

Climate-related phenology of *Mauritia flexuosa* in the Colombian Amazon

Ligia E. Urrego · Andrea Galeano · Cristina Peñuela · Mauricio Sánchez · Esaú Toro

Received: 19 February 2016/Accepted: 23 August 2016/Published online: 1 September 2016 © Springer Science+Business Media Dordrecht 2016

Abstract Mauritia flexuosa is a keystone species with a broad geographic distribution throughout the Amazon. Environmental changes can impact the reproductive success in a keystone species such as M. flexuosa, which results in a cascade of events that impacts many other species. The present study examined the reproductive phenology in the palm M. flexuosa between December 2010 and November 2012. A 1-ha plot was established in the central Amazon and all palms ≥ 14 m tall were labelled for measuring. The following five phenophases were recorded monthly for each labelled palm: (i) spadix formation; (ii) buds; (iii) open flowers; (iv) infructescences with green fruits; and (v) infructescences with ripe fruits. ANOVA and multiple range tests were used to evaluate significant differences among variables for each year. The phenological activity index for each phase was related with regional climate variables, including maximum and minimum daily temperature, monthly accumulated precipitation, cloudiness, flood and water table levels in the plot using a redundancy

Communicated by Joy Nystrom Mast.

C. Peñuela

Universidad Regional Amazónica IKIAM, Tena, Ecuador

analysis. Overall, fruiting and flowering AIs exhibited significant differences; however, increased synchronous flowering was recorded during the first year associated with maximum temperatures and a drought period; the second year indicated precipitation sufficient for higher fruit production. Climate also influenced seedling mortality, recruitment, and establishment.

Introduction

Mauritia flexuosa L.f. is one of the most widespread palm species in the Amazon (Ter Steege et al. 2013) and Orinoquia (Lasso et al. 2013) regions of South America. Most populations are concentrated along flooded and poorly drained zones of fluvial plains; these sites are known as várzea forest (white water) and igapó forest (black water) (Prance 1979; Henderson et al. 1995). Flooding cycles, geomorphological processes, and soil features restrict and shape the species local environment, which are determined by river dynamics (Junk et al. 2013). M. flexuosa often form dense, monospecific stands. Stand density increases due to prolonged flooding periods and poor soil drainage conditions, resulting in impoverished soils, which impede colonization of intolerant species to hydromorphic soil conditions (Urrego 1997;

L. E. Urrego (⊠) · A. Galeano · M. Sánchez · E. Toro Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Sede Medellín, Calle 59A No. 63-20, Medellín, Colombia e-mail: leurrego@unal.edu.co

Galeano et al. 2015). Therefore, population persistence depends in part on maintenance of these specific environmental conditions and the role of specific animal dispersers. *M. flexuosa* is vital in feeding several wildlife species, and is therefore recognized as a keystone species (Rodríguez et al. 2006; Holm et al. 2008).

The reproductive cycle of M. flexuosa transitions from annual to supra annual (Urrego 1987; Khorsand-Rosa 2013). Urrego (1987) reported that the species was influenced by climatic variables, including the number of sunshine hours per day and extreme air temperatures, which might trigger the current season's flowering or fruiting. Higher flood levels with longer flooding times might also negatively influence reproductive cycles, including seed germination and seedling establishment (Urrego 1987; Khorsand-Rosa 2013; Galeano et al. 2015). Despite reports of moderate seed germination percentages (50 %), seedling survival might drop (23-44 %) after 6 months of flooding (Urrego 1987; Galeano et al. 2015), likely related to density dependent factors and anthropogenic disturbance intensity among sites (Isaza et al. 2013; Khorsand-Rosa 2013; Galeano et al. 2015).

Mauritia flexuosa has multiple uses and therefore high economic potential (Sampaio et al. 2008; Trujillo et al. 2011) in the Amazon. However, despite the species wide geographic distribution and dense stands, *M. flexuosa* is seriously threatened by management practices, which involves cutting down female palms to harvest fruits (Holm et al. 2008; Isaza et al. 2013). Moreover, according to the local people of the Colombian Amazon, *M. flexuosa* stands exhibit changes in fruit crop frequency, which might be related to current global climate change, recorded by Phillips et al. (2010) in Amazon vegetation.

