## Strategies to Maximize the Wood Production in Amazon Forest

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## Research

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## TITLE PAGE

## Strategies to maximize the wood production in Amazon forest

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## To the Editor-in-Chief:

Dear Sir,
We would like to submit the manuscript "Strategies to maximize the wood production in Amazon forest" to possible publication in the Forest Ecosystems Journal, we strongly believe our theme fits within its scope.

We confirm that the manuscript was not published or it is not under evaluation elsewhere in substantially the same or abbreviated form, either in print or electronically. The innovation of this paper was the use of the analysis of the original structure of the forest combined with growth models to predict the optimal wood production in Amazon forest. It may be used by forest managers and forest law-makers, aiming to maximize sustainable wood production in the Amazon Forest.

Forest Ecology and Management was the most cited journal in our paper and

Sincerelly,<br>Patrícia Póvoa de Mattos

## Strategies to maximize the wood production in Amazon forest


#### Abstract

Background: This study aimed to develop a procedure to determine which logging diameter would achieve optimal wood production by species, aiming to support sustainable management of the Amazon forest. Two main methodologies of analysis by species were combined: probability density function (PDF) and growth modeling. The growth models were used to derive the volume increment curves at the individual tree level. To detect the points of maximum annual increment in volume at the population tree level we used PDF with adjusted growth equations.


Results: The population maximum annual volumetric increments occurred in smaller diameters compared to that of the individual-level. When combining shorter cutting cycles with the population biological rotation point considered as the minimum cutting diameter (MCD), we observed higher annual increments in volume than that achieved using the Brazilian law criteria $(\mathrm{MCD}=50 \mathrm{~cm})$ or other MCD tested.

Conclusion: The procedure proposed may be used by forest managers and forest lawmakers, aiming to maximize sustainable wood production in the Amazon forest.

Keywords: dendrochronology; forest modeling; minimum cutting diameter

## Background

Natural forests are steadily accumulating biomass, reflected in the production of carbon and wood. The forest functions must be maintained after logging, and the remaining stocks must allow a continuous production of wood for the next interventions, ensuring forest management sustainability (Ong; Kleine, 1996; Van Gardingen et al., 2006; Braz et al., 2015; Avila et al., 2017). The management must be carefully planned and be
consistent with the initial natural forest structure (e.g., density, diametric distribution, growth, mortality, and regeneration) of the species of interest (Seydack et al., 1995; Bick et al., 1998).

According to Seydack (2012), a challenge for forestry scientists is to combine modeling and simulation tools to understand tropical forest dynamics, enabling production maximization. Minimum cutting diameters (MCD) should be defined for all commercial species, representing a powerful tool in maximizing increment for tropical forests under management as in the Amazon region.

Knowledge of the natural forest balance allows identification of the ideal moment of intervention and its production potential (Bick et al., 1998). The forest balance equation depends on how tree increment occurs over time. Studies of species growth at individual-level, structure, and reproductive biology are the basis for defining the management guidelines that guarantee sustainability for wood production in tropical forests (Vanclay, 1989; Miranda, D. L. C. et al., 2018; Dionisio et al., 2018).

Forest growth goes through youth, maturity, senescence, and stagnation phases. Its basic unit is the tree, which has a distinct sigmoidal growth pattern, tending to a biological limit (Odum, 1988). Trees that were established decades ago will grow within the ingress criteria for classes with larger diameters, will stagnate or eventually die. Thus, a diametric distribution of natural forest is the result of several tree establishments over different periods.

Diametric distribution is a useful factor to describe the forest properties since the diameter is easily obtained and correlated with other variables such as volume, which defines the economic value of the forest area (Bailey; Dell, 1973). Diameter is widely used in the forest sector to assess the effect of environmental and anthropogenic disturbances (Kohyama, 1986; Coomes et al., 2003; Wright et al., 2003; Bettinger et al.,

2009; Hossain et al., 2015), to describe successional patterns (Kohyama, 1986; Wright et al., 2003; Wang et al., 2009) and for the prediction of the future stock of a stand (De Liocourt, 1898; Meyer, 1952; Carvalho, 1981; Condit et al., 1998; Bettinger et al., 2009; Hossain et al., 2015; Orellana; Figueiredo Filho, 2017). However, future stock projection is difficult for tropical forest due to its great diversity (Orellana, Figueiredo Filho, 2017). Moreover, information about individual species distribution pattern is scarce.

Describing forest growth trajectory requires long-term information when permanent plots are used as data source (Bick et al., 1998). The successive measurements can make it difficult or even imply a failed simulation, due to the time spent to replicate a structure that represents the initial diametric classes up to the biological diameter limit of the species (Brienen; Zuidema, 2006a; Miranda D. L. C. et al., 2018).

Most studies of the species forest growth in the Amazon basin were carried out with permanent plots (Silva, 1989; 1997; Higuchi, 1996; Fortini et al., 2015; Avila et al., 2017; D'Oliveira et al., 2017) and supported the management guidelines in the Brazilian legislation (Silva, 1989, 1997; Higuchi, 1996). However, in some species less than one individual per hectare occurs in Amazonian primary forest structure, especially when considering trees with commercial dimensions (Miranda, D. L. C. et al., 2018), and extensive sample areas are therefore required to properly represent a population of individual species (Groenendijk et al., 2017; Miranda, D. L. C. et al., 2018.).

In addition to area size, time scale is also a limiting factor in studying forest dynamics with permanent plots (Brienen; Zuidema, 2006a; Miranda, D. L. C. et al., 2018). In Brazil, permanent plots monitored for more than 40 years are rare. These periods are short compared to the age of commercial trees, which are rarely less than 100 years old (Brienen; Zuidema, 2006a; Schöngart, 2008; Rosa et al., 2017).

Growth series obtained by dendrochronology became more popular as an alternative to permanent-plot data to supply the demand for information and growth models of species (Brienen, 2005; Brienen; Zuidema, 2006a; Schöngart, 2011; Mattos et al., 2015; Canetti et al., 2017; Groenendijk et al., 2017; Miranda, D. L. C. et al., 2018). Growth ring analysis is a fast and reliable tool for assessing tree age, determining its growth rates over the life cycle, and identifying growth differences between species (Groenendijk et al., 2017; Rosa et al., 2017).

This study aimed to develop a procedure based on the diametric structure and growth models to set the minimum cutting diameter (MCD) for optimal wood production. The procedure was tested on four species in the Brazilian Amazon. The results may be used as a basis for forest management plans and to aid in the revision and modernization of forest law in countries with humid tropical forests.

## Methods

This study was conducted in the Sinop micro-region ( $11^{\circ} 50 \mathrm{~S} ; 54^{\circ} 50^{\prime} \mathrm{W}$ ), Mato Grosso (MT) state, within the Brazilian Legal Amazon. The region comprises 9 municipalities, encompassing nearly 40 thousand $\mathrm{km}^{2}$ (IBGE, 2010). The region's vegetation is characterized by a transition zone between open tropical rainforest and deciduous tropical rainforest, and is the largest area composed of this ecotone in the world (IBGE 1992; SIVAM 2002). The micro-region presents flat relief and tropical climate with a dry season between autumn and winter (Alvares et al., 2013). All compartments from which data were collected were included in sustainable forest management plans authorized by the State Environmental Agency (SEMA-MT).

The species Apuleia leiocarpa (Vogel) J.F. Macbr., Erisma uncinatum Warm., Hymenolobium excelsum Ducke, and Trattinnickia burserifolia Mart. were studied.

Together, these species represent $25 \%$ of the commercial volume logged in the microregion of Sinop, the second-largest tropical wood production hub in Brazil (Ribeiro et al., 2016).

