



Management implications of long-term tree growth and mortality rates: A modeling study of big-leaf mahogany (*Swietenia macrophylla*) in the Brazilian Amazon



Christopher M. Free^{a,*}, R. Matthew Landis^{b,c}, James Grogan^{d,e}, Mark D. Schulze^{e,f,g}, Marco Lentini^e, Oliver Dünisch^h

^a Rutgers University, Institute of Marine and Coastal Sciences, New Brunswick, NJ 08901, USA

^b Middlebury College, Department of Biology, Middlebury, VT 05753, USA

^c ISciences, Burlington, VT 05401, USA

^d Mount Holyoke College, Department of Biological Sciences, South Hadley, MA 01075, USA

^e Instituto Floresta Tropical, Rua dos Mundurucus, 1613, Jurunas, Belém, Pará 66.025-660, Brazil

^f HJ Andrews Experimental Forest, Blue River, OR 97413, USA

^g Oregon State University, Department of Forest Ecosystems and Society, Corvallis, OR 97331, USA

^h Meisterschule Ebern für das Schreinerhandwerk, Gleusdorfer Str. 14, 96106 Ebern, Germany

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ABSTRACT

Knowledge of tree age-size relationships is essential towards evaluating the sustainability of harvest regulations that include minimum diameter cutting limits and fixed-length cutting cycles. Although many tropical trees form annual growth rings and can be aged from discs or cores, destructive sampling is not always an option for valuable or threatened species. We used an individual-based population model developed for big-leaf mahogany (*Swietenia macrophylla*, Meliaceae) in southeast Amazonia, Brazil to simulate stem age-size relationships and examine forest management implications of mortality and diameter increment growth. Growth trajectories of 10,000 simulated mahogany trees were consistent with growth trajectories reconstructed from 32 mahogany discs with annual rings. Trajectories were highly variable and strongly autocorrelated; diameter was a poor predictor of tree age even when accounting for up to 10 years of previous growth history. Commercial-sized trees (60 cm diameter) ranged in age from 33 to 180 years (74 yr median). Only 12.5% of seedlings survived to this size, but survival and time to reach commercial size depended strongly on early growth history (first 10 years of life). A tree grown at the 75th percentile growth rate throughout its lifetime requires 70 years to attain commercial size, but Brazilian forest management regulations imply a rotation length of 60 years. These results demonstrate that individual-based models parameterized with typical census data can incorporate individual variation and growth autocorrelation and realistically simulate tree growth and mortality. In the absence of tree ring data, such models can be used to evaluate the consequences of long-term growth and mortality for sustainable management. In the case of mahogany, our results suggest that non-detrimental harvests cannot be achieved without lengthening cutting cycles, increasing commercial tree retention rates, and regularly applying silvicultural treatments designed to increase stem diameter growth rates. Forest managers can have the greatest effect on the rate of commercial recruitment in the first 10 years after a harvest by implementing treatments ensuring that adequate numbers of new stems establish and recruit to dominant positions in recovering canopy gaps. Regrettably, sustainable mahogany management systems developed based on understanding of the species' ecology will not be as simple as current harvest regulations in Brazil imply.

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1. Introduction

“How old is that tree?” Forest managers and researchers in the tropics rarely can tell unless they know that it established after some verifiable disturbance event in the recent or distant past

* Corresponding author. Address: Institute of Marine & Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901, USA.

E-mail addresses: cfree14@gmail.com, cfree@swietking.org (C.M. Free).

(Snook, 2003; Baker et al., 2005). But the ability to age trees would offer a powerful tool to forest managers attempting to sync harvest and silvicultural practices to biological realities in the field. Aging trees is key to understanding population and stand dynamics, including knowing whether harvest regulations that include minimum diameter cutting limits (MDCL) and fixed-length cutting cycles are sustainable or not. Rotation length for a species or a stand – the time necessary for regeneration from seed to minimum commercial size – should be determined by age at minimum commercial size (Smith et al., 1997). If, for example, a 60-cm diameter tree representing the minimum commercial size requires 90 years on average to attain that size, but the cutting cycle represents a shorter interval than this (typically 25–30 years across most of the tropics), then timber yields will inevitably fall over multiple cutting cycles if densities of sub-commercial stems are low compared to commercial-sized trees. This condition is common for many high-value timber species in tropical America (Grogan et al., 2008; Schulze et al., 2008a, b).

Trees can be aged by counting annual growth rings on cross-sectioned stem discs or radial cores, especially in northern and southern temperate zones where each year's winter dormancy leaves a clearly demarcated ring (Bormann and Berlyn, 1981). A growing body of evidence indicates that many tropical species also form annual growth rings, especially those occurring in seasonally dry climates (Worbes, 1999; Dünisch et al., 2002, 2003; Fichtler et al., 2003; Worbes et al., 2003; Brienen and Zuidema, 2005). As a result, tree ring analyses are beginning to be used as a tool in tropical forest management (Rozendaal and Zuidema, 2011), and have provided important insights into the role of growth autocorrelation (Brienen et al., 2006; Brienen and Zuidema, 2007), age-size variation (Brienen and Zuidema, 2006; Schöngart, 2008), and canopy accession patterns (Baker and Bunyavejchewin, 2006; Brienen and Zuidema, 2006; Brienen et al., 2010). Even so, relatively few ring studies have been conducted to date in the tropics, and the most reliable of these – based on cross-sectioned discs rather than radial cores – are destructive to the trees in question or depend on previously harvested trees. Although increment cores can be obtained without harming trees (Baker and Bunyavejchewin, 2006; Buckley et al., 2007) and could be used to sample a broad range of size classes even for valuable or threatened species (Zuidema et al., 2011), stem discs are more reliable due to the presence of wedging rings in many tropical trees (Worbes, 2002).

