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Original Paper

Morphometry of the fruits of *Genipa americana* (Rubiaceae): a case study from the southern coast of Bahia, Brazil

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Abstract
We conducted a study to assess the morphometric attributes of *Genipa americana* fruit, and their relationship with variations in elevation and distances between sampling sites on the southern coast of Bahia, Brazil. Eight fruit were used per sampling site (ten sites; n = 80). Mantel's test revealed that the spatial distance between sample sites, and elevation of all sampling sites were significantly correlated with the similarities found in fruit diameter (DF), fruit length (FL), and fresh fruit mass (FFM), but the spatial distance between sites, independently of the elevation, was only correlated with the number of seeds per fruit (NSF) and total fresh mass of seeds per fruit (FMSF). The morphometric attributes of fruits, and their associated relationships with elevation and distance between sampling sites are demonstrated.
Key words: Brazilian Atlantic Forest, elevation, native species, spatial distance.

Resumo
Nós conduzimos um estudo com o objetivo de acessar os atributos morfométricos de frutos de *Genipa americana* e suas semelhanças associadas a elevação e distância entre locais de coleta no Litoral Sul da Bahia, Brasil. Foram utilizados oito frutos por local de amostragem (dez locais; n = 80). O teste de Mantel revelou que a distância espacial e a elevação de todos os locais de amostragem estavam significativamente correlacionadas com as semelhanças encontradas no diâmetro do fruto (DF), comprimento do fruto (FL) e massa fresca do fruto (FFM), mas a distância espacial apenas se correlacionou com o número de sementes por fruto (NSF) e a massa fresca total de sementes por fruto (FMSF). Foi demonstrado que os atributos morfométricos de frutos e suas semelhanças associadas na elevação e distância entre os locais de amostragem.
Palavras-chave: Mata Atlântica Brasileira, elevação, espécies nativas, distância espacial.

Introduction

Genipa americana L. (Rubiaceae) is a neotropical tree with a wide distribution in the Brazilian territory. It is known as "genipapo" in Portuguese, "iá-nipaba" in Tupi-Guarani, or "genipap" in English. *Genipa americana* fruits are of the globose berry type, measure 6–8 cm in diameter, weigh 200–400 g, and have a slightly fermented odor when ripe (Lorenzi 2008). Because they are fleshy and juicy, they can be consumed in natural or processed form. They are used by the food industry when manufacturing sweets, juices, and liqueurs (Prudente 2002). Thus, the fruit has great socio-economic importance in some parts

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of northeastern Brazil (Magistrali *et al*. 2013; Virgens *et al*. 2019). The fruit stands out as having a pleasant taste and can be used to treat numerous diseases (Rezende 2010). Some studies report that these characteristics are related to the antioxidant activity of vitamins and bioactive compounds, such as monoterpenes and flavonoids (Seifried *et al*. 2007; Santana-Neta 2014; Rezende 2010). *Genipa americana* is a very hardy, and fast-growing species, with commercially important fruit and wood (Lorenzi 2008; Rolim *et al*. 2019). Because of these characteristics, *G. americana* can be an excellent choice for cultivation in agroforestry systems on small farms in the tropics (Montagnini *et al*. 2004).

According to Ducke (1946) and Moraes *et al*. (1994), *G. americana* is probably native to Amazonian regions with alluvial and periodically flooded soils. Historical reports indicate that its fruit was consumed and used for body paintings by indigenous people along the Brazilian Atlantic rainforests before European colonization (Filgueiras & Peixoto 2002; Tomchinsky & Ming 2019). For example, of the reports from 18 authors who visited Brazil in the 16th and 17th centuries [compiled by Tomchinsky & Ming (2019)], 13 cited *G. americana* as a plant Brazilians used as food. Tomchinsky & Ming (2019) also reported that after *M. esculenta* (manioc), *G. americana*, *Ananas comosus* L. (Merr.) (pineapple), and *Ipomoea batatas* L. (Lam.) (sweet potato) were the plants most commonly referenced for food use in Brazil during the 16th/17th centuries.

