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## Population dynamics of *Pentaclethra macroloba*, a hyperdominant tree in the Amazon River estuary


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**Abstract:** *Pentaclethra macroloba* is a hyperdominant tree of the Amazon estuary and highly exploited in the region, because the oil of its seeds has medicinal properties. Little is known about the influence of the flood polymodal cycle on the population dynamics of trees in the Amazon estuary. We evaluated the influence of tree diversity, climate, soil properties and flood level on the population dynamics of *P. macroloba*. During five years of monitoring (from 2011 to 2015), population density and mortality, recruitment and growth rates data were obtained of three populations of *P. macroloba* (Mazagão Velho, Maracá and Ajuruxi areas). Four transects were used in each area and 20 permanent plots were installed in each transect to study the population dynamics. Linear models were used to evaluate the relationship between biotic/abiotic factors and population density of *P. macroloba*. The population density of the three populations analyzed showed a significant decrease between the period from 2011 to 2015 ( $F = 381.3$ ;  $p < 0.001$ ). The Maracá area had a higher mortality rate ( $4.50\% \text{ year}^{-1}$ ) compared to Mazagão Velho ( $3.24\% \text{ year}^{-1}$ ) and Ajuruxi ( $1.96\% \text{ year}^{-1}$ ). The recruitment rate in Ajuruxi and Mazagão Velho were  $1.05\% \text{ year}^{-1}$  and  $0.32\% \text{ year}^{-1}$ , respectively, and in Maracá there were no recruits. Annual growth rate of the Maraca area was higher ( $0.93 \text{ cm}^{-1} \text{ year}^{-1}$ ) compared to Ajuruxi ( $0.75 \text{ cm}^{-1} \text{ year}^{-1}$ ) and Mazagão Velho ( $0.65 \text{ cm}^{-1} \text{ year}^{-1}$ ) populations. The flood level had a negative and significant correlation with the population density of *P. macroloba* in the Maracá ( $F = 39.7$ ;  $p < 0.01$ ), Ajuruxi ( $F = 9.9$ ;  $p < 0.05$ ) and Mazagão Velho ( $F = 19.6$ ;  $p < 0.05$ ) areas. Only the Ajuruxi area had a positive and significant correlation with arboreal richness ( $\beta = 0.14$ ;  $p < 0.05$ ). The flood gradient is an environmental driver that regulates the population growth of *P. macroloba*. The hyperdominant characteristic of this species is the result of its adaptability and interactions between soil fertility and tree diversity.

**Keywords:** polymodal tide, forest management, demographic rate, late secondary species, diametric growth


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## Introduction

The Amazon floodplain forests are ecosystems characterized by climatic seasonality, high rainfall and the hydrological cycle of flooding of the rivers that bathe them (Wittmann et al., 2006). With a coverage area of around 400,000 km<sup>2</sup> (Melack & Hess, 2010), these ecosystems occupy approximately two thirds of the Amazonian wetlands, with about 70% of their area covered by forests (Wittmann et al., 2010).

The interannual hydrological cycles of the floodplain forests provide a complex climate system to these areas (Rudorff et al., 2014), favoring the establishment of a rich flora with many endemic species (Albernaz et al., 2012). The rich floristic composition of floodplain forests is incomparable to other flooded ecosystems in the world (Wittmann et al., 2006). More than 70% of the trees in these ecosystems are used for multiple purposes (Wittmann & Wittmann, 2010). Wittmann et al. (2010) investigated the use of 186 arboreal species from floodplain forest, of the total number of species sampled, 135 (72.6%) are used by the riverside population, and 49 of these species (36.3%) are used for a single purpose and the majority are used for multiple purposes. Among the species studied, 98 species produce non-wood products, a large part of which is used in traditional medicine.

Among the species with high non-timber potential for exploitation in floodplain forests *Pentaclethra macroloba* (Willd.) Kuntze stands out, popularly known in the Amazon region by the name of *pracaxi*. *P. macroloba* has a wide geographic distribution in Neotropical America (Dantas et al., 2021a), forming three subpopulations adjacent to Costa Rica, Venezuela and Western Brazilian Amazon (Hartshorn, 1983). This species occupies the 10th position in the rank of the hyperdominant plants of the Amazon (ter Steege et al., 2020), it can be found in upland, floodplain and *igapó* forests (Ferreira et al., 2005; Condé & Tonini, 2013; Carim et al., 2016). *P. macroloba* is considered a long-lived late secondary species (ecological classification proposed by Budowski (1970)), seedlings can persist for up to 21 years in the shade of the understory and adult trees reaching up to 102 years of age in the floodplain forests of the Amazon estuary (Dantas et al., 2022). This species colonizes secondary forests and gaps very well, even improving soil microbiota and nitrogen fixation (McGee et al., 2020).

Little is known about the ecological and management aspects of the population of *P. macroloba* in western Amazonia (Dantas et al., 2021a, 2021b, 2022), making it a worrying situation, as the species is historically exploited by riverside populations and currently by the cosmetics industries. The oil

extracted from its seeds has medicinal properties against muscle pain, inflammation, snakebite and even in the treatment of cancer according to reports from the local population of the island of *Cotijuba* in the State of Pará, Brazil (Crespi & Guerra, 2013). Seed oil is effective in healing the skin and treating keloids (Banov et al., 2014). The chemical properties of the oil have a high concentration of fatty acids, mainly behenic and lignoceric acids, which moisturize the skin and provide softness to the hair (Costa et al., 2014). The aqueous extract of the bark has triterpenoid saponins that have anti-hemorrhagic action against the venom of the *Bothrops jararaca* snake (Silva et al., 2007).

In the Amazon estuary, the polymodal low-amplitude flood cycle (Junk et al., 2011) selects the species best adapted to survive this flooding regime. However, due to the low scientific knowledge about the interaction of plants with the flood dynamics and the climatic seasonality of these forests, a specific management plan for these areas and for species with non-timber potential such as *P. macroloba* is difficult to develop.

Knowledge of forest dynamics is one of the requirements for any initiative for the management and conservation of species (Weissenhofer, 2005), because this type of study tells us the parameters of the population over time such as growth, recruitment and mortality. The study of forest dynamics over time is important to assess the influence of edaphoclimatic factors on population parameters of tree species and to assist in public policies for the management of timber and non-timber species.