In the absence of tree rings, either because they do not form or because destructive sampling is not an option, long-term stem diameter increment rates combined with observed mortality rates across the full range of stem sizes for a given species can provide insights into stem age-size relationships. However, aging trees by projecting observed growth rates back into time to 'reverse grow' them to the time of establishment is problematic. Stem growth rates may vary as a function of diameter (Grogan and Landis, 2009), requiring robust sample sizes to adequately capture population-level patterns. Growing conditions may change multiple times during a tree's lifetime, either gradually or abruptly, accelerating or suppressing growth as surrounding forest canopies open and close following disturbances large and small (Baker and Bunyavejchewin, 2006; Brienen and Zuidema, 2006). And tree-specific factors such as crown vine loading, fruit production rates, structural injury, disease, and genetics may complicate age-size relationships. For these reasons, long-term permanent plot data should be treated as a collection of time-series snapshots of individual tree growth patterns approximating the range of growing conditions and growth and mortality rates that trees of all sizes will encounter at a given forest site.

In this paper, we use an individual-based population model developed for big-leaf mahogany (*Swietenia macrophylla*, Meliaceae) in southeast Amazonia, Brazil to simulate stem age-size rela-

tionships for this iconic tropical timber species. In 2002, mahogany became the first widely traded timber species to be listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Blundell, 2004). Mahogany's Appendix II listing addressed concern over the sustainability of industrial harvest practices, which typically removed up to 95% of adult trees from primary forests without regard for seedling regeneration necessary for stand replacement (Snook, 1996; Zimmerman et al., 2001; Grogan et al., 2008). Because Appendix II listing requires exporting nations to verify that timber supplies originate from sustainably managed forests (Grogan and Barreto, 2005), thorough understanding of mahogany population dynamics is necessary to transform historic logging practices into sustainable forest management.

The mahogany population model incorporates observed growth autocorrelation following a straightforward parameterization method and yields realistic simulations of individual tree characteristics and population dynamics (Grogan et al., 2014). We offer further validation by comparing individual tree growth trajectories generated by the model to actual growth trajectories reconstructed from stem disc analysis at field sites west of our research site (Dünisch et al., 2003). We use the model to examine forest management implications of mortality and diameter increment growth by: (1) simulating tree lifetime growth trajectories from seedling to senescence in order to estimate the age ranges of trees at reproductive maturity (30 cm diameter) and minimum commercial size (60 cm diameter); (2) estimating the age of trees at reproductive maturity and commercial size when grown at optimal growth rates, which we define as the 75th percentile of simulated growth rates; and (3) examining the importance of fast-growing trees to observed population structures and the role that silviculture must play towards achieving sustainable harvests. We conclude by discussing the causes of mahogany age-size variation and implications for current legal harvest regulations in Brazil.

2. Materials and methods

2.1. Study species

Mahogany is a fast-growing, light-demanding, late successional canopy emergent tree associated with seasonally dry tropical forests from Mexico to Bolivia (Lamb, 1966). In southeastern Amazonia, it is commonly distributed along seasonal streams or rivers, occurring at highly variable but consistently low densities, up to 1.2 trees >20 cm diameter ha⁻¹ (Veríssimo et al., 1995; Grogan et al., 2002, 2008). Within the study region, mahogany trees larger than 5–10 cm diameter shed their crowns each dry season, reflushing new crowns after a deciduous period lasting from 5 to 10 days (Grogan, 2001; Grogan and Schulze, 2012; Grogan and Loveless, 2013). The few published studies of growth and mortality by adult mahogany trees in natural forests have been summarized by Grogan and Landis (2009). Previous studies have shown that mahogany trees form annual growth rings in some regions (Worbes, 1999; Dünisch et al., 2002; 2003).

2.2. Study site

The study site is a 4100-ha forest industry-owned management area called Marajoara, located at 7°50'S, 50°16'W in the southeast corner of the state of Pará. Climate is tropical dry. Annual precipitation during 1995–2001 averaged 1859 ± 82 mm (SE), with >90% falling between November and May; in some years, no rain fell for 3–4 mo during the dry season (Grogan and Galvão, 2006). This pronounced seasonality increases the likelihood that tree species in this region, including mahogany, form annual growth rings

(Worbes, 2002). Topographic relief is slight; all streams are seasonal within the principal research area of 2050 ha. The forest is dominated by evergreen trees intermixed with deciduous species. Marajoara was selectively logged for mahogany from 1992 to 1994, reducing landscape-scale densities from 0.65 to 0.19 mahogany trees >20 cm diameter ha^{-1} , and from 0.39 to 0.04 mahogany trees >60 cm diameter ha^{-1} , the current minimum commercial diameter in Brazil (Grogan et al., 2008). An additional 5 secondary timber species were logged at that time, producing an estimated $3 \text{ m}^3 \text{ ha}^{-1}$ of roundwood including mahogany. The site is surrounded by pasture and heavily logged and burned forest.

