Journal of Agricultural Science; Vol. 15, No. 2; 2023
ISSN 1916-9752 E-ISSN 1916-9760
Published by Canadian Center of Science and Education

Diameter Distribution of *Vouacapoua americana* Aublet in the Brazilian Amazon

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Received: December 9, 2022 Accepted: January 5, 2023 Online Published: January 15, 2023
doi:10.5539/jas.v15n2p82 URL: https://doi.org/10.5539/jas.v15n2p82

Abstract

Vouacapoua americana Aublet was classified as endangered in 2013 and its extraction banned in 2014. Forest management allows conservation and sustainable production, but, for this, knowledge of diameter distribution is fundamental. This study aimed to characterize and analyze diameter distribution patterns of the species at different sites in the Brazilian Amazon. Data on trees with diameter ≥ 10 cm were acquired from continuous forest in permanent sample plots and preharvest forest inventories (PHFIs) of nine forest management areas. Absolute density, diameter distribution, and De Liocourt quotient (q) were calculated. Diameter distributions were fitted by a linearized Meyer type I distribution function, and the similarity between distributions was analyzed by the nonparametric Kruskal-Wallis test (H-test). The species showed high density (6.31 to 25.55 trees/ha). Mensrured diameters ranged from 10.00 to 127.32 cm. A decreasing behavior was observed in all diameter distributions, with few discontinuous distributions and mostly truncated distributions. The De Liocourt quotient (q) did not show constancy or proximity, with values ranging from 0.4 to 23.48. Diameter distributions did not differ by the Kruskal-Wallis test ($H = 15.45$, $p = 0.3479$). Diameter distributions fitted by the Meyer model resulted in an inverted "J"-like curve. The diameter structure showed a high density of individuals, a decreasing distribution from smaller to larger diameter classes, a characteristic inverted "J" pattern, and unbalanced diameter distributions.

Keywords: endangered species, species conservation, species management

1. Introduction

The species *Vouacapoua americana* Aublet, belonging to the family Leguminosae (Fabaceae) and subfamily Caesalpinioideae, occurs in the Brazilian Amazon in Maranhão, Pará, Amapá, and Amazonas States (Silva et al., 1988; Pinagé & Paiva, 2011), where it is known as acapu, acapuzeiro, angelim-da-folha-larga, and ritangueira. The species is also found in the Guianas and Suriname, where it is called brownheart, partridgewood, bruinhart, wakapoe, wacapoe, vacapon, wacapou, and sarabebeballi, among other names (Pinagé & Paiva, 2011). *V. americana* is characteristic and exclusive to the Amazon rainforest dry lands, where it is moderately frequent but of irregular and discontinuous dispersion. It occurs, predominantly, within primary forests on flat lands with clay soils well supplied with moisture (Lorenzi, 1998; Silva & Leão, 2006).

Because of its widely appreciated beauty and mechanical resistance, *V. americana* has a long history of use in Pará State, being intensively applied in the manufacture of floors and other building structures. However, in recent decades, *V. americana* has been mostly commercialized for the production of fence posts and pickets, corrals, and tutor sticks for pepper and passion fruit crops (Homma, 2014). This demand for *V. americana* wood is met through timber extraction without appropriate forest management techniques, which ultimately resulted in the classification of the species as "endangered (EN), A2cd" in the Official National List of Endangered Plant

Species (Martinelli & Moraes, 2013). As of December 17, 2014, *V. americana* extraction is prohibited under Ordinance No. 443 of the Brazilian Ministry of Environment.

An economic conservation strategy to ensure sustainable wood production from *V. americana* is to adopt forest management practices. However, it is only possible to apply appropriate silvicultural and conservation practices with sufficient knowledge about the characteristics of each species (Cruz et al., 2021). Thus, efficient management of *V. americana* necessitates understanding its ecological, structural, silvicultural, and economical variables, among others.

Tree size distribution analysis is a simple but effective tool for describing tree populations and forest stands (Lima et al., 2015), contributing to decision-making in forest management (Santos et al., 2016; Orellana et al., 2017). Diameter distributions, when evaluated at the species level, provide information on species-specific regeneration strategies, demographic rates, and population trends (Knight, 1975; Wright et al., 2003). Given the differences in growth rates and the great variations in age among trees, the diameter structure differs between forest typologies, succession stages, and species or groups of species analyzed individually (Cysneiros et al., 2017).

Forest diameter distribution profiles can be classified as decreasing, unimodal, and multimodal (Scolforo, 2006). The decreasing diameter distribution, also known as inverted "J" distribution, is characterized by a decrease in the number of trees per unit area with increasing tree diameter and is mainly observed in native forests (Marcon et al., 2015). This type of diameter distribution may indicate a continuous flow of natural regeneration (Meyer, 1952; Canalez et al., 2006). Unimodal distributions are characteristic of young and coeval forest stands (Marcon et al., 2015) and may indicate that regeneration occurs in cycles (Scolforo, 2006). Finally, multimodal distributions, characterized by more than one high-frequency peak, may be indicative of species differing in performance or age, different site qualities within the forest, or differences in silvicultural treatments (Marcon et al., 2015).

For Orellana et al. (2014), it is of fundamental importance to conduct studies on the diameter distribution of species at the individual level for assessing natural regeneration dynamics or defining criteria for sustainable extraction. Diameter distribution curves allow to infer on the conservation level of forest communities, as they allow visualizing the existence or not of proportionality in the number of individuals in each diameter class and the shape and intensity of the distribution curve (Lima et al., 2013).

In view of these observations, the following question arose: What is the diameter distribution pattern of *V. americana* in the Brazilian Amazon? Using PHFIs (100% of individuals) and CFIs carried out in forest management areas in the Brazilian Amazon, in addition to a literature review, we sought to answer the above question and test the hypothesis that *V. americana* exhibits an inverted "J" diameter distribution curve. Thus, this study aimed to characterize the diameter structure and identify the distribution pattern by diameter class of *V. americana* at different sites of the Brazilian Amazon, generating knowledge to guide management and conservation actions for the species in natural forests in the study region.

