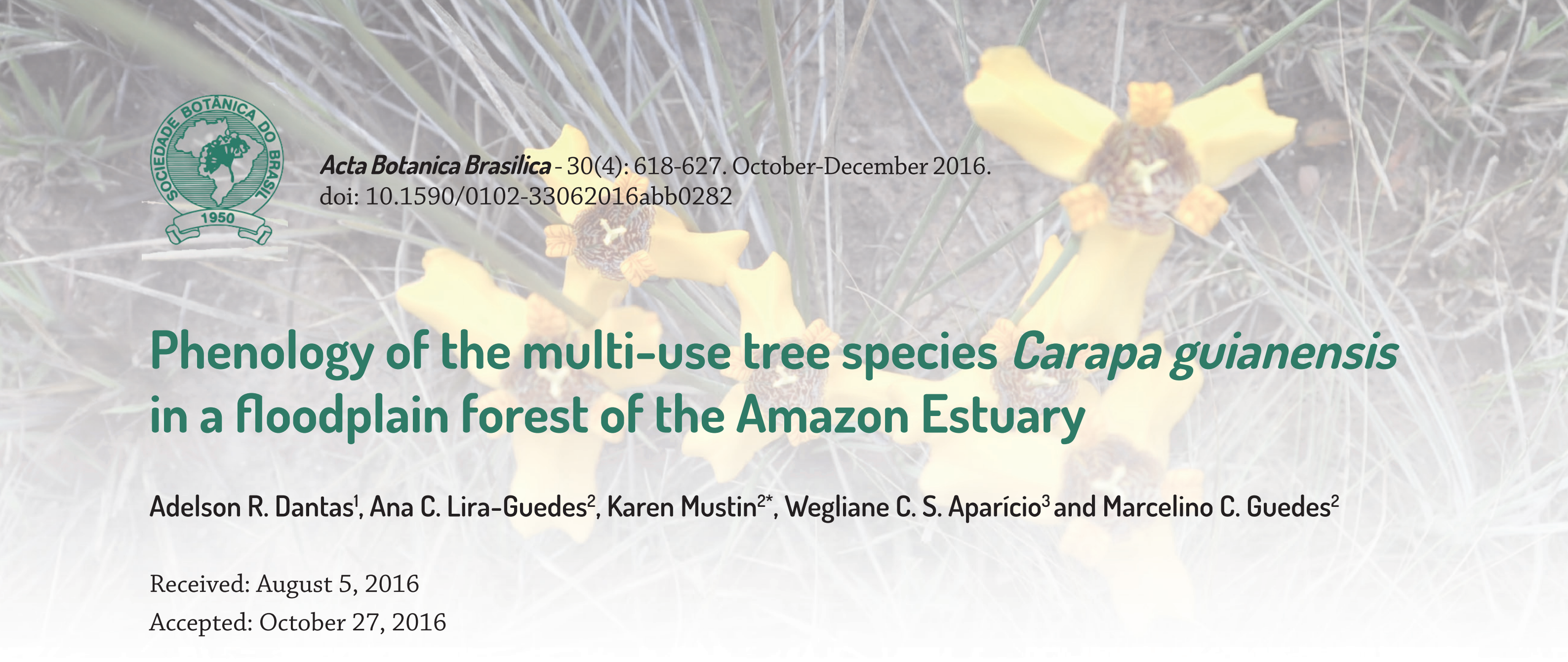

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Phenology of the multi-use tree species *Carapa guianensis* in a floodplain forest of the Amazon Estuary

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ABSTRACT

Carapa guianensis is a multi-use tree species that is used for the production of timber and non-timber forest products (NTFPs) that are used and sold by rural Amazonian populations. Here we aimed to evaluate the phenophases of *C. guianensis* in várzea forest and relate them to climatic seasonality. Phenophases of flowering (flower buds and open flowers), fruiting (unripe and ripe fruits), and leaf flush and leaf fall were recorded for 30 individual trees during a 25 month period. Relationships between rainfall and the proportion of trees in each phenophase were tested using Generalised Linear Models with quasi-binomial errors. Flowering was found to peak in the driest months of the year (September to December), while fruiting peaked during the wettest months of the year when river levels are at their highest (January to May). Leaf flush and leaf fall occurred simultaneously throughout the year, regardless of seasonality. Strong seasonality in flowering and fruiting of *C. guianensis* likely represents a reproductive strategy that maximizes pollination and hydrochorous seed dispersal. This study has the potential to aid in planning the timing of seed collection and oil extraction activities, thus contributing to the sustainable exploitation of this tree.

Keywords: Amazon, *Carapa guianensis*, crabwood tree ecology, Florestam, Meliaceae, phenology, phenophases, sustainable forest management

Introduction

The trees of várzea forest are an important source of timber and non-timber forest products that are used and sold by rural Amazonian populations (Wittmann *et al*. 2010). Indeed, it has been shown that at least 72 % of tree species in these forests are used by local people, most of which are used in popular medicine (Wittmann *et al*. 2010). *Carapa guianensis,* a species from the family Meliaceae, popularly known in the Amazon region as andirobeira (Ferraz *et al*. 2002), and in English as crabwood, is one such multiple-use tree. *C.guianensis* has various medicinal properties: its bark contains alkaloids such as carapina, which possess antipyretic properties; the oil extracted from its seeds contains tetranortriterpenoid limonoids which have anti-inflammatory and anti-allergic properties (Henriques & Penido 2014), and acts as a natural insect repellent; and teas made from its leaves and fruits are used to relieve itching and treat intestinal worms (Praciak 2013). In the pharmaceutical and homeopathic industries, the oil is sold as capsules to treat diabetes and rheumatism (Santos & Guerra 2010).

