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ORIGINAL PAPER

Species-specific growth models inform sustainable management of *Rhizophora mangle* in the Colombian Caribbean

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Abstract Mangrove ecosystems provide crucial ecological services but face threats from climate change and unsustainable resource use. This highlights the need for science-based forest management initiatives. Cispatá Bay, located in the Colombian Caribbean, hosts the country's only mangrove under a regulated sustainable use model. Yet, current management guidelines rely on generalized silvicultural criteria, such as a uniform minimum logging diameter (MLD) of 10 cm and a 14 year cutting cycle (CC), which do not reflect species-specific growth dynamics, potentially compromising sustainability. This study aims to improve sustainable forest management in Cispatá Bay by developing species-specific growth models for *Rhizophora mangle*, a dominant and heavily harvested species. We introduce a novel methodological framework for sustainable forest management in mangrove ecosystems, integrating dendrochronology and biometric modeling to derive ecological management parameters. We combined tree-ring data from 26 dead individuals with forest inventory measurements and applied nonlinear mixed-effects modeling, accounting for autocorrelation and growth eccentricity. The resulting models yielded biologically meaningful ontogenetic traits, including a maximum mean diameter (A_{max}) of 40.35 cm, a weighted average growth rate (WAGR) of 0.42 cm year^{-1}, a lifespan (t_{span}) of 95.12 years, and a halflife ($t_{0.5}$) of 41.09 years. Additionally, we estimated an MLD of 24 cm and a CC of 20 years—both substantially higher than current thresholds. These findings suggest that continued application of generalized metrics may compromise forest regeneration, reduce volume recovery, and undermine long-term sustainability. By integrating dendrochronological techniques with biometric modeling, this research provides a replicable framework for evidence-based forest governance in mangroves.

Keywords Mangrove silviculture · Tree-rings · Ontogenic traits · Silvicultural parameters

Introduction

Mangroves provide a wide range of ecosystem services, including carbon sequestration, water regulation, and protection against extreme climatic events such as floods and hurricanes (Bimrah et al. 2022; Mitra 2020). They also support local livelihoods by supplying essential resources for food, fuel, and construction (Hussain and Badola 2010; Palacios and Cantera 2017). Despite their ecological and

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socioeconomic importance, mangroves are increasingly threatened by climate change, urban expansion, and high deforestation rates (Bhowmik et al. 2022; Kumari and Pathak 2023). Ensuring their persistence requires conservation and forest management strategies grounded in robust silvicultural parameters that enable sustainable resource use.

Sustainable forest management in tropical ecosystems relies on accurate information about structural and dynamic parameters such as diameter, height, volume growth, age, and regeneration processes (Conde et al. 2024; Martínez et al. 2025; Schöngart 2008). Traditionally, tropical tree growth has been assessed through periodic measurements in permanent sampling plots (Dauber et al. 2005; Vanclay 1994) or through dendrochronological techniques that reconstruct annual growth patterns from tree rings (Andrade et al. 2019; Inga and del Valle 2017; Martínez et al. 2025; Xu et al. 2014). Dendrochronology is generally less expensive and time-consuming than long-term plot monitoring and offers higher temporal precision, providing continuous annual records that span the entire lifespan of individual trees (Inga and del Valle 2017). Given the need for reliable long-term growth and age data in mangrove ecosystems (Chowdhury et al. 2023a), dendrochronology presents a particularly efficient and accessible approach for species that form distinct annual growth rings.

Mangrove species' growth is influenced by various environmental drivers, among which salinity is the primary limiting factor (Lovelock et al. 2016). Salinity in mangrove environments fluctuates seasonally in response to rainfall and freshwater inflows; during dry periods, reduced freshwater input increases salinity, imposing additional energetic costs that constrain growth (Kodikara et al. 2017; Lovelock et al. 2016). These fluctuations are recorded in the anatomical structure of growth rings (Chowdhury et al. 2023b). Annual growth rings have been observed in several mangrove species, including *Excoecaria agallocha* (Siddique et al. 2021), *Laguncularia racemosa* (Estrada et al. 2008), *Sonneratia apetala* (Chowdhury et al. 2008), *Rhizophora mangle* (Menezes et al. 2003; Ramírez-Correa et al. 2010; Souza et al. 2016), *R. mucronata* (Verheyden et al. 2004), *Xylocarpus granatum* (Chowdhury et al. 2023b), and *Heritiera fomes* (Chowdhury et al. 2008), among others.

The annual formation of growth rings in *R. mangle* has been confirmed in Brazil (Menezes et al. 2003; Souza et al. 2016) through radiocarbon analyses and by comparing ring counts with independently determined tree ages. Similar validation has been reported for Cispatá Bay, Córdoba, Colombia (Ramírez-Correa et al. 2010), where tree age was likewise matched to the number of growth rings. This confirmation supports the application of dendrochronological methods to study growth dynamics and estimate silvicultural metrics for the species, providing valuable information to inform sustainable forest management practices.

Between 1938 and 1945, the diversion of the Sinú River allowed seawater to intrude into Cispatá Bay, creating favorable conditions for mangrove colonization in areas previously used for rice cultivation (Suárez 2004). Since then, the local economy has become heavily dependent on mangrove resources, particularly timber from *R. mangle*. Approximately 94% of the local population relies on *R. mangle* wood as a primary source of fuel for cooking and heating (Dupont et al. 2025), with additional uses including local construction and commercialization (CVS and INVEMAR 2010). However, intensive extraction has led to significant ecological changes in mangrove populations, particularly affecting forest structure through reductions in basal area and shifts in regeneration dynamics (Agudelo et al. 2015). In response, the Corporación Autónoma Regional de los Valles del Sinú y del San Jorge (CVS) and the Instituto de Investigaciones Marinas y Costeras (INVEMAR) launched an Integrated Management Plan (IMP) in 2008 to promote the sustainable use of mangrove resources (CVS and INVEMAR 2010).

The IMP was developed using forest inventory data collected from permanent sampling plots, which provided valuable insights into forest structure, composition, growth, and mortality. Nevertheless, some measurements—such as tree height—were recorded with limited precision (rounded to the nearest meter), introducing potential bias into structural analyses. Using these data, the plan established a 14 year cutting cycle (CC) for *R. mangle*. However, other critical silvicultural parameters, including the minimum logging diameter (MLD), were not derived from species-specific ecological data but instead followed national legislation that applies a uniform MLD of 10 cm to all tree species across Colombia (República de Colombia 1996). Under this framework, timber extraction was organized using a polycyclic system that divided

Cispatá Bay into 14 sectors, each harvested sequentially while the remaining sectors regenerated.

