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Original Article

Selection of genotypes of sapodilla (*Manilkara zapota*) based on fruit morphometric and chemical traits

Seleção de genótipos de sapoti (*Manilkara zapota*) com base em características morfo-biométricas e químicas de frutos

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Abstract

Sapodilla (*Manilkara zapota*) is a tropical fruit tree valued for its nutritional and economic potential and is increasingly important in northeast Brazil. This study aimed to evaluate genetic variability and identified superior genotypes based on morphometric and chemical fruit traits. We evaluated nine genotypes (162 fruits) from the *in situ* germplasm bank at the State University of Maranhão. Morphometric traits included fruit weight, fruit longitudinal and transversal length, fruit penetration resistance, peel and pulp characteristics, and seed attributes. Chemical traits included pH, total soluble solids (TSS), total titratable acidity (TAA), and the TSS/TAA ratio. Genetic parameters were estimated using the Restricted Maximum Likelihood/Best Linear Unbiased Prediction method (REML/BLUP), using SELEGEN software. High broad-sense heritability (>0.5) and high accuracy (>0.9) were observed for fruit longitudinal length and seed area, indicating strong genetic control. Moderate heritability estimates (0.26–0.41) for TSS, pulp weight, and pulp yield suggest potential for indirect selection. Significant negative genetic correlations (r=−0.48 to −0.71; p<0.05) between seed yield and pulp-related traits indicate trade-offs important for breeding decisions. Multivariate analyses and Mulamba & Mock index identified genotypes G2, G1, and G7 as the most promising, combining high pulp yield, sweetness, and low acidity that are suitable for both fresh consumption and processing. These results demonstrate the presence of genetic variability in the evaluated germplasm and indicate promising genotypes in the *ex situ* colletion, that can be used in sapodilla in future breeding programs.

Keywords: exotic fruits, plant breeding, REML/BLUP methodology, *ex situ* germplasm banks, *Achras sapota*, *Manilkara achras*.

Resumo

O sapoti (*Manilkara zapota*) é uma frutífera tropical de alto valor nutricional e econômico, e que tem ganhado relevância no Nordeste do Brasil. Avaliaram-se a variabilidade genética e a seleção de genótipos superiores de *M. zapota,* baseadas em características morfométricas e químicas dos frutos. Foram avaliados nove genótipos (162 frutos) do banco de germoplasma *in situ* da Universidade Estadual do Maranhão. As características morfométricas incluíram peso, comprimento longitudinal e transversal do fruto, resistência à penetração, características da casca, da polpa, e das sementes. As características químicas incluíram pH, sólidos solúveis totais (SST), acidez titulável total (ATT) e a relação SST/ATT. Os parâmetros genéticos foram estimados utilizando o método de Máxima Verossimilhança Restrita/Melhor Predição Linear Não Viesada (REML/BLUP), pelo software SELEGEN. Alta herdabilidade em sentido amplo (>0,5) e alta acurácia (>0,9) foram observadas para os parâmetros comprimento longitudinal do fruto e a área da semente, indicando forte controle genético. Estimativas moderadas de herdabilidade (0,26–0,41) para SST, peso e rendimento de polpa sugerem potencial para seleção indireta. Correlações genéticas negativas significativas (r=−0,48 a −0,71; p<0,05) entre o rendimento de sementes e características da polpa demonstram fatores importantes para decisões de melhoramento. Análises multivariadas e o índice de Mulamba & Mock identificaram os genótipos G2, G1 e G7 como promissores, pois combinam alto rendimento de polpa, doçura e baixa acidez, sendo adequados para consumo *in natura* e para processamento. Os resultados confirmam a existência de variabilidade genética entre os genótipos de sapoti da coleção e destacam genótipos-chave para futuros programas de melhoramento.

Palavras chave: frutíferas exóticas, melhoramento genético, REML/BLUP, bancos de germoplasma *ex situ*, *Achras sapota*, *Manilkara achras*.

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1. Introduction

Sapodilla [*Manilkara zapota* (L.) P. Royen], also known as "chicozapote", is a fruit tree of the Sapotaceae family (Milind-Parle and Preeti, 2015) native to the Yucatán Peninsula in Mexico and to other lowland forests in Central America. These trees grow slowly, have high longevity, and can reach heights of 15 to 30 meters. They produce a sticky white latex called "chicle gum", which was widely explored for gum production at the end of the 19th century (Mathews, 2022). Sapodilla has also been used for latex, timber, and fruit production (Reyes-Gómez et al., 2018). It is commonly cultivated in humid tropical and subtropical regions (Ravishankar et al., 2021). The species was introduced in South America, especially in Venezuela and Colombia, and adapted well to hot and humid regions of Brazil, such as the Northeast region (Moura and Silva Junior, 1999; Silva Junior et al., 2014).

Manilkara zapota fruits, also known as sapota, are round and brown with a rough yellow-brown skin. They have a soft, grainy, and sweet pulp with a pleasant aroma (Bangar et al., 2022). Their sweetness comes from simple sugars such as fructose, glucose, and sucrose (Tulloch et al., 2020). Sapota is also rich in essential nutrients (including vitamins A, C, and niacin), minerals (iron, potassium, and calcium), and bioactive phytochemicals such as gallotannins, phenolic acids, and flavonoids, which show great potential for diverse pharmacological applications (Rivas-Gastelum et al., 2023).