2.3. Field methods

The sample population at Marajoara consists of 358 mahogany trees >10 cm diameter that survived selective logging within 2050 ha of the larger forest management area. These trees were censused annually for survival, stem diameter growth, and fruit production from 1995 to 2010 (see Grogan and Landis (2009) for detailed description of field methods). Due to selective logging prior to the study (Grogan et al., 2008), mortality and growth rates may reflect a small post-logging increase (De Graaf et al., 1999). Demographic rates for trees <10 cm diameter were estimated from nursery-grown seedlings ($N = 237$) experimentally outplanted into large (0.65-ha) artificial clearings (Grogan, 2001). This was necessary due to the scarcity of natural regeneration in gap environments. Nursery-grown seedlings were outplanted in 1996 and censused annually until 2010. Competing vines and secondary vegetation were removed manually for the first three years following outplanting. Because growth and survival rates of these juveniles were likely higher than natural regeneration, these data represent optimistic estimates of juvenile performance.

2.4. Model construction and simulating growth trajectories

The mahogany population model was constructed using R version 3.0.2 (R Core Team 2012) including the nlme, MASS, and rms packages (Pinheiro and Bates, 2000; Harrell, 2001; Venables and Ripley, 2002). The individual-based model simulates population dynamics over annual time steps. Similar to matrix-based models, the model is non-spatial and does not incorporate density-dependence. Unlike matrix-based models, it incorporates growth autocorrelation, the tendency for fast-growing trees to remain fast-growing, which has been shown to strongly influence modeling results (Brienen and Zuidema, 2007; de Valpine, 2009; Zuidema et al., 2009). See Grogan et al. (2014) for a full description of model parameterization and validation.

We used the model to simulate the growth and mortality of 10,000 trees over 300 years. All simulated trees were assumed to have begun as seedlings growing in a canopy gap sufficiently large for successful recruitment (minimum radius 10 m or 314 m^2 ; Grogan et al., 2003; Grogan et al., 2005). At each time step (one year), mortality probability and diameter increment (cm yr^{-1}) were estimated for each tree using regression equations derived from annual census data. Diameter increment was estimated as a function of stem diameter using generalized least squares to incorporate an autoregressive error term to account for growth autocorrelation over the preceding 10 years. Mortality probability was estimated as a binary logistic regression derived from current-year stem diameter and diameter increment (Pinheiro and Bates, 2000; Grogan and Landis, 2009; Grogan et al., 2014).

2.5. Model validation

We validated simulated growth trajectories in two ways. First, we compared simulated growth trajectories to actual growth

trajectories reconstructed from a tree ring analysis of mahogany growing in a forest 50 km west of the city of Aripuanã, Mato Grosso, Brazil ($10^{\circ}09'S$, $59^{\circ}26'W$; ~ 1040 km from Marajoara). Dünisch et al. (2003) constructed tree ring chronologies for 33 of 47 mahogany trees based on stem discs collected immediately after felling. Chronologies could not be constructed for 14 trees in which the annuality of growth rings, especially during the juvenile stage, could not be verified through microscopical analyses and cross-dating. One tree harvested outside the forest was excluded from our analysis for a total of 32 chronologies. Discs were polished and the widths of increment zones were measured along four perpendicular radii. Annual growth increments, marked by terminal parenchyma bands (Dünisch et al., 2002), were identified by light microscopy of the discs or in microtone cross-sections of the xylem blocks. The widths of the increment zones were obtained using a measuring ocular lens. Ring width chronologies were used to reconstruct lifetime age-diameter trajectories. See Dünisch et al. (2003) for a full description of the study site and tree ring analysis. We refer henceforth to these as the 'Dünisch trees'. Second, we compared simulated growth trajectories to ring counts from cross-sectional stem discs taken from 10 dead mahogany trees at Marajoara ranging from 24 to 103 cm diameter. Stem discs were cut by chainsaw, sanded, and stained before counting rings along 3–4 radial axes per disc, averaging ring counts to estimate tree age. Rings are assumed to form annually due to the pronounced seasonality of the study region.

2.6. Data analysis

We simulated individual tree growth trajectories to estimate the range of tree diameters after 30 years (cutting cycle length) and after 60 years (assumed rotation length). Growth trajectories also provided estimates of the range of tree ages at reproductive maturity (30 cm diameter; Grogan and Loveless, 2013) and at the minimum commercial size in Brazil (60 cm diameter). To characterize variability in the age-size relationship, we also estimated the age of trees at 90, 120, and 150 cm diameter. We calculated the median, minimum, and maximum ages of trees at each diameter. These analyses were performed on growth trajectories both simulated in the model and reconstructed from the Dünisch trees.

Not unexpectedly, stem diameter proved to be a poor predictor of tree age (Harper, 1977; Enright and Hartshorn, 1981; Sarukhan et al., 1984; Villalba et al., 1985; Worbes et al., 2003). To see whether growth history might improve the predictive power of stem diameter, we estimated tree ages using diameter and growth history combined by classifying the average growth increment of the preceding 2 years and 10 years into 10% growth performance quantiles and calculating the 5–95% age range of trees within each diameter-growth performance category. We essentially asked: what is the range of simulated ages for all trees attaining a given size (e.g., 60 cm diameter) that grew at a given observed 10% quantile rate during the preceding 2 or 10 years (e.g., 70–80th percentile)? We used 2 years of growth history assuming that forest managers might be able to collect this information in preparation for harvest operations, and 10 years of growth history for comparison.