While these products play a crucial role in the subsistence of a large part of the population living within and around Amazonian forests (Tonini *et al*. 2009), the species is also

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much valued for timber, with high market demand in Japan, the USA and Germany, and subsequently the disappearance of the species from logging frontiers (Ferraz *et al*. 2002; Shanley & Londres 2011). Good management practices and the development of plans for sustainable use are therefore necessary to protect the natural resources these trees provide. To do so requires an improved understanding of the reproductive ecology of this species, and in particular its phenology. A better understanding of phenology would mean a clearer definition of the period of greatest seed production, which would facilitate planning for sustainable crabwood seed collection practices, and subsequent oil extraction. At present there is no technology available in the region that allows for longer-term storage of seeds, and as such, crabwood oil extraction is an activity completely controlled by the timing of seed production periods.

The species is found in both terra firme (not inundated by flooded rivers) and várzea (inundated by flooded rivers) forests, and is widely distributed in Africa and the American Tropics (Pennington 1981). Individuals can reach 55 m in height, have a cylindrical and straight trunk (20 - 30 m in height) with buttresses at the base, and bark shed in pieces, and the canopy is quite branched (Fournier 2003). The leaves are alternipinnada, with between four and eigth alternate leaves along the rachi. The species is monoecious, possessing both male and female inflorescences in white or beige flowers (Hiura & Sarquis 2008). The fruit is a spherical capsule, dry and indehiscent, with four valves usually containing between two and four brown seeds (Ferraz *et al*. 2002). Seeds of *C.guianensis* are an important food source for various animals, including armadillos, collared peccaries (*Pecari tajacu*), pacas (*Cuniculus spp.*), deer and agoutis (*Dasyprocta spp.*), and these species also contribute to seed dispersal. Rodents are particularly important seed dispersers for *C.guianensis* as the rate of seed predation by these animals is relatively high (McHargue & Hartshorn, 1983). There are also numerous insect seed predators associated with *C.guianensis,* including grubs of Meliaceae, *Hypsipyla ferrealis* and *Hypsipyla grandella* (Lepidoptera: Pyralidae), that attack the fruit and can damage all or most of the seeds inside (Jesus-Barros *et al*. 2015).

Várzea forests of the Amazon region are characterised by high rainfall, climatic seasonality and highly dynamic hydrology resulting from the flood pulses of the Amazon river (Wittmann *et al*. 2006), which are mono-modal and predictable (Junk 1989) resulting in a terrestrial and aquatic phase during the year (Junk 1997). In the Amazon Estuary, flood levels also vary daily in relation to semi-diurnal tides (National Geospatial-Intelligence Agency 2014). Studies have shown that many *várzea trees show seasonal patterns of* flowering and fruiting, with most species flowering in the dry season and fruiting in the rainy season, which is likely an adaptation to the flood regime, facilitating hydrochorous seed dispersal (Pires-O'Brien & O'Brien 1995; Cattanio *et al*. 2004; Haugaasen & Peres 2005; Ferreira & Parolin 2007; Parolin *et al*. 2010). However, a study of 80 species in the Central Amazon showed that 35 % of tree species flowered in the rainy season, and 52 % produced fruits in the dry season (Alencar 1998). Specifically for *C. guianensis*, there is geographic variation in described phenology of flowering, in both várzea and terra firme, across regions of the Amazon. In populations in Acre (Boufleuer 2004), Pará (Maués 2006), Roraima (Pereira & Tonini 2012) and Amapá (Freitas *et al*. 2013) flowering occurs in the dry season. However, in the southeast of Acre two peaks of flowering occur, one in the dry season and one in the rainy season (Klimas *et al*. 2012). Plowden (2004) also report flowering in the period of highest rainfall in the Tembé Indigenous Reserve in the state of Pará. That being said, all of these studies concur that fruiting of *C. guianensis* occurs in the rainy season. This strategy, of producing fruits in the rainy season, appears to be crucial for establishment and survival of *C. guianensis*, especially in várzea forest, as the seeds are dispersed mainly by hydrochory (Scarano *et al*. 2003).

The present study aims to evaluate the phenophases of a population of *Carapa guianensis* in the Fazendinha Protected Area in relation to climatic seasonality, in order to increase our understanding of the reproductive phenology of this species in tropical várzea, and to generate information to aid in its conservation management in the region.