Due to the diverse biological activities of its compounds, different parts of *M. zapota* are widely used in phytotherapy (Sharma et al., 2024). The active compounds in the leaves have analgesic, antihyperglycemic, antilipidemic, hypocholesterolemic, hepatoprotective, astringent, antioxidant, antiviral, antibacterial, and even anti-cancer properties (Rao et al., 2014; Barbalho et al., 2015; Shaniba et al., 2019; Alrashood et al., 2020). Compounds in the flowers and fruits help regulate nervous system functions, including anxiety, depression, stress, and insomnia (Sharma et al., 2024). Given all these nutritional and medicinal properties, identifying highly productive genotypes is essential to strengthening sapodilla production.

One of the bottlenecks for expanding *M. zapota* commercial orchards is the lack of high-quality genetic material (Kaur et al., 2020). In this context, *ex situ* germplasm banks play a key role in preserving the genetic diversity needed to select desirable agronomic traits, increase productivity, and enhance resilience to environmental changes (Ravishankar et al., 2021). However, further research is needed to expand trait databases for this species (Budiarto et al., 2023).

Success in crop improvement depends on broad genetic diversity, which provides the foundation for advancing breeding programs (Cooper et al., 2021). Phenotypic variation among individuals largely results from genetic differences, a key factor guiding both breeding programs and conservation strategies (Begna, 2021). To develop effective breeding approaches and select superior germplasm, it is important to estimate reliable genetic parameters using easily measured biometric traits (Rosado et al., 2018). Resende (2016) proposed the Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) method, which has been widely applied in tree breeding. This approach allows for accurate estimation of genetic parameters and maximizes genetic gains through selection. REML/BLUP also enables modeling of both fixed and random effects, accounts for the heterogeneity in genetic variances, and performs well in unbalanced data, supporting the prediction of individual genetic potential (Carias et al., 2014).

Morphometric traits are reliable tools for identifying promising genotypes, especially in tropical fruit species with economic importance and in early stages of domestication (Costa et al, 2025; Morillo et al., 2023). They support germplasm management, breeding, and conservation efforts. In this context, this study aimed to assess the genetic variability of sapodilla genotypes maintained in an *ex situ* germplasm collection at the School Farm of the State University of Maranhão, using fruit morphometric and chemical traits. Specifically, we addressed the following questions: (1) Is the phenotypic diversity observed in sapodilla fruits mainly due to genetic or environmental factors?; (2) Which morphometric and chemical fruit traits are most closely related, and how are they correlated?; (3) Which genotypes show the greatest potential for selection and multiplication in the *ex situ* bank to improve fruit productivity in future generations?

2. Materials and Methods

2.1. Study area, plant material, and fruit harvesting

In this study, we evaluated nine sapodilla genotypes from an *ex situ* collection at the School Farm of the State University of Maranhão (UEMA, Universidade Federal do Maranhão), located in São Luís, Maranhão, Brazil (2°35'11.32" S and 44°12'29.62" W). The region has a humid tropical climate, with an average annual temperature of 26.15°C, relative humidity of 82%, and annual rainfall of 2,107 mm (INMET 2024). The local vegetation is typical of the Amazon Rainforest. The soil is Ultisols, according USDA Soil Taxonomy (Soil Survey Staff, 2022). The 20-year-old sapodilla trees were managed uniformly for irrigation, fertilization, and pest management. Genotypes were monitored from flowering to fruiting between August 2024 and January 2025 (Table 1; Figure 1A, 1B, and 1C). As a climacteric fruit, sapodilla was harvested when a yellowish color was observed in the inner mesocarp (Figure 1D).

A total of 162 fruits (12 to 20 per genotype) were randomly collected from different positions within the canopy of each plant. All fruits were uniform in size and free from visible injuries. They were stored in paper bags at the Post-Harvest Laboratory of the State University of Maranhão (LAPOC/UEMA, Laboratório de Pós-Colheita, Universidade Estadual do Maranhão) until full maturation, when biometric and chemical analyses were performed.

Table 1. Characteristics of sapodilla (*Manilkara zapota*) mother trees from the *ex situ* collection at the School Farm of the State University of Maranhão.

Genotype	Latitude	Longitude	DBH (cm)	Height (m)
G-01	02° 35.178' S	44° 12.491' W	91.17	5.85
G-02	02°35.179´ S	44° 12.485´ W	99.81	7.00
G-03	02°35.178´ S	44° 12.481´ W	37.55	3.15
G-04	02°35.178´ S	44° 12.477´ W	91.33	5.40
G-05	02°35.179´ S	44° 12.476´ W	65.00	6.15
G-06	02°35.180´ S	44° 12.471´ W	48.85	5.50
G-07	02°35.178´ S	44° 12.464´ W	63.10	5.20
G-08	02°35.179´ S	44° 12.464´ W	142.84	6.70
G-09	02°35.180´ S	44° 12.462´ W	97.82	6.50

DBH: diameter at breast height.



Figure 1. Visual appearance of *Manilkara zapota* trees from the *ex situ* germplasm collection. A) Productive mother tree; B) Hermaphrodite flowers; C) Branches during the fruiting period; D) Fruit at the sampling stage for biometric analysis.

2.2. Morphometric fruit traits

Morphometric characterization was performed by direct measurements of individual fruits. Mass parameters were determined using a semi-analytical balance (M214A, Quimis), whereas morphometric traits were measured using a digital caliper (Zaas Precision®, Amatools). Fruit firmness was evaluated using a penetrometer (PTR-100, Instrutherm). Pulp yield (PUY, %) and seed yield (SEY, %)

were calculated from pulp and seed weight using formulas described by Guimarães et al. (1992).