To evaluate the importance of early growth performance to commercial recruitment, we classified trees into growth performance quartiles (slowest, slow, fast, fastest) based on diameter attained in the first ten years of life, and compared the proportion surviving and the proportion attaining commercial size among the four early growth performance categories.

For both simulated and observed (Dünisch) trees, we calculated the median, minimum, and maximum passage time – the number of years spent in a size category – for each 10-cm size class between 0 and 60 cm diameter. In order to assess the contribution of each size class to age variation at commercial size, we analyzed

the effect of passage time in each size class on age at 60 cm diameter using multiple regression that included all size classes (Brienen and Zuidema, 2006).

We calculated the 75th percentile growth rate – what we consider an ‘optimal’ growth rate achievable through silviculture – using a linear quantile regression forced through the origin in the R package *quantreg*. To evaluate the potential for silviculture to increase the sustainability of current harvest standards, we calculated the time required to grow a tree to the 60 cm MDCL at this growth rate.

3. Results

3.1. Mahogany growth trajectories and validation

Growth trajectories by 10,000 simulated mahogany trees were highly variable but similar to patterns revealed by long-term census data (Fig. 1; Grogan et al., 2014).

Growth trajectories of trees from the Dünisch et al. (2003) ring study closely resembled simulated growth trajectories, with all 32 observed trajectories falling within 5th and 95th percentile diameter ranges for simulated trees (Fig. 2A). Approximately equivalent numbers of Dünisch trees grew above and below median simulated increment rates until the time of harvest. The tendency for trees to maintain a consistent growth rate over multiple years, either fast- or slow-growing, was apparent in the Dünisch tree ring chronologies, further demonstrating the prevalence and importance of growth autocorrelation in mahogany trees.

Stem disc ring counts from 10 mahogany trees at Marajoara yielded estimated ages that fell well within 5th and 95th percentile diameter ranges for simulated trees (Fig. 2B). Ages for seven of these trees fell within 2nd and 3rd quartile age ranges (25th to 75th percentiles). Five of 10 trees with ring counts were aged close to the median value for simulated trees at their respective diameters; the largest aged tree (103 cm diameter, ~141 years old) was close to the median value for the corresponding median simulated age-size (150 years), indicating that the model performs well across long timescales.

Almost 60% of simulated trees lived fewer than 10 years; 21.9% of simulated trees survived to reproductive maturity (30 cm diameter), 12.5% survived to commercial size (60 cm diameter), and <1% survived to 150 cm diameter (Fig. 3A). The median diameter of 30-yr-old trees was 21.0 cm (range 3.3–55.8 cm); the median diameter of 60-yr-old trees was 43.5 cm (range 4.7–98.7 cm). The

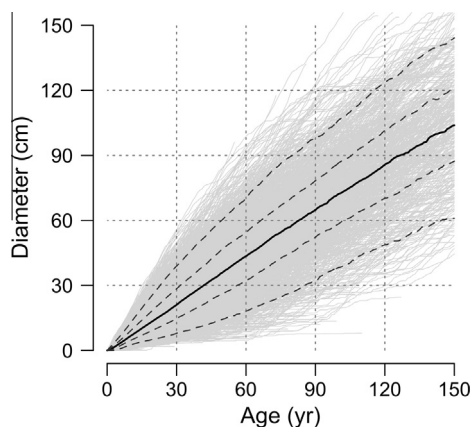


Fig. 1. Growth trajectories by 10,000 simulated trees through 150 years (gray lines) showing stem diameter as a function of age. The solid black line indicates median values (50th percentile); dotted lines show 5th, 25th, 75th, and 95th percentile trajectories from bottom to top. The 75th percentile trajectory represents our estimate of the ‘optimal’ growth rate achievable through silviculture.

growth model’s autocorrelation function resulted in periods of consistent diameter increment growth, with a given tree experiencing both above- and below-average growth rates over time (Fig. 1). On average, early fast-growing trees – that is, trees growing faster than median values during the first 10 years of simulations – lived longer than early slow-growing trees (mean of 76 vs. 56 years, respectively; Fig. 3A). Similarly, early fast-growing trees attained commercial size earlier and with higher frequency than early slow-growing trees (Fig. 3B).

3.2. Age-size relationships

Both simulated and observed mahogany trees demonstrated large variation in growth trajectories and age-size relationships. Simulated trees ranged widely in age at a given diameter, from 16 to 130 years at 30 cm based on 2191 ‘surviving’ trees, 33–180 years at 60 cm (1246 trees), and 76–255 years at 120 cm (274 trees); median ages at these diameters were 38, 74, and 144 years, respectively (Table 1, Fig. 1). The much smaller sample of Dünisch trees yielded narrower age ranges at these diameters: 34–87 years at 30 cm (30 trees), 65–115 years at 60 cm (18 trees), and 140 years at 120 cm (1 tree).