This reliance on generalized regulations reflects a broader issue in tropical forest governance. Government-mandated criteria often overlook interspecific variability, resulting in either overexploitation or underutilization of forest resources (Andrade et al. 2019; Conde et al. 2024; Dauber et al. 2005; López et al. 2013). Given the high diversity of tropical forests, such uniform prescriptions are ecologically inadequate. Although some forest management systems have begun adopting species-specific parameters (De Ridder et al. 2013; Schöngart 2008), this approach remains rare in mangrove management.

This study introduces a novel methodological framework for sustainable mangrove forest management using tree-ring data and forest inventory measurements. Specifically, we aim to (i) characterize *R. mangle* growth in diameter, height, and volume; (ii) estimate reliable ontogenetic traits and silvicultural parameters through biometric modeling and growth analysis; and (iii) compare the estimated metrics for *R. mangle* with those currently used in Cispatá Bay in order to propose evidence-based recommendations for its management. We hypothesize that silvicultural parameters currently applied to *R.mangle* in Cispatá Bay, which were established without species-specific growth information, are not optimally aligned with its growth dynamics. Consequently, the prescribed MLD and/or CC are expected to deviate from those required to ensure long-term sustainability and adequate volume recovery after harvesting.

Material and methods

Study area

The study was conducted in Cispatá Bay (9°23'17''N, 75°50'55''W), located in the Colombian Caribbean region of South America (Fig. 1). The study area exhibits a mean annual temperature of 27.87 ± 0.38 °C and an average annual precipitation of 1,266.76 ± 210.14 mm. A distinct dry season extends from December to March, during which monthly rainfall remains below 40 mm. The wet season occurs from May to November, with monthly precipitation typically exceeding 110 mm.

Cispatá Bay is part of the IMP for Cispatá, La Balsa, Tinajones, and adjacent ecosystems. The plan encompasses a total area of 27,171 ha, of which 8,571 ha are mangrove forests (CVS and INVEMAR 2010). These mangroves are characterized by elevated salinity and periodic inundation—conditions that strongly influence species composition. *R. mangle* is the dominant species and the first to colonize the ecotone between marine and terrestrial environments, followed by *Avicennia germinans* and *L. racemosa*.

Forest inventories

The forest inventories were established with the development of the IMP (CVS and INVEMAR 2010), and data from seven transects of fringe mangroves in Cispatá Bay were provided by INVEMAR. Due to substantial variability in topographical and hydrological conditions (e.g., the presence of streams and lagoons), continuous sampling was not feasible, resulting in transect areas ranging from 0.45 to 1.46 ha. Within each transect, 10 × 10 m plots were delineated to identify species and to measure tree diameter and height for all individuals with a diameter greater than 3.5 cm. For *A. germinans* and *L. racemosa*, diameter at breast height (DBH) was recorded, whereas for *R. mangle* diameter was measured 30 cm above the highest aerial root, in accordance with its characteristic stilt-root structure and established mangrove measurement protocols (Kauffman and Donato 2012a, b; Komiyama et al. 2005).

Sampling and tree-ring analyses

Due to the complex wood anatomy of mangrove species, including the occurrence of false or wedging rings (Chowdhury et al. 2016, 2024; Rahman et al. 2020), cross-sections were collected instead of increment cores. Because tree harvesting is regulated under the IMP, 26 cross-sections were obtained from dead or felled *R. mangle* trees, sampled as close to the base as possible but above the aerial roots. The felled trees were selected using size and visible condition, prioritizing individuals with diameters greater than 10 cm that still retained foliage or showed no visible signs of decay. Sampling trees with diameters greater than 10 cm increases sample depth in the older classes by maximizing the number of measurable rings (Speer 2010), while still capturing age–growth

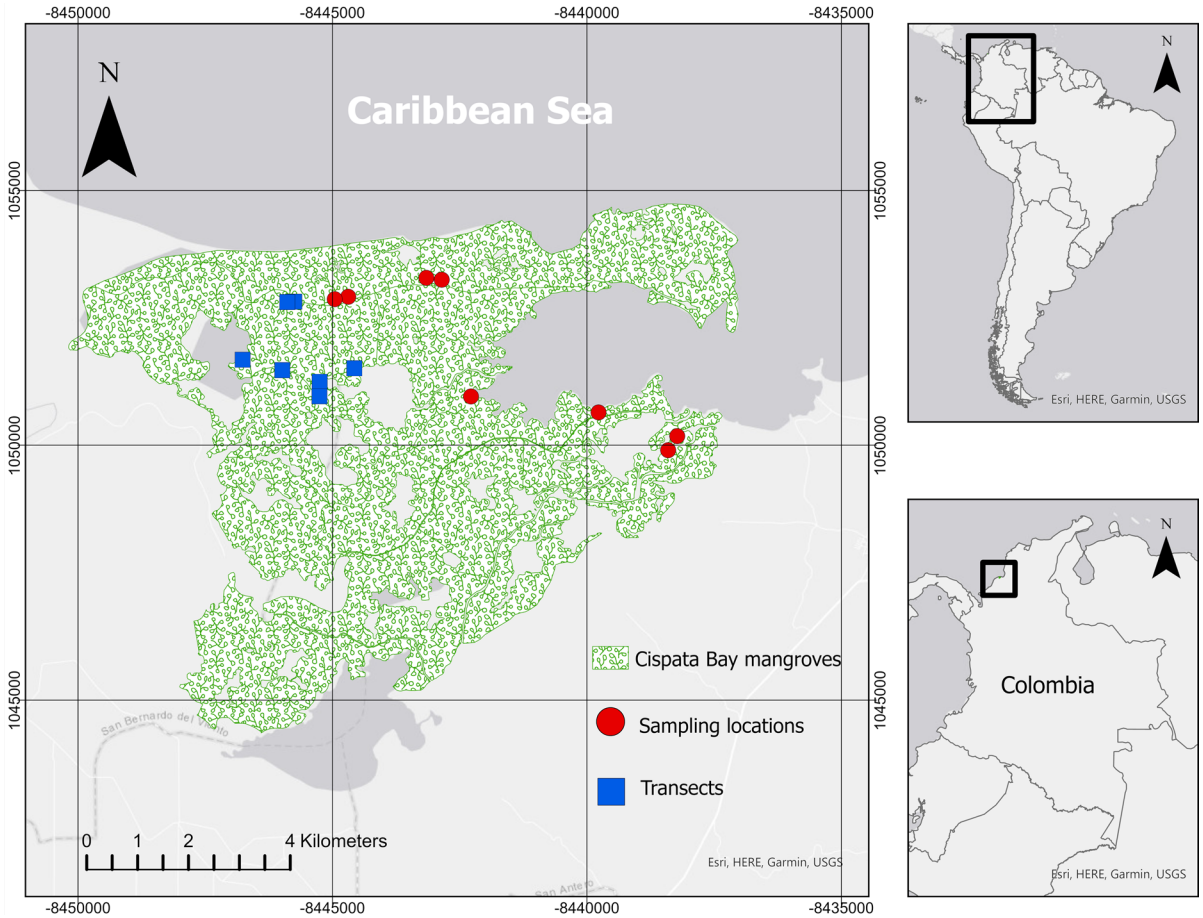


Fig. 1 Location of the sampling sites and inventory transects in Cispatá Bay. Red dots represent the sampling locations where cross-sections were obtained. Blue squares are the locations of the forest inventory transects established during the formulation of the IMP by the INVEMAR (CVS and INVEMAR, 2010)

