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Assessment of the conservation status of big-leaf mahogany, Spanish cedar, and three lesser-known timber species populations in the forestry concessions of the Maya Biosphere Reserve, Petén, Guatemala

Project Finnfor, CATIE

Final Report

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EXECUTIVE SUMMARY

The 2.1 million hectare Maya Biosphere Reserve (MBR) in the department of Petén, Guatemala was established in 1990. Shortly after its creation, Guatemala passed a law that allowed for allocation of forest concessions to both private businesses and community-based entities in the 560,000-ha Multiple Use Zone (MUZ). Over the past 20 years, 14 such concessions have been granted, of which nine community forest enterprises and two 'industrial' or private enterprises are active today, overseen by the National Council on Protected Areas (CONAP).

In this report we ask: **What is the conservation status of *Swietenia macrophylla* (big-leaf mahogany), *Cedrela odorata* (Spanish cedar), *Lonchocarpus castilloi* (manchiche), *Bucida buceras* (pucté), and *Calophyllum brasiliense* (santa maría) tree populations in the Multiple Use Zone of the Maya Biosphere Reserve? What are the impacts of current forest management practices on the commercial density and regeneration of these five timber species, which represent 95% of the timber volume currently harvested in active concessions?** This study interprets 'conservation status' in CITES terms, and evaluates whether current management regimes in the concessions establish a level and form of harvest that is non-detrimental to the long-term maintenance of these species' populations on the landscape. We assume that 'sustainable' means 'sustained timber yield over multiple harvests'. We apply the best available empirical knowledge to these questions through use of life history-based models to simulate population dynamics of species' population structures in 2005 and 2006 Annual Forest Operational Plans (POAFs) in 11 concessions representing the active production forests of the MBR.

Methodology

This study relied on both historical data of logging activity in concessions and new fieldwork. 100%-area inventory data for commercial and sub-commercial trees > 30 cm diameter in 2005 and 2006 POAFs were obtained in digital format from CONAP, including indication of whether individual trees were harvested or not. In May–June 2014, 265 one-hectare strip transects were installed at 1%-area intensity within all POAFs to provide density estimates for seedlings, saplings, and pole-sized trees. These two sources provided the pre- and post-harvest population structure data necessary for modeling commercial recovery after one or more harvests.

Separate modeling platforms were used to analyze response by *Swietenia* on the one hand, and by *Cedrela* plus three lesser-known timber species on the other. The *Swietenia* model was adapted from a model constructed to evaluate the impact of current legal forest management practices on future harvests in Brazil (Grogan et al. 2014). This model is based on large-scale 20-year field studies of all phases of mahogany's life history, including size-related mortality, diameter growth, and fruit production rates. The model 'harvests' and 'grows' POAF populations over the course of three cutting cycles and four harvests, reporting median values from 100 simulations for commercial density and volume recovery. Our analysis of the available long-term forest monitoring data in MUZ concessions indicates that application of this model is valid in the Petén.

The model used for *Cedrela* and the three lesser-known species simulates population responses after the original harvest (2005/2006) and a single cutting cycle (Grogan et al. 2008, Schulze et al. 2008). The lack of empirical knowledge regarding seedling, sapling, and pole-sized tree dynamic rates (survival, diameter growth) of these four species limited our ability to simulate population dynamics beyond the second harvest.

Results

While model simulations for *Swietenia* populations in MUZ concessions demonstrated a range of future-harvest outcomes, in most POAFs current forest management practices appear sustainable over multiple harvests. That is, **given the forest management parameters applied in 2005 and 2006 POAFs and anticipated during future harvests, model simulations indicate that mahogany populations will recover initial commercial densities and volumes during cutting cycles between successive harvests**. These outcomes derive from two main sources: extremely favorable population densities and population structures across much of the landscape, and a method established for calculating cutting intensity that is based on biological reality rather than on short-term financial exigency. CONAP's method of basing allowable cutting intensities on expected growth and recruitment to commercial size by inventoried populations of sub-commercial trees is both intuitively obvious and exceptionally rare in the world of tropical forest management.

Modeling outcomes for populations of *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* after a single cutting cycle were highly variable but generally positive in terms of population persistence. All four of these species occur at lower commercial densities than mahogany, especially *Cedrela*. They are also more spatially patchy at the landscape scale, especially *Bucida*, possibly related to specialized site requirements for seedling establishment, growth, and recruitment. While *Cedrela* is simply rare and *Lonchocarpus* apparently has limited ability to persist and grow through successive size classes, *Bucida* and *Calophyllum* present more options for silvicultural practices aimed at reducing mortality and accelerating growth rates.

For all five species, commercial recovery rates during the first cutting cycle were constrained by the decision to harvest more commercial basal area during the first harvest than the formula for calculating cutting intensity indicated. This occurred due to the concessions' requests and CONAP's approval to harvest 'non-recoverable basal area', which appears to be a common practice. This means that higher commercial volumes were removed from POAF-level populations than could be replaced by recruitment to commercial size during the first cutting cycle, with implications for the definition of 'sustained yield'.

Transect surveys found higher average densities of *Swietenia* seedlings, saplings, and small pole-sized trees in 2005 and 2006 POAFs compared to 2015 POAFs. This strongly suggests that **logging apparently encourages higher densities of mahogany regeneration.** Silvicultural practices intended to accelerate growth rates could now be applied to these elevated densities of seedling and saplings in order to increase future yields, should industry and communities choose to invest in these practices.

Conclusions

We conclude that, based on results presented here, **forest management practices in the Maya Biosphere Reserve Multiple Use Zone represent state-of-the-art best-practices for species-level management in tropical forests.** The practice of determining and implementing cutting intensities based on species biology represents a genuine advance towards sustained yield timber production that deserves recognition and replication in other regions. Specific conclusions include:

- With a high degree of certainty, *Swietenia* populations will recover pre-harvest commercial densities during the first cutting cycle between harvests, on average, and this outcome appears sustainable over repeated harvests under current forest management practices.

- Recovery of *Swietenia* commercial volume production will lag behind tree density recovery during the first cutting cycle, leading to smaller second harvests, on average. Timber volume production should recover to initial harvest levels or higher during third and fourth harvests, assuming that current management parameters are followed.

- With a low degree of certainty, most *Cedrela* populations occurring at extremely low landscape-scale densities will recover pre-harvest commercial densities during the first cutting cycle, but timber volume production will be much lower during second harvests compared to first harvests.

- Estimated landscape-scale densities of *Cedrela* pole-sized trees, saplings, and seedlings are very low overall and patchily distributed on the landscape, suggesting that repeated harvests may not be possible in many POAFs.

