SPATIAL DISTRIBUTION OF A POPULATION OF *Pentaclethra macroloba* (Willd.) KUNTZE IN A FLOODPLAIN FOREST OF THE AMAZON ESTUARY[1]

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ABSTRACT – We analyzed the spatial distribution pattern of *Pentaclethra macroloba* to assist in the development of management plans and conservation of this species in estuarine floodplain forests. The study was conducted in an area of floodplain forest of 55.94 ha, in Mazagão, Amapá, Brazil. A census was performed and all individuals of $\geq$ 30 cm circumference at breast height (CBH), living and dead, were georeferenced. Ripley's K function was used to analyze the spatial distribution of the population, including mortality and diameter classes. The relationships between distance to the edge of inundation and density and basal area of the population were analyzed using linear regression. We recorded 993 live individuals and 22 dead. The distribution of the population was found to vary with the topographic gradient associated with the distance to the edge of the inundation. Diameter classes 1 ($\leq$ 13.2 cm) and 2 ($\leq$ 18.6 cm) were spatially aggregated close to the water and randomly distributed far from the water. Classes 3 ($\leq$ 24.0 cm) and 4 ($\leq$ 29.5 cm) were aggregated at all distances, and classes 5 ($\leq$ 34.9 cm), 6 ($\leq$ 40.3 cm), 7 ($\leq$ 45.7 cm) and 8 ($\leq$ 51.2 cm), were randomly distributed at all distances. Mortality was randomly distributed. The population density was 18 trees ha^{-1} with a basal area of 49 m^2 ha^{-1}, and both density ($r^2=0.51$; $p=0.0195$) and basal area ($r^2=0.67$; $p=0.0039$) increased with the distance from the edge of the inundation. We conclude that the spatial distribution and successful establishment of this species in floodplain forest are related to the dynamics of flooding and the resultant impacts on dispersal processes.

Keywords: Autoecology of oil bean tree; Ripley's K function; Dispersal.

DISTRIBUIÇÃO ESPACIAL DE UMA POPULAÇÃO DE Pentaclethra macroloba *(Willd.) KUNTZE EM FLORESTA DE VÁRZEA DO ESTUÁRIO AMAZÔNICO*

RESUMO – Analisou-se o padrão de distribuição espacial de Pentaclethra macroloba *para auxiliar em planos de manejo e conservação desta espécie nas florestas de várzeas estuarinas. O estudo foi realizado em floresta de várzea de 55,95 ha, na cidade de Mazagão, Amapá. Foi realizado um censo e georreferenciamento de todos os indivíduos, vivos e mortos, que apresentavam a Circunferência na Altura do Peito (CAP)* $\geq$ *30 cm. A Função K de Ripley foi utilizada para analisar o padrão de distribuição populacional, da mortalidade e das classes diamétricas. A relação da distância de inundação com a densidade e a área basal da população foi analisada utilizando regressão linear. Foram inventariados 993 indivíduos vivos e 22 mortos. A população obteve padrão agregado ao longo do gradiente topográfico de inundação. As classes de diâmetro 1 (*$\leq$ *13,2 cm) e 2 (*$\leq$ *18,6 cm) iniciaram com padrão agregado, finalizando com padrão aleatório. As classes 3 (*$\leq$ *24,0 cm) e 4 (*$\leq$ *29,5 cm) obtiveram padrão totalmente agregado e nas classes seguintes, 5 (*$\leq$ *34,9 cm), 6 (*$\leq$ *40,3 cm), 7 (*$\leq$ *45,7 cm) e 8 (*$\leq$ *51,2 cm) o padrão foi aleatório. O padrão da mortalidade foi aleatório. A densidade* *populacional foi 18 indivíduos ha^{-1} e área basal de 49 m² ha^{-1} dos indivíduos vivos. A densidade (r^2=0,51; p = 0,0195) e a área basal (r^2 = 0,67; p = 0,0039) dos pracaxizeiros aumentam com o afastamento do gradiente de distância do rio. A dinâmica de inundação e o processo de dispersão são fatores relacionados com o padrão espacial e o sucesso no estabelecimento da espécie.*

Palavras-chave: Autoecologia de pracaxi; Função K de Ripley; Dispersão.

1. INTRODUCTION

High rainfall and climatic seasonality lead to periodic flooding of areas along the main river systems of the Amazon (Wittmann et al., 2006), with areas flooded by white water being known as várzeas or floodplain forests (Wittmann et al., 2010). Floodplain forests are energetically open systems that contain large volumes of freshwater and sediments, and are driven by daily (Rabelo, 2000) and annual (Junk, 1989) cycles of flooding. The flood pulse is unimodal and predictable, leading to a terrestrial and an aquatic phase (Junk, 1997). Due to constant flooding, a large amount of sediment, originating in the Andes or pre-Andes (Mcclain and Naiman, 2008), is carried to these areas (Rabelo, 2000) which leads to highly fertile soils (Rabelo, 2000). Floodplain forests play an important role in the organic carbon balance in the Amazon Basin, are areas of high rates of productivity of aquatic plants and are important sources of methane for the troposphere (Melack et al., 2009).