2. Method

2.1 Characterization of Study Sites

The study was conducted in a region of occurrence of *V. americana* in the Brazilian Amazon. Data collection was performed at 15 study sites, each comprising an annual production unit in one of nine forest management areas in the municipalities of Almerim, Anapú, Breu Branco, Mojú, Novo Repartimento, Paragominas, and Portel in Pará State and Mazagão in Amapá State, Brazil (Figure 1). Characterization of study sites (Table 1) was performed using data from forest management plans and their respective annual operational plans. The climate of study sites is classified in the Köppen-Geiger classification system as humid tropical (Am), with average temperatures in the coldest month always above 18 °C, a short dry season, and large amounts of rainfall (Beck et al., 2018). Predominant soils are classified according to the Brazilian Soil Classification System (Santos, 2018). Vegetation classification follows the Technical Manual of Brazilian Vegetation (IBGE, 2012).

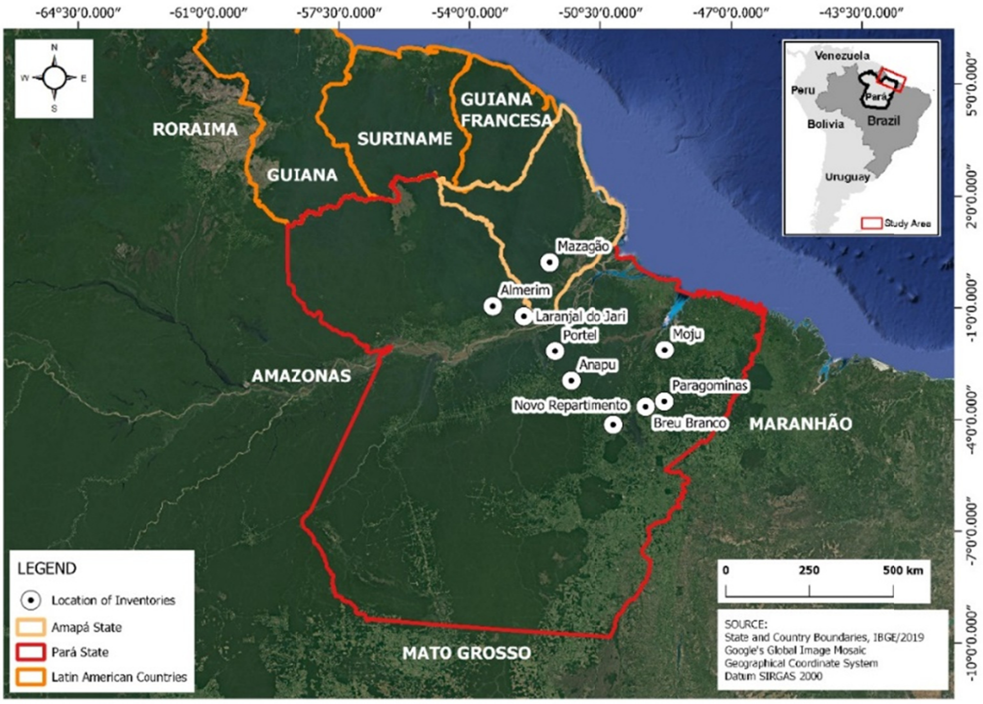

Figure 1. Location map showing the distribution of study sites for collection of acapu (*Vouacapoua americana* Aublet) populations in Pará and Amapá States, Brazil.

Table 1. Physical description of study sites of acapu (*Vouacapoua americana* Aublet) populations in Pará (PA) and Amapá (AP) States, Brazil

Municipality, State (study sites)	Area (ha)	Latitude	Longitude	Annual rainfall (mm)	Predominant soils	Vegetation
Paragominas, PA (Paragominas)	969*	-3.52	-48.79	1800	Yellow Latosol, Yellow Argisol	Submontane DOF
Moju, PA (Moju)	11**	-2.127	-48.78	2500	Yellow Latosol, Red-Yellow Argisol	Submontane DOF
Breu Branco, PA (Breu)	21.8**	-3.6628	-49.2849	2000	Yellow Argisol, Dystrophic Red-Yellow Argisol, Yellow Latosol	Submontane DOF
Novo Repartimento, PA (Repartimento)	167.41*	-4.1448	-50.149	2000	Red-Yellow Argisol, Red-Yellow Latosol	Submontane OOF with palm trees
Anapu, PA (Anapu2, Anapu6, Anapu7)	1387.56*	-2.96	-51.29	2200	Red-Yellow Latosol	Submontane DOF
Portel, PA (Portel1, Portel2, Portel3)	5280.41*	-2.16	-51.72	2400	Dystrophic Yellow Latosol	Lowland DOF
Mazagão, AP (Mazagão)	25**	0.22	-51.865	2400	Red-Yellow Latosol	Submontane DOF
Laranjal do Jari, PA (Jari)	6**	-1.22	-52.55	2400	Yellow Latosol, Red-Yellow Argisol	Submontane DOF
Almerim, PA (Almerim4, Almerim5, Almerim6)	5177.16*	-0.95	-53.38	2200	Yellow Latosol, Red-Yellow Argisol	Submontane DOF

Note. DOF: dense ombrophilous forest; OOF: open ombrophilous forest.

* Area of the annual production unit where pre-harvest forest inventory and continuous forest inventory was carried out in the permanent plots.