- With an intermediate degree of certainty, most *Lonchocarpus*, *Bucida*, and *Calophyllum* populations will recover pre-harvest commercial densities during the first cutting cycle. Timber volume production will be lower, on average, during second harvests compared to first harvests, but the decline will not be as extreme as for *Cedrela*.

- The method for determining cutting intensity represents an important advance in natural forest management in the tropics, but should be improved both empirically and from a regulatory standpoint. The use of 0.4 cm $year^{-1}$ as the median growth rate to determine cutting intensity is not clearly backed up by empirical evidence. Data from permanent plots in the MUZ indicate that this rate is possibly low for *Swietenia*, approximately correct for *Lonchocarpus*, too high for *Bucida*, and too low for *Calophyllum*. Insufficient monitoring data exists to make any conclusion regarding *Cedrela*. Declines in volume production during second harvests seen in the model are primarily due to the approval of cutting intensities higher than those indicated by the method.

- Harvest operations appear to encourage seedling establishment and short-term post-harvest growth.

- The data from permanent monitoring plots that has been collected until now is valuable but not sufficient to guide fully informed decision-making.

Recommendations

Recommendations for improving sustainable, science-based forest management in the MUZ include:

i) **Improve knowledge of species' size-dependent growth and mortality rates through improvements to the network of permanent monitoring plots in order to increase the accuracy of cutting intensity calculations and the predictive power of model simulations**. Currently, CONAP uses a single linear annual growth rate of 0.4 cm for all species. If this rate is lower than reality for a given species, current harvest authorizations are more conservative than necessary for population recovery. Conversely, if the rate is higher than reality, harvest authorizations may lead to population declines.

ii) **Improve knowledge of species' regeneration and recruitment requirements**. While *Swietenia* regeneration ecology is fairly well understood, knowledge about seed production, dispersal, and germination, seedling establishment, and growth and mortality by seedlings, saplings, and poles is lacking for *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum.* Such information is vital in order to better predict population recovery following harvests.

iii) **Systematic sampling of juvenile stems (seedlings, saplings, pole-sized trees) and use of a tailored, user-friendly version of the model applied here should be incorporated into annual management operations and decision-making**. Incorporating transect surveys into standard operational protocols for 5-year plan or annual POAF preparation would make them affordable and efficient and allow managers to quantify size classes that will grow to commercial size beyond the next harvest. The NetLogo model is a user-friendly version of the models applied in this analysis. Its modification for Petén-specific use to look at *Swietenia* population recovery following harvests would allow CONAP, regents, and concession managers to make more informed decisions regarding cutting intensity and other management parameters.

iv) **Implement target cutting intensities more consistently**. Approving extraction of extra volume from the non-recoverable basal area is likely to produce population declines over time. Adjustments should be approved with caution if at all, and be attached to requirements for silvicultural treatment that will accelerate the recuperation of basal area.

v) **Emphasize silvicultural practices designed to reduce mortality and increase growth rates by commercial, future crop, and juvenile trees**. As an example, pre- and post-harvest vine cutting to free crowns of commercial species is the single most effective way to reduce mortality and accelerate long-term diameter growth rates.

vi) **Ensure that incentives for long-term management are in place by extending the length of concession contracts through multiple cycles**. This study has demonstrated the strong influence of present-day decisions on the future forest. However, concessionaires currently lack strong incentives to collect additional long-term data, or to not request additional cutting intensity above recuperable basal area, because there is no legal surety that their concession contracts will be extended beyond the first harvest.

1 INTRODUCTION

1.1 Location of the study region

The Maya Biosphere Reserve in Petén is a 2.1 million hectare protected area that includes most of the Guatemalan portion of the great *Selva Maya* (**Fig. 1**). This subtropical humid rainforest contains different broadleaf ecosystems primarily distinguished by altitude (which ranges from 275–770 meters above sea level) and rainfall (from 1160–1700 mm year^{-1}). The Selva Maya, which includes parts of Belize, Guatemala, and Mexico, is a region of historical, social, and biological significance as Mesamerica's largest contiguous forest area, the cradle of the Maya civilization, and home to 180,000 people. Its ecosystems are the habitat of numerous resident and migratory fauna species and refuge of threatened or endangered flora and fauna. Among these species are the high-value timber trees *Swietenia macrophylla* (big-leaf mahogany, locally known as 'caoba' and henceforth in this report referred to as *Swietenia* or mahogany) and *Cedrela odorata* (Spanish cedar, locally known as 'cedro' and henceforth *Cedrela*), both of which have been listed since 2002 on CITES Appendices II and III, respectively, after decades of overharvesting throughout their native range in tropical America.

The UNESCO-designated Maya Biosphere Reserve (MBR), established by the Guatemalan government in 1990, consists of a core zone, which includes several national parks under strict protection; a multiple use zone (MUZ); and a buffer zone. Shortly after creating the MBR, Guatemala passed a law permitting allocation of forest concessions to both private businesses and community-based entities in the 560,000-hectare MUZ. Since the mid-1990s, 14 such concessions have been granted, of which nine community forest enterprises and two 'industrial' or private enterprises are active today (**Table 1, Fig. 2**). These concessions are overseen by the Guatemalan government's National Council on Protected Areas (CONAP).

1.2 Justification

Many stakeholders are keenly interested in understanding the impacts that logging has had on the forest ecosystems of the MUZ, whether positive or negative, in order to evaluate the concession system in both ecological and economic terms and to hold a more informed discussion regarding its medium- and long-term viability.

The financial model of the concessions has been heavily reliant on sales of *Swietenia* and, to a lesser extent, *Cedrela,* although recent years have seen greater exploration and use of lesser-known species. In 2013, 55% of harvested volumes and 85% of community forest businesses' income still came from these two species according to CONAP and FORESCOM data. Most of the remaining harvested volume (40%) came from three additional species: *Lonchocarpus castilloi* (locally known as 'manchiche', henceforth *Lonchocarpus*), *Bucida buceras* ('pucté', henceforth *Bucida*), and *Calophyllum brasiliense* ('santa maría', henceforth *Calophyllum*). A critical aspect of evaluating the viability of the MUZ forest management model in both ecological and financial terms is therefore understanding the resilience of these species' populations under current harvest practices and intensities.

While a variety of studies have been conducted on *Swietenia* and *Cedrela* in the MUZ, as of 2014 a comprehensive study at appropriate spatial and temporal scales had not yet been done to evaluate their conservation status. The design of existing long-term forest monitoring plots does not provide adequate sample size or data to answer questions about a given species' resilience under logging regimes (Marmillod 2012), although they can provide valuable information regarding a given tree species' life cycle. Nor have any studies attempted to project current distribution and density patterns into the future in order to understand the long-term implications of today's management decisions.