The following fruit morphometric traits were analyzed: fruit weight (FRW, g), fruit longitudinal length (FLL, mm), fruit transversal length (FTL, mm), ratio between longitudinal and transversal fruit diameter (LD/TD, unit), peel thickness (PET, mm), pulp thickness (PUT, mm), peel weight (PEW, g), pulp weight (PUW, g), pulp yield (PUY, %), seed weight (SEW, g), seed yield (SEY, %), seed area (SA, mm^3), number of seeds per fruit (NSF, units), fruit penetration resistance (PR, kg/F), seed length (SL, mm), seed width (SW, mm), and seed thickness (ST, mm).

2.3 Chemical pulp traits

Chemical traits were determined using standardized laboratory analytical procedures on homogenized pulp samples. The hydrogen ion potential (pH) was measured using a pH meter (PHS-3C, JuanJuan). Total soluble solids (TSS, °Brix) were determined by direct reading with an analog refractometer (RF001, JuanJuan). Total titratable acidity (TTA, %) was measured by titration with a 0.1N sodium hydroxide solution. The chemical ratio (RT) was calculated as the ratio of TSS and TTA, according to AOAC guidelines (AOAC, 2016).

2.4 Estimation of genetic parameters

Genetic parameters [broad-sense heritability (h^2a), selection accuracy ($r_{a\hat{a}}$), genetic coefficient of variation (CVg, %), experimental coefficient of variation (CVexp, %), and relative coefficient of variation (CVr) that corresponds to CVg/CVexp] were estimated using the Restricted Maximum Likelihood (REML) method combined with the Best Linear Unbiased Prediction (BLUP) approach, according to the following model (Equation 1):

$$y = Xu + Zg + e \quad (1)$$

Where y is the vector of observed data, u is the vector of fixed effects (overall mean), g is the vector of random genotypic effects, and e is the vector of residual errors. X and Z are the incidence matrices for u and g, respectively.

The magnitudes of h^2a and raâ were classified according to Resende et al. (1998) (Table 2). The variance components were estimated using the Expectation-Maximization (EM) algorithm with REML, based on the following mixed model equations

(Equations 2, 3, and 4):

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\left((1-h^2)/h^2\right) \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{g} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \quad (2)$$

$$\hat{\sigma}_e^2 = [y'y - \hat{b}'X'y - \hat{g}'Z'y] / [N - r(X)] \quad (3)$$

$$\hat{\sigma}_g^2 = \left[\hat{g}'A^{-1}\hat{g} + \sigma_e^2 \; tr \; C^{22}\right] / N_g \quad (4)$$

C^{22} is from the form (Equation 5):

Table 2. Classification of heritability $\left(h_a^2\right)$ and selection accuracy ($r_{a\hat{a}}$) magnitudes used to estimate the genetic parameters of *Manilkara zapota*.

Classification	Individual heritability	Selective accuracy
Low	$0.01 < h_a^2 < 0.15$	$0.10 < r_{a\hat{a}} < 0.40$
Moderate	$0.15 < h_a^2 < 0.50$	$0.40 < r_{a\hat{a}} < 0.70$
High	$h_a^2 > 0.50$	$r_{a\hat{a}} > 0.70$

$$\begin{bmatrix} C^{11} & C^{12} \\ C^{21} & C^{22} \end{bmatrix} = \begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}(\sigma_e^2 / \sigma_g^2) \end{bmatrix}^{-1} \quad (5)$$

Where $r(X)$ is the rank or number of linearly independent columns in X, N_g is the number of random elements (individuals), A is the additive genetic relationship matrix, tr is the trace operator (sum of the diagonal elements of the matrix), N is the total number of observations, and h^2 is the broad-sense individual heritability, calculated as: $h^2 = \hat{\sigma}_g^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_e^2)$).

For the statistical analyses, we used the software SELEGEN-REML/BLUP (Statistical System and Computerized Genetic Selection by Mixed Linear Models), version 2016, model 20 (Resende, 2016). Deviance Analysis (ANADEV) or Likelihood Ratio Test (LRT) was performed using the Chi-square (χ^2) statistic, at a 1% significance level with one degree of freedom. The evaluated genotypes were compared to those estimated using the full model (with and without the genotype effect), as proposed by Resende (2007).

2.5 Selection index

Predicted genotypic values were used to calculate the selection index based on the sum of ranks method, as proposed by Mulamba and Mock (1978). Genotypes were ranked for each trait individually, and the rank values were summed across all traits for each genotype. The resulting total was used as a global selection index, allowing genotype classification based on overall performance (Cruz et al., 2014).

2.6 Multivariate analyses and graphs

Pearson´s genetic correlations between variables were calculated using the genotypic values estimated by the model (μ + g). Principal component analysis (PCA) was applied to these values to identify the traits contributing most to the observed variation. All analyses were performed in RStudio (version 2024.12.1+563) using R version 4.3.2 (R Core Team, 2020). The following R packages were used to compute results and generate graphs: *ggcorrplot, corrplot, readr, Hmisc, writexl*, and *devtools* (Wickham, 2016).

3. Results

3.1 Genetic parameters

ANADEV using LRT evidenced statistically significant differences among the *M. zapota* genotypes for most of the evaluated traits, except TTA and ST (Table 3). The variability in TTA and ST seems largely influenced by environmental factors rather than genetic components.