** Accumulated sampling area of the permanent plot, with only continuous forest inventory.

2.2 Database

Data on trees with a diameter at breast height (DBH, 1.3 m from the ground) greater than or equal to 10 cm were obtained from CFIs carried out in permanent plots at the 15 study sites (Table 1 and Figure 1). Data on trees with DBH ≥ 40 cm were acquired from PHFIs or forest censuses of 11 study sites (Table 1).

2.3 Data Analysis

For assessment of the population structure of trees with DBH ≥ 10 cm, joint analysis of PHFI and CFI data was performed. Each of the 15 study sites (Table 1) represented a sample. PHFI and CFI data were assessed considering tree density (number of trees per hectare), given that the study sites had different sizes.

Preliminary information on the diameter structure of the species was obtained by using descriptive statistics (frequency, minimum, maximum, mean, standard error, variance, standard deviation, mode, median, quartiles, skewness, kurtosis, geometric mean, and coefficient of variation).

Participation of the species in managed forests was determined by calculating the absolute density, which indicates the mean number of individuals per unit area (hectare) (Lamprecht, 1962). The cumulative value of the absolute density (ind/ha) was grouped into diameter classes, with a class interval of 10 cm starting from the minimum DBH of 10 cm. Diameter distributions were tested for normality and homoscedasticity of variances using Shapiro-Wilk and Levene's tests, respectively. In the case of non-normal distribution, data were log-transformed and tested again for normality and homoscedasticity of variances.

Comparison of variables between study sites and analysis of similarity between diameter distributions were performed using the nonparametric Kruskal-Wallis test (*H*-test) at a significance level of 5%, followed by Dunn's multiple comparison post hoc test, when necessary (Siegel & Castellan Jr., 2006).

On the basis of diameter distribution data, the De Liocourt quotient (*q*) (De Liocourt, 1898) was calculated by dividing the number of individuals in a diameter class by the number of individuals in the immediately higher diameter class. In this study, the De Liocourt quotient was used to identify the balance of diameter distribution.

To assess whether diameter distributions could be fitted by a negative exponential curve, as expected for native species (Scolforo, 1998), we used the linearized Meyer (1952) type I distribution function (Equation 1) to fit distributions (Hess et al., 2014; Meira et al., 2016; Santos et. al., 2018).

$$\ln(y_i) = \beta_0 + \beta_1 X_i + \varepsilon_i \tag{1}$$

where, y_i is the number of trees per hectare per diameter class, X_i is the central value of the diameter class, β_0 and β_1 are model parameters expressing the vegetation structure in relation to diameter distribution, and ε_i is the random error. For classes that did not contain individuals, y_i was defined as 1. The goodness of fit of the model was assessed by the criterion of the adjusted coefficient of determination (adjusted R^2) and the relative standard error.

From the adjusted distribution function (Equation 1), the q quotient intrinsic to the vegetation was calculated using Equation (2), taking into account the ratio of the frequency of a given diameter class (X_i) to that of the subsequent class ($X_i + 1$) (Hess et al., 2014).

$$q = \frac{e(\beta_0 + \beta_1 X_i)}{e(\beta_0 + \beta_1 X_i + 1)} \tag{2}$$

3. Results

A total of 36,609 trees were recorded at the 15 data collection sites in a total sampled area of 13,045.34 ha. *V. americana* diameters ranged from 10 to 127.32 cm, resulting in broad range (64.17 to 117.32 cm) and high dispersion (CV = 16.19-60.58%) of diameters between the studied sites (Table 2). As a result, a wide range of diameter classes was obtained (classes 7 to 12).

Table 2. Descriptive statistics of the diameter structure of *Vouacapoua americana* Aublet individuals with a diameter at breast height of ≥ 10 cm inventoried in Pará and Amapá States, Brazil

Item	**Paragominas**	**Moju**	**Breu**	**Repartimento**	**Amapu2**	**Amapu6**	**Amapu7**	**Portel1**	**Portel2**	**Portel3**	**Mazagão**	**Jari**	**Almerim4**	**Almerim5**	**Almerim6**
Area (ha)	969	11	21.8	167.41	415.05	440.89	531.62	1663.72	1804.12	1812.57	25	6	2416.29	2324.58	2436.28
Count	9288	131	557	1411	7111	2174	2619	3396	2628	1493	99	149	1228	1686	2639
Min	10.30	10.00	10.00	10.03	17.51	10.00	10.50	14.01	10.03	10.03	12.41	10.28	11.46	10.50	10.31
Max	108.23	94.90	74.17	92.63	125.99	127.32	114.59	111.41	105.04	98.68	92.31	100.90	120.96	114.59	108.23
Range	97.93	84.90	64.17	82.60	108.48	117.32	104.09	97.40	95.02	88.65	79.90	90.62	109.50	104.09	97.91
Sum	358461	3830.7	14786.5	52555.7	287910	118441	144263	190304	150666	83398.5	4874.92	5552.66	81187.5	102041	161942
Mean	38.59	29.24	26.55	37.25	40.49	54.48	55.08	56.04	57.33	55.86	49.24	37.27	66.11	60.52	61.36
SE	0.14	1.55	0.55	0.37	0.17	0.29	0.22	0.16	0.19	0.25	1.62	1.60	0.35	0.29	0.23
Variance	190.33	313.78	167.50	193.34	200.43	176.72	132.11	82.30	96.05	93.18	260.22	383.76	153.70	137.41	145.59
SD	13.80	17.71	12.94	13.90	14.16	13.29	11.49	9.07	9.80	9.65	16.13	19.59	12.40	11.72	12.07
Median	35.97	23.80	23.87	39.79	38.20	52.84	52.52	54.11	56.34	54.75	48.38	33.42	64.30	59.21	60.48
Mode	31.83	20.00	44.56	35.01	35.01	47.75	47.75	50.93	50.93	50.93	63.66	32.47	63.66	60.48	57.30
Q1	27.37	15.4	15.5	26.83	29	46.15	47.75	49.97	50.93	50.93	37.88	20.37	57.93	52.2	52.84
Q3	47.43	38.6	36.02	45.93	49.34	62.39	60.48	60.8	63.66	60.48	61.43	51.09	73.21	67.88	68.44
Skewness	0.87	1.22	0.67	-0.26	0.86	0.39	0.80	0.59	0.31	-0.35	0.20	0.72	0.08	0.38	0.43
Kurtosis	0.56	1.05	-0.40	-0.16	0.73	2.77	2.67	2.25	2.94	4.10	0.27	-0.03	2.70	1.51	1.16
GM	36.32	24.81	23.53	33.92	38.19	52.64	53.86	55.30	56.42	54.82	46.25	32.22	64.76	59.33	60.13
CV	35.75	60.58	48.75	37.33	34.97	24.40	20.87	16.19	17.09	17.28	32.76	52.57	18.75	19.37	19.66