The range of ages predicted for trees of a given stem diameter based on diameter plus observed growth history was generally narrower than predictions based on diameter alone, but remained wide. For example, a simulated 60-cm diameter tree growing at 90–100th percentile growth rates during the two previous years ranged from 38 to 108 years old (5–95th percentile ages); having 10 years of growth history in hand only narrowed that range to 37–91 years (5–95th percentile ages; Table 2, Fig. 4). We therefore conclude that it is not possible to create an age-size table for mahogany in the study region that predicts tree age with any degree of precision, even when incorporating recent observed growth history.

3.3. Passage times

Although median passage times were similar for all 10-cm diameter size classes, differences between the minimum and maximum passage times were largest in the first size class (0–10 cm diameter) and decreased towards larger size classes (Table 3). This pattern was mainly caused by decreasing maximum passage times as trees grew larger; minimum passage times varied little among size classes. The contribution of passage time through each size class to age at 60 cm diameter was assessed by partial correlation coefficients (PCC). PCC values decreased as size classes grew larger (Table 3), indicating that growth during the smallest size classes is most important to determining tree age at 60 cm diameter.

3.4. Optimal growth rate

A tree growing at the ‘optimal’ growth rate, defined here as the 75th percentile rate, grew 0.85 cm yr^{-1} over the long term (diameter = $0.85 \cdot \text{years}$; pseudo- $r^2 = 180.21$). A tree growing at this rate requires 36 years to reach reproductive maturity (30 cm diameter) and 70 years to reach commercial size (60 cm diameter). A 60-yr-old tree grown at the optimal growth rate will attain 51.2 cm diameter (Fig. 1).

4. Discussion

The close resemblance of model simulations to actual growth trajectories of mahogany trees in the Brazilian Amazon demonstrates that models based on permanent plot data can incorporate individual variation and growth autocorrelation to realistically

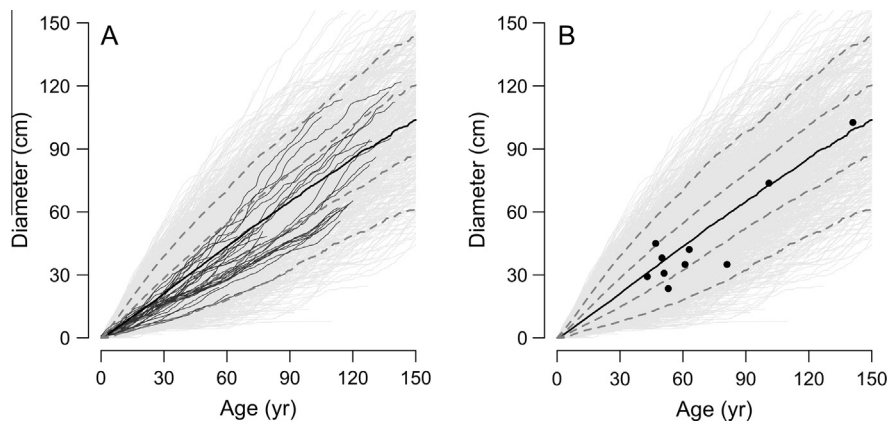


Fig. 2. (A) Growth trajectories of 32 Dünisch trees (dark gray lines) compared to simulated trees (light gray lines) as in Fig. 1. Dashed black lines indicate 5th, 25th, 75th, and 95th percentile simulated diameters; the solid black line shows median (50th percentile) simulated values. (B) Filled circles represent 10 trees aged from cross-sectional discs at Marajoara; simulated trees and lines as in (A).

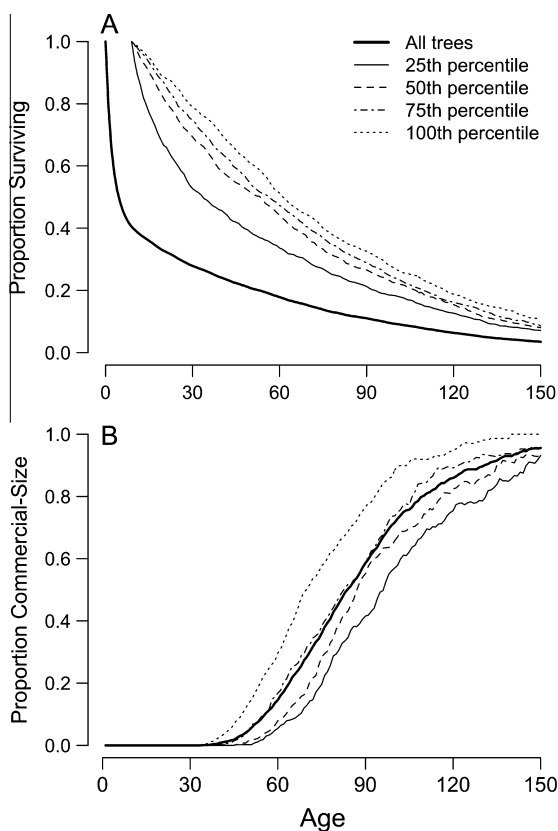


Fig. 3. The impact of seedling growth rate during the first 10 years of simulations on (A) survival probabilities and (B) commercial recruitment probabilities over time. Seedlings growing at 25th, 50th (median), 75th and 100th percentile growth rates during this period experienced successively lower mortality and higher commercial recruitment rates. Heavy black lines indicate survival and commercial recruitment probabilities for all simulated trees, including those surviving fewer than 10 years.