Environmental factors contributed substantially to trait variation, as environmental variance (σ^2e) exceeded genotypic variance (σ^2g) for most of the evaluated traits, except for FLL and SA (Table 3). These two traits also showed the highest individual heritability ($h^2a > 0.5$) and high selective accuracy (raâ > 0.7), indicating a strong genetic influence and promising potential for genetic gain trough selection (Table 3).

Four traits showed moderated heritability combined with high selective accuracy: TSS (h^2a=0.42; $r_{aâ}$=0.86), SL (h^2a=0.36; $r_{aâ}$=0.83), SW (h^2a 0.23; $r_{aâ}$ 0.74), and RT (h^2a 0.16; $r_{aâ}$ 0.66). Most pulp-related traits and one related to fruit size (FRW, PET, PUT, PUW, PUY, and SEY) also showed moderate heritability ($0.15 < h^2a < 0.5$) but with moderate accuracy ($0.4 < r_{aâ} < 0.7$). These results suggest that genetic components contribute to phenotypic variation in these traits and indicate additional targets for selection aimed at genetic gain (Table 3). The lowest broad-sense heritability values ($0.01 < h^2a < 0.15$) were observed for FTL, LD/TD, PEW, SEW, NSF, PPN, TTA, PH, and ST (Table 3). This suggests that the environmental factors exerted a stronger influence on the phenotypic variation in these traits.

The highest selection accuracy values ($r_{aâ} > 0.7$) were observed for FLL, SA, PUW, PUY, SEY, TSS, and SL (Table 3). As many of these traits are related to pulp, they represent reliable phenotypic descriptors for use in sapodilla breeding programs.

3.2 Correlation between evaluated traits

Figure 2 presents Pearson´s correlation coefficients between all evaluated traits. FRW showed strong, positive, and statistically significant correlations with FLL (0.82), FTL (0.77), PUW (0.97), and PEW (0.43). PUW showed

Table 3. Genetic parameters estimated from fruit traits of *Manilkara zapota.*

Traits	σ_g	σ_e	σ_f	h^2a	h^2mc	$r_{aâ}$	$CV_{g(\%)}$	$CV_{e(\%)}$	CVr	Mean
FRW (g)	219.49*	748.13	967.62	0.22	0.54	0.73	12.58	23.23	0.54	117.73
FLL (mm)	32.93*	24.27	57.20	0.57	0.84	0.92	10.25	8.80	1.16	55.95
FTL (mm)	7.76*	43.31	51.07	0.15	0.41	0.64	5.06	11.94	0.42	55.08
LD/TD	0.004*	0.02	0.02	0.18	0.47	0.68	25.02	52.88	0.47	0.26
NSF	0.76*	4.10	4.87	0.15	0.42	0.65	17.72	41.12	0.43	4.93
PET (mm)	0.007*	0.02	0.03	0.23	0.54	0.73	8.51	15.54	0.54	1.03
PEW (g)	1.86*	23.54	25.41	0.07	0.24	0.49	9.11	32.40	0.28	14.98
pH	0.015*	0.13	0.15	0.10	0.31	0.56	2.87	8.38	0.34	4.31
PR (kg/F)	0.14*	1.25	1.39	0.09	0.30	0.55	30.18	91.62	0.33	1.22
PUT (mm)	3.26*	16.74	20.00	0.16	0.44	0.66	9.22	20.90	0.44	19.58
PUW (g)	210.83*	583.52	797.35	0.26	0.59	0.77	14.56	24.29	0.59	99.67
PUY (%)	5.42*	16.19	21.61	0.25	0.57	0.76	2.76	4.77	0.57	84.33
RT (TSS/TTA)	418.83*	2,142.12	2,560.95	0.16	0.44	0.66	15.22	34.42	0.44	134.46
SA (mm^3)	0.03*	0.02	0.06	0.60	0.85	0.92	12.57	10.33	1.22	1.51
SEW (g)	0.21*	2.17	2.38	0.08	0.27	0.53	14.56	46.83	0.31	3.14
SEY (%)	0.65*	1.22	1.86	0.35	0.68	0.82	29.41	40.33	0.73	2.73
SL (mm)	2.96*	5.16	8.12	0.36	0.70	0.83	11.55	15.25	0.76	14.88
ST (mm)	0.03ns	0.65	0.68	0.05	0.17	0.41	3.72	16.47	0.22	4.90
SW (mm)	0.42*	1.43	1.86	0.23	0.54	0.74	7.17	13.15	0.54	9.10
TSS (°Brix)	1.69*	2.42	4.11	0.41	0.73	0.86	5.61	6.72	0.83	23.16
TTA (%)	0.07 ns	3.43	3.50	0.02	0.08	0.28	9.19	63.93	0.14	2.89

Parameters: σg: genotypic variance, σe: residual variance, σ_f: individual phenotypic variance, h^2a: broad-sense heritability of individual plots, h^2mc: heritability of genotype means, $r_{aâ}$: genetic accuracy, CVg (%): genotypic variation coefficient, CVe (%): coefficient of residual variation, CVr: coefficient of relative variation. **Traits**: FRW: fruit weight (g), FLL: fruit longitudinal length (mm), FTL: fruit transversal length (mm), LD/TD: ratio between longitudinal and transversal fruit diameter, NSF: number of seeds per fruit (unit), PET: peel thickness (mm), PEW: peel weight (g), pH: hydrogen ion potential (unit), PR: penetration resistance (kg/F), PUT: pulp thickness (mm), PUW: pulp weight (g), PUY pulp yield (%), RT: Chemical Ratio (TSS/TTA), SA: seed area (mm^3), SEW: seed weight (g), , SEY Seed Yield (%), SL: Seed length (mm), ST: seed thickness (mm), SW: Seed width (mm), TSS: total soluble solids (°Brix) and TTA: total titratable acidity (%). *Significant at 5% via the LRT test, *ns*: not significant at 5%.

