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ORIGINAL ARTICLE

Volume increment modeling and subsidies for the management of the tree *Mora paraensis* (Ducke) Ducke based on the study of growth rings

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Abstract

Key message **First study that demonstrated the formation of annual growth rings in Amazonian Estuary trees. Growth patterns of *Mora paraensis* and specific management criteria, such as felling cycle, are presented.**

Abstract The aim of the present study was to contribute to increased sustainability in the timber management of *Mora paraensis*, through the estimation of minimum logging diameter (MLD) and felling cycle, using volume increment models based on tree-ring analysis and allometric relationships. We collected stem discs from 17 trees of five diameter classes. The diameters and heights of the trees were also measured. We estimated tree ages by ring-counting and the radial increment rates by measuring the ring widths with a digital analysis system. We built growth models based on relationships between age, diameter and tree height to estimate volume increment along the tree's whole life cycle. The maximum current diameter increment in *M. paraensis* occurs at an age of around 26 years, reaching 4.91 mm year-1. The MLD was 46.4 ± 0.6 cm (standard error), which trees achieve at an age of about 115 years. The felling cycle, estimated by the mean passage time through 10 cm diameter classes until achieving the MLD, was 24.7 ± 1.3 years. These results corroborated the norms of the current Brazilian legislation that regulates forest management of high intensity in the Amazon basin. In future, more specific growth models are needed for other commercial tree species in the Amazonian Estuary to define the optimal harvest rate to maintain sustainable timber resource management practices. Through such practices, the conservation of these ecosystems and their multiple services and functions, as well as the welfare of the forest-dependent human populations can be secured.

Keywords Floodplain forests · Várzea · Pracuúba · Tree rings · Minimum logging diameter · Felling cycle

Introduction

The occurrence of annual growth rings in the tropics was denied for a long time, and as such studies applying tree-ring analyses in tropical regions are not as common as in temperate regions (Lieberman et al. 1985). However, several studies have shown evidence of the formation of annual growth rings in tropical trees (Worbes 2002; Rozendaal and; Zuidema 2011; Zuidema et al. 2012) that are formed when tropical trees pass through a period of cambium dormancy during the year, which occurs due to unfavorable environmental growth conditions such as annual inundations in nutrient-rich white-water floodplain forests (*várzea*) resulting in anoxic conditions in the soil (Schöngart et al. 2002). Several studies have described annual tree rings in species occurring in the floodplains of the Amazon and Orinoco

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river systems (Worbes 1985, 1989; Dezzeo et al. 2003; Schöngart et al. 2002, 2004, 2005).

The analysis of tree-ring series is important for the estimation of tree age and the characterization of growth patterns along the entire life span, in turn improving the understanding of forest dynamics and thus helping to develop adequate forest management systems (Brienen and Zuidema 2006, 2007; Schöngart et al. 2007; Rosa et al. 2017). The estimates of timber production which consider the between-species and between-environment variations in tree growth are needed to ensure the continuous supply from, and maintenance of, natural forest management systems (Brienen and Zuidema 2007; Schöngart 2008). This is particularly important in the Amazonian *várzea* floodplains, where logging activities are concentrated on just a few commercial tree species (Schöngart and Queiroz 2010).

The *várzeas* of the Amazon Estuary have been managed for over 300 years and timber exploitation is part of a diverse livelihood strategy that often includes cropping, fishing, hunting and production of palm fruits (*Euterpe oleracea*) (Fortini and Zarin 2011; Fortini and Carter 2014). Timber exploitation in the floodplain forests of the Amazonian Estuary is mainly focused on the supply of timber for local and regional markets, with timber used largely for construction purposes. *Mora paraensis* (Ducke) Ducke (popular name: *pracuúba*) is considered to be endemic to the estuarine floodplains of the Amazon (Wittmann et al. 2013), presenting a high dominance in this ecosystem (Queiroz et al. 2005; Carim et al. 2008; Lima et al. 2014). The species stands out among other commercial tree species in the region due to its high timber stocks of up to 40 m^3 ha^{-1} of commercial volume (Lima et al. 2014) and its high wood density of about 0.90–1.00 g cm^{-3} (Silva 2002). This drives high demands for the timber of this species in regional markets. As such, there is an urgent need to understand whether existing norms surrounding exploitation of this species defined by Brazilian forest legislation meet the biological reality of its growth potential. Data on tree ages and growth patterns, and subsequent growth modeling, allow for the development of species-specific management criteria. In this study, we show that *M. paraensis* forms annual tree ring by cambial wounding. In the next step, we analyze tree ring series of 17 trees from different diameter classes to model tree growth in diameter, height and volume, to define a specific felling cycle and minimum logging diameter (MLD).