Our objective was to evaluate the demographic parameters of *P. macroloba* over time and the environmental factors of the habitat that influence its population dynamics to understand its hyperdominance and assist in management plans for its natural resources. Our hypotheses are: (1) climax species diversity decreases with higher density of *P. macroloba* (late secondary species) and more exposed to sunlight; and (2) the population density and growth rate of *P. macroloba* are controlled by the flood gradient of the Amazon River. To clarify our hypotheses, we evaluated the population dynamics of *P. macroloba* over five years in permanent plots and related demographic parameters of the population with surrounding vegetation, degree of canopy luminosity, soil properties, climate, and river flood level.

## Material and Methods

### Study site

The study was carried out in the permanent plots of the Florestam project (Ecology and forest

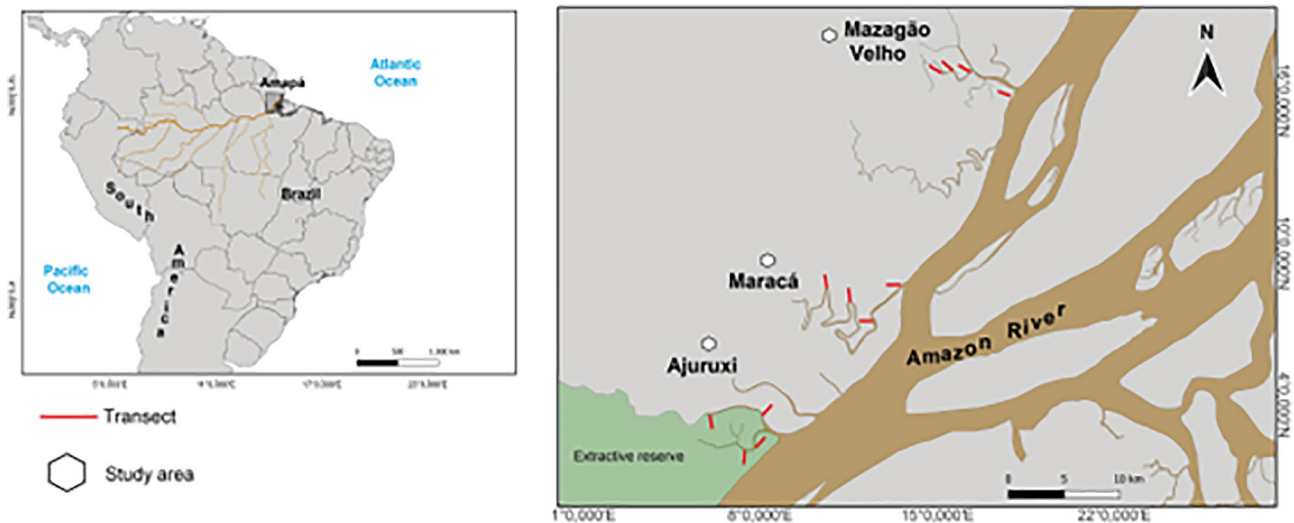


Fig. 1. Study of the population dynamics of *Pentaclethra macroloba* in the Amazon River estuary, Amapá, Brazil

management for multiple use of floodplains of the Amazon estuary) located in three riverside areas called Mazagão Velho (0°15'04"S and 51°22'03"W), Maracá (0°27'22"S and 51°28'27"W) and Ajuruxi (0°32'67"S and 51°32'78"W). These areas are located in the city of Mazagão, State of Amapá, Brazil and close to a sustainable use conservation unit (Resex Cajari) (Fig. 1). The areas are inhabited by traditional riverside populations that use forest resources as a livelihood source.

The climate system of the region is of the type Am, tropical rainy (Alvares et al., 2013). The average annual temperature is around 27 °C and the average annual rainfall is 2,550 mm, with the rainy season occurring between January and May. At the mouth of the Amazon River there are fluctuations in the tide level that can reach 2 to 3 m (Fortini et al., 2006).

The soils are characteristic of the floodplain region of the Amazon estuary. They are Melanic Gleysols, with a silty texture and with predominance of smectite, illite, kaolinite, goethite, anatase and quartz (Pinto, 2014). The forest typology of the area is classified as Ombrophilous Dense Alluvial Forest (IBGE, 2012). The most dominant species, among the 98 species recorded, are: *Mora paraensis* (Ducke) Ducke (Fabaceae), *Astrocaryum murumuru* Mart. (Arecaceae), *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae), *Carapa guianensis* Aubl. (Meliaceae) and *Matisia paraensis* Huber (Malvaceae) (Carim et al., 2016).

## Monitoring of population dynamics

For the study of population dynamics, four transects of 1000 m length were installed in each area. The transects were allocated perpendicularly to the main river, with a distance of at least 1 km between them, to ensure maximum sample representativeness and independence. In each transect, 20 permanent

plots (10 m × 25 m) were installed, totaling 2 ha of vegetation sampling per area (6 ha in total). The plots were allocated along each transect, following a micro-relief gradient of the area, trying to cover areas with good and bad drainage (Miranda et al., 2018).

The inventories were carried out for five uninterrupted years, from 2011 to 2015. In 2011, the first inventory (T1) was carried out in the three locations, in which all trees with DBH (Diameter at Breast Height) ≥ 5 cm were measured, numerically identified (with zinc plate) and marked with red ink at the measurement site. The second (T2), third (T3), fourth (T4) and fifth (T5) inventories were carried out in 2012, 2013, 2014 and 2015 respectively. From the second inventory onwards, the individuals of the first inventory were remeasured, the trees that reached the minimum DBH of inclusion (recruits) were measured and included in the sampling and the trees found dead were counted. As this study is part of a broader project, in addition to the *P. macroloba* species, all trees and palm within the plots were inventoried. This allowed relating the influence of floristic diversity on the demographic parameters of *P. macroloba*.

## Measurement of the canopy luminosity degree

The luminosity degree of the canopy was measured only in the plots of the Mazagão Velho and Ajuruxi areas. The degree of light incidence in the understory was obtained through hemispherical photographs. In the center of each plot, a digital camera (Canon model EOS T2i 550 D), with an 8 mm hemispherical lens (fisheye), was positioned on top of a tripod of 1.30 m. The photographs were always taken in the morning (7:00 am to 9:00 am) or in the late afternoon (4:30 pm to 6:30 pm) (Ferreira, 2013).