Note. SE: standard error; SD: standard deviation; Q1: first quartile; Q3: third quartile; GM: geometric mean; CV: coefficient of variation.

At all sites, *V. americana* density was high, ranging from 6.31 to 25.55 trees/ha (Table 3).

Table 3. Diameter distribution of acapu (*Vouacapoua americana* Aublet) individuals per hectare according to 10 cm interval classes starting at a diameter at breast height of ≥ 10 cm for study sites in Pará and Amapá States, Brazil

Diameter class (cm)	**Central value (cm)**	**Paragominas**	**Moju**	**Breu**	**Repartimento**	**Amapu2**	**Amapu6**	**Amapu7**	**Portel1**	**Portel2**	**Portel3**	**Mazagão**	**Jari**	**Almeirim4**	**Almeirim5**	**Almeirim6**
10-20	15	4.0000	4.6364	9.7706	9.2667	6.0000	7.8000	3.6000	6.6667	7.4286	12.0000	1.6667	6.0000	3.2000	3.1111	3.6364
20-30	25	3.1094	3.2727	6.8807	4.5239	4.6452	6.4000	2.8000	4.6667	5.1429	2.6667	1.0000	4.3333	1.6000	2.2222	2.9091
30-40	35	2.5913	1.0909	3.9908	2.5681	4.4718	1.8000	1.4000	1.3333	6.2857	0.6667	0.8800	4.8333	1.2000	1.7778	2.1818
40-50	45	1.9267	0.8182	3.5321	3.5071	3.7032	1.7918	1.7813	0.5013	0.2677	0.1765	1.1200	3.3333	0.8000	0.1235	0.1580
50-60	55	1.1486	1.2727	1.1927	1.1214	2.3708	1.4720	1.7381	0.9082	0.6613	0.3829	0.5200	2.6667	0.1544	0.2396	0.3657
60-70	65	0.4964	0.5455	0.1376	0.2357	1.2384	0.8664	0.7900	0.4550	0.3503	0.1909	0.7200	2.0000	0.1618	0.1936	0.2984
70-80	75	0.2105	0.0909	0.0459	0.0714	0.3783	0.4808	0.3800	0.1352	0.1291	0.0535	0.2400	0.6667	0.1279	0.1226	0.1777
80-90	85	0.0413	0.0909		0.0143	0.1253	0.0862	0.1110	0.0240	0.0233	0.0050	0.0800	0.8333	0.0377	0.0301	0.0521
90-100	95	0.0206	0.0909		0.0071	0.0337	0.0272	0.0376	0.0054	0.0044	0.0022	0.0800		0.0141	0.0060	0.0176
100-110	105	0.0031				0.0169	0.0091	0.0113		0.0022			0.1667	0.0041	0.0026	0.0037
110-120	115					0.0024	0.0113	0.0038	0.0006					0.0008	0.0004	
120-130	125					0.0024	0.0045							0.0004		
Total (trees/ha)		**13.55**	**11.91**	**25.55**	**21.32**	**22.99**	**20.75**	**12.65**	**14.70**	**20.30**	**16.14**	**6.31**	**24.83**	**7.30**	**7.83**	**9.80**

Diameter distributions of *V. americana* (Table 3) were found to be non-normally distributed, as assessed by the Shapiro-Wilk test, even after log transformation. The Kruskal-Wallis test did not show significant differences between medians ($H = 15.45$, $p = 0.3479$).

At all sites, there was a higher density of trees in the smallest diameter classes (10-40 cm) (Table 3 and Figure 2), and density decreased with increasing diameter (≥ 40 cm), indicating a decreasing trend in the diameter distribution of *V. americana*. Trees of all diameter classes were recorded at all sites except Portel1 and Jari, where at least one of the diameter classes was not recorded, resulting in a discontinuous diameter distribution (Table 3 and Figure 2). Except in Paragominas, Breu, Anapu2, and Anapu6, there was a marked increase (leap) in the number of trees in a diameter class in relation to the previous class, causing discontinuity in the decrease in the number of individuals with increasing diameter classes, resulting in a truncated distribution (Table 3). It was evident for all study sites that the first diameter classes (10-40 cm) concentrated a high number of trees per hectare (Table 3).