## Fitting probability density function of the diametric structure of species

The data were obtained from $100 \%$ inventories of six forest compartments carried out in the municipalities of Santa Carmem, Sinop, and União do Sul, totaling 5,432 ha. Forest inventories were conducted from 2011 to 2014, by measuring all trees with diameter at 1.30 m above ground level $(\mathrm{dbh}) \geq 40 \mathrm{~cm}(\mathrm{n}=3,617$ for A. leiocarpa, 13,655 for $E$. uncinatum, 1,814 for $H$. excelsum, and 16,162 for T. burserifolia).

Data from sample units of 0.25 ha ( $10 \mathrm{~m} \times 250 \mathrm{~m}$ ) were also used to complement the densities of the smaller diameter trees ( $20 \leq \mathrm{dbh} \leq 40 \mathrm{~cm}$ ), not covered in the $100 \%$ inventories. These plots were measured in four compartments in the municipalities of Santa Carmem and Feliz Natal, MT. All trees with $\mathrm{dbh} \geq 20 \mathrm{~cm}$ were measured. Altogether, data from 138 plots were used, adding up to 36 ha inventoried. On average, there were 35 trees ha ${ }^{-1}$ with $20 \leq \mathrm{dbh}<40 \mathrm{~cm}$ ( 5 of $A$. leiocarpa, 11 of $E$. uncinatum, 4 of $H$. excelsum, and 121 of $T$. burserifolia).

The dbh data for each species were grouped into diametric classes of 10 cm -range to fit probability density functions (PDFs). Normal, Beta, Gamma, Log-Normal, Johnson's SB, and Weibull with three parameters (Scolforo, 1998) PDFs were fitted. The diametric structure of each species included the largest diameter class in which live individuals were found in the $100 \%$ inventories. To avoid total numbers of individuals less than one tree per ha per species (as occurred for A. leiocarpa and H. excelsum), the densities of individuals were considered on a 10 -ha scale (i.e. number of trees $10 \mathrm{ha}^{-1}$ ).

The goodness-of-fit tests of PDFs by species were performed in two steps, using the Kolmogorov-Smirnov test $(\alpha=0.05)$. Initially, the goodness-of-fit of the theoretical

PDFs to the empirical data was tested in each forest compartment. In the second stage, the goodness-of-fit of the PDFs fitted to the data of the entire Sinop micro-region (i.e., for the total data set) were tested considering sample inventories and $100 \%$ inventories. The best PDF for each species was selected based on the lowest maximum absolute value between theoretical PDF and observed data ( $\mathrm{D}_{\text {calc. }}$. For Kolmogorov-Smirnov test) and lowest error index (Reynolds et al., 1988).

## Modeling diametric growth by species

Stem sections (discs) with approximately $5-\mathrm{cm}$ thick were collected from trees from different forests compartments in the Sinop micro-region. These samples were obtained from the base of the first commercial log, approximately 1 m above the ground level, or immediately above the sapopemas. We collected 9 discs samples from A. leiocarpa, 10 from E. uncinatum, 13 from H. excelsum, and 11 from T. burserifolia. The samples were dried and polished and the growth rings were measured with an accuracy of 0.01 mm on a LINTAB measurement table (Frank Rinn, Heidelberg, Germany), using the TSAPWin software (Rinn, 1996). Crossdating was carried out among radii of each tree and among trees.

The mean increment and passage time were analyzed by dbh class. We adjusted the growth models of Gompertz, Johnson-Schumacher, Lundqvist-Korf, Logistic, Monomolecular, and Schumacher for each species (Burkhart; Tomé, 2012).

The values of the asymptotes $\left(\beta_{0}\right)$ were fixed at the upper limit of the largest diametric class recorded in the $100 \%$ inventories used. To increase modeling accuracy, we used the non-parametric Bootstrap method with 100 interactions (Miller, 2004), previously used in studies of modeling growth in diameter (Brienen, 2005; Mattos et al., 2015; Canetti et al., 2017). The models were fitted by non-linear regression using the PROC NLMIXED procedure in the $\mathrm{SAS}^{\circledR}$ software. The most suitable growth model by
species was selected based on the relative residual standard error ( $\mathrm{S}_{\mathrm{yx} \%}$ ), corrected Akaike and Bayesian information criteria.

## Obtaining growth curves in individual volume for each species

Initially, the commercial height at each diameter was obtained to estimate the commercial volume at each age and to relate it to the diametric growth curve. The commercial height/dbh ratio of 30 trees (randomly selected) per species was fitted by non-linear regression (PROC NLMIXED procedure in the SAS ${ }^{\circledR}$ software) according to equation 1 (Schöngart, 2008). Of the 30 trees, four came from sampling inventories (20 $\leq \mathrm{dbh}<40 \mathrm{~cm}$ ) and 26 from $100 \%$ inventories ( $\mathrm{dbh} \geq 40 \mathrm{~cm}$ ). This selection method was adopted due to the difference of inclusion levels among inventories and the varying sizes of the measured areas.

To calculate the wood volume, we used commercial height and dbh for each age (obtained from the diametric growth equation), and taper functions developed for the municipality of Santa Carmem (MT) to calculate the wood volume. For E. uncinatum and T. burserifolia, we used species-level taper functions (equations 2 and 3, respectively) developed by Lanssanova (2012). For A. leiocarpa and H. excelsum we used the general taper function for the municipality (equation 4) developed by Lanssanova et al. (2018).

The $\mathrm{di} / \mathrm{dbh}$ ratio of the growth samples was applied to calculate the youngest diameters at the dbh, from which the volume at each age was calculated. As a result, the volume growth curve of the individual tree was obtained for each species. From the volume growth curves, the mean annual volume increment $\left(\mathrm{MAI}_{\mathrm{v}}\right)$ and current annual volume increment $\left(\mathrm{CAI}_{\mathrm{v}}\right)$ curves for individual trees were obtained according to equations 5 and 6.
$H=\frac{d b h \beta_{0}}{d b h+\beta_{1}}$

$$
\begin{align*}
& {\frac{d_{i}}{d b h_{\text {E.uncinatum }}}}=1.20+2.97 \frac{h_{i}}{H}+10.95\left(\frac{h_{i}}{H}\right)^{2}+21.15\left(\frac{h_{i}}{H}\right)^{3}+19.51\left(\frac{h_{i}}{H}\right)^{4}+6.80\left(\frac{h_{i}}{H}\right)^{5}  \tag{2}\\
& {\frac{d_{i}}{d b h_{T . b u r s e r i f o l i a ~}}}=1.13+1.89 \frac{h_{i}}{H}+7.16\left(\frac{h_{i}}{H}\right)^{2}+14.02\left(\frac{h_{i}}{H}\right)^{3}+12.56\left(\frac{h_{i}}{H}\right)^{4}+4.15\left(\frac{h_{i}}{H}\right)^{5}  \tag{3}\\
& {\frac{d_{i}}{d b h_{G e n e r a l}}}=1.21+2.94 \frac{h_{i}}{H}+10.94\left(\frac{h_{i}}{H}\right)^{2}+20.46\left(\frac{h_{i}}{H}\right)^{3}+17.93\left(\frac{h_{i}}{H}\right)^{4}+5.90\left(\frac{h_{i}}{H}\right)^{5}  \tag{4}\\
& M A I_{v}=\frac{v_{t}}{t}  \tag{5}\\
& C A I_{v}=v_{t+1}-v_{t} \tag{6}
\end{align*}
$$

where: $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm}) ; \mathrm{d}_{\mathrm{i}}=$ diameter at the sample collection height (disc sample, cm ); $\mathrm{h}_{\mathrm{i}}=$ height of sample collection (m); $\mathrm{H}=$ commercial height of the tree (m); $\beta_{0}$ and $\beta_{1}$ $=$ model parameters fitted by non-linear regression; $\mathrm{MAI}_{\mathrm{v}}=$ mean annual volume increment $\left(\mathrm{m}^{3}\right) ; \mathrm{CAI}_{\mathrm{v}}=$ current annual volume increment $\left(\mathrm{m}^{3}\right) ; \mathrm{v}_{\mathrm{t}}=$ accumulated commercial volume $\left(\mathrm{m}^{3}\right)$, at different ages; $\mathrm{t}=$ age (years), according to the diametric growth curve.

