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Original article

Management criteria for *Ficus insipida* Willd. (Moraceae) in Amazonian white-water floodplain forests defined by tree-ring analysis

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Abstract – *Ficus insipida* Willd. (Moraceae) is a fast growing tree species of early successional stages in the Amazonian nutrient-rich white-water floodplains (várzea). The species is one of the most economically important low-density wood species in the community-based forest management project in the Mamirauá Sustainable Development Reserve (MSDR) in Central Amazonia, where timber species are managed using a polycyclic selection system with a minimum logging diameter (MLD) of 50 cm and a cutting cycle of 25 years. In this study we analyze the floristic composition, stand structure and forest regeneration of a natural 20 year-old stand at an early successional stage and we model tree growth of diameter, height and volume of *F. inspida* based on tree-ring analysis to define management criteria. The volume growth model indicates that the preferred period for logging should be at a tree age of 17 years when the current annual volume increment peaks. This age corresponds to a diameter of 55 cm, which would be an appropriate MLD.

Amazon / floodplain forest / tree ring / cutting cycle/ minimum logging diameter (MLD)

Résumé – Critères de gestion dérivés de l'analyse de cernes pour *Figus insipida* Willd. (Moraceaea) dans des forêts inondables amazoniennes. *Ficus insipida* Willd. (Moraceae) est une essence à croissance rapide présente dans les premiers stades de succession dans les forêts inondables sur sols riches d'Amazonie (« varzea »). Cette essence est l'une des plus importantes essences productrice de bois de faible densité, dans le cadre du projet de gestion forestière communautaire durable de la réserve de Mamiraua, en Amazonie Centrale. Ces forêts sont gérées sur le principe d'un système polycyclique avec récolte des arbres présentant un diamètre minimal de 50 cm et une révolution de 25 ans entre récoltes. La présente étude analyse la composition floristique, la structure des peuplements et la régénération dans une forêt naturelle âgée de 20 ans et issue d'une phase de régénération. Un modèle de croissance en diamètre, hauteur et volume a été adapté à *Ficus insipida* sur la base d'une analyse de cernes, afin de définir des critères de gestion. Le modèle de croissance en volume indique que l'âge de récolte optimal est d'environ 17 ans, au moment du pic de production courante annuelle. À cet âge, les arbres atteignent un diamètre de 55 cm, qui constituerait ainsi un diamètre minimal de récolte (DMR) tout à fait approprié.

Amazonie / forêt inondable / cerne / révolution / diamètre minimal de récolte

1. INTRODUCTION

Amazonian floodplains periodically inundated by nutrient-rich and sediment-loaded white-water rivers are called várzea; they occur on an area of about 200 000 km^2 in the Amazon basin [13, 23]. Forests composed by almost 1 000 tree species cover about 50–75% of the várzea [38]. These serve multiple ecological functions: they regulate the hydrology of the river-floodplain system, act as sinks and sources in biogeochemical cycles, serve as habitat for a huge number of endemic plant and animal species, function as food resources for many fish species thus guaranteeing the nutrient supply for the human population, and deliver timber and non-timber products for the local population [15, 16].

For centuries the várzea has been settled and used largely because of its ease of accessibility, high soil fertility, and richness in natural resources [15]. Floodplain forests in the Amazon region are endangered due to their conversion for agriculture and pasture, and their exploitation by an expanding timber and plywood industry [12,35]. Because of low energy costs for logging, skidding, and transport during the flooded period [4] between 60% and 90% of the local and regional markets in the Western Amazon basin of Brazil and Peru are still provided with timber from the várzea [42]. More than 50 tree species of the floodplain forests are used for several purposes [16,21,42], but only a few timber species are of commercial interest. These include *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Virola surinamensis* (Rol. ex Rottb.) Warb. (Myristicaceae), *Calophyllum brasiliense* Cambess. (Clusiaceae) and *Cedrela odorata* L. (Meliaceae). Due to unsustainable logging practices, lack of information about growth rates and regeneration, these species disappeared from local and regional markets within a few decades [17]. These were then replaced in the harvest by others such as *Hura crepitans* L. (Euphor-

