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Growth and population structure of the tree species *Malouetia tamaquarina* (Aubl.) (Apocynaceae) in the central Amazonian floodplain forests and their implication for management

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ABSTRACT

The long-term success of forest management depends primarily on the sustainability of timber production. In this study we analyse the population structure, tree age and wood increment of *Malouetia tamaquarina* (Aubl.) (Apocynaceae) to define a species-specific minimum logging diameter (MLD) and felling cycle by modelling volume growth. Contrary to other timber species in the nutrient-rich white-water floodplains forests (várzea), *M. tamaquarina* grows in the subcanopy of old-growth várzea forests. The wood of this species is utilized by local inhabitants in the floodplains for handicraft. In 35 plots of 25 m × 50 m we measured diameter at breast height (DBH) and tree height of all trees taller than 150 cm height. From 37 individuals with DBH > 15 cm we sampled two cores by increment borers to determine the wood density, tree age and diameter increment rates. In the management area of a várzea settlement with about 150 ha recently harvested trees of *M. tamaquarina* have been recorded and DBH was measured. The species presents an inverse *J*-shaped diameter distribution indicating that the species is obviously regenerating in the old-growth forests. Tree-ring analysis indicates a mean age of 74.5 years for a DBH of 22.7 cm for a studied population comprising 37 trees with maximum ages of up to 141 years for an individual with a DBH of 45.7 cm. The tree species has low annual diameter increment rates (3.16 ± 0.6 mm) despite a low wood density (0.36 ± 0.05 g cm^{-3}). The volume growth model indicates a MLD of 25 cm and a felling cycle of 32.4 years. In the management area 35 trees with a mean DBH of 24 cm were recorded, similar to the defined MLD. The abundance of trees above the MLD is 2.7 trees ha^{-1}, or 405 trees, when extrapolated to the whole management area. Considering a felling cycle of 32.4 years (annual production unit of 4.63 ha) this results in total of 12.5 harvestable trees, almost three times less than actually harvested. The actual practice of harvesting *M. tamaquarina* risks the overexploitation of this slow-growing species.

1. Introduction

The conservation of tropical forests has become a huge challenge in our time in the background of global climate change and increasing human populations especially in the tropics with high deforestation rates. A promising way to conserve tropical forests is the development of sustainable management systems which guarantee the long-term use of natural resources such as timber and non-wood forest products (NWFP) and maintain the multiple ecological functions and services of the forests. But a great difficulty for a sustained management of tropical forests is obtaining reliable data on tree growth, which is a prerequisite for determining harvesting volumes and felling cycles (Boot and Gullison, 1995; Brienen and Zuidema, 2006, 2007; Schöngart, 2008).

For centuries, the nutrient-rich Amazonian floodplains (várzea) have been used and settled by a human population of high density that carried out agriculture, pasture, fishing and hunting, as well as the extraction of timber and NWFPs (Junk et al., 2000). Consequently, várzea floodplain forests are one of the most stressed and threatened forest ecosystems in the Amazon. Many várzea trees are utilized and commercially harvested for a variety of different purposes comprising timber and NWFPs (Phillips et al., 1994; Parolin, 2000; Kvist et al., 2001; Bentes-Gama et al., 2002; Wittmann et al., 2009). In general, floodplain inhabitants have preserved an inti-

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Fig. 1. *M. tamaquarina* is a frequent tree species in the sub-canopy of late successional stages of the várzea floodplain forests used for the manufacture of handicrafts by riverine populations.

mate knowledge of the floodplain environment and its resources (e.g., Hiraoka, 1992; Padoch, 1988; Junk et al., 2000), but intensive commercial exploitations of a few tree species, carried out without knowledge of their growth rates, population structures, and regeneration processes, have locally exhausted merchantable stocks and caused already the disappearance of some timber species from local and regional markets within only a few decades (Ayres, 1993; Lima et al., 2005; Schöngart and Queiroz, 2010). The majority of commercially harvested trees in the várzea belong to emergent tree species of the canopy achieving large diameters such as *Hura crepitans* (Euphorbiaceae), *Maquira coriacea* (Moraceae), *Ceiba pentandra* (Malvaceae), *Cedrela odorata* (Meliaceae), *Ocotea cymbarum* (Lauraceae), *Calycophyllum spruceanum* (Rubiaceae) and *Calophyllum brasiliense* (Clusiaceae) (Schöngart and Queiroz, 2010). Molongó, the local name for *Malouetia tamaquarina* (Aubl.) A.DC. (Apocynaceae), however, is a small, abundant evergreen low-canopy tree of várzea's late successional stages (Fig. 1). The timber is used mainly for the manufacture of handicrafts (Cabalzar, 2003).