variability. Although trees with diameters smaller than 10 cm were not sampled directly, tree-ring analysis allows growth to be reconstructed from the first year of establishment for each sampled individual. All samples were oven-dried at 60 °C for four days. To enhance ring visibility, each sample was polished using a sanding machine with progressively finer abrasive paper (grits 60–600). The prepared samples were then processed at the Laboratorio Bosques y Cambio Climático of the Universidad Nacional de Colombia, where they were digitized at a resolution of 2400 dpi using an Epson 10000XL scanner.

Growth rings in *R. mangle* were delimited using variations in vessel density (Fig. S1). Ring-width measurements (radial increments) were obtained using the Coorecorder software (v. 7.8; Cybis Elektronik and Data AB 2014a) and a composite reference chronology was developed with Cdendro (v. 7.8; Cybis Elektronik and Data AB 2014b). Subsequent analyses of ring-width data were conducted in the R environment (v. 4.1.1; R Core Team 2024) using the dplR package (Bunn et al. 2022).

Because the material originated from dead and fallen trees, we applied a five-level dendrochronological decay suitability classification based on visual wood condition and the feasibility of growth-ring measurement. This system comprised the following categories: (1) no visible decay; (2) minor decay; (3) moderate decay, making ring delimitation difficult; (4) advanced decay, permitting ring measurement in only one radius; and (5) severe decay, rendering the sample unsuitable for analysis (Fig. 2).

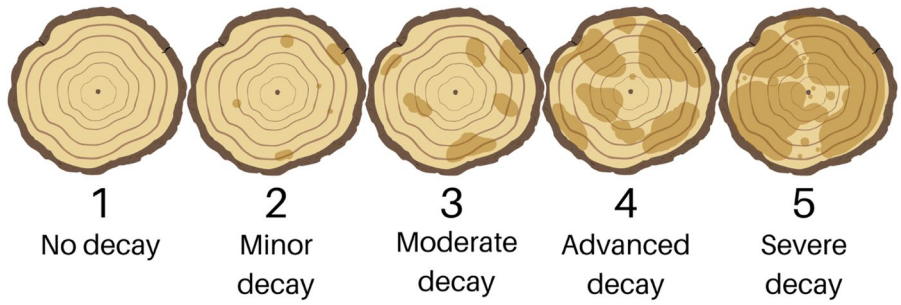


Fig. 2 Graphical representation of the samples decay. (1) no decay, (2) minor decay, (3) moderate decay, (4) advanced decay, and (5) severe decay

Growth modelling

The tree diameter was calculated as twice the radius, with the radius determined from the cumulative ring width. However, this value may be inaccurate when the pith does not coincide with the geometric center of the cross-section (Chowdhury et al. 2024; Giraldo and del Valle 2011). To address this, an eccentricity correction factor was applied to each measurement following Giraldo and del Valle (2011):

$$RW_c = \frac{\frac{P_c}{2\pi}}{r_m} RW_m \quad (1)$$

where RW_c is the corrected ring width, P_c is the perimeter of the sample, r_m is the radius length at which the ring widths were measured, and RW_m is the measured ring width.

Although two radii were measured for most samples, only one was randomly selected for diameter growth modeling, while the second radius was used for statistical validation. In samples where only one radius was available, that measurement was included directly in the modeling dataset.

Diameter growth was modeled using the von Bertalanffy growth equation (von Bertalanffy 1934), which describes organism growth as the balance between anabolic and catabolic processes. In the context of tree growth, anabolism corresponds to photosynthetic production, whereas catabolism represents respiratory consumption:

$$\frac{dD}{dt} = \eta D^m - \gamma D \quad (2)$$

where $\frac{dD}{dt}$ denotes the growth rate, D is the diameter, t is the age, and ηD^m and γD are the photosynthesis and respiration rates, respectively.

Since tree-ring data provide measurements beginning from the first year of growth, a diameter of zero was assumed at $t=0$. Integrating Eq. (2) under these conditions yields:

$$D(t) = (\frac{\eta}{\gamma})^{\frac{1}{1-m}}(1 - e^{-\gamma(1-m)t})^{\frac{1}{1-m}} \quad (3)$$

A nonlinear mixed-effects (NLME) approach was applied to model Eq. (3). The photosynthetic parameters (η,m) were treated as random effects, while the respiration parameter (γ) was modeled as a fixed effect common to all trees, following Martínez et al. (2025). The general expression of Eq. 3 within the NLME framework can be formulated as follows:

$$D_{ij} = f(t_{ij}, \varphi_{ij}) + \epsilon_{ij} i = 1, \ldots, M; j = 1, \ldots, n_i \quad (4)$$

where f is a nonlinear response function with respect to φ_{ij}, t_{ij} is the diameter of observation j and tree i, M is the number of trees, and n_i is the number of observations within the tree I, $\in_{ij}$ is the unexplained error. The parameter vector for a single observation is defined in matrix form as follows:

$$\varphi_{ij} = A_{ij}\beta + B_{ij}b_i \quad (5)$$

where β is the vector of fixed parameters, b_i is the vector of random parameters, and A_{ij} and B_{ij} are the design matrices that link the fixed and random effects to the nonlinear parameters φ_{ij}.

Because tree-ring data consist of repeated measurements from the same individual, they may exhibit temporal dependence or autocorrelation (Mehtätalo and Lappi 2020). Therefore, after estimating model (4), we examined the residual correlation structure and tested several autoregressive integrated moving average (ARIMA) specifications

to account for potential autocorrelation among observations (Martínez et al. 2025).

To estimate height growth, 80% of the forest inventory data were used to fit an allometric diameter-height model, while the remaining 20% were reserved for model validation. The relationship between diameter and height was described using a two-parameter Michaelis–Menten equation, a nonlinear theoretical model originally developed for enzyme kinetics (Michaelis and Menten 1913; Srinivasan 2022), but also widely applied in tropical forests to characterize diameter-height allometry (Conde et al. 2024; Schöngart 2008). In this model, the parameters represent the mean maximum tree height and the rate at which it is approached. The Michaelis–Menten equation can be written as follows:

$$H = \frac{\alpha}{1 + \left(\frac{\beta}{DBH}\right)} \tag{6}$$

where H denotes total height, DBH denotes diameter at breast height, α represents the asymptote (mean maximum height), and β is the parameter defining the rate of approach to the asymptote.