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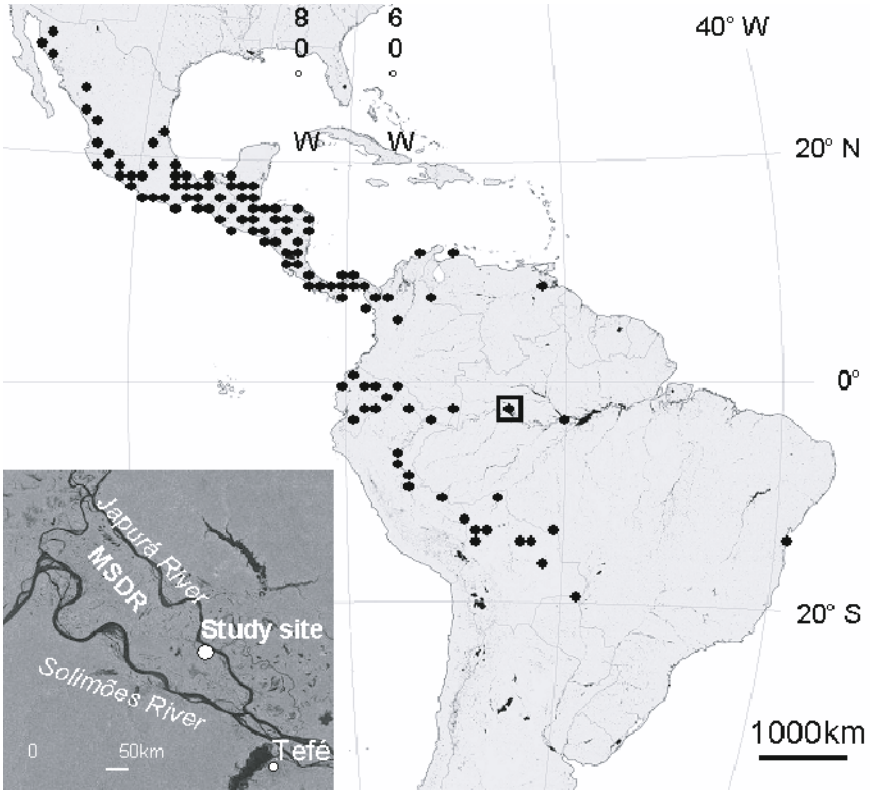

Figure 1. Occurrence of *Ficus insipida* in the Neotropics (data from the Missouri and New York Botanical Gardens). Study site in the Mamirauá Sustainable Development Reserve (MSDR) is located at the confluence of the white-water rivers Japura and Solimões in the Central Amazon basin.

biaceae), *Couroupita subsessilis* Pilg. (Lecythidaceae), *Ocotea cymbarum* Mez (Lauraceae) and *Sterculia elata* Ducke (Malvaceae) [1, 2, 42]. Management of natural forests and timber resources in the Brazilian Amazon is regulated by legal restrictions and normative instructions requiring a polycyclic system with a cutting cycle between 25–35 years and minimum logging diameters of 45–50 cm [27, 42].

A timber species with increasing importance for the Amazonian plywood sector is *Ficus insipida* Willd. (synonym *Ficus antelminthica* Mart.), Moraceae, with a wood density of 0.38 ± 0.03 g cm^{-3} [22]. Though generally a riparian species in early successional stages of the Central and Western Amazonian várzea [26, 34], *F. insipida* is frequent in diverse forest types of the Neotropics (Fig. 1).

The predictable several months long annual flooding, defined as flood-pulse [14], results in phenological, morphological and physiological responses in tree species [28, 40]. Flooding causes annually recurring anaerobic conditions for the roots, hinders the water-uptake by the root hairs and leads to leaf shedding [39]. This ultimately results in a cambial dormancy [28] and the formation of an annual tree ring boundary in the wood during the flooded period [29, 39]. Tree growth starts immediately after leaf flush at the end of the flooded period (July/August) and monthly diameter increment rates remain high during the terrestrial phase (vegetation period) starting within the dry season (August) and ending within the rainy season (February/March) [28]. Ring width corresponds to the length of the vegetation period, which is prolonged during El Niño years [29]. The existence of annual tree rings allows the application of dendrochronological methods to determine tree age and growth rates [25, 39].

