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Original Article

Natural history of the hyperdominant tree, *Pentaclethra macroloba* (Willd.) Kuntze, in the Amazon River estuary

História natural da árvore hiperdominante, *Pentaclethra macroloba* (Willd.) Kuntze, no estuário do rio Amazonas

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Abstract

Pentaclethra macroloba is a hyperdominant species with multiple uses in the Amazon. This species tolerates varying flood amplitudes, however the effect of flood topographic gradient on its ecophysiology remains unclear. We want to know if individuals from the high (10 trees) and low (20 trees) *várzea* show distinct phenological patterns as a function of the flood gradient, as well as their colonization strategies and their seed predators. From February 2018 to December 2019, we monitored the phenology of *P. macroloba*. There was no difference in phenological patterns between the two environments, but flooding caused different phenological responses. The increase in temperature favored the production of flower buds and increased precipitation reduced the proportion of flowering trees in both environments. The increase in rainfall and river flood level favored the ripe fruit only in the low *várzea* where individuals were most exposed to flooding. When the flood level increased, there was a greater proportion of trees losing leaves in both environments. The species produces high variability in seed size (length: $H = 49.2$, $p > 0.001$; width: $H = 62.5$, $p > 0.001$; weight: $H = 70.4$, $p > 0.001$). The seed predation rate was 5%, mainly caused by *Carmenta surinamensis* moth larva. The flood gradient established different phenological responses in the species, directing trees to have a better reproductive performance. The low predation rate and the variability in seed size are factors that contribute to the formation of large population densities in the Amazon River estuary.

Keywords: topographic gradient, colonization, daily flood, phenophases, pracaxi oil.

Resumo

Perntaclethra macroloba é uma espécie de múltiplas utilidades da Amazônia. Essa espécie tolera a variadas amplitudes de inundação. Mas, o efeito do gradiente topográfico de inundação na sua ecofisiologia ainda é desconhecido. Nós objetivamos saber se indivíduos da várzea alta (10 árvores) e baixa (20 árvores) apresentam padrões fenológicos distintos em função do gradiente de inundação, bem como suas estratégias de colonização e seus predadores de sementes. De fevereiro de 2018 a dezembro de 2019, monitoramos a fenologia de *P. macroloba*. Não houve diferença nos padrões fenológicos entre os dois ambientes, mas as inundações provocam respostas fenológicas diferentes. O aumento da temperatura favoreceu a produção de botões florais e o aumento da precipitação diminuiu a proporção de árvores florindo em ambos os ambientes. O aumento das chuvas e do nível de inundação do rio favoreceu os frutos maduros apenas na várzea baixa, onde os indivíduos estão mais expostos às inundações. Quando o nível de inundação aumentou, houve maior proporção de árvores perdendo folhas em ambos os ambientes. A espécie produz alta variabilidade no tamanho das sementes (comprimento: $H = 49,2$, $p > 0,001$; largura: $H = 62,5$, $p > 0,001$; peso: $H = 70,4$, $p > 0,001$). A taxa de predação de sementes foi de 5%, causada principalmente pela larva da mariposa *Carmenta surinamensis*. O gradiente de inundação estabelece diferentes respostas fenológicas às espécies, para que as árvores se ajustem para ter um melhor desempenho reprodutivo. A baixa taxa de predação e a variabilidade no tamanho das sementes são fatores que contribuem para a formação de grandes densidades populacionais no estuário do Rio Amazonas.

Palavras-chave: gradiente topográfico, colonização, inundação diária, fenofases, óleo de pracaxi.

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1. Introduction

The Amazon estuary is influenced by the Amazon River and is in the coastal region of Amapá and Pará States, north of Brazil. The forests surrounding this region are called "*várzea*" and cover an area of about 400,000 km^2 (Melack and Hess, 2010). These forests are subject to the daily flood cycle, or flood pulse, by the Amazon River tide, which reaches a mean amplitude of 1.30 m (Junk et al., 2011).

Pentaclethra macroloba (Willd.) Kuntze is a species of the Fabaceae family, popularly known in the Amazon by the name "pracaxi" or "pracaxizeiro" (Dantas et al., 2017). This species is a hyperdominant Neotropical tree in the Amazon Basin (ter Steege et al., 2020), particularly in the floodplain forests of the Amazon River estuary (Carim et al., 2016). In the Neotropical Region, there are three large populations of *P. macroloba*. The first population, widely studied, is concentrated in Costa Rica, mainly in the *La Selva* Forest Reserve, where it is monodominant. The second population is concentrated in the extension of Panama towards Colombia. The third and last population is in the north of the Brazilian Amazon, and its natural history is little known (Hartshorn, 1983).

P. macroloba has multiple non-timber uses, as the trunk bark has terpenoid saponins with an anti-hemorrhagic action against the venom of *Bothrops* genus vipers (Silva et al., 2007). The main non-timber product of this species is the seed which has oil with medicinal properties, widely exploited by the *ribeirinhos,* or those who live of the Amazon estuary. The oil is highly coveted by the cosmetics industries, as it has a high concentration of fatty acids that moisturize the skin (Costa et al., 2014). In the international market, a liter of oil can cost from US$ 50 to US$ 75, and the cosmetic industries use the oil to make bar of soap, moisturizing cream, washes and shampoo (Teixeira et al., 2020).

Little is known about the ecological and reproductive strategies of *P. macroloba* in the Amazon Basin. This is worrisome, as this species has been exploited for decades without any management to ensure the sustainability of its seed production. In this case, phenological studies should be prioritized, because they are very useful in supporting the management and conservation strategies of economically important species. Phenology studies document time of reproductive and vegetative cycles of the plant and their relationship with the environment (Lieth, 1974). The challenge of phenology is to determine the main phenological triggers that drive the flowering and fruiting stages (Pereira et al., 2022).