Because inventory data is collected from plots within transects, a two-level, nested, mixed-effects nonlinear model (NLME) was used to fit Eq. 6:

$$H_{ijk} = f\left(D_{ijk}, \varphi_{ijk}\right) + \epsilon_{ijk} i = 1, \ldots, M; j = 1, \ldots, M_i; k = 1, \ldots, n_{ij} \tag{7}$$

where f is a nonlinear response function with respect to φ_{ijk}, D_{ijk} is the diameter of tree k in plot j and transect i, M is the number of transects, m_i is the number of plots within transect i, n_{ij} is the number of trees, and $\in_{ijk}$ is the unexplained residual error.

Model performance was assessed by testing all possible combinations of random parameters, using the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and log-likelihood (logLik) as model selection metrics. The model exhibiting the lowest AIC and BIC values and the highest logLik was selected as the best-fitting model. Subsequently, the diameter values derived from the tree-ring data were substituted into Eq. 6 to estimate the height of each tree throughout its lifespan. All models in this study were fitted using maximum likelihood estimation (MLE) implemented in the nlme package (Pinheiro et al. 2021) within the R software environment (R Core Team 2024).

The presence of heteroscedasticity was assessed graphically for both diameter-growth and diameter-height models. When evidence of heteroscedasticity was detected, variance functions were incorporated into the models to stabilize residual variance, including the power function of the covariate (*VarPower*), the exponential function of the covariate (*VarExp*), and different variances among analytical units (e.g., trees, transects) using *VarIdent* structures. Additionally, the assumption of normality was evaluated through visual inspection of residual frequency histograms.

We evaluated the model's fit using the validation dataset. The following measurements of bias, precision, and performance, as proposed by Vanclay (1994), were calculated:

Average bias (AB):

$$AB = \frac{\sum_{i=1}^{n} \left(y_i - \widehat{y}_i\right)}{n} \tag{8}$$

where y_i is the *ith* observation, $\widehat{y}_i$ is the *ith* predicted value of the model, and n is the number of observations of the validation dataset.

To measure precision, the mean absolute error (MAE) was calculated:

$$MAE = \frac{\sum_{i=1}^{n} \left|y_i - \widehat{y}_i\right|}{n} \tag{9}$$

The model efficiency (ME) was also calculated:

$$ME = 1 - \frac{\sum_{i=1}^{n} (y_i - \widehat{y}_i)^2}{\sum_{i=1}^{n} (y_i - \overline{y})^2} \tag{10}$$

where $\overline{y}$ is the response variable's average.

EM is analogous to R^2 for nonlinear regression. A perfect fit is indicated by a value of one, while negative values represent a poor fit of the model.

Annual tree volume was estimated by applying a form factor of 0.657, previously reported for *R. mucronata* (Roberts and Ruara 1967). This species belongs to the same genus as *R. mangle* and exhibits a highly similar stem architecture, making the form

factor an appropriate proxy for the studied species. The annual volume was estimated as follows:

$$V_t = \pi(\frac{D_t}{2})^2 \cdot H_t \cdot f \quad (11)$$

where V_t, D_t, and H_t is the volume, diameter, and height at time t, respectively, and f is the form factor.

We calculated the current and mean annual increment of the volume (CAI_V and MAI_V) as follows:

$$CAIv_t = CV_{t+1} - CV_t \quad (12)$$

$$MAIv_t = \frac{CV_t}{t} \quad (13)$$

where CV_t represents the cumulative volume at time t.

Ontogenic traits and silvicultural parameters

Based on the diameter growth model, several ontogenic traits proposed by Inga and del Valle (2017) were calculated. The maximum mean diameter (A_{max}), represents the asymptote of diameter in centimeters and corresponds to the theoretical upper limit of D as time (t) approaches infinity:

$$A_{max} = (\frac{\eta}{\gamma})^{\frac{1}{1-m}} \quad (14)$$

The weighted absolute growth rate (WAGR) is an age-independent estimation of the growth rate throughout the lifespan of the species:

$$WAGR = \frac{(\frac{\eta}{\gamma})^{\frac{1}{1-m}} \cdot \gamma \cdot (1-m)}{2 \cdot (m+1)} \quad (15)$$

Lifespan (t_{span}) is the time in years required for the population to reach A. It is calculated as the quotient of A and $WAGR$:

$$t_{span} = \frac{2 \cdot (m+1)}{\gamma \cdot (1-m)} \quad (16)$$

Half-life ($t_{0.5}$) represents the time in years needed to reach half of A_{max}:

$$t_{0.5} = -\frac{ln(1-(0.5)^{1-m})}{\gamma(1-m)} \quad (17)$$

The MLD and CC were determined following the Growth-Oriented Logging (GOL) concept proposed by Schöngart (2008). According to this concept, trees should be harvested at an age between the maximum values of the CAI_V and MAI_V to optimize the species' growth potential. Harvesting trees before or after this interval results in suboptimal resource use and reduced yield efficiency. The MLD is defined as the diameter reached by the species at the age corresponding to the maximum CAI_V.

The CC was calculated as the average time required for the species to grow from one diameter class of 10 cm to the next:

$$CC = \frac{age_{MLD}}{MLD \cdot 0.1} \quad (18)$$

Results

Forest structure

The total tree abundance in Cispatá Bay was estimated at 1,014.89 ± 300.66 individuals ha^{-1}, of which 888.62 ± 211.75 individuals ha^{-1} (88%) corresponded to *R. mangle* trees (diameter ≥ 3.5 cm). The abundance of *R. mangle* followed a reverse J-shaped distribution across diameter classes (Fig. 3a). The average diameter and height were 11.8 ± 9.6 cm and 9.6 ± 3.2 m, respectively. The species had a volume stock of 129.15 m^3 ha^{-1}, with 95% exceeding the current MLD of 10 cm applied in Cispatá Bay. The volume distribution by diameter class was unimodal, peaking between 30–40 cm, with sharp declines in both smaller and larger classes (Fig. 3b).

Tree-ring data and growth trajectories

Twenty-two samples exhibited moderate or lower decay, allowing measurement of two radii per sample, while two samples with advanced decay allowed measurements from only one radius. Two severely decayed samples were excluded from the analysis (Table S1).