## Soil collection

Soil samples were collected in all plots and areas in December 2012. For the analysis of soil fertility and granulometry, five simple soil samples were collected (four withdrawn at the ends and one at the center of each plot) at a depth of 0 to 20 cm with the aid of a Dutch Auger. The samples were homogenized to form a single sample composed per plot. For physical analysis, an undisturbed sample (obtained in the depth of 0–5 cm) was collected in the center of the plot, with the aid of a metal ring (98 cm<sup>3</sup>) coupled to an auger. The rings were packed in aluminum foil to help keep the sample undisturbed and prevent moisture loss (Pinto, 2014). The samples were sent to the Soil Laboratory at Embrapa Amapá for physical and chemical analysis.

The chemical attributes obtained from the soil were: active acidity (pH), potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), aluminum (Al), potential acidity (H+Al), base sum (SB), Cation Exchange Capacity (CEC) and the physical attributes were: particle density, humidity, clay, silt, sand and porosity. The analyses were performed according to standardized norms of the Brazilian Agricultural Research Corporation (Nogueira & Souza, 2005).

## Hydroclimatic variables

The mean maximum temperature and total precipitation variables were obtained from the Climatological Station of Macapá (less than 4 km, in a straight line, from the study areas), stored in the historical meteorological database of the National Institute of Meteorology (INMET, 2019). The mean annual inundation of the Amazon River was obtained from the Fluviometric Station of *Laranjal do Jari* (less than 3 km, in a straight line, from the study area), stored in the National Water Agency database (ANA, 2022).

## Data analysis

The demographic parameters calculated were population density (Equation 1), mortality rate (Sheil et al., 1995; Equation 2), recruitment rate (Sheil et al., 2000; Equation 3), half-life (Equation 4), time of doubling (Korning & Balslev, 1994; Equation 5) and relative rate of diametric growth (Shen et al., 2013; Equation 6).

$$PD = \frac{N_i}{a} \quad (1)$$

$$M = \frac{\ln(N_0) - \ln(N_1)}{t} \quad (2)$$

$$R = \frac{\ln(N_{N1+t}) - \ln(N_1)}{t} \quad (3)$$

$$T_{0.5} = \frac{\ln(0.5)}{0.01 \times M} \quad (4)$$

$$T_2 = \frac{\ln(2)}{0.01 \times R} \quad (5)$$

$$RGR = \frac{\log(dbh_1) - \log(dbh_0)}{t} \quad (6)$$

in which: PD – population density (individual ha<sup>-1</sup>);  $N_i$  – number of individuals in inventory  $i$ ;  $a$  – size of the sample area (ha);  $M$  – annual mortality rate (% year<sup>-1</sup>);  $N_0$  – number of individuals in the first inventory;  $N_1$  – number of individuals surviving in the last inventory;  $t$  – time elapsed between the first and the last inventory (4 years);  $R$  – annual recruitment rate (% year<sup>-1</sup>);  $N_{N1+t}$  – number of surviving individuals in the last inventory, added to the number of recruited individuals;  $T_{0.5}$  – half-life parameter;  $T_2$  – population doubling time; RGR – relative diametric growth rate (cm<sup>-1</sup> year<sup>-1</sup>);  $dbh_0$  – diameter measured in the first inventory; and  $dbh_1$  – diameter measured in the last inventory.

The diameter structure of the populations was evaluated over time and the diameters of the trees were ordered by size classes according to the formula proposed by Sturges (1926) (Equation 7). Basal area (Equation 8) was evaluated in terms of loss (Equation 9), gain (Equation 10) and internal growth (Equation 11) (Marín et al., 2005).

$$C = 1 + 3.333 \ln(N_0) \quad (7)$$

$$g_i = \frac{\pi \cdot dbh}{40000}; BA = \sum_{i=1}^n g_i \quad (8)$$

$$L = \frac{\ln(BA_0) - \ln(BA_{s1})}{t} \quad (9)$$

$$G = \frac{\ln(BA_r) - \ln(BA_{s1})}{t} \quad (10)$$

$$I = \frac{\ln(BA_1) - \ln(BA_{s1})}{t} \quad (11)$$

$C$  – number of diameter classes;  $g_i$  – basal area of tree  $i$ ;  $dbh$  – diameter measured at breast height 1.30 m;  $BA$  – total basal area of the population (m<sup>2</sup> ha<sup>-1</sup>);  $L$  – loss in basal area (% year<sup>-1</sup>);  $BA_0$  – basal area of living trees in the first inventory;  $BA_{s1}$  – basal area of surviving trees in the last inventory;  $G$  – gain in basal area (% year<sup>-1</sup>);  $BA_r$  – basal area of trees recruited in the last inventory;  $I$  – internal growth of basal area



(% year<sup>-1</sup>); and BA<sub>1</sub> – basal area of living trees in the last inventory.

The demographic parameters between the three areas were compared by ANOVA test (Miranda et al., 2018). The Kolmogorov-Smirnov test (D) was applied to assess whether there was difference in the diameter structure of the population between the first (T1) and last (T5) measurement (Brown & Rothery, 1993).

As some plots did not register the presence of *P. macroloba*, we used Generalized Linear Models (GLMs) to relate the absence (value 0) or presence (value 1) of *P. macroloba* in the plots with the soil parameters (physical and chemistry properties) and vegetation (luminosity, richness and diversity). For this, the number of individuals found in each plot of a given transect was divided by the total number of individuals in the transect to obtain a proportional value. The analyses were performed by area and by transect, being our sampling unit the plots (n = 20 for each transect). The percentage of canopy opening was calculated from the images that presented the best contrast between the canopy and the sky, using the Gap Light Analyzer software vs. 2.0 (Frazer et al., 1999).

We applied simple linear models to evaluate the relationship of annual variation in population density, basal area and growth rate of *P. macroloba* with the annual mean variables of total rainfall, maximum temperature and flood level. All statistical analyses were performed using the R program (R core Team, 2019).

## Results

### Parameters of population dynamics

The population density showed a significant difference between the three areas analyzed comparing the year 2011 with the year 2015 ( $F = 381.3$ ;  $p < 0.001$ ) (Fig. 2). The reduction was more accentuated in the Maracá area, in the year 2011 the initial density obtained was 50.5 individuals ha<sup>-1</sup> and in the year 2015 the final density was 42 individuals ha<sup>-1</sup> (decrease of 8.5 individuals ha<sup>-1</sup>). In the Mazagão Velho

area, in the year 2011 the initial density obtained was 44 individuals ha<sup>-1</sup> and in the year 2015 the final density was 39 individuals ha<sup>-1</sup> (decrease of 5 individuals ha<sup>-1</sup>). In the Ajuruxi area, in the year 2011 the initial density obtained was 52 individuals ha<sup>-1</sup> and in the year 2015 the final density was 49 individuals ha<sup>-1</sup> (decrease of 3 individuals ha<sup>-1</sup>). The Mazagão Velho area presented the highest number of plots with absence of *P. macroloba* (31 plots) and the other areas presented the same amount (25 plots each).