These forests contain an important diversity of trees, with approximately 1,000 tree species tolerant to the patterns of flooding already recorded from the Amazon Basin (Wittmann et al. 2006). These trees are an important source of resources for a majority of the rural population of the Amazon (Wittmann et al., 2010), providing a variety of timber and, most importantly, non-timber forest products (NTFPs) that are sources of food, pharmaceutics and cosmetics. These NTFPs include: fruits (taperebá, urucuri), oils (andiroba, pracaxi), barks (andiroba, ucuúba, pracaxi), resins (breu-branco), and latex (seringueira), etc.

One species of particular importance as a source of NTFPs is *Pentaclethra macroloba* (Willd.) Kuntze. This species belongs to the family Fabaceae and is popularly known in the Amazon region as "pracaxi". *P.macroloba* reaches a height of approximately 14 m and a DBH (Diameter at Breast Height) of up to 59 cm (Projeto Florestam). The leaves are bipinnate. The inflorescences are in the form of terminal or subterminal spikes, with 200 bisexual flowers per stem. The fruits are dry, dehiscent green pods that turn brown when ripe. The seeds are dark brown and opaque with superficial depressions forming prominent lines that are sometimes reticulated close to the base of the seed (Flores, 2003). Flowering occurs between July and September, the dry season, and fruits mature and seeds are dispersed between January and April, the period of highest rainfall (Freitas et al., 2003). The primary dispersal mechanism is autochory, with seeds dispersed by explosive dehiscence (Flores, 2003). Beyond this, in the Amazonian floodplains *P. macroloba* has hydrochory as a secondary dispersal mechanism (Williamson and Costa, 2000). Approximately 90% of seeds germinate (Flores, 2003). The species is a pioneer (Condé and Tonini, 2013), occurring in high densities in the Amazon Estuary (Carim et al., 2017), and being characterised by rapid growth and a high capacity for regeneration (Sears and Pinedo-Vasquez, 2005). The bark of this species is used to dye the skin and also as a medicine to treat dysentery and diarrhoea (Cordero and Boshier, 2003), and the leaves can be used to treat fungal infections (Shebitz et al., 2013). However, its greatest potential is in the oil extracted from its seeds, that has medicinal properties (Pesce, 2009; Costa et al., 2013) that could make it very attractive to the cosmetics and herbal medicine industries, although it is not yet marketed on a large-scale.

Ecological studies that aim to investigate the spatial distribution of this species within the forest are fundamental for programmes of management and conservation. According to Condit et al. (2000), the spatial distribution of a species allows for an understanding of both reproductive processes and how the resources available in the community are used. Indeed, understanding how individuals of a species distribute themselves in a community is one of the first steps to understanding forest dynamics (Hay et al., 2000), natural history and ecological interactions between populations (Forget et al., 1999).

The objective of this study was to analyse the spatial distribution pattern of *P. macroloba* to aid in the development of management plans and in the species' conservation, aiming to support sustainable exploitation of this species in estuarine floodplain forests.

2. MATERIAL AND METHODS

2.1. Characterization of the study area

The study was conducted in the "Campo Experimental do Mazagão - CEM", owned by Embrapa Amapá. The CEM is located in the municipality of Mazagão, in the south of the state of Amapá, at 00°02'33" south and 51°15'24" west, and at an altitude of 15 m (Yokomizo et al., 2010). It has an area of 55.95 ha of floodplain forest. The relief is fairly smooth, with a declivity in the north/east. Owing to this declivity and patterns of flooding, the area consists of three habitat types. When the water from the Mazagão river channel overflows to the forest interior, part of the area is submerged (lowland floodplain forest), and the other part, located more to the north/south remains un-submerged (highland floodplain forest). However, when the river levels are at their highest (period of highest flood level during the new and full moons) the whole area is submerged. In the centre of the area there is a lower area in which water remains dammed throughout the year, forming a habitat referred to as "igapó" (Dantas et al., 2014).

The climate of the region is classified as Am, characteristic of rainy tropical climates (Alvares et al., 2014). According to data from the Embrapa meteorological station, located less than 20 km from the study area, the average annual temperature reaches a maximum of 31.6ºC and a minimum of 23.1ºC. The average annual precipitation is 2,584.7 mm, with 85.87% of the accumulated precipitation being concentrated in the months of January to July (Lopes Filho, 2016).

The predominant vegetation type is Dense Alluvial Rainforest (IBGE, 2012), with a high frequency of palms and large, commercially valuable trees, particularly: andiroba (*Carapa guianensis*), ucuúba (*Virola surinamensis*), pracuuba (*Mora paraensis*), pau-mulato (*Calycophyllum spruceanum*), seringueira (*Hevea brasiliensis*), macacaúba (*Platymiscium ulei*), macucu (*Licania* sp.), cedro (*Cedrella odorata*), pracaxi (*Pentaclethra macroloba*), mututi (*Pterocarpus amazonicus*), ananim (*Symphonia globulifera*), mauba (*Licaria mahuba*), ventosa (*Hernandia guianensis*), and others (Rabelo, 2005).