The ages of sampled trees ranged from 30 to 92 years. Growth trajectories revealed a clear growth depensation pattern (i.e., increasing intraspecific variability over time; Fig. S2). Applying the eccentricity correction factor significantly modified the growth

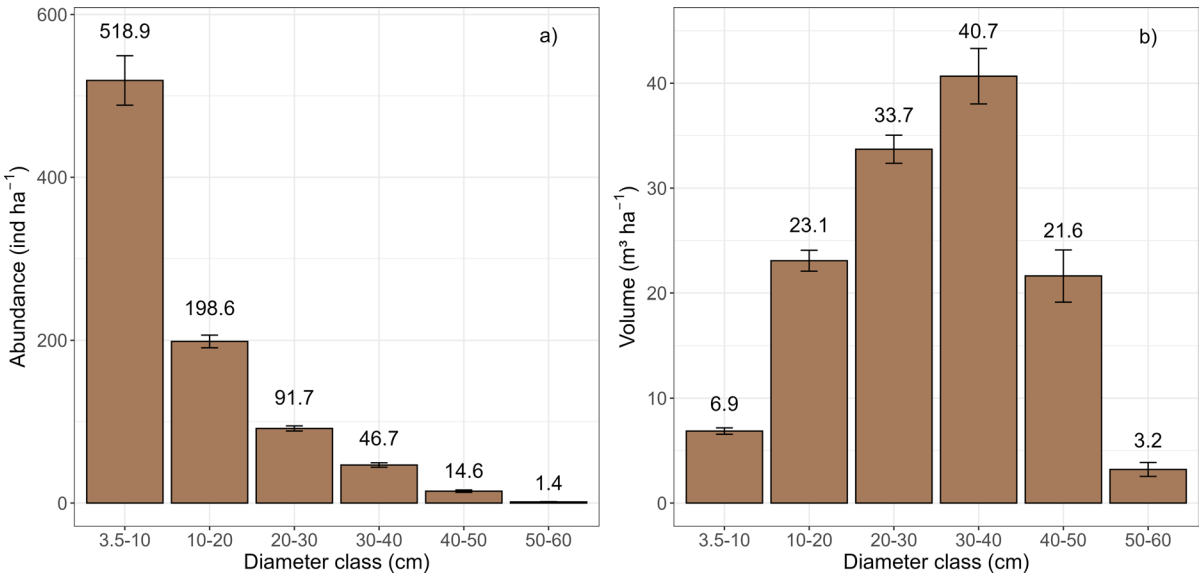


Fig. 3 *Rhizophora mangle* density **a** and volume stock **b** distributions on diameter classes of 10 cm in Cispatá Bay. Bars' height represents the mean value, and whiskers the standard error

trajectories, reducing some of the observed variability (Fig. S2). For example, the two uncorrected diameters calculated for the tree Z6 were 39.0 cm and 50.6 cm, while the corrected circumference-based value was 33.7 cm (Table S1). After correction, the 26 analyzed trees exhibited diameters ranging from 12.6 to 42.6 cm (Table S1).

Growth models

The von Bertalanffy (1934) equation, combined with a mixed-effects modeling approach and autocorrelation correction, provided an excellent fit for *R. mangle* diameter growth (Fig. 4). Model validation indicated low bias (AB = 0.005), high precision (MAE = 0.15), and strong performance (ME = 99.95%). Before incorporating the correlation structure, the residuals displayed a stochastic autocorrelation trend, which was effectively corrected using an ARIMA(1, 1, 0) specification (Fig. S3). Residual histograms indicated normal distribution, and homogeneous variance was confirmed without requiring an additional variance function (Fig. S3). All parameters were significant at the 99% confidence level (Table 1). Parameters η and m varied among trees from 0.31 to 0.52 and 0.47 to 0.63, respectively (Table S2).

Substantial variability was observed in the diameter-height relationship (Fig. 5). The model treating α and β as random parameters demonstrated the best fit, based on the lowest AIC and BIC and the highest Loglik (Table 2,, A3), and was therefore selected to model diameter-height allometry (Fig. 5). The final model showed AB = 0.066, ME = 68.2%, and MAE = 1.28 (Table 2), with all parameters statistically significant at the 99% confidence level (Table 1). The initial model exhibited increasing variance with diameter, which was successfully addressed by adding a power variance function (Fig. S4). The residuals were normally distributed (Fig. S4).

Based on the CAI_V curve, *R. mange* reached its maximum (0.015 m^3 $year^{-1}$) at 49 years, while the maximum MAI_V occurred at 81 years (0.009 m^3 $year^{-1}$) (Fig. 6).

3.4. Ontogenic traits and silvicultural parameters

According to the diameter growth model, the estimated parameters were: $A_{max} = 40.09$ cm, WAGR = 0.42 cm $year^{-1}$, $t_{span} = 95.12$ years, and $t_{0.5} = 41.09$ years (Table 3). Using the volume estimates, the optimal harvesting period was determined to occur between 49 and 81 years, with a CC of 20 years. During this period, an average tree

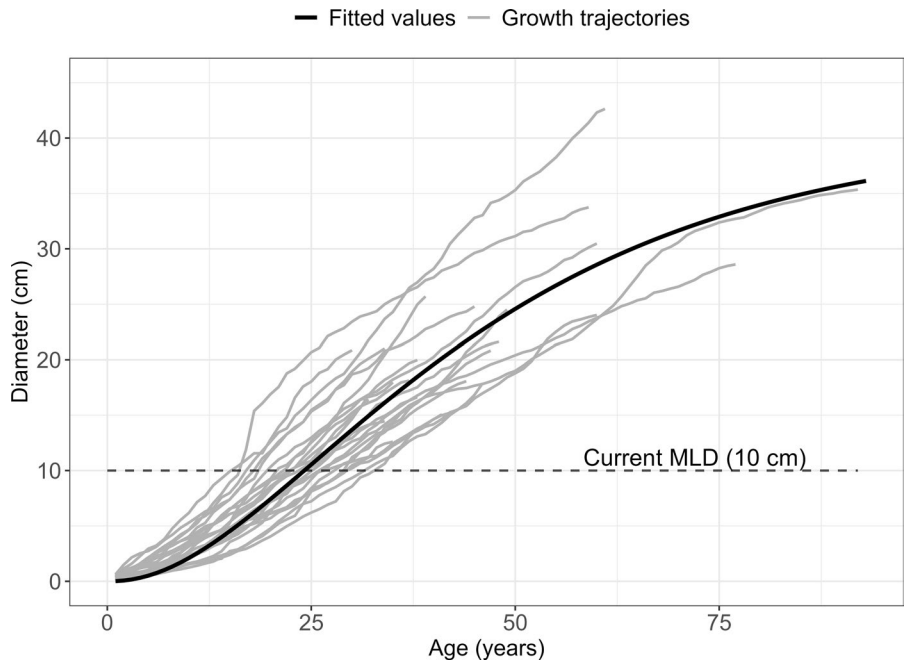


Fig. 4 Fitted values of the von Bertalanffy model (1934; black) and diameter growth trajectories of *Rhizophora mangle* (grey). The dashed line represents the current minimum logging diameter (MLD) used in Cispatá Bay

Table 1 Estimated parameters for diameter growth and diameter-height models for R. mangle