simulate tree growth in the absence of tree ring data. In the past, growth modeling studies often assumed deterministic growth trajectories, did not consider variability among trees, and failed to account for autocorrelated growth rates (Howard and Valerio, 1996; Alder and Silva, 2000; Dauber et al., 2005). These simplifications have been shown to generate unrealistic growth projections and underestimate long-term tree growth (Brienen, 2005; Brienen and Zuidema, 2007). More recently, growth modeling studies have incorporated growth variation and autocorrelation

with matrix models (Sist et al., 2003; Zuidema et al., 2009) and spatially explicit community models (Kammesheidt et al., 2001; Phillips et al., 2004; Gourlet-Fleury et al., 2005); although these models are more realistic, they are often complex and data intensive. Our model uses a straightforward individual-based modeling approach based on typical census data to incorporate individual variation and growth autocorrelation and realistically simulate tree growth and mortality.

The large variation observed in the age-size relationship makes it difficult to predict the age of mahogany trees of a given diameter with any degree of precision. Age range predictions were narrower when based on diameter plus growth history compared to diameter alone, but remained imprecise nonetheless. Among-tree autocorrelated growth, such as that observed in mahogany (Grogan and Landis, 2009), leads to large differences in long-term growth rates between trees and results in large age variation among trees with the same diameter (Pfister and Stevens, 2002; Arets, 2005; Brienen et al., 2006; but see Fujiwara et al., 2004). For mahogany, growth autocorrelation is likely driven by a combination of factors: (1) explanatory variables (e.g. crown vine coverage) remaining constant over time; (2) growth capacity varying among trees because of differences in crown form and size; (3) cryptic microsite differences in soil fertility or water availability; or (4) genetic differences (Grogan and Landis, 2009). Bullock et al. (2004) showed that age estimates based on size and growth rates with only moderate autocorrelation will result in large variation, reaffirming that diameter is a poor indicator of tree age (Harper, 1977; Sarukhan et al., 1984).

In the present study, age ranges of observed (the Dünisch trees) and simulated mahogany trees at 60 cm diameter spanned 65–115 and 33–180 years, respectively. Our large sample of trees, juveniles, saplings, and seedlings at Marajoara and this study's long observational time horizon provide many examples of the biological realism of these age ranges for a commercial-sized tree. For example, naturally occurring seedlings tagged as recent germinants in 1995 still persisted in understory shade at <80 cm height in September 2013 during our most recent annual census, albeit at very low survival rates. Naturally occurring saplings measured in 1996/1997 between 2.7 and 4.6 cm diameter persisted in partial to full shade until 2013 while growing at annual rates of 0.22–0.26 cm diameter yr^{-1} (that is, hardly at all). Meanwhile 16 trees in our sample that ranged in 1997 from 19 to 99 cm diameter grew during the 16 years since at average increment rates <0.2 cm yr^{-1} . These examples, combined with exceptionally fast-growing individuals at the high end of the growth spectrum at Marajoara, account for the wide range of possible ages by 30- and 60-cm

Table 1

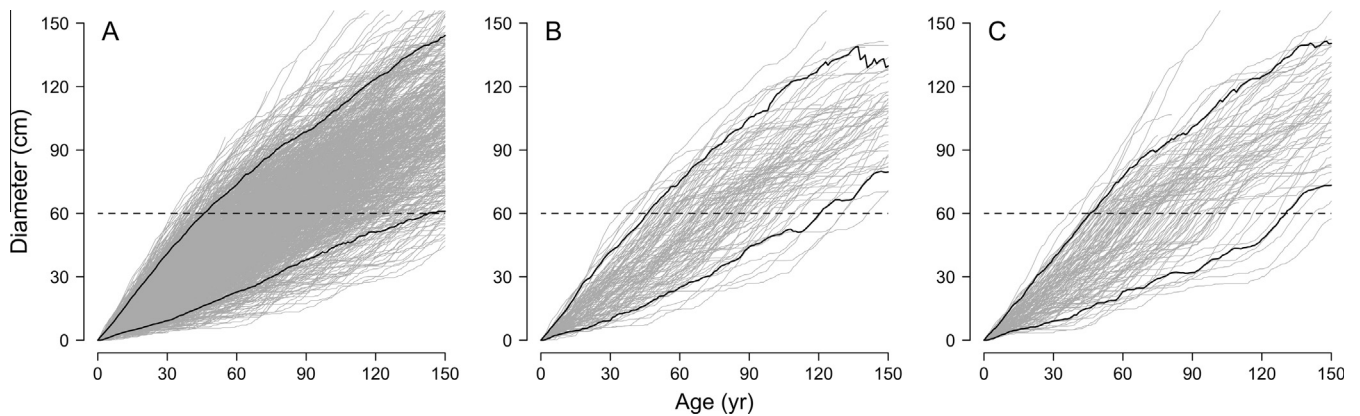
Ages of simulated (SIM) vs. Dünisch (DÜN) trees at reproductive maturity (30 cm diameter), commercial size (60 cm diameter), and larger.