Materials and methods

Study area

The study was carried out in Mazagão, in the state of Amapá, northern Brazil (0°13′00′ S, 51°26′00″ W), in areas of the FLORESTAM Project (Ecology and forest management for multiple use of floodplains in the Estuary of the Amazon River), coordinated by Embrapa Amapá. Mean annual temperature is around 27 °C and average daily temperature varies by less than 3 °C during the year. Mean annual precipitation is 2550 mm and occurs mainly in the wet season from January to May. This part of the Amazon Estuary is characterized by a tidal fluctuation of about 2–3 m, driven by the Atlantic Ocean. Because of the elevated river level during the wet season, the forests are inundated twice a day during high tides (Fortini and Carter 2014). The typical soils are Gleysols, with a predominance of silty texture and high fertility (Santos and Tardin 2003). The vegetation is classified as alluvial rainforest or tidal floodplain forest, locally known as *várzea* (ZEE 2000; Junk et al. 2011). According to a more recent classification, the typology of the vegetation of these flooded forests can be considered an alluvial dense rainforest (IBGE 2012).

Data collection and analysis

To confirm growth patterns and annual ring formation for this species, in the period from August to September 2010, secondary cambium was wounded at breast height on four trees of *M. paraensis* using squares of approximately 3 cm in size (Mariaux 1967; Sousa 2011). In October 2013, the trees were felled and their discs were sampled to test whether the rings formed after wounding corresponded to 3 years of tree growth. The discs were polished and the rings were marked and measured along the eight radii where rings could be best visualized. At each radius, we measured the increment rates after the scar of cambial wounding corresponding to the 3-year period. We compared these measured increment rates with the values obtained from the growth model in the present study, for the past 3 years before the corresponding age of each tree.

We collected 17 trees of *M. paraensis* using stratified sampling at five different classes of diameter at breast height (DBH): (1) $15 < \mathrm{DBH} < 20$ cm, (2) $25 < \mathrm{DBH} < 30$ cm, (3) $35 < \mathrm{DBH} < 40$ cm, (4) $45 < \mathrm{DBH} < 50$ cm, and (5) $\mathrm{DBH} > 55$ cm (Table 1). Diameters were derived from the circumference at breast height (CBH), measured at 1.30 m above the ground, using a measuring tape with a precision of 1 mm, dividing CBH by Pi. We also used the measuring tape to obtain commercial and total tree height of all individuals after felling. To estimate tree age, we used stem discs (cross-section of the trunk) collected at the height at which CBH was measured. The samples were transported to the laboratory at Embrapa Amapá, and after drying polished with sandpaper with progressive grit sizes up to 600. For the anatomical characterization of the growth rings, we used the ring patterns described by (Coster 1927), adapted by Worbes (1989, 2002).

Table 1 Diameter and height of the 17 *Mora paraensis* trees harvested for the analysis of growth rings in the estuary of the Amazon River, northern Brazil

Tree	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Classes	1	1	1	1	2	2	2	3	3	3	3	3	4	4	5	5	5
DBH (cm)	17.2	18.5	19.9	17.8	27.4	25.8	26.4	38.8	36.9	34.7	36.6	39.5	45.5	47.2	63.7	64.3	57.3
Commercial height (m)	8.0	6.0	4.0	10.0	8.0	10.0	8.7	11.6	14.5	18.2	17.0	18.0	16.0	14.5	15.0	14.0	16.0
Total height (m)	18	20	15	23	23	22	22	22	23	25	30	30	28	28	30	30	28

We estimated ages for the 17 trees through direct ring-counting and measured ring width using a digital analysis system with precision of 0.01 mm (LINTAB, Rinntech, Germany) supported by the software TSAP-Win (Time Series Analyses and Presentation, Rinntech, Germany), to produce the individual time series of radial growth (Schöngart et al. 2005).

We calculated current diameter increments and used them to build cumulative diameter growth curves for each individual, which were adjusted to the measured DBH (Brienen and Zuidema 2007; Schöngart 2008). The age–diameter relationship based on 17 curves was adjusted by a sigmoidal regression model (Schöngart et al. 2007), which describes the biological phases of juvenile, mature and senescent growth:

$$\mathrm{DBH} = \left(\frac{a}{1 + \left(\frac{b}{\mathrm{age}}\right)^{c}}\right), \tag{1}$$

where DBH is the diameter at 1.30 m from the ground (cm) and *a, b*, and *c* are the parameters obtained from the adjustment of the sigmoidal regression considering standard errors.