The age of biological rotation of individual tree was obtained at the intersection point of the $\mathrm{CAI}_{\mathrm{v}}$ and $\mathrm{MAI}_{\mathrm{v}}$ curves. If the age of biological rotation was not reached with the ages of the available samples, we extrapolated the growth equation in diameter to estimate that age. For the extrapolated diameters, the commercial volume and $\mathrm{CAI}_{v}$ and $\mathrm{MAI}_{\mathrm{v}}$ were calculated, following the same procedures.

## Obtaining growth curves in volume of the population of each species

To obtain growth in volume per unit area for the population of each species over time, individual growth curves in volume were associated with the PDFs. It was assumed that a species diametric distribution follows the same pattern that occurred in the past (Gotelli, 2008; Lundqvist, 2017). From this premise, the maximization of the population volume increments was obtained. The population was defined hereby as the number of trees from the first to the last diametric class in which there were individuals alive until the moment " t ".

The input of the PDFs is the dbh of the trees and the output is the estimated number of trees per unit area. The growth equations developed to generate the diameter values were used to estimate the number of trees alive at each time " t ", considering the species' growth curve. The procedure illustrated in Fig. 1 allowed us to estimate the population's diametric evolution over time (time x number of trees $\mathrm{ha}^{-1}$ ). As the actual diametric distributions were established with data from $\mathrm{dbh} \geq 20 \mathrm{~cm}$, the calculations were performed from that diameter, according to the following procedure:
I. The number of trees at each time " t " (identified by the PDF) was multiplied by the volume of the individual tree (v) at each time, resulting in the population production curve $(\mathrm{V})$ at each time referring to the species growth curve;
II. From the population volume production curve, $\mathrm{MAI}_{\mathrm{v}}$ and $\mathrm{CAI}_{\mathrm{v}}$ were derived (equations 5 and 6).

|  | Obtained from: |  |  |  | $\qquad$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\begin{gathered} \text { Pdf } \\ 2 \end{gathered}$ | Dbh growth equation < 5 |  | Taper equations , 5 | $\begin{aligned} & \mathrm{Nxv} \\ & 2 \end{aligned}$ |  |  |
| $\begin{gathered} \mathbf{N} \\ \text { (trees ha-l} \end{gathered}$ | $\begin{gathered} \text { Time } \\ \text { (years) } \end{gathered}$ | Dbh (cm) | $\underset{\left(m^{v}\right.}{ }$ | $\underset{\left(m^{3} h a^{-1}\right)}{V}$ | $\begin{gathered} \text { MAIv } \\ \left(\mathrm{m}^{3} \mathrm{ha}^{-1} \text { year }^{-1}\right) \end{gathered}$ | $\begin{gathered} \text { CAIv } \\ \left(\mathrm{m}^{3} \mathrm{ha}^{-1} \text { year }{ }^{-1}\right) \end{gathered}$ |
| 0.0955 | 70 | 27.8696 | 0.3783 | 0.0361 | $5.16 \times 10^{-4}$ | $1.86 \times 10^{-3}$ |
| 0.0957 | 71 | 28.4297 | 0.3971 | 0.0380 | $5.35 \times 10^{-4}$ | $1.88 \times 10^{-3}$ |
| 0.0958 | 72 | 28.9951 | 0.4166 | 0.0399 | $5.54 \times 10^{-4}$ | $1.91 \times 10^{-3}$ |
| 0.0958 | 73 | 29.5656 | 0.4368 | 0.0419 | $5.73 \times 10^{-4}$ | $1.93 \times 10^{-3}$ |
| 0.0957 | 74 | 30.1413 | 0.4577 | 0.0438 | $5.92 \times 10^{-4}$ | $1.95 \times 10^{-3}$ |
| 0.0955 | 75 | 30.7221 | 0.4793 | 0.0458 | $6.10 \times 10^{-4}$ | $1.97 \times 10^{-3}$ |

Fig. 1. Scheme showing the methodological process for obtaining the curves of volume increment of the population. The boxes with red outline inform the data source of the column to which the arrows are directed. $\mathrm{PDFs}=$ probability density functions; $\mathrm{N}=$ number of trees per hectare; $\mathrm{dbh}=$ diameter at 1.30 m above ground level; $v=$ volume of individual tree; $V=$ species population volume $\left(\mathrm{m}^{3} \mathrm{ha}^{-1}\right) ; \mathrm{MAI}_{\mathrm{v}}=$ mean annual volume increment; and $\mathrm{CAI}_{\mathrm{v}}=$ current annual volume increment.

Management simulations

The projection method by diametric class (Alder, 1995) was used to compare the volumetric increments obtained from the different combinations of cutting cycle and minimum cutting diameter (MCD), according to the following management scenarios:
I. $\mathrm{MCD}=50 \mathrm{~cm}$ and cutting cycle $=35$ years, according to current legislation (Brasil, 2006);
II. MCD defined by the biological rotation age of the population (intersection of the $\mathrm{MAI}_{\mathrm{v}}$ and $\mathrm{CAI}_{\mathrm{v}}$ curves) and cutting cycle $=35$ years;
III. MCD defined by the maximum $\mathrm{CAI}_{\mathrm{v}}$ and biological rotation age of the population and cutting cycle calculated using equation 7 (Schöngart, 2008).

Cutting cycle (years) $=\frac{\text { Age }_{\text {Max.CAIv }}}{0.1 d b h_{\text {Max.CAIv }}}$
where Cutting cycle (years) $=$ time interval between explorations in the forest (Schöngart, 2008); $\mathrm{dbh}_{\text {Max.CAlv }}=$ minimum cutting diameter, defined as the diameter at which the species reaches the maximum $\mathrm{CAI}_{v} ; \mathrm{Age}_{\text {Max.CAlv }}=$ age at which the species reaches the MCD .
IV. MCD defined by dbh in which the maximum CAIv occurs at the individual tree level and cutting cycle calculated according to Schöngart (2008);
V. MCD defined by the dbh of biological rotation age of the population in volume and increasing cutting cycles ( 10 to 70 years).

The mathematical procedure for simulations in the projection method by diametric class is presented in equation 8 (Alder, 1995).
$N_{k, t+1}=N_{k, t}+I_{k}-O_{k}-M_{k}-H_{k}$
where $\mathrm{N}_{\mathrm{k}, t+1}=$ number of trees in dbh class $k$ in period $t+l ; \mathrm{N}_{\mathrm{k}, \mathrm{t}}=$ number of trees in class $k$ in period $t ; \mathrm{I}_{\mathrm{k}}$ $=$ ingrowth in class $k$ during the period; $\mathrm{O}_{\mathrm{k}}=$ number of trees passing from class $k$ to subsequent classes, $\mathrm{M}_{\mathrm{k}}=$ mortality in class $k ; \mathrm{H}_{\mathrm{k}}=$ trees logged during the period.