The flood pulse of floodplain forests has a pronounced effect on the life cycle of the trees that inhabit this environment. In the Central Amazon, every year the trees experience flood amplitudes up to 7 m in height which can last up to 270 days inside the forest (Wittmann et al., 2010). This flooding regime causes physiological stress on the trees, which forces them to enter a process of cambial dormancy and lose their leaves, a survival strategy that prevents the tree from drowning (Schöngart et al., 2002). In the Amazon estuary, little is known about the effect of the low-amplitude daily tide of the Amazon River on the phenology and growth of trees that inhabit the flood gradient (Cattanio et al., 2004; Dantas et al., 2021a). The topographic gradient of these areas establishes challenging conditions for the survival of the trees, with some elevated areas experiencing less intense flooding while lower elevation areas experience daily flooding because they are at a lower level of the terrain. *P. macroloba* is one of those species that establishes itself in varied topographic flood gradients, so we might expect multiple phenological survival strategies from *P. macroloba*.

Trees that produce a variety of seed sizes, within individuals and within populations, can reveal various colonization strategies, a key feature of plant evolutionary biology. These variations can be related to the genetic inheritance of the parental tree and the position of the fruit in the crown (Simons and Johnston, 2000). The flood gradient, the topographic heterogeneity and the nutritional status of the Amazon wetlands are factors that influence the seed size of several plant species adapted to flooding (Parolin, 2000). In the Amazon estuary, the daily tide of the Amazon River is an effective seed dispersal agent (Cunha et al., 2017), as the flood dynamics maximizes long-distance dispersal and increases the probability of the plant of colonizing new areas. In this sense, high variability in seed sizes produced by trees can be expected, mainly by *P. macroloba* due to its dominance in this region.

The identification of the main propagule predators of tropical trees is a key factor to understand the demographic pattern of plants and assist in management and conservation plans of natural resources. This is because seed predators have a significant impact on the production of ecologically and economically important species, which may influence the demographics of the trees (Silman et al., 2003). However, it is known that the seeds of *P. macroloba* produce secondary compounds, which are toxic to most animals (Janzen, 1970; McKenna and McKenna, 2006) and this may be one of the factors that explain its dominance in the forests from Central America and Amazon. In this case, low rates of seed predation for *P. macroloba* are expected in our study area.

Our objective was to evaluate the influence of the topographic flood gradient on the phenology of *P. macroloba*, as well as to determine its colonization strategies and its main seed predators to assist in the management and conservation of its natural resources. Our hypotheses are: (1) the phenological patterns of *P. macroloba* vary along the topographic and flood gradient; (2) there is high variability in the size of seeds produced by populations of *P. macroloba* along the Amazon estuary; and (3) *P. macroloba* has a low rate of post-dispersal seed predation.

2. Materials and Methods

2.1. Study area

Phenological monitoring, production quantification and evaluation of seed predation were conducted in the Mazagão Experimental Field Site (hereafter CEM), belonging to the Brazilian Agricultural Research Corporation (Embrapa Amapá). CEM has 55.95 ha of forest flooded daily by the Amazon River, located in Mazagão city, in the Southeast of Amapá State, Brazil (00°06' S, 51°16' W) (Dantas et al., 2020). The morphometric variability of seeds was evaluated in three areas with natural occurrence of *P. macroloba*: CEM (area of this study), Fazendinha Environmental Protection Area – hereafter *APA da Fazendinha* – (data provided by Dantas et al., 2021b) and Santana Island – hereafter IS – (data provided by Soares et al., 2019). *APA da Fazendinha* and IS are 17 km (00°4'33" S, 51°10'18" W) and 12 km (00°3'10" S, 51°7'38" W), respectively, distance from the CEM (Figure 1).

In CEM, the sloping soil establishes different levels of flooding in the area, forming environments of high *várzea* (HV) and low *várzea* (LV) (Wittmann et al., 2002). In the LV, the flooding reaches the soil daily and can reach up to 60 cm on the tree trunks during the rainy season (Dantas et al., 2022). In the HV, the soil has a slope from 3 to 3.5 m high, hindering the entry of the daily tide in this environment. However, the HV is partially flooded in the rainy season, where flooding level reaches 10 cm on the tree trunks (Dantas et al., 2020).

The climate type in the region is Am – rainy tropical (Alvares et al., 2013). In the Amapá State, the rainy season starts in December and ends in August. Peak rain is above 60 mm in March. The dry season starts in September, when the rainfall is below 60 mm monthly. Data from 1968 to 2016 show the mean annual rainfall is 2560 mm, with a maximum temperature of 31.4 °C and minimum temperature of 23.5 °C (Vilhena et al., 2018).

The soil of the Amazon estuary is classified as Melanic Gleysol, with a silty texture and predominance of smectite, illite, kaolinite, goethite, anatase and quartz (Pinto 2014). The vegetation is classified as Dense Alluvial Ombrophilous Forest (IBGE, 2012) and species include: *Mora paraensis* (Ducke) Ducke, *Astrocaryum murumuru* Mart., *Pentaclethra macroloba*, *Carapa guianensis* Aubl. and *Virola surinamensis* (Rol.) Warb. (Carim et al., 2016).

2.2. Phenological and diametric growth monitoring

We surveyed 55.95 ha of the study area and identified the presence of 1015 *P. macroloba* trees with a diameter at breast height (DBH) > 5 cm (Dantas et al., 2017). Twenty trees in the LV and ten trees in the HV with good phytosanitary aspect, dominant and co-dominant in the canopy and of different diameter classes were selected for phenological monitoring.

The phenological phases of flowering, fruiting and leaf change were categorized into the following phenophases: floral bud and flower in anthesis (flowering); immature fruit, ripe fruit and seed dispersal (fruiting); and new leaf, mature leaf and leaf fall (leaf change) (Dantas et al., 2021a). The phenophases were observed at 15-day intervals, during the period from February 2018 to December 2019, with the aid of binoculars with a magnification of 60x. The intensity of each phenophase was determined by a semi-quantitative scale composed of four categories of 25% amplitude (Fournier, 1974) which are: 0 – absence of phenophase, 1 – presence of phenophase with intensity between 1% to 25%, 2 – presence of phenophase with intensity between 26% to 50%, 3 – presence of phenophase with intensity between 51% to 75% and 4 – presence of phenophase with intensity between 76% to 100%. The diameter growth of *P. macroloba* was monitored using dendrometer bands installed at a height of 1.30 m on the trunk of each tree. We installed dendrometer bands in July 2018 and after one month of adjustment, the diametric increment was measured monthly with a digital caliper (Carbografite® model 150, accuracy of 0.01 mm).