Timber extraction in Amazonian forests requires a management plan based on legal regulations and normative instructions (IN) established by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA). The established IN no. 5 (11 December 2006) defines diameter cutting limits (DCLs) and felling cycles (Schöngart, 2008) for regular management plans with a felling cycle of 25–35 years and maximum yields of up to 30 m^3 ha^{-1} or, alternatively, management plans with low yield intensities (<10 m^3 ha^{-1}) applying a shorter felling cycle of 10 years (in várzea floodplain forests yields can exceed 10 m^3 ha^{-1}, but must be restricted to 3 harvested trees ha^{-1}). The IN no. 5 requires the establishment of species-specific diameter cutting limits based on ecological and technical criteria, but if this information is not available for a timber species, a common DCL of 50 cm is applied.

The GOL concept (Growth-Oriented Logging) developed by Schöngart (2008) is an approach to the sustainable management of tropical timber resources in nutrient-rich central Amazonian várzea forests using species-specific DCLs, in term of an optimized minimum logging diameter (MLD), and felling cycles derived from growth models of 12 commercial tree species. Growth modelling is based on tree-rings, which are annually formed in the wood as a consequence of the annual flood-pulse (Worbes, 1989; Schöngart et al., 2002, 2004, 2005). In this study we examine the population structure and tree growth of *M. tamaquarina* using tree-ring analysis to construct models for diameter and volume growth (Schöngart et al., 2007). From these growth models we derive an estimate for a felling cycle and MLD and discuss our results in the background of current Brazilian forest legislation and actually practised resource management in the study region.

2. Methods

2.1. Study area

The study was located in the Mamirauá Sustainable Development Reserve (MSDR) in the Amazonas state located at the confluence of the Solimões and the Japurá Rivers, approximately 70 km northwest of the municipality of Tefé. The MSDR comprises 11,240 km^2 of várzea floodplains. The climate in the study area is characterized by a mean daily temperature of 26.9 °C and an annual precipitation of almost 3000 mm, with a distinct dry season from July to October. Mean water level fluctuation of the Japurá River during the period 1993–2000 is 11.38 m (Schöngart et al., 2005). The várzea is a landscape patchwork of water bodies, aquatic and terrestrial macrophytes and different forests types which cover about 50–75% of the floodplains (Wittmann et al., 2006). Erosion and sedimentation processes continuously rearrange the floodplains, creating a mosaic of small-scale landscapes corresponding to different successional stages with ages up to 300–400 years (Schöngart, 2003).

The MSDR was the first conservation unit in the Brazilian várzea, established in 1990 as an Amazonas State Ecological Station and transformed into a Sustainable Development Reserve in 1996 by the State's Governor as a new category of conservation unit in Brazil. Together with the Amanã Sustainable Development Reserve, Jaú and Anavilhanas National Parks, the MSDR forms the "Central Amazon Conservation Complex" with a total area of about 6 million hectares. This region was declared a world natural heritage site by UNESCO in the year 2000 and recognition was extended in 2003 (Ayres et al., 2005).

Since 1992, a variety of community-based management systems have been implemented in the MSDR based on socio-economic and biological-ecological studies, including fisheries, agriculture, agroforestry, eco-tourism, and forestry (Ayres et al., 1998). Since 1998, several cooperatives have been founded within the MSDR to conduct controlled timber extractions. This forest management aims to keep a multi-aged stand through timber cutting at intervals (felling cycle) by establishing a diameter cutting limit (polycyclic system). The felling cycle defines the return interval in years between timber harvests in the same area. Due to the harvest of only a few selected trees above the defined diameter cutting limit, the uneven-aged structure of the forest is maintained by the establishment of seedlings in small gaps and in the understorey (de Graaf et al., 2003). To achieve a more or less constant annual harvest, the total area for the forest management is divided in several blocks (annual production units) with similar size corresponding to the number of years of the felling cycle. The community Nova Colômbia in the MSDR traditionally uses the wood of *M. tamaquarina* for handicrafts and sells the products at local markets supported by the program for the production of handicrafts of the Mamirauá Institute for Sustainable Development. The semicircular management area comprises approximately 150 ha of forests which the locals can reach within a one hour foot walk (terrestrial phase) or canoe (aquatic phase) from the community (Fig. 2). The annual average income for the seven families of the community Nova Colômbia practising the production of handicrafts was 8845.00 Brazilian Reais (US$ 5025.00) during the period 2007–2009 and contributed considerably to the annual rent and welfare of the local riverine people.