The matrices were built from the $30-\mathrm{cm}$ dbh class, for every 5 years $(\mathrm{t})$, until reaching the desired cutting cycle. We considered the wood volume of trees with a dbh higher than the MCD the volume to be harvested $\left(\mathrm{H}_{\mathrm{k}}\right)$. The following data were used:
I. Initial diametric structure $\left(\mathrm{N}_{\mathrm{k}, \mathrm{t}}\right)$ : obtained from PDFs fitted by species, considering $\mathrm{dbh} \geq 30 \mathrm{~cm}$;
II. Mean increment by diameter class (obtained from the growth equations). The number of trees passing to the subsequent classes $\left(\mathrm{O}_{\mathrm{k}}\right)$ was calculated from the passage time between diametric classes (equation 9), as described by Alder (1995).

$$
\begin{equation*}
O_{k}=\frac{t . i}{w} \tag{9}
\end{equation*}
$$

where: $\mathrm{O}_{\mathrm{k}}=$ number of trees migrating from class $k$ to subsequent classes during the period considered; i $=$ mean increment $\left(\mathrm{cm}\right.$ year $\left.^{-1}\right)$ of the diametric class $k$ (obtained from the growth series); $\mathrm{w}=$ interval between diametric classes ( 10 cm in the present study); $\mathrm{t}=$ period considered.
III. Ingrowth $\left(\mathrm{I}_{\mathrm{k}}\right)$ : the number of trees in the $20-\mathrm{cm}$ diameter class (smallest dbh class obtained) was considered as ingrowth.
IV. Mortality $\left(\mathrm{M}_{\mathrm{i}}\right)$ : the mortality was estimated using equation 10 adapted from Lundqvist (2017).
$M_{i}=100\left(1-{\frac{N_{i+1} i_{i+1}}{N_{i} i_{i}}}^{\frac{2}{t_{i}+t_{i+1}}}\right)$
where: $\mathrm{M}_{\mathrm{i}}=$ percentage of annual mortality in diametric class $i ; \mathrm{N}_{\mathrm{i}}=$ number of trees in class $i ; \mathrm{N}_{\mathrm{i}+1}=$ number of trees in the class subsequent to $i ; \mathrm{i}_{\mathrm{i}}$ and $\mathrm{i}_{\mathrm{i}+1}=$ mean annual increment in diameter $(\mathrm{cm})$ of classes $i$ and $i+1$ (obtained from the growth equation); $\mathrm{t}_{\mathrm{i}}$ and $\mathrm{t}_{\mathrm{i}+1}=$ passage time (years) from the diametric classes $i$ and $i+1$ to the subsequent classes (obtained from the growth equation).

After obtaining the final diametric structure of the projection matrix by diametric class， the number of trees was converted into volume（applying the taper functions previously described）to obtain the total wood production in the considered period．This production was divided by the cutting cycles，in order to proportionally compare the production of the tested MCD and cutting cycles．

## Results

## Diametric structure

When testing the adherence of general probability density functions（PDFs）adjusted to the measured density distributions for each species and for each forest compartment，the majority of tested PDF fitted（Table 1）．The only exceptions found were the Normal function（all areas）and the Beta function（areas 3， 4 and 6）for T．burserifolia．

Table 1．Goodness－of－fit test of the probability density function（PDF）fitted considering the total data set to the observed diametric distributions in each study area by the Kolmogorov－Smirnov test．

| Species | D | PDF | Area 1 | Area 2 | Area 3 | Area 4 | Area 5 | Area 6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{gathered} \frac{5}{5} \\ \hline 0 \end{gathered}$ | Normal | 0.048 | 0.100 | 0.078 | 0.139 | 0.089 | 0.063 |
|  |  | Beta | 0.047 | 0.094 | 0.081 | 0.141 | 0.092 | 0.062 |
|  |  | Gamma | 0.054 | 0.100 | 0.070 | 0.154 | 0.077 | 0.054 |
|  |  | Log Normal | 0.075 | 0.109 | 0.080 | 0.167 | 0.060 | 0.048 |
|  |  | Johnson＇s SB | 0.045 | 0.095 | 0.075 | 0.147 | 0.085 | 0.060 |
|  |  | Weibull 3p | 0.044 | 0.095 | 0.076 | 0.145 | 0.087 | 0.061 |
|  |  | $\mathrm{D}_{\text {tab．}}$ | 0.410 | 0.410 | 0.521 | 0.565 | 0.432 | 0.375 |
| $\begin{array}{ll} \text { 音 } \\ \text { 音 } \\ \text { 音 } \\ & \end{array}$ | $\begin{gathered} \frac{5}{5} \\ 0 \end{gathered}$ | Normal | 0.049 | 0.256 | 0.084 | 0.055 | 0.082 | 0.044 |
|  |  | Beta | 0.072 | 0.190 | 0.151 | 0.107 | 0.026 | 0.050 |
|  |  | Gamma | 0.069 | 0.261 | 0.081 | 0.045 | 0.099 | 0.060 |
|  |  | Log Normal | 0.095 | 0.278 | 0.063 | 0.068 | 0.122 | 0.085 |



Area $=$ sampled forest compartment; Dcalc. $=$ maximum absolute value between fitted PDF and observed values in each compartment; Dtab. $=$ critical value of Kolmogorov-Smirnov test $(\alpha=0,05) ; *=$ the PDF did not fit to the observed values (Dtab. $\leq$ Dcalc.).

When considering the adherence of all PDFs tested to the total set of observed data by species all functions fitted. The Gamma function fitted better to the observed data for $A$. leiocarpa, the Normal function for E. uncinatum and $H$. excelsum, and the Weibull with three parameters for T. burserifolia (Fig. 2). A unimodal pattern was observed for the diametric distributions of A. leiocarpa, E. uncinatum, and H. excelsum. On the other hand, T. burserifolia decreased in a regular number of trees, similar to the negative


Fig. 2. Probability density functions with better fitting for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C) and Trattinnickia burserifolia (D). Dbh $=$ diameter at 1.30 m above ground
level $(\mathrm{cm}) ; \Gamma=$ gamma function; Dcalc. $=$ maximum absolute value between fitted pdf and observed values in each compartment; $\mathrm{IR}=$ error index (Reynolds et al., 1988).

## Height/dbh ratio

The fitted height/dbh model showed satisfactory statistics and residual distribution for all species (Fig. 3). The species that reached the highest commercial heights were $E$. uncinatum and $H$. excelsum. The largest commercial height range occurred before reaching $60-\mathrm{cm} \mathrm{dbh}$, ranging from 6.5 to 10.9 m . After $60-\mathrm{cm} \mathrm{dbh}$, the commercial heights tended to stabilize, ranging from 10.9 to 13.4 m .


Fig. 3. Heigh/dbh models of Apuleia leiocarpa, Erisma uncinatum, Hymenolobium excelsum, and Trattinnickia burserifolia. $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm}) ; \beta_{0}$ and $\beta_{1}=$ equation parameters fitted by non-linear regression; $\mathrm{S}_{\mathrm{yx} \%}=$ relative residual standard error (\%)

## Diametric increment in dbh classes

The mean increment by dbh class and passage time are shown in Fig. 4 and 5. Apuleia leiocarpa presented an initial increase in dbh increment, and a decrease for the upper diameter classes (Fig. 4A), characterizing the U shape for the passage time (Fig. 5A). Erisma uncinatum, H. excelsum, and T. burserifolia showed a higher increase in the upper classes (Fig. $4 \mathrm{~B}, \mathrm{C}$ and D), assuming a decreasing passage time (Fig. $5 \mathrm{~B}, \mathrm{C}$ and D).





Fig. 4. Boxplot of the mean annual periodic increment by diameter class of Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). Markers (x) represent the mean increment per diameter class, which were calculated only for the diameter classes with three or more trees. $\mathrm{Dbh}=$ diameter at 1.30 m above ground level.


