



## Environmental drivers for regeneration of *Mauritia flexuosa* L.f. in Colombian Amazonian swamp forest



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### ABSTRACT

*Mauritia flexuosa* L.f. (swamp forest palm) stands are widely distributed in the poorly drained zones of flood plains and low terraces. They provide several economic and cultural resources for local human communities and play an important ecological role in Amazonia. To identify the main factors involved in the natural regeneration dynamics of *M. flexuosa*, we surveyed the recruitment, mortality, and survival rates of seedlings from June 2010 to November 2012 on a 1-ha plot in a flooded forest area of Colombian Amazonia. The recorded mortality and recruitment rates of *M. flexuosa* were higher compared to its survival rates over time. These three parameters, included in a CCA, were positively correlated to the basal area (BA) of *M. flexuosa* adults. The CCA the first two axes explained 88% of data variance. While recruitment was positively related to flooding levels, mortality was positively related to basal area of species other than *M. flexuosa* and to the lowest organic matter percentages in the topsoil. In a PCA first two axes explained 57% of variance and showed positive correlation of both basal area and seedling abundance of *M. flexuosa* to soil organic matter content, and to poorly drained soils. Pore water pH and percentages of sand and clay increased with improved soil drainage conditions.

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### 1. Introduction

*Mauritia flexuosa* L.f. (swamp forest palm) stands are widely distributed in the poorly drained zones of flood plains and lower terraces in Amazonian alluvial valleys that extend across Colombia and Venezuela, toward São Paulo and Mato Grosso states in Brazil (Henderson, 1995). *M. flexuosa* is a highly dominant species in the Amazonia region (Ter Steege et al., 2013). *M. flexuosa* stands are characterised by notably acidic organic soils (Histosols) with permanent or seasonal flooding (Kahn, 1988; Urrego, 1997; Oliveira et al., 2007; Junk et al., 2013). Such soils occur in both várzea and igapó type forests (Sioli, 1975; Urrego, 1987). While várzea forests grow on alluvial plains flooded by Andean white water rivers, with a pH between 6.9 and 7.4, igapó forests are flooded by Amazonian black and clear water rivers, with a pH between 4.6 and 5.2 (Prance, 1979; Prance, 1979). Differences in soil pH between these forests are related to the percentage of organic matter and nutrient availability in the soils, the latter being higher in várzea forests (Prance, 1979; Revilla, 1990; Wittmann et al., 2004).

Vegetation structure, diversity and floristic composition of *Mauritia* stands vary according to the spatial heterogeneity derived from the interaction of physical and biological features at a regional scale (Hutchings et al., 2003), especially fluvial dynamics (Salo et al., 1986). For instance, *M. flexuosa* dominated stands located in the Orinoquia region grow in permanent or seasonally flooded savannahs, and are characterized by a dense herbaceous layer and few species in the understory. In contrast, *M. flexuosa* stands located in Amazonia grow in permanent or seasonally flooded basins, and have a richer mix of canopy and understory tree species (Urrego et al., 2013; Urrego et al., 2013).

The natural regeneration dynamics of plants play an important role in maintaining the diversity of flooded forests (Cintra and Horna, 1997). The recruitment of seedlings and species distribution in flooding forests are determined by local physical conditions, such as geomorphology, sedimentation rates, distance from river beds, as well as soil texture, drainage, nutrient, and organic matter accumulation. However, they are also influenced by proximate biological factors such as forest canopy structure (light availability), successional state, the adjacent terra firme vegetation composition and inter and/or intra-specific competence (De Granville, 1974; Urrego, 1997; Ponge et al., 1998; Wittmann and Junk, 2003; Farris-Lopez et al., 2004; Turner, 2004; Wittmann et al., 2004; Budke et al., 2008). The size of the tree population and seedling and sapling establishment are also affected by rain seasonality and extreme flooding

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pulses that are heavily influenced by the El Niño Southern Oscillation (ENSO) cycle (Schöngart and Junk, 2007). Thus, these factors represent the most important ultimate influences on the physical settings of these forests (Prance, 1979; Urrego, 1997; Schöngart and Junk, 2007). In fact, the highest seedling establishment takes place at the beginning of the dry season (Parolin et al., 2004).