In the present study we analyze stand structure, floristic composition and regeneration of an early successional stage dominated by *F. insipida.* Growth parameter models for *F. insipida* in diameter, tree height and volume are based on ring-width measurements. From these models we derive specific management recommendations for the cutting cycle in terms of an optimum minimum logging diameter (MLD) for this species. Based on results of our structure analysis and growth modeling we discuss the development of a specific management plan for *F. insipida*, and compare it with current management practices in the study area.

2. STUDY SITE AND METHODS

2.1. Study site

The study was conducted in the Mamirauá Sustainable Development Reserve (MSDR), located between the Solimões and the Japurá Rivers at their confluence, approximately 70 km northwest of the city of Tefé, in the Brazilian Amazon (Fig. 1). The climate in the study area is characterized by a mean daily temperature of 26.9 °C and an annual precipitation of almost 3 000 mm, with a distinct dry season during July-November. Mean amplitude of the annual water fluctuation is 11.38 m for the period 1993–2000 (data: Institute for Sustainable Development Mamirauá – ISDM). The MSDR was founded in 1990 and comprises 11 240 km^2 of várzea floodplains. Since 1992 the ISDM has commenced a variety of community-based management systems in the MSDR for fishery, agriculture, agro-forestry, eco-tourism and forestry based on socio-economic and biological-ecological studies [3]. The forest management program established in 1998 is a polycyclic selection system [10, 17] with a MLD of 45 cm and a cutting cycle of 25 years with a maximum yield of 5 trees ha^{-1}. These restrictions are based on legal regulations and normative instructions established by the Brazilian Federal Environmental Institute (IBAMA). Commercial timber species facing extinction such as *C. odorata, C. brasiliense, C. pentandra, V. surinamensis*, *Platymiscium ulei* Harms (Fabaceae) and *Xylopia frutescens* Aubl. (Annonaceae) are excluded from the forest management [42]. The most important timber species logged in the year 2003 were mainly low-density wood species (*F. insipida*, *H. crepitans*, *C. guinanesis*, *Maquira coriacea* (H. Carst.) C.C. Berg (Moraceae)) and some high-density wood species including *O. cymbarum*, *Calycophyllum spruceanum* (Benth.) Hook. f ex K. Schum. (Rubiaceae) and *Piranhea trifoliata* Baill. (Euphorbiaceae). Wood prices in 2007 at the riverbank for low-density timber species ranged between R$ 30.00 m^{-3} and R$ 45.00 m^{-3} (US$ 15.00–22.50 m^{-3}), high-density timber species were sold for R$ 62.00 m^{-3} (US$ 31.00 m^{-3}) (1 US$ = R$ 2.00).

2.2. Structure analysis

The study was conducted in a natural early successional stage near the Japurá River (02° 54' S, 64° 53' W) that submerges annually for 144 days by an average flood-height of 3.50 m [27] defined as low várzea forests [38]. Despite the small-scale geomorphological variation of the floodplains, várzea forests are dominated by a high proportion of generalists, widely distributed tree species [38] such as *F. insipida* (Fig. 1). Especially the low várzea exhibits high floristic similarity over large geographic distance due to long-distance dispersal by currents and fishes [2, 38]. Thus the studied stand is representative for large areas of várzea floodplains in Central Amazonia. The stand is a result of primary succession that developed on recently deposited sediments because of the changing river channel [26]. The stand is more or less even-aged with an age of 20 ± 3 years, determined using ring counting of more than 100 individuals of dominating tree species such as *Pseudobombax munguba* (Mart. & Zucc.) Dugand (Malvaceae), *Luehea cymulosa* Spruce ex Benth. (Malvaceae) and *Nectandra amazonum* Nees (Malvaceae) [27] which form annual tree rings as a consequence of the annual long-term flooding [28, 39]. In a 1-ha area divided into 16 quadrates (25 m × 25 m = 625 m^2) all trees $\geqslant$ 10 cm diameter at breast height (dbh) were mapped and inventoried, measuring dbh with a diameter tape and total tree height with a Blume Leiss BL 6 (Zeiss, Jena). In the center of each plot a circular subplot was marked (area of 62.5 m^2), where forest regeneration (> 1 m tree height and < 10 cm dbh) was registered, giving a total sample area of 1 000 m^2. For every tree with representatives $\geqslant$ 10 cm dbh we determined absolute and relative frequency, abundance and dominance values to calculate the Importance Value Index (IVI) [7].