Fig. 5. Mean passage time by diameter class for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D) and their respective tendency lines. Only passage times for diameter classes with three or more trees were considered. $\mathrm{Dbh}=$ diameter at 1.30 m above ground level.

## Modeling accumulated diameter growth and generating increment curves

The Johnson-Schumacher model better fitted the time series of $A$. leiocarpa and $H$. excelsum, while the Gompertz was better for E. uncinatum and T. burserifolia. For diameter growth, A. leiocarpa and H. excelsum reached the point of maximum tangency close to 35 cm and 50 cm , respectively, registering lower increments after these diameter classes (Fig. 6 A and C). However, E. uncinatum and T. burserifolia did not reach this point within the measured diameters (Fig. 6 B and D), showing upward growth throughout the entire time series.


Fig. 6. Accumulated diametric growth equations fitted for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). The growth equations were fitted for the ages represented by three or more samples. $\mathrm{Dbh}=$ diameter at 1.30 m above ground level; $\mathrm{t}=$ time (years); $\mathrm{S}_{\mathrm{yx} \%}=$ Relative Residual Standard Error (\%).

Apuleia leiocarpa, E. uncinatum, and T. burserifolia reached the maximum current annual increment in volume $\left(\mathrm{CAI}_{\mathrm{v}}\right)$ when considering the available data (Fig. $7 \mathrm{~A}, \mathrm{~B}$ and D). The maximum $\mathrm{CAI}_{\mathrm{v}}$ for $H$. excelsum was estimated at approximately 245 years (Fig. 7C).

For the four species, the growth equation was used to estimate the biological rotation age, which for individual trees occurred at the $95-\mathrm{cm}$ dbh for A. leiocarpa, $121-\mathrm{cm}$ for H. excelsum, and $165-\mathrm{cm}$ for E. uncinatum and T. burserifolia. The maximum $\mathrm{CAI}_{\mathrm{v}}$
occurred close to the $60-\mathrm{cm}$ dbh for $A$. leiocarpa, $80-\mathrm{cm}$ for $H$. excelsum, and $120-\mathrm{cm}$ for $E$. uncinatum and $T$. burserifolia (Table 2).

Table 2. Estimated ages and diameters on the biological rotation and the maximum current annual increment of individual tree volume for the species.

| Species | Biological rotation |  | Maximum CAI $_{\mathrm{v}}$ |  |
| :--- | :--- | :--- | :--- | :--- |
|  | Dbh (cm) | Age (years) | Dbh (cm) | Age (years) |
| Apuleia leiocarpa | 95 | 455 | 63 | 231 |
| Erisma uncinatum | 165 | 409 | 119 | 257 |
| Hymenolobium excelsum | 121 | 480 | 80 | 245 |
| Trattinnickia burserifolia | 165 | 319 | 118 | 203 |

Dbh = diameter at 1.30 m above ground level; maximum $\mathrm{CAI}_{\mathrm{v}}=$ maximum current annual increment for individual tree volume; Biological rotation $=$ intersection of the $\mathrm{CAI}_{\mathrm{v}}$ and $\mathrm{MAI}_{\mathrm{v}}$ (current and mean annual increment for individual tree volume) curves.


Fig. 7. Volumetric increment curves (black) and dbh growth equation (red) for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). In the primary yaxis: $\mathrm{MAI}_{\mathrm{v}}=$ mean annual volumetric increment; $\mathrm{CAI}_{\mathrm{v}}=$ current annual volumetric increment. On the secondary y-axis: $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm})$ (growth equation fitted within the measured data range); $\mathrm{Edbh}=$ accumulated diameter at 1.30 m above ground level (growth equation outside the measured data range).

## Growth by species population

The maximum $\mathrm{CAI}_{\mathrm{v}}$ and biological rotation ages of the population volume (Table 3; Fig. 8) occurred in lower diameters than those recorded for individual trees (Fig. 7; Table 2). Those ages were reached for diameters within the stem samples. There was therefore no need for the extrapolation of the volume growth equations that was required for the individual diameter growth (Fig. 7).

Table 3. Estimated ages and diameters on the biological rotation and the maximum current annual increment by species population.

| Species | Biological rotation |  | Max. $\mathrm{CAI}_{\mathrm{v}}$ |  |
| :--- | :--- | :--- | :--- | :--- |
|  | Dbh (cm) | Age (years) | Dbh (cm) | Age (years) |
| Apuleia leiocarpa | 58 | 203 | 44 | 160 |
| Erisma uncinatum | 86 | 192 | 64 | 154 |
| Hymenolobium excelsum | 52 | 150 | 37 | 106 |
| Trattinnickia burserifolia | 58 | 116 | 34 | 80 |

$\mathrm{Dbh}=$ diameter at 1.30 m above ground level; $\mathrm{Max} . \mathrm{CAI}_{\mathrm{v}}=$ maximum current annual increment for population volume; biological rotation $=$ intersection of the curves of $\mathrm{CAI}_{\mathrm{v}}$ and mean annual increment in volume for individual tree.


Fig. 8. Volumetric and diametric increment curves for the population of Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C) and Trattinnickia burserifolia (D) ( $\mathrm{dbh} \geq 20 \mathrm{~cm}$ ). In the primary y-axis: $\mathrm{MAI}_{\mathrm{v}}=$ mean annual increment in volume; $\mathrm{CAI}_{\mathrm{v}}=$ current annual increment in volume. In the secondary $y$-axis: $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm})$, obtained from the growth equation.

## Minimum cutting diameter (MCD) and cutting cycle simulations

The MCD criteria determined by the biological rotation age of the population and with short cutting cycles (10 years) (Table 4) resulted in a higher annual volume yield for the four species. For $A$. leiocarpa, H. excelsum and T. burserifolia, the maximum $\mathrm{CAI}_{\mathrm{v}}$ age of the population and the cutting cycle, as suggested by Schöngart (2008), resulted in the least increment $\left(\mathrm{m}^{3} \mathrm{ha}^{-1}\right.$ year $\left.^{-1}\right)$ of all criteria. For $E$. uncinatum the management criteria defined in the legislation resulted in the least increment.

Table 4. Simulation results using different criteria for defining the minimum cutting diameter and cutting cycle.

| Species | MCD | Law | Rot. pop. | Rot. pop. | $\mathrm{CAI}_{\mathrm{v}}$ | $\mathrm{CAI}_{\mathrm{v} \text { ind. }}$ | Rot. pop. | Rot. pop. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Cutting cycle | Law | Law | SM | SM | SM | Short | Long |
| $\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\mathrm{MCD}(\mathrm{cm})$ | 50 | 57 | 57 | 44 | 63 | 57 | 57 |
|  | Cycle (years) | 35 | 35 | 37 | 37 | 37 | 10 | 70 |
|  | Inc. $\left(m^{3} \mathrm{ha}^{-1}\right.$ year $\left.^{-1}\right)$ | 0.0078 | 0.0107 | 0.0106 | 0.0055 | 0.0113 | 0.0159 | 0.0086 |
|  | Vol. ( $\mathrm{m}^{3} 100 \mathrm{ha}^{-1}$ ) | 27.46 | 37.52 | 39.09 | 20.49 | 41.82 | 15.86 | 60.53 |
| InInE0000 | MCD (cm) | 50 | 86 | 86 | 64 | 119 | 86 | 86 |
|  | Cycle (years) | 35 | 35 | 22 | 22 | 22 | 10 | 70 |
|  | Inc. $\left(\mathrm{m}^{3} \mathrm{ha}^{-1}\right.$ year $\left.^{-1}\right)$ | 0.0238 | 0.1140 | 0.1238 | 0.0643 | 0.0800 | 0.1427 | 0.0795 |
|  | Vol. ( $\mathrm{m}^{3} 100 \mathrm{ha}^{-1}$ ) | 83.27 | 398.90 | 272.28 | 141.51 | 176.01 | 142.74 | 556.66 |
|  | MCD (cm) | 50 | 52 | 52 | 37 | 80 | 52 | 52 |
|  | Cycle (years) | 35 | 35 | 31 | 31 | 31 | 10 | 70 |
|  | Inc. $\left(m^{3} \mathrm{ha}^{-1}\right.$ year $\left.^{-1}\right)$ | 0.0051 | 0.0054 | 0.0055 | 0.0029 | 0.0049 | 0.0069 | 0.0046 |


| Vol. $\left(\mathrm{m}^{3} 100 \mathrm{ha}^{-1}\right)$ | 17.69 | 18.84 | 17.03 | 8.86 | 15.31 | 6.90 | 31.86 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |



Fig. 9. Annual volume increment by the MCD defined by the population's biological rotation age and different cutting cycles for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D).