*M. flexuosa* stands are estimated to represent a very important carbon sink among Amazonian forest stands (Gonzalez and Rial, 2011). These stands provide valuable commercial and cultural resources for local human communities (Holm et al., 2008). The ecological importance of *M. flexuosa* is due to its ability to colonise flooded and poorly drained soils (Gonzalez and Rial, 2011); however, this characteristic may increase the vulnerability of *M. flexuosa* stands to environmental alterations associated with climate change (Colinvaux et al., 1996; Rull, 1998; Mayle et al., 2000). Predicted increases in flood levels and frequency (IPCC, 2014) may prolong soil anoxic conditions, and increase seedling mortality and sedimentation rates on alluvial valleys which in turn may alter local geomorphology by creating new available sites colonization of other species and change forest composition. This study aimed to answer the following questions: (1) does the natural regeneration distribution of *M. flexuosa* occur homogeneously at small spatial and short temporal scales? and (2) which biotic and abiotic factors influence this distribution? We postulate as a hypothesis that the natural regeneration distribution pattern of *M. flexuosa* is influenced by rain seasonality in combination with locally heterogeneous conditions, such as drainage, flooding levels and slope, which allow terra firme forest species to establish on better-drained sites and displace *M. flexuosa* seedlings.

## 2. Methods

### 2.1. Study area

This study was carried out in an igapó forest dominated by *M. flexuosa*. The site was positioned on a poorly drained low terrace near the transition to terra firme forests (3°56'48.89"S and 69°53'1.83"W) in the black water Calderón river basin, 28 km away from Leticia city in the Colombian Amazonia. Mean annual precipitation in the zone is 3335 mm, and the area is classified as tropical rain forest (Af) in the Köppen climate classification (Rubel and Kotttek, 2011). The rainy season extends from November to May with maximum precipitation occurring in April. The dry season extends from June to October, with the driest period occurring in August. The mean annual temperature is 26 °C (15–36 °C), and the mean relative humidity is higher than 90% (IDEAM, 2010–2012; IDEAM, 2010–2012). The prevalent El Niño conditions in 2010 left the well-drained areas of the 1-ha plot without flooding, whereas the La Niña conditions that occurred in 2011–2012 (NOAA, 2013) generated minimum flooding levels of 4 cm throughout the plot. The site is flooded by the Calderón river and some of its tributaries during the rainy season. The Calderon valley is narrow and elongated with a multiannual average flow rate of 324 m<sup>3</sup> s<sup>-1</sup> (Hoyos et al., 2005).

### 2.2. Sampling

A 1-ha rectangular plot (250 × 40 m<sup>2</sup>) was subdivided into 100 sub-plots of 100 m<sup>2</sup> (10 × 10 m<sup>2</sup>). In these sub-plots, the diameter at breast height (DBH) and the total height of all trees with DBH ≥ 10 cm were measured and labelled. The botanical identification of all collected specimens was performed at the herbarium of the National University in Medellín (MEDEL) and in the Amazonian Herbarium (COAH). The importance of the identified species was ranked based on the calculation of the importance value index (IVI) (Curtis and McIntosh, 1951). Species diversity and dominance

were calculated by the Fisher and Simpson diversity indexes (Krebs, 1999), respectively. The occupation index (OI) of *M. flexuosa* was calculated as the proportion of the 1-ha plot area occupied by the basal area (BA) of adult plants of this species.