The soils of the area are classified as Melanic Gleysols (Embrapa, 2013), soils that have a medium texture, poor drainage and medium to high natural fertility (Yokomizo et al., 2010). According to surveys by pedologist Raimundo Cosme Oliveira Júnior (Embrapa Amazônia Oriental) carried out in the project "ecologia e manejo para uso múltiplo de florestas de várzea do estuário amazônico - Florestam", all the soils of this region of the estuarine floodplain are classified as Melanic Gleysols Ta Eutrophic, with a predominance of silt textures. Both the sediment and the soil are formed by smectite, ilite, kaolinite, goethite, anatase and quartz (unpublished data).

2.2. Data collection

A census was carried out in July and August 2014, in which all living and dead individuals of *P. macroloba* with a CBH (Circumference at Breast Height) $\geq$ 30 cm (measured with a tape measure with an accuracy of 0.1 cm) were registered. Data were collected along twelve transects (that were open trails in the year 2011, when the first inventory of the study area was carried out) inside the forest. The transects were installed in parallel in a north-south direction, perpendicular to the "Mazagão channel", with 50 m between transects and a varied length according to the sinuosity of the edge of the study area (Figure 1). The inventories were initiated at the margin of the Mazagão channel and continued towards the highland floodplain forest, always going out and back along the same transect, and trees were inventoried in a 25 m strip on the right side of the transect, both in the outward and return trips. Thus it was possible to carry out a 100% inventory.

All the inventoried individuals were identified numerically with aluminium plates placed at the time of CBH measurement. Georeferencing of all individuals was performed using a GPS (Garmin 60CSx), which showed an error of at most 6 m, mainly close to midday when satellite signals were weakened, and generally of between 3 and 4 m.

2.3. Data analysis

CBH data were transformed to DBH (Diameter at Breast Height). The spatial distribution pattern of the population, mortality and diameter classes were analysed using the x and y coordinates (in UTM) of each individual in the sample. The spatial distribution pattern was determined by the univariate Ripley's K Function (Ripley, 1981). This

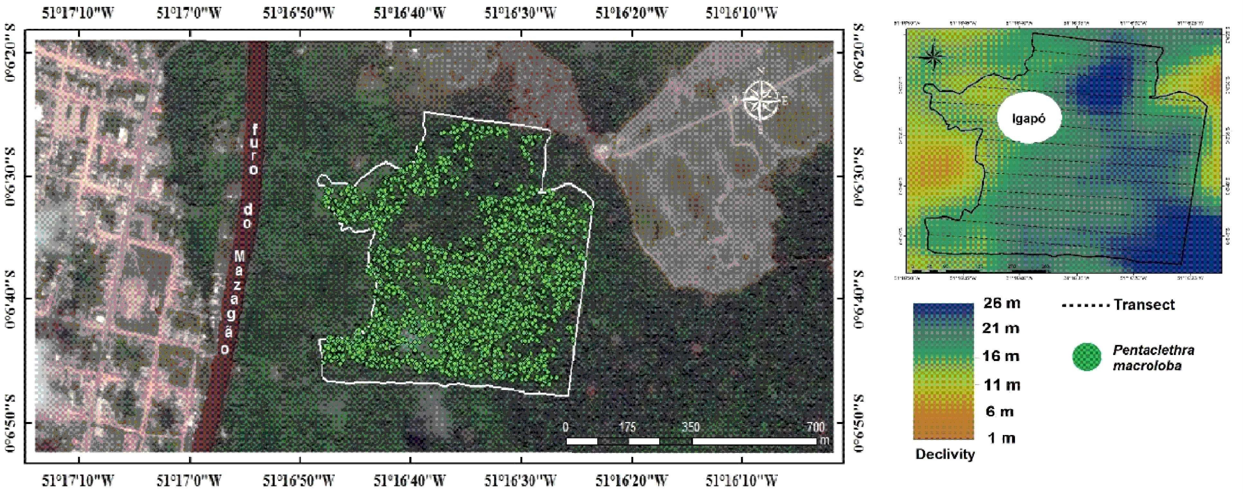

Figure 1 – Spatial distribution map of the population of *Pentaclethra macroloba* (Willd.) Kuntze (left) and topographic gradient (right) of the floodplain forest, "Campo Experimental do Mazagão - CEM".

Figura 1 – *Mapa da distribuição espacial da população de* ***Pentaclethra macroloba*** *(Willd.) Kuntze (à esquerda) e o gradiente topográfico (à direita) da floresta de várzea do Campo Experimental da Embrapa Amapá no município de Mazagão.*

analysis tool describes the characteristic of a point on several scales of distance (Dixon, 2002). The method basically consists of plotting a circle of radius "s" around each point (individual tree registered), and quantifying the number of other individuals within the circle (Silva et al., 2012). In the case of the univariate function, the null hypothesis is that of Complete Spatial Randomness (CSR).