Climate fluctuations related to El Niño Southern Oscillation (ENSO) frequencies induced longer dry seasons (Phillips et al. 2010), prevalence (Laurance et al. 2004), and flood intensity in the Amazon, which might affect *M. flexuosa* stands as follows: (i) increase adult and seedling mortality (Bradsmith and Bravo 2006) due to heightened sedimentation rates associated with river overflows covering fluvial plains during extreme precipitation events; (ii) water table and soil humidity changes due to alterations in floristic composition by invasion of upland plant species (Phillips et al. 2009; Galeano et al. 2015); and (iii) phenological cycle modifications in plant species due to enhanced dry seasons, which extend the flowering period, shorten fruiting, and/or diminish fruit production, as reported in other Amazon species (Clark 2007). Studies showed changes in fruit production affected local fruit consumption and played an integral role in animal trophic chains, as animals feed on *M. flexuosa* fruits (Brightsmith and Bravo 2006; Holm et al. 2008).

Current climate change effects on plant species populations are widely recognized, however to achieve an accurate understanding of such complex effects for individual species represents a long-term task, particularly when addressing species phenology. Data related to long-term phenological and extreme climate event data and relationships with phenological changes are largely absent. M. flexuosa is the dominant species in the Amazon (Ter Steege et al. 2013); therefore, it is important to assess the species response facing climate change. In the present study, we examined the following two questions: (i) what are the main environmental features influencing M. flexuosa reproductive phenology; and (ii) how does the inter-annual climate variability affect reproductive phenology of a well-preserved stand of M. flexuosa in two consecutive years in the Colombian Amazon.

Study area

The study area was established in a M. flexuosa stand located on a poorly drained low terrace of the Calderón River watershed in the Colombian Amazon (3°56' 48.9"S, 69°53'1.83"W), 28 km from Leticia city (Fig. 1). A 1 ha permanent plot was established in the M. flexuosa stand and the Calderón River and some of its tributaries flood over the plot during the rainy season. The zone is classified as tropical rain forest (Af) in the köppen climate classification (Rubel 1884). Mean annual temperature and precipitation are 26 °C (15-36 °C) and 3335 mm, respectively (IDEAM 2010–2012), which excluding the Andean piedmont, corresponds to the Amazon basin zone with the highest recorded precipitation (Espinoza et al. 2009). Intertropical convergence zone (ITCZ) displacements modulate precipitation in the basin; however, inter-annual variations are influenced by ENSO (Espinoza et al. 2009). November to May represents the rainy season, with a maximum in April; and the dry season extends from June to October, with August recorded as the driest month (IDEAM 2010-2012). Notable drought



Fig. 1 Map of the study area. Location of the sampled *M. flexuosa* stand in the Colombian Amazon

conditions were recorded in the Amazon from July 2010 to April 2011 (IDEAM 2011), despite predominant "La Niña" like conditions across the country, particularly in the Andes and Caribbean regions. In the northwestern Amazon, the most severe drought since 1998 was recorded; the drought was influenced by the meridional sea surface temperature (SST) gradient in the tropical atlantic (Espinoza et al. 2009; Xu et al. 2011; Marengo 2013). Galeano et al. (2015) documented that precipitation and flooding levels increased and reached 4 cm of the mean flooding level following the second half of 2011 to the first of 2012.

Methods

Phenological measures were obtained from 154 palms with heights ≥ 14 m; the minimum height at which

flowering palms were identified in a 1 ha permanent plot. Reproductive phenology observations were conducted between December 2010 and November 2012 on 89 individuals that flowered and/or fruited during this period. The following five phenophases were recorded monthly: (i) spadix formation; (ii) buds; (iii) open flowers; (iv) infructescences with green fruits; and (v) infructescences with ripe fruits. Phenophase duration for the population was calculated by averaging phenophase duration for all measured palms in the plot. Phenological patterns and population synchrony were calculated using the activity index (AI) (Bencke and Morellato 2002). Seven palms from 35 (20 %) produced fruit in December 2010 and February 2012 and were measured to evaluate fruit production. Infructescence number was counted and one infructescence per palm was randomly chosen to evaluate the number of fruiting branches per infructescence as follows: (i) fruit number/branch; (ii) fruit number/ infructescence; (iii) length of 40 % of infructescence fruits; (iv) width of 40 % of infructescence fruits; and (v) weight of 40 % of infructescence fruits. The 40 % was considered representative based on fruit size variance. The number of fruits/palm was estimated based on these measurements. Flooding and water table levels were measured every month close to each adult female palm using a marked stick (cm).

Maximum and minimum daily air temperatures $(T_{\text{Max}} \text{ and } T_{\text{Min}}, \text{respectively})$, cloudiness, and precipitation data were obtained from the (IDEAM 2010–2012) meteorological station located at the Vásquez Cobo Leticia (Amazonas) airport (Figs. 2, 3). Interannual differences in climatic variables and fruit production were established using a one-way ANOVA and multiple range tests (MRT) in STATGRAPHICS (Centurion XV, Version15.1.02). A principal component analysis (PCA) was applied to identify any phenological data structure that best explains the data variance and whether each reproductive phenophase was restricted to a specific time of year. The relationship between phenological phases and climate

variables was established through a redundancy analysis (RDA) performed with CANOCO 4.5 (Ter Braak and Smilauer 2002). Fruit production differences between 2011 and 2012 were examined using ANOVA and MRT.