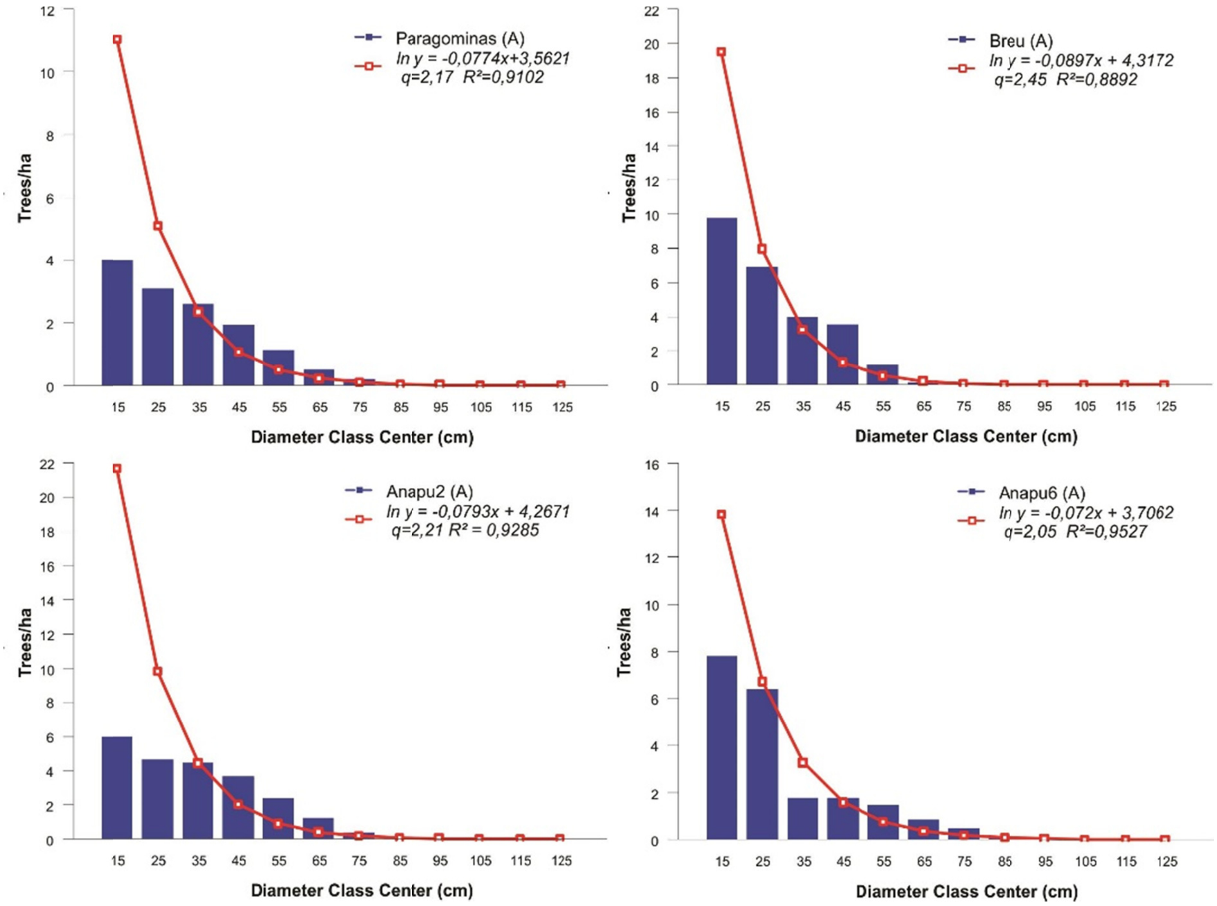

Figure 2. Observed and estimated diameter distributions without leaps or discontinuities for acapu (*Vouacapoua americana* Aublet) populations with a diameter at breast height of ≥ 10 cm according to study site

The occurrence of at least one "leap" in the diameter distribution of 11 of the 15 sites (Table 3) was corroborated by the results of the De Liocourt quotient (*q*), which did not demonstrate constancy or proximity, varying from 0.4 to 23.48 (Table 4). The greatest variation in *q* values occurred from *q*4 to *q*7 (Table 4), corresponding to the diameter classes in which leaps occurred (Table 3). For all sites, *q* values were mainly below their respective mean value (Table 4).

Table 4. The De Liocourt quotient (*q*) of acapu (*Vouacapoua americana* Aublet) populations according to 10 cm interval classes starting at a diameter at breast height of ≥10 cm for study sites in Pará and Amapá States, Brazil

Diameter class (cm)	***q* class**	**Paragominas**	**Moju**	**Breu**	**Repartimento**	**Amapu2**	**Amapu6**	**Amapu7**	**Portel1**	**Portel2**	**Portel3**	**Mazagão**	**Jari**	**Almerim4**	**Almerim5**	**Almerim6**
10-20	*q*1	1.29	1.42	1.42	2.05	1.29	1.22	1.29	1.43	1.44	4.50	1.67	1.38	2.00	1.40	1.25
20-30	*q*2	1.20	3.00	1.72	1.76	1.04	3.56	2.00	3.50	0.82	4.00	1.14	0.90	1.33	1.25	1.33
30-40	*q*3	1.34	1.33	1.13	0.73	1.21	1.00	0.79	2.66	23.48	3.78	0.79	1.45	1.50	14.40	13.81
40-50	*q*4	1.68	0.64	2.96	3.13	1.56	1.22	1.02	0.55	0.40	0.46	2.15	1.25	5.18	0.52	0.43
50-60	*q*5	2.31	2.33	8.67	4.76	1.91	1.70	2.20	2.00	1.89	2.01	0.72	1.33	0.95	1.24	1.23
60-70	*q*6	2.36	6.00	3.00	3.30	3.27	1.80	2.08	3.36	2.71	3.57	3.00	3.00	1.27	1.58	1.68
70-80	*q*7	5.10	1.00		5.00	3.02	5.58	3.42	5.63	5.55	10.78	3.00	0.80	3.40	4.07	3.41
80-90	*q*8	2.00	1.00		2.00	3.71	3.17	2.95	4.44	5.25	2.25	1.00		2.68	5.00	2.95
90-100	*q*9	6.67				2.00	3.00	3.33		2.00				3.40	2.33	4.78
100-110	*q*10					7.00	0.80	3.00						5.00	6.00	
110-120	*q*11					1.00	2.50							2.00		
Total (trees/ha)		**13.55**	**11.91**	**25.55**	**21.32**	**22.99**	**20.75**	**12.65**	**14.7**	**20.3**	**16.14**	**6.31**	**24.83**	**7.3**	**7.83**	**9.8**
Mean *q*		**2.66**	**2.09**	**3.15**	**2.84**	**2.46**	**2.32**	**2.21**	**2.95**	**4.84**	**3.92**	**1.68**	**1.44**	**2.61**	**3.78**	**3.43**
Intrinsic *q*		**2.17**	**1.70**	**2.45**	**2.53**	**2.21**	**2.05**	**1.96**	**2.47**	**2.53**	**2.64**	**1.46**	**1.46**	**2.24**	**2.31**	**2.02**