Diameter (cm)	Sample N		Age (yr)							
			Median		Min–Max		5–95%		25–75%	
	SIM	DÜN	SIM	DÜN	SIM	DÜN	SIM	DÜN	SIM	DÜN
30	2191	30	38	51	16–130	34–87	22–73	36–68	30–49	45–62
60	1246	18	74	91	33–180	65–115	46–122	66–114	60–91	74–109
90	620	10	109	111	53–254	88–129	71–168	89–127	93–130	99–119
120	274	1	144	140	76–255	140	97–211	140	122–166	140
150	95	–	174	–	99–268	–	124–230	–	156–197	–

Table 2

Age ranges (5–95th percentiles) of simulated trees based on diameter plus growth performance during the previous (A) two and (B) ten years at reproductive maturity (30 cm diameter), commercial size (60 cm diameter), and larger.

Diameter (cm)	0–10%	10–20%	20–30%	30–40%	40–50%	50–60%	60–70%	70–80%	80–90%	90–100%
A										
30	29–86	26–86	25–74	26–71	26–69	23–69	22–62	22–68	21–64	19–55
60	52–142	49–127	50–132	48–123	51–114	49–113	49–112	46–110	45–112	38–108
90	81–163	82–152	73–168	76–173	77–151	74–167	70–164	74–173	70–169	61–156
120	100–194	105–212	113–211	100–198	105–214	112–213	108–221	101–218	97–198	83–187
150	171–226	145–240	127–206	117–197	131–202	119–215	136–230	125–235	140–226	148–245
B										
30	34–93	31–82	29–77	28–69	26–69	26–61	25–63	23–57	22–49	18–45
60	62–156	52–122	58–122	50–113	50–112	50–113	44–110	46–116	45–95	37–91
90	90–161	81–163	89–176	76–183	77–154	77–174	80–161	61–142	65–159	59–143
120	102–198	110–236	116–218	113–215	112–200	97–175	98–200	99–182	112–205	83–195
150	183–231	158–215	148–202	144–186	128–225	156–217	114–185	103–260	138–226	143–212

**Fig. 4.** Growth trajectories of simulated mahogany trees: (A) attaining commercial size ($N = 1246$); (B) growing at the 70–80th percentile growth rate over the two years prior to attaining commercial size ($N = 124$); and (C) growing at the 70–80th percentile growth rate over the ten years prior to attaining commercial size ($N = 124$). Solid black lines indicate the 5th and 95th percentile growth trajectories in each scenario. Dashed black line indicates commercial size (60 cm diameter).**Table 3**Observed, simulated, and 'optimal' passage times (yr) through 10-cm diameter size classes. Optimal passage times represent passage time requirements of a tree grown at the 75th percentile growth rate. Partial correlation coefficients (PCC) indicate the effect of passage time through size categories on age at 60 cm diameter and were obtained through multiple regression analysis. The regression model and all PCC values were highly significant ($p < 0.001$).

Size class (cm)	Dünisch et al. (2003) (yr)			Growth model (yr)				
	Min–Max (Mean)	Range	N	Min–Max (mean)	Range	N	Optimal	PCC
0–10	12–39 (20.5)	27	32	5–84 (15.2)	79	3253	11	0.55
10–20	10–26 (17.6)	16	32	4–75 (13.4)	71	2609	12	0.53
20–30	7–27 (15.6)	20	30	3–62 (12.5)	59	2191	12	0.49
30–40	8–25 (15.2)	17	27	3–59 (11.8)	56	1854	11	0.43
40–50	6–23 (14.8)	17	23	3–53 (12.0)	50	1546	12	0.47
50–60	7–16 (11.3)	9	18	4–56 (12.2)	52	1246	12	0.47

diameter mahogany trees, and the wide range of possible stem sizes after 30 and 60 years of growth. As a long-lived, light-demanding, fast-growing, late successional canopy emergent, mahogany's surprising shade tolerance makes it particularly suited

for immense intraspecific growth variation (Lieberman et al., 1985).

The age variation among trees of a given diameter observed by Dünisch et al. (2003) and by trees simulated in our model is

consistent with studies of other tropical tree species. Tree ring analyses by [Brienen and Zuidema \(2006\)](#) of several tropical species in southwest Amazonia found the following age ranges for 60 cm diameter trees: *Amburana cearensis* (Fabaceae), 77–159 years; *Bertolletia excelsa* (Lecythidaceae), 121–239 years; *Cedrela odorata* (Meliaceae), 42–172 years; *Cedrelinga catenaeformis* (Fabaceae), 55–95 years; and *Peltogyne heterophylla* (Fabaceae), 88–230 years. Other studies of tropical trees have reported similar magnitudes of variation in the age-size relationship across all size classes (e.g., [Enright and Hartshorn, 1981](#); [Villalba et al., 1985](#); [Worbes et al., 2003](#)).

The variation in ages at large diameters (>60 cm) was mainly caused by variation in the passage time of trees through smaller size classes. In real trees, variation is likely due to large differences in light conditions among individuals in the early size categories ([Chazdon and Fetcher, 1984](#); [Montgomery and Chazdon, 2002](#)). The age of large canopy trees is thus largely determined by the time they require to become 30 cm diameter. Passage times for the Dünisch mahogany trees through juvenile size classes to 30 cm diameter (8–88 years) were similar to model simulations (16–130 years). [Brienen and Zuidema \(2006\)](#) reported similar passage times for six Bolivian rain forest species and further demonstrated the importance of passage time through early size classes on the age variation of large trees. The potential for long passage times through the early size classes indicates the importance of silvicultural practices promoting fast growth through the juvenile stages, especially given that early fast-growers contribute disproportionately to trees attaining commercial size. Higher mortality rates and slower commercial recruitment rates by slow-growing seedlings underline the importance of silviculture and fast growth during the early years of life ([Landis and Peart, 2005](#); [Rozendaal et al., 2010](#)).