Materials and methods

Study area

The study was conducted in the Fazendinha Protected Area (136.59 ha, hereafter referred to as 'Fazendinha PA'), consisting predominantly of Alluvial Rainforest (IBGE 2012), and located in the Amazon Estuary at 00º03'04,24"S, 51º07'42,72"W in the municipality of Macapá, Amapá, Brazil (Fig. 1). The data were collected from trees in tidal várzea forest which is directly influenced by the waters of the River Amazon owing to seasonal, and twice daily tidal, inundations. Soils in tidal várzea in this region, following the Brazilian classification, are classified as Typical Eutrophic Ta Melanic Gleysols (Embrapa 2006).

Data collection

Phenological data

From the six-hundred and eighty individual crabwood trees of ≥ 15 cm DBH registered in the Fazendinha PA during a 2008 inventory (Abreu *et al*. 2014), 30 productive, adult trees were selected to record phenological data for the present study. The selection criteria used were: a minimum distance of 30 m between trees; possession of a wide canopy and excellent tree health; and ease of viewing of phenological events. Phenological observations were

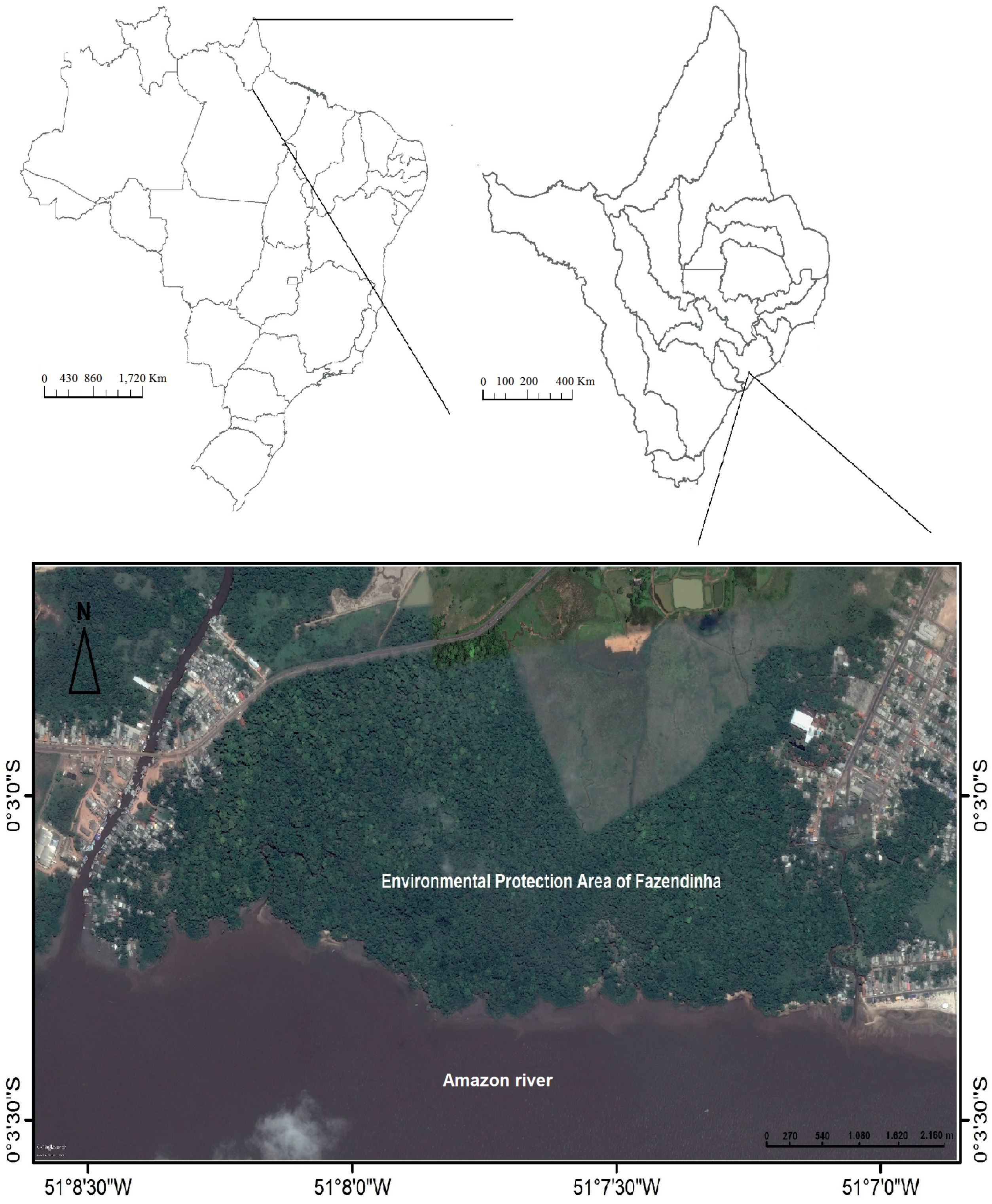

Figure 1. Fazendinha Protected Area, located on the banks of the River Amazon in the state of Amapá, Brazil.

made fortnightly, using binoculars (Bushmaster R2050, with 20x magnification) during the period from October 2009 to October 2011.