In analyzing the occurrence or not of leaps and discontinuity in the diameter distribution of *V. americana* it was possible to identify three types of diameter distributions: (i) without leaps or discontinuity (Paragominas, Breu, Anapu2, and Anapu6) (Figure 2), (ii) with one leap or discontinuity (Moju, Repartimento, Anapu7, Portel1, Portel3, Almerim4, Almerim5, and Almerim6) (Figure 3), and (iii) with two leaps or discontinuities (Portel2, Mazagão, and Jari) (Figure 4).

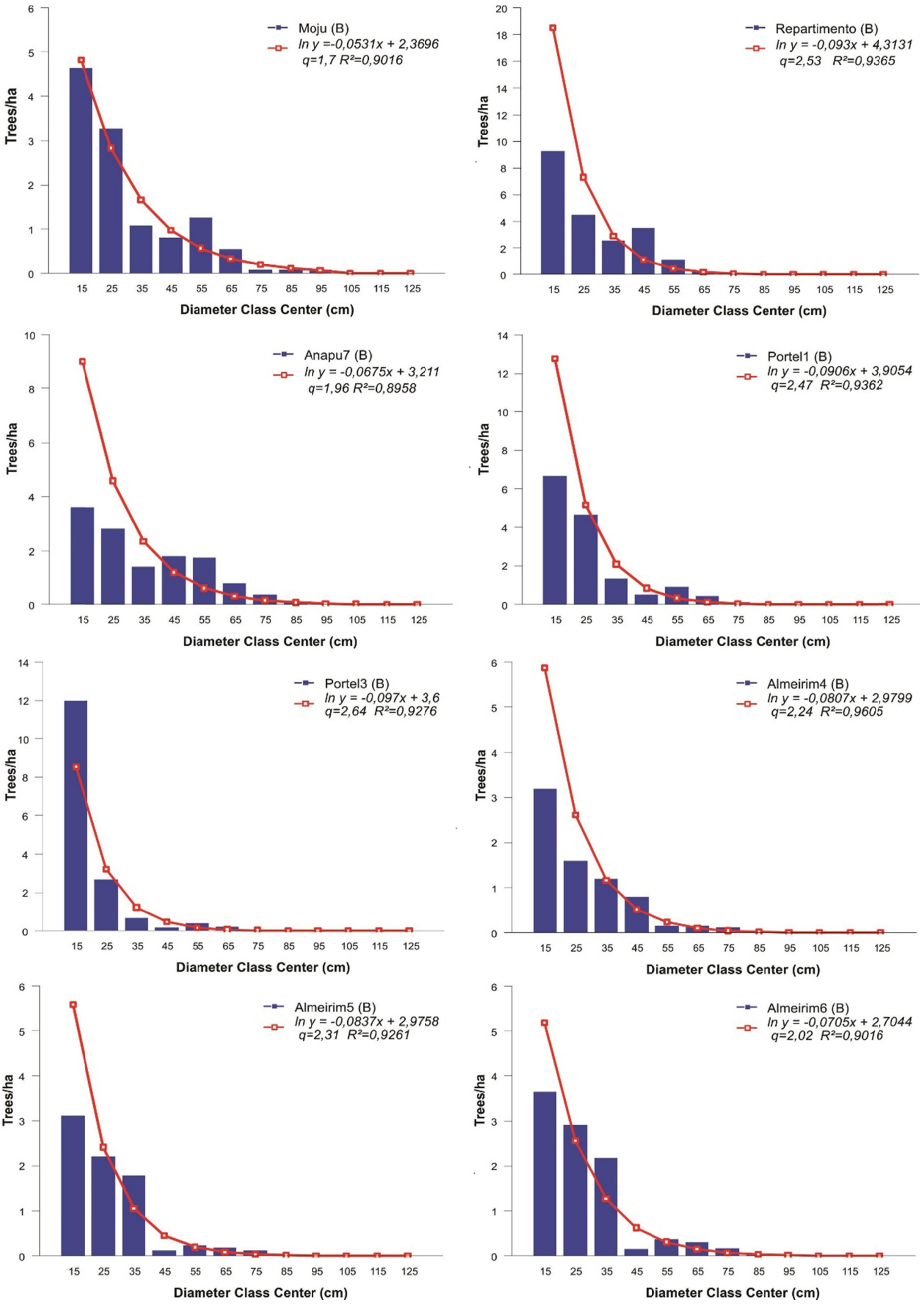

Figure 3. Observed and estimated diameter distributions with one leap or discontinuity for acapu (*Vouacapoua americana* Aublet) populations with a diameter at breast height of ≥ 10 cm according to study site