2.3. Dendrochronological analyses and growth modeling

Two wood cores were sampled from 30% of the individuals of *F. insipida* from different size-classes ($n = 18$ trees) with an increment borer (diameter 5 mm) at dbh. To avoid growth anomalies cores were taken at regular formed segments of the bole. At larger trees cores were sampled at circumferences above the buttresses achieving up to 3 m above the ground. The samples were glued on a wooden support and polished consecutively with sandpaper (up to a grain of 600). Tree ring structure was analyzed by wood anatomical patterns, defined as alternating fiber and parenchyma tissues as is typical for the family Moraceae [39] (Fig. 2). The ring width was measured to the nearest 0.01 mm using a digital measuring device (LINTAB) supported by additional software for time series analyses and presentation (TSAP). The measured annual current increments on two cores were averaged and summed for every tree to construct individual cumulative diameter growth curves. From a total of 465 ring-width measurements a mean diameter growth curve was calculated and fitted to a sigmoidal regression model. The relationship between dbh and tree height of 54 individuals was adapted to a non-linear regression. Combining the diameter growth model with the dbh-height relationship results in a model to estimate height growth of *F. insipida*. The basal area was multiplied by the tree height and a reduction factor of 0.6 to estimate the volume for every tree age [5, 20]. From the models for dbh, height and volume growth we derived the mean annual increment *MAI* and the current annual increment *CAI* by the following equations [24]:

$$MAI = \frac{CGW_t}{t} \tag{1}$$

$$CAI = CGW_{t+1} - CGW_t \tag{2}$$

where *CGW* is the cumulative growth in different years *t* over the entire life span. Growth modeling was performed with the software program X-Act (SciLab).

3. RESULTS

3.1. Species composition and stand structure

A total of 838 trees ha^{-1} $\geqslant$ 10 cm dbh, belonging to 30 tree species and 19 families were recorded in the 20 year-old stand at an early successional stage. The frequency, abundance, dominance and the *IVI* of the five most frequent tree species are presented in Table I. The highest tree densities were characterized by *L. cymulosa* and *P. munguba*, the two species comprising almost 52% of the total abundance. From *F. insipida* 56 individuals were registered with a basal area of 8.4 m^2 ha^{-1}, corresponding to 27.6% of the stand's basal area (30.5 m^2 ha^{-1}). The five most frequent tree species comprised 79% of the total abundance, 82% of the stand's basal area and almost 69% of the total *IVI*. The diameter distribution of the stand showed a J-reverse pattern characterized by an exponential decreasing tree density with increasing diameter class (Fig. 3a). The average dbh of the *Ficus* population was 40.1 cm with 16 individuals exceeding the MLD of 50 cm while the other tree species had a mean dbh of only 19.2 cm. The greatest contribution to total basal area of *F. insipida* was found at a dbh between 55 and 59 cm, for the other species at