Located in the Brazilian Atlantic rainforest, the southern coastal region of the state of Bahia is characterized by its proximity to the Atlantic Ocean and has a typically humid, tropical climate (Mori *et al*. 1983). In addition, this region's topography has marked variations in elevation, characterized by the presence of several mountains reaching approximately 1,000 m above sea level (masl) (Amorim *et al*. 2009; Thomas *et al*. 2009; Rocha & Amorim 2012). This region has been inhabited by indigenous people for thousands of years, and by Europeans since the beginning of the 16th century (Cerqueira & De Jesus 2017). Despite being affected by anthropogenic disturbances for centuries, southern Bahia still has one of the greatest diversities of tree species in the world (Martini *et al*. 2007). In southern Bahia, as well as in other parts of northeastern Brazil, the fruits of *G. americana* have been consumed for centuries in the form of fresh fruits, sweets, or liquors, which are much appreciated during the traditional June festivities. Even today however, the exploitation of *G. americana* occurs mainly in an extractive way, through the actions of small farmers, without the use of technology or agronomic practices. Interestingly, in southern Bahia, Brazil this species is not found in primary or secondary forests (*e.g*., Mori *et al*. 1983; Martini *et al.* 2007; Piotto *et al*. 2009; Thomas *et al*. 2009) and is generally found sub-spontaneously in areas close to human settlements, such as cocoa rustic agroforest systems (Sambuichi *et al*. 2012), traditional home gardens, and abandoned pastures. This trend in location may be evidence that the species is not native to this region, but instead may have been spread by indigenous people on a dispersion route that began in the Amazon to the south of Brazil.

Morphometric variations of tree fruits have been associated with differences in elevation and soil characteristics, even on small spatial scales (Itoh *et al*. 2003; Davies *et al*. 2005). Elevation integrates and defines several physical variables, such as soil texture, and nutrient concentrations (Daws *et al.* 2002; Costa *et al*. 2005; John *et al*. 2007; Quesada *et al*. 2009). The relationships between elevation, vegetation, and soil have always been determinants of ecological processes (Dearborn & Danby 2017; Román-Sánchez *et al*. 2018; Sanaei *et al*. 2018). At the regional scale, spatial heterogeneity in vegetation and soil is attributed to variations in topography and climate (Lybrand & Rasmussen 2015). On a local scale, topographic factors such as slope, and slope aspect, can significantly influence vegetation, thereby affecting radiation, temperature, water, and nutrients (Ranney *et al*. 2015; Dearborn & Danby 2017). Topographic factors have important effects on vegetation dynamics (Bernards & Morris 2017; Dearborn & Danby 2017; Méndez-Toribio *et al*. 2017). Variations in the topography of ecosystems influence the responses of plant species and functional groups to increased elevation. Thus, topography is expected to affect the morphological diversity of genipap fruit along the south coast of Bahia.

Because *G. americana* is still managed as a sub-spontaneous tree, and very little is known about its desirable agronomic characteristics, the objective of this study was to assess the morphometric attributes of *G. americana* fruits and their associated relationship with elevation and distance between sampling sites in the southern coast of Bahia, Brazil.

Materials and Methods

Study area and collection of plant material

The study was carried out in the citizenship territory of the southern coast of Bahia (CTSB). The CTSB is composed of 26 municipalities, with a total area of 14,664.54 km^2 and approximately 772,683 inhabitants (Cerqueira & De Jesus 2017). Per Köppen's classification (Alvares *et al.* 2013), the region is a humid (or super-humid) tropical climate of the *Af* type, does not have a dry season, and has an average monthly temperature of 24–26 °C. The total rainfall exceeds 1,500 mm annually, with the greatest rainfall from March–August, and even the driest month receives over 60 mm of rainfall. In the warmer months (January and February) the temperature is 24–25 °C.

Fruits from *G. americana* were collected from where they were spontaneously growing on small rural properties, and from open markets in different areas of the CTSB (Fig. 1). Collections were carried out from April–July 2019 from ten sites throughout six municipalities (Ilhéus - 1,760.0 km^2, Itabuna - 432.2 km^2, Buerarema - 230,5 km^2, São José da Vitória - 72.5 km^2, Ibicaraí -231.9 km^2, and Jussari - 356.8 km^2), within a total area of 3,083.9 km^2 and an elevation gradient of 29–400 masl (Tab. 1). The latitude and longitude of the different sample sites were obtained using a GPS (Global Positioning System). Only healthy and fully ripe fruit were used. Maturation was determined when a natural separation of the fruit and branch occurred, or when a healthy fruit was found in the soil of the sampling site (without herbivory and deformation to the pericarp, or other visible damage). The fruits, once harvested and/or purchased (with the same characteristics as above), were packed in plastic boxes and transferred to the Plant Physiology Laboratory of the Universidade Estadual de Santa Cruz (UESC), Ilhéus, Bahia, Brazil, for later measurements.