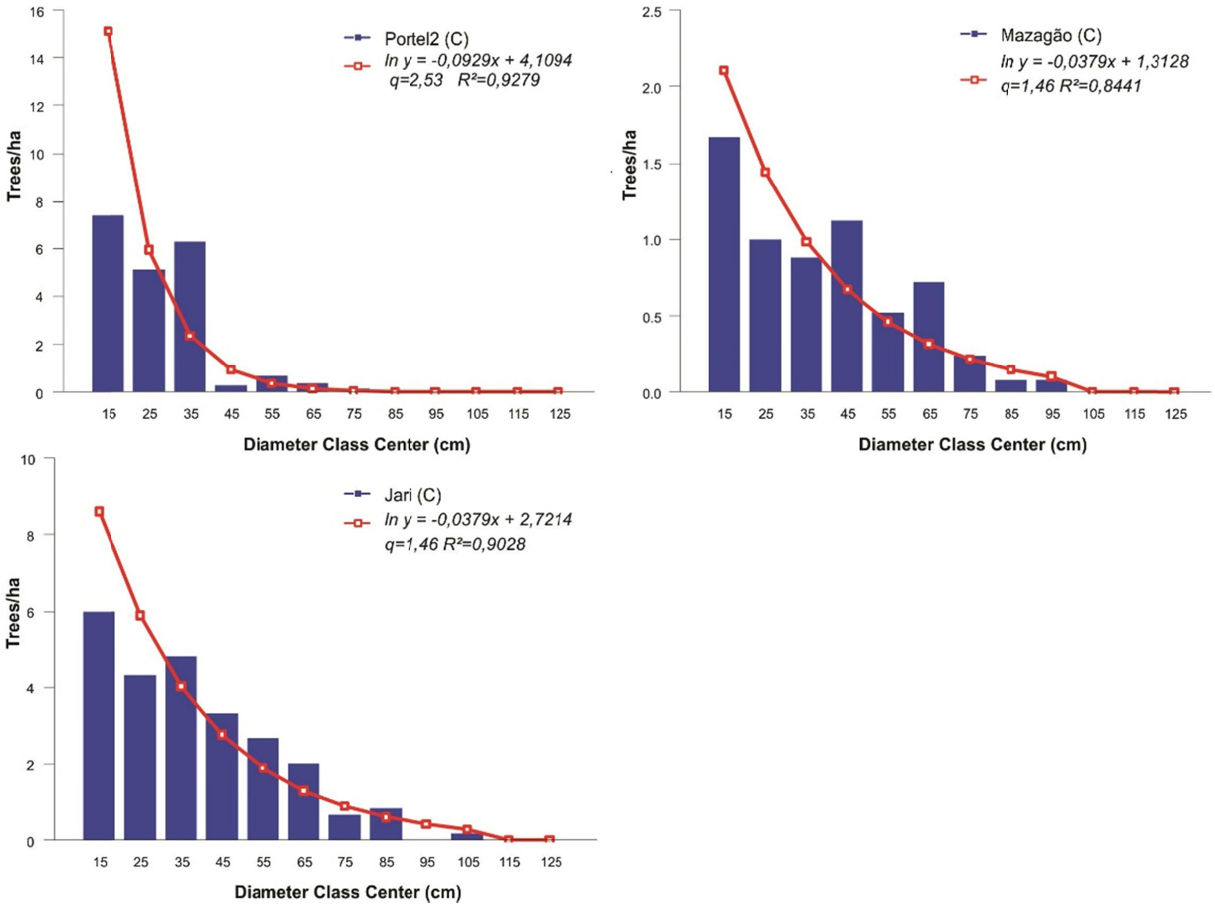

Figure 4. Observed and estimated diameter distributions with two leaps or discontinuities for acapu (*Vouacapoua americana* Aublet) populations with a diameter at breast height of ≥ 10 cm per study site

Although *V. americana* had discontinuous or truncated diameter distributions at some sites (Table 3, Figures 3 and 4), it was observed that. Overall, tree density decreased with increasing DBH classes. This behavior was confirmed by adjusting diameter distribution curves using Meyer's model in its linearized form, resulting in a curve resembling an inverted "J" (Table 3 and Figures 2, 3, and 4).

4. Discussion

Previous studies on *V. americana* occurring in the Amazon region with DBH ≥ 10 cm reported lower (Almeida et al., 1993; Carim et al., 2013) and similar (Francez et al., 2009; Souza et al., 2011; Carim et al., 2015; Coelho et al., 2017; Silva et al., 2017) absolute density values. In any case, high density can be considered a structural characteristic of the species.

Overall, the diameter distribution of *V. americana* decreased markedly with increasing diameter classes. Discontinuities or leaps were observed in the diameter distributions of some populations. The discontinuity observed in 2 of the 15 study sites may be considered common and predictable. It is known that the diameter distribution of a given species may be discontinuous (Barros, 1996). Alves Junior et al. (2009), in analyzing the diameter distribution of *Plathymenia foliolosa*, identified discontinuity in more than one class and/or in several successive classes. The existence of large discontinuities or flattening of distributions, sometimes reaching total absence of young individuals, is related to the population ecology of species (Felfili, 1997). Considering that diameter class discontinuity occurred in a small number of populations and that populations were in a primary forest environment, it can be considered that *V. americana* has a continuous diameter distribution, representing a structural characteristic of the species. However, it cannot be disregarded that the continuity or discontinuity of diameter distributions is related to forest typology and the formation of forest communities, both influenced by topography.

The leap in the number of trees in at least one diameter class observed in the majority of sites (11 sites) may be an indicator of the occurrence and influence of natural disturbances. Such disturbances might have promoted high mortality of trees of the diameter class immediately below the leap. Another possible explanation is that environmental conditions (light and space) allowed the entry of individuals from the lower class to the immediately higher class. However, these conditions were not created for other classes, resulting in a leap in the diameter distribution of the species. A leap in diameter distribution was also observed in other studies with the same species (Souza et al., 2011; Carim et al., 2013). Oliveira et al. (2008) argued that the decreasing behavior of the distribution curve suggests that the forest environment, up to the time of the inventory, had not suffered severe disturbances, with little to no anthropogenic pressure. Machado et al. (2004) related the difficulty of some species in recruiting new individuals of smaller diameter classes to factors inherent to fragmentation, such as dispersing agents and area size and shape. Given that many inventory studies were carried out in primary contiguous (not fragmented) forests of considerable extension, these characteristics might have influenced tree density. Insertion, and recruitment in relation to the mortality observed in the first three DBH classes.