To describe the relationship between DBH and height, we applied a non-linear regression model (Nebel 2001; Nebel et al. 2001; Schöngart et al. 2007),

$$H = \left(\frac{\mathrm{DBH} \times a}{\mathrm{DBH} + b}\right), \tag{2}$$

where *H* is the total height (m), and *a* and *b* are parameters generated in the non-linear regression analysis with indicated standard errors.

We used the cumulative growth in diameter and height to calculate the annual current and mean increment rates at each age by the equations,

$$CAI = CGr_{(t+1)} - CGr_{(t)}, \tag{3}$$

$$MAI = \frac{CGr_{(t)}}{t}, \tag{4}$$

where CAI is the current annual increment, MAI is the mean annual increment and CGr is the cumulative growth in different years *t* along the total life cycle of the plant.

We estimated volume growth for each age using the allometric equation by Cannell (1984), as there are no specific allometric models available for *M. paraensis*,

$$V = \left[\pi \times \left(\frac{\mathrm{DBH}}{2}\right)^2 \times H \times 0.6\right], \tag{5}$$

where *V* is the volume (in m^3), DBH is the diameter at breast height (in cm), and *H* is the total tree height (in m).

The annual rates of current and mean volume increment during the plant lifetime can be derived from the cumulative volume growth, by applying Eqs. (3) and (4).

Based on the Growth-Oriented Logging (GOL) concept, the volume growth model forms the basis of specific management criteria for commercial tree species' through the estimation of minimum logging diameters and felling cycles (Schöngart 2008). CAI defines the growth in volume over a 1-year period, and MAI refers to the average growth per year that a tree or group of trees have shown, up to a specified age. The CAI curve reaches its maximum before the MAI curve, and these two curves intersect at the maximum MAI point. Harvesting before the maximum CAI age is an unsustainable practice, whereas harvesting after maximum MAI means that the trees have already passed the economically optimum rotation age. Thus, the period between the maximum CAI and the maximum MAI of volume growth represents the optimal interval for harvesting the tree to take advantage of the growth potential without depleting the resource (timber). The ideal minimum logging diameter (MLD) for the species was obtained by the diameter at maximum CAI in volume growth using the age–diameter relationship (Schöngart 2008). The felling cycle (FC) which represents the mean time through 10-cm diameter classes until reaching the specific MLD was calculated using Eq. (6) (Schöngart et al. 2007),

$$\mathrm{FC} = \frac{\mathrm{age}_{(\mathrm{MDH})}}{\mathrm{MDL} \times 0.1}, \tag{6}$$

where FC is the felling cycle of the species and age$_{(\mathrm{MLD})}$ is the age of the tree when it reached the MLD.

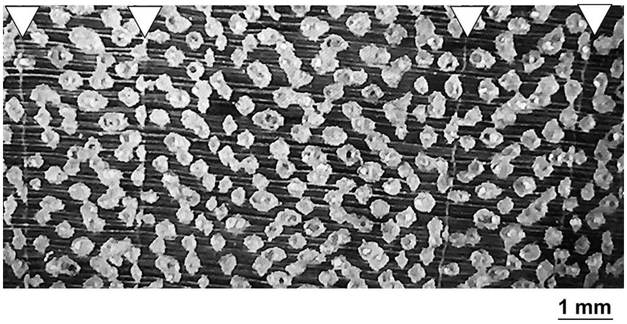

Fig. 1 Anatomical wood structure of tree rings of *M. paraensis* (Fabaceae) growing in the floodplains of the Estuary of the Amazon River, northern Brazil. Growth rings are limited by marginal parenchyma bands, which are indicated by arrows

Results

Growth rings of *M. paraensis* were delimited by marginal parenchyma bands, typical for tree species of the family Fabaceae (Worbes 2002). In the earlywood, we observed a band with a lower density of vessels (Fig. 1). Macroscopic wood characteristics of *M. paraensis* include (1) axial parenchyma visible to the naked eye; (2) confluent aliform paratracheal; (3) confluent vasicentric; (4) pores clearly visible under a 10× magnification lens, medium, solitary with frequent presence of multiples; (5) vascular lines appear at a regular basis in the tangential longitudinal plane; (6) radius visible under a 10× magnification lens on the transversal and tangential face, non-stratified, mirrored, poorly contrasted; (7) distinct growth layers, individualized by darker tangential fibrous zones; and (8) the presence of marginal parenchyma (Fig. 1). More detailed information on wood anatomy can be found in the study by Sousa (2011).

During the 3-year study period between cambial wounding and sampling the stem discs for analysis, three growth rings were formed (Fig. 2). The average age of the four trees marked by cambial wounding was 32.5 years and in the 3-year growth period after the incision the mean annual diameter increment was 1.48 ± 0.53 mm (Table 2).