The radius "s" used for this study ranged from 0 to 350 m, because this value corresponds to approximately one half of the smallest side of the study area, which according to Diggle (2003), avoids bias in the distance estimator of the function and errors of estimates. To test the CSR hypothesis, confidence intervals were created using the Monte Carlo method, from 1000 permutations and using the total number of sample records, guaranteeing a probability level of 1%.

The Ripley's K function was transformed into the function L (h) to better visualize the results and to compare the estimates with the CSR hypothesis. The graph of the transformed L (h) function, whose X-axis represents the radius "s" (in meters) allows for deviations from the null hypothesis to be visualised (Ripley, 1981). If the pattern is completely random, the L (h) function is presented as a horizontal line within the confidence intervals. Spatially aggregated distributions lead to more trees than expected by the CSR, and the function will have positive values. If the trees are regularly spaced, the number of trees will be fewer than expected by the CSR and the function will have negative values (Silva et al., 2012).

The relationships between distance to the edge of the inundation and population density and basal area were verified using simple linear regression analysis. For this, the study area was divided in to 10 parcels of 25,000 m^2 in ArcGis 10.1 (ArcMap). The significance of the regression was verified using Analysis of Variance (ANOVA), and a 5% probability level. All the statistical analyses were performed in Program R version 3.1.0 (R Development Core Team, 2014), and for the spatial distributions the package "Splancs" was used (Rowlingson and Diggle, 2013). The number of diametric classes and their amplitudes were calculated using the Sturges formula (Sturges, 1926). The map of the spatial distribution of individuals was created in ArcMap version 10.1.

3. RESULTS

One-thousand-and-fifteen individuals were inventoried, of which 22 were dead. Considering only living individuals, the sample population showed an aggregate distribution pattern (Figure 1). The L (h) function fell above the confidence interval, rejecting the null hypothesis of complete spatial randomness and showing an aggregate pattern at all scales of distance (Figure 2a).

The spatial pattern found for tree mortality was random (Figures 2b), as the L (h) function fell within the confidence intervals and as such the null hypothesis of complete spatial randomness is supported.

In the study area, living individuals were distributed according to the topographic gradient, with the highest concentration occurring in the highest (highland floodplain forest, 11 individuals ha^{-1}) and lowest (lowland floodplain forest, 6 individuals ha^{-1}) parts of the area. Few individuals were found in the igapó (1 individuals ha^{-1}) (Figure 1).

Eleven diameter classes were formed with a 5.4 cm amplitude between classes (Figure 3). Classes 9, 10 and 11 of the living individuals presented only one individual. There was mortality of individuals only in classes 1 to 5 (Figure 3). The spatial distribution by diametric class revealed that the individuals belonging to classes 1 ($\leq$ 13.2 cm) and 2 ($\leq$ 18.6 cm) alternated between aggregated and random patterns. In class 1 (Figure 4a), the spatial pattern was aggregated between 0 and 300 m from the edge of the inundation and random at 301 to 350 m. Class 2 (Figure 4b) was spatially aggregated at 0 to 250 m from the edge of the inundation, and randomly distributed at 251 to 350 m. Classes 3 ($\leq$ 24.0 cm, Figure 4c) and 4 ($\leq$ 29.5 cm, Figure 4d) showed totally a aggregated pattern. In the largest diameter classes, classes 5 ($\leq$ 34.9 cm, Figure 4e), 6 ($\leq$ 40.3 cm, Figure 4f), 7 ($\leq$ 45.7 cm, Figure 4g) and 8 ($\leq$ 51.2 cm, Figure 4h), the pattern was random at all distances analysed. For classes 9 ($\leq$ 56.6 cm), 10 ($\leq$ 62.0 cm) and 11 ($\leq$ 67.4 cm), no analyses were performed, since only one individual was recorded per class (Figure 3).

The population density of living individuals was 18 individuals ha^{-1}, with a total basal area of 49 m² ha^{-1}. The regression analysis revealed that density (r2 = 0.51, p = 0.0195) and basal area (r2 = 0.67, p = 0.0039) are linearly related to the distance to the Mazagão channel, with both density and basal area of the population increasing with distance from the edge of the inundation (Figure 5). The significance level of the regression was satisfactory for both population density (F1.8 = 8.479 *, p = 0.019; * significant) and basal area (F1.8 = 16.07 **, p = 0.004; ** highly significant) according to the ANOVA test with a 5% probability error level.