2.3. Production and predation of seeds

For the monitoring of fruit and seed production, we did not distinguish between high and low *várzea*, as our objective was to estimate the production capacity of the study area for forest management purposes. In addition

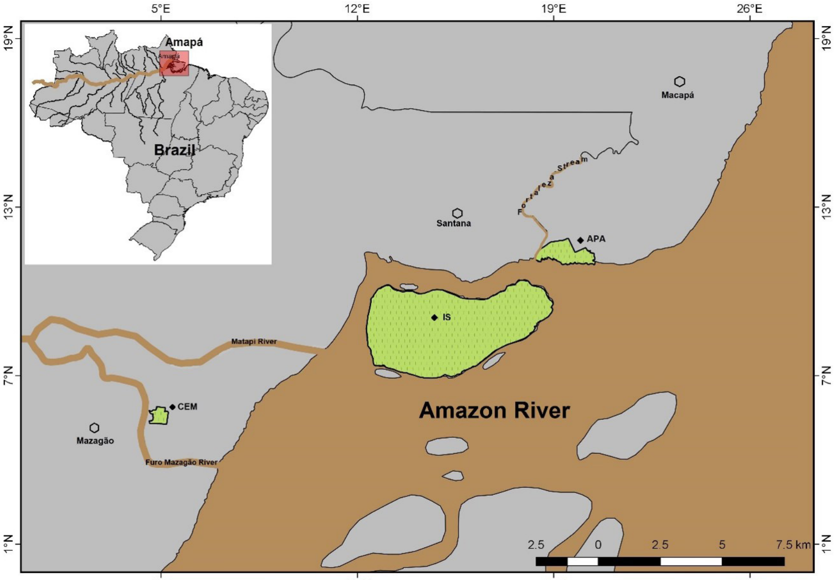

Figure 1. Three populations of *Pentaclethra macroloba* distributed along the Amazon River estuary: Mazagão Experimental Field (CEM), Santana Island (IS) and Fazendinha Environmental Protection Area (APA).

to the 30 trees selected for phenology, three other trees were added to quantify fruit production (33 trees). Fruit production was estimated by observation and counting directly in the tree crown (Minor and Kobe, 2019), with the aid of binoculars. Seven trees, out of the 33, were selected to quantify seed production. The seven trees were surrounded with a polyethylene screen of 1 m high (Figure S1a), capturing the entire crown projection area on the ground (Figure S1b) (Wadt et al., 2017). The production of fruits and seeds was monitored during the period from February to December 2019 at 15-day intervals.

The seeds inside the fence were collected, stored in bags with the numerical identification of the tree to which it belongs and transported to the Seed Laboratory of Embrapa Amapá. We separate the predated seeds from the healthy seeds. From healthy seeds, morphometric data of length (mm), width (mm), thickness (mm) and fresh weight (g) were obtained with the aid of a digital caliper and analytical balance (Shimadzu® model AUW22OD, accuracy of 0.001 g).

To identify the moth larva, we collected 15 ripe fruits directly from the crown of a *P. macroloba* tree using a pruning stick, at a 17 m. Three fruits pierced by the larva (Figure S5a and b) were identified and the predated seeds were removed. The seeds were placed in a plastic tray at ambient temperature and monitored daily to visualize the emergence of adults.

2.4. Hydroclimatic data

The environmental variables collected were flood height in the tree trunk, maximum mean temperature and monthly rainfall. The flood height was measured on white strings installed parallel to the trunk of each monitored tree. The river water, rich in sediment, stains the white string and leaves the height of the flood recorded, facilitating measurement with a tape measure. At each assessment, the strings were exchanged for new ones for subsequent measurement (Dantas et al., 2021a). The maximum mean temperature and monthly rainfall data were obtained from the Macapá Climatological Station (00°02’07” S, 51°05’55” W), about 19 km from the CEM (INMET, 2019).

2.5. Seed morphometry

We analyzed the variability in seed size produced in three populations of *P. macroloba* found along the Amazon estuary. For this, 379 seeds from the CEM, 134 seeds from *APA da Fazendinha* (data provided by Dantas et al., 2021b) and 100 seeds from IS (data provided by Soares et al., 2019) were collected (Table S1; Supplementary Material).

2.6. Data analysis

The phenological data were analyzed comparing high and low *várzea* environments. We did not observe variation in Fournier amplitude scales from one fortnight to another, so the data were analyzed monthly with the selection of the highest value obtained. The intensity of each phenophase was determined by the Fournier formula (Fournier, 1974).

We applied an ANOVA test to evaluate the statistical differences in phenophase intensity between high and low *várzea* environments (Haugaasen and Peres, 2005). The Shapiro-Wilk test was applied to evaluate whether the distribution of phenological data is normal in relation to the hydrometeorological variables and diameter growth. The relationship between phenophases with diameter growth and hydroclimatological variables was evaluated using Generalized Linear Models (GLMs) with quasi-binomial error (Newbery et al., 2006; Dantas et al., 2016, 2021a). For this, we use binary phenological data, assigning “0” for absence and “1” for the presence of a phenophase. We applied circular statistics to assess the magnitude of the seasonality of *P. macroloba* phenological events (Morellato et al., 2010). For this, the 12 months of the year were converted at angles, with an interval of 30º, where 0º corresponds to the month of January (first month) and 330º corresponds to the month of December (last month). The mean angle (a) and the vector (r) were calculated with the objective of evaluating the period of manifestation and the intensity of seasonality, respectively. The vector (r) ranges from 0 to 1 with greater seasonality when the value approaches 1 (Morellato et al., 2010). The Rayleigh (Z) test was applied to evaluate the occurrence (null hypothesis H_0) or not (alternative hypothesis H_A) of data uniformity around the circle (Morellato et al., 2010). The Watson-Williams (W) test was applied to compare mean angles between the two environments (Zar, 2010).

In the analysis of fruit and seed production, we did distinguish between high and low *várzea*. Descriptive statistics were performed on the morphometric samples to obtain the values of the mean, standard deviation and coefficient of variation of all characteristics related to seed production. A Kruskal-Wallis test (H) was applied to evaluate the morphometric variations of the seeds produced by the three populations of *P. macroloba* along the Amazon estuary. The seed predation rate was determined by the quotient between the number of seeds predated and the total number of seeds collected, with the result multiplied by 100 (Lira-Guedes and Jesus-Barros, 2017). All analyzes were performed using the R program (R core Team, 2019) and the “circular” statistical package was used for the circular statistical analyses (Agostinelli and Lund, 2017).