Measurement of phenotypic morphometric attributes of fruits

For eight fruit per sampling site were used (ten sites: S1 to S10; n = 80). We measured fruit diameter (FD, cm), fruit length (FL, cm), fresh fruit mass (FFM, g), the number of seeds per fruit (NSF), total fresh mass of seeds per fruit (FMSF, g), total dry mass of seeds per fruit (DMSF, g), and

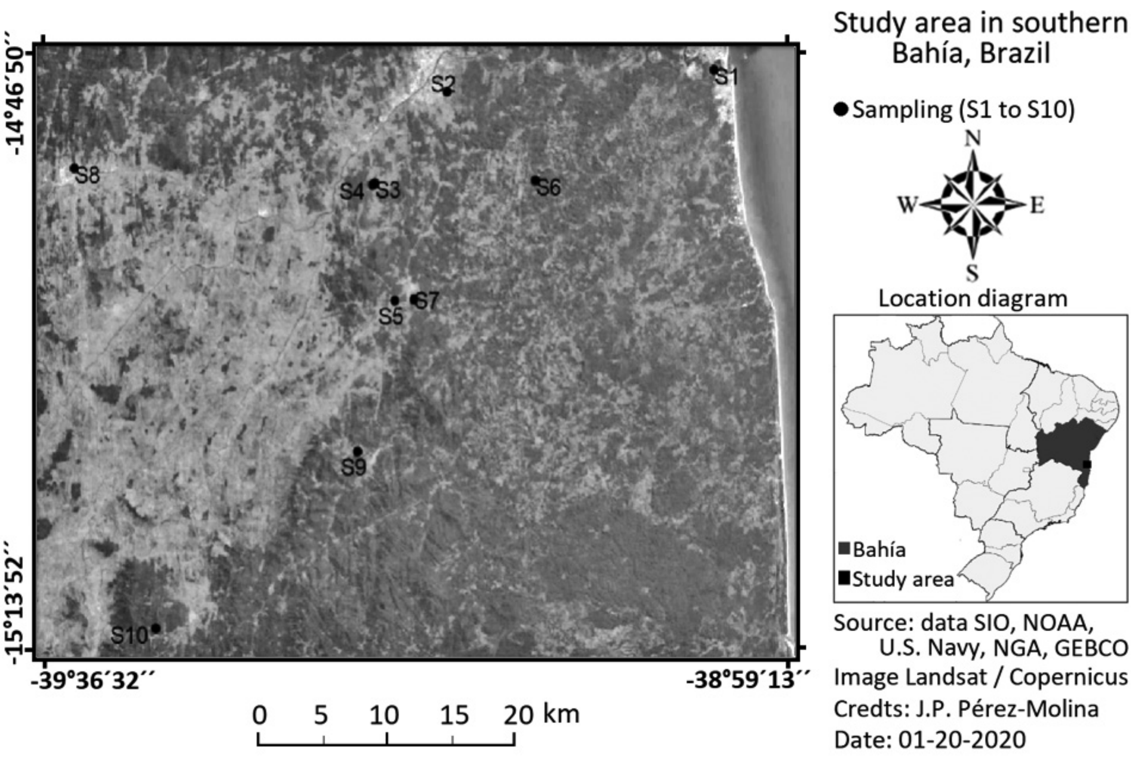

Figure 1 – Collection areas of the fruits of *Genipa americana* in southern Bahia, Brazil. Sampling sites: S1 to S10.

Table 1 – Characteristics of the collection areas of the fruits of *Genipa americana*, in southern Bahia, Brazil.

Origin	City	Site	Coordinate	Elevation (masl)
Tree	Ilhéus I	S1	39º02’23’’W; 14º48’26’’S	29
	Itabuna I	S2	39º15’57’’W; 14º48’50’’S	85
	Buerarema I	S5	39º18’56’’W; 14º57’59’’S	118
	Ilhéus II	S6	39º11’38’’W; 14º52’58’’S	131
	Buerarema II	S7	39º17’59’’W; 14º57’58’’S	158
	São José da Vitória	S9	39º21’05’’W; 15º04’31’’S	208
Free market	Itabuna II	S3	39º19’45’’W; 14º52’44’’S	114
	Itabuna III	S4	39º19’52’’W; 14º52’48’’S	115
	Ibicaraí	S8	39º34’57’’W; 14º51’24’’S	170
	Jussari	S10	39º31’29’’W; 15º11’47’’S	400