4. DISCUSSION

Various biotic and abiotic factors can determine the distribution of a species within its habitat (Fangliang et al., 1997), including for example: dispersal processes, environmental dynamics and topography. The aggregated spatial distribution of *P. macroloba* found in this study may be related to the type of dispersal and to flood dynamics of the study area. This species' primary dispersal mechanism is via autochory, with seeds being expelled from the mature, dry fruits via explosive dehiscence (Flores and Rivera, 1989). However, in estuarine floodplain forests, this type of dispersal alone cannot carry the seeds far enough away from the matrix to explain the pattern of distribution observed. The distribution pattern is strongly related to the secondary dispersal mechanism of the species, hydrochory. In this case, after the buoyant seeds are dispersed by autochory, they are subsequently carried over long distances by the currents of the flooded channels (igarapés) (Williamson and Costa, 2000). Trunks, litter, branches, roots and banks of earth act as natural barriers, intercepting the seeds and allowing for considerable concentrations of propagules in one place. As such, in higher areas (highland floodplain forest) large aggregations of saplings are found, with seeds having been carried there from lower ground areas by the rising flood waters. The dispersal process of *P. macroloba* observed in this study corroborates the hypothesis forwarded by Janzen (1970), in which the number of seeds is expected to decline with increasing distance from the parent tree.

According to Ricklefs (2010), the spatial structure of plant populations follow environmental variations. As a result, species tend to settle in suitable habitats. In the floodplain forests, the diverse microhabitats formed by the flood dynamics are sources of vital biological processes that define the establishment and survival of plant species in their initial stages of development (Nebel et al., 2001). The results of this study suggest that the adequate habitat of *P. macroloba* (in the floodplain forest of this study) are the lowest and highest areas of the terrain, which do not suffer long periods of flooding, and where most of the population is concentrated. These two parts of the terrain receive high nutrient inputs from the Amazon River, due to tidal inundations that twice-daily flood the area. Long periods of flooding may be a limiting factor for the establishment of *P. macroloba* as in the

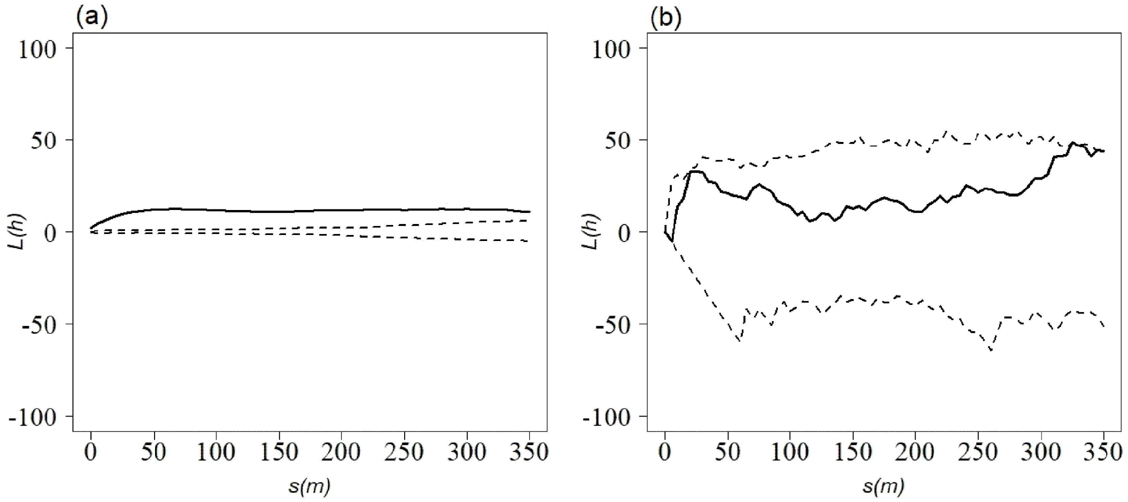

Figure 2 – Distribution pattern of the population (a) and mortality (b) of *Pentaclethra macroloba* (Willd.) Kuntze (on a scale of 0-350 m) in floodplain forest of the "Campo Experimental do Mazagão - CEM" (Continuous line = transformed K function; Discontinues line = confidence intervals).

Figura 2 – *Padrão de distribuição da população (a) e da mortalidade (b) de* ***Pentaclethra macroloba*** *(Willd.) Kuntze (nas escalas de 0 a 350 m) na floresta de várzea do Campo Experimental da Embrapa Amapá no município de Mazagão (Linha continua = função K transformada; linha descontinua = envelopes de confiança).*