In the field, a soil sample was collected from each 100 m<sup>2</sup> subplot to determine soil granulometry and organic matter content. In each subplot, we measured the slope with a clinometer and pore water pH with a multi-parameter portable meter (Hanna-HI9811-5). The water table depth and flooding levels were measured using PVC tubes buried in the ground; the zero value was located at the forest floor level. The drainage conditions were established according to the categorical classification (1–5) of the FAO (1977), where the lowest value (1) corresponds to the poorest drainage conditions. In the laboratory, the Bouyoucus and acid–base titration methods were used to determine soil texture and organic matter content, respectively (Jaramillo, 2011). Differences among the environmental variables of the sub-plots were established through ANOVA using Statgraphics Centurion XVI.

To quantify recruitment in each subplot, all seedlings smaller than 1 m of height were measured and counted in four semi-annual periods between June 2010 and November 2012. The finite survival rate of *M. flexuosa* was calculated for each subplot and semi-annual period as the proportion of live seedlings at the end of each period relative to the number of live seedlings at the beginning of this period. The mortality rate was calculated by subtracting the finite survival rate from 1. The finite recruitment rate is the number of new seedling recorded in each semi-annual period (Krebs, 1999). In each semi-annual period, environmental variables were also measured. The abundance of seedlings of other species was measured in a smaller sample (57 subplots).

Relationship among canopy structure, *M. flexuosa* natural regeneration dynamics and environmental variables was established through canonical correspondence analysis (CCA) using CANOCO 4.5 (Ter Braak and Smilauer, 1998). A principal component analysis (PCA) was used to identify the relationship between the physical soil conditions and the basal area of adult palms, and the number of seedlings of *M. flexuosa*. These analyses were carried out with software R 3.0.1. (R development Core Team, 2014). To explore sedimentation rates that influenced the soil and vegetation in the 1-ha plot, two sediment cores were extracted from drainage sites with contrasting conditions (subplots 8–58). Sedimentation rates were calculated based on a time scale obtained from measurements of <sup>210</sup>Pb decay method in 12 samples extracted from the first 100 cm of the top of each soil core. The analysis was conducted by Mycore Scientific Inc., Canada.

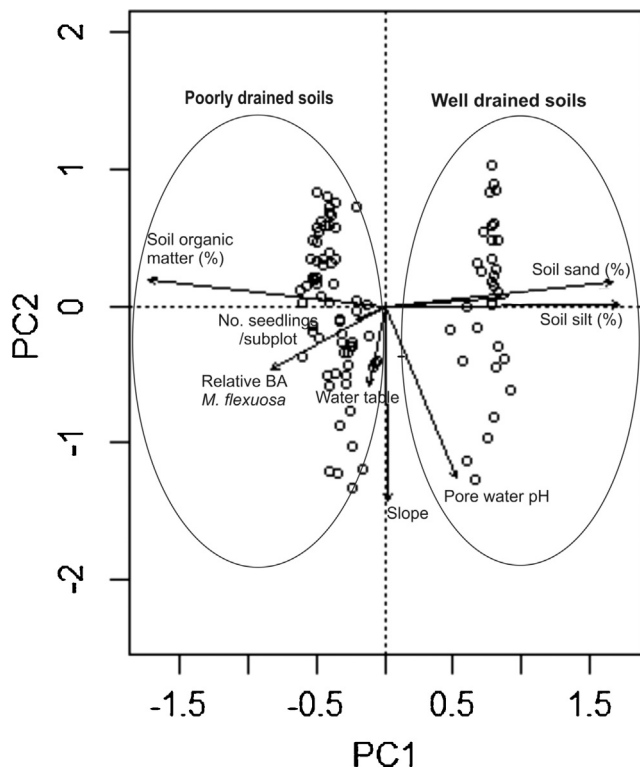
## 3. Results

### 3.1. Vegetation structure and floristic composition

In the 1-ha plot, 735 *M. flexuosa* individuals with DBH > 10 cm and 162 tree species were recorded. The most important species was *M. flexuosa* (IVI = 82%) (A.1). The second most important species was *Sacoglottis amazonica* Mart., a terra firme forests species, followed by certain palms that are able to grow in both environments, such as *Euterpe precatória* Mart., *Socratea exorrhiza* (Mart.) H. Wendl. and *Oenocarpus bataua* Mart. While the total BA was 31 m<sup>2</sup> ha<sup>-1</sup>, that of *M. flexuosa* was 14 m<sup>2</sup> ha<sup>-1</sup>. The OI of *M. flexuosa* was 0.45, while that of all other species was 0.48. The diversity was 100 based on the Alpha Fisher index, while the Simpson dominance index was 0.08.