The phenophases observed were: i) flowering (flower buds), which begins when small reproductive buds appear in the inflorescence and ends when the flowers begin to open, ii) flowering (open flowers), which is the phase in which the corolla opens, observed either in the tree canopy, on the forest floor or in litter and seed traps installed underneath the canopy, iii) , fruiting (unripe fruits), which begins when it is possible to see the first fruits on the stem of the inflorescence, iv) fruiting (ripe fruits), when fruits fall to the forest floor, v) leaf flush, which begins with the eruption of small reddish-coloured leaflets at the tips of the stems, and ends when the leaflets turn green, and vi) leaf fall, in which the leaves change colour from green to yellow and fall easily, leaving gaps in the canopy. These phenological phases follow the classification used by Morellato *et al*. (2000).

In order to confirm that the species in the study area is indeed *C. guianensis*, specimens including fertile material were sent to the IAN herbarium at Embrapa Amazônia Oriental (Belém, Pará, Brazil). The identification report was released on 13th May 2013, with the material registered under the number 189029.

Climate data

Monthly rainfall (mm) data were recorded at the Macapá weather station, located 1km from the study area (Instituto Nacional de Metereologia 2015). Maximum daily flood level data for the Amazon River were obtained from the tidal monitoring station at the Port of Santana 6 km from the study area, and were averaged across the month (Centro de Hidrografia da Marinha 2016).

Data analysis

The proportion of trees expressing signs of each phenophase was calculated for each fortnightly sample. These values were then averaged to give a single value for each month of the 25 month study period, which was used as the response value for the analyses.

The relationships between proportion of trees in each phenophase and total monthly rainfall (mm), and between the proportion of trees with ripe fruits and river water levels, were verified using univariate Generalised Linear Models (GLMs) with quasi-binomial errors in the programming language R (R Core Team 2015). The relationship between the proportion of trees with ripe fruits and river water levels was modelled to test the hypothesis that fruiting peaks coincide with peak water levels in order to facilitate long-distance dispersal via hydrochory. The relationship between water levels and the other phenophases was not tested as there was no theoretical basis upon which to hypothesise that the seasonal changes in river level, and subsequent inundations of the forest, would affect the phenology of other ecological processes.

To estimate synchrony in the phases of flowering and fruiting, Augspurger's (1983) index of population synchrony (Z) was calculated as follows:

$$Z = \frac{1}{n}\sum_{i=1}^{n} X_i$$

Where: n is the total number of individuals in the sample and Xi is the synchrony between individual i and its conspecifics, calculated using the following formula:

$$Xi = \left(\frac{1}{n-1}\right)\frac{1}{f_i}\sum_{j=1}^{1} e_j$$

Where: fi is the number of months in which individual i flowered or fruited and ej is the number of months in which individuals i and j flowered or fruited at the same time (where $i \neq j$).

The intensity of synchrony was categorised on the following scale: 0 - absence of synchrony; 0.1 to 0.27 - minimal synchrony; 0.28 to 0.45 - low synchrony; 0.46 to 0.69 - medium synchrony; 0.70 to 0.99 - high synchrony; and 1 - perfect synchrony.

Results

September, October and November were the driest months, and the wettest months were from January to June (Fig. 2 - INMET 2015). Tidal flooding occurs daily, reaching its maximum amplitude in March and April, coinciding with the equinox and the period of most intense rainfall (Pereira *et al*. 2002).

In the following sections the results relating to the phenophases of flowering, fruiting and leaf flush and fall are reported.

Flowering

During the study period there were three peaks in flowering (flower buds), firstly in November and December 2009 (83 % of trees), then in September and October of 2010 (90 % of trees), and finally in September of 2011 (100 % of trees). There were also three peaks in flowering (open flowers), in November of 2009 (52 % of trees), October of 2010 (76 % of trees), and finally in September of 2011 when flowering peaked at 100 % of trees (Fig. 2). The peaks of flowering (both buds and open flowers) coincide with the driest months of the year (Fig. 2).

There is a significant negative relationship between the proportion of trees flowering (flower buds - GLM: $\beta = -0.017$; SE = 0.0037; $p<0.001$), and flowering (open flowers - GLM: $\beta = -0.016$; SE = 0.0043; $p = 0.0011$) and the total monthly rainfall (Tab. 1, Fig. 3).

With regards to flowering (both buds and open flowers), most individuals (80 % of trees) showed medium synchrony, and most of the rest (16.6 % of trees) showed high synchrony. The population as a whole showed intermediate synchrony with regards to flowering (Z = 0.66; Tab. S1 in supplementary material).