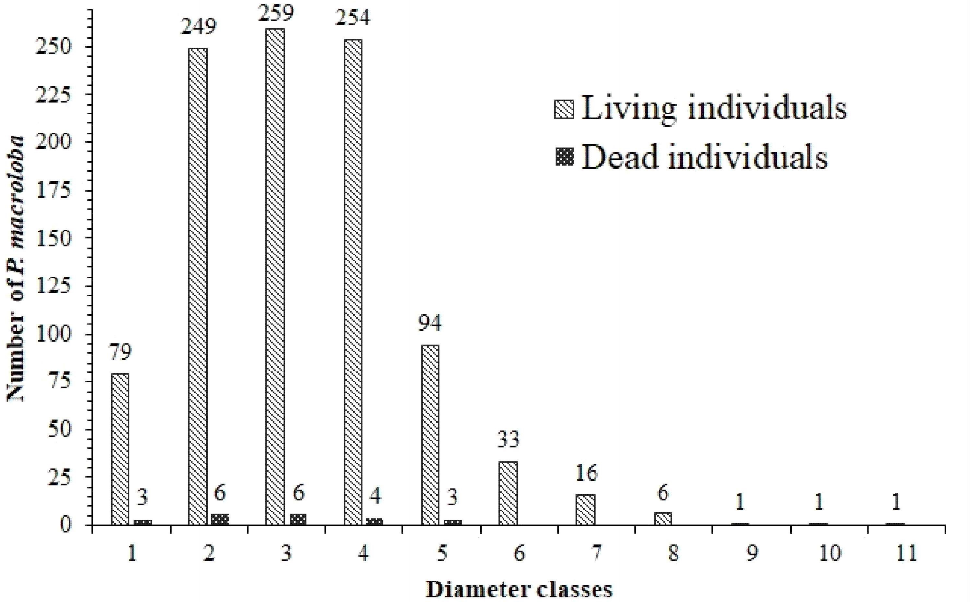

Figure 3 – Diametric distribution of *Pentaclethara macroloba* (Willd.) Kuntze in floodplain forest of the "Campo Experimental do Mazagão - CEM": class 1 [≤ 13.2 cm]; class 2 [≤ 18.6 cm]; class 3 [≤ 24.0 cm]; class 4 [≤ 29.5 cm]; class 5 [≤ 34.9 cm]; class 6 [≤ 40.3]; class 7 [≤ 45.7 cm]; class 8 [≤ 51.2 cm]; class 9 [≤ 56.6]; class 10 [≤ 62.0]; and class 11 [> 67.4].

Figura 3 – *Distribuição diamétrica de* ***Pentaclethra macroloba*** *(Willd.) Kuntze na floresta de várzea do Campo Experimental da Embrapa Amapá no município de Mazagão: classe 1 [≤ 13,2 cm]; classe 2 [≤ 18,6 cm]; classe 3 [≤ 24,0 cm]; classe 4 [≤ 29,5 cm]; classe 5 [≤ 34,9 cm]; classe 6 [≤ 40,3]; classe 7 [≤ 45,7 cm]; classe 8 [≤ 51,2 cm]; classe 9 [≤ 56,6]; classe 10 [≤ 62,0]; e classe 11 [> 67,4].*