3. Results

3.1. Phenology in low and high várzea

3.1.1. Flowering

The mean flowering time in both environments was four months, with peak intensities during drought. There was no significant difference in the intensity of the phenophases of flower buds (F = 0.03; p = 0.87) and flowers in anthesis (F = 0.003; p = 0.95) between the two analyzed environments. However, the flower bud peak was 2%-3% higher in the low *várzea* (September 2018, 24% intensity and October 2019, 25% intensity; Figure 2a) in comparison with the high *várzea* (September to October 2018, 22% intensity and October 2019, 22% intensity; Figure 2b).

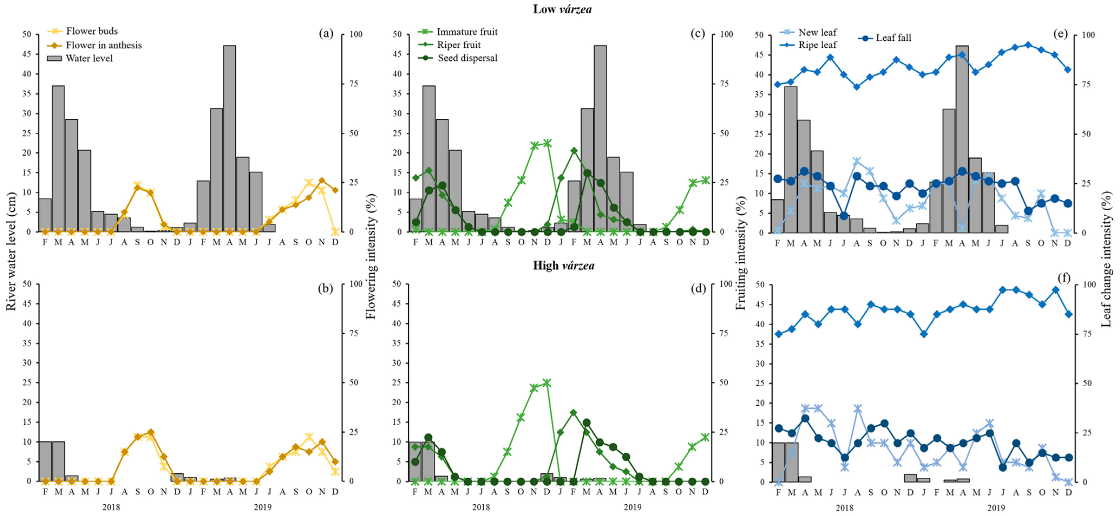

Figure 2. Flowering (a, b), fruiting (c, d) and leaf change (e, f) intensity of *Pentaclethra macroloba* along a flood gradient in high and low *várzea* environments in the Amazon River estuary.

The peak of flowers in anthesis in 2018 was 3% lower in the low *várzea* (September, 22% intensity) compared to the high *várzea* (October, 25% intensity). In 2019, the opposite occurred; the peak of flowers in anthesis was 6% higher in the low *várzea* (November, 26% intensity) in relation to the high *várzea* (November, 20% intensity).

The flower buds (low *várzea*: vector r = 0.85, $p < 0.001$; high *várzea*: vector r = 0.81, $p < 0.001$) and flowers in anthesis (low *várzea*: vector r = 0.76, $p < 0.001$; high *várzea*: vector r = 0.79, $p < 0.001$) phenophases were highly seasonal for trees in both environments (Figure 3a and b). Trees started (July) and finished (December) flowering at the same time in both environments. However, the flower bud phenophase in the low *várzea* lasted five months, while in the high *várzea* this phenophase lasted six months. There was a statistical difference in the flowering period for the flower bud (W = 0.29, $p < 0.01$) and flowers in anthesis (W = 0.23, $p < 0.05$) phenophases between the environments (Table S2, see angle and date means).

There was a negative and significant association between flower bud (low *várzea*: $\beta = -0.013$, $p < 0.001$; high *várzea*: $\beta = -0.012$, $p < 0.001$) and flowers in anthesis (lower *várzea*: $\beta = -0.011$, $p < 0.001$; high *várzea*: $\beta = -0.013$, $p < 0.001$) phenophases with rainfall (Figure 4a and b; Tables S3 and S4) for the two analyzed environments. There was a negative and significant association between flower buds ($\beta = -0.61$, $p < 0.05$) and flowers in anthesis ($\beta = -0.74$, $p < 0.001$) phenophases with the river flood level only for individuals from the low *várzea* (Figure 4c and d). With the maximum temperature, there was a positive and significant correlation between flower buds (low *várzea*: $\beta = 2.19$, $p < 0.001$; high *várzea*: $\beta = 1.77$, $p < 0.001$) and flowers in anthesis (low *várzea*: $\beta = 1.86$, $p < 0.001$; high *várzea*: $\beta = 1.85$, $p < 0.001$) phenophases for trees in both environments (Figure 4d and e). There was no significant relationship between tree phenophases and cambial increment (Table S3).

3.1.2. Fruiting

The mean fruiting time in both environments was five months, with immature fruits in the dry period and ripe fruits and seed dispersion in the rainy period. There was no significant difference in the intensity of the phenophase of immature fruit (F = 0.02, p = 0.89), ripe fruit (F = 0.53, p = 0.53) and seed dispersal (F = 0.01, p = 0.92) between the two environments. However, the immature fruit peak was 5% more intense in the high *várzea* (December 2018, 50% intensity; Figure 2d) than in the low *várzea* (December 2018, 45% intensity; Figure 2c). For the ripe fruit phenophase, the peak was 14%-6% more intense in the low *várzea* (March 2018, 31% intensity and February 2019, 41% intensity; Figure 2c) compared to the peak that occurred in the high *várzea* (February-March 2018, 17% intensity and February 2019, 35% intensity; Figure 2d). The seed dispersal peak was 2% more intense in the low *várzea* (April, 24% intensity) than in the high *várzea* (March, 22% intensity) for the year 2018. In the year 2019, the seed dispersal peak presented the same intensity (March, 30% intensity) for both environments.

