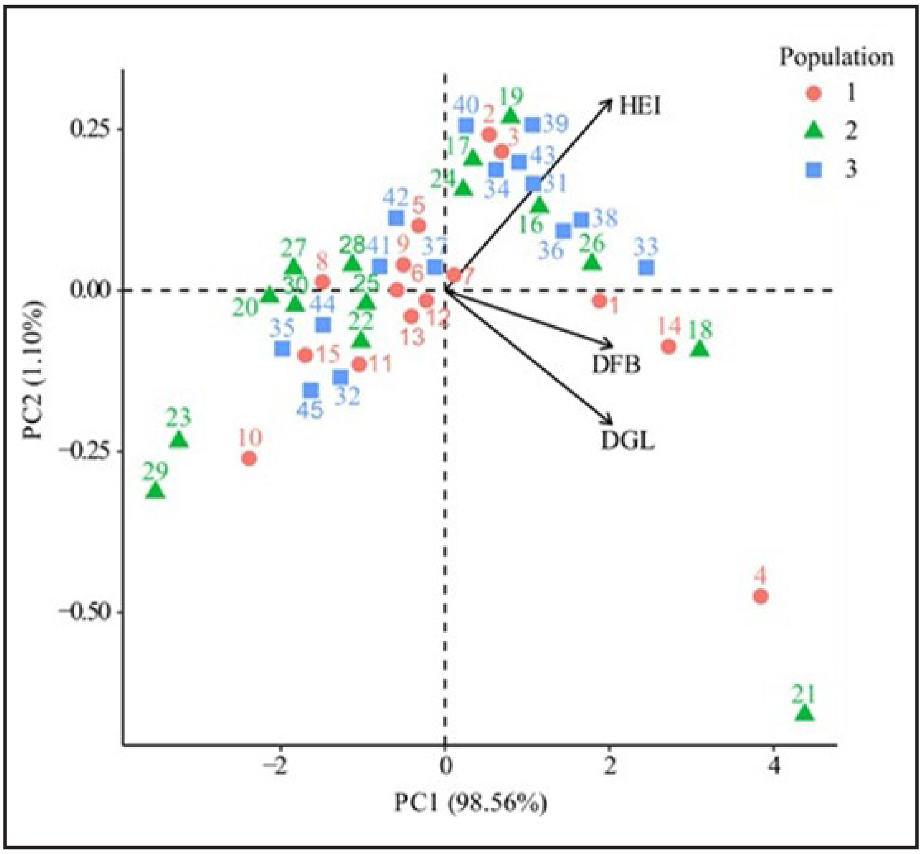
(N_e = 130.18) estimated for the test was similar to the reference effective population size (N_{ef} = 150) required to guarantee short-term genetic conservation. The minimum viable population (MVP) needed to ensure the genetic variability of *P. platycephala* in the short and long term, or the number of individuals needed to obtain N_{ef} values of 150 and 1,500, would be 474 and 4,736 individuals, respectively.

Our results suggest that the greater the selection intensity carried out, the lower the genetic gains obtained; however, with higher selection intensities, the effective population size is retained, and the genetic variability of the provenance and progeny test will not be compromised. By applying restrictive selection intensities to an original population, fixation rates and loss of alleles per generation at a rate of $1/4N_e$ may be favoured, and as a consequence, the existing variability will be reduced by $1/(2N_e)$ with each generation (RESENDE, 2015). According to Aguiar *et al*. (2019), the selected population must have the highest possible N_e to ensure genetic conservation and selection strategies that guarantee genetic variability. Sebbenn *et al*. (2007) also point out that, for such purposes, low-intensity management (thinning) is an efficient strategy that ensures genetic variability, as it will not result in a drastic reduction in the effective size of the population.

The effective population size (N_e) estimated for the *P. platycephala* provenance and progeny test was smaller than the sample size, which may indicate kinship between the evaluated progenies (VENCOVSKY; NASS; CORDEIRO, 2007). As noted above, the values of N_e fluctuate according to the selection intensity. Therefore, the best selection strategy will be that based on a combined analysis that considers both the genetic gains to be obtained and the effective population size. As such, severe genetic complications in subsequent generations can be avoided, such as a reduction in fitness of the progenies due to genetic drift, inbreeding or increases in inbreeding, as well as the consequent reductions in the genetic variability of the base population.

Based on the PCA, the first two principal components explained 99.66% of the existing variability between BLUPs for HEI, DGL, and DFB. The progenies to the right of the graph stand out as they present the best genetic values (BLUP) for HEI, DGL, and DFB (Figure 5). The more proximal the progenies are on the cartesian plane, the more genetically similar they are.

Figure 5 – Graphical dispersion of the scores of 45 *Parkia platycephala* Benth. progenies (coded as 1 – 45), estimated from the BLUP of the quantitative traits height (HEI), diameter at ground level (DGL), and diameter below the first bifurcation (DFB), in a provenance and progeny test at 34 months



Source: Authors (2020)

For breeding purposes, crossing between phenotypically related progenies will reduce the chances of success through artificial selection (VENCOVSKY; NASS; CORDEIRO, 2007). As allogamous species already tend to present high rates of inbreeding depression (SOUZA JÚNIOR, 2001), crossing between similar progenies can lead to the effects of inbreeding in the segregating population. This situation requires caution because the *P. platycephala* provenance and progeny population already shows signs of inbreeding. Thus, conservation and improvement strategies must be carried out that aim to maintain and increase the observed genetic variability. To this end, the test can be enriched with progenies from other sources, and individuals with inferior phenotypic traits can be removed from the test.

4 CONCLUSIONS

Although the evaluated traits show low to moderate genetic control (0.00 – 0.39), the *P. platycephala* provenance and progeny test has potential for use in breeding programs, with the possibility of genetic gains if selection is made between and within populations based on diameter at ground level (DGL). The ex situ genetic conservation of the species is ensured as the effective population size is retained in the provenance and progeny test. An initial thinning of up to 25% of poorer performing individuals will not compromise the genetic variability necessary for conservation, the development of breeding programs, or future transformation of the test into a seedling seed orchard (SSO). Thinning will also reduce the chance of crossbreeding between phenotypically related individuals. Finally, we suggest that the test is continually monitored and evaluated as the trees age to ensure accurate operational decision making.

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