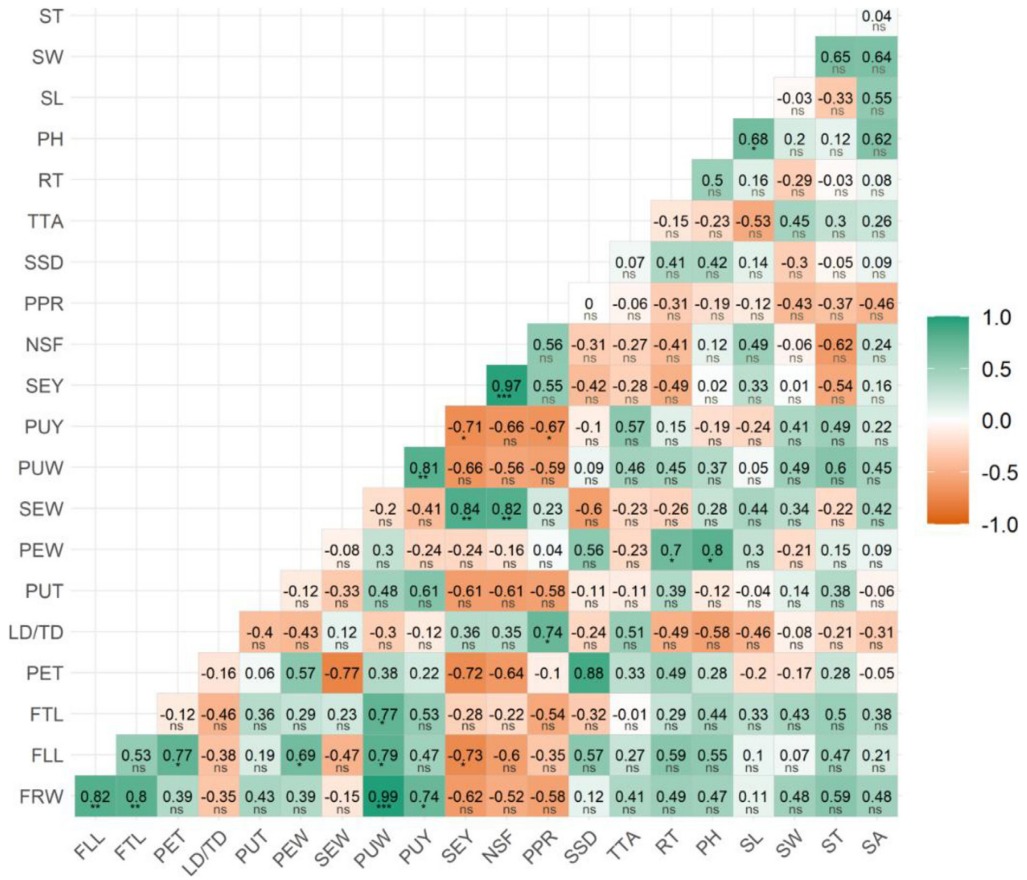


Figure 2. Pearson's correlation coefficient (r) between the morphometric and chemical traits of fruits from nine *Manilkara zapota* genotypes**. Statiscal** Legend: ns: not significant, *: p<0.05 significance, **: p<0.01 significance. Traits Legend: FRW: fruit weight (g), FLL: fruit longitudinal length (mm), FTL: fruit transversal length (mm), PET: peel thickness (mm), PUT: pulp thickness (mm), PEW peel weight (g), SEW seed weight (g), PUW pulp weight, PUY pulp yield (%), SEY Seed Yield (%), NSF number of seeds per fruit (unit), SSD: soluble solids (°Brix), TTA: total titratable acidity (%), RT: Chemical Ratio SSD/TTA, PH: hidrogenionic potencial (unit), SL: Seed length (mm), SW: Seed Width (mm), ST: seed thickness (mm), SA: Seed area (mm^3).

additional strong correlations with PUY (0.84), FLL (0.70) and FTL (0.75), as well as PET and TTA (0.88). A moderate positive correlatios was found between TSS and PUY (0.42) (Figure 2).

The number of seeds per fruit (NSF) was positively correlated with SEY (0.97) and negatively correlated with PUY (-0.66). SEY also showed strong negative correlations with PUY (-0.71), PUW (-0.66), and PUT (-0.61). Likewise, TTA was negatively correlated with PET (-0.72), PUT (-0.61), PUY (-0.60), and PUW (-0.59). As expected, seed biometric traits (SL, SW, ST, and SA) were strongly positively correlated with one other (Figure 2).

3.3 Principal component analysis

PCA revealed that the first two components explained 57.26% of the total variance (Figure 3). The first component (PC1, X axis) accounted for 35.5% of the genotypic variance, while the second component (PC2, Y axis) explained 21.7% (Figure 3A).