The relationship between age and diameter was highly significant for *M. paraensis* (Fig. 3), which allowed diameter growth and increments to be modeled ($r^2 = 0.82$; $p < 0.001$). The growth model indicates that the maximum current diameter increment *M. paraensis* occurs at approximately 26 years of age, with a growth rate of 4.91 mm year^{-1} (Fig. 4). The relationship between diameter and height was significant ($r^2 = 0.71$; $p < 0.001$) (Fig. 5). The

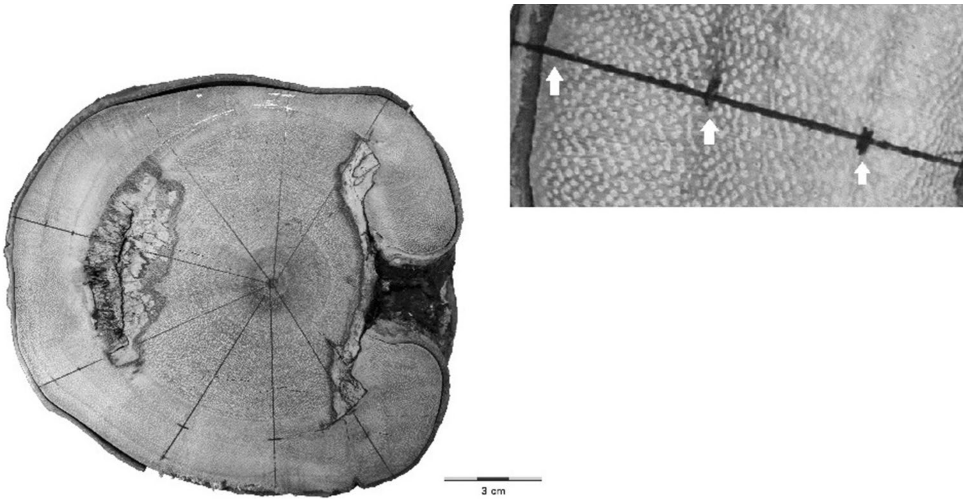

Fig. 2 Stem disc of *Mora paraensis* in the estuarine floodplains of the Amazon River, northern Brazil, sampled in October 2013, 3 years after the application of cambial wounding on two sides of the tree resulting in a dated scar in the wood

Table 2 Estimated age as a function of diameter, and current increment in the past 3 years before the age defined according to the GOL model (Schöngart 2008) for *Mora paraensis*. The increments of 3 years, measured in eight radii of each disc, is presented, after the incision mark in 4 *M. paraensis* trees collected in the estuary of the Amazon River

Sampled	Estimated age (years)	DBH (cm)	Current increment GOL model (cm)	Current increment (cm)
01	22	9.1	1.39	0.77 ($n = 8$, max = 2.0 min = 0.2)
02	46	21.0	1.34	2.15 ($n = 8$, max = 2.8, min = 1.5)
03	32	14.2	1.39	1.68 ($n = 8$, max = 2.4, min = 0.5)
04	30	13.2	1.41	1.32 ($n = 8$, max = 2.0 min = 0.2)
Mean ± DV	32.5 ± 9.2		1.38 ± 0.02	1.48 ± 0.53

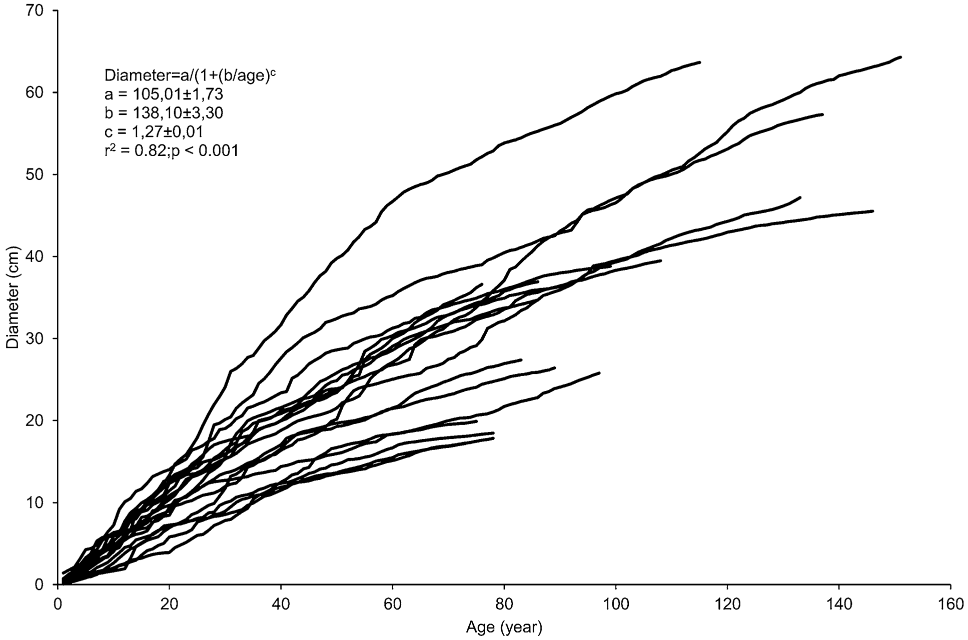

Fig. 3 Cumulative diameter growth curves of 17 individuals of *Mora paraensis* and adjusted model for the mean age–size relationship