the mass of 1,000 seeds (MTS, g). FL was measured from the base to the apex, and FD was measured on the median line (accuracy ± 0.1 mm). After FL and FD measurements, the fruits were pulped, and the seeds were immediately washed in water and dried with paper towels to obtain FMSF. Fruit and seed weights were obtained using an analytical balance accurate to ± 0.001 g. The DMSF was obtained after the seeds were dried on paper towels in the shade at room temperature for approximately one week. Based on the values of FMSF and DMSF the average water content of the seeds in fresh fruits was approximately 82%. Finally, the MTS was calculated in order to estimate the mass of seeds in fresh fruits. The MTS was calculated from the equation adapted from the Ministry of Agriculture and Supply’s seed analysis rules (Mapa 2009): MTS = (1,000 × FMSF) / NSF.

Data analysis

All variables were evaluated using analysis of variance (Fisher’s test) or Kruskal-Wallis for the factor: sampling site (S1 to S10). Bonferroni’s tests were applied to compare the means between sampling sites. All statistical assumptions were checked. Spearman (r_s), or Pearson (r_ρ) correlation coefficients between all pairs of variables were calculated. Mantel’s test correlations (r_m) were made, contrasting the similarities of the phenotypic morphometric attributes of fruit and seeds, with the spatial distances (km) between sites, and the similitude of sample site elevations. These similarities were calculated by the differences of the variables between two sampling sites in a comparison matrix; the spatial separation was calculated by Euclidean distance. The elevation was defined by calculating the average value in a diameter of 1 km around each sampling point (S1 to S10), using *ArcGIS* version 10.7.1. The Mantel test was calculated with permutations of the Monte-Carlo test method (n = 2000 interactions). This test measures the correlation between two matrices (biological variable and spatial distance), and is one way of testing for spatial autocorrelation (Crabot *et al*. 2019; Giraldo Caballero & Camacho-Tamayo *et al*. 2018). All statistical analyses were performed using *R* programming language version 3.6.1, (RCoreTeam 2019) with a significance level of α = 0.05.

To assess the divergence between sites (S), a cluster analysis was performed. The distance matrix of that analysis was calculated using the Euclidean dissimilarity Gower (1985) measure, and Ward’s grouping method (Ward 1963). The definition of the group number was established using the pseudo t^2 index (Duda & Hart 1973). In order to efficiently visualize the relationship between biometric variables and sites, a heat map was constructed. We used red, white, and blue color palettes. The colors are referenced according to the average values of each variable, considering all the sites studied. The red and blue colors indicate values above and below the average, respectively, and the white color relates to values similar to the average. All analyses were performed using R software (R Core Team 2019).

Results

All morphometric attributes of fruit showed significant differences between sampling sites (S1 to S10), ordered from lowest to highest elevation (Fig. 2). Despite this finding, no pair of variables showed the same pattern of magnitude between sampling sites. However, significant correlations were found between the elevation of sampling sites and FD, FL, and FFM (r_s = 0.56, 0.42, and 0.24, respectively; Fig. 3). As expected, all other variables showed a significant correlation with each other, except for MTS with FFM and FMSF ($P > 0.05$).

Mantel's test revealed that the spatial distances between, and elevations of, all sampling sites were significantly correlated with the similarities found in FD, FL, and FFM (r_m = 0.23, 0.29, and 0.26, respectively; $P < 0.001$; Tab. 2) , but the spatial distance between sites, independently of the elevation, only correlated with NSF and FMSF (r_m = 0.09 and 0.10, respectively; $P < 0.05$). DMSF and MTS showed no significant correlation with Mantel ($P > 0.05$).

Cluster analysis showed the formation of two groups in relation to the sites (S), and two groups in relation to the set of variables. For the sites, group I consisted of sites S1, S2, S3, and S4, and group II of sites S5, S6, S7, S8, S9, and S10. For the variables, group I was formed by the variables FMSF, FFM, DMSF, and NSF, and group II by the variables FD, FL, and MST. Group I sites compared to group II had a lower value for morphometric variables, except for MTS (Fig. 4). In contrast, most sites in group II had low MTS values.