The immature fruit (low *várzea*: vector r = 0.83, $p < 0.001$; high *várzea*: vector r = 0.87, $p < 0.001$), ripe fruit (low *várzea*: vector r = 0.76, $p < 0.001$; high *várzea*: vector r = 0.78, $p < 0.001$) and seed dispersal (low *várzea*: vector r = 0.87, $p < 0.001$; high *várzea*: vector r = 0.83, $p < 0.001$) phenophases were highly seasonal for trees in both environments (Figure 3c and d). Trees started fruiting at the same time in August in both environments. However, the trees finished fruiting in June in the low *várzea* (11 months of fruiting) and in July in the high *várzea* (12 months of fruiting). There was a statistical difference in the fruiting period for the immature fruit (W = 0.59, $p < 0.001$), ripe fruit (W = 0.32, $p < 0.01$) and seed dispersal (W = 0.48, $p < 0.001$) phenophases (Table S2, see angle and date means).

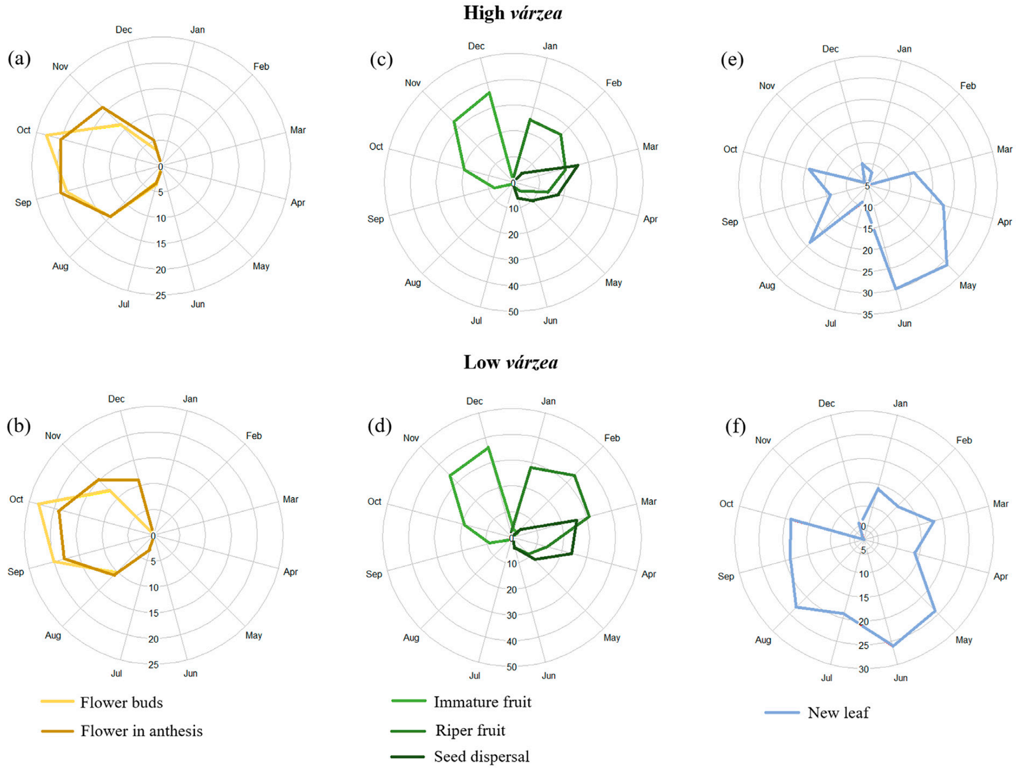

Figure 3. Flowering (a, b), fruiting (c, d) and leaf change (e, f) seasonality of *Pentaclethra macroloba* along a flood gradient in high and low *várzea* environments in the Amazon River estuary.

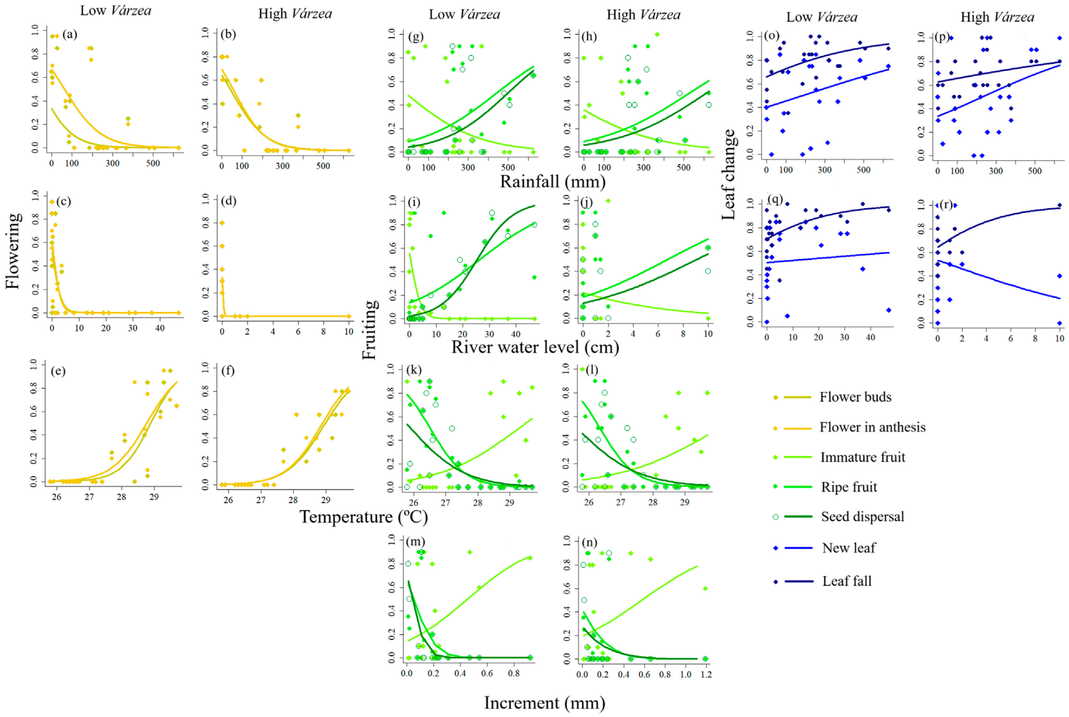

Figure 4. Relationship of hydroclimatic variables and cambial increment in the flowering (from [a] to [f]), fruiting (from [g] to [n]) and leaf change (from [o] to [r]) phases of *Pentaclethra macroloba* along a flood gradient in high and low *várzea* environments in the Amazon River estuary.