Results

Climatic setting

The maximum difference between extreme temperatures (range 11–17 °C) was recorded during the dry period in August of both years, when precipitation, cloudiness, and flood levels were lowest (Figs. 2, 3). In addition, flood levels were lower in 2011 than in 2012, from February to August (Fig. 2). Whereas precipitation exhibited a positive, significant relationship with cloudiness (R = 0.58; $F_{1,22} = 11.09$; P < 0.05), it showed a weak, non-significant relationship to flood levels. Following the maximum temperature amplitude and drought period recorded in August 2011, precipitation, cloudiness, and flood



Fig. 3 Distribution of monthly extreme temperatures between December 2010 and November 2012 in the Colombian Amazon



levels increased progressively, reaching maximum values in March 2012. A comparison of climatic variable distribution among 2010–2012 study years was used to identify extreme climate conditions. One-way ANOVA and MRTs showed significantly lower maximum ($F_{2,33} = 16.58$; $P \le 0.000$) and higher minimum temperatures ($F_{2,33} = 19.82$; $P \le 0.000$) in 2010 ($T_{\text{max}} = 33.6 \text{ °C}$, $T_{\text{min}} = 21.5 \text{ °C}$), when compared to values recorded in 2011 ($T_{\text{max}} = 35.4 \text{ °-C}$, $T_{\text{min}} = 18.1 \text{ °C}$) and 2012 ($T_{\text{max}} = 35.9 \text{ °C}$, $T_{\text{min}} = 18.0 \text{ °C}$).

Phenology

The flowering phase, from spadix formation until flowers opened, occurred during the dry season in both years (2011–2012). However, in 2011 the beginning of the flowering phase was observed in April, which was earlier than during the normal dry season (Fig. 4); in 2012, the phase began in June. The 2011–2012 period exhibited inflorescences in different developing stages concurrently within the population. However, flowering synchrony was significantly higher in 2011 (42 %) than 2012 (26 %). Fruit development, from green to ripe fruits, occurred over an ~10 month period, from July 2011 to April 2012 (Fig. 4). Contrary to flowering, fruiting synchrony reached a higher value (23 %) in 2012 compared with 2011 (16 %); 14 % of adult palms flowered during both years.

PCA (Fig. 5) showed phenophase development occurred concurrently in 2011 and 2012. The first two PCA axes explained 90 % of the variance, with eigenvalues of 0.65 and 0.25. Flowering phases were

grouped in the upper right quadrant of the biplot, with maximum values in September and October of both years, although open flowers in 2011 initiated earlier, i.e., in August (Fig. 5). The green fruit phase was grouped to the left upper and lower quadrants of the biplot and included samples from January to November of 2011 and 2012. These results represented the long development period for green fruits. The ripe fruit phase, lower right quadrant of the PCA biplot, occurred in June and July of both years, although in 2012 the phase lasted until August.

RDA results of the relationships between AI and climatic variables (Fig. 6; Table 1) explained 52 % of the variance along the first two RDA axes, with eigenvalues of 0.41 and 0.11. Cloudiness and maximum air temperature exhibited the highest regression coefficients and interset correlations (Table 1). Maximum AI values for flowering phases (spadix formation, flower buds, and open flowers) were associated with T_{Max} recorded from August to November 2011 and 2012, when precipitation and cloudiness were lowest, and the amplitude between T_{Max} and T_{Min} was greatest. Green fruit development was related to the highest cloudiness and precipitation values. Increased T_{Min} values in June and July of both years showed a relationship with ripe fruits.