## Discussion

## Diametric distribution pattern of the species

Most of the probability density functions (PDFs) (Table 1) fitted to data in each forest compartment. Thus, a single PDF per species was fitted at the Sinop microregion (Fig. 2). Fitting only one PDF per species across the microregion suggests the existence of similarities in the species diametric structure in the typology, contrasting to the claim that ecosystems are chaotic and disordered (O'Hara, 2014). According to this same author, ecosystems are not deterministic or ordered, due to the occurrence of repeated disturbances on small scales, which prevent the forest from being homogeneous over
time. However, for Larson (1992), the occurrence of environmental or anthropic disturbances combined with the genetic variation of mixed forest does not imply that forest development patterns cannot be discerned.

Also, the micro-region's pattern agrees with the demographic equilibrium theory, which states that the diameter distribution balance may be scalar (Muller-Landau et al., 2006). The forest structure is regulated by general principles of growth, mortality (Wang et al., 2009) and ecological succession (Oliver, 1992).

Even in distant or geographically isolated regions, species with resembling physiological and morphological characteristics can have a similar population structure (Oliver, 1992). This occurs because the structures repeat over time in the forest (Gotelli, 2008). Diametric structure models allow us to infer the diameter in which tree number reduces as a result of stagnant growth and increased mortality (Durrieu de Madron; Forni, 1997; Braz et al., 2014).

Ecologists use the diametric structure to indicate the health of the forest. A high number of smaller trees, as recorded for T. burserifolia (Fig. 2D), would represent forest sustainability, since it would restore the upper classes (Kohyama, 1986; Muller-Landau et al., 2006; Wang et al., 2009). These considerations originated from De Liocourt's (1898) and Meyer's (1952) theories that state the concept of a balanced forest following a negative exponential pattern.

However, several studies have found that some forest types and many individual species may not follow such a negative exponential model (Condit et al., 1998; Dawkins; Philip, 1998; Nyland, 2002; Pascal, 2003; Braz, 2010; Braz et al., 2014; Hossain et al., 2015), as occurred for three of the species in this study (Fig. 2 A, B and C).

A minor number of smaller trees, as recorded for A. leiocarpa, E. uncinatum and $H$. excelsum, could indicate that the populations are declining (Condit, 1998; Hossain et al.,
2015). However, the forest diametric structure is not the only indicator defining population maintenance. Schaaf et al. (2006) pointed out that the highest density does not guarantee the species maintenance in the community, but their ability to compete within the ecological niche does. The authors stated that if the species has few trees with smaller diameters, but if the individuals tolerate competition for light in the lower canopy, they can remain in the forest. Therefore, it is necessary to consider other factors, particularly the species growth in the diameter classes (Condit et al., 1998). Braz et al. (2014) identified over $60 \%$ of the basal area in the upper stratum in the Sinop micro-region, a situation described by Pascal (2003). This author stated that the deficit of trees in some dbh classes or the accumulation in larger dbh classes can result from different causes. For example, a massive fruiting and germination due to favorable climatic conditions can engender an overstock of trees in a particular dbh class. These individuals can outgrow to larger dbh classes after a certain time, resulting in an imbalanced diametric structure curve. These same individuals may be stagnated in a certain dbh class when under the closed canopy of the forest.

An over-stocked upper stratum may have its regeneration constrained due to inadequate access to light by trees in the lower canopy (Yegang; Jinxuan, 1988; Lamprecht, 1990; Felfili, 1997; Nyland, 2002; Bettinger et al. 2009). In such cases, some species may need a longer time scale to regenerate (Felfili, 1997). Over time, this factor decharacterizes both the negative exponential structure (Braz, 2010; Bettinger et al., 2009) and the whole forest increment (Dawkins; Philip, 1998).

## Production modeling at individual tree level

Commercial height is an essential dendrometric variable for modeling production forests since it is used for volume prediction (Lappi, 1997). Fitting parameters for the commercial height/dbh ratio (Fig. 3) allows us to calculate commercial volumes of
individual trees and stands more accurately where there is no field measuring. Other authors used the commercial height/dbh ratio to model the wood volume in the Amazon Forest (Brienen; Zuidema, 2006a; Fortini; Zarin, 2011; Miranda, Z. P. et al., 2018). According to Alder (1995), in natural forests the initial growth of trees is slow, followed by a phase of higher increments until it reaches its maximum. After that maximum point, growth reduces until stagnation. Apuleia leiocarpa, E. uncinatum and $T$. burserifolia followed this pattern (Fig. $4 \mathrm{~A}, \mathrm{~B}$ and D and $5 \mathrm{~A}, \mathrm{~B}$ and D), while $H$. excelsum maintained constant growth during five diameter classes, not exceeding 0.5 cm year ${ }^{-1}$, except in the $65-\mathrm{cm}$ class (Fig. 4C). The constant growth of $H$. excelsum until larger sizes is a feature of late and emerging secondary species (Silva et al., 1985), whose crowns extend above the canopy average level. These functional groups have several micro-habitats during their ontogenesis (Clark; Clark, 1992). They are characterized as partial sciophytes, shade-tolerate in the early development stages. However, they require a high degree of illumination to overcome the intermediate stages to maturity, increasing its growth during canopy opening (Maciel et al., 2017).

The decreasing tendency of passage time (Fig. $5 \mathrm{~B}, \mathrm{C}$, and D) for the late secondary species (E. uncinatum, H. excelsum, and T. burserifolia) is also a feature of partial sciophytes, that are shade tolerant, but do not demand shade for growth (Maciel et al., 2017).

The U-shaped passage time of the initial secondary species (A. leiocarpa) has already been pointed out by Brienen and Zuidema (2006b) for Bertholletia excelsa Bonpl., an initial secondary species (Gouveia et al., 2011). The same tendency was also registered for Goupia glabra Aubl. in the micro-region of Sinop-MT (Oliveira et al., 2015), which shows maximum growth in the $25-\mathrm{cm}$ and $35-\mathrm{cm}$ diameter classes, despite being a late secondary species (Araújo et al., 2009), as occurred for A. leiocarpa (Fig. 5A).

The biological rotation and maximum $\mathrm{CAI}_{\mathrm{v}}$ ages (Fig. 7; Table 2) were consistent with the increment by diameter class (Fig. 4). Apuleia leiocarpa, an initial secondary species, reached biological rotation and maximum $\mathrm{CAI}_{\mathrm{v}}$ ages in smaller diameters, while $H$. excelsum reached it in intermediate sizes. The other two species achieved biological rotation for an estimated dbh higher than 160 cm . The maximum $\mathrm{CAI}_{\mathrm{v}}$ of an individual tree were used in scientific studies to define minimum cutting diameters and cutting cycles for species in Amazonas State (Schöngart, 2008; Rosa et al., 2017; Miranda D. L. C., 2018), and has already been included in State forest law (Amazonas, 2010). If logging happens before the maximum $\mathrm{CAI}_{\mathrm{v}}$ or after the maximum $\mathrm{MAI}_{\mathrm{v}}$, the volumetric production will be inefficient. In this case, the species would not have reached or would have passed their optimal growth (Schöngart, 2008; Braz; Mattos, 2015). Therefore, knowing the maximum $\mathrm{CAI}_{\mathrm{v}}$ and $\mathrm{MAI}_{\mathrm{v}}$ per species is essential for sustainable forest management in the Amazon forest.