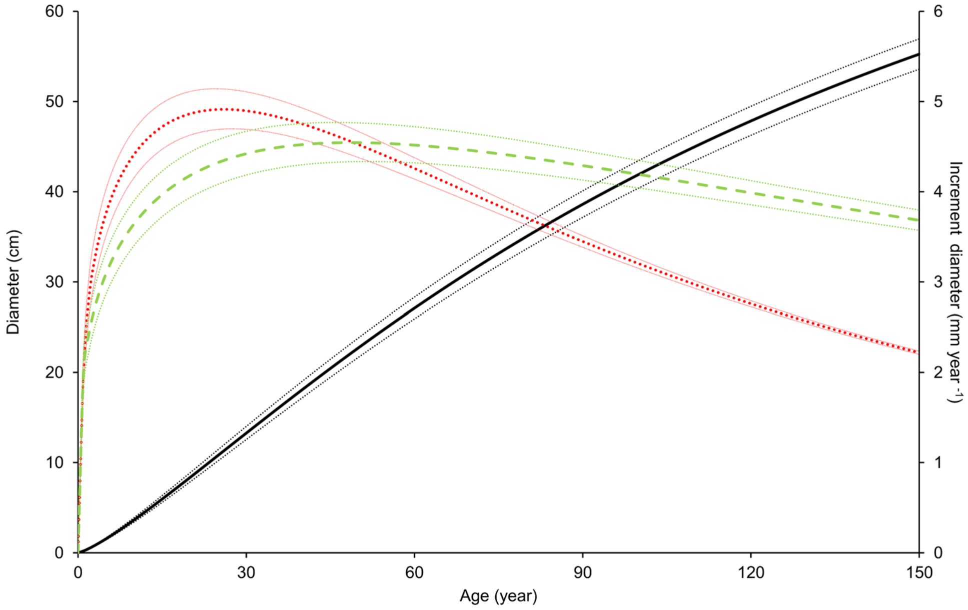

Fig. 4 Diameter growth model of *Mora. paraensis* (solid black line), current annual increment—CAI (dotted red line) and mean annual increment—MAI (dashed green line). The dotted lines represent the standard error of each curve

maximum height increment rate was 0.67 m year^{-1} (Fig. 6) and occurred at approximately 6 years of age.

The volume growth curve was constructed using the age–diameter and age–height relationships, and based on this the optimal harvesting period for adult trees was determined. The maximum current volume increment (CAI_{max}) of *M. paraensis* was achieved at an age of 115 years (Fig. 7). At this age, the trees showed an average DBH ± standard deviation of 46.4 ± 0.6 cm, which defines the MLD. The felling cycle was estimated as 24.7 ± 1.3 years, representing the time needed for the population just below the MLD to pass through a DBH class of 10 cm in that environment to replace what had been exploited, and maintain the productive capacity.

Discussion

The floodplain forests of Central Amazonia have a predictable annual cycle of flood and droughts, defined as a monomodal flood pulse (Junk et al. 1989). Trees in this environment form annual growth rings, as a consequence of the annually, occurring anoxic conditions in the root system (Worbes 1989; Schöngart et al. 2002, 2004, 2005). However,