Most of the evaluated genotypes clustered in Group 1, which was associated with traits like FRW, FLL, FTL, LL/TL, FLL, ST, SA, PUW, PUT, PUY, RT, TSS, and TTA (Figure 3A). Group 2 included fewer genotypes, which were more strongly associated with NSF, SEW, SEY, ST, SL, TTA, PR, and PET (Figure 3A). The four traits that contributed most to separation along PC1 were PUW, FRW, FLL, and SEY (Figure 3B). In contrast, SL, PH, SEW, and SA contributed most to the separation along PC2 (Figure 3C). PCA revealed that the main differences among the genotypes were primarily associated with fruit size traits and, secondarily, with traits related to pulp acidity and seed biometric parameters.

3.4 Mulamba and Mock index ranking

Based on eight evaluated traits, genotypes G2, G1, G7, G3, G9, and G6 showed the highest overall rankings according to the Mulamba and Mock index (Table 4, Figure 4). The results indicate that different genotypes are suitable for distinct breeding purposes. For example, G2, G9, and G7 were superior in pulp yield and fruit weight, while G2, G1, G3, and G9 stood out for their low titratable acidity and high total soluble solids, reflecting greater sweetness.

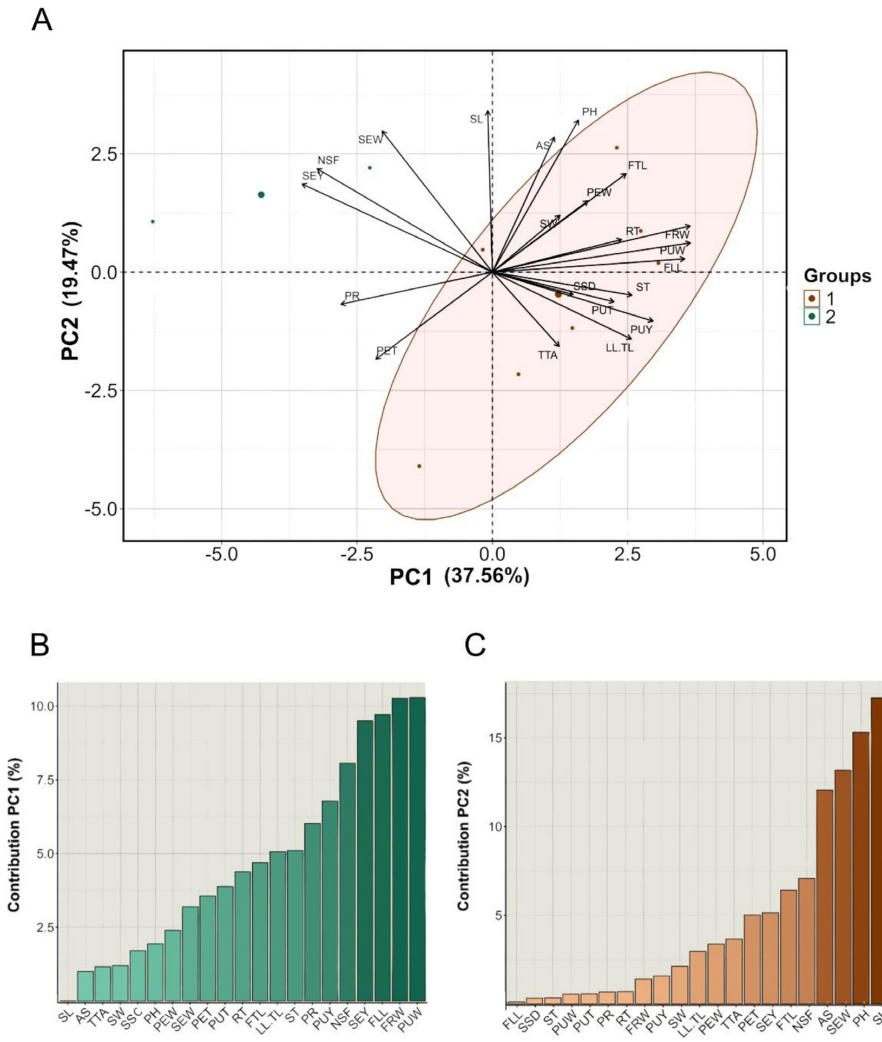


Figure 3. Principal component analysis (PCA) of morphometric and chemical traits of *Manilkara zapota*. A) PCA bi-plot of the nine genotypes based on all evaluated traits; B) Relative contribution of each trait to principal component 1 (PC1); and C) Relative contribution of each trait to principal component 2 (PC2).

Table 4. Classification of 9 genotypes of *Manilkara zapota* based on the Mulamba and Mock (1978) average ranking index.

Trait*	Genotype								
	G2	**G1**	**G7**	**G3**	**G9**	**G6**	**G8**	**G5**	**G4**
FRW (+)	2	5	4	3	1	7	6	8	9
PET (-)	1	5	6	3	7	4	8	2	9
PUT (+)	2	3	1	6	7	4	5	8	9
PEW (-)	8	4	1	9	6	7	2	3	5
PUW (+)	2	5	4	3	1	7	6	8	9
PUY (+)	5	3	2	6	1	8	4	7	9
TSS (+)	5	1	9	4	3	2	7	8	6
TTA (-)	5	7	6	1	9	4	8	2	3
Mean Rank	**3.75**	**4.13**	**4.13**	**4.38**	**4.38**	**5.50**	**6.00**	**7.50**	**9.00**

*Traits: FRW: fruit weight (g), PET: peel thickness (mm), PUT: pulp thickness (mm), PEW: peel weight (g), PUW: pulp weight (g), PUY pulp yield (%), TSS: total soluble solids (°Brix) and TTA: total titratable acidity (%).