Fruit production

Fruiting-associated parameters were higher in February 2012 compared with December 2010 (Table 2). Significant differences between both years were detected in the number of infructescences/palm **Fig. 4** Fluctuation of the activity index of flowering and fruiting of *M. flexuosa* between December 2010 and November 2012 in the Colombian Amazon



Fig. 5 Biplot corresponding to the first two axes of the principal component analysis of the activity index of flowering and fruiting phenophases of *M. flexuosa* between December 2010 and November 2012 in the Colombian Amazon



corresponding to the first two axes of the redundancy analysis between the activity index of flowering and fruiting phenophases of *M. flexuosa* between December 2010 and November 2012 and the climate variables. *MINT* Minimum temperature, *MAXT* Maximum temperature in the Colombian Amazon



Table 1 Statistical results from the first two redundancy analysis (RA) axes, based on environmental variables measured in the *M*. *flexuosa* stand in the Colombian Amazon study area

| Environmental variables | Interset correlations | | Regression coefficients | |
|-------------------------|-----------------------|--------|-------------------------|--------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| T _{Max} | 0.553 | -0.339 | 0.533 | -0.753 |
| $T_{\rm Min}$ | -0.451 | -0.380 | -0.168 | 0.485 |
| Monthly precipitation | -0.569 | 0.039 | -0.126 | 0.306 |
| Cloudiness | -0.688 | -0.290 | -0.464 | -0.708 |
| Flooding | -0.222 | 0.065 | -0.199 | 0.521 |

Bold values represent the coefficients of the most important variables for each axis

 $(F_{1,8} = 8.33; P \le 0.05)$; weight of fruit/infructescence $(F_{1,8} = 6.78; P \le 0.05)$; and weight of fruits/ palm $(F_{1,22} = 13.40, P \le 0.01)$.

Seedling recruitment and mortality

Seedling recruitment and survivorship comparisons between both years were based on data from Galeano et al. (2015). Primary results are shown in Fig. 7. Significant differences were detected between years in seedling recruitment ($F_{2,170} = 14.25$, $P \le 0.00$);

mortality ($F_{2,170} = 4.18$; $P \le 0.05$), and seedling height ($F_{2,337} = 7.155$, $P \le 0.000$); however, significant differences were not observed in survivorship between 2011 and 2012.

Discussion

Results showed that climate variability throughout the 2-year study period was associated with the reproductive phenology of *M. flexuosa*. Observed interannual

| Table 2 Fruit production parameters in <i>M. flexuosa</i> | Parameter | Period 1 (2010–2011) | Period 2 (2011–2012) |
|--|--|----------------------|----------------------|
| for period 1 and period 2 | Average fruit size: length \times width (cm) | 5×4 | 5 × 4 |
| | | N = 778 | N = 1423 |
| | Average fruit number infructescence ⁻¹ | 315 | 527 |
| | Average infructescence number palm ⁻¹ | 2.6 | 3.6 |
| | | N = 19 | N = 24 |
| | Average fruit number palm ⁻¹ | 846 | 1849 |
| | Number palms fruiting ha ⁻¹ | 24 | 35 |
| | Number palms flowering ha ⁻¹ (flowering) | 65 | 40 |
| | Total population fruit number ha ⁻¹ | 9154 | 19,475 |
| | Fruit production (ton ha^{-1} year ⁻¹) | 0.93 | 2.22 |



Fig. 7 Fruit production and seedling regeneration of *M. flexuosa* in 2010 and 2012 in the Colombian Amazon. The number of fruits was divided by 100 in order to reduce the scale of the bar

differences related to ENSO were identified, despite the modulation effects of ITCZ in Amazon rainfall distribution (Nobre et al. 2010). A substantial La Niña affected the neotropics from July 2010 to May 2011 and was recorded as the strongest in several decades in Colombia (IDEAM 2011). A La Niña causes increased precipitation rates and reduced air temperatures (Poveda and Mesa 1997), although in over one-half of the Colombian Amazon, precipitation deficits were reported, consequently lower river flood levels occurred during this period (IDEAM 2011) (Fig. 2). Precipitation, flood levels, and the water table were lower than historical averages at the study site (Espinoza et al. 2011). The drought of 2010-2011 was recorded as the most extreme in the major part of the Amazon since 1998 (Espinoza et al. 2011; Xu et al. 2011; Marengo et al. 2013) and was related to the tropical Atlantic north-south SST gradient (Marengo et al. 2011), that caused the 2005 drought (Phillips et al. 2009). From July to December 2011, regional precipitation showed an increased trend and reached maximum values during the rainy season, whereas during the same period in 2010, precipitation exhibited a notable decrease in this region of the Amazon (Espinoza et al. 2011; IDEAM 2011; Marengo et al. 2011).

Thus, the harsh climate conditions recorded in 2010–2011 might result in earlier flowering (in April 2011) initiation and the highest AI in the recorded flowering, as documented in several tropical species (Haugaasen and Peres 2005; Sakai et al. 2006) interpreted based on global climate change. Sakai et al. (2006) attributed mass flowering in aseasonal Asian tropical forests with extreme droughts related to ENSO, Li et al. (2011) reported El Niño effects were the main drivers of interannual climatic variability

causing increased temperatures and declined rainfall. However in our study region, Marengo et al. (2011) found that La Niña conditions were obscured by an intensified Atlantic north–south SST gradient, which caused decreased precipitation and increased maximum temperatures, which triggered *M. flexuosa* flowering in 2011. Observations recorded in other Amazon-flooded forests (Parolin et al. 2002) reported strong drought conditions increased soil dissolved carbon and nutrient concentrations, which might facilitate a higher carbohydrate load in *M. flexuosa* palms, required for gregarious flowering and result in profuse flowering at the end of the drought.