Model	Fixed effects			Random effects		Correlation structure	Variance structure
Diameter growth	η	m	γ	σ_η	σ_m		
	0.376***	0.571***	0.077***	0.061	0.048	ARIMA(1,1,0); ϕ : 0.28***	VarConst
Diameter—Height	α	β	–	$\sigma_{\alpha i}/\sigma_{\alpha j}$	$\sigma_{\beta i}/\sigma_{\beta j}$	–	VarPower;δ : 1.32
	15.593***	7.535***	–	1.215/1.118	0.909/1.838		

σ_η and σ_m are the standard deviations of the random parameters η y m of the diameter growth model, respectively; $\sigma_{\alpha i} y \sigma_{\beta i}$ are the standard deviations at transect level of the random parameters α and β, while $\sigma_{\alpha j} y \sigma_{\beta j}$ are the standard deviations at plot level; ARIMA (p,d,q): Autoregressive Integrated Moving Average model as the correlation structure, where p, d, and q are the order of the autoregressive polynomial (AR), differencing, and moving average (MA) polynomials, respectivel; ϕ are the estimated parameters of the AR structure. VarConst refers to constant variance among the residuals, while VarPower refers to the power of variance function which accounts for increase in variance of the residuals as fitted values increases. δ is the parameter of the variance function

would reach a diameter of 24–34 cm. The specific MLD for *R. mangle* was estimated at 24 cm, typically achieved at 49 years—more than double the current legal MLD of 10 cm, which is reached at 24 years (Fig. 6 and Table 3).

Discussion

This study examined the sustainable management of *R. mangle*, a dominant and heavily harvested mangrove species in the Colombian Caribbean. We combined tree-ring and forest inventory data to model diameter, height, and volume growth, from which ontogenic traits and silvicultural parameters were derived. Although similar approaches have been applied in other tropical forests, this represents the first application in mangrove ecosystems.

Forest structure

Cispatá Bay showed a total tree abundance of 1014.89 ± 300.66 individuals ind ha^{-1} with diameter > 3.5 cm. When considering individuals with a

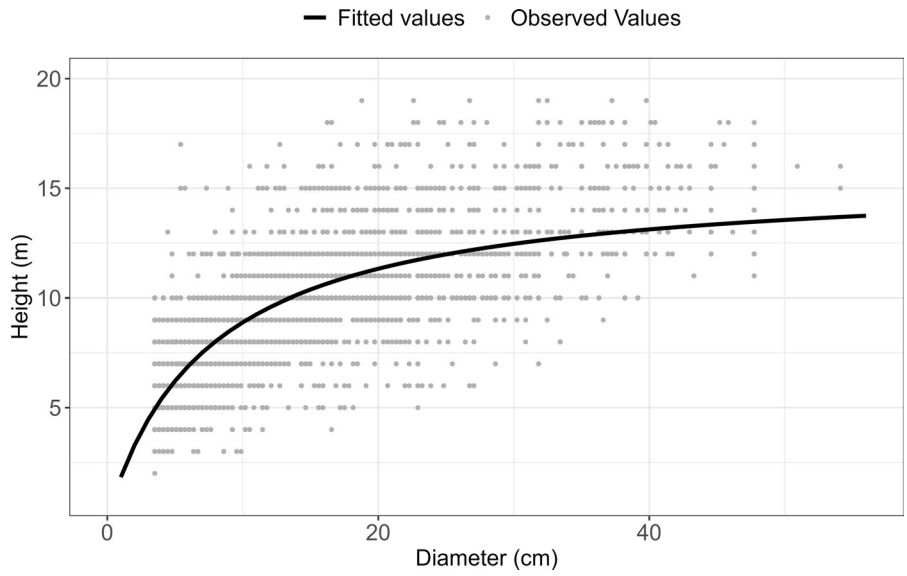


Fig. 5 Diameter-height allometry and fitted values of the Michaelis–Menten (1913) model

diameter > 5 cm, abundance was lower than that of well-preserved fringe mangroves in the Colombian Caribbean (Urrego et al. 2009) but comparable to sites under intensive wood extraction and degradation (Urrego et al. 2014). The inverse J-shaped distribution of *R. mangle* abundance observed here is consistent with other fringe mangrove ecosystems (Urrego et al. 2014), reflecting high regeneration rates driven partly by gap formation following harvesting, which facilitates seedling establishment (Duke 2001; Sherman et al. 2000; Urrego et al. 2014).

Tree-ring sampling and growth trajectories

The use of cross-sections from felled or naturally dead trees enabled reliable tree-ring analyses, allowing precise estimates of diameter growth, ontogenetic traits and silvicultural parameters for *R. mangle*. While tree-ring studies of dead trees are common in extratropical regions (Bocking et al. 2017; Speer 2010), they are rarely applied in tropical settings due to indistinct rings and high decomposition rates (Fichtler et al. 2003; Groenendijk et al. 2015). Mangrove environments, however, are saline and anoxic, which retard decomposition, making this method feasible (Ouyang et al. 2017; Simpson et al. 2023). Frequent disturbances such as storms and deforestation (Asari et al. 2021; Chowdhury et al. 2017) also yield recently fallen trees suitable for sampling. This study, therefore, supports the use of non-destructive sampling in mangroves where timber extraction is limited.

We observed substantial variability in diameter growth trajectories, consistent with growth depensation reported for *R. mangle* in Brazil (Menezes et al. 2003) and for many tropical species (Andrade et al. 2019; Brienen et al. 2010; Free et al. 2014; Martínez et al. 2025). Such intraspecific variation arises from persistent environmental effects, periods of suppression and release, autocorrelation, and genetic diversity (Brienen et al. 2010; Brienen and Zuidema 2006; Martínez et al. 2025). Importantly, we demonstrated that neglecting growth eccentricity can substantially bias diameter estimates and model outputs (Fig. S2), with over- or underestimation of up to 50% and 30%, respectively (Table S1). Similar findings were reported by Visser et al. (2023), who showed that ignoring eccentricity can distort basal area increment estimates by up to 55%. Eccentric growth—often linked to wind exposure, crown asymmetry, competition, and slope— is seldom considered in tropical

Table 2 Validation parameters for the diameter growth and diameter-height models

Model	AB	MAE	ME (%)
Diameter growth	0.005	0.147	99.956
Diameter—Height	0.066	1.278	68.206