The primary actors in the MUZ – community and private concessionaires, CONAP, and technical assistance providers – therefore identified a need to analyze the conservation status and impacts of current harvest practices on populations of *Swietenia*, *Cedrela*, and the three commercially significant lesser-known species with a view to ensuring their long-term health. CATIE's Forest Production and Conservation Program implemented the present study in collaboration with Rainforest Alliance; the Association of Community Forest Concessions (ACOFOP); FORESCOM, a processing and sales service provider to the community enterprises; and CONAP.

1.3 Objectives

1. Determine the conservation status of populations of five species under forest management in the Maya Biosphere Reserve (*Swietenia*, *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum*). In practice this study interpreted 'conservation status' in CITES terms, and attempted to evaluate whether the current management regime in the concessions establishes a level and form of harvest that is non-detrimental to the long-term maintenance of these species' populations on the landscape at a level consistent with their role in the ecosystems in which they occur, in line with requirements under CITES (cf Article III, paragraph 2(a); Article IV paragraph 3), Guatemalan law, and the Forest Stewardship Council, under whose standard all MUZ concessions are required to be certified.

2. Determine the impacts of silvicultural practices used in the concessions on the density and regeneration of these five timber species, in order to determine appropriate levels of harvest in Management Plans and POAFs. It is important to note here that due to data availability, this study is limited to understanding density and regeneration in areas defined as 'harvestable' by CONAP and the concessionaires, which excludes certain forest types such as particularly low-lying seasonally flooded forest.

3. Based on the results of this assessment of conservation status, formulate recommendations to review and adjust (if necessary) the guidelines, strategies, and practices of management, harvest, monitoring, and conservation for the species in the study. In addition to feeding directly into planning by the key actors in the MUZ, this information is intended to contribute to efforts by the Guatemalan government and the international community to protect CITES-listed plant species. Finally, the information generated will enable all interested parties to evaluate new, empirically sound evidence regarding the MUZ concession model and make necessary improvements to the current monitoring regime that, in turn, will allow for ongoing adaptive management.

1.4 Analytical approach

To achieve these objectives, this study conceptualized species populations in terms of past (pre-harvest) densities, present (post-harvest) densities, and the future densities which will be direct outcomes of today's harvest practices. Past and present densities can be derived from commercial census data that describes the distribution of diameter size classes by species within annual harvest areas in each concession, and indicates which individual trees are removed by logging. To project future densities over timeframes relevant to forest managers in the MBR, we used population models that were developed specifically for this purpose to simulate tree growth and harvests over one to three cutting cycles, depending on the species. Each species' conservation status was evaluated based on its population resilience (recovery rates) in the face of repeated harvests: to what degree do the data and models predict that tree densities and commercial volume production will recover during cutting cycles between first and second harvests and beyond, given the forest management parameters applied since the late 1990s in the MBR? In other words, how do projected future populations compare to present and past populations on the Petén landscape?

Fig. 1. *The Maya Biosphere Reserve (MBR) in the Petén region of northern Guatemala, showing neighboring countries Mexico, Belize, and Honduras.*

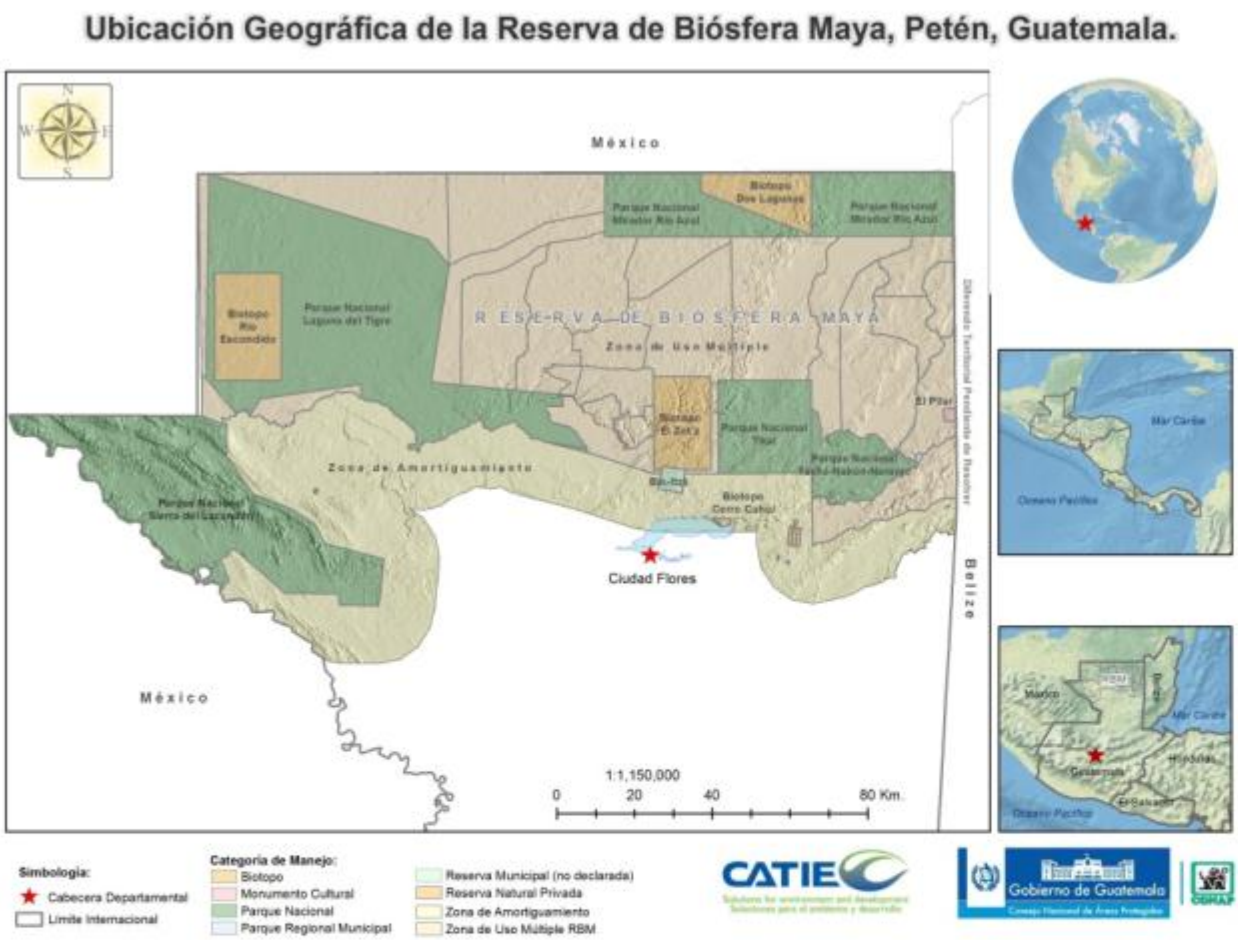
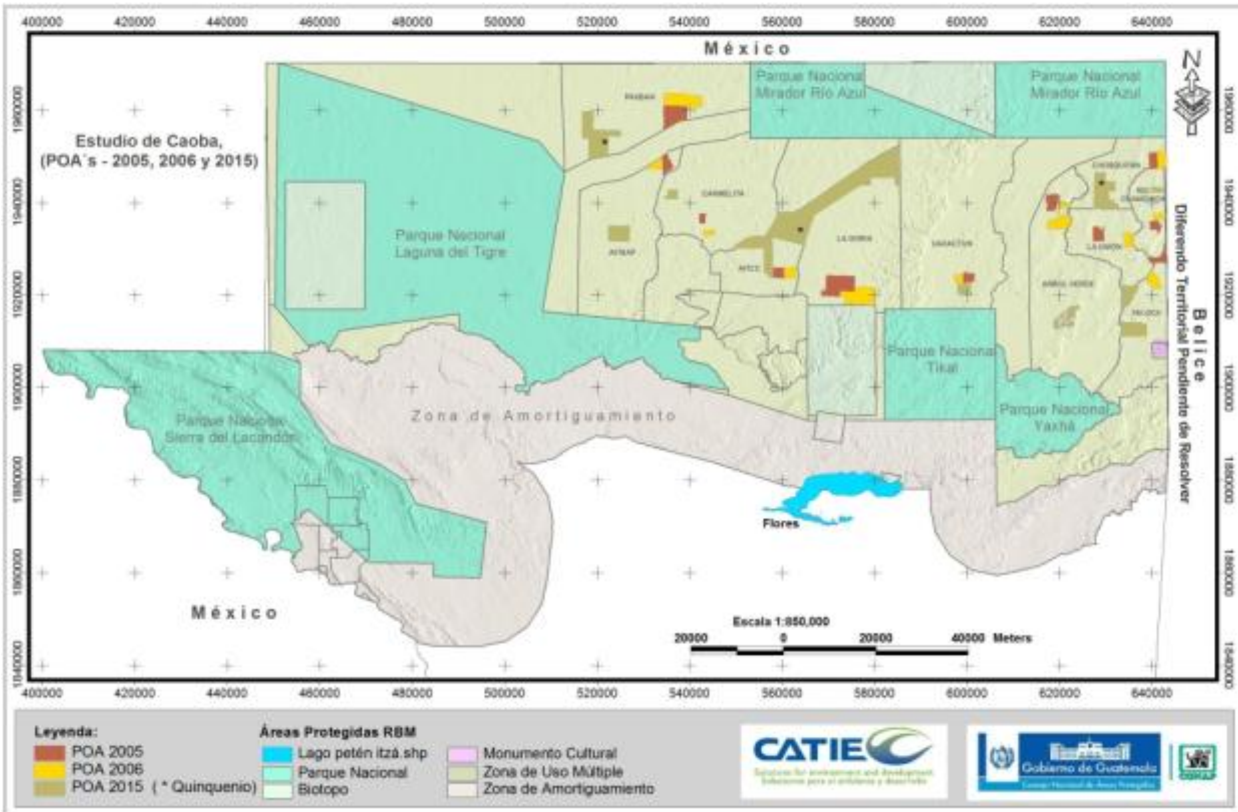