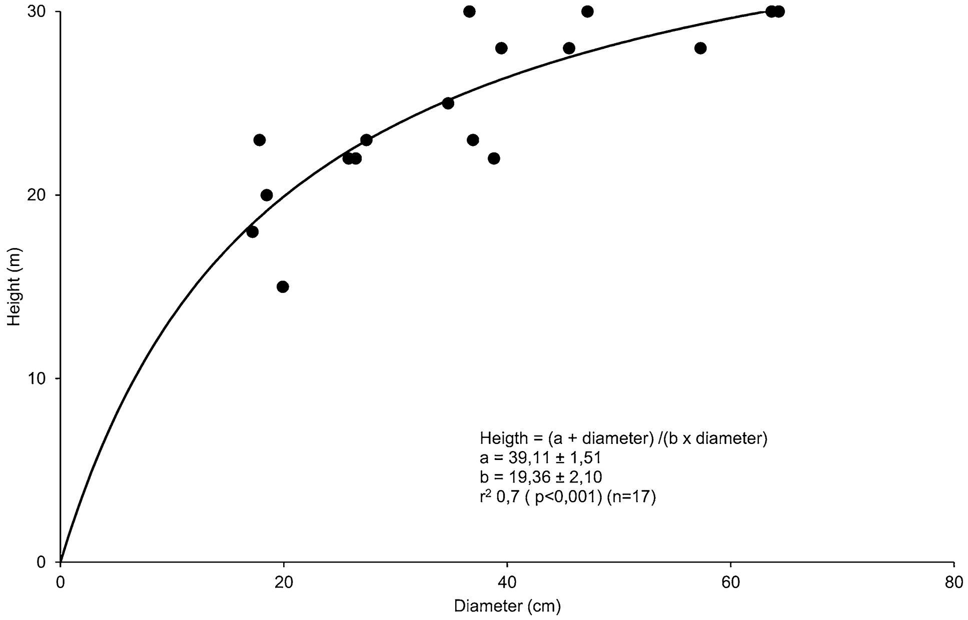

Fig. 5 Relationship between diameter and height of 17 individuals *M. paraensis*, and estimates of the parameters for the adjustment of the non-linear regression model

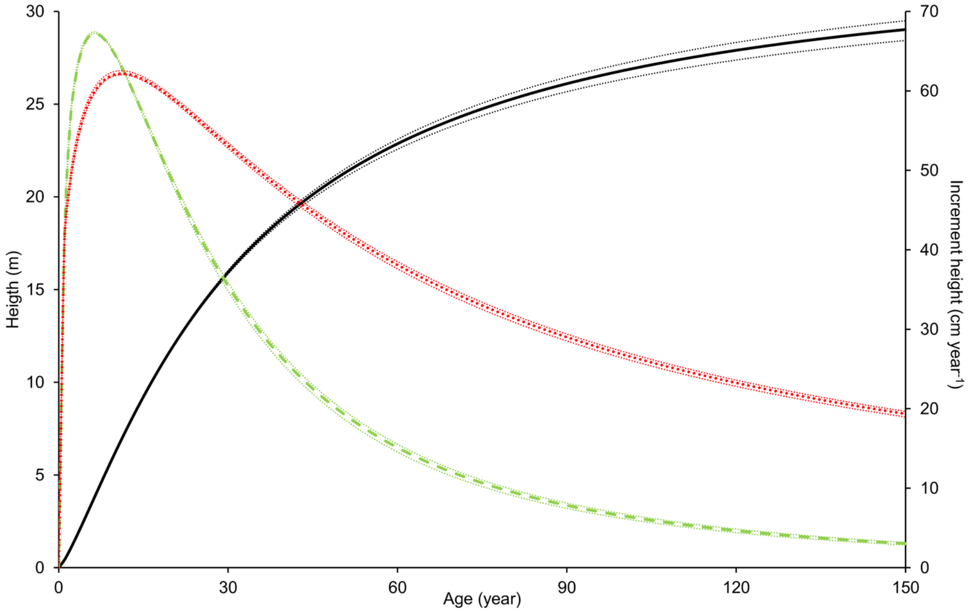

Fig. 6 Height growth model of *M. paraensis* indicating the cumulative height growth (solid black line), the current (dotted red line) and mean height increment (dashed green line). The dotted lines represent the standard error of each curve

for the floodplains of the Amazon Estuary where river level dynamics are driven by a predictable polymodal flood pulse (Junk et al. 2011), characterized by two daily cycles of floods and ebbs resulting from the influence of oceanic tides, there has been no evidence so far of the rhythm of tree-ring formation. The formation of growth rings evidenced by cambial wounding suggests an annual growth rhythm of tree species in the estuarine floodplain with a period of cambial dormancy. However, it is not clear which external factors induce the annual growth rhythm, indicating the need for further studies. Tree growth might be restricted during the very rainy season, when the floodplain area extends much further into the forest, and the water levels are higher due to higher discharges of the Amazon River.