### 3.2. Environmental features

In the PCA the subplots were classified in two groups according to drainage conditions. The first group gathered subplots on



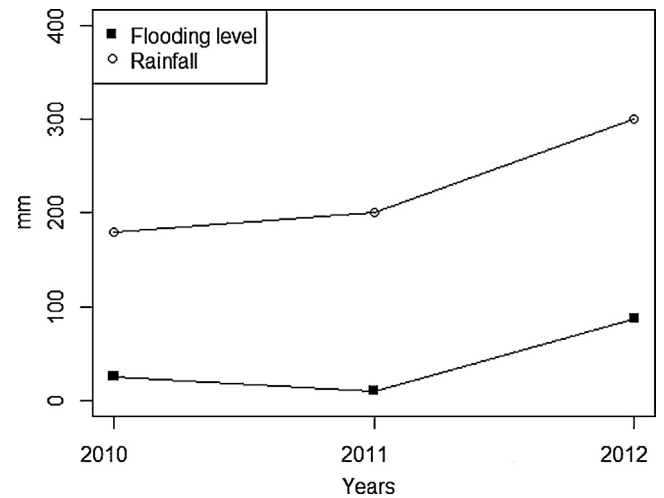
**Fig. 1.** Principal component analysis (PCA) diagram. The biplot shows the first two ordination axes. Vectors indicate both biological and physical variables measured in the 10 m<sup>2</sup> subplots. Biological variables measured in each subplot: basal area of adult palms (BA). Number of seedlings of *M. flexuosa*. Physical variables measured in each subplot: content of sand, silt and organic matter in the soils, water table, slope and pore water pH. Circles represent the 10 m<sup>2</sup> subplots ordered by drainage conditions within 1 ha plot.

poorly drained soils and the second the subplots on moderately well drained soils. While the high soil organic matter content, water table, and both BA and seedling abundance of *M. flexuosa* were associated to poorly drained soils, the pore water pH and percentage of sand and clay increased with improved drainage conditions. The first two axes of the PCA with eigen-values of 0.4–0.1, respectively, explain 57% of data variance (Fig. 1). A total of 77% of the subplots were termed “swamps” and were characterized by slopes <5%, organic soils (OM > 15%), and had low interstitial water pH (4.0), poor to imperfect drainage and flooding levels between 0 and 6 cm (A.2). The remaining 23% of the subplots were located on slopes between 5% and 15%, mineral rich soils (clayey to silty clay soils), higher pore water pH values (4.6) and low flooding levels.

In addition, flooding levels showed a direct relationship with the distribution of seasonal precipitation; in 2010, precipitation and flooding levels reached intermediate levels when compared to the subsequent two years. In 2011, the lowest precipitation and flooding levels were recorded during the dry season. In contrast, in 2012, both parameters increased synchronically, reaching the highest levels during the rainy season (Fig. 2). A number of subplots, especially those located on the transition between poor to moderately drained soils, were only flooded when precipitation and river flooding were at the highest levels in 2012.

### 3.3. Natural regeneration of *M. flexuosa*

Natural regeneration in the swamps was dominated by *M. flexuosa* seedlings. In contrast, natural regeneration in well drained areas was dominated by other species, such as *Calathea striata* H. A. Kenn., *Adiantum latifolium* Lam. and *Lepidocaryum tenue* Mart.



**Fig. 2.** Changes in mean monthly precipitation and mean monthly flooding levels between 2010 and 2012 in the Calderon river basin.