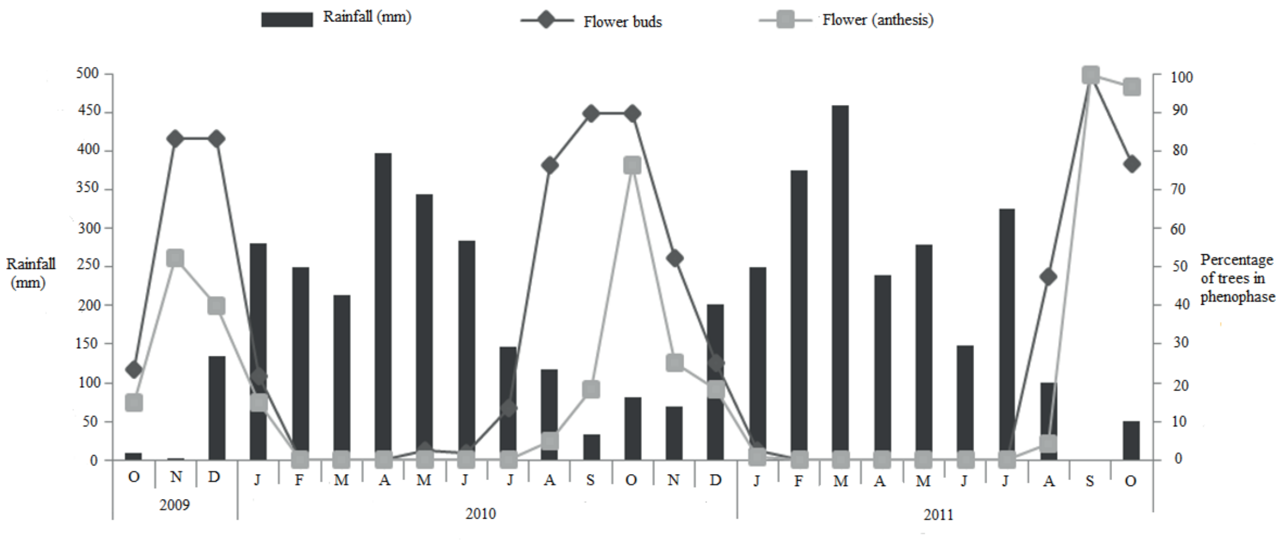

Figure 2. Proportion of trees flowering (flower buds – diamonds, and open flowers - squares) within the study population of *Carapa guianensis* in the Fazendinha Protected Area – Macapá, Amapá, Brazil, shown in relation to total monthly rainfall (bars) throughout the study period (October 2009 to October 2011).

Table 1. Effect sizes (β), standard errors (SE) and significance levels (*significant at 0.05, **significant at 0.01, ***significant at 0.001, ^{NS}not significant) of the relationships between phenological phases and rainfall (rain) and river water level (water), based on GLMs with quasi-binomial error structures. NT = not tested.

Response variable	β_{rain}	SE_{rain}	β_{water}	SE_{water}
% trees flowering (flower buds)	-0.017***	0.0037	NT	NT
% trees flowering (open flowers)	-0.016**	0.0043	NT	NT
% trees fruiting (unripe fruit)	0.0091**	0.0031	NT	NT
% trees fruiting (ripe fruit)	0.016 ***	0.0041	10.16**	2.96
% trees in leaf flush	-0.0008^{NS}	0.0019	NT	NT
% trees in leaf fall	0.0014^{NS}	0.0020	NT	NT

Fruiting

During the study period there were three peaks in fruiting (unripe fruits), firstly in March 2010 (93 % of trees) and then in January 2011 (100 % of trees), with a smaller peak occurring again from March to May 2011 at a level of 93 %. There were two peaks in fruiting (ripe fruits), between March and May 2010 (93 % of trees) and between March and May 2011 at a level of 93-97 % (Fig. 4). The peaks of fruiting (both unripe and ripe fruits) coincide with the wettest months of the year (Fig. 4).

There is a significant positive relationship between the proportion of trees with unripe (GLM: $\beta = 0.0091$; SE = 0.0031; $p = 0.008$), and ripe (GLM: $\beta = 0.016$; SE = 0.0041; $p < 0.001$) fruits and the total monthly rainfall (Tab. 1, Fig. 5). The relationship between the proportion of trees with ripe fruits and river water level was also significant and positive (GLM: $\beta = 10.16$; SE = 2.96; $p = 0.0023$; Tab. 1, Fig. 6)

All but two individuals produced fruits during the study period, and showed high synchrony in the fruiting phases, contributing to overall high synchrony of fruiting at the population level ($Z = 0.85$; Tab. S2 in supplementary material).

Leaf flush and fall

Budding of new leaves (leaf flush) and leaf fall occurred concurrently, and there was no clear seasonal pattern in peaks throughout the study period (Fig. 7). There was also no significant relationship between leaf flush or leaf fall, and rainfall (Tab. 1).

Discussion

There is clear seasonal variation in the production of flowers and fruits of *Carapa guianensis* in the study region. Peaks of flowering occur between September and December, the driest months of the year, and the proportion of trees flowering is strongly and significantly negatively related to