The diameter increments found in the present study are very similar to the values obtained by Fortini and Zarin (2011), who monitored populations of *M. paraensis* in permanent plots in the same region from 2004 to 2007, indicating a mean diameter increment of 0.5 cm year^{-1}. In the floodplain of the Central Amazon, tree-ring analyses have allowed for the identification of significant relationships between age and diameter for many species (Schöngart et al. 2007; Schöngart 2008; Scabin et al. 2012; Marinho et al. 2013; Rosa et al. 2017). This relationship is required for

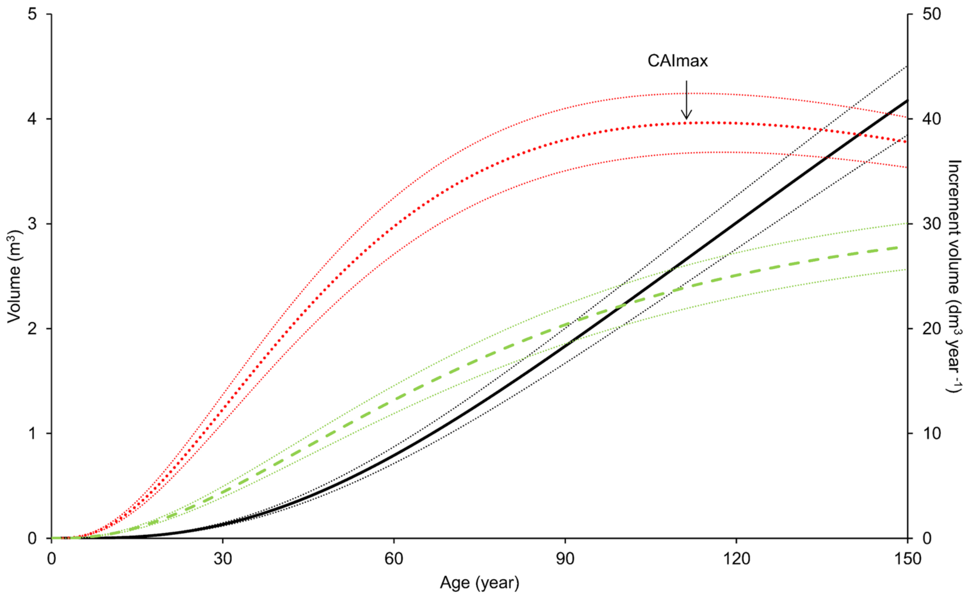

Fig. 7 Volume growth model of *M. paraensis* indicating the cumulative volume growth (solid black line), current annual (dotted red line) and mean annual volume increment (dashed green line). The maximum point (CAImax) of the current annual increment represents the minimum logging diameter (MLD), which is derived from the species-specific age–diameter relationship (Schöngart 2008, 2010a). The dotted lines represent the standard error of each curve

the GOL modeling approach applied in this study. For the species *M. paraensis*, in the Estuary of the Amazon River, this relationship was also predictable and highly significant, despite the natural variation among the 17 trees sampled.

Growth variation in trees of the same species is natural in tropical native forest environments (Furch 1997), depending on factors such as environmental differences and genetic characteristics of each individual. The growth in diameter of individual trees of *M. paraensis* as a function of age varied considerably, but without affecting the significance of the model. Other studies have also found significant relationships based on the samples of between 15 and 20 trees, for other species in a tropical environment (Schöngart et al. 2015; Rosa et al. 2017).

There is a strong relationship between diameter increment rates and specific wood density (Worbes et al. 1992; Schöngart 2008). Tree species with high wood densities that are associated with low increment rates are frequently found in late-successional tree species (Worbes et al. 1992; Schöngart et al. 2010). In the Central Amazonian floodplains, species with medium and high wood densities varying from about 0.65 to 0.87 g cm^{-3} (Parolin and Ferreira 1998; Schöngart et al. 2010) have mean diameter increment rates varying from 2.4 to 10.6 mm year^{-1} (Worbes 1989; da; Fonseca Júnior et al. 2009). The range therefore includes the values found in the present study for *M. paraensis*. Among angiosperms, high wood density provides resistance to deterioration (Chave et al. 2009).

The growth models suggest that *M. paraensis* invests first in height growth, attaining maximum increment rates around 6 years. The current diameter increment culminates at approximately 26 years of age. This strategy is an important adaptation for floodplain trees to take their leaves above the flood level, in order for photosynthesis to take place (Parolin 2002).

The population structure of *M. paraensis* shows an inverted 'J' distribution (Fortini and Zarin 2011), which indicates that the population is stable and auto-regenerative. Species with such distribution patterns have high potential to replace harvested trees, maintaining the productive capacity for the next felling cycle. Polycyclic systems are recommended to manage species with such structural population patterns (Schöngart 2008). In polycyclic management systems, the ideal period for extraction and the MLD are estimated when the species expresses its highest growth potential in volume. This period occurs between the maximum current and the maximum mean increment rates (Schöngart 2008). In the floodplain forest of Central Amazon, tree species with high wood density (0.65 to 0.94 g cm^{-3}) achieve an MLD of 50 cm within a period of 106–151 years, whereas species with low wood densities (0.23–0.57 g cm^{-3}) reach this limit at ages between 15 and 67 years (Schöngart 2008; Da Fonseca Júnior et al. 2009). *M. paraensis* takes less time to reach the 50-cm MLD in the Estuary of the Amazon River than species with a similar wood density in the Central Amazon. For the species *Piranhea trifoliata* of Central Amazon, which has a wood density (0.94 g cm^{-3}) similar to *M. paraensis*, the estimated age to reach a diameter of 50 cm was 152 years (Schöngart 2008), whereas *M. paraensis* reaches that diameter in 128 years. Consequently, the felling cycle of *P. trifoliata* estimated in 32 years with an MLD of 70 cm is longer than the felling cycle of 25 years with an MLD of 46 cm estimated for *M. paraensis*. This difference is probably related to the flood regime or edaphic conditions.