Significant differences were recorded for mortality ( $F_{2,297} = 13.44$ ,  $P$ -value < 0.0001), recruitment ( $F_{2,297} = 26.07$ ,  $P$ -value < 0.000) and survival ( $F_{2,297} = 22.12$ ,  $P$ -value < 0.00002) among the three measurement periods (Fig. 3). Mortality rates were higher than survival rates in the three semi-annual measurements. The highest seedling recruitment was recorded in February 2012, after a season (July 2011) with notably high fruit production (Toro, 2014).

### 3.4. Relationship among natural regeneration, forest structure and the environment

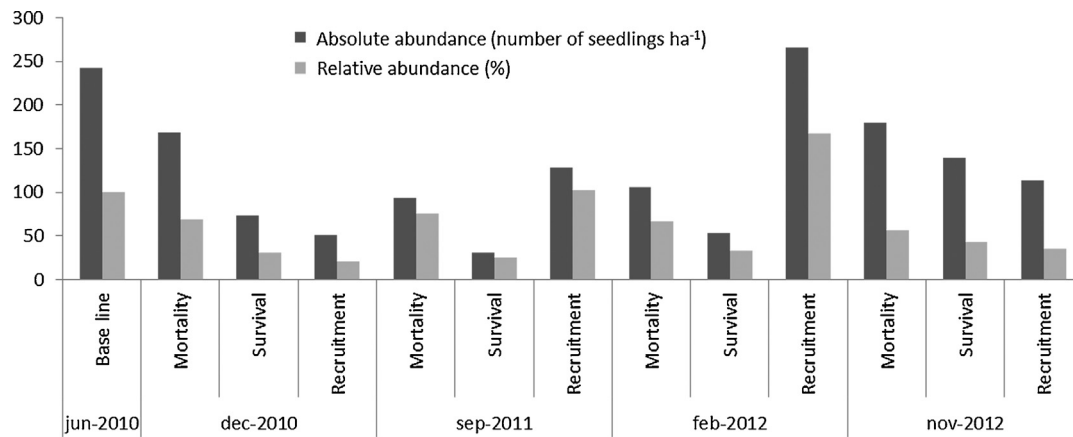
The first two axes of the CCA had eigen-values of 0.49–0.17, and explained 88% of the data variation (Fig. 4). Seedling mortality of *M. flexuosa* was negatively related to the percentage of organic matter in the soil, the BA and the height of other tree species. In contrast, *M. flexuosa* recruitment was positively related to flooding levels and pore water pH, but negatively related to drainage conditions and the height of *M. flexuosa* in the canopy. Survival rates were negatively correlated to drainage conditions; it means that survival was lower in drier soils.

The sedimentation rates recorded in the sampled cores (Fig. 5) showed no statistically significant differences. However, the curves of the sedimentation rates were not synchronous with one another. In the first four decades of the previous century, sedimentation rates reached approximately 0.4 cm yr<sup>-1</sup> in both cores, and increased synchronously until 1960. However, between 1960 and 1990, the sedimentation rates of the two cores exhibited opposite trends; sedimentation rates decreased towards the poorly drained site, but increased in the transition to moderately drained sites. From 1990 to present day, the trends at the two sites were again inverted.

## 4. Discussion

### 4.1. Structure, composition and neighbouring vegetation

The *M. flexuosa* forests studied here showed higher diversity compared to similar forest types (Freitas, 1996; Urrego, 1997; Wittmann et al., 2013). This may be due to our location near the transition from poorly drained terraces to terra firme forests. In addition, the alternation of contrasting slopes, along with the texture and drainage conditions of the soils, are also responsible for the patchy distribution of species from both well- and poorly drained forests at small spatial scales, and, hence, high alpha and