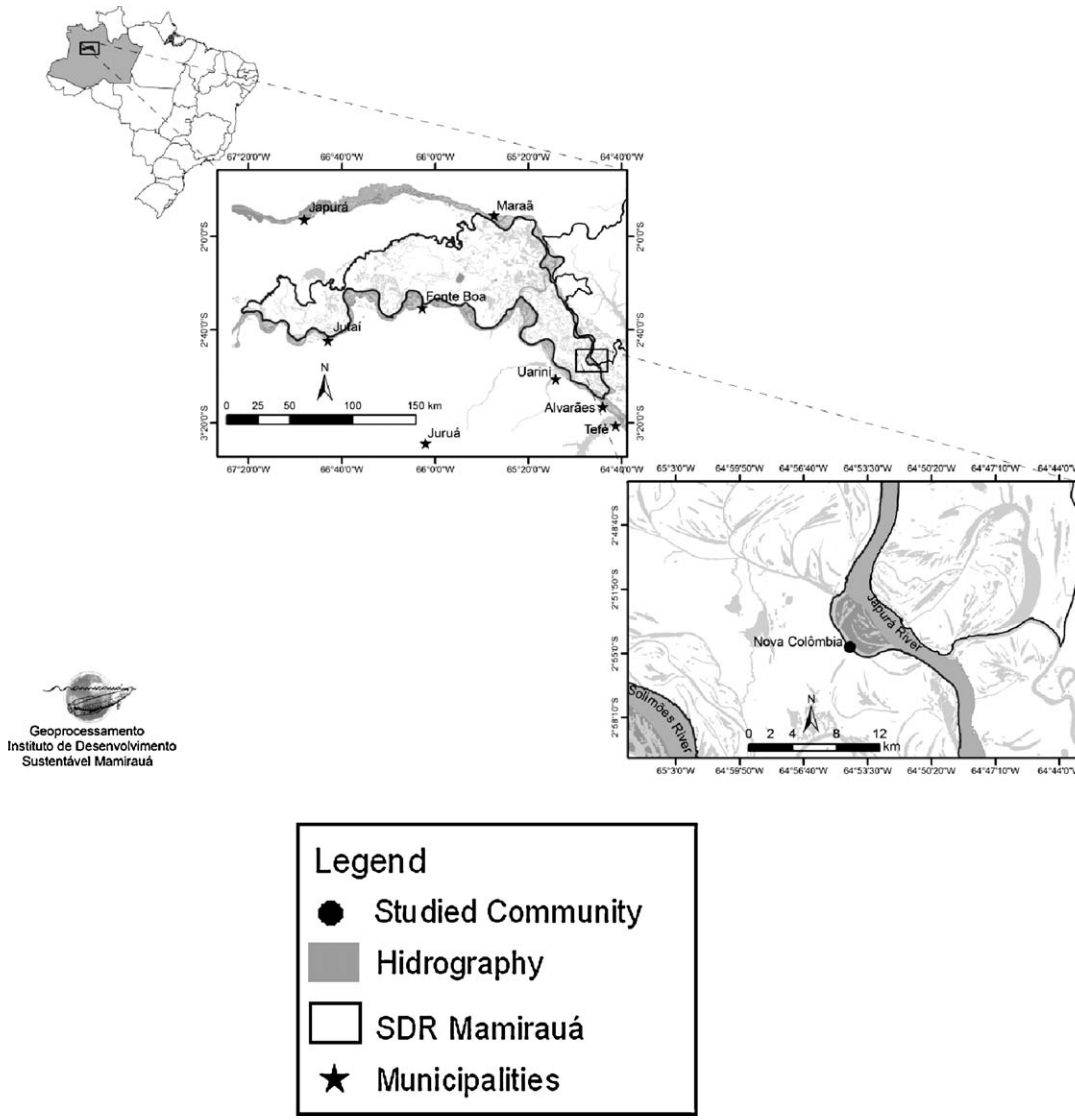

Fig. 2. Study area with the location of the Mamirauá Sustainable Development Reserve and the community Nova Colômbia in the Jarauá sector.