In the low *várzea*, there was a positive and significant association between the ripe fruit ($\beta = 0.005$, $p < 0.05$) and seed dispersal ($\beta = 0.006$, $p < 0.05$) phenophases with rainfall (Figure 3g; Tables S3 and S4) and there was no significant association with the immature fruit (Table S3). In the high *várzea*, no phenophase had association with rainfall (Figure 3h; Table S3). Ripe fruit ($\beta = 0.07$, $p < 0.05$) and seed dispersal ($\beta = 0.15$, $p < 0.001$) phenophases were associated positively and significantly with river flood level only in the low *várzea* (Figure 3i and j). The ripe fruit (low *várzea*: $\beta = -1.83$, $p < 0.001$; high *várzea*: $\beta = -1.81$, $p < 0.001$) and seed dispersal (low *várzea*: $\beta = -1.18$, $p < 0.05$; high *várzea*: $\beta = -1.04$, $p < 0.05$) phenophases associated negatively and significantly with the maximum temperature in both environments (Figure 3k and l). There was no significant association between immature fruit and maximum temperature in both environments (Table S3). The ripe fruit ($\beta = -13.01$, $p < 0.05$) and seed dispersal ($\beta = -21.02$, $p < 0.05$) phenophases had a negative and significant association with the cambial increment only in the low *várzea* (Figure 3m and n).

3.1.3. Leaf change

There was no significant difference in the intensity of the phenophase of new leaf ($F = 0.002$, $p = 0.97$), mature leaf ($F = 1.78$, $p = 0.19$) and leaf fall ($F = 2.62$, $p = 0.11$) between the two environments. The trees in both environments retained mature leaves throughout the year and there was no defined intensity peak for this phenophase (Figure 2e and f). The same behavior occurred for the new leaf and leaf fall phenophases, but with less intensity than the mature leaf phenophase. Only the new leaf phenophase showed seasonality in production in the low (vector $r = 0.23$, $p < 0.05$; Figure 3e) and high (vector $r = 0.24$, $p < 0.05$; Figure 3f) *várzea*. There was a statistical difference in the period of occurrence for the new leaf ($W = 0.24$, $p < 0.05$) and mature leaf ($W = 0.31$, $p < 0.01$) phenophases between the environments (Table S2, see angle and date means). For the leaf fall phenophase there was no statistical difference ($W = 0.14$, $p > 0.10$).

In the low *várzea*, there was a positive and significant association only between the leaf fall phenophase with rainfall ($\beta = 0.003$, $p < 0.05$; Figure 4o) and river flood level ($\beta = 0.06$, $p < 0.05$; Figure 4q). In the high *várzea*, only the leaf fall phenophase was positively and significantly associated with the river flood level ($\beta = 0.31$, $p < 0.05$; Figure 4r). The new leaf phenophase had no association with any hydrometrological variable in both environments. There was no association between leaf change phenophases with the cambial increment. (Table S3).

3.2. Fruit and seed production

We quantified 261 fruits in the crown of the 33 monitored trees, with a mean of 9 fruits per tree (± 8 fruits/tree) and with high variability in production between trees (CV 89%). The seven monitored trees produced a total of 380 seeds (2 kg), a mean of 54 seeds/tree (± 50 seeds/tree) and with high variability in production (CV 92%). The population of *P. macroloba* from CEM showed little variability in seed size produced between trees (Table S5).

3.3. Seed size variability in three populations of Pentaclethra macroloba

Along the Amazon estuary there was a high morphometric variability of seed produced by populations of *P. macroloba* from CEM, *APA da Fazendinha* and IS (except for thickness measurement due to data loss) for the measures of length ($H = 49.2$; $p > 0.001$; Figure S2a), width ($H = 62.5$; $p > 0.001$; Figure S2b), thickness ($H = 137.2$; $p > 0.001$; Figure S2c) and fresh weight ($H = 70.4$; $p > 0.001$; Figure S2d). The seeds from the IS area had greater length (49 cm) and weight (11 g) mean than the seeds from the CEM (length: 46 cm and weight: 10 g) and *APA da Fazendinha* (length: 44 cm and weight: 8 g).

3.4. Seed predation

Of the three hundred and eighty seeds were analyzed, 18 were found predated and the predation rate was 5%. Of the 18 seeds predated, 50% of predation was caused by moth larvae (Figure S3a and b), 28% by fungi (Figure S3d) and 22% by rodents (Figure S3c). it was possible to identify the presence of the *Carmenta surinamensis* (Möschler) (Lepidoptera: Sesiidae) moth as the main predator of fruits and seeds de *P. macroloba* (Figure S4a, b and c).

4. Discussions

4.1. Phenology in low and high várzea

We found no distinction in the phenological pattern of *Pentaclethra macroloba* with respect to topography (elevation) and flood gradient within *várzea*. However, the phenophases of flower buds, flowers in anthesis, ripe fruits, seed dispersal and leaf fall of the low *várzea* trees had a high and significant relationship with the flood pulse than the high *várzea* trees (Figure 4; Table S3). Haugaasen and Peres (2005) analyzed the phenological patterns of tree communities in upland and floodplain forests (Central Amazonia) and found that the major determinant of phenological patterns in the floodplain forest is flooding, while in the upland forest it is rainfall and solar radiation. Hawes and Peres (2016) observed similar phenological patterns between tree communities in the transition between upland forests and floodplain forests in western Amazonia. However, the authors found a greater interaction of the trees in the floodplain forest with the flood. For example, seed dispersal was greater during the flood season, because trees used the flood peak to disperse their seeds, an adaptive strategy.