The origin of tree mortality was all natural, caused by the wind or natural senescence of the species. The Maracá area had a higher mortality rate (4.50% year<sup>-1</sup>) compared to Mazagão Velho (3.24% year<sup>-1</sup>) and Ajuruxi (1.96% year<sup>-1</sup>). The recruitment rate of the *P. macroloba* population in the Maracá area was zero during the five years of monitoring. The Ajuruxi area had a recruitment rate of 1.05% year<sup>-1</sup> and the Mazagão Velho area the rate was 0.32% year<sup>-1</sup>. The population decline for the Maracá, Mazagão Velho and Ajuruxi areas was estimated to occur in 15, 21 and 35 years, respectively (Table 1). It was not possible to predict the doubling time of the *P. macroloba* population in the Maracá area, as during the study period there were no recruit trees. As for the populations of the Mazagão Velho and Ajuruxi areas, the doubling time was 215 and 66 years, respectively.

The diametric structure showed a significant difference between the three areas analyzed ( $F = 3.42$ ;  $p < 0.05$ ). The population of *P. macroloba* in the Mazagão Velho area had a higher mean DBH (22 cm  $\pm$  9 cm), with a maximum diameter of 47 cm, compared to populations in the Ajuruxi areas (19 cm  $\pm$  9 cm; maximum 42 cm) and Maracá (18 cm  $\pm$  7 cm; maximum 44 cm). The populations of Ajuruxi and Maracá were structured in eight diameter classes,

Table 1. Demographic parameters of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest

Demographic parameters	Mazagão Velho	Maracá	Ajuruxi
Mortality (% year <sup>-1</sup> )	3.24	4.50	1.96
Recruitment (% year <sup>-1</sup> )	0.32	0	1.05
Half-life (year)	21	15	35
Doubling time (year)	215	0	66

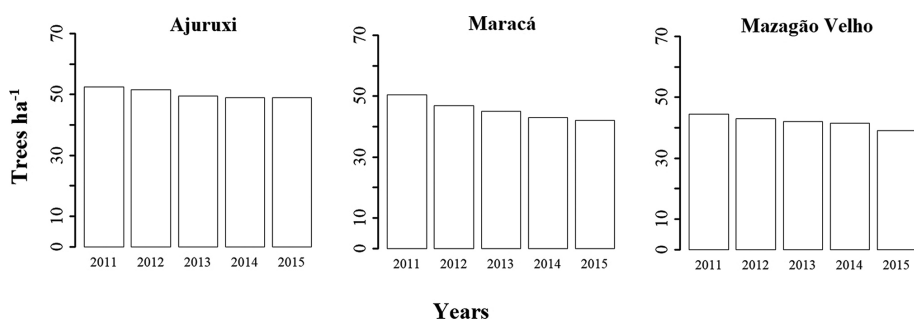


Fig. 2. Population density of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest

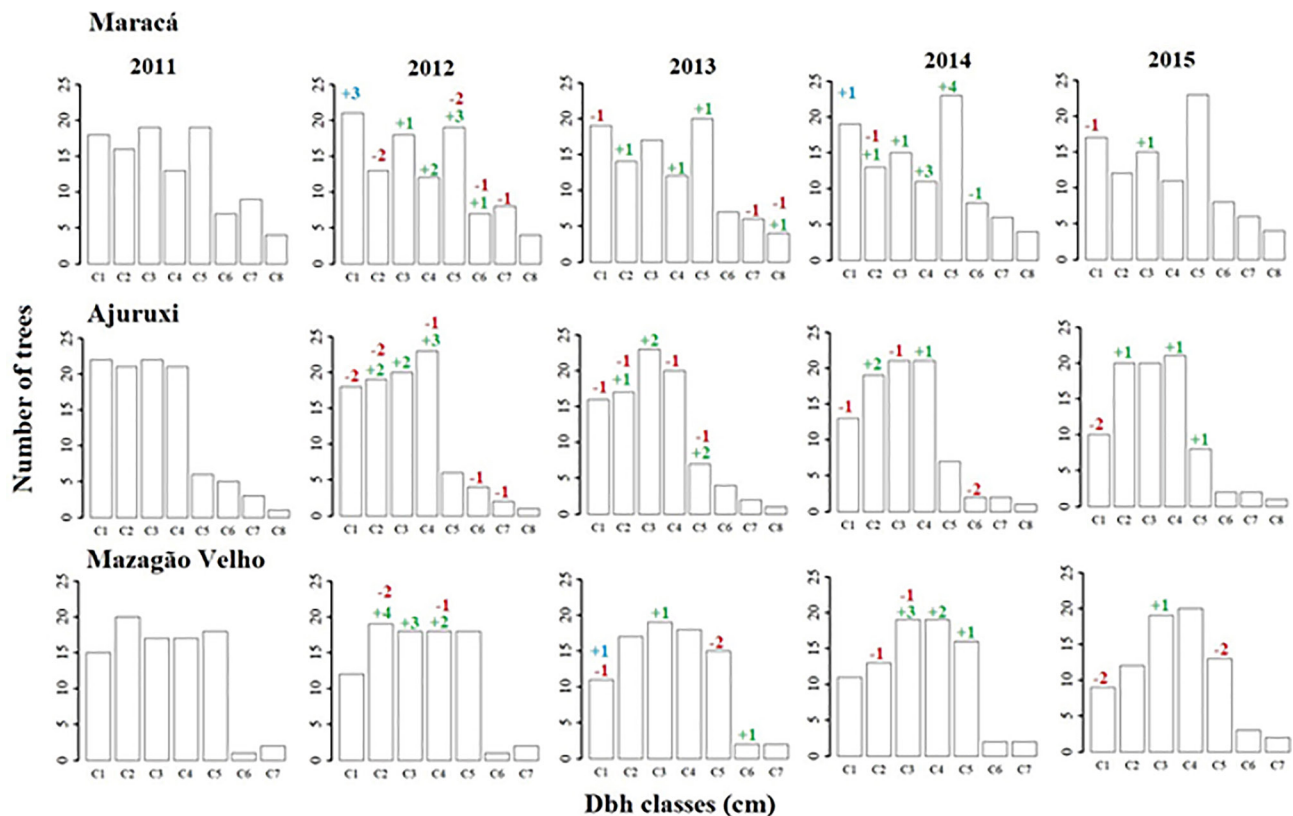


Fig. 3. Dynamics of the diametric structure of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest: the numbers with a + sign in blue represent the number of recruits; numbers with sign (+) in green represent the number of individuals who transitioned from one class to another; and the numbers with sign (-) in red represent the number of individuals who died