2.2. Forest inventories

Population structure of *M. tamaquarina* was studied from August to September 2007 in the MSDR (Fig. 2). In 35 randomly distributed plots (separated by at least 300 m distance) of 25 m × 50 m (total area of 4.375 ha) within the management area of Novo Colômbia all trees of *M. tamaquarina* ≥ 1.5 m tree height were recorded. Diameter at breast height (DBH) – measured 1.30 m above the ground – and the flood-height of every tree, visible as a distinct mark of the last high-water period on the trunk, were noted and tree height was measured using a Blume-Leiss BL 6 device. From 37 randomly selected individuals with DBH > 15 cm we sampled two cores with 5 mm diameter to determine tree age, diameter increment rates and wood density. The bore hole was closed with carnauba wax to protect the tree against the attack by xylophagous organisms. In the traditional management area of the community Nova Colômbia a survey was made to record and measure DBH of all harvested trees of *M. tamaquarina* in the year 2007.

2.3. Tree-ring analysis and growth modelling

Wood samples were prepared and processed at the Dendroecological Laboratory at the National Institute of Amazon Research (INPA) in Manaus. One sample was used to estimate wood density by the relationship between fresh volume and dry weight after drying at 105 °C for 72 h (Schöngart et al., 2005). The other sample was polished by increasingly fine grain sandpaper until wood structure was clearly evident. Growth rings were macroscopically analysed under a Leica MZ 8 dissecting microscope and the wood anatomical features of the tree rings was described following the definition of four basic types of growth ring formation according to Coster (1927, 1928) and Worbes (1989). It was useful to moisten the surface of the sample with some drops of water to increase contrast between different wood tissues and the distinctiveness of growth zones. In a next step ring width was measured with a digital measuring device (LINTAB) to the nearest 0.01 mm supported with software for tree-ring measurement, analysis and presentation (TSAP-Win, Rinntech, Heidelberg, Germany) providing radial growth curves for each individual. The wood samples contained in 77% of the cases the pith allowing an age determination referring to the tree age at the height of DBH. For the other trees which did not included the pith the age was estimated by the ratio radius/average radial increment (Schöngart et al., 2005). The increment rates ($n = 1955$) measured on the wood samples, from pith to bark, were accumulated to form individual growth curves related to the measured diameter (Brienen and Zuidema, 2006, 2007). The relationship between age

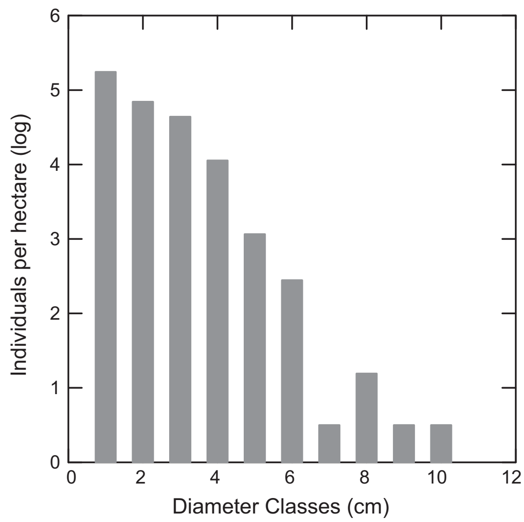

Fig. 3. Diameter distribution of *M. tamaquarina* in nine 5-cm diameter classes: (1) 0.5–4.9 cm, (2) 5.0–9.9 cm, (3) 10.0–14.9 cm, (4) 15.0–19.9 cm, (5) 20.0–24.9 cm, (6) 25.0–29.9 cm, (7) 30.0–34.9 cm, (8) 35.0–39.9 cm, (9) 40–44.9, (10) >45 cm.