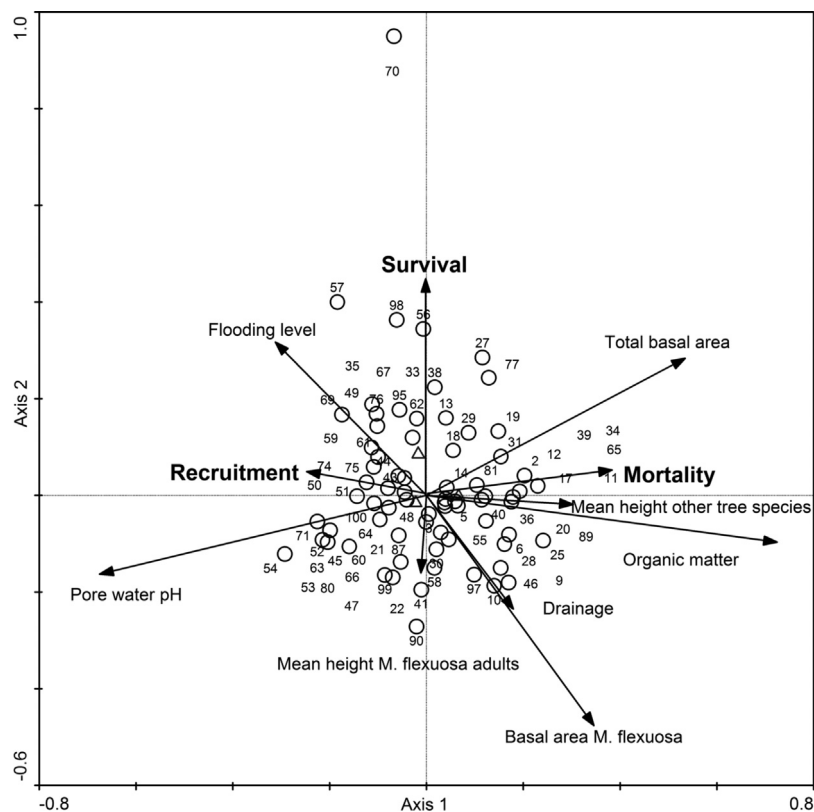


**Fig. 3.** Changes in mortality, recruitment and survival of *M. flexuosa* seedlings between 2010 and 2012. The finite survival rate of *M. flexuosa* for each subplot and semi-annual period was calculated as the proportion of live seedlings at the end of each period relative to the number of live seedlings at the beginning of this period. The mortality rate was calculated by subtracting the finite survival rate from 1. The finite recruitment rate is the number of new seedling recorded in each semi-annual period (Krebs, 1999).

beta diversity (Wittmann et al., 2002). The low relative abundance of *M. flexuosa* (25%) in the 1-ha plot supports of the hypothesized competition from other plant species of well-drained forests found on non-flooded sites (e.g. *S. amazonica*, *L. tenue* and *C. striata*). These plants contribute to the high species richness recorded in these swamps (Freitas, 1996; Urrego, 1997; Wittmann et al., 2004, 2006; Teixeira and Assis, 2005). The ecotonal location of these forests also explains the higher Alpha Fisher index values that were recorded when compared with an igapó forest dominated by *M. flexuosa* in the Colombian Caquetá region (Urrego, 1997). However, the obtained values were lower compared to those recorded in seasonally flooded forests by white water rivers (várzeas), which

are also located closer to terra firme forests in the Brazilian Amazonia (*sensu* Wittmann et al., 2004) (Table 1). Our results confirm the influence of geomorphologic location and flooding frequency on the diversity and floristic composition of *M. flexuosa* forests.

The positive correlation between seedling density and BA of *M. flexuosa* adults indicates that the spatial heterogeneity of the soils and the floristic composition of the canopy strongly influence the natural regeneration of this species, as documented for other gregarious palm populations (Svenning, 1999). However, both factors are closely related to seasonal and inter-annual variability in precipitation, flooding levels, and drainage conditions, which, in turn, affect seedling establishment at these sites (Kubitzki, 1989; Gurnell,