The curves of individual wood volume increment indicate the ideal parameters for sustainable management of each species. However, other variables representing the species dynamics must be considered for decision-making. For example, it is essential to define available stock of trees by diameter class and survival rates (Sebben et al., 2008; Free et al., 2014; Groenendijk et al., 2017; Free, 2017).

## Volumetric population growth

The maximum $\mathrm{CAI}_{\mathrm{v}}$ estimated from the population increment curves occurred for diameters lower than 50 cm for A. leiocarpa, H. excelsum, and T. burserifolia, and at $64-\mathrm{cm}$ diameter for E. uncinatum (Table 3; Fig. 8). The dbh when biological rotation age occurs, at which $\mathrm{CAI}_{\mathrm{v}}$ and $\mathrm{MAI}_{\mathrm{v}}$ curves intersected, was around 50 cm for $A$. leiocarpa, H. excelsum, and T. burserifolia, while for E. uncinatum this occurred at 86 cm . Erisma uncinatum has increased growth (Fig. 4) and a high concentration of trees in
the upper diameter classes, which explains its yield culmination in larger dbh sizes. This feature suggests the maintenance of larger dbh trees in the forest. In polycyclic management systems, the trees available for logging must reach at least the diameters with the highest growth potential in volume (Miranda, Z. P. et al., 2018) represented by the MCD. For this reason, it is essential to determine the diameter that provides the highest wood production for each species, based on the individual growth and the population demographic characteristics.

According to Miranda, Z. P. et al. (2018), the species management in the mixed forest should be carried out within the diameters of the higher $\mathrm{CAI}_{v}$ and the biological rotation of the population to maximize the volume. However, we observed a large range between the maximum $\mathrm{CAI}_{\mathrm{v}}$ and the biological rotation ages, of at least 36 years and $14-\mathrm{cm}$ dbh (Table 3; Fig. 8). It remains unclear which MCD should be applied the highest wood yield for the next cutting cycle.

The $\mathrm{CAI}_{\mathrm{v}}$ curves and biological rotation ages for all species population culminated in lower diameters and ages compared to the increment curves at the individual level (Fig. 7; Table 2). The inclusion of the number of trees per diameter class anticipates the culmination since it indirectly represents the population mortality and survival rates (Assmann, 1970; Rubin et al., 2006). As trees increase in size, the number of trees decreases due to mortality, causing a deceleration in the gross wood production, even though the remaining trees become larger (Seydack, 2000; Lundqvist, 2017). Therefore, even if individual trees are growing, the total production per unit area will decline much earlier (Assmann, 1970).

According to Seydack (2000) the population demographic factors of commercial species are essential to determine the optimal parameters for forest management. In the natural forest structure, the available stock of trees by diameter class is a crucial factor for yield
projection in terms of the number of trees, basal area and volume (Ong; Kleine, 1996), since they indicate survival by diameter class. The recovery time of the wood volume in a post-intervention cycle is related to the species-specific growth, and also to the number of trees in the smaller diameter classes to the intervention diameter (Brienen; Zuidema, 2006a). Therefore, methods based on the inflection point age at the population level are recognized for being more accurate in predicting maximum volume yield in a natural forest than methods that consider only the individual tree growth.

## Volumetric production using different management criteria

The increments $\left(\mathrm{m}^{3} \mathrm{ha}^{-1}\right.$ year ${ }^{-1}$ ) of each species were, in general, compatible with other studies carried out in the Amazon, using permanent plots (Reis et al., 2010; Braz et al., 2018). Reis et al. (2010) obtained similar increments for E. uncinatum (Table 4), considering the cutting cycle and MCD of the Brazilian forest law (Brasil, 2006).

The cutting cycles and alternative MCD from those defined in Brazilian forest law produced higher volumetric increment for the 4 studied species, similar to that obtained by Groenendijk et al. (2017) in tropical rainforest in Cameroon. Erisma uncinatum produced approximately seven times higher wood volume ( $\mathrm{ha}^{-1}$ year ${ }^{-1}$ ) applying short cutting cycle (10 years) and MCD $70 \%$ larger ( 86 cm ) than the Brazilian mandatory MCD $(50 \mathrm{~cm})$. Erisma uncinatum presented the highest yield gain with the alternative MCD and cutting cycles, due to the higher number of trees and growth in dbh classes above 50 cm (Fig. 2 and 7). All results, especially those of E. uncinatum, showed the potential of maximizing the forest management yield considering population characteristics at the species level. The ideal MCD can increase volumetric increments, even without silvicultural treatments, and so should be considered to increase management productivity (Avila et al., 2017).

The MCD defined by the dbh of the biological rotation of the population produced higher annual increments for the four species, especially for shorter cutting cycles (Table 4). It is important to consider the optimal population increment rate instead of average growth data. This was previously considered by Ong and Kleine (1996) and Bick et al. (1998) when studying natural forests in Malaysia. These authors obtained the population growth from zero using permanent plots and simulations of forest production and found the maximum sustainable yield population, defining optimum logging rates and cutting cycles. Glauner et al. (2003) pointed out that the underlying principle of management is to improve the forest condition, converting its stock to an optimum level of increment of the commercial species.

In this study the dbh of the maximum $\mathrm{CAI}_{\mathrm{v}}$ (lowest among those tested as MCD) produced the lowest volume increments considering the tested cycles (Table 4). According to Bick et al. (1998), the harvested volume of two cycles must oscillate in the population growth curve between a lower and an upper limit of the maximum yield volume (i.e., the age of maximum $\mathrm{CAI}_{\mathrm{v}}$ ). These authors recommended an MCD above the dbh of maximum $\mathrm{CAI}_{\mathrm{v}}$. Our results are consistent with these recommendations, since the yield was higher when the logging was carried out at an age after the maximum population $\mathrm{CAI}_{\mathrm{v}}$, such as the biological rotation age.

When considering only the individual tree growth curve to define the logging parameters we observed that the MCD was always higher, although the volumetric increments were lower, except for $A$. leiocarpa (Table 4). Contrary to the statement of Sebbenn et al. (2008) and Lacerda et al. (2013), the excessive MCD increase does not always imply higher forest productivity for all species. As mentioned, after reaching their productivity peak the trees grow at moderate rates and the mortality is high. Slow
growth trees should be logged before dying, through selective logging of mature trees of declining vigor (Seydack, 2012; Lundqvist, 2017).

The cutting cycles must be long enough so that remaining trees reach the MCD (Seydack et al., 1995). However, it cannot be too long, to ensure the trees' potential growth and forest economic sustainability (Mattioli et al., 2015). The simulations revealed that long cutting cycles resulted in smaller volumetric increments for all species (Fig. 9), reaching a loss higher than $60 \%$ compared to the 10 -year cutting cycle, considering the same MCD (defined by population biological rotation). Therefore, increasing the cutting cycle indefinitely (Sebbenn et al., 2008) represents a technical error in a productive forest (Braz et al., 2015). Moreover, increasing the cut cycle requires long-term investment (Glauner et al., 2003), which is difficult in unstable political-economic environments (Groenendijk et al., 2017). On the other hand, short cutting cycles require logging planning, following the reduced-impact logging standards.