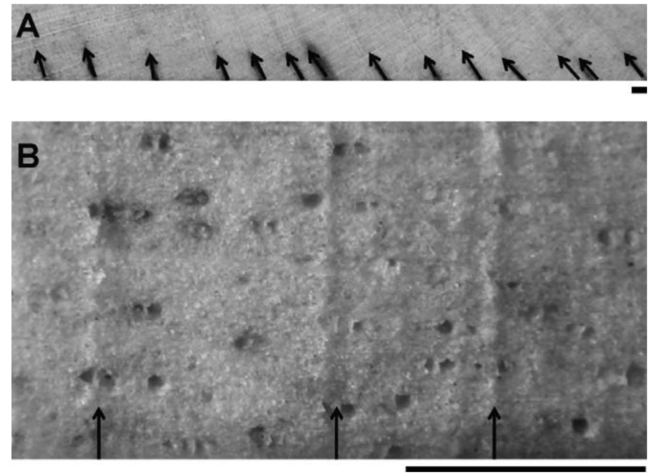

Fig. 4. (A) Tree-ring series of *M. tamaquarina* indicating distinct annual growth boundaries. (B) Even when narrow the macroscopic analysis allowed a confidential identification of the ring's wood anatomical structure indicated by terminal parenchyma bands. Arrows indicate the ring boundaries; horizontal bars indicate 1 mm length.

and DBH was adapted to a sigmoidal regression model, from which annual rates of current and mean diameter increment were derived (Schöngart et al., 2007; Schöngart, 2008). Height growth of a tree species was estimated by combining the age-diameter relationship and the relationship between diameter and tree height measured in the field fitted to a non-linear regression model. Thus, for every tree age over the lifespan of *M. tamaquariana*, the diameter and corresponding tree height can be estimated. Cumulative volume growth was calculated for every year by the basal area multiplied with the corresponding tree height and a common form factor of 0.6 (Cannell, 1984):

$$V_t = \pi \times \left(\frac{\mathrm{DBH}_t}{2}\right)^2 \times h_t \times f \qquad (1)$$

where V_t is the volume at age t; DBH_t is the diameter at age t; h_t is the tree height at age t, and f is the form factor (the ratio of tree volume to the volume of a cylinder with the same basal diameter and height).

From the cumulative volume growth over the life span the current and mean annual volume increment rate was derived to define management criteria following the methodology described in Schöngart (2008) who used the age at maximum current volume increment to define the corresponding MLD by the age-diameter relationship. Harvests before this age would lead to an inefficient use of the growth potential of a tree species. To estimate the felling cycle the mean time through 10-cm diameter classes until achieving the specific MLD was calculated.

The estimated felling cycles by mean passage times through 10-cm diameter classes can easily be transferred to the forest inventory data.

3. Results and discussion

In the total inventoried area of 4.375 ha 315 trees have been recorded corresponding to an average of 72.9 trees ha^{-1}. Only one individual has a DBH > 50 cm, which is the minimum size for felling according to the Brazilian forest legislation (IN no. 5, 11 December 2006). The annual mean flood height of the trees is 2.5 ± 0.6 m. The population structure indicates a decreasing abundance with increasing diameter class, known as an inverse *J*-shaped distribution (Fig. 3). This indicates that recruitment is continuous and mortality distributed over all size classes resulting in a negative exponential distribution. Generally, such species have a stable or expanding population under the environmental conditions of the old-growth várzea forests (Sokpon and Biaou, 2002). However, further studies should monitor population structure of *M. tamaquarina* to obtain reliable data on regeneration process, recruitment and mortality of this species. A total of 35 trees with an average DBH of 24 cm (10.3–37.4 cm) have been harvested during the year 2007 by the locals of the community Nova Colômbia corresponding to 0.23 trees ha^{-1}.

The tree rings of *M. tamaquarina* are distinct and of annual nature (Worbes, 1995; Schöngart et al., 2002). Wood anatomical structure of tree rings combines two ring characteristics: The variation of cell wall thickness and cell lumen diameter results in a clear shift from light earlywood to a dark latewood limited by a light terminal parenchyma band. These bands allow the definite identification of the annual rings, even when they are narrow (Fig. 4).

M. tamaquarina has a relative low wood density of 0.36 ± 0.05 g cm^{-3} (Table 1). The tree age for the average DBH (22.7 cm) of the analysed collective is 74.5 years resulting in a mean annual diameter increment of 3.16 ± 0.6 mm year^{-1}. The maximum age was 141 years for an individual with 45.7 cm DBH (Table 1). The tree age explained 81% of the variation in diameter (Fig. 5A) allowing an estimate for diameter growth and annual current and mean increment rates over the tree's life span (Fig. 5b). Also tree age and mean annual diameter increment were significantly correlated ($R^2 = 0.25$, $F_{1,36} = 11.74$, $p < 0.02$), while wood density was independent of tree age ($R^2 = 0.02$, $F_{1,22} = 0.57$, $p > 0.1$). Diameter and tree height were significantly correlated ($R^2 = 0.29$, $p < 0.01$) (Fig. 5C). The volume growth model indicates that *M. tamaquarina* reaches its optimum in current volume increment at an age of 81 years which corresponds to a MLD of 25 cm (Fig. 5D). The felling cycle, estimated by the mean passage time through 10 cm-diameter classes, betrays 32.4 years (81 years to reach the MLD of 25 cm divided through 2.5 diameter classes of 10 cm).