Discontinuity and leaps in diameter distributions resulted in a high variation (0.4 to 23.48) of the De Liocourt quotient, not demonstrating constancy or proximity between study sites. A constant q value indicates that the population is balanced or in equilibrium (Meyer, 1952). When the q quotient is not constant. there is a discrepancy between mortality and recruitment rates, which can lead to changes in forest structure (Felfili et al., 1998; Nascimento et al., 2004). The wide range of q values showed that diameter distributions were not balanced with regard to the relationship between recruitment and mortality over time.

The De Liocourt quotients $q1$, $q2$, and $q3$ for the first three DBH classes (10-40 cm) were sometimes higher than the mean of quotients and did not show constancy or proximity. Nevertheless, it can be stated that, at all sites, the species had a balanced diameter distribution in the first three DBH classes. This behavior is in agreement with the statements of Santos et al. (2016), who argued that the diameter structure of a forest characterized by small trees of the smallest diameter classes indicates balanced distribution trends, given the regeneration capacity of plant species. Furthermore, a high number of individuals in small diameter classes suggests that the species has great regenerative potential and capacity to maintain current density levels (Lehn et al., 2008).

However, some authors consider that variation in the De Liocourt quotient may indicate that the area has suffered disturbances in the past and that, the greater the variation in the quotient, the more severe the disturbance (Alves Junior, 2010). According to Machado et al. (2004), the distribution of a large number of individuals in smaller diameter classes shows that the disturbance is relatively intense and continuous. Nunes et al. (2003) reported that areas subjected in the past to severe disturbances have a higher density of thin and low trees, characteristic of the initial regeneration stage. The fact that the studied populations were in a primary forest, not having suffered anthropogenic disturbances, only natural disturbances, is in agreement with the statements of Alves Junior (2010), Machado et al. (2004), and Nunes et al. (2003), supporting that natural disturbances contributed to the leap in diameter distribution and the variation in q values, explaining the species dynamics of recruitment and mortality according to diameter class.

The DBH range of 40 to 80 cm had the greatest variation in q values and the largest number of discontinuities in diameter distributions (Tables 3 and 4). It is likely that the frequency and intensity of natural disturbances in the study sites promoted tree mortality at a higher rate than entry of individuals from a lower class to the immediately higher class. According to Gomide et al. (2009), a high density of individuals in small diameter classes may translate into the entry of some of their representatives in subsequent classes. Ricklefs (2009) stated that a higher density of individuals in the first diameter classes indicates that the forest has sufficient stock of thin trees to replace larger trees that will be eliminated over time or by management programs, representing an ecological strategy of the population to maintain self-perpetuation. Imbalance in recruitment and mortality rates in the DBH range of 40-80 cm generated a leap in the diameter distribution, resulting in unbalanced distribution.

For DBH values ≥ 80 cm, the variation in q values, the leap in distribution, and tree density were smaller than in previous intervals. Natural disturbances likely affected individuals of this DBH range in the same manner as in lower DBH ranges (40 to 80 cm). It is possible that the species was unable to establish a larger number of trees in larger diameter classes because few individuals were able to overcome interspecific competition. According to Delonga et al. (2018), a smaller number of trees in larger diameter classes is in accordance with natural forest dynamics, whereby competition for better growth conditions allows only a few individuals to reach large dimensions. In this DBH range, the reduced number of trees per hectare might be due to a high mortality rate, combined with recruitment problems associated with high mortality in lower classes.

Three types of *V. americana* diameter distributions were identified, based on the presence or absence of leaps and discontinuities. However, when fitted using Meyer's model, all distribution curves resembled an inverted "J" indicating that the behavior of the species was in line with that predicted for uneven-aged forests, in which tree number decreases exponentially with increasing diameter class (De Liocourt, 1898; Meyer, 1952; Alves Junior et al., 2009; Carvalho et al., 2016). The inverted "J" shape of diameter distributions suggests that *V. americana* has good capacity for self-regeneration and maintenance of current density levels (Nascimento et al., 2004). Canalez et al. (2006) stated that an inverted "J" distribution demonstrates that the species can maintain regeneration in a continuous flow.

Balanced diameter distributions (tending toward inverted "J" curves), in which recruitment compensates for mortality over time, have relatively constant *q* values (Felfili et al., 1998; Nascimento et al., 2004; Lehn et al. 2008). This pattern of constant *q* values and inverted "J" distribution curves can be applied to diameter distributions of forest stands; however, such behavior may differ at the species level, as observed in the present study. Despite the apparent imbalance between mortality and recruitment and the consequent variation in *q* values, the diameter distribution curves of *V. americana* still tended toward an inverted "J" shape.

It is not possible to affirm whether a species is in equilibrium or not solely by analyzing diameter distributions; it is also necessary to investigate other aspects of its ecology, such as vertical structure, ecological group and dynamics. The inverted "J" behavior was characteristic of the diameter distribution of *V. americana*, in agreement with previous studies on primary forests (Campos et al., 2002; Souza et al., 2011).

V. americana has the following diameter characteristics:

- diameters greater than 1 m (100 cm) and mean diameters of 48 cm;
- high density at occurrence sites, predominantly of trees of small diameter classes (< 40 cm);
- unbalanced diameter distribution, resulting from the presence of leaps and/or discontinuities in the number of trees in one or more diameter classes; and
- a decreasing distribution from smaller to larger diameter classes, tending toward an inverted "J" diameter distribution.

The structural features identified for *V. americana* demonstrate the capacity and high resilience of tree stocks of lower diameter classes (< 40 cm) to regenerate. These characteristics are positive for the application of forest management techniques, ensuring conservation in the face of the predatory exploitation currently suffered by the species.

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