Although there was no phenological distinction between high and low *várzea*, *P. macroloba* trees showed significant interactions with hydrometerological variables. A greater intensity of flowering in the period of low level of river flood may be associated to an ecophysiological and reproductive strategy of the species to emit larger amounts of inflorescences without the interference of environmental stressors. According to Ferner et al. (2012) the flooding causes a drop in oxygen in the rhizosphere, triggering an energy crisis in the plant. Due to this, the mitochondrial respiration is substituted by alcoholic fermentation that produces less energy equivalents. The trees in the low *várzea* had a higher flowering peak in the dry season, when the flooding is less intense, than the trees in the high *várzea*. The phenophase intensity may vary from year to year, but this depends on the intrinsic characteristics of the species and the environmental factors of the habitat. However, a greater flowering intensity for trees of the low *várzea* shows that individuals seek more attraction for pollinators, as flowering during the dry season may be crucial for plant reproduction in environments more exposed to flooding, since flooding can interfere in plant metabolism.

The flowering seasonality in the dry season, in both environments, is an advantage for the species, due to the activity of pollinating insects, such as bees and wasps (Dantas et al., 2021a), being more active in this season of low rainfall and high temperature (Lawson and Rands, 2019). The flowering time between the two environments does not occur simultaneously (significant difference between the mean angles). This may indicate evolution of variation in flowering season to not overlap pollinators in a single period and increase chance of fertilization of the flower. In addition, the flowering concentration in the dry season directs the fruiting and seed dispersal stages to coincide with the rainy season and peak river flood. The low flowering intensity in the high *várzea* during the dry season, comparing with the low *várzea*, shows the influence of water stress on trees in this environment, this can be compared to non-flooded forests.

Ferreira and Parolin (2007) analyzed the phenology of 29 tree species in an *igapó* forest in Central Amazonia, found that the flowering intensity for *P. macroloba* varies along the flooding gradient. In a floodplain forest in the Macapá city, Amapá, Brazil, Dantas et al. (2021a) studied the phenology of *P. macroloba* and found a flowering peak in the dry period. For a forest community on *Ilha da Marchanteria*, Central Amazon, Schöngart et al. (2002) found a flowering peak for a tree community during high river flood level, but there are species that produce flowers at the end of the flood or in the middle of the dry season.

The river flood level had no significant relationship in the phenophases of ripe fruits and seed dispersal in the high *várzea*, but a high significant relationship of this variable was observed in the low *várzea* (Figure 4 and Table S3). This may be related to the different dispersion mechanisms of the species and the flood degree that the trees are subjected. Dispersal in low *várzea* is more efficient through water, as the seed has mechanisms adapted for hydrochoric dispersal, such as an air pocket between the cotyledons for better flotation in the water (Williamson and Costa, 2000), hence a greater association with flooding. In the high *várzea*, the water reaches the tree trunks only at the river flood peak, which coincides with the rainy season (January to March), and reaches a few centimeters on the tree trunk (up to 10 cm), allowing that the tree does not depend of the water to disperse their seeds, so *P. macroloba* can utilize its autochoric dispersal by explosive fruit dehiscence, which may be more efficient in this environment.

The flowering time of *P. macroloba* in the dry season favors fruit ripening and seed dispersal in the rainy season. This strategy guarantees an ideal temperature in the dry period for fruit ripening and the moisture needed from the rainy season to hydrate the dry fruit and trigger its explosive dehiscence mechanism.

In the low *várzea*, *P. macroloba* showed a reduction in the cambial increment during the period of ripe fruits and seed dispersal. This phase of the species is crucial for seed propagation, requiring maximum concentration of energy for fruit development (Wang et al., 2013). Another fact that may be affecting the cambial activity of the species is the increase in the flood level. The permanence of water within the forest causes a stress in the tree root that hinders the oxygen assimilation, due to the flooding causing hypoxemia in the soil (Parolin and Wittmann, 2010). To get around this situation, the tree uses the lenticels present in the trunk to breathe and carry out gas exchange from internal to external environment, causing a low rate of cambial activity (Schöngart et al., 2002).

The trees remain with a complete canopy of leaves throughout the year, independent of the season, in the two environments analyzed. This strategy ensures a higher rate of photosynthetic absorption (Wagner et al., 2016), mainly in the northeast of the Amazon where there is a greater solar incidence. Our study revealed a greater leaf fall during the rainy season and high river flooding in the low *várzea*, which may be related to the response of trees to the physiological stress caused by increased flooding. According to Schöngart et al. (2002), leaf fall in a flooded environment can be a root response to low oxygen availability in the rhizosphere due to flooded soil. The result is low water conductance through the trunk and water stresses in the crown, forcing the tree to shed its leaves. On the other hand, Cattanio et al. (2004) found a greater leaf fall during the dry season and low river level for a forest community in the Amazon estuary, *Ilha do Cambu*, Pará, Brazil. Dantas et al. (2021b) extensively studied the phenology of *P. macroloba* in the *APA da Fazendinha*, area less than 6 km from our study area, and found no relationship between leaf fall and river flooding.

4.2. Fruit and seed production

The population of *P. macroloba* from the Amazonian estuary has higher fruit production, compared to the population of the species in Central America. Minor and Kobe (2019) estimated the fruit production of *P. macroloba* in the *La Selva* Biological Station in Costa Rica, using the same method of this study, found that 367 monitored trees, with DBH between 18 cm and 119 cm, produced in total 188 fruits. While the 33 trees in our study, with DBH between 17 cm and 55 cm, produced 261 fruits. The variability in fruit production between the two populations may be related to the soil nutrient content. The soil of *La Selva* is of ancient origin and of low fertility, located in swamp areas of Costa Rica (McDade and Hartshorn, 1994). The soils of the floodplain forests of the Amazon estuary have a high concentration of nutrients such as calcium, magnesium, potassium and phosphorus (Montagnini and Muñiz-Miret, 1999), due to being bathed by the Amazon River which carries a high load of sedimentary material of the Andean and pre-Andean regions (Meade, 2008).

P. macroloba showed high variability in the number of fruits and seeds produced between trees, an intrinsic characteristic of tropical trees. According to Obeso (2002), reproductive activity of a plant requires significant expenditure of energy and nutritional resources allocation. This can lead the tree to produce more in one year, due to the investment in nutritional content and energy for this, and in the following year the tree can be energetically depleted, producing less fruits. According to Lucas-Borja and Vacchiano (2018), this pattern of production, which varies from year to year and between individuals, is a key factor in the natural recruitment of tree populations.