Table 1
Average values (± indicates the standard deviation, number in brackets are minimum and maximum values) of flood height, DBH, mean diameter increment, tree age and wood density of *M. tamaquarina* in várzea floodplain forests of central Amazonia.

Mean water column above the forest floor (m)	2.5 ± 0.6
DBH (cm)	22.7 (15.2–45.7)
Mean diameter increment (mm ano^{-3})	3.16 ± 0.6
Tree age (years)	74.5 (35–141)
Wood density (g cm^{-3})	0.36 ± 0.05

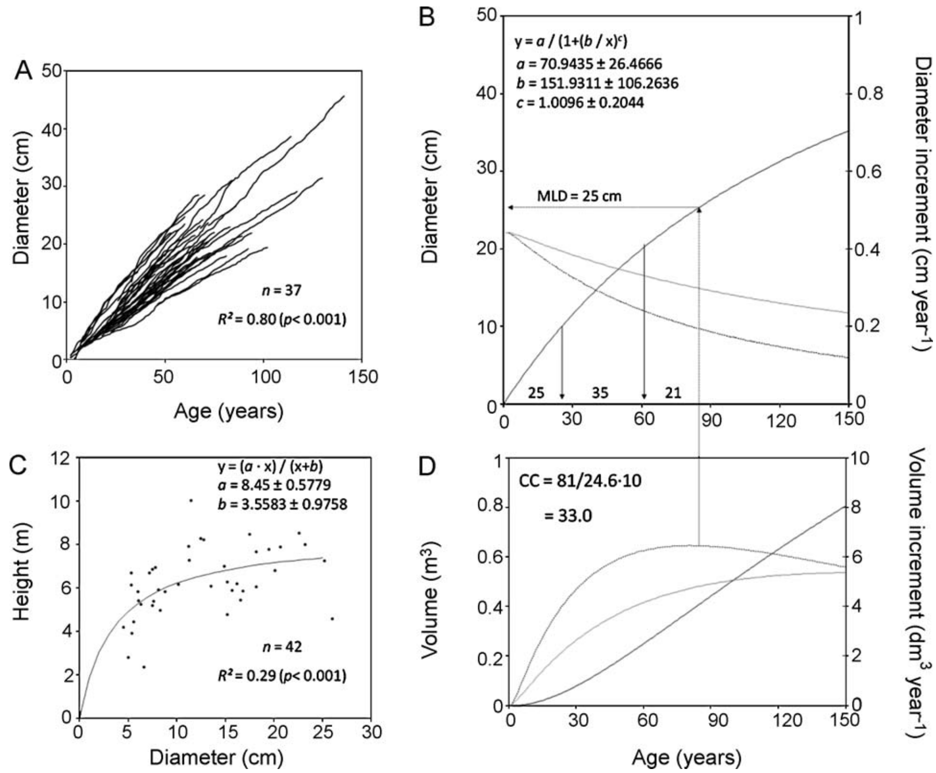

Fig. 5. (A) Growth modelling of *M. tamaquarina* based on a significant relationship of diameter and tree age indicate by 37 individual cumulative diameter growth curves. (B) Significant relationship between tree age and diameter fitted to a sigmoidal regression model (black line). From this model the current (spotted line) and mean (gray line) annual increment were derived. (C) Significant relationship between diameter and tree height of 42 trees of *M. tamaquarina* fitted to a non-linear regression model. (D) For every age along the lifespan of *M. tamaquarina* volume was estimated by DBH and corresponding tree height ($V = \pi \times (\text{DBH}/2)^2 \times h \times 0.6$) by combining age-diameter and diameter-height relationships. From the volume growth model current (spotted line) and mean (gray line) annual increment were derived. The minimum logging diameter (MLD) is defined in the peak of the current volume increment by the age-diameter relationship. The felling cycles are estimated by the passage time through 10-cm diameter classes until reaching the defined MLD (indicated by numbers upon the *x*-axis in figure B).