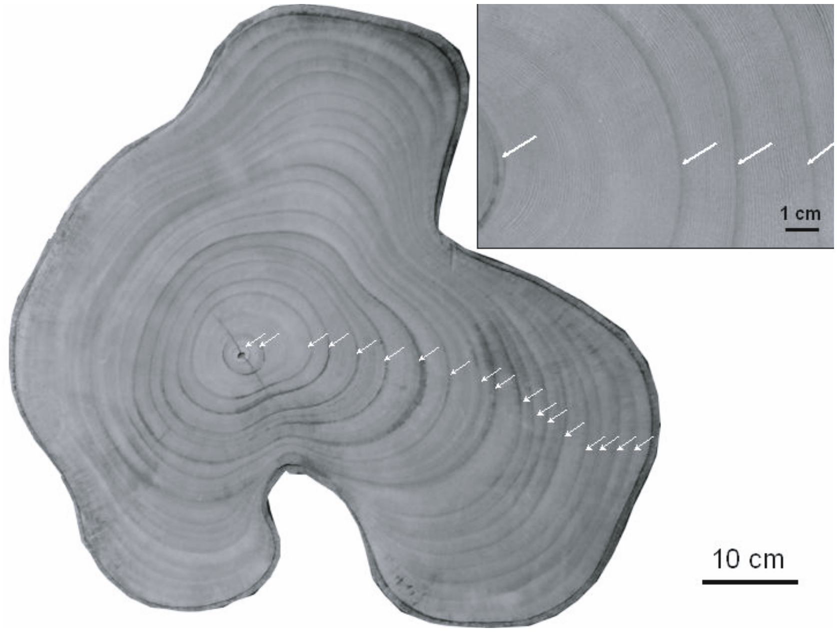

Figure 2. Cross section of a 19 year-old *Ficus insipida* with a dbh of 58 cm. Tree rings are characterized by alternating fiber and parenchyma bands (right above) allowing a confidential tree-ring analysis. Arrows indicate the ring boundaries.

Table I. Absolute and relative frequency, abundance (tree density) and dominance (basal area) of the five most important tree species of a 1-ha plot in a 20 year-old early successional stage ranged by the Importance-Value-Index (IVI = rel. frequency + rel. abundance + rel. dominance).

		Frequency		Abundance		Dominance		IVI	
Tree species	Family	abs.	rel.	*n*	rel.	m^2	rel.	abs.	rel.
Luehea cymulosa	Malvaceae	100	9.8	245	29.2	5.13	16.8	55.8	18.6
Pseudobombax munguba	Malvaceae	100	9.8	190	22.7	6.50	21.3	53.7	17.9
Ficus insipida	Moraceae	81.25	7.9	56	6.7	8.41	27.6	42.2	14.1
Nectandra amazonum	Lauraceae	87.5	8.5	119	14.2	3.25	10.7	33.4	11.1
Rhodostemonodaphne sp.	Lauraceae	93.75	9.1	54	6.4	1.74	5.7	21.3	7.1
Five most important tree species		462.5	45.1	664	79.2	25.03	82.1	206.4	68.8
Total stand (30 tree spp.)		1025.0	100.0	838	100.0	30.5	100.0	300.0	100.0

a dbh between 20 and 24 cm (Fig. 3b). The average height of the stand was 14.8 ± 4.5 m, with maximum tree heights over 25 m (*F. insipida*).

Species composition of forest regeneration differs considerably from that of trees $\geqslant$ 10 cm dbh. On the entire regeneration research area of 0.1 ha we recorded 230 individual saplings (corresponding to 2 300 individuals ha^{-1}) belonging to 20 tree species and 16 families. Most of the species recorded within the regeneration component are absent from the mature flora. However, frequent tree species present in both the mature flora and the regeneration were *Ilex inundata* Poepp. ex Reissek (Aquifoliaceae), *L. cymulosa*, *N. amazonum* and *P. munguba*. No representatives of *F. insipida* are found within the younger recruiting, regeneration age classes.

3.2. Growth models of *Ficus insipida*

Tree age of *F. insipida* varied between 3 and 20 years. The relationship between tree age and dbh of *F. insipida* is statistically significant ($r = 0.82$, $P < 0.001$) allowing the modeling of cumulative diameter growth curves (Fig. 4a). After 15 years an average tree reaches the current MLD of 50 cm. From the mean diameter growth curve we derive the current and mean diameter increment (Fig. 4b). Trees reach their maximum current diameter increments at an age of 4–5 years with a rate averaging 4 cm $year^{-1}$, while the highest increment rate observed exceeded 8 cm $year^{-1}$. Diameter and total tree height for diameters varying between 10.9 and 73.3 cm (corresponding ages between 3 and 20 years) is significantly correlated ($r = 0.74$, $P < 0.001$) and described by a non-linear regression model (Fig. 4c). Substituting the dbh variable in the diameter growth model (Fig. 4b) by the significant relationship between dbh and tree height (Fig. 4c) results in a model for height growth (Fig. 4d). Current height increment peaks at an age of 2 years, with rates of almost 3.5 m $year^{-1}$. The combination of the regression analyses of the age-dbh and dbh-height relationships results in a volume growth model for the entire life span (Fig. 4e). The optimal period to harvest the trees is at the peak