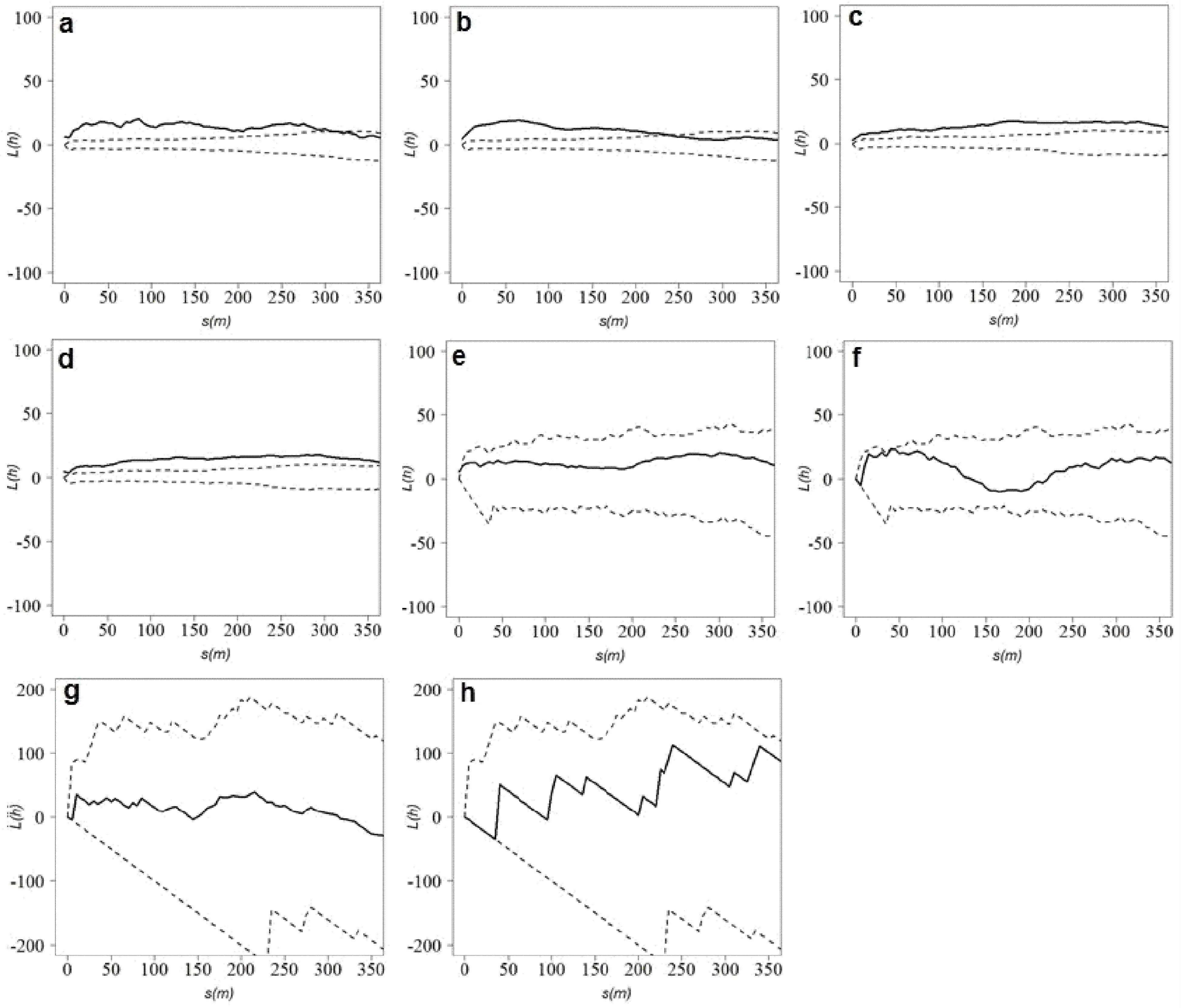

Figure 4 – Spatial distribution pattern of the population of *Pentaclethra macroloba* (Willd.) Kuntze, per diameter class (on a scale of 0-350 m) in floodplain forest of the "Campo Experimental do Mazagão - CEM": (a) class 1 [≤ 13.2 cm]; (b) class 2 [≤ 18.6 cm]; (c) class 3 [≤ 24.0 cm]; (d) class 4 [≤ 29.5 cm]; (e) class 5 [≤ 34.9 cm]; (f) class 6 [≤ 40.3]; (g) class 7 [≤ 45.7 cm]; and (h) class 8 [≤ 51.2 cm] (Continuous line = transformed K function; Discontinues line = confidence intervals).

Figura 4 *– Padrão de distribuição espacial da população* ***Pentaclethra macroloba*** *(Willd.) Kuntze, por classe diamétrica (nas escalas de 0 a 350 m) na floresta de várzea do Campo Experimental da Embrapa Amapá no município de Mazagão: (a) classe 1 [≤ 13,2 cm]; (b) classe 2 [≤ 18,6 cm]; (c) classe 3 [≤ 24,0 cm]; (d) classe 4 [≤ 29,5 cm]; (e) classe 5 [≤ 34,9 cm]; (f) classe 6 [≤ 40,3]; (g) classe 7 [≤ 45,7 cm]; e (h) classe 8 [≤ 51,2 cm] (Linha continua = função K transformada; linha descontinua = envelopes de confiança).*

igapó (the lowest site of the terrain, where tidal water is dammed during most of the year), the concentration of individuals was found to be very low. This is due to the extremely anoxic conditions around the tree roots, making it difficult for species that are not adapted to these conditions to establish (Wittmann and Parolin, 2005). The spatial distribution map of the species generates some hypotheses about *P. macroloba*'s strategies of dispersal and colonization, which need to be investigated in specific studies.

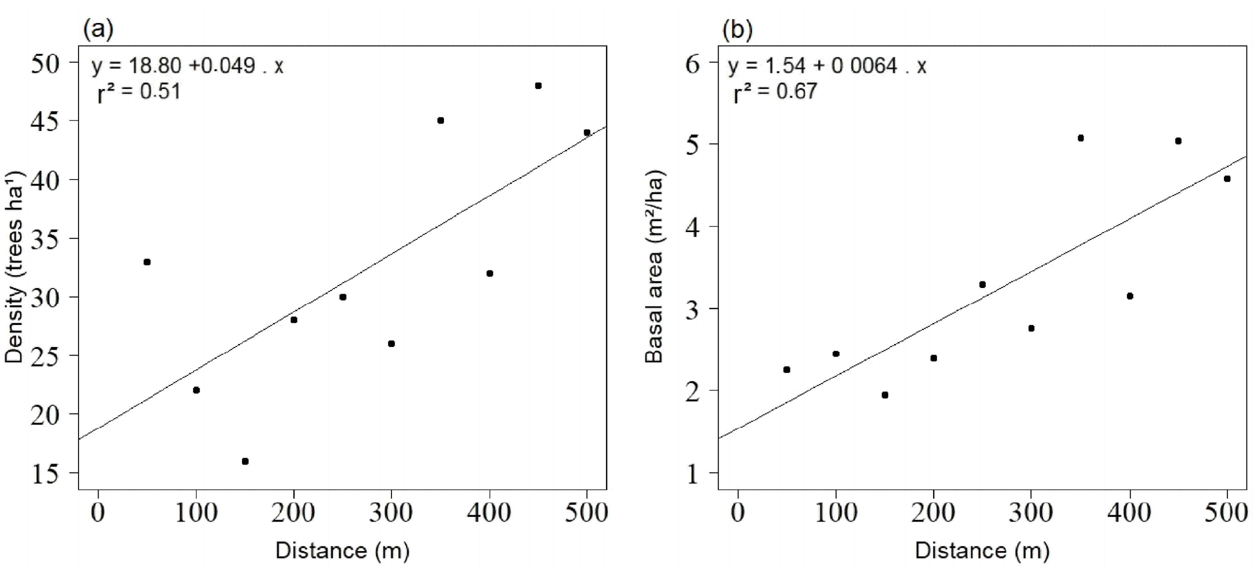

Figure 5 – Relationship between distance to the edge of the inundation and density (a) and basal area (b) of the population of *Pentaclethra macroloba* (Willd.) Kuntze in floodplain forest of the "Campo Experimental do Mazagão - CEM".