Suitable cutting cycles depend on economic considerations (Bick et al., 1998) besides the MCD and the forest remaining structure. Economic analysis should support selecting the best cutting cycle for each specific case, considering the optimal parameters and exploitation feasibility for each species. Cost-benefit analyses can help assess forest management's economic and social aspects (Rosa et al., 2017). Moreover, higher MCD requires studies on tree health and risks of rot in older and bigger trees.

## Conclusions

The diametric distribution of each species is similar throughout the transition zone between open tropical rainforest and deciduous tropical rainforest in Brazilian Amazon. Modifications of the standard diametric structure by species can be combined with
growth models for inferring tropical forest dynamics, as done in this study. The diametric distribution should support wood production planning and be the basis for monitoring forest logging.

The optimum population minimum cutting diameter (MCD) of a species can significantly increase the volumetric increment and the total wood volume, maximizing the forest production under management. After determining the MCD, the best cutting cycle must be defined according to economic analysis, which will specify the best intervention time for the productive forest.

The methodology for species-level MCDs proved to be a useful tool and superior to the fixed parameters defined in the Brazilian law or the methodologies that consider only the individual tree growth. The procedure provides higher reliability for the maximized wood production. The ideal MCDs based on dendrochronology substantially reduces costs and time spent collecting data for forest modeling.

## Availability of data and materials

The data that support the findings of this study are available from Embrapa Florestas and Elabore Projetos e Consultoria Florestal but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of Embrapa Florestas and Elabore Projetos e Consultoria Florestal.

## Abbreviations

CAIv: current annual volume increment
DBH: diameter at 1.30 m above ground level
MAIv: mean annual volume increment

MCD: minimum cutting diameter PDF: probability density function

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## Authors' contributions

AC participated of elaborating the paper conceptualization and methodology, made the formal analysis and wrote the original draft of the paper.

EMB participated of elaborating the paper conceptualization and methodology, collected field data and supervised the paper writing and design. PPM participated of elaborating the paper conceptualization and methodology and supervised the paper writing and design.

ROB participated of elaborating the paper conceptualization and collected field data.
AFF participated of elaborating the paper conceptualization and methodology and supervised the paper writing and design.

## Ethics approval and consent to participate

Not applicable

## Consent for publication

Not applicable

## Competing interests

The authors declare that they have no competing interests.

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Figures

Obtained from:

| $\begin{aligned} & \text { Pdf } \\ & \stackrel{y}{5} \end{aligned}$ | Dbh growth equation |  | Taper equations | $\begin{aligned} & \mathrm{Nxv} \\ & \end{aligned}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\begin{gathered} \mathrm{N} \\ \text { (trees ha-l} \end{gathered}$ | Time (years) | Dbh <br> (cm) | $\begin{gathered} \mathbf{v} \\ \left(\mathbf{m}^{3}\right) \end{gathered}$ | $\begin{gathered} \mathrm{V} \\ \left(\mathrm{~m}^{3} \mathrm{ha}^{-1}\right) \end{gathered}$ | $\begin{gathered} \text { MAIV } \\ \left(\mathrm{m}^{3} \mathrm{ha}^{-1} \text { year }^{-1}\right) \end{gathered}$ | $\begin{gathered} \text { CAIV } \\ \left(\mathrm{m}^{3} \text { ha }^{-1} \text { year }{ }^{-1}\right) \end{gathered}$ |
| 0.0955 | 70 | 27.8696 | 0.3783 | 0.0361 | $5.16 \times 10^{-4}$ | $1.86 \times 10^{-3}$ |
| 0.0957 | 71 | 28.4297 | 0.3971 | 0.0380 | $5.35 \times 10^{-4}$ | $1.88 \times 10^{-3}$ |
| 0.0958 | 72 | 28.9951 | 0.4166 | 0.0399 | $5.54 \times 10^{-4}$ | $1.91 \times 10^{-3}$ |
| 0.0958 | 73 | 29.5656 | 0.4368 | 0.0419 | $5.73 \times 10^{-4}$ | $1.93 \times 10^{-3}$ |
| 0.0957 | 74 | 30.1413 | 0.4577 | 0.0438 | $5.92 \times 10^{-4}$ | $1.95 \times 10^{-3}$ |
| 0.0955 | 75 | 30.7221 | 0.4793 | 0.0458 | $6.10 \times 10^{-4}$ | $1.97 \times 10^{-3}$ |

## Figure 1

Scheme showing the methodological process for obtaining the curves of volume increment of the population. The boxes with red outline inform the data source of the column to which the arrows are directed. PDFs = probability density functions; $\mathrm{N}=$ number of trees per hectare; dbh = diameter at 1.30 m above ground level; v = volume of individual tree; $\mathrm{V}=$ species population volume ( $\mathrm{m}^{3}$ ha- 1 ); MAlv = mean annual volume increment; and CAlv = current annual volume increment.


$$
\begin{array}{r}
f(d b h)=\frac{d b h^{8.883-1} e^{\frac{-d b h}{6.657}}}{6.657^{8.883} \Gamma(8.883)} \\
\mathrm{D}_{\text {calc. }}=0.003 \\
\mathrm{RI}=0.025
\end{array}
$$

$\square$ Observed frequency
-Gamma
A




## Figure 2

Probability density functions with better fitting for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C) and Trattinnickia burserifolia (D). Dbh = diameter at 1.30 m above ground level (cm); $\Gamma$ = gamma function; Dcalc. = maximum absolute value between fitted pdf and observed values in each compartment; IR = error index (Reynolds et al., 1988).


## Figure 3

Heigh/dbh models of Apuleia leiocarpa, Erisma uncinatum, Hymenolobium excelsum, and Trattinnickia burserifolia. $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm}) ; \beta 0$ and $\beta 1=$ equation parameters fitted by non-linear regression; Syx\% = relative residual standard error (\%)


Figure 4
Boxplot of the mean annual periodic increment by diameter class of Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). Markers (x) represent the mean increment per diameter class, which were calculated only for the diameter classes with three or more trees. $\mathrm{Dbh}=$ diameter at 1.30 m above ground level.


Figure 5
Mean passage time by diameter class for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D) and their respective tendency lines. Only passage times for diameter classes with three or more trees were considered. Dbh = diameter at 1.30 m above ground level.


Figure 6

Accumulated diametric growth equations fitted for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). The growth equations were fitted for the ages represented by three or more samples. Dbh = diameter at 1.30 m above ground level; $\mathrm{t}=$ time (years); Syx\% = Relative Residual Standard Error (\%).


Figure 7

Volumetric increment curves (black) and dbh growth equation (red) for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D). In the primary y-axis: MAlv $=$ mean annual volumetric increment; CAlv = current annual volumetric increment. On the secondary $y$ axis: $\mathrm{dbh}=$ diameter at 1.30 m above ground level (cm) (growth equation fitted within the measured data
range); Edbh = accumulated diameter at 1.30 m above ground level (growth equation outside the measured data range).


Figure 8

Volumetric and diametric increment curves for the population of Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C) and Trattinnickia burserifolia (D) (dbh $\geq 20 \mathrm{~cm}$ ). In the primary y-axis:

MAlv = mean annual increment in volume; CAlv = current annual increment in volume. In the secondary yaxis: $\mathrm{dbh}=$ diameter at 1.30 m above ground level $(\mathrm{cm})$, obtained from the growth equation.


Figure 9

Annual volume increment by the MCD defined by the population's biological rotation age and different cutting cycles for Apuleia leiocarpa (A), Erisma uncinatum (B), Hymenolobium excelsum (C), and Trattinnickia burserifolia (D).