__Fig. 2__. Locations of 11 forest concessions participating in this study. See __Table 1__ for full and abbreviated names. Colored blocks within the concessions indicate location of POAFs sampled by this study as described in section 3.2.



2 FOREST MANAGEMENT BACKGROUND

2.1 Brief review of forest management history in the MBR area

Some level of selective *Swietenia* logging has probably occurred in the Petén for several centuries, but the 1960s through the 1980s saw a particularly intensive period of exploitation. Under the watch of a largely military-administered state enterprise called Fomento y Desarrollo de Petén (FYDEP), 13 logging companies were given 3- to 5-year renewable contracts to log as much as they wanted, paying a simple volume-based tax. Anecdotal sources suggest logging intensities of up to six mahogany trees per hectare were common in at least certain areas of what is now the Reserve.[1]

The FYDEP system of forest harvest licenses ended in 1989 and all logging contracts were revoked with the Biosphere Reserve's creation the following year. Although the regulations creating the MBR in 1990 allowed for the possibility of granting concessions, overcoming political and technical barriers to putting this system into place took time, and most new enterprises began logging under 25-year contracts only in the early 2000s. Substantial donor support and technical assistance from USAID, Rainforest Alliance, and CATIE, among others, played a notable role in this process (Kent et al. 2014).

Between 2000 and 2013, fourteen concessions extracted 284,555 m^3 of timber at an average intensity of 2.16 m^3 ha^{-1}. Eleven concessions remained active as of late 2014: nine community forest concessions occupy 352,907 ha (73% of the total concessioned area) while two private concessions cover 132,303 hectares (23%).

2.2 Key forest management requirements

CONAP is the regulatory entity for forest management in the MUZ under the Protected Areas Law Decree 4-89 (Article 19) and Forest Law Decree 101-96. Over the years, regulations have been adjusted in response to concerns and needs as these have emerged; regulations are detailed in the "Protected Area Forestry Administration Manual".

All concessions in the MUZ are required to elaborate and operate according to three nested sets of plans prepared with assistance from their regent, a professional forester certified by the national forester's guild who is legally responsible for ensuring proper execution of planning and harvest.

- *Management Plan:* Each enterprise must adjust its overall plans for managing the concession every five years. The management plan should describe strategies for ecological and economic sustainability in the extraction of both timber and non-timber species.
- *Five-Year Plan (Quinquenal):* This intermediate planning tool, first implemented in 2005 to attempt to minimize year-to-year variation in operations and revenues, requires concessions to define the boundaries of their next five annual harvesting parcels by estimating volumes of *Swietenia* and establishing a roughly equal annual distribution of volumes across a five-year block (which can result in annual harvest parcels of very different size). Complete commercial inventories (> 30 cm diameter) are conducted within parcels that represent a 3%-area sample of the block.

[1] Carlos Díaz, director of planning, Baren Comercial, who was a forester at FYDEP during those years.

- *Annual Operational Forest Plan (POAF):* On a yearly basis the concession must submit a detailed plan for the annual harvest area (AAA) or parcel. The POAF is a 100%-area and geo-referenced census or inventory of individuals of commercial trees larger than 30 cm diameter found in the AAA. Note that the AAA only includes harvestable or 'effective' area, which is typically less than the complete area inside POAF boundaries as it excludes steep slopes (exceeding 55% grade), seasonally flooded lowlands, water recharge zones, riparian areas, archeological sites, and other high conservation-value areas. Data is taken on stem diameter (a proxy for basal area), stem quality (graded from 1 'straight and healthy' to 6 'dead or fallen tree'), function (extract, future harvest, protect, salvage, decrepit, seed tree), and commercial height. Particularly healthy, well-formed and emergent individuals are left standing as 'seed trees' to produce seeds and seedling regeneration; there is no fixed requirement for how many must be left. The POAF must include maps showing the location of all commercial trees (both current and future), planned skid roads, secondary and tertiary roads, and log landings.