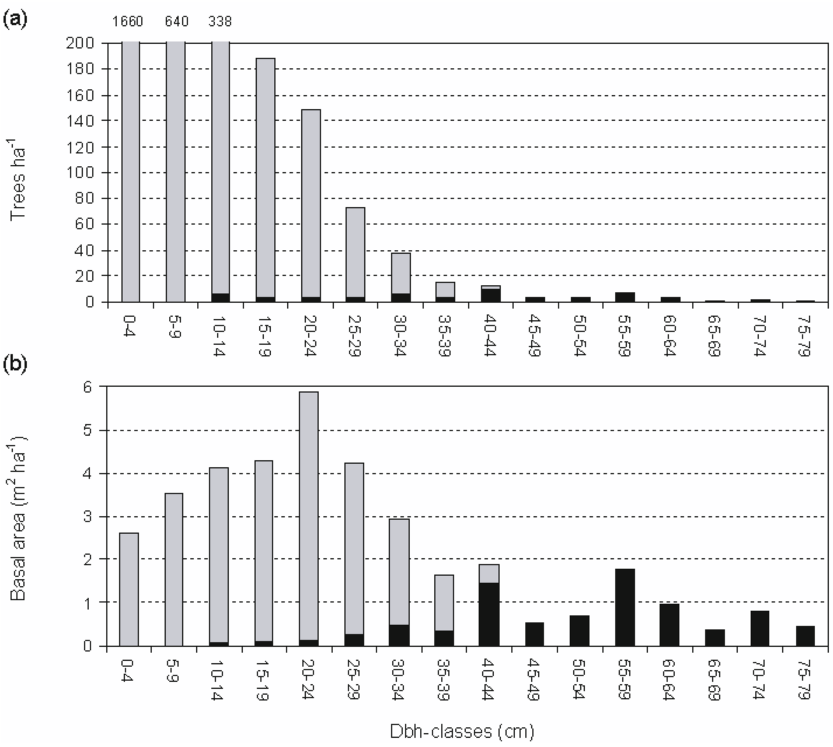

Figure 3. Distribution of (**a**) tree densities and (**b**) basal area of *Ficus insipida* (black bars) and other tree species (gray bars) for 5 cm dbh classes in the 20 year-old early successional stage.

of the current volume increment [30, 31], when trees of *F. insipida* have an average age of 17 years. The diameter at the maximum current volume increment indicates the preferred time for logging, and corresponds to a dbh of 55 cm, this derived from the model for diameter growth (Fig. 4b), which would be an appropriate MLD for this species. The cutting cycle, calculated by the mean passage of time through 10 cm dbh classes until the tree reaches the MLD of 55 cm (Fig. 4b), is 3.1 years.

4. DISCUSSION AND CONCLUSION

The development of sustainable forest management systems requires data about wood production of stands and single tree species. Polycyclic silvicultural systems practiced in the tropical forests so far manage a large number of timber species with only one fixed cutting cycle, and one defined MLD [10, 17, 36]. However, these time and diameter limitations are estimations or legal restrictions rather than being derived from scientific data. The definition of species-specific and site-specific management criteria based on wood growth data and structural analysis of the natural stands in the tropics is quite rare [20, 30, 32]. In this study we show how management criteria can be defined on species-specific basis by growth models employing dendrochronological analyses. The application of tree-ring data to define management options for tropical timber species is not a new discovery. During 1855–1862 in the British colony Burma (today Myanmar), Dietrich Brandis (1824–1906) had already developed a specific management plan for teak (*Tectona grandis* L., Verbenaceae). From stand inventories performed along transects (linear taxation) and ring counting of stumps, he estimated a cutting cycles of 24 years (mean passage time through a size class) and a MLD of 4 cubits (~58.8 cm) to guarantee the sustainable use of the teak stocks [8, 11].