We only obtained 2 years of phenological data for our study area, which indicated the climate was atypical; however, PCA results showed synchrony (sensu Newstrom et al. 1994) in the M. flexuosa flowering pattern for both years in seasonal and aseasonal forests (Ervik 1993; Storti 1993; Ponce 2002; Isaza 2013; Nuñez and Carreño 2013). Similar to other annual flowering species differences in flowering time and duration were recorded. Seasonal forests (e.g., savannahs) in the Llanos Orientales, Colombia and the eastern Amazon, Brazil (Storti 1993; Khorsand-Rosa 2013; Nuñez and Carreño 2013), with annual precipitation <2200 mm, supported M. flexuosa individuals that flowered during or at the beginning of the wet season. Aseasonal forests of the central Amazon experience annual rainfall >3000 mm; however, these forests do exhibit a drier season, and M. flexuosa flowered at the end of this season (Ervik 1993; Cabrera and Wallace 2007; Isaza et al. 2013). However, during January to June 2011 drier conditions prevailed, a pattern similar to stands of seasonal forests in Llanos Orientales, Colombia (Nuñez and Carreño 2013).

Mauritia flexuosa fruiting at the study site also exhibited an annual pattern (Figs. 4, 5), consistent with other Amazon *M. flexuosa* stands (Storti 1993; Ponce 2002; Isaza 2013; Nuñez and Carreño 2013), although green fruit production was observed for ~9 months. Results showed that fruit production was associated with precipitation, increased cloudiness, and minimum air temperatures. Haugaasen and Peres (2005) reported that lengthy green fruit production was more common in flooded Amazon forests and particularly in *M. flexuosa* (Da Silva 2009; Tobler 2010; Khorsand-Rosa 2013). However, ripe fruits exhibited a peak between June and July in both years. In 2011 ripe fruits started earlier and in lower proportion than in 2012. *M. flexuosa* maximized fruiting during the rainy season and under high water levels, comparable to many other species from flooded forests (Parolin et al. 2002; Ferreira and Parolin 2007). Parolin (2010) showed increased fruit maturation at the onset or during the rainy season, which maximized dispersal syndromes, i.e., hydrochory and ictiochory (Haugaasen and Peres 2005), and attracted notable numbers of birds and mammals that feed on the fruits (Mendieta-Aguilar et al. 2015).

However, significant differences in fruiting AI between the two consecutive years (Fig. 4) might be related to a water deficit and the strong drought recorded during the first study period (2011) (IDEAM 2011; Marengo et al. 2013). Ponce (2002) reported similar observations for seasonal M. flexuosa forests in the eastern Amazon (Brazil). Here, these conditions affected not only the number of females shedding fruit (24 females ha^{-1} in 2010–2011 compared to 35 females ha^{-1} in 2012), but also fruit production, which was much lower in the first $(0.9 \text{ ton } ha^{-1} \text{ year}^{-1})$ compared with the second (2.2 ton $ha^{-1} year^{-1}$) year. Haugaasen and Peres (2005) showed interannual fruiting variation in species from Amazon flooded forests and in many other tropical forest species due to strong changes in rainfall and temperature, with ENSO responsible for the most notable variability in the Amazon (Phillips et al. 2010; Khorsand-Rosa 2013). However, new data now indicate other climate forces, such as the Atlantic SST (Espinoza et al. 2011; Marengo et al. 2013), might also influence Amazon plant phenology.