Generally, the conditions for sustainable and integrated forest management and conservation are more favourable in the várzea than in other forest types in Amazonia, as the former consists of highly productive forest ecosystems. The Amazonian várzea forests are among the most productive tropical forests worldwide with a net primary production 13.3–31.8 Mg ha^{-1} year^{-1} (MSDR) (Schöngart et al., 2010) as a consequence of the annual flood-pulse which deposits sufficient nutrients to maintain long-term fertility of the alluvial soils (Furch, 1997). Diameter growth is significantly higher in the várzea than in the nutrient-poor counterparts, the black-water floodplain forests (igapó), as shown for *Macrolobium acaciifolium* (Schöngart et al., 2005), *Vatairea guianensis* and *Tabebuia barbata* (da Fonseca et al., 2009), species that occur in both systems. But there are huge differences also comparing diameter growth of different species within the várzea (Schöngart, 2008). Tree species with low wood densities like *Pseudobombax munguba* have high diameter and volume increment rates, while tree species with high wood densities like *Piranhea trifoliata* tend to have lower diameter and volume increment rates. The tree species of this study, *M. tamaquarina*, has a low wood density of 0.36 ± 0.05 g cm^{-3} comparable to the wood density of the várzea tree species *F. insipda* with 0.38 ± 0.03 g cm^{-3} of which tree growth has been analysed in the same study area (Schöngart et al., 2007). Mean diameter increment rate of *M. tamaquarina*, however, is more than 10 times lower than those of *F. insipda*. The felling cycle of *M. tamaquarina* with 32.4 years is in the same range as estimated for *P. trifoliata*, but mean wood density of the latter species is 0.94 g cm^{-3} (Schöngart, 2008). As *M. tamaquarina* is a sub-canopy tree species with tree heights of up to 10 m (Fig. 5b) growing under relative low insolation, mean diameter increment rates are much lower than those of species established in the upper canopy (Korning and Balslev, 1994; Clark and Clark, 1996, 1999; Worbes, 1997; Schöngart, 2003). Diameter distribution and the low diameter increment rates characterize *M. tamaquarina* as a shade-tolerant tree species (Swaine and Whitmore, 1988) despite the low wood density which normally is typical for fast growing pioneer species.

The estimated MLD of 25 cm corresponds with the mean diameter of 24 cm of harvested trees by the local inhabitants. The abundance of trees *M. tamaquarina* considering individuals which passed over the MLD is 2.7 trees ha^{-1} and we estimate a total abundance of 405 harvestable trees in the total management area of the community. Applying the estimated felling cycle of 32.4 years results in an annual production unit of 4.63 ha with a total of about 12.5 trees above the MLD of 25 cm. The annual harvest of 35 trees in the current management practises of the community, however, is almost three times higher. Therefore the traditional use of *M. tamaquarina* is not sustainable and might have negative future impacts for the species population as well as for the local inhabitants since they have to go to more distant places to find harvestable trees for the production of handicrafts.

The IN no. 5 from IBAMA requires the use of a common diameter cutting limit of 50 cm. The application of this diameter cutting limit makes the management of *M. tamaquarina* unviable, because rarely this species reaches diameters of that size. However, the IN no. 5 allows the establishment of specific diameter cutting limits if technological and ecological criteria are available. In the case of *M. tamaquarina* we suggest a MLD of 25 cm which is similar to the mean diameter of harvested trees by local people which consider technical criteria to produce the handicraft. Further, the IN no. 5 allows to operate with a 10-year felling cycle in the modus of low yield intensity restricted to a selective logging of 3 trees ha^{-1}. Such a management option would endanger the population of *M. tamaquarina* as the annual production unit of the total forest area would be 15 ha with a total amount of about 40.5 harvestable trees (2.7 individuals ha^{-1}). This is even more than the actual harvest practised by the local inhabitants.

This study suggests a species-specific management of *M. tamaquarina* applying a MLD of 25 cm and a felling cycle of 33 years. An alternative to reduce the exploitation pressure on the natural populations of *M. tamaquarina* would be the performance of reforestation of abandoned agricultural and degraded areas in the várzea floodplains or plantings in agricultural crops such as cassava or maize. Therefore, however, studies on germination and regeneration under varying environmental factors are necessary.

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