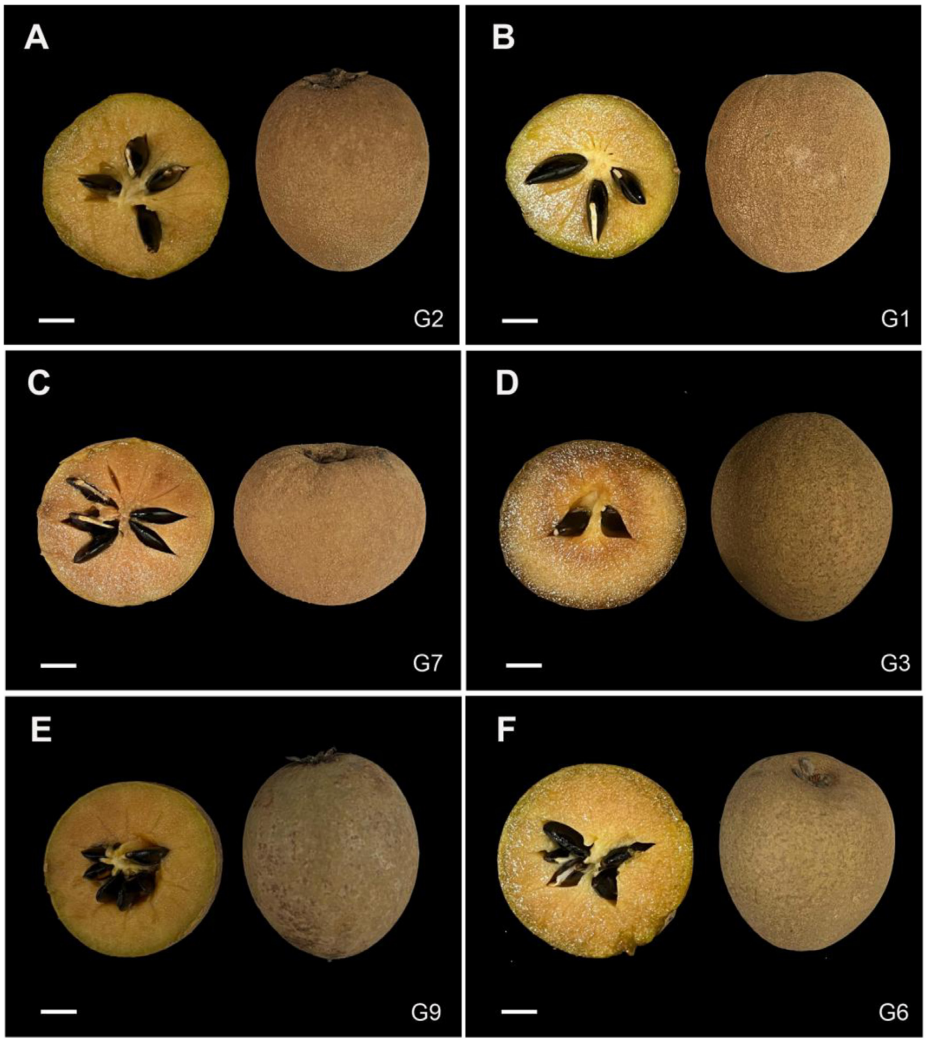


Figure 4. Visual appearance of *Manilkara zapota* fruits from the six top-ranked genotypes selected using Mulamba & Mock mean rank index. A) G2, B) G1, C) G7, D) G3, E) G9, and F) G6. Scale bar: 4 cm.

As shown in Figure 4, genotypes G1 and G2 have brown peels with a slightly smoother texture than G3, G6, and G9, which display a rougher peel texture. Pulp color varied from yellowish-brown in G1, G2, and G6 to orange-brown in G7, G3, and G9. Genotypes G1, G6, and G9, which ranked highest for total soluble solids, also have a juicy pulp texture. In contrast, G7 and G2 have firmer and more opaque pulp. The number of seeds per fruit ranged from 2 to 6. Fruit shape varied across genotypes, from elongated oval (G2, G3, and G6) to oval (G1, G7, and G9) and round (G7).

4. Discussion

The evaluation of germplasm collections is a critical step in plant breeding programs, as it ensures the conservation of genetic diversity and facilitates the identification of superior genotypes with agronomic, nutritional, and commercial potential (Costa et al., 2023; Santos et al., 2024; Costa et al., 2025). In the face of intensified climate change and biodiversity loss, focusing on underutilized fruit species with high socioeconomic and nutritional value, such as *M. zapota*, is important for enhancing food security and promoting agroecological resilience. Previous studies have also emphasized that the conservation and evaluation of sapodilla germplasm are essential to support breeding programs and to expand the cultivation of this species in tropical regions (Lederman et al, 2001; Silva Junior et al., 2014).

Our study confirmed substantial phenotypic variability among *M. zapota* genotypes for most biometric and chemical fruit traits, consistent with patterns reported in *Endopleura uchi* (Costa et al., 2025) and *Psidium cattleyanum* (Santos et al., 2024). This diversity highlights the potential for genotype differentiation and targeted selection. Similarly, Singh et al. (2025) identified wide morphological and agronomic variation in *Tamarindus indica*, while

Dangi et al. (2024) and Tripathi et al. (2025) reported high variability among genotypes of *Prunus avium* and *Cordia myxa*, respectively, further supporting the value of multivariate approaches for identifying superior individuals. These findings align with the present results and highlight the importance of exploiting intraspecific variation in perennial fruit crops.