Figura 5 *– Relação da distância do gradiente de inundação do furo do Mazagão com a densidade (a) e a área basal (b) de uma população de* ***Pentaclethra macroloba*** *(Willd.) Kuntze na floresta de várzea do Campo Experimental da Embrapa Amapá no município de Mazagão.*

The fact that the spatial distribution was aggregated in the smallest diametric classes and random in the largest indicates that young individuals settle away from their parent tree, corroborating the Janzen hypothesis (Janzen, 1970). This classic author states that the further the young individual establishes from the parent tree, the greater the chances of survival of the species. This behaviour is typical of a pioneer species, such as *P. macroloba*, as it is unlikely that an early-successional species would survive under the shadow of its parent tree. In classes 1 and 2 the behaviour was different from the other classes, with a spatial pattern that alternated between aggregated and random patterns. Capretz et al. (2012), suggest that this behaviour is due to competition among the individuals of the population in the young phase. According to the author, competition for resources causes the mortality rate to increase in the vicinity of an individual, and consequently the population density declines with mortality, leading to spatial randomness.

The spatial pattern of dead trees may be caused by spatial heterogeneity of the area or by primary disturbance agents (Lin et al., 2004). In the area, mortality of individuals of *P. macroloba* was caused by gales affecting both pracaxi and other species. Large and old trees were most affected by the gales and also caused greater damage to the individuals around them, destroying a considerable number of trees in their surroundings as they fell and opening up large clearings in the forest. One of the factors that may cause spatial randomness in tree mortality is the effect of aggregate density. This effect was more obvious in diametric classes 1, 2, 3 and 4, which had larger numbers of dead individuals (Figure 3) and more aggregated distributions (Figure 1a, 1b, 1c, 1d). The spatial randomness of mortality may also be related to the low number of dead individuals registered (22 individuals).

The increase in population density with increasing distance from the edge of the inundation (the "Mazagão channel") suggests a strategy of survival and settlement in the flooded habitat by *P. macroloba*. According to Wittmann et al. (2010), in floodplain forests, the water current is stronger near the river bank, and consequently sedimentation and soil erosion rates are higher, making it difficult for some tree species to establish. However, in the area of this study, some individuals were registered close to the margins of the Mazagão channel, suggesting that they are more resistant to the energy of the current than individuals in the highland floodplain forests. Abreu et al. (2014) also found an increase in population density of *Carapa guianensis* with increasing distance from the banks of the Amazon.

The increase in basal area with increasing distance to the margin of the Mazagão channel can be explained by the constant transport of organic matter and nutrients from the river to the highest part of the terrain, where most of the large diameter individuals were recorded, by the rising tide. In the highest parts of the terrain the canopy is not very closed, allowing sunlight to penetrate to the understorey. This favours pioneer species, such as *P. macroloba* (Condé and Tonini, 2013), allowing them to obtain higher rates of photosynthetic absorption, and thus greater diametric increases. In this area, drainage occurs more intensely than in the lowland floodplain forest or igapó, and as such the roots spend less time in anoxic conditions, leading to better absorption of nutrients and improved metabolism of the plant.

The increase in basal area towards the highest parts of the terrain may also be related to the physiological response of the species, depending on the duration and height of the flood. In a study by Schöngart et al. (2002) in the floodplain forest of Marchanteria Island (Manaus), trees showed high rates of diameter increase during the “terrestrial phase” (i.e. when water levels are low). The inverse occurred during the “aquatic phase” (i.e. when water levels are high), when metabolic rates of individuals decreased, indicating dormancy of cambial activity. A similar result was also found in the study by Myster (2013) in permanent plots installed in the floodplain forests of the Peruvian Amazon. The author observed a reduction of the basal area of the tree community in areas subject to longer periods of flooding, and the result was the reverse for areas with a shorter period of exposure.

5. CONCLUSION

The population of *P. macroloba* shows an aggregate distribution pattern that varies among diametric classes. Trees of smaller diameters are distributed in an aggregate form or alternate between aggregate (at greater distances from the edge of the inundation) and random patterns (at smaller distances), and trees of larger diameters are randomly distributed in the study area. Tree mortality was randomly distributed.

The spatial distribution map of the population produced in this study will aid in the development of management strategies for the species, such that it is possible to map the main seed producing matrices. This will minimize operating costs in the field and help riverside communities to plan for seed extraction activities, and thus in turn to augment their family income with oil extraction activities.

The flood dynamics of the study area are closely related to the spatial distribution pattern of the species, and are one of the determining factors for establishment success of *P. macroloba* in estuarine floodplain habitats.

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