Minor and Kobe (2019) suggest that fruit and seed production in tropical trees can be very uneven among plants of the same species due to environmental factors. Klimas et al. (2012), studying the production of *Carapa guianensis* seeds in floodplain and upland forests for four years, in the Amazon, found that the floodplain trees produce more seeds than the upland trees. The authors attribute these results to better fertility of the floodplain soils, which contributes to the increase in production. Another factor that affects the plant's reproductive activity is climate change. Wright and Calderon (2006) verified, in an arboreal community of Barro Colorado Island in Panama, that moderate El Niño events contributed to an increase in the seed production rate. According to the authors, the moderate increase in temperature and solar radiation probably contributed to the increase in tree productivity, as their crowns would be more exposed to light, increasing the photosynthetic rate of the plant.

4.3. Seed size variability

The variability in the size of the *P. macroloba* seed along the estuary, may indicate multiple colonization strategies. According to Williamson and Costa (2000), large seeds have greater buoyancy in water, because they have an air pocket between the cotyledons which favors the floating in the river current and the colonization of areas distant from mother tree. Smaller seeds sink and remain close to the parent tree (Lopez, 2001) and have a higher probability of dying suppressed in the shade of the parent tree canopy. For the tree, the production of small seeds becomes an advantage, as it requires little energy for the formation of this seed (Parolin, 2000). On the other hand, embryo development and seedling survival rates increase at larger seeds, as they have greater endosperm mass and nutritional reserves (Michaels et al., 1988; Moegenburg, 1996).

4.4. Seed predation

The low seed predation rate (5%) of *P. macroloba* suggests the existence of defensive barriers against herbivory. This is possibly due to the seeds haveing toxic compounds such as alkaloids and free amino acids (Hartshorn, 1972), which makes them unpalatable to most herbivores. For *C. guianensis*, which also occurs in the Amazon estuary, but does not have natural pesticides against herbivory, the rate of predation by larvae of moths of the genus *Hypsipyla* can reach 62% (Pinto et al., 2013).

In this study area, *P. macroloba* seeds were frequently predated by moth larvae. At the *La Selva* Biological Station in Costa Rica, McKenna and McKenna (2006) found that the main predator of *P. macroloba* seeds is the larva of the moth *Carmenta surinamensis* (Möschler) (Lepidoptera: Sesiidae), which reduced germination and growth rate of the seedling. Estimates of seed losses for natural predation and the collection time must be considered for the extraction of pracaxi oil, as the high humidity of the floodplain forest favors the rapid attack by fungi and larvae insects.

Only a few vertebrates are capable of digesting the toxic seeds of *P. macroloba* (Guariguata et al., 2000). In *La Selva*, parrots (*Pionus senilis* (Spix,1824)) and squirrels (*Sciurus variegatoides* Ogilby, 1839) are known predators that consume small amounts of *P. macroloba* seeds (Guariguata et al., 2000). In our study, the gnawed seeds may have been attacked by agoutis (*Dasyprocta azarae* Lichtenstein, 1823), which often appear in search of *C. guianensis* seeds. These rodents can, to some extent, tolerate toxic alkaloid compounds that are present in the seeds of many plant species (Guimarães et al., 2003).

5. Conclusions

The topographic flood gradient does not influence the intensity of the phonological processes of *Pentaclethra macroloba* between the two environments. However, flowering and fruiting times were different between the two environments. There is a greater interaction of the trees in the low *várzea* with environmental variables, mainly with the flood level. The low predation rate of *P. macroloba* seeds and the variability in the size of the seeds produced by this species contribute to the formation of dense populations in the Amazon River estuary and to its hyperdominance in the Brazilian Amazon. Our results may provide information to formulate public policies aimed at *P. macroloba* management and conservation.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1: Seed morphometry of three populations of Pentaclethra macroloba in the Amazon estuary: Experimental Field of Mazagão (CEM, 379 seeds), Fazendinha Environmental Protection Area (APA, 134 seeds) and Santana Island (IS, 100 seeds).

Table S2: Parameters of the circular statistic of Pentaclethra macroloba phenophases in environments of the high and low várzea in the Amazon River estuary. SD = standard deviation, **** mean date not displayed because there was no statistical significance by the Rayleigh test.

Table S3: Relationship of Pentaclethra macroloba phenophases with hydroclimatic variables and cambial increment in high and low várzea environments in the Amazon estuary.

Table S4: Generalized linear models of the relationship between climate and diameter increment with the phenophases of Pentaclethra macroloba in high and low várzea environments in the Amazon River estuary. X_{FB} = Flower buds, X_{FA} = Flower in anthesis, X_{IF} = Immature fruit, X_{RF} = Ripe fruit, X_{SD} = Seed dispersal, X_{NL} = New leaf, X_{LF} = Leaf fall, $y_{water(LV)}$ = water level in the low várzea, $y_{water(HV)}$ = water level in the high várzea, $y_{increment(LV)}$ = diametrical increment in the low várzea and $y_{increment(HV)}$ = diametrical increment in the high várzea.

Table S5: Seed production morphometry of a Pentaclethra macroloba population in a floodplain forest of the Amazon estuary. N = number of seeds; = sample mean; CV = coefficient of variation; SD = standard deviation.

Figure S1: Installation of fence to seed collect of Pentaclethra macroloba in a floodplain forest of the Amazon estuary: (a) installation of the fence around the tree; and (b) Layout of the fence seen from above.

Figure S2: Leaf change intensity of Pentaclethra macroloba as a function of the flood gradient in environment of the high and low várzea in the Amazon River estuary.

Figure S3: Variability in length (a), width (b), thickness (c) and fresh weight (d) of seeds from three populations of Pentaclethra macroloba in floodplain forests along the Amazon estuary.

Figure S4: Predation by moth larvae (a and b), rodents (c) and fungi (d) in seeds of Pentaclethra macroloba in floodplain forest of the Amazon estuary.

Figure S5: Main predator of Pentaclethra macroloba seeds: fruit pierced by the larva (a); after piercing the fruits, the larvae feed on the seeds and lodge in their cocoons (b); and adult moth individuals (c).

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