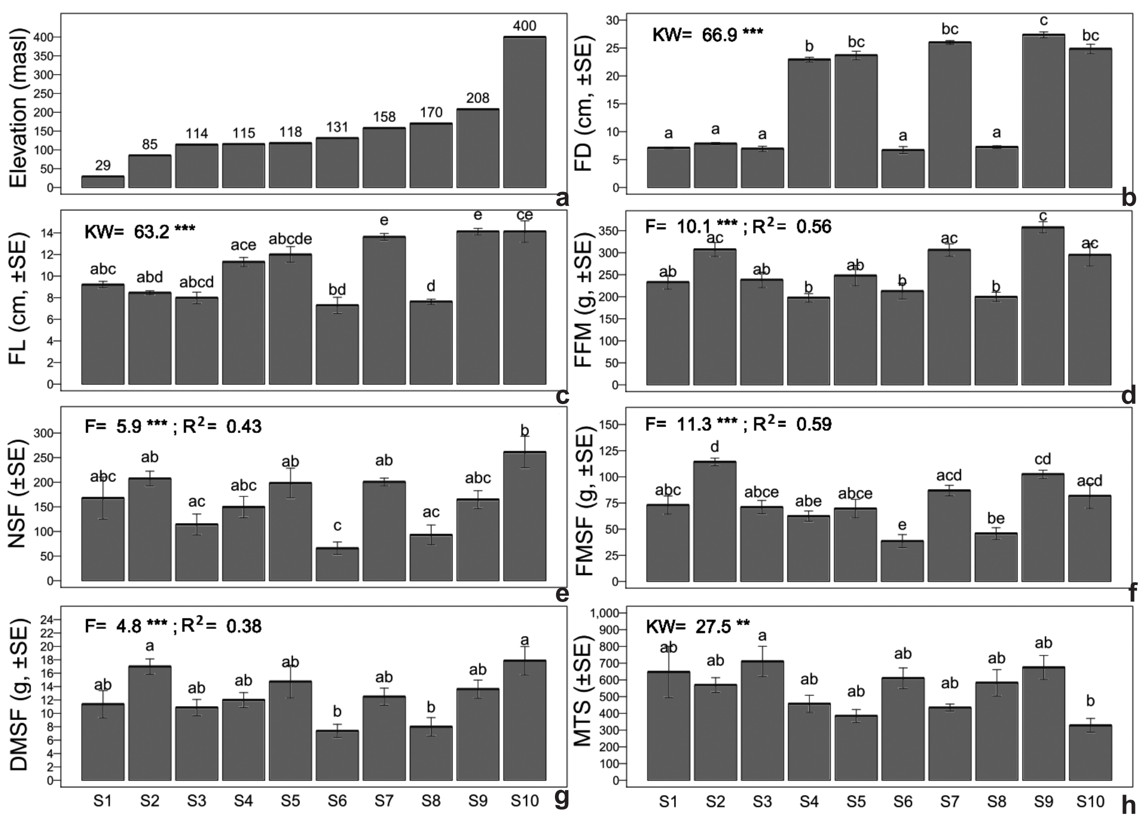

Figure 2 – a-h. Phenotypic morphometric attributes of fruits of *Genipa americana* in southern Bahia, Brazil (n = 8 per sampling sites, S1 to S10) – a. elevation (meters above sea level); b. FD = fruit diameter; c. FL = fruit length; d. FFM = fruit fresh mass; e. NSF = number of seeds per fruit; f. FMSF = total fresh mass of seeds per fruit; g. DMSF = total dry mass of seeds per fruit; h. MST = and mass of 1,000 seeds. Equal letters indicate no statistically significant difference between sampling sites. ($P > 0.05$, Bonferroni's test; KW = Kruskal-Wallis test; F = Fisher value; d.f. = 9, 70; $R2$ = coefficient of determination; ** = $P < 0.01$; *** = $P < 0.001$. SE = standard error).

Discussion

Genipa americana is a neotropical tree, with a wide distribution throughout the Brazilian territory (Judd *et al*. 2008; Souza & Lorenzi 2005). Because of human use of this species, especially by Brazilian indigenous people, it is likely that its current distribution pattern reflects a complex association between ecological and historical processes. These factors may have contributed to shaping the distribution pattern of *G. americana* in the area covered by this study, since the variability found in the morphometric attributes associated with the distribution and elevation of the sites was more accentuated when the sites were closer together.