The contracts signed between each concession and the Guatemalan government stipulate that these three plans, once approved by CONAP, must be followed, and lay out the conditions for revoking a concession in the case of persistent non-compliance. These contracts also require that each enterprise have plans for management of natural regeneration, reforestation and/or restoration of the timber resources in the Management Unit, which may include activities such as enrichment planting.

In addition to the standards required by the Guatemalan government, all concessions must obtain and uphold FSC certification. This requirement was established in 1999 by CONAP in response to social and political pressures regarding the importance of using best practices when harvesting within protected areas such as the MBR. Seven community concessions operate under a group certification held by FORESCOM, while two community concessions and both industrial concessions have their own certificates. FSC audits are conducted annually, currently by RACert (formerly SmartWood), historically one of the FSC auditing bodies with the most experience and disposition to audit community forestry operations.

CONAP conducts an inspection before approving the POAF to verify that mapped trees and volumes correspond to the AAA. A second inspection is conducted during logging to oversee harvest practices, and a third inspection occurs afterwards to verify that regulations and harvest parameters were upheld and post-harvest practices such as cleaning up skid trails were followed. In all cases CONAP uses a sampling methodology for these inspections.[2] The concessionaires are also obligated by FSC certification to conduct post-harvest evaluations and monitor for impacts; their certification audit reports are publically available.

2.3 Description of important management parameters

Cutting cycle, minimum diameter cutting limit, and cutting intensity are central, interconnected elements to any strategy of sustainable forest management. The following describes how these parameters are defined and used by CONAP and/or concessionaires in the MBR Multiple Use Zone.

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[2] F. Baldizon, pers. comm.

2.3.1 Cutting cycle

The cutting cycle is the interval established between logging in any given annual parcel (AAA). In a 'sustainable' system, this interval should be sufficient for the forest to recuperate more or less all of the basal area of those species removed during the previous logging episode. Guatemala's forest law regulations do not specify a particular cutting cycle interval. CONAP's technical norms for sustainable forest management state that the duration of the cutting cycle shall be determined as a function of growth rates of the species under management, abundance of those species, and the owner's socioeconomic factors, with a minimum of 20 years (CONAP n.d. a, cited in Manzanero 2005). The different concessions have defined cutting cycles ranging from 25–40 years; in theory these cycles could change if new information regarding growth rates and regeneration indicate that such would be appropriate. (It is however important to note that under current law the concessions are only granted for 25-year periods.)

2.3.2 Minimum diameter cutting limit (MDCL)

The minimum diameter cutting limit is the smallest size of a tree that can be legally harvested, using the standard forestry measurement of diameter at breast height (1.3 meters above the ground, with modifications used for trees that have tall buttress roots or other irregularities). This parameter should ideally also be defined in relation to the cutting cycle and species' growth rate and fruiting patterns, so as to ensure that both seed sources and adequate basal area remain in the forest for regeneration and recuperation between logging episodes. Like the cutting cycle, MDCL is a technical norm that CONAP allows each concession to define for each species. Technical guidelines mandate that operators consider species abundance, size-class distribution, growth rate studies, phenological studies, forest type, ecological integrity, and market demand (CONAP n.d.b). Almost all MDCLs lie within the 50–60 cm diameter range. See **Tables 6 & 7** for MDCL by species by concession.

2.3.3 Cutting intensity (CI)

The cutting intensity – how much can be harvested from a given POAF in a given year – is arguably the single most important factor in determining the sustainability of a logging operation. In many countries, cutting intensity is defined with simple maximum and minimum cut-offs. For example, Brazilian rules for *Swietenia* harvests establish a 20% retention rate for commercial-sized trees (i.e., up to 80% of all trees in a given area can be legally harvested), as long as the resulting density does not drop below 5 trees per 100 hectares (Grogan et al. 2014).

In Petén, several aspects of the way this parameter is defined stand out. First, CI is defined using basal area rather than number of trees; basal area has the advantage of relating more directly to volume production. Second, CI is defined via a calculation based on growth rates, cutting cycles, and tree stem size classes, that explicitly limits harvest to a level not greater than what will grow into commercial stem size classes before the next harvest.

The box below shows the basic steps that CONAP and concessions use to calculate CI in a given POAF, using an example from real data (CONAP n.d.b). The methodology was adopted through work with CATIE and NPV in the 1990s.

All non-harvest categories (seed trees, decrepit, and dead trees) are excluded from these calculations. Trees larger than 90 cm diameter are also excluded and may be harvested at up to

65% intensity. CONAP guidelines also allow the authorities to adjust CI upwards in situations of relatively low abundance, adding as much as 20% of 'non-recoverable basal area' – in other words, volume beyond that which is expected to grow back during the cutting cycle – to the original calculated intensity. Data from the 2005 and 2006 POAFs indicates that CONAP has frequently made use of this adjustment. This is an important point to which we will return in later sections. The upper limit or maximum CI is currently defined as 80% for all species, but in the original 1999 Manual for Forestry Administration in Protected Areas these rules were not as clear. This Manual stated that "for Peten's forests, it is considered adequate to leave as seed trees 15% of the trees above the minimum cutting diameter." Based on this statement, an 85% ceiling of cutting intensity was used in early years, including in 2005 and 2006.

Example of cutting intensity calculation for Swietenia*, using data from an MUZ concession POAF, the growth rate assumed by CONAP (0.4cm yr^{-1}), a 30-year cutting cycle, and minimum diameter cutting limit of 60 cm.*

Steps in calculating Cutting Intensity	Example
Median annual diameter growth increment is multiplied by the number of years in the coming cutting cycle to calculate how much stem diameter trees are expected to add before the next harvest.	0.4 cm yr^{-1} * 30 years = 12 cm diameter growth
Expected growth is then subtracted from the minimum diameter cutting limit (MDCL) to determine the threshold diameter above which current sub-commercial trees can be expected to move into commercial size classes.	60 cm (MDCL) – 12 cm = 48 cm diameter This means that 2.4 stem size classes (each 5 cm) will grow to commercial size before the next harvest.
The basal area (derived from tree diameters) that will be added by trees between this threshold diameter and the MDCL is calculated using census data and growth increments. This is known as the recoverable basal area.	In the census data for this example, recoverable basal area from these 2.4 size classes is 224.5 m^2. The total commercial basal area represented by trees 60–90 cm is 320.9 m^2.
The recoverable basal area is divided by the total commercial basal area to determine the percentage representing the permissible cutting intensity.	(224.51/320.87) * 100 = 70% The POAF in this example is allowed a cutting intensity of 70%.