Mauritia flexuosa fruit phenology and production exhibited temporal and spatial variation. Urrego (1987) generated preliminary *M. flexuosa* fruiting data from a várzea forest in the northern Colombian Amazon and recorded fruit production (9.1 tons ha⁻¹ $year^{-1}$) much higher than our 2011–2012 igapó forest fruit production (average 1.6 tons $ha^{-1} year^{-1}$). However, our production result was spatially and temporally similar to another M. flexuosa stand, and subsequently production was comparable (1.45 ton ha^{-1} year⁻¹; Isaza et al. 2013). Fruit production comparisons among *M. flexuosa* stands within the Amazon are challenging, even within years, due to spatial variation in rainfall and species distribution. Khorsand-Rosa (2013) characterized Roraima (northern Amazon) during 2010 as an abnormally wet year and the Central Amazon as extremely dry; however, fruiting was related to the wet season, and fruit production was higher during wetter years. In the present study, we also found that fruit production was higher during the wetter year (2012). In addition, increased fruit production was recorded in the forest rather than the ecotone and the disturbed savannah (Khorsand-Rosa 2013). Fruit production in 2012 was higher in our study area (2.2 tons ha⁻¹year⁻¹), where forest conservation is considerably better due to an increased distance to human settlements, compared to fruit production reported by Isaza et al. (2013) (1.45 ton ha⁻¹ year⁻¹) in more disturbed forests, where evidence of harvested and cut down palms were discovered.

Galeano et al. (2015) showed that M. flexuosa seedling germination and recruitment were highly influenced by climatic fluctuations. Suitably wet conditions for fruiting might also be required for seed germination and seedling establishment. In addition, extreme dry conditions increased seedling mortality. December 2010 indicated seedling mortality was highest, with the lowest fruit production and seedling recruitment (Fig. 7). February 2012 exhibited the highest fruit production and seedling recruitment. Due to high seedling mortality in December 2010, seedling growth measures were not possible; however, the highest mean seedling height was recorded 2 months after the increased rainfall in September 2011. Williamson and Ickes (2002) reported that ENSO associated droughts showed increased effects in southeast Asian forests, where post-drought seedling recruitment was also very high, based on the post-ENSO seedling release hypothesis. Therefore, flooding and/ or soil water availability clearly affected seedling establishment, consistent with several species distributed in frequently flooded forests (Kubitzki and Ziburski 1994). Our results also showed that prolonged drought conditions might cause high M. flexuosa seedling mortality congruent with other floodplain species (Parolin et al. 2010), but benefits the colonization of species from terra firme forests, which might occur at the expense of M. flexuosa seedling establishment (Galeano et al. 2015). Ferreira and Stohlgren (1999) suggested that M. flexuosa establishment was influenced by the species establishment strategy under flooding conditions, but we also showed phenological pattern was strongly driven by climatic fluctuations.

Our data provided evidence that short-term climatic fluctuations influenced M. flexuosa flowering and fruiting patterns. According to climate change projections (IPCC 2013) in the Central Amazon, temperatures will increase between 0.6 and 2 °C by 2100, under the most conservative scenario, and precipitation will decrease between 20 and 30 %. These projections imply disturbing climate and subsequent environmental changes will occur, which will likely impact the phenological response of M. flexuosa, a keystone Amazon plant species and therefore a vital resource for many other species. While massive flowering might occur more frequently, fruit production could diminish if late season precipitation is not sufficient to compensate soil water scarcity. Alternatively, changes in soil water availability might restrict M. flexuosa seedling establishment and promote colonization of adjacent species from terra firme forest sites. These changes could affect M. flexuosa dispersal and subsequent distribution patterns, but most importantly, survival of this species integral to the Amazon.

Acknowledgments The authors are grateful to Dirección Nacional de Investigaciones de la UNIVERSIDAD NACIONAL DE COLOMBIA for financial support and to El Zafire biological station for logistic support in the field. We are also in debt to the Amazonian indigenous people, especially Ever Kuiru, Miguel Arcangel and Anisley Silva, and our colleagues Omaira Valencia and Diana Sucerquia, who made the field work possible.

References

- Bencke C, Morellato P (2002) Comparação de dois métodos de avaliação da fenología de plantas, sua interpretação representação. Rev Brasil de Bot 25:269–275
- Bradsmith D, Bravo A (2006) Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in *Mauritia* palm swamps. Biodivers Conserv 15:4271–4287
- Cabrera H, Wallace R (2007) Patrones fenológicos de ocho especies de palmeras en el bosque amazónico de Bolivia. Rev Boliv de Ecol y Conserv Ambient 21:1–18
- Clark DA (2007) Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. Biotropica 39:4–19
- Da Silva PA (2009). Orthopsittaca manilata (Boddaert, 1783) (Aves: psittacidae) Abundância e atividade alimentar em relação à frutificação de Mauritia flexuosa L.F. (Arecaceae) numa vereda no triângulo minero. Dissertation, Universidade Federal de Uberlândia
- Ervik F (1993) Notes on the phenology and pollination of the dioecious palms *Mauritia flexuosa* (Calamoideae) and

Aphandra natalia (Phytelephantoideae) in Ecuador. In: Barthlott W, Naumann C, Schmidt-Loske C, Schuchmann K (eds) Animal-plant interactions in tropical environments. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, pp 7–12