Patterns of forest diversity depend strongly on how tree species are spatially distributed in relation to the environment (Zuleta *et al*. 2018; Jucker *et al*. 2018; Thomas *et al.* 2015). The spatial heterogeneity of community structures stems from environmental variables, or community processes (Antonelli *et al*. 2018; Badgley *et al*. 2017). In both cases, spatial distribution has a functional role in ecosystems (Borcard & Legendre 2002), and is

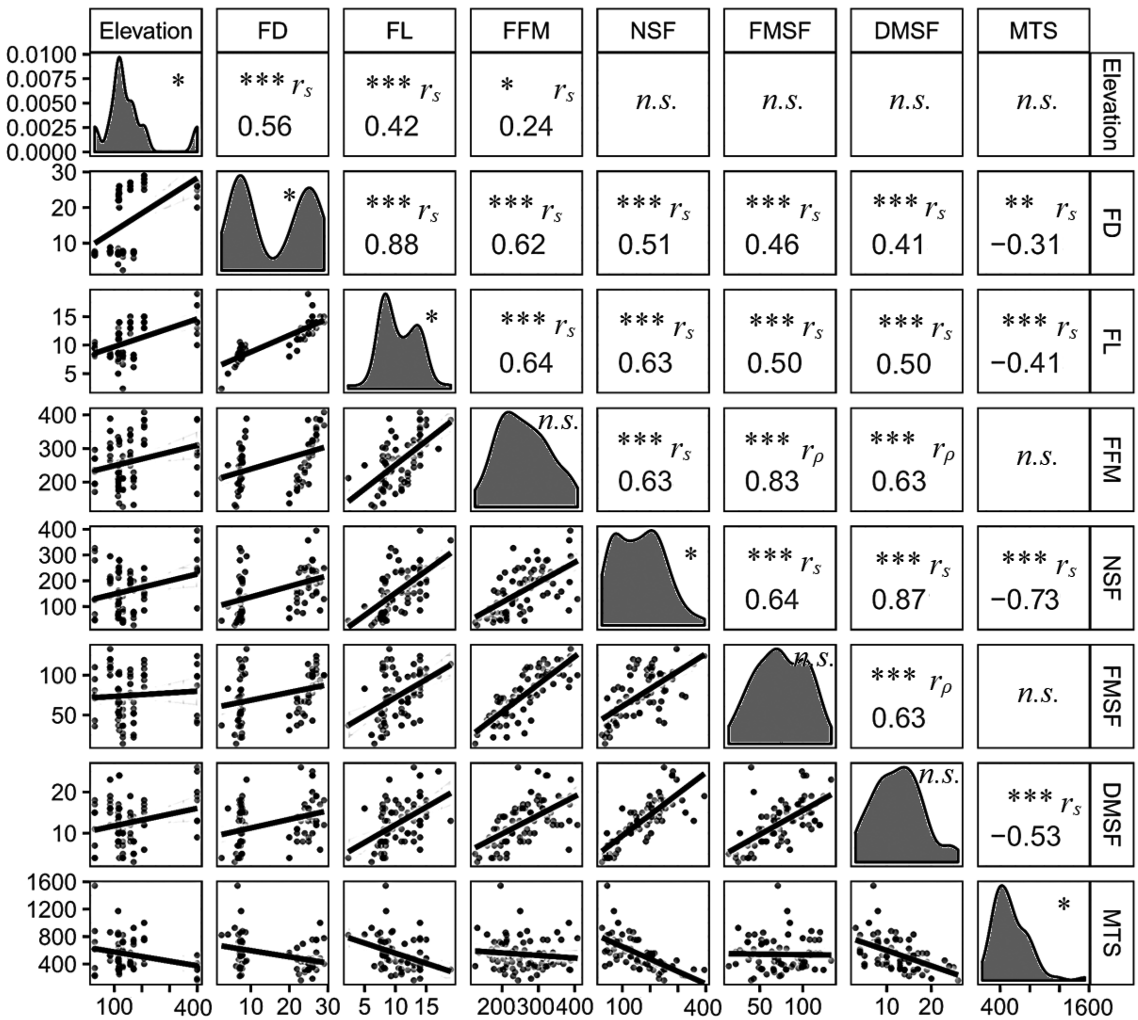

Figure 3 – Matrix of relationships between pairs of phenotypic morphometric attributes of fruits of *Genipa americana* in southern Bahia, Brazil (n = 80). Subplots in the upper diagonal represent the correlation coefficient between pairs of variables (r_s and r_ρ are Spearman and Pearson correlation coefficient, respectively). The subplot on the diagonal shows the probability density curve (Shapiro-Wilks's test, α = 0.05; Normal distribution, p > 0.05). Subplots in the lower diagonal represent the dispersion between pairs of variables (solid line shows the best fit of a linear regression model). *n.s.* = not significant; * = P < 0.05; ** = P < 0.01; *** = P < 0.001. The meaning of the abbreviations sees Fig. 2.