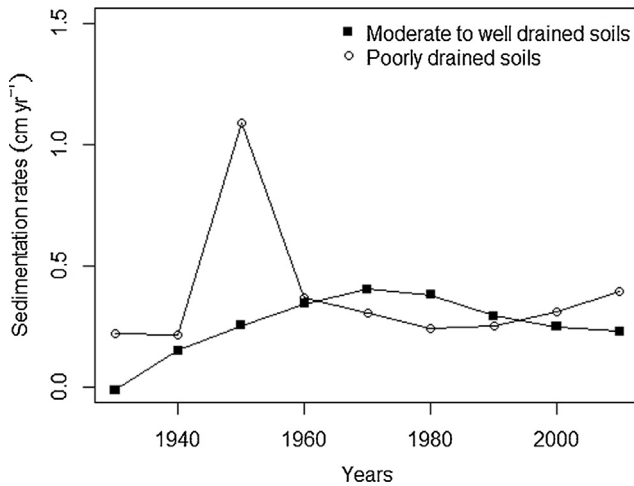
**Fig. 4.** CCA ordination biplot of the structural parameters in the 1-ha plot of *M. flexuosa* forest (mean total height of *M. flexuosa*; mean total height tree species other than *M. flexuosa*; basal area of *M. flexuosa*; total basal area of tree species other than *M. flexuosa*), environmental variables (organic matter content in the soil, drainage conditions, flooding levels and pore water pH) and natural regeneration parameters of *M. flexuosa* seedlings (mortality, recruitment and survival).



**Table 1**

Comparison of Alfa Fisher's index values of flooded forests growing on different landscapes. BDLT (bad drained low terrace), HV (high varzea), LV (low varzea).

Reference	Landscape	Mean annual flood levels (m)	Area	Minimum DBH	No. of trees	No. of species	Fisher	Fisher's (1000 ind)
Wittmann et al., 2004	LV	7	1 ha	10	498	43	11.32	22.74
Urrego, 1997	LV	7	1 ha	10	1074	172	72.48	67.49
Wittmann and Parolin, 2005	LV	6.5	1 ha	10	434	91	34.78	80.13
Wittmann et al., 2002	HV	3	1 ha	10	469	177	134.6	286.98
Urrego, 1997	BDLT	7.5	1 ha	10	940	75	100.07	106.45
This study	BDLT	1.2	1 ha	10	735	162	100.12	136.22
Freitas, 1996	BDLT	NA	1 ha	10	580	158	108.75	187.5

**Fig. 5.** Sedimentation rates of the two sediment cores based on a time scale obtained with the <sup>210</sup>Pb decay method.

1997; Wittmann et al., 2010; Teixeira et al., 2011). For instance, at the well-drained subplots in our 1-ha plot (i.e. without permanent inundation), *M. flexuosa* seedlings were not found. Instead, *C. striata*, *A. latifolium* and *L. tenue*, which usually grow in terra firme soils, dominated the seedling community. Thus, we postulate that the flooding duration and frequency, which are closely associated with seasonal precipitation distribution and geomorphology, are the most important factors that regulate the distribution, richness and diversity of várzea and igapó forests (Wittmann et al., 2004). The high environmental variability of this region generates high diversity, because more plant niches are available.

#### 4.2. *M. flexuosa* natural regeneration dynamics

In our 1-ha plot, the highest density-dependent recruitment and survival rates of *M. flexuosa* seedlings were recorded on the most poorly drained sites, where the highest flooding levels and highest BA of *M. flexuosa* adults were also recorded. In fact, the topography, drainage conditions and BA of the adult tree population are recognised as the main drivers of seedling survival and recruitment in tropical forests (Metz, 2012; Lin et al., 2012). In contrast, the highest *M. flexuosa* seedling mortality occurred on the best-drained and least flooded areas of the plot, where the richness of terra firme forest species was the highest (Kalliola et al., 1991; Wittmann and Junk, 2003; Wittmann et al., 2004).