with an amplitude between classes of 4.4 cm and 4.9 cm, respectively. In the area of Mazagão Velho, the population was structured in seven diameter classes, with an amplitude of 5.9 cm. The interclass transition of trees (individuals that have grown in diameter and will migrate from a lower diametric class to a higher) was more dynamic in the population of *P. macroloba* from the Ajuruxi (21 transition), followed by the population from the Mazagão Velho (20 transition) and Maracá (18 transition) (Fig. 3). Despite the occurrence of interclass transition, there was no significant change in the diametric structure between 2011 and 2015 for the Ajuruxi ( $D = 0.07$ ;  $p = 0.93$ ), Maracá ( $D = 0.17$ ;  $p = 0.11$ ) and Mazagão Velho areas ( $D = 0.13$ ;  $p = 0.40$ ).

The annual growth rate of *P. macroloba* showed a significant difference between the three areas analyzed ( $F = 3.31$ ;  $p < 0.05$ ). The annual growth rate of the population of *P. macroloba* from Maracá was more expressive ( $0.93 \text{ cm}^{-1} \text{ year}^{-1}$ ) than the populations of Ajuruxi ( $0.75 \text{ cm}^{-1} \text{ year}^{-1}$ ) and Mazagão Velho ( $0.65 \text{ cm}^{-1} \text{ year}^{-1}$ ). The relationship between diametric increment and DBH was significant and negative for the areas of Ajuruxi ( $F = 22.19$ ;  $p < 0.001$ ), Maracá ( $F = 10.55$ ;  $p < 0.001$ ) and Mazagão Velho ( $F = 14.88$ ;  $p < 0.001$ ) (Fig. 4).

The basal area of *P. macroloba* showed a significant difference between the three areas analyzed ( $F = 4.80$ ;  $p < 0.001$ ). The three populations of *P. macroloba* showed a decrease in basal area over the years

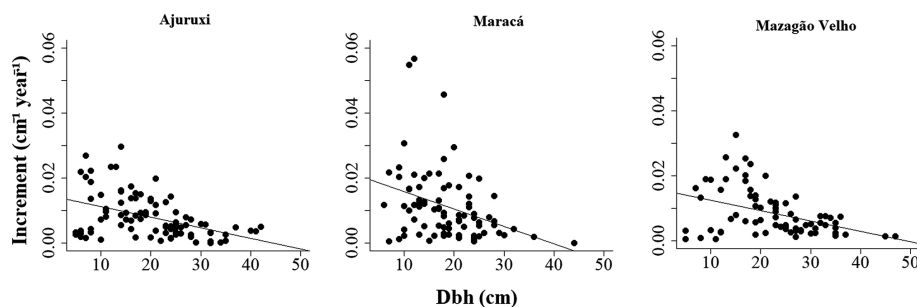


Fig. 4. Influence of diameter size (DBH) on diametric growth rate of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest

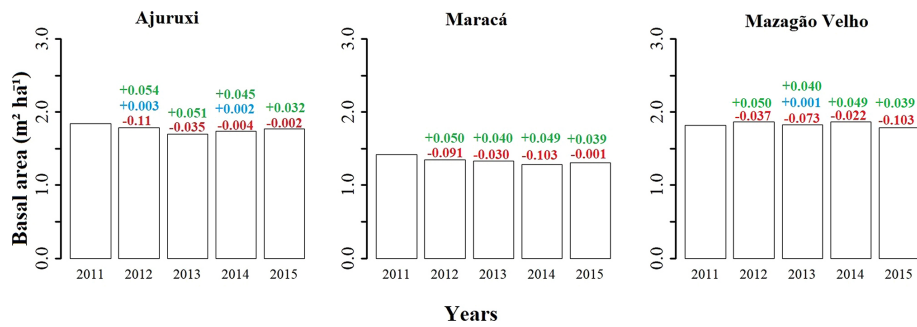


Fig. 5. Basal area dynamics of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest: numbers with minus sign (-) in red represent the loss in basal area of dead individuals; numbers with a plus sign (+) in blue represent the gain in basal area with the entry of new individuals; and the numbers with a plus sign (+) in green color represent internal growth in basal area