Age-size relationships described by the Dünisch trees and our simulations suggest that mahogany cannot be sustainably harvested under the current legal minimum diameter cutting limit (MDCL, 60 cm) and cutting cycle (25–30 years) in Brazil ([Grogan et al., 2014](#)). We estimate that 84 years are required for most mahogany trees to attain 60 cm diameter; 60% and 73% of surviving trees will have attained commercial size after 90 and 100 years, respectively. This biological reality implies a polycyclic harvest system with three cutting cycles per rotation, the time required to reach commercial size. Whether populations can supply commercial timber at steady rates on this schedule depends on the density and condition of sub-commercial stems at the time of first harvest. Simulations of the Marajoara population, a relatively high-density population compared to populations at other sites across southern Amazonia ([Gullison et al., 1996](#); [Dünisch et al., 2003](#); [Grogan et al., 2008](#)), indicate that repeated harvests under these harvest parameters will lead to steep population decline and commercial depletion within 60–90 years ([Grogan et al., 2014](#)). If 60 cm diameter is the most desirable MDCL, then longer cutting cycles and higher retention densities than currently required for mahogany in Brazil (20% of commercial-sized trees must be retained per cutting cycle) will be required to promote population recovery and sustained yield. As well, long-term replacement of existing juvenile and commercial-sized trees will depend on investment in silvicultural practices designed to increase densities of seedling regeneration, whether naturally occurring or artificially established in logging gaps (enrichment).

Mahogany is the most prominent example of a class of high-value tropical timber species that are shade intolerant, long-lived, and characterized by low to very low densities of sub-commercial stems and advance regeneration. Current legal harvest rules in Brazil for these non-mahogany species, including Spanish cedar (*Cedrela odorata*, Meliaceae), ipê (*Tabebuia* spp., Bignoniaceae), and jatobá (*Hymenaea courbaril*, Fabaceae), allow even higher harvest

intensities (up to 90% of commercial-sized trees per cutting cycle) and guarantee population declines and commercial depletion over repeated harvests for similar reasons ([Schulze et al., 2008a, b](#)).

[Verwer et al. \(2008\)](#) found that recovery of overexploited mahogany populations in Bolivia is enhanced by application of intermediate levels of silvicultural treatments. These authors suggest that sustainable harvests may be possible by maintaining optimal growing conditions through such treatments as liana cutting. Our results indicate that silvicultural practices encouraging mahogany trees to grow consistently at the 75th percentile growth rate could mitigate population declines and make forest management systems including mahogany more economically viable over the long term. A tree grown at the 75th percentile rate through every size class will reach commercial size (60 cm) in approximately 70 years. This would require silvicultural treatments targeting each diameter size class, a level of intervention that may not appear attractive through the lens of financial discount rates. However, our simulations suggest that much of this reduction in rotation length – the time from seed to commercial size – can be accomplished through maintenance of enrichment plantings in logging gaps in the first decade after each harvest; silvicultural interventions such as crown liberation are much more effective for sapling and pole-sized individuals than for larger trees with crowns already achieving intermediate or canopy dominant status ([Grogan et al., 2005](#); [Grogan and Landis, 2009](#)). Experimental tests with mahogany regeneration support the idea that intervention in the initial years following seedling establishment can exert a large influence on canopy (overstorey) recruitment rates ([Keefe et al., 2009](#); [Snook and Negreros-Castillo, 2004](#); [Grogan et al., 2005](#); [Navarro-Cerrillo et al., 2011](#)).

5. Conclusions

“How old is that tree?” Without counting annual rings from cores or radial discs, it is not possible to know. Even with 10 years of growth history data, we cannot estimate the age of mahogany in any size-class with precision. The large age-size variation among individuals is mostly due to persistent growth autocorrelation, which emerges as a result of differences in crown vine coverage, form, or size, microsite characteristics, and genetics ([Grogan and Landis, 2009](#)). Accounting for this variation, we show that it will be difficult to sustain mahogany timber yields in Brazil without lengthening cutting cycles, increasing commercial tree retention rates, and regular application of silvicultural treatments designed to increase stem diameter (and thus commercial volume) growth rates. Both direct and deferred costs associated with producing mahogany timber and satisfying CITES non-detriment requirements for Appendix II species are thus likely to be significant. However, a small but growing body of evidence suggests that it is possible to incorporate enrichment planting and targeted crown liberation into profitable management systems, at least for a premiere timber species like mahogany ([Wadsworth and Zweede, 2006](#); [Schulze 2008](#); [Keefe et al., 2009, 2012](#); [Navarro-Cerrillo et al., 2011](#)). Our results suggest that managers can have the greatest effect on the rate of commercial recruitment in the first 10 years after a harvest by implementing treatments ensuring that adequate numbers of new stems establish and recruit to dominant positions in recovering canopy gaps. Regrettably, sustainable mahogany management systems developed based on understanding of the species' ecology will not be as simple as current harvest regulations in Brazil imply.

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