The ability of *M. flexuosa* to survive in anoxic soil conditions, which are typical of poorly drained and highly flooded sites, makes it one of the most successful competitor species in Amazonian flooded forests (Wittman and Junk, 2003; Piedade et al., 2010; Junk et al., 2013; Ter Steege et al., 2013). In fact, in areas where *M. flexuosa* was dominant among both the seedling population and adult palms, the highest soil organic matter content and lowest pore water pH were recorded, as a result of low plant

decomposition rates. In both, seedlings and adults, this species has several mechanisms to facilitate that establishment and survival. For instance, pneumatophores facilitate root respiration in adult palms (De Granville, 1974). In addition, seedling establishment is facilitated by hydrochorious and barochorous seed dispersal to flooded sites, with the degree of competition with plants from well-drained forests that are not adapted to these soil conditions being low. Nevertheless, seedling establishment is negatively affected by seed consumption, especially by peccaries that are considered the major consumers of *M. flexuosa* seeds (Antonik, 2005; Parolin et al., 2013).

Local environmental variability in the level, frequency and duration of flooding are related to regional inter-annual precipitation fluctuations and the global frequency of ENSO (Schöngart and Junk, 2007). These factors, combined with local drainage conditions (Marinho et al., 2010), affect natural regeneration patterns and plant population dynamics (Kubitzki, 1989; Gurnell, 1997). These ENSO anomalies might also explain the contrast in the sedimentation rates between the two sampled cores. During El Niño prevalent conditions (2010), the moderately to well-drained sites of the 1-ha plot were not flooded, nor were sediments deposited. In contrast, the poorly to negligibly drained sites were flooded by river water and sediments. However, during La Niña conditions (February 2012), the entire plot was flooded, and sediments were deposited across the entire 1-ha plot, regardless of drainage conditions. The current change in climate is altering precipitation patterns in Amazonia by primarily increasing the mean annual precipitation and ENSO intensity (IPCC, 2013). Thus, climate change might also increase flooding levels and river overflows; consequently causing changes to the geomorphology, alluvial sedimentation rates and diminution in the thickness of the organic matter layer in the soils, in addition to causing shifts in vegetation composition and structure towards a terra firme forest dominated by successional species, as proposed for other wetlands (Wittmann et al., 2006, 2010; Teixeira et al., 2011).

In 2010, *M. flexuosa* mortality rates exceeded recruitment and survival rates, and were associated with low levels of precipitation and flooding. In contrast, the high flooding levels recorded in the two subsequent years (2011–2012) favoured *M. flexuosa* seedling recruitment, even in well-drained areas where this species is usually a poor competitor. Yet flooding levels and spatial variability alone do not explain the differences obtained among semi-annual measurements, because biological interactions also play an important role in mortality, recruitment and survival. The highest recruitment of *M. flexuosa* occurred in 2012, following high fruit production recorded in 2011 (Toro, 2014). However, high mortality was also recorded during the same period for seedlings that grew under parental palms, which may be related to fronds that fall on them, as documented by Peters et al. (2004). Ponce et al. (1996) also found that *M. flexuosa* seedling mortality is associated with herbivory, and accidental death. In addition, we suggest that inter-specific competition is important for *M. flexuosa* seedling survival: the dominance of terra firme forest species diminishes *M. flexuosa* seedling survival on well-drained subplots.

The results of this study indicate that the natural regeneration dynamics of *M. flexuosa* forests is regulated by environmental gradients that operate at different temporal and spatial scales. In addition, regeneration of this species is influenced by the interaction of various abiotic and biotic factors, such as micro-topography, drainage conditions, precipitation seasonality and forest structure and composition, as recorded for other flooded forests (Vormisto et al., 2004; Costa et al., 2009; Albernaz et al., 2012). In summary, the variability in time and space not only of biotic (i.e. interspecific competition) but also of environmental drivers (i.e. flood and water table levels, drainage conditions and organic matter content in the soils) can strongly affect the natural regeneration pattern of *M. flexuosa*.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [10.1016/j.aquabot.2015.02.001](https://doi.org/10.1016/j.aquabot.2015.02.001).

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