2.4 Study species

Swietenia macrophylla (big-leaf mahogany or caoba, in the family Meliaceae) is the world's premier tropical timber species. It occurs in seasonally dry tropical forests from Mexico's Yucatan Peninsula to lowland forests of Bolivian Amazonia. Like most tropical tree species, *Swietenia* occurs at low landscape-scale densities which vary widely from region to region and even within localities. Population densities in Central America, and especially in the great Maya Rainforest straddling Guatemala, Belize, and Mexico, tend to be much higher than in South

America. *Swietenia* is a giant canopy emergent tree at maturity, capable of rapid vertical and diameter growth under optimal growing conditions which include high light, high available soil nutrients, and deep, well-drained soil. Mahogany seeds are relatively large, winged, and wind dispersed during the dry season, typically landing on the forest floor within 100 meters of parent trees. Germination occurs rapidly after the onset of wet season rains. Seedling survival and growth depends mainly on light availability after establishment. While median diameter growth rates range from 0.3–0.7 cm $year^{-1}$, sustained growth rates exceeding 1 cm $year^{-1}$ are possible under optimal conditions.

Cedrela odorata (Spanish cedar or cedro, also in the family Meliaceae) is a close relative of mahogany with many similar timber and life history characteristics. It is a neotropical species whose range overlaps *Swietenia*'s while extending further into the Caribbean, east across northern Amazonia into the Guianas, and much further south into the Brazilian Atlantic forest and Argentina. Across its range *Cedrela* population densities tend to be lower than *Swietenia*'s, with exceptions (see, for example, high densities of *Cedrela* on steep topography at Tikal and adjacent forests). *Cedrela* is a large canopy emergent, possibly a faster grower than *Swietenia* under ideal conditions, which remain poorly understood, and probably shorter-lived. Its seeds are winged and wind dispersed but much smaller than *Swietenia* seeds, produced in much higher numbers, and dispersed over much greater distances and areas. Seed germination and seedling establishment rates are low. Regeneration requirements are poorly understood.

Lonchocarpus castilloi (manchiche, in the family Fabaceae-Papilionoideae) is a tropical timber species whose natural range is restricted to southern Mexico and Central America. It is a medium-sized canopy overstory tree only occasionally exceeding 100 cm diameter. While typically associated with *Bucida burceras* (see below) and *Brosimum alicastrum* (ramon, Moraceae) in seasonally dry forests, little published information is available about its population density patterns or life history.

Bucida burceras (pucté, Combretaceae) occurs from the Caribbean and southern Mexico to the Guianas across northern South America. Like *Lonchocarpus* it is a medium-sized canopy overstory tree. *Bucida* is a light-demanding tree that competes best on marginal sites where available soil moisture may limit growth by other species. For this reason it is often associated with swales and seasonal streams in dry foothills. Based on data from concessions in this study, *Bucida* is slow-growing relative to the other four species. Seeds are small (~38,000 per kg) with low germinability; dispersal mechanisms are poorly understood (Francis 1989). Little is known about size-specific mortality and growth rates.

Calophyllum brasiliense (santa maría, Clusiaceae) occurs from the Caribbean and Mexico to Peru, Bolivia, Brazil, and the Guianas. It is a relatively shade tolerant, medium-sized canopy overstory tree. *Calophyllum* is a site and soil generalist, generally occurring where annual rainfall totals exceed 1500 mm, growing best where conditions are wet and humid but also tolerating excessively draining soils (Devall & O'Rourke 1998). Fruit and seeds are dispersed by bats, birds, rodents, and, in intermittently flooding forests, by fish. Like *Lonchocarpus* and *Bucida*, little is known about its size-specific mortality and growth rates.

3 METHODOLOGY

Population models developed by the authors were deemed the best tool available to address this study's objective, which is to evaluate probable impacts of forest management practices dating back to the early 2000s on populations of *Swietenia, Cedrela,* and three lesser-known timber species in the Maya Biosphere Reserve Multiple Use Zone (MUZ). These models simulate growth of populations into the future, applying growth, mortality, and reproduction functions to the current distribution of tree diameter size classes on an annual basis according to rules describing the best understanding of how a given species' population persists under natural conditions. Confidence in modeling outcomes increases with quality of data both for observed population structures and for the mathematical functions that are applied in order to simulate populations over time. In this study we use two modeling approaches with differing confidence levels.

In the first approach, used only for *Swietenia*, we apply a sophisticated population model developed from a 20-year study of all aspects of mahogany's life cycle in the Brazilian Amazon, in forests similar in structure and diversity to those in the Petén region. This model describes growth and mortality from seed to adult senescence, while also accounting for annual seed production and canopy disturbances necessary for seedling survival and growth. Because this *Swietenia* model incorporates growth and mortality functions for seedlings, saplings, and pole-sized trees – that is, for diameter size classes smaller than are typically covered by commercial census data – it allows us to grow mahogany populations many decades into the future. Further, the model accounts for seeds that will produce trees not present in today's forest. The *Swietenia* model has been validated through the peer-review process at high-quality scientific journals (see Grogan & Landis 2009, Free et al. 2014, Grogan et al. 2014). Our confidence in this modeling approach over the time-frames analyzed here – three cutting cycles, or 75 to 120 years into the future – is high.

Data describing growth and mortality by trees smaller than 30 cm diameter, and reproductive effort by adult trees, is unavailable for *Cedrela* and the three lesser-known species, constraining the type of modeling approach available for them. In the second modeling approach, we use a simpler model that simulates populations of these species during a single cutting cycle – 25 to 40 years – based on observed growth rates measured in permanent plots in MBR concessions since 2001, combined with a fixed annual probability of mortality for all trees. This modeling approach has also been validated through the peer-review process at high-quality scientific journals (Grogan et al. 2008, Schulze et al. 2008). Over the time-frame analyzed, a single cutting cycle, we are moderately confident that outcomes reported here are representative of near-term population growth. In addition, we simulate mahogany populations using this second modeling approach for comparative purposes with the *Swietenia* model.

Modeling population dynamics of tropical timber species subject to harvests at specified time intervals (the cutting cycle) requires two types of data as inputs:

1) *Descriptive data* indicating the relative densities by stem size class at which a species occurs within a given forest area; that is, how many seedlings (*brinzales*), saplings (*latizales bajos*), small poles (*latizales altos*), poles (*fustales*), sub-commercial trees, and commercial trees are there on the landscape, whether known or estimated?

2) *Dynamic data* describing stem size-specific rates of mortality, diameter growth, seed production, seed germination, seedling establishment, and recruitment by juveniles to adult (commercial) size classes. For light-demanding species dependent on natural forest gaps for recruitment such as *Swietenia* and *Cedrela*, dynamic data should ideally also describe the rate at which forest disturbances suitable for sustained growth occur.