AB average bias, *MAE* mean absolute error, *ME* model efficienc

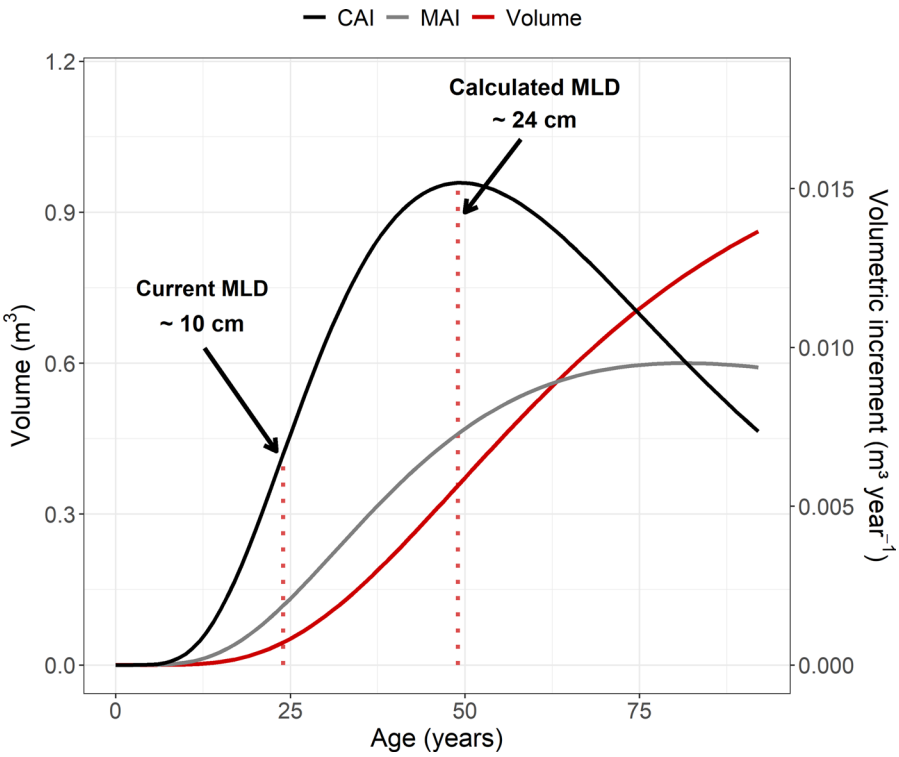


Fig. 6 Mean cumulative volume growth (red), and current (CAIV; black) and mean (MAIV; grey) annual volume increments for *Rhizophora mangle*. Red dotted lines indicate the current and calculated minimum logging diameters (MLD) used in Cispatá Bay. The calculated MLD corresponds to the diameter attained at the age when CAIV reaches its maximum value

growth studies (Brienen and Zuidema 2006; Conde et al. 2024; Free et al. 2014; Šilhán 2019). Measuring multiple radii (Visser et al. 2023) or applying perimeter-based correction factors (Gebrekirstos et al. 2008; Giraldo and del Valle 2011) can effectively minimize these errors, as implemented in this study.

Table 3 Ontogenic traits and silvicultural parameters derived from growth models for *Rhizophora mangle's* population in Cispatá Bay

Parameter	Value
Amax	40.35 cm
WAGR	0.42 cm year^{-1}
t_{span}	95.12 years
$t_{0.5}$	41.09 years
MLD	24 cm
Age_{MLD}	49 years
$Age_{D=10}$	24 years
CC	20 years

Amax maximum mean diameter or the estimated asymptote for the diameter model, *WAGR* weighted absolute growth rate; t_{span} lifespan, $t_{0.5}$ half-life, *MLD* minimum logging diameter, Age_{MLD} age at which the minimum logging diameter is reached, $Age_{D=10}$ age at which the current minimum logging diameter used in Cispatá Bay (10 cm) is reached, *CC* cutting cycle

Growth modeling

The von Bertalanffy (1934) model, applied through an NLME framework, effectively described *R. mangle*'s diameter growth and variability. Model performance was further improved by incorporating an ARIMA specification, which captured the species' growth autocorrelation; failing to do so could otherwise bias long-term estimates by underestimating growth in fast-growing trees (Brienen et al. 2006). The estimated *m* parameter was biologically consistent with the metabolic theory underlying the model (Richards 1959), with values between 0.48 and 0.63. This allowed meaningful interpretation of the calculated η (0.376) and γ (0.077) parameters as proportional coefficients of photosynthesis and respiration (Martínez et al. 2025), offering insights into species physiology. *R. mangle* exhibits ontogenetic shifts in light requirements, showing shade tolerance in early stages and accelerated growth under canopy openings (da Silva et al. 2015; Ellison and Farnsworth 1993). The estimated η (0.376) for *R. mangle* closely matches

that for *Humiriastrum procerum* as shade-tolerant in the Chocó biogeographic region (η = 0.384) and is substantially lower than *Apeiba macropetala* (η= 0.999), a fast-growing heliophyte in the same region (Martínez et al. 2025).

The diameter–height allometric model derived from inventory data displayed considerable variability, unlike the stronger fit (R^2=0.85) reported by Méndez-Alonzo et al. (2015) for *R. mangle* in La Mancha Lagoon, Mexico. Variations in soil salinity, phosphorus availability, and light conditions largely explain such differences between sites (Cisneros-de la Cruz et al. 2018). The higher variability in this study may also stem from measurement error due to the 1-m precision of the instrument used for height estimation.

Ontogenic traits and silvicultural parameters

The growth models enabled the calculation of ontogenic traits and volume growth over the species' lifespan, supporting the derivation of silvicultural parameters under the GOL concept. While several studies have analyzed similar parameters in tropical forests (Andrade et al. 2019; Conde et al. 2024; Inga and del Valle 2017; Lisboa et al. 2025; Martínez et al. 2025; Schöngart 2008), this represents the first such assessment in mangroves. We calculated an A_{max} of 40.09 cm, WAGR of 0.42 cm y^{-1}, t_{span} of 95.12 years, and $t_{0.5}$ of 41.09 years. The maximum diameter may be influenced by salinity, temperature, and storm events (Lovelock et al. 2016). For instance, dwarf *R. mangle* populations dominate in subtropical Florida (Coronado-Molina et al. 2004), whereas mangroves in the Colombian Pacific, considered the tallest in the Americas, can reach diameters of 96.7 cm (Castellanos-Galindo et al. 2021). Our A_{max} value thus represents a theoretical population mean, not an upper physical limit. The highest-growth individuals (Table S2) reached diameters consistent with the largest trees in Cispatá Bay (56 cm). The WAGR estimated here agrees with radial increment rates (0.13–0.33 cm y^{-1}) reported for Brazil (Menezes et al. 2003) and provides a more age-independent indicator of performance than absolute growth (Inga and del Valle 2017). The lifespan estimated for *R. mangle* was shorter than the 250-year maximum reported by Chen and Twilley (1998) for Mexico, likely reflecting smaller diameters in our population. To our knowledge, this is the first study to estimate $t_{0.5}$ for *R. mangle*.