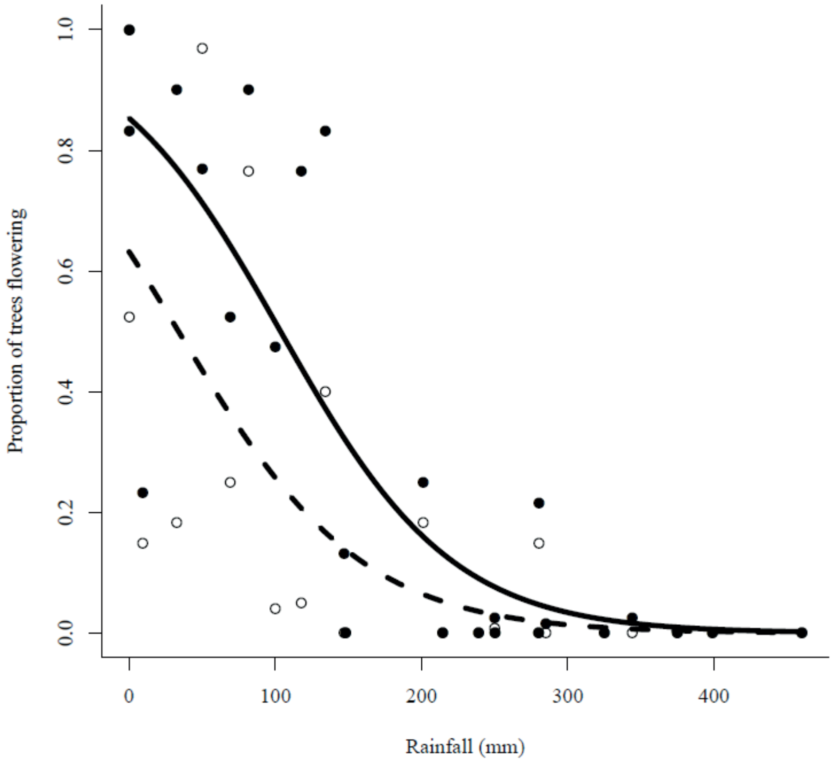

Figure 3. Relationship between proportion of individuals in the population of *Carapa guianensis* flowering (flower buds) – closed circles, solid line, and flowering (open flowers) – open circles, dashed line, and rainfall (mm) in the Fazendinha Protected Area – Macapá, Amapá, Brazil.

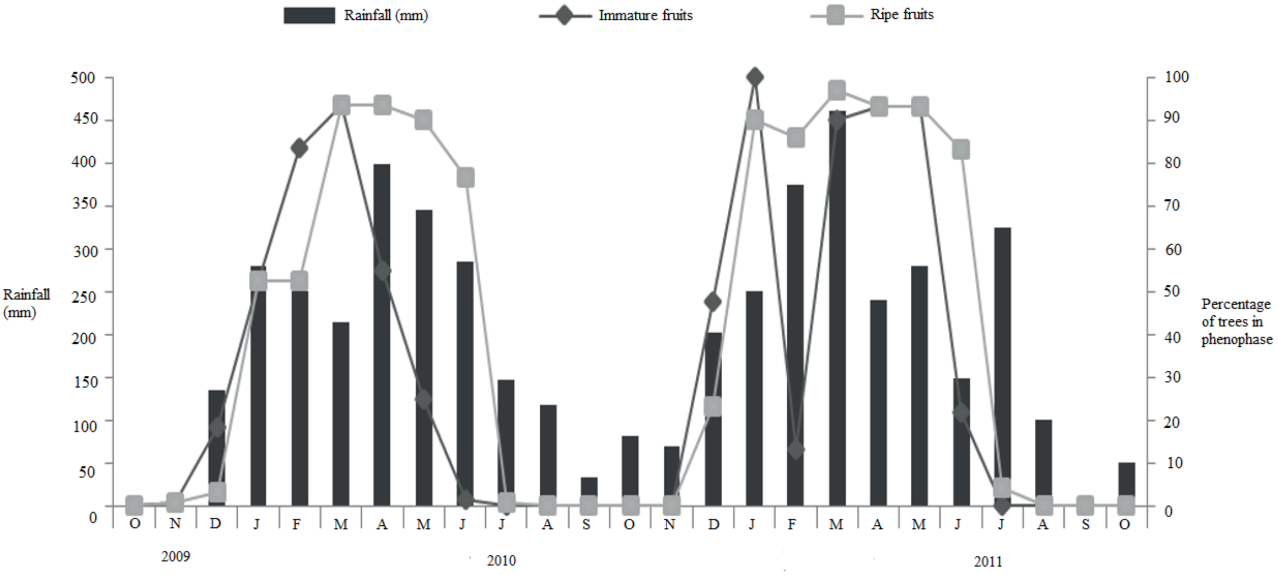

Figure 4. Proportion of trees fruiting (unripe fruits - diamonds, and ripe fruits – squares) within the study population of *Carapa guianensis* in the Fazendinha Protected Area – Macapá, Amapá, Brazil, shown in relation to total monthly rainfall (bars) throughout the study period (October 2009 to October 2011).