Data necessary for this study were obtained from a wide range of sources as described below. We also further describe origins of the *Swietenia* and lesser-known species population models and modifications made to accommodate MBR data.

3.1 Descriptive data for building population structures

3.1.1 POAF commercial census data for trees > 30 cm diameter

Swietenia: First-harvest timber production in the MUZ is provided by commercial-sized trees (trees larger than the minimum diameter cutting limit or MDCL) harvested at an intensity pre-determined by the rate at which sub-commercial trees are assumed to grow to commercial size during the cutting cycle between first and second harvests (see **section 2.3.3** on cutting intensity). Second-harvest timber production, 25–40 years after initial harvests, will be provided by commercial trees that survived the initial harvest, and by sub-commercial trees that grow to commercial size during the cutting cycle.

100%-area commercial census data for mahogany trees > 30 cm diameter were obtained in digital format from CONAP for 2005, 2006, and 2015 POAFs within the 11 active forest concessions in the study region. Additional operational and descriptive information about each POAF was obtained from concession managers responsible for implementing annual harvests. In some cases census data for 2015 POAFs was incomplete because concession managers had yet to digitize this information.

Commercial census data was organized according to a standard protocol in separate Excel spreadsheets for each POAF. Tree names, codes, stem quality classifications, and whether logged or not during the first harvest were compared to hard-copy documentation on file with CONAP to ensure data quality. Finally, these spreadsheets were combined into a single database for analysis.

Census data describe tree populations > 30 cm diameter within total harvestable or 'effective' areas in a given POAF. The effective area excludes trees located within protected zones – for example, around archaeological features – as well as trees located in areas deemed by managers as unsuitable for logging due to steep slopes or seasonal flooding. Across concessions, 13% of the total area within 2005/2006 POAFs was off-limits (**Table 2**); the effective area was used as the basis for population density measurements.

The census data also indicate which trees were harvested in 2005/2006 POAFs, allowing actual cutting intensity to be calculated and compared with the cutting intensity registered by CONAP. Because concessions are managed independently from each other, with different technical staff implementing inventories, coding systems for tree function and stem quality varied among concessions, requiring careful standardization and quality control before analysis to ensure that the model generated first-harvest outcomes equivalent to actual operational outcomes (**Table 3**). In fact, a slightly different coding system used by one concession (La

Gloria) created the impression that 100% of commercial trees were harvested in 2005/2006 POAFs. This coding problem will be resolved during preparation of results for publication in a scientific journal.

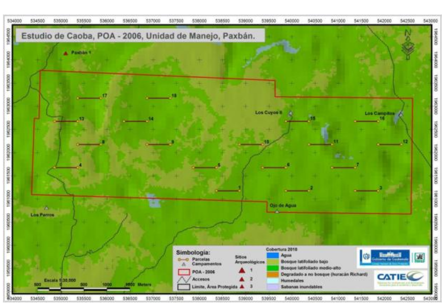
<u>*Cedrela + three lesser-known timber species*</u>: Commercial census data for *Cedrela* and three lesser-known timber species came from the same data sources as described above for *Swietenia*. However, in several POAFs, the 100%-area census data did not include sub-commercial trees (from 30 cm diameter to the MDCL) for all three species' populations (in seven POAFs for *Lonchocarpus*, eight for *Bucida*, and six for *Calophyllum*; **Table 4**). For these 21 populations, we filled this data gap by deriving diameter distributions from five-year plan surveys, which used 20 x 250 m (0.5-ha) strip transects to survey 3% of each concession area. This means that in POAFs where these sub-commercial trees were not surveyed by the concessionaires, the data will show identical diameter distributions in both years. Since no five-year plan existed for the La Gloria concession, initial populations for *Lonchocarpus*, *Bucida*, and *Calophyllum* in the La Gloria 2005 POAF could not be constructed or analyzed. In addition, a subset of species populations in other concessions were not analyzed because they occurred at insufficient densities for harvests in those POAFs (**Table 4**).

Again, data coding issues from several concessions persist in the results presented here; these will be corrected during preparation of results for publication in a scientific journal.

3.1.2 Field transect data for trees < 30 cm diameter

Third and fourth harvests in 50+ years will be provided by currently sub-commercial trees that grew too slowly to recruit to commercial size during the first cutting cycle, and by seedlings, saplings, and pole-sized trees that eventually grow to commercial size during repeated cutting cycles. Because this data is not collected during commercial censuses, fieldwork was necessary to estimate densities of stems < 30 cm diameter for all five species considered in this study. 20 m x 500 m strip transects (1 ha) were systematically placed within 2005/2006/2015 POAFs (**Fig. 3**) and surveyed for small poles (*latizales altos* 5–10 cm diameter) and pole-sized trees (*fustales*10–30 cm diameter). Seedlings (*brinzales* 30–150 cm height) and saplings (*latizales bajos* > 150 cm height to < 5 cm diameter) were surveyed in a 2 m x 500 m transect (0.1 ha) centered within each 1-ha transect. POAF-level sampling intensity was 1% for poles and 0.1% for seedlings and saplings. To collect this data, 265 1-ha transects were geo-located and installed during May–June 2014 within 11 concessions and 33 POAFs across the MUZ (**Table 2**). See the field manual by Manzanero & Pinelo (2014) for details on field methods, data collection, and transect locations. Transect data were digitized and processed for analysis in July 2014.

Fig. 3. *Systematically located 1-ha strip transects in the Paxbán 2006 POAF. 18 transects were installed within an effective area of 1816 ha (see* ***Table 2****).*



3.2 Dynamic data: growth and other demographic rates

3.2.1 Demographic rates for *Swietenia*

Dynamic data describing the complete arc of a species' life history are rarely available for tropical timber species. These data are available for *Swietenia*, however, from an ongoing 20-year research program at five forest research sites across southern Amazonia in Brazil (Grogan et al. 2008, 2014, Free et al. 2014). There, observational studies based on annual recensuses since 1995 of several thousand naturally occurring and experimentally outplanted seedlings, saplings, poles, and adult trees have allowed detailed description of size (diameter)-specific mortality, growth, and seed production rates across mahogany's life cycle (Grogan & Landis 2009, Grogan & Schulze 2012, Free et al. 2014). Spatial aspects of seed dispersal have been described (Grogan & Galvão 2006a, Norghauer et al. 2012), while experimental studies have examined seed germination, seedling establishment, and seedling growth requirements across light and soil nutrient gradients (Grogan et al. 2003a&b, 2005, Grogan & Galvão 2006a). Landscape ecology, including forest disturbance rates at the primary research site in southeast Pará, a seasonally dry forest similar structurally to MBR forests, has also been described (Grogan & Galvão 2006b). These data form the basis for a population dynamics model originally constructed for the purpose of evaluating the sustainability of current legal forest management parameters for *Swietenia* in Brazil (Grogan et al. 2014).