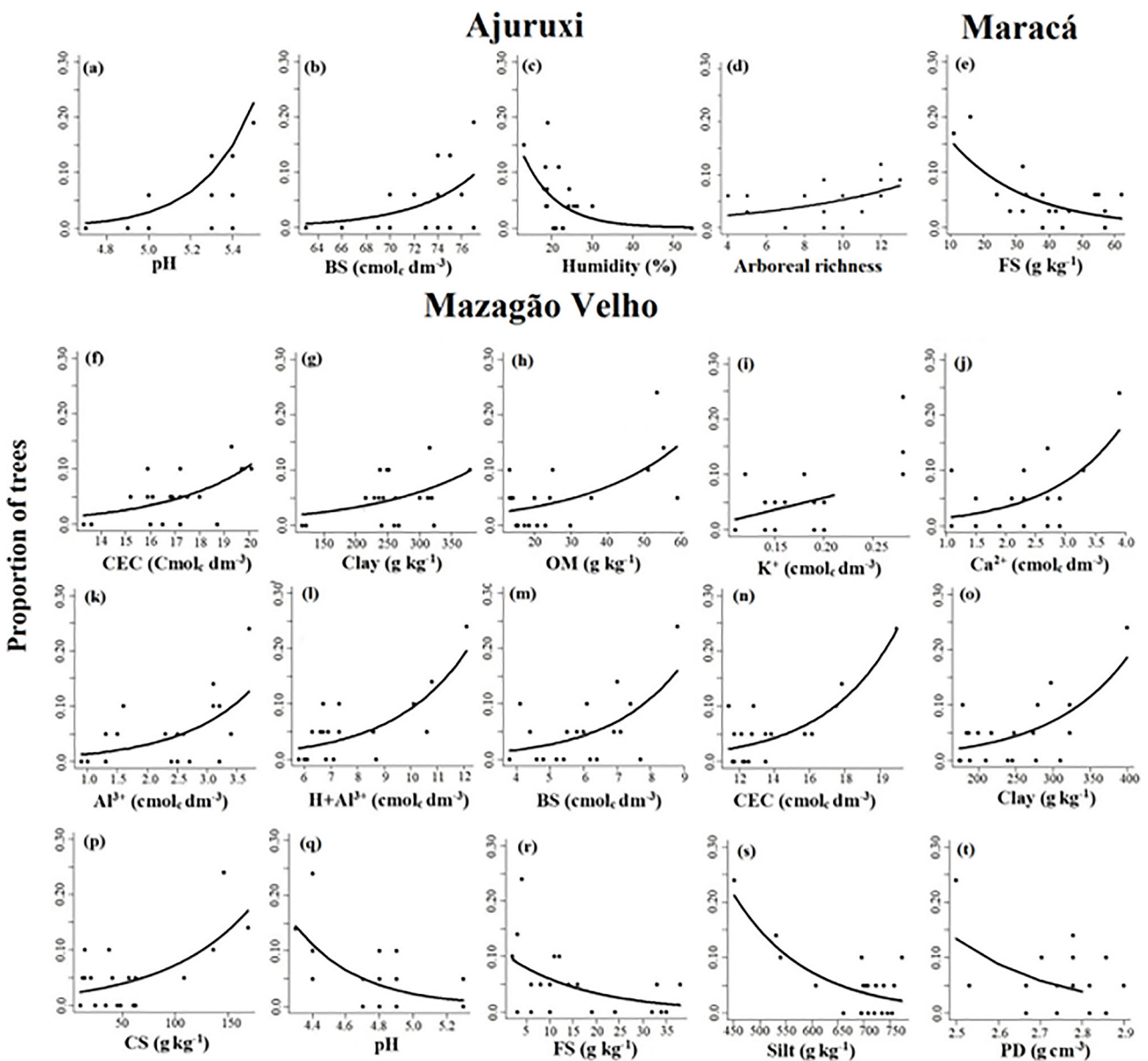


Fig. 6. Influence of soil and vegetation variables on the establishment of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest. BS = Base Sum; pH = Potential Hydrogeonic; FS = Fine sand; CEC = Cation Exchange Capacity; OM = Organic Matter; CS = Coarse Sand; PD = Particle Density; K<sup>+</sup> = Potassium; Ca<sup>2+</sup> = Calcium; Al<sup>3+</sup> = Aluminum

(Fig. 5). In the first inventory (T1), the population of *P. macroloba* in the Maracá area presented a basal area of  $1.42 \text{ m}^2 \text{ ha}^{-1}$  and at the end of the monitoring (T5) the basal area was  $1.31 \text{ m}^2 \text{ ha}^{-1}$ , representing a loss of  $4.9\% \text{ year}^{-1}$ . This population did not show gain in basal area, since it did not recruit any individuals, and the internal growth was  $2.9\% \text{ year}^{-1}$ . In the Ajuruxi area, the basal area in the inventory T1 was  $1.84 \text{ m}^2 \text{ ha}^{-1}$  and in the inventory T5 was  $1.77 \text{ m}^2 \text{ ha}^{-1}$ , a loss of  $3.6\% \text{ year}^{-1}$ . The gain in basal area of this population was  $0.1\% \text{ year}^{-1}$  and the internal growth was  $2.6\% \text{ year}^{-1}$ . In the Mazagão Velho area, the basal area in the inventory T1 was  $1.82 \text{ m}^2 \text{ ha}^{-1}$  and in the inventory T5 was  $1.79 \text{ m}^2 \text{ ha}^{-1}$ , a loss of  $3.1\% \text{ year}^{-1}$ . The gain in basal area was  $0.01\% \text{ year}^{-1}$  and the internal growth was  $2.7\% \text{ year}^{-1}$ .

### Influence of soil and vegetation properties on population density

In the Ajuruxi area, there was a positive and significant correlation between the proportion of *P. macroloba* in the plots with the edaphic variables of pH ( $\beta = 3.95$ ;  $p < 0.05$ ; Fig. 6a) and base sum ( $\beta = 0.19$ ;  $p < 0.05$ ; Fig. 6b), and negative correlation with soil moisture ( $\beta = -0.12$ ;  $p < 0.05$ ; Fig. 6c). In the Maracá area, only the fine sand variable ( $\beta = -0.04$ ;  $p < 0.01$ ; Fig. 6e) had a negative and significant correlation with the proportion of *P. macroloba* in the plots.

In the Mazagão Velho area, there was a positive and significant correlation between the proportion of *P. macroloba* in the plots and the edaphic variables of CTC (Transect 1,  $\beta = 0.28$ ;  $p < 0.01$ , Fig. 6f; Transect 4,  $\beta = 0.25$ ;  $p < 0.001$ , Fig. 6n), clay (Transect 3,  $\beta = 0.006$ ;  $p < 0.05$ , Fig. 6g; transect 4,  $\beta = 0.009$ ;  $p < 0.01$ , Fig. 6o), organic matter ( $\beta = 0.04$ ;  $p < 0.01$ , Fig. 6h), K ( $\beta = 12.20$ ;  $p < 0.01$ , Fig. 6i), Ca ( $\beta = 0.85$ ;  $p < 0.05$ , Fig. 6j), Al ( $\beta = 0.83$ ;  $p < 0.05$ , Fig. 6k), potential acidity ( $\beta = 0.36$ ;  $p < 0.001$ , Fig. 6l), base sum ( $\beta = 0.47$ ;  $p < 0.05$ , Fig. 6m) and coarse sand ( $\beta = 0.01$ ;  $p < 0.01$ , Fig. 6p) and negative with pH ( $\beta = -2.65$ ;  $p < 0.01$ , Fig. 6q), fine sand ( $\beta = -0.04$ ;  $p < 0.01$ , Fig. 6r), silt ( $\beta = -0.007$ ;  $p < 0.01$ , Fig. 6s) and particle density ( $\beta = -4.12$ ;  $p < 0.05$ , Fig. 6t) Only the Ajuruxi area had a positive and significant correlation with a vegetation variable, which was arboreal richness ( $\beta = 0.14$ ;  $p < 0.05$ ; Fig. 6d). There was no significant relationship between the proportion of *P. macroloba* in the plots and the luminosity of the canopy for any population (Supplement S1).