The existence of annual growth rings of tree species in Central Amazonian floodplain forests has been demonstrated for many evergreen and deciduous tree species [28, 29, 39–41, 43] using a combination of independent dendrochronological methods such as wood anatomical descriptions, cambial wounding, measurements of the cambial resistance, radiocarbon dating, phenological observations, densitometry and climate-growth relations. The existence of annual tree rings allows the application of dendrochronology to model tree growth in the Amazonian floodplain forests [27]. Due to the controversial discussion existing in literature about the existence of annual tree rings in the wood of tropical tree species, the application of dendrochronological methods to model tree growth is quite rare in the tropics. Simulations of diameter growth curves based on tree-ring data so far exist only for some tree species in Cameroon [43], Zimbabwe [33], Tanzania [30], Venezuela [41] and the Central Amazonian floodplains [28, 42]. The majority of growth models are based on indirect methods such as repeated diameter measurements of trees from different size classes, this performed during some years in permanent sample plots to simulate growth trajectories [6, 18, 20, 31, 32]. These models however represent only a

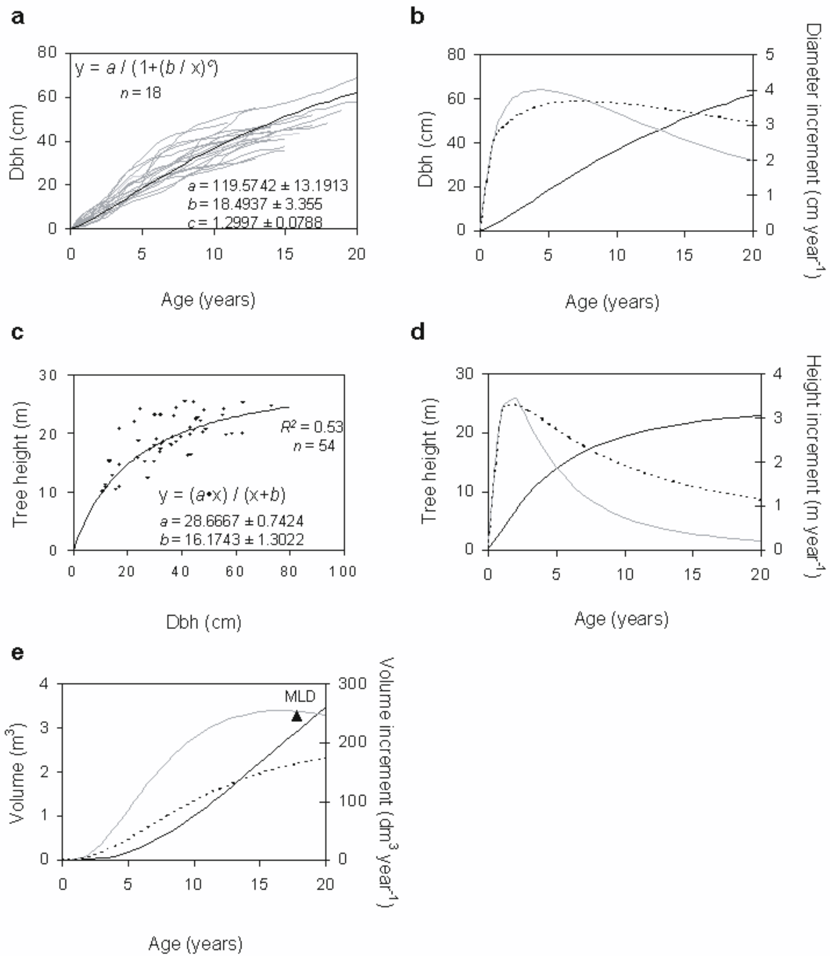

Figure 4. (**a**) Cumulative diameter growth curves of 18 individuals of *Ficus insipida* (gray lines) and the mean curve (black line), fitted with a sigmoidal regression model. (**b**) Model of diameter growth (black line), current annual increment *CAI* (gray line) and mean annual increment *MAI* (spotted line). (**c**) Relationship between diameter and tree height of 54 individuals, fitted with a non-linear regression analysis. (**d**) Model of height growth (black line), current height increment (gray line) and mean height increment (spotted line). (**e**) Volume growth model derived from the diameter growth model combined with the height growth model (volume was estimated by the basal area multiplied with the tree height and a form factor of 0.6). The minimum logging diameter is defined in the peak of the current volume increment.

short period of tree growth, while tree-ring analysis applied in this study describes the growth of an individual over its whole life span.