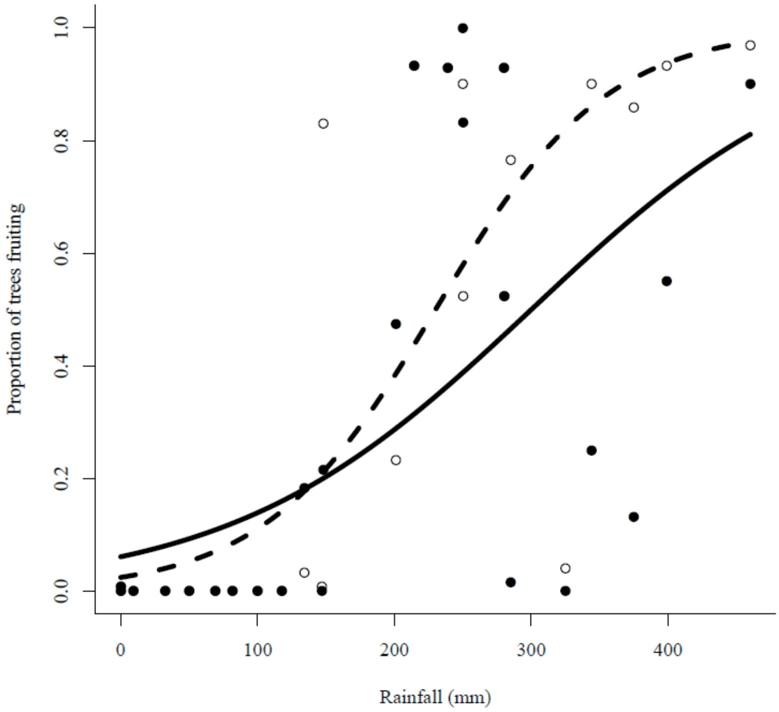

Figure 5. Relationship between proportion of individuals in the population of *Carapa guianensis* with unripe (closed circles, solid line) and ripe fruits (open circles, dashed line), and rainfall (mm) in the Fazendinha Protected Area– Macapá, Amapá, Brazil.

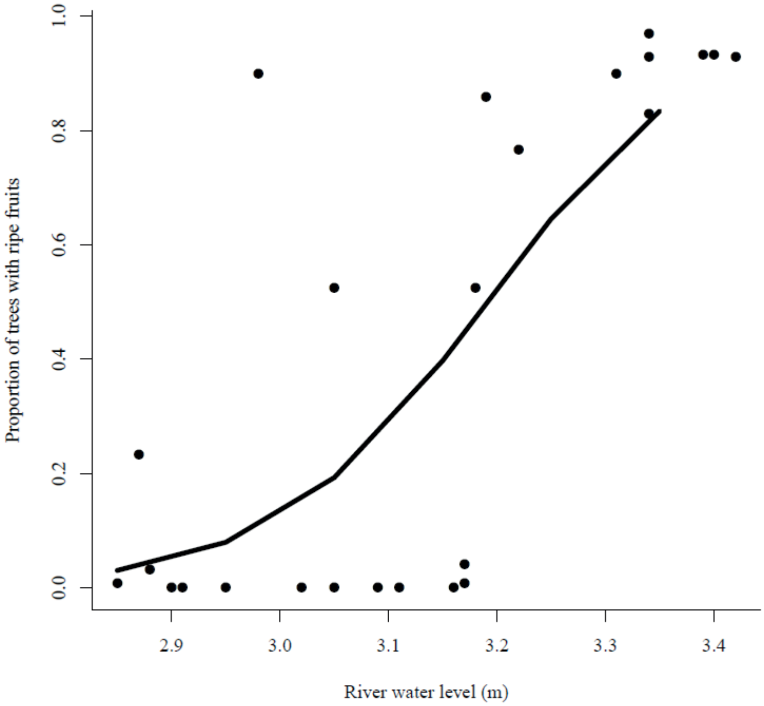

Figure 6. Relationship between proportion of individuals in the population of *Carapa guianensis* with ripe fruits and river water level (m) in the Fazendinha Protected Area– Macapá, Amapá, Brazil.