Table 2 – Mantel's test correlations (r_m) between the similarities of the phenotypic morphometric attributes of fruits *vs.* the spatial separation and the similarities of elevation of all sampling sites. *n.s.* = not significant. * = P < 0.05; ** = P < 0.01; *** = P < 0.001. The number of permutations based on Monte-Carlo test were of *n* = 2000 interactions. The meaning of the abbreviations sees Fig. 2.

Variable	FD	FL	FFM	NSF	FMSF	DMSF	MTS
Spatial distance	0.23 ***	0.29 ***	0.26 ***	0.09 *	0.10 *	0.08 *n.s.*	0.07 *n.s.*
Elevation	0.23 **	0.24 **	0.16 ***	0.08 *n.s.*	0.05 *n.s.*	0.07 *n.s.*	0.08 *n.s.*

associated with changes in elevation. In our study, we found high variability in the morphometric attributes evaluated between the sampling sites, which may be related to the anthropization of these areas, and the associated variations in elevation. In addition, within the same species there are individual variations owing to the influences of genetic and environmental factors during seed development (Marcos-Filho 2015). In the present study, the morphometric variations occurred both within, and between, the different locations, resulting in the formation of two clusters depending on the elevation and morphometric characteristics. The sites with the highest elevations are those that also had the highest morphometric values; in fact, environmental factors also seem to affect the variations found. Several studies have shown that tropical tree species have high variability in fruit size, the number of seeds, and fresh weight of fruit (Braga *et al*. 2007; Matos *et al*. 2014; Zuffo *et al*. 2014; Virgens *et al*. 2019).

Studies have shown that the effects of abiotic factors are more evident at larger spatial scales, while biotic factors are more important at smaller scales (Yang *et al*. 2016; Muscarella *et al*. 2019). The spatial variations in ecosystem composition are more evident on larger scales (Jucker *et al*. 2018; Muscarella *et al.* 2019). However, we found that even on smaller scales, it was possible to observe the effects of environmental factors on variations in morphometric characteristics found between, and within the studied sites. Thus, the size and mass of seeds can vary between plants of the same species (caused by the climatic conditions of the year), and within the same plant (Piña-Rodrigues & Aguiar 1993). In addition, the number of seeds per fruit can be affected by the climatic conditions of an area, mainly by water availability during

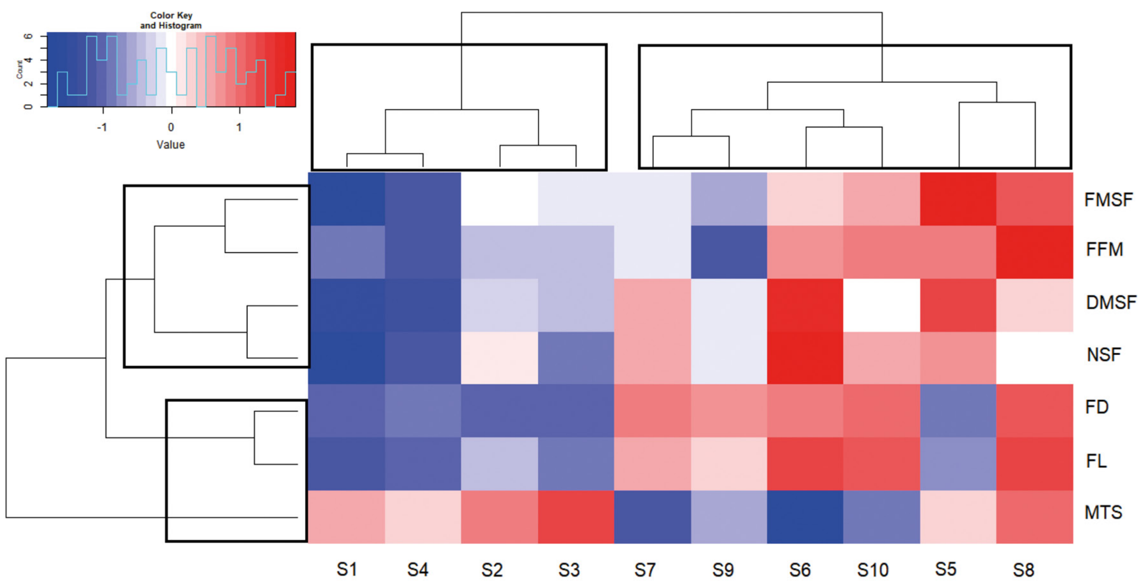

Figure 4 – Cluster analysis with heat map in relation to the sites (horizontal axis) and phenotypic morphometric attributes of fruits of *Genipa americana* in southern Bahia, Brazil. (n = 80) (vertical axis); S = Site.