### Influence of hydrometeorological variables on population density, basal area and growth rate

Annual rainfall and mean maximum temperature had no significant correlation with population density, basal area, and growth rate of the three populations of *P. macroloba* (Supplement S1). The Amazon

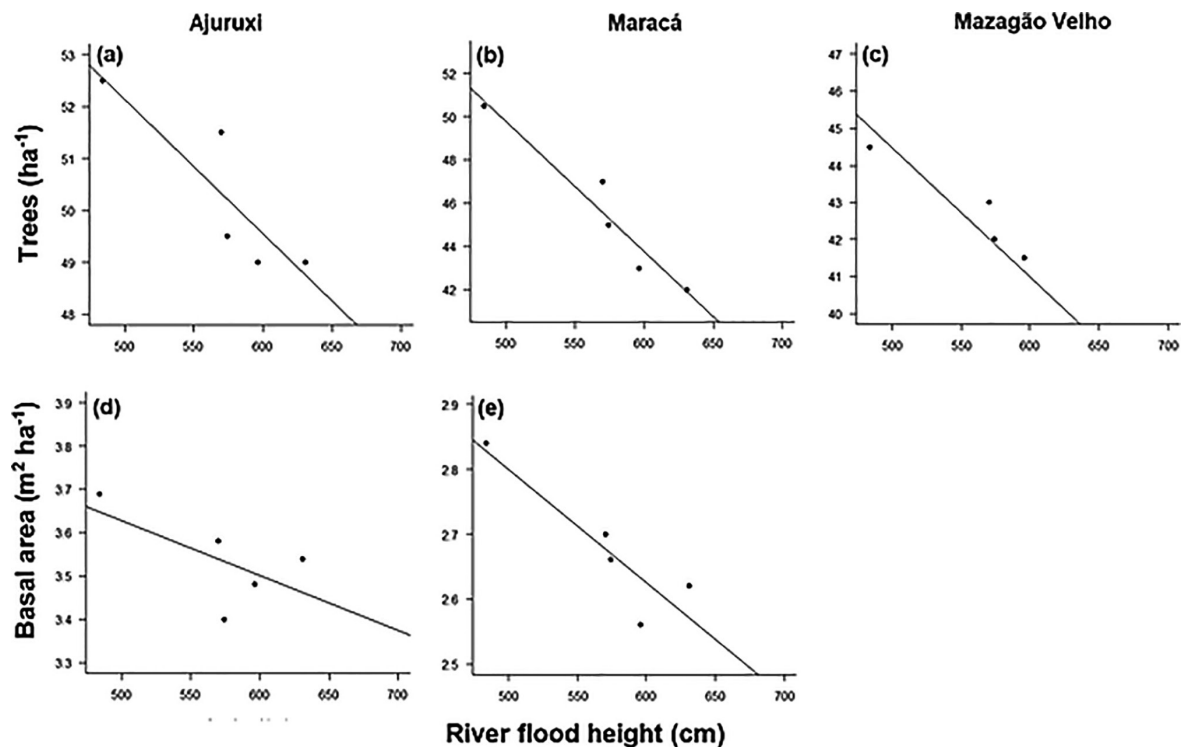


Fig. 7. Annual relationship of the mean maximum height of the Amazon River flood level with the population density and basal area of three populations of *Pentaclethra macroloba* from the Amazon River estuarine floodplain forest



River water level in the study region had a negative and significant correlation with the population density of *P. macroloba* in the areas of Maracá (Fig. 7a;  $F = 39.7$ ;  $p < 0.01$ ), Ajuruxi (Fig. 7b;  $F = 9.9$ ;  $p < 0.05$ ) and Mazagão Velho (Fig. 7c;  $F = 19.6$ ;  $p < 0.05$ ). There was also a significant and negative correlation between the basal area and the river flood level for the areas of Maracá (Fig. 7e;  $F = 12.9$ ;  $p < 0.05$ ) and Ajuruxi (Fig. 7d;  $F = 9.4$ ;  $p < 0.05$ ). While for the Mazagão Velho area, there was no significant correlation between the flood level and the basal area. The climatic and hydrological variables were not correlated with the diametric growth of *P. macroloba* (Supplement S1).

## Discussion

Our study showed a low population dynamism in the demographic parameters of *Pentaclethra macroloba*, mainly reflected in low rates of mortality and recruitment, that may be related with the ecological characteristics of the species, with the conservation status of the forest and with the flood dynamics of the Amazon River.

The decrease in population density presented by *P. macroloba* is related to the fact that the mortality rate has exceeded the recruitment rate, an intrinsic characteristic of the species of the late early successional stage in a forest with a high degree of conservation. The three study areas are adjacent to the Rio Cajari Extractive Reserve, a Conservation Unit that favors a dense forest with climax trees that dominate the canopy. In this condition, few individuals of *P. macroloba* are dominant in the canopy and most are suppressed by the dense tree canopies, causing the death and low growth rate, since the sunlight that penetrates the preserved forest canopy is insufficient to stimulate growth of the understory individuals. Carvalho et al. (2017) observed that the density of pioneer trees in an upland forest with logging historic in western Amazonia is higher, compared to more conserved areas, where the density of these trees tends to decrease in the closed canopy. The low mortality rate of *P. macroloba* is reflected in the low dynamism of the population. According to Nascimento et al. (2005) tree mortality is the main mechanism of renewal and recruitment of trees in the population.

The light that penetrates the understory did not influence the population density of *P. macroloba*, this was reflected in the low rate of recruitment of the species. Ferreira (2012) evaluated the degree of openness of the canopy in our study area and found a dense and preserved canopy, with an openness index between 4.66% to 29.66% for the Mazagão Velho area and between 5.08 to 30.97% for the Ajuruxi area. Sunlight has always been a triggering factor in

the growth process of *P. macroloba*. This was demonstrated in the study of Dantas et al. (2022), in which they analyzed the width of the growth rings and observed past events of suppression and release in the growth of 38 *P. macroloba* trees in a floodplain forest in eastern Amazonia. The authors found that most individuals grew directly towards the forest canopy (15 events = 47%). This indicates that *P. macroloba* seedlings develop very well in the gaps that form from the fall of trees.