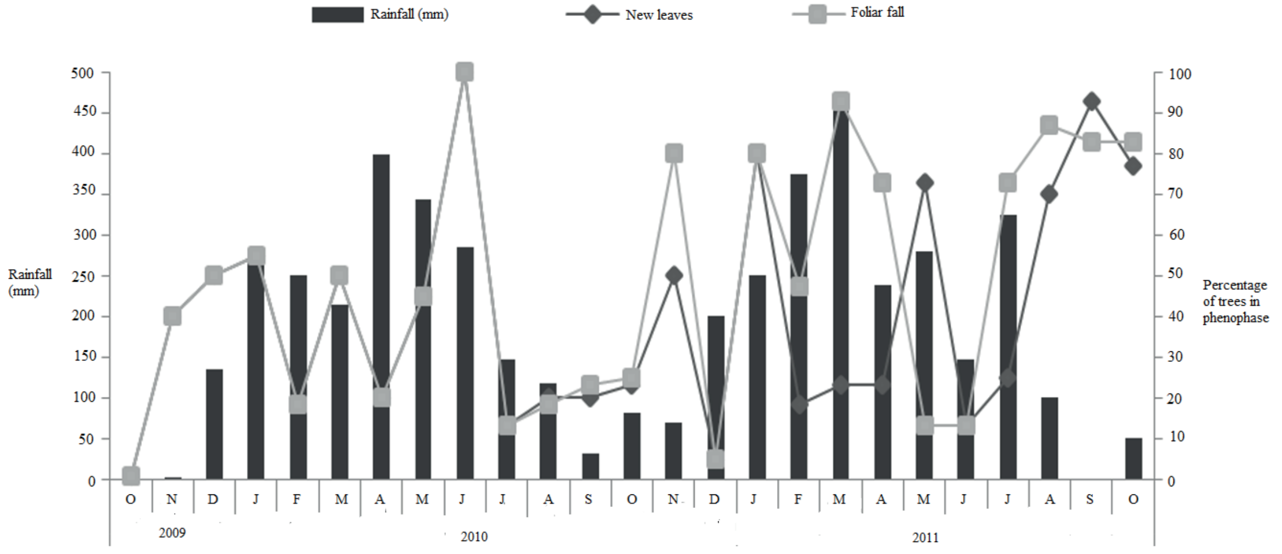

Figure 7. Proportion of trees with changing leaves (new leaves -diamonds, and leaf fall - squares) within the study population of *Carapa guianensis* in the Fazendinha Protected Area – Macapá, Amapá, Brazil, shown in relation to total monthly rainfall (bars) throughout the study period (October 2009 to October 2011).

total rainfall. Conversely, peaks of fruiting occur between January and May, the wettest months of the year, and the proportion of trees fruiting is strongly and significantly positively related to total rainfall. Leaf flush and fall occur concurrently, and did not show a strong seasonal pattern.

Flowering in the dry season, as shown in this population of *C. guianensis*, is a sensible reproductive strategy in tree species of the Amazonian várzea. Intense rainfall at other times of the year could cause structural changes to the flower, potentially affecting pollination through reductions in viability of the pollen or receptivity of the stigma. This could be particularly true for *C. guianensis* which has very small, delicate flowers. Pires-O'Brien & O'Brien (1995) further highlight that heavy rainfall could dilute nectar and thus interfere with attraction and motility of pollinators, such as micro-lepidoptera and meliponinae in the case of *C. guianensis* (Maués 2006). In the Amazon region, the period of heaviest rainfall is also associated with higher river levels, and flooding of várzea forest. The concentration of flowering in the period of lower river levels may therefore also be part of a strategy to concentrate fruiting during periods of higher water levels, facilitating hydrochory (Ferreira & Parolin 2007). We found medium intensity synchrony of flowering for *C. guianensis*, and other studies have previously shown high (Pereira & Tonini 2012) and no (Maués 2006) synchrony. High synchrony could help to attract pollinators (Rathcke & Lacey 1985), though it could also reduce overall movement of pollinators between trees, potentially reducing genetic diversity. Furthermore, high synchrony could attract beetles and larvae of lepidoptera, increasing rates of flower predation.

The occurrence of fruiting during periods of highest rainfall, as found in this study, supports evidence from other phenological studies of *C. guianensis,* carried out in other parts of the Amazon, in both terra firme and várzea (Boufleuer 2004; Plowden 2004; Maués 2006; Klimas *et al*. 2012; Pereira & Tonini 2012; Freitas *et al*. 2013). Here we show that the probability of fruiting is very low (<0.2) when precipitation levels are less than 150 mm per month, and the probability of appearance of ripe fruits increases markedly when average monthly river water levels rise above 3.2m. This coincidence of fruiting with the rainy season and high river levels facilitates hydrochoric seed dispersal as torrential rain and high winds knock ripe fruits from the trees, and seeds are then carried long distances by the waters of the Amazon and its tributaries (Scarano *et al*. 2003). Furthermore, when river levels are higher more of the várzea is inundated, more individual trees are reached, and therefore more seeds will be dispersed. In tidal várzea, when the tide falls, seeds accumulate in lower-lying areas, which may help to maintain soil humidity and therefore facilitate plant growth during the Amazonian summer (September to November) when rainfall is low and the influence of the tides do not reach as far in to the forest. While, in common with a large proportion of riparian and wetland plant species, *C. guianensis* displays hydrochorous seed dispersal, this occurs in combination with other dispersal syndromes, principally zoochory (dispersal by animals). This may help to explain why synchrony was higher in the fruiting than flowering phase, as a higher density of fruits may attract larger numbers of dispersers (Rathcke & Lacey 1985).

Leaf flush and fall occurred simultaneously and gradually throughout the year. Populations of *C. guianensis* in Acre, Pará, Roraima and in the south-east of the state of Amapá have also been found to show this perennial pattern in both terra firme and várzea (Schöngart *et al*. 2002; Boufleuer 2004; Maués 2006; Pereira & Tonini 2012). The fact that the canopies of these trees are always green is advantageous because it increases the area of photosynthetic uptake, and therefore carbohydrates available during the reproductive phase, leading to greater seed production (Farias & Hoppe 2004). Furthermore, it has been suggested that continuous budding of leaves helps the tree to store greater quantities of carbohydrates to be used during reproductive phases (Klimas *et al*. 2012).

Strong seasonality in flowering and fruiting of *C. guianensis* likely represents a reproductive strategy to maximise pollination and hydrochorous seed dispersal. The phenological information provided by this study, particularly the identification of the exact period of highest seed production, will facilitate the inclusion of crabwood oil extraction in the management plan for the Fazendinha PA. Furthermore, the results presented here contribute to an improved understanding of the reproductive behaviour of *C. guianensis* in tidal várzea, essential information for planning for the sustainable use of this species.

Acknowledgements

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