- Espinoza JC, Ronchail J, Guyot JL, Cochonneau G, Naziano F, Lavado W, De Oliveira E, Pombosag R, Vauchel P (2009) Spatio-temporal rainfall variability in the Amazon basin countries (Brazil, Peru, Bolivia, Colombia, and Ecuador). Int J Climatol 29:1574–1594
- Espinoza JC, Ronchail J, Guyot JL, Junquas C, Vauchel P, Lavado W, Pombosa R (2011) Climate variability and extreme drought in the upper solimões river (Western Amazon Basin): understanding the exceptional 2010 drought. Geophys Res Lett 38:1–6
- Ferreira LV, Parolin P (2007) Tree phenology in central Amazonian floodplain forests: effects of water level fluctuation and precipitation at community and population level. Pesqui Bot 58:139–156
- Ferreira LV, Stohlgren TJ (1999) Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120:582–587
- Galeano A, Urrego L, Sánchez M, Peñuela CM (2015) On spatio-temporal distribution of natural regeneration of *Mauritia flexuosa* in a community in the southern Colombian Amazonia. Aquat Bot 123:47–53
- Haugaasen T, Peres CA (2005) Tree phenology in adjacent Amazonian flooded and unflooded forests. Biotropica 37:620-630
- Henderson A, Galeano G, Bernal R (1995) Field guide to the palms of the Americas. Princeton University Press, New Jersey, p 352
- Holm JA, Millar CJ, Cropper WP Jr (2008) Population dynamics of the dioecious amazonian palm *Mauritia flexuosa*: simulation analysis of sustainable harvesting. Biotropica 40:550–558
- IDEAM (2010–2012) Datos sistema de información nacional ambiental Leticia, Colombia In: http://www.institucional ideamgovco/jsp/clima49. Accessed 2015
- IDEAM (2011) Análisis del impacto del fenómeno "La Niña" 2010–2011 en la hidroclimatología del país. http://www. ideam.gov.co/documents/21021/418818/An%C3%A1lisis+ Impacto+La+Ni%C3%B1a.pdf. Accessed 2015
- IPCC (2013) Working Group I Contribution To The IPCC fifth assessment report climate change 2013: The Physical Science Basis
- Isaza C, Galeano G, Bernal R (2013) Manejo actual de Mauritia flexuosa para la producción de frutos en el sur de la Amazonia colombiana. In: Lasso CA, Rial A, González-Boscán V (eds) VII Morichales y canangunchales de la Orinoquia y Amazonia: Colombia—Venezuela, 1st edn. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá, pp 243–273
- Junk WJ, Piedade MTF, Lourival R, Wittmann F, Kandus P, Lacerda LD, Bozelli RL, Esteves FA, Nunes Da Cunha C, Maltchik L, Shöngart J, Schaeffer-Novelli Y, Agostinho AA (2013) Brazilian wetlands: their definition, delineation,

and classification for research, sustainable management, and protection. Aquat Conserv 24:5-22

- Khorsand-Rosa RS (2013) Influence of habitat on the reproductive ecology of the amazonian palm, *Mauritia flexuosa*, in Roraima, Brazil. Dissertation, Florida International University. Paper 842. http://www.digitalcommonsfiuedu/ etd/842
- Kubitzki K, Ziburski A (1994) Seed dispersal in floodplain forest of Amazonia. Biotropica 26:30–43
- Laurance WF, Oliveira AA, Laurance SG, Condit R, Nascimento HEM, Sanchez-Thorin AC, Lovejoy TE, Andrade A, D'Angelo S, Ribeiro JE, Dick CW (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. Nature 428:171–174
- Li W, Zhang P, Ye J, Li L, Baker PA (2011) Impact of two different types of El Niño events on the Amazon climate and ecosystem productivity. J Plant Ecol 4:91–99
- Lasso CA, Rial A, Matallana C, Ramírez W, Señaris J, Díaz-Pulido A, Corzo G, Machado-Allison A (eds) (2013) Biodiversidad de la cuenca del Orinoco II Áreas prioritarias para la conservación y uso sostenible. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Ministerio del Ambiente, Vivienda y Desarrollo Territorial, WWF, Colombia, Fundación Omacha, Fundación La Salle de Ciencias Naturales e Instituto de Estudios de la Orinoquia Universidad Nacional de Colombia, Bogotá
- Marengo JA, Tomasella J, Alves L, Soares W, Rodriguez DA (2011) The drought of 2010 in the context of historical droughts in the Amazon Region. Geophys Res Lett 38:1–5
- Marengo JA, Borma LS, Rodríguez DA, Pinho P, Wagner R, Soares WR, Alves LM (2013) Recent extremes of drought and flooding in amazonia: vulnerabilities and human adaptation. Am J Clim Change 2:87–96
- Mendieta-Aguilar G, Pacheco LF, ROLDAN A (2015) Dispersión de semillas de *Mauritia flexuosa* (Arecaceae) por frugívoros terrestres en Laguna Azul, Beni, Bolivia. Acta Amazon 45:45–56
- Newstrom LE, Frankie GW, Baker HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at la selva, Costa Rica. Biotropica 26:141–159
- Nobre C, Obregón GO, Marengo JA, Fu R, Poveda G (2010) Characteristics of amazonian climate: main features. Amazon Glob Chang Geophys Monogr Ser 186:149–162
- Nuñez LA, Carreño J (2013) Biología reproductiva de Mauritia flexuosa en Casanare, Orinoquia colombiana. In: Lasso CA, Rial A, González-Boscán V (eds) VII Morichales y canangunchales de la Orinoquia y Amazonia: Colombia— Venezuela, 1st edn. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá, pp 119–150
- Parolin P, Armbruester N, Wittmann F, Ferreira LV, Piedade MTF, Junk WJ (2002) A review of tree phenology in central Amazonian floodplains. Pesqui Bot 52:195–222
- Parolin P, Lucas C, Piedade MT, Wittmann F (2010) Drought responses of flood-tolerant trees in Amazonian floodplains. Ann Bot 105:129–139
- Phillips OL, Aragão LE, Lewis SL et al (2009) Drought sensitivity of the amazon rainforest. Science 323:1344–1347