Management implications

Timber extraction has been shown to alter regeneration dynamics in mangrove ecosystems by increasing the abundance of small trees, likely driven by establishment facilitation following canopy gap formation during harvesting (Fig. 3; Agudelo et al. 2015; Urrego et al. 2014). Although the smallest diameter class (3.5–10 cm) presented the highest abundance of *R. mangle* in Cispatá Bay, trees within this class were not sampled directly for growth-ring analysis. Instead, we relied on dendrochronological methods to reconstruct growth from the year of establishment of larger sampled individuals (> 10 cm), thereby indirectly incorporating early growth stages into the analyses. Consequently, growth dynamics relevant to early diameter classes were incorporated into the modeling framework, ensuring that management implications reflect stand development across size classes.

The MLD and CC are key criteria for sustainable tropical forest management. Consistent with our hypothesis, the estimated MLD and CC deviated from those currently applied in Cispatá Bay. We calculated an MLD of 24 cm, achieved at 49 years—more than double the 10 cm currently applied, which is reached at 24 years of age. Similar discrepancies have been reported when the GOL-based parameters are used (Andrade et al. 2019; Conde et al. 2024; Schöngart 2008). The existing 14-year CC defined in the local management plan differs significantly from our 20-year estimate based on tree-ring data. This difference reflects the higher temporal precision of dendrochronological methods, which account for growth autocorrelation and individual variability (Brienen and Zuidema 2006; Inga and del Valle 2017; Martínez et al. 2025).

The current silvicultural parameters used in Cispata Bay may not be optimal for ensuring long-term sustainability and stand recovery. A low MLD may reduce the number of trees able to reach larger size classes, while a short CC prevents residual trees from reaching the next diameter class, hindering volume recovery. Adjusting these metrics would better align harvesting practices with species growth dynamics and ecosystem resilience. However, implementing stricter criteria may conflict with local livelihood

practices. Firewood collection remains the main energy source, typically involving small-diameter trees below the current MLD (CVS and INVEMAR 2010; Dupont et al. 2025). Recent surveys indicate that 94% of households use *R. mangle* for fuelwood, extracting intensively for up to 100 days per year (Dupont et al. 2025). Although essential for subsistence, this practice is a major anthropogenic driver of mangrove degradation (Chowdhury et al. 2017; Huxham et al. 2017).

Alternative strategies have proven successful elsewhere. In Saadani National Park, Tanzania, promoting alternative fuels among higher-income households reduced unsustainable harvesting while boosting incomes through enhanced shrimp fisheries (McNally et al. 2011). In Indonesia, the selective use of deadwood is permitted to satisfy firewood demand without cutting live trees (Mugi et al. 2022; Sillanpää et al. 2017). Nevertheless, further study is needed to evaluate the ecological effects of deadwood removal, given its role in nutrient cycling and habitat provision (Chisika and Yeom 2021; Wijas et al. 2024). In Cispatá Bay, similar approaches—including deadwood utilization, promotion of alternative fuels, and targeted application of silvicultural criteria for construction and commercialization—could reconcile conservation goals with community well-being.

The effectiveness of management plans depends not only on regeneration and recruitment but also on volume recovery after each rotation (Andrade et al. 2019; Schöngart 2008). To enhance regeneration, we recommend active planting in canopy gaps, as *R. mangle* seedlings perform best under open canopies (Ellison and Farnsworth 1993). Enrichment planting and controlled pruning can accelerate growth in *Rhizophora* species (Ferreira et al. 2015; Kathiresan et al. 2019). Similarly, crown liberation, widely used in managed tropical forests, can increase productivity and shorten the time needed to reach MDL while providing sustainable firewood (Grogan and Landis 2009). Given the high current density of *R. mangle* in Cispatá Bay, we recommend low-intensity harvesting that maintains large individuals essential for ecosystem services such as coastal protection, flood mitigation, and erosion control (Alongi 2008; Asari et al. 2021). To support this, the silvicultural thresholds proposed in this study provide science-based criteria that can guide the revision of local management plans and support updates to national forestry regulations for mangrove ecosystems. Achieving long-term sustainability, however, also requires active community participation, integration of socio-cultural needs, and adaptive monitoring of forest recovery to guide future interventions.

During the study, we encountered some limitations related to both sampling and modeling. Due to the origin of the material from fallen and dead trees, growth-ring delimitation presented certain challenges in some samples due to varying degrees of wood decay. To minimize potential bias, we included only radii showing no significant decay. For samples classified as having advanced decay, only one measurable radius was used, while samples with severe decay were excluded from the analysis.

With regard to the modeling and estimation of silvicultural metrics, socio-cultural constraints were considered in a simplified manner. However, future studies should explore these aspects in greater depth and integrate more detailed socio-economic scenarios. Incorporating tree mortality into future analyses would further improve the modeling and estimated metrics. Addressing both factors would allow for more realistic long-term estimates of volume availability, cutting intensities, and sustainable harvesting strategies.

Conclusions

The integration of dendrochronological methods with biometric modeling enabled the derivation of revised silvicultural parameters for *Rhizophora mangle* in Cispatá Bay, revealing substantial discrepancies relative to the parameters currently in use. These results suggest that prevailing criteria may encourage premature harvesting, thereby constraining forest recovery and undermining long-term sustainability.

Incorporating adjusted models that explicitly account for autocorrelation improved predictive performance and strengthened the physiological interpretation of growth parameters. In addition, correcting for stem eccentricity reduced biases that are frequently overlooked in tropical studies. Collectively, these methodological refinements position the proposed approach as a useful reference for adaptive management in mangrove systems subject to access or extraction restrictions.

Nonetheless, implementation of the revised criteria should proceed gradually and be supported by continuous monitoring, particularly given local communities' reliance on small-diameter timber. A transition toward evidence-based management requires meaningful community participation and the incorporation of local needs into the implementation process, with particular attention to regeneration dynamics and equitable access to resources.

Overall, this study advances a robust, science-based framework for forest governance that is potentially transferable to other species and regions, while underscoring the need for experimental validation. Progress toward genuinely sustainable forestry in Caribbean mangroves and comparable systems will depend on interdisciplinary collaboration, long-term monitoring, and the explicit integration of social and ecological values.

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Author contributions All authors contributed to the study's conception and design. Material preparation and data collection were carried out by David Valderrama and Valeria Aguirre. Data analysis was conducted by David Valderrama and Sergio Orrego. The first draft of the manuscript was written by David Valderrama, and the final version was prepared by David Valderrama, Jaime Polanía, and Sergio Orrego. Jaime Polanía secured funding for the project, and both Jaime Polanía and Sergio Orrego supervised the research. All authors read and approved the final manuscript.

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Data availability Tree-ring data used in this study are publicly available in the Mendeley Data repository at https://doi.org/10.17632/z42tbzp2n5.1. Forest inventory data are not publicly available as they are the property of a private organization and subject to restrictions.

Declarations

Conflict of interest The authors declare no competing interests.

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