The derived management criteria from the growth models for *F. insipida* show discrepancies to the currently practiced forest management (cutting cycle of 25 years, MLD of 50 cm). The volume growth model indicates that trees of *F. insipida* with a diameter of 50 cm still have not reached their optimum volume increment rate. A cutting cycle of 25 years is inappropriate and inefficient for managing the timber resources of this fast-growing tree species. The estimated cutting cycle derived from the growth model is only 3.1 years, calculated as the mean passage time through 10 cm dbh classes. However, polycyclic selection systems are appropriate for shade tolerant timber species with a characteristic J-reverse pattern in the density distribution [36]. Natural regeneration of *F. insipida* is absent. The most reasonable explanation for this are the unfavorable light conditions on the forest floor, which experiences only a 17.3 ± 4.2% level of relative photosynthetically active radiation compared to that reaching open disturbed areas or the canopy roof [37]. The harvest level of 5 trees ha^{-1} maximum, would probably not create the favorable light conditions needed on the forest floor for a successful regeneration of *F. insipida*. Thus, a polycyclic selection system is not appropriate for the management of this fast-growing tree species. *F. insipida* is a shade intolerant/light demanding pioneer naturally occurring in more or less even-aged young successional stages in the Amazonian floodplain forests [26, 34] and thus adequate for a monocyclic silvicultural system [17, 36]. The application of a monocyclic system for *F. insipida* could be a rotation period of 17 years when trees reach their optimum volume increment rates. Monocyclic systems should, however, avoid clear-cuts, because young successional stages are mostly located close to the river margins where they have an important ecological function to protect the soils against erosion. A modified monocyclic system could be the logging of all *F. insipida* with dbh over 55 cm creating large gaps in the stand to favour the regeneration of light-demanding tree species such as *F. insipida*. The enlargement of these gaps could be repeated in 2-3 intervals of 3 year corresponding to the mean passage time through 10-cm dbh classes until the previous stand is completely removed and substituted by a new stand which has grown up during that period. In that phase enrichment-plantings with *F. insipida* are thinkable to improve the regeneration with a higher level of economic tree species if natural regeneration is absent. Further studies should therefore focus on the germination, growth and mortality rates of seedlings of *F. insipida* and their relationship to environmental factors (light, inundation) [37]. This would help to develop an appropriate silvicultural treatment based on scientific data increasing the sustainability of the participative forest management in the MSDR leading to higher incomes and benefits for the local populations and maintaining the forest's multiple ecological functions. The new established Normative Instruction No. 5, from December 11 2006, enables a management plan for timber resources applying cutting cycles of 25–35 years with a maximum yield of 30 m^3 ha^{-1}, or alternatively a low impact management with a cutting cycle of 10 years not exceeding 3 trees ha^{-1} (the maximum yield is 10 m^3 ha^{-1}, for the vàrzea higher yields are possible but are restricted to 3 trees ha^{-1}). However these management options are still not sufficient to allow an efficient management of the fast growing timber resource of *F. insipida*.

Timber exploitation in most non-flooded Amazonian forests (terra firme) faces the problem of the soil's low nutrient status, leading to rapid depletion of nutrient stocks after removal of large amounts of wood biomass [19]. In the nutrient-rich várzea the annual floods replace the loss of nutrients caused by wood extraction. The amount of deposited nutrients is sufficiently high to allow the long-term use of floodplain soils, even by monocultures of fast growing timber species [9]. The high tolerance against prolonged flooding and the high growth rate indicates the great potential of this species for reforestation of degraded floodplain areas such as abandoned areas traditionally used for agriculture and pasture. The plantation of the species in different forms (enrichment plantations, monocultures) in combination with other flood tolerant timber species or agro-forestry systems can help to decrease the pressure on the few remaining areas of intact floodplain forests. In addition, a further benefit to be gained would be the improvement of the economic situation of the local riverine population in a relatively short period.

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