- Phillips OL, van der Heijden G, Lewis SL et al (2010) Droughtmortality relationships for tropical forests. New Phytol 187:631–646
- Ponce M (2002) Patrones de Caída de frutos em *Mauritia flexuosa* L.f y fauna involucrada en los procesos de remoción de semillas. Acta Bot Venez 25:119–142
- Poveda G, Mesa OJ (1997) Metodologías de predicción de la hidrología colombiana considerando el evento de El Niño Oscilación del Sur (ENOS). Rev Atmós 17:26–39
- Prance GT (1979) Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31:26–38
- Rodríguez M, Alberico JM, Trujillo F, Jorgenson J (eds) (2006) Libro rojo de los mamíferos de Colombia Serie libros rojos de especies amenazadas de Colombia Conservación Internacional Colombia and Ministerio de Ambiente, Vivienda y Desarrollo Territorial Bogotá, Colombia
- Rubel F, Kottek M (2011) Comments on: the thermal zones of the earth by Wladimir Köppen (1884). Meteorol Z 20:361–365
- Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yasunari T, Chong L, Nakashizuka T (2006) Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. Am J Bot 93:1134–1139
- Sampaio M, Belloni I, Benedetti I (2008) Harvesting effects and population ecology of the buriti palm (*Mauritia flexuosa* L f, Arecaceae) in the Jalapão Region. Cent Braz Econ Bot 62:171–181

- Storti E (1993) Biología floral de *Mauritia flexuosa* L.f na regiao de Manaus, AM, Brasil. Acta Amazon 23:371–381
- Ter Braak CJ, Smilauer P (2002) CANOCO reference manual and CanoDraw for windows user' guide: software for canonical community ordination (ver 45). Microcomputer Power, Ithaca
- Ter Steege H, Pitman NC, Sabatier D et al (2013) Hyperdominance Amazon tree flora Sci 342:325–334
- Tobler MW, Janovec JP, Cornejo F (2010) Frugivory and seed dispersal by the lowland tapir *Tapirus terrestris* in the Peruvian Amazon. Biotropica 42:215–222
- Trujillo JM, González MA, Torres M, Castañeda E (2011) La palma de Moriche (*Mauritia flexuosa* Lf) un ecosistema estratégico. Orinoquia 15:62–70
- Urrego LE (1987) Estudio fenológico preliminar de la fenología de la Canangucha (*Mauritia flexuosa* L F). Colomb Amazón 2:57–81
- Urrego LE (1997) Los bosques inundables en el Medio Caquetá: Caracterización y sucesión Serie estudios en la Amazonia Colombiana. Fundación Tropenbos Colombia XIV, Bogotá
- Williamson GB, Ickes K (2002) Mast fruiting and ENSO cycles—does the cue betray a cause? Oikos 97:459–461
- Xu L, Samanta A, Costa M, Ganguly S, Nemani R, Myneni R (2011) Widespread decline in greenness of amazonian vegetation due to the 2010 drought. Geophys Res Lett 38:1–4