Algorithms describing demographic rates for mahogany derived from these studies are presented in **Table 5**. As can be seen, the relationships among rates are complex. For example, both mortality and diameter growth rates vary by stem size and are influenced by previous growth history, an autocorrelation effect known to significantly impact modeling behavior at the population level. Seed production is also strongly influenced by stem size and previous growth history (Grogan & Landis 2009).

3.2.2 Demographic rates for *Swietenia*: Brazil vs. Petén populations

We compared mortality and growth rates from natural forest populations in Brazil and other regions to growth data from permanent plots (PPMs) established in MBR concessions in the late 1990s to mid 2000s by forest managers in cooperation with CONAP. This comparison is necessary to evaluate whether a model built with mortality and growth rates from Brazil can reasonably be used to simulate Guatemalan *Swietenia* populations. No other dynamic data is available from the Petén.

Though mortality rates vary by stem size, a large sample of mahogany trees > 10 cm diameter (N = 342) averaged 1.25% annual mortality over an 18-year period at a study site in Brazil (Grogan & Landis 2009, Grogan et al. 2014). For comparison, Mize & Negreros-Castillo (2006) found 1% annual mortality in a 15-year study in Quintana Roo, Mexico. Baima (2001) reported 1.197% annual mortality for a large sample of mahogany trees > 10 cm diameter in Brazilian Amazonia over a 3-year period; Gullison et al. (1996) reported 1.6% annual mortality by trees > 2.5 cm diameter in Bolivia over a 2-year period (**Table 6**). No other published data describing mortality by mahogany trees in natural forests is available, including from the MUZ. Based on these comparisons we conclude that the size- and growth history-dependent mortality function from Brazil provides the best estimate of *Swietenia* mortality rates in the MUZ.

Median annual diameter growth increment by trees 10–60 cm diameter was 0.66 cm year^{-1} over 18 years at the study site in Brazil (Grogan et al. 2008, 2014, Grogan & Landis 2009; **Fig.**

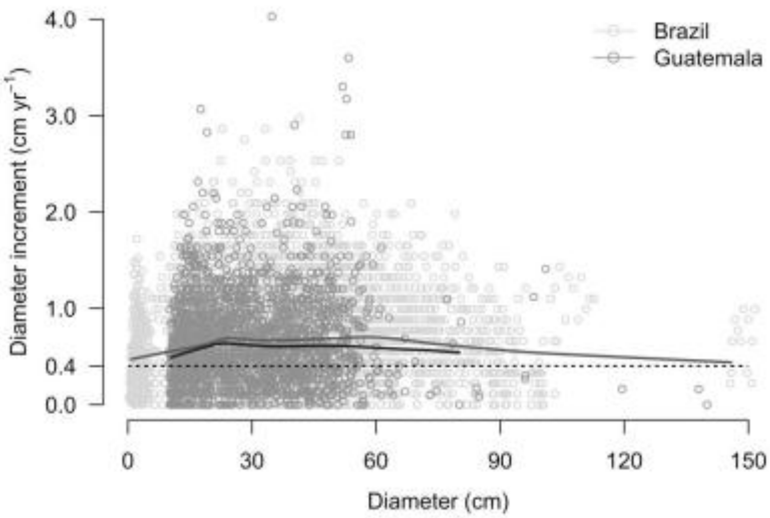
4). The few published reports describing natural forest diameter growth rates for *Swietenia* in other regions demonstrate both a consistent range of values similar to those in Brazil and wide variability among regions and between forests within regions (**Table 6**). In Quintana Roo, Mexico, Argüelles et al. (1998, p. 73) reported median diameter growth rates ranging from 0.16–0.66 cm year^{-1} for trees 10–60 cm diameter over an 8-year period. Negreros-Castillo & Mize (2014) found rates between 0.22–1.97 cm in a 6-year study in Quintana Roo.

In Guatemala, CONAP has partnered with MUZ concession managers to conduct long-term studies of diameter growth rates in permanent plots since 1998. Pooled data from seven permanent plots within five forest concessions found a median diameter growth rate of 0.60 cm year^{-1} by mahogany trees 10–60 cm diameter over periods of 3 to 11 years (**Fig. 4**; CONAP *unpublished data*; Hoil *unpublished data*). Manzanero (2005, p. 4 Fig. 3) reported median diameter growth rates by sub-commercial mahogany trees ranging from 0.41–0.43 cm year^{-1} over 1- to 7-year study periods in permanent plots in three concession forests.

In the absence of long-term diameter growth data for specific populations within each concession, the Brazil data represents the best available choice for simulating mahogany population dynamics in MUZ concessions for the following reasons: 1) The Brazil data match permanent plot data from MUZ concessions extremely well over the range of stem size classes represented within permanent plots (predominantly 10–60 cm diameter, see **Figure 4**); 2) The Brazil data matches studies from other regions in Central and South America both well and poorly, highlighting the variability that is characteristic of different populations growing under different conditions. 3) The Brazil data represents a very large sample of trees of all diameter size classes re-censused annually with great precision for 18 years as of 2014, noting that very little data is available from MUZ concessions for trees > 60 cm diameter. 4) Growth, mortality, and seed production rates (see next paragraph) are interlinked in the Brazil demographic model; substituting the limited growth data from MUZ concessions would disable these linkages and introduce uncertainty in model performance.

Other dynamic rates derived from Brazil populations include the probability and quantity of annual fruit production as a function of tree size (stem diameter), the distance to which seeds disperse, and seed germination and seedling establishment and survival rates. Seed production rates at the primary Brazil study site (Grogan & Galvão 2006a, Grogan & Landis 2009, Grogan et al. 2014) are strongly stem size-dependent and compare well with published reports from a nearby site in southeast Pará (Jennings & Baima 2005) and in Quintana Roo, Mexico (Snook et al. 2005). Other vital rates for seeds and seedlings in the Brazil study forest are in the public record (Grogan et al. 2003, 2005, Grogan & Galvão 2006a).

***Fig. 4**. Observed diameter increment rates (cm year^{-1}) for* Swietenia *from studies in Brazil (light gray; n = 4277) and Guatemalan Maya Biosphere Reserve concessions (dark gray; n = 2131). Solid lines indicate Lowess smoothers through each dataset (light = Brazil, dark = Guatemala). The horizontal dashed line indicates the 0.4 cm year^{-1} median diameter increment assumed by Guatemalan harvest regulations and used in the calculation of cutting intensity.*



3.2.3 Demographic rates for *Cedrela* + three lesser-known timber species