flowering (Marcos-Filho 2015) affecting the vigor and resistance of storage, as well as the uniformity of the seeds. In tropical forests, at spatial scales smaller than one square kilometer, variation in soil properties can also influence the distribution of tree species (John *et al*. 2007) and affect the characteristics of *G. americana* fruits, as observed in our study.

It should be noted that variations in FMSF may be associated with the high initial water content of the seeds, which reflects the intermediate behavior regarding the storage of *G. americana* seeds (Carvalho & Nascimento 2000; Magistrali *et al*. 2015). The FMFS is also related to the time after extraction of seeds from the fruits (Oliveira *et al*. 2011) and the water availability in the environment (Toublanc-Lambault *et al*. 2019). As the FMFS was measured just after the extraction of the seeds from the fruits, the high values of FMFS in our study may explain the higher values of MTS in comparison with similar studies published with *G. americana* (Paiva-Sobrinho *et al.* 2017; Virgens *et al.* 2019). Moreover, considering that the fruits used in our study were collected in areas of the Atlantic forest (in ecosystems with high, regular, and distributed rainfall throughout the year), the climatic characteristics of the areas may have contributed to the high values of FMSF. The high moisture content of fruits and seeds can also be related to the site elevation. As precipitation increases and evapotranspiration decreases with elevation, a higher elevation can result in higher soil and fruit moisture content (Zhu & Lin, 2011; Wang *et al.* 2017). However, significant relationships between elevation with FMSF and TMS were not observed in our study.

Our results showed that native tree species which are not yet domesticated, but are found in areas of anthropization, present highly variable morphometric characteristics, as previously verified for this (and other) species (Virgens *et al*. 2019; Paiva-Sobrinho *et al.* 2017; Sangalli *et al*. 2012; Silva Junior *et al*. 2012; Zuffo *et al.* 2014). Thus, knowledge of the morphometric variations of fruit characteristics is important for the improvement of these characteristics (Gonçalves *et al.* 2013). From a genetic perspective, studying the relationship between fruit and seeds is efficient for understanding the dynamics of the morphometric characteristics of each species (Gonçalves *et al*. 2013; Souza *et al.* 2016; Maurya *et al.* 2015; Zuffo *et al.* 2016), as these correlations can help identify which mechanisms are involved in the species' diversity of expression. In our study, it was possible to observe strong correlations between FL and FD, and between FMSF and MTS. In addition, sites S10, S9, and S7 showed a stronger correlation between these variables than others, and indicate the possibility of developing procedures to estimate the production of seeds for commercial purposes from assessments in the areas of seed collection.

We also demonstrated that fruits of *G. americana* with different spatial distributions and elevations in the southern region of Bahia showed highly variable morphometric attributes. Differences in the variability of these characteristics can be indicative of the degree of the sites' anthropization. It should also be noted that exploitation of *G. americana* in the southern region of Bahia is mainly extractive. However, the commercialization of fruits in the region mainly occurs in open markets, on the edges of highways where species occur, or on rural properties where cocoa is planted based on the *cabruca* production system, under the shade of native trees such as *G. americana*. Thus, studies such as this one can inform the selection of native trees in a humid tropical climate based on the morphometric characteristics of fruits, to indirectly select important variables for the conservation or exploitation of the genetic resources of these species.

In summary, all morphometric attributes of fruits showed a significant difference between sampling sites. Significant correlations were found between the elevation of sampling sites and fruit diameter, and fruit length and fresh fruit mass. Mantel's test revealed that the spatial distance between sites and elevation of all sampling sites were significantly correlated with the similarities found in fruit diameter, fruit length, and fruit fresh mass, but the spatial distance between sites, independently of the elevation, was only correlated with the number of seeds per fruit and total fresh mass of seeds per fruit. The morphometric attributes of fruit and seeds, and their associated similarities in elevation and distance between sampling sites have been demonstrated.

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