In some plots we did not register the presence of *P. macroloba*, something unusual for this species with ecological plasticity to adapt to various environmental gradients. In addition to the closed canopy and low incidence of light, another factor that may be limiting the presence of *P. macroloba* is the river flood. The permanently flooded soil makes it difficult to transport oxygen and the gas exchange of the root with the environment, creating an anoxic environment in the rhizosphere, where few trees manage to establish themselves in these conditions (Wittmann & Parolin, 2005). Dantas et al. (2017) analyzed the spatial structure of *P. macroloba* in the floodplain forest of *Estação Experimental do Mazagão*, distant less than 10 km from our study area, found a high density of *P. macroloba* in the transition between an area periodically flooded by a low-amplitude flood pulse (low floodplain) and another area only floods during the rainy season (high floodplain). In areas with permanent flooding (a depression in the ground that accumulates water), the authors did not register the presence of *P. macroloba*.

The mortality rate for the three populations analyzed in this study (Ajuruxi 1.96% year<sup>-1</sup>; Mazagão Velho 3.24% year<sup>-1</sup>; Maracá 4.50% year<sup>-1</sup>) is considered low for tropical late secondary species. The average mortality rate for this ecological group is between 7% year<sup>-1</sup> and 10% year<sup>-1</sup> (Condit et al., 1995). In *La Selva* Forest Reserve, Costa Rica, Hartshorn (1972) found a mortality rate of 20% year<sup>-1</sup> for *P. macroloba*. This mortality rate found in *La Selva* may be related to the human population advance around the reserve or may also be the result of interspecific competition, since of all the trees in the reserve more than 40% are *P. macroloba* (McDade & Hartshorn, 1994). While in our study area, the permanent plots are close to a conservation unit and inhabited only by riverside populations, perhaps this favors a high degree of conservation of the neighboring vegetation, reflecting in a low tree mortality rate.

The diametric structural pattern of *P. macroloba* over the years, log-normal, shows a typical pattern of late secondary successional stage species that recruit few young trees and concentrate most of the adult trees in the central diameter classes. This pattern was also observed in other floodplain areas of the Amazon estuary (Dantas et al., 2017, 2022) and

Costa Rica (Galván et al., 2003) in populations of *P. macroloba*. Young trees have a greater diameter increment than older trees (Fig. 4), showing that young trees can develop in a conserved environment with a closed canopy, this guarantees the renewal of the future population.

The increase in pH (tending to the neutral range) and exchangeable cations ( $\text{Base Sum} = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^{+}$ ) in the soil, showed a significant relationship with increasing population density of *P. macroloba* in the Ajuruxi area (Fig. 6a and 6b). Soil acidity is controlled by the increase and leaching of basic cations such as Ca, Mg, K and Na (Neina, 2019). This shows a preference of *P. macroloba* for soils with neutral pH, where most mineral nutrients are available to the plant. On the other hand, very moist soils can limit the establishment of *P. macroloba* (Fig. 6c). Dantas et al. (2017), studying the special distribution of *P. macroloba* in estuarine floodplain forest, observed that in soils with low drainage capacity and which remain waterlogged for most of the year limited the establishment of *P. macroloba*.

In the Mazagão area, the fine sand content was the only soil variable to explain the increase in *P. macroloba* trees in the plots. High levels of fine sand in the soil, together with clay and silt, contribute to making the soil firmer and more structured, reducing the impact of tidal dynamics on the sedimentation of these soils and providing greater firmness to the roots of the trees. Soils with a high content of fine sand have a greater capacity to fix potassium (Mushkina et al., 2007), a mineral element important for plant growth and cell osmotic balance (Taiz et al., 2017).

In the Maracá area, the increase in soil variables such as CTC, clay, organic matter, K, Al, potential acidity, base sum and coarse sand provided an increase in the number of *P. macroloba* trees in the plots. The high content of organic matter and clay favors a greater retention of mineral nutrients, through the increase of CTC, essential for the development and growth of the plant. According to Targhetta et al. (2015) low levels of clay and basic cations in the soil negatively affected the distribution and richness of tree species in a flooded environment in Central Amazonia. In white-sand vegetation (*campinarana*), influenced by flooding, in Central Amazonia, there is a greater diversity of plants in soils with high clay contents, which contributes to greater fertility of these soils (Damasco et al., 2013). However, *P. macroloba* is highly adaptable to soils with low nutritional content, as this species is an excellent nitrogen fixer (McGee et al., 2020).

The increase in aluminum content in the soil was positively correlated with the density of trees, which may indicate that *P. macroloba* can help in the phytoremediation of soils with high aluminum content. Mori

et al. (2021) also found a positive relationship between the increase of aluminum in the soil with the functional traits of productivity of a forest community in flooded environments in the Central Amazon.

On the other hand, when the pH and the levels of silt, fine sand and particle density increase, the density of *P. macroloba* decreases in the plots. This shows that *P. macroloba* is adaptable to different types of soils and can establish itself in different pH ranges (4 to 7). Damasco et al. (2013) found that plant diversity increases in soils with acidic pH in flooded *campinaranas* in Central Amazonia. However, the authors found in other plots that the correlation was negative between diversity and soil pH, when the pH rises towards the neutral range, plant diversity increases.

Our results show that high levels of flooding may be a limiting factor for the establishment and increment in basal area of *P. macroloba*. Dantas et al. (2022) showed that the high level of flooding in the rainy season of the Amazon estuary reduced the cambial activity of *P. macroloba*. In the lower levels of flooding, a high population density of *P. macroloba* is found (Dantas et al., 2017). This shows that the low-amplitude, polymodal flood cycle is fundamental for the survival of tree species that are adapted to low flood levels. In a floodplain forest in Central Amazonia, Luize et al. (2015) found that species richness and diversity decrease in areas with higher flood amplitudes.

The population parameters presented by *Pentaclethra macroloba* are reflections of its successional life history and of the environmental interactions with the flood dynamics of the floodplain forest. The presence of a late secondary stage hyperdominant species, such as *P. macroloba*, is not a factor that inhibits the presence of neighboring trees, on the contrary, *P. macroloba* had a positive interaction with the floristic richness of the region. The high fertility of the Amazon estuary soils favors the establishment and higher population density of *P. macroloba*. The flood gradient is an environmental drive that regulates the population growth of *P. macroloba*, so that areas with low flood amplitude favor the establishment of the species. Our long-term study will be essential to establish public policies for the sustainable management of seeds and natural populations of *P. macroloba*.

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