The felling cycle of 25 years found in this study matches the management criteria indicated by Normative

Instruction no. 5 from IBAMA (Brasil 2006), which recommends felling cycles of 25–35 years and an MLD of 50 cm for timber resource management applying the conventional sustainable forest management plan, includes the use of heavy equipment for skidding and transport of logs. In this category, the maximum logging intensity is 30 m^3 ha^{-1}, independent of the species. In the case of floodplain forests, where the use of heavy equipment is not possible (Schöngart and Queiroz 2010), forest managers can apply the low-intensity category which allows a maximum logging intensity of 10 m^3 ha^{-1}, with a felling cycle of 10 years and an MLD of 50 cm, regardless of the tree species. The competent organ can, based on article 6 of Normative Instruction nº 5 and, authorize logging above 10 m^3 ha^{-1} (limited to 3 trees ha^{-1}).

In the case of floodplain forests, the application of the low-intensity category felling cycle cannot be recommended based on the results of the present study, based on modeling individual trees. The application of a felling cycle of 10 years will possibly degrade populations of this endemic species in the estuarine floodplain ecosystem.

Normative Instruction no. 009 (of 15th November 2010) was implemented to regulate the harvest of timber from the *várzea* floodplains of the state of Amazonas. Based on the GOL concept (Schöngart 2008), it predicts the application of 12 years felling cycles for tree species with wood densities below 0.60 g cm^{-3} and 24 years for those with wood densities above 0.60 g cm^{-3}, applying species-specific MLDs. This innovative law represents a huge advance, increasing the level of sustainability for the management of timber resources in these regions.

However, felling cycles for the same tree species vary considerably between ecosystems. There is evidence from the Central Amazonian floodplains that diameter growth and volume production can be highly variable within the same species, depending on edaphic conditions and flooding regime, such as has been observed for *Macrolobium acaciifolium, Handroanthus barbatus, Vatairea guianensis* and *Calophyllum brasiliense* (Schöngart et al. 2005; Da Fonseca Júnior et al. 2009; Schöngart 2010a, b, c; Scabin et al. 2012; Assahira et al. 2017; Rosa et al. 2017). The analysis of growth rings is a powerful tool to determine increment rates, which consider the entire life history of a species (Worbes et al. 2003). Such analyses allow for the construction of the cumulative growth curve of a tree species, and based on that the definition of specific criteria to manage timber resources, differentiating between species and environments (Schöngart 2008; da Fonseca et al. 2009; Scabin et al. 2012; Rosa et al. 2017).

Conclusions

Mora paraensis presents distinct annual growth rings, whose analysis along its lifespan allowed for patterns of growth in diameter, height, and volume to be modeled. Thus, specific criteria for the management of its timber resources in the floodplain forest of the Estuary of the Amazon River can be estimated. The modeling approach based on tree rings, as suggested by the GOL concept, can also be applied to other commercial tree species of the estuarine floodplain forest such as *Calycophyllum spruceanum* (Rubiaceae), *Platymiscium filipes* (Fabaceae) and *Carapa guianensis* (Meliaceae), to validate if the established norms and regulations of Brazilian forest legislation in terms of felling cycles and MLDs meet the biological reality of their growth potential.

We recommend carrying out further studies on the population structure and dynamics, as well as large-scale inventories of commercial timber stock of the most abundant and harvested species in the estuarine floodplains, for the planning of smallholder and community-based forest management. It is also necessary to build capacity for correct botanical identification in the field and provide knowledge on species reproduction, as well as specific growth modeling in distinct environments of the estuary, such as fluvial islands of different sizes and ages.

Author contribution statement ZPM: data collection in the field, data analysis and main editor of the article, which is one of the chapters of his doctoral thesis. MCG: work planning, obtaining funding, collecting and analyzing data and reviewing the manuscript. Advisor of thesis work and project coordiantor to which the work is linked. SAR: laboratory analysis. JS: analysis, growth modeling and discussion of the results, and revision of the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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