Despite the genetic diversity observed, environmental variance exceeded genetic variance for most traits, in line with findings for *Mangifera indica* (Costa et al., 2023). This suggests that phenotypic expression in *M. zapota* is strongly influenced by environmental factors, particularly under field conditions where microvariations in soil, climate, and management practices can mask underlying genotypic differences. For example, in *Theobroma grandiflorum*, water restriction significantly reduced fruit production, showing the sensitivity of perennial fruit species to abiotic stresses (Alves et al., 2021). Thus, distinguishing environmentally plastic traits from genetically stable ones is crucial to enable effective selection in breeding programs.

Notably, fruit longitudinal length and seed area exhibited high broad-sense heritability ($h^2a > 0.50$) and selective accuracy ($ra > 0.70$), indicating strong genetic control and high reliability for selection. These results suggest that both traits can be effectively improved through direct selection. Similar findings have been reported in *Attalea speciosa* and *T. indica*, where fruit size and pulp traits also showed high heritability and genetic gain (Pinheiro et al., 2025; Singh et al., 2025). Selective accuracy values above 0.70 are considered robust indicators of true genetic performance (Leão et al., 2023; Costa et al., 2023).

Other traits, such as soluble solids content, pulp weight, and pulp yield, showed moderate heritability and selective accuracy, indicating potential for indirect selection, especially in breeding programs focused on sensory quality. Traits with moderate heritability can be efficiently improved through indirect selection when they are correlated with traits under stronger genetic control (Lagos-Santander et al., 2024). These patterns are consistent with findings reported in *P. cattleyanum* (Santos et al., 2024), *M. indica* (Costa et al., 2023), and *T. grandiflorum* (Alves et al., 2021), where similar traits showed moderate genetic control and relevance to fruit quality improvement.

Beyond heritability, genetic correlations provided additional insights into trait interdependence and selection strategies. Fruit weight was positively correlated with both longitudinal length and pulp weight, suggesting that selecting for larger fruit size could indirectly enhance pulp production. In contrast, seed yield was negatively correlated with both pulp weight and pulp yield, indicating a trade-off between allocation in seeds and pulp. This type of resource partitioning is common in fruit species and has also been reported in *T. grandiflorum* (Alves et al., 2021). Similarly, titratable acidity was negatively correlated with pulp-related traits, suggesting that sweeter, juicier fruits tend to have lower acidity, which is desirable for both fresh consumption and processing. Such trade-offs were also reported by Singh et al. (2025) in *T. indica*, where pod yield was inversely related to pulp percentage. Recognizing and managing these biological constraints is essential for breeding programs aiming to optimize both productivity and quality.

On the other hand, low heritability estimates for peel thickness, pH, and seed number may reflect a narrow genetic base or strong environmental influence. Similar results have been reported for fruit color in mango, where trait expression is highly affected by environmental conditions (Costa et al., 2023). These findings reinforce the need to expand germplasm collections by incorporating new genotypes from contrasting ecogeographic regions to broaden the genetic base for selection (Cooper et al., 2021). This recommendation is particularly relevant for sapodilla, as global germplasm collections remain relatively limited and are concentrated in only a few countries, highlighting the importance of expanding conservation efforts and conducting further characterization studies (Silva Junior et al., 2014).

Multivariate analysis identified genotypes G2, G1, G7, and G9 as the most promising based on the integration of biometric, chemical, and statistical data. G2 and G7 stood out for their pulp yield, while G1 and G9 combined high soluble solids content and low titratable acidity. These genotypes are strong candidates for clonal propagation or use as parents in future breeding programs. Similar strategies have been applied by Singh et al. (2025) and Dangi et al. (2024), who used multivariate clustering to select elite genotypes in tamarind and sweet cherry, respectively, highlighting the robustness of these tools in perennial fruit crop improvement.

Finally, the REML/BLUP mixed model used here proved to be a powerful tool for evaluating perennial species with unbalanced datasets and complex genetic structures. Its effectiveness, previously demonstrated in *E. uchi* (Costa et al., 2025), lies in its capacity to enhance predictive accuracy and improve the reliability of selection. By combining field-based phenotyping, multivariate clustering, and advanced statistical modeling, this study establishes a solid framework for the selection and conservation of *M. zapota*. Future research should prioritize multi-environment trials and the genomic identification of target traits, including the use of molecular markers to assist selection. Integrating these tools into breeding and conservation programs will aind in developing improved cultivars adapted to diverse agroecological conditions (Rivas et al., 2025).

5. Conclusion

The evaluation of the genetic variability of *M. zapota* genotypes (based on morphometric and chemical fruit traits) identified promising genotypes for breeding. The evaluated genotypes showed significant genetic variability, confirming the value of *ex situ* germplasm collections for breeding under tropical conditions. Genotypes G2, G1, and G7 emerged as promising candidates for clonal propagation and hybridization, combining desirable traits such as high pulp productivity, sweetness, and low acidity.

Fruit longitudinal length and seed area showed high heritability and selection accuracy, indicating

strong genetic control and potential for direct selection. Pulp-related traits, including total soluble solids and pulp yield, showed moderate heritability, supporting their use in indirect selection strategies. Future studies should incorporate multi-environment trials and molecular validation to improve selection efficiency and accelerate the development of cultivars adapted to diverse agroecological conditions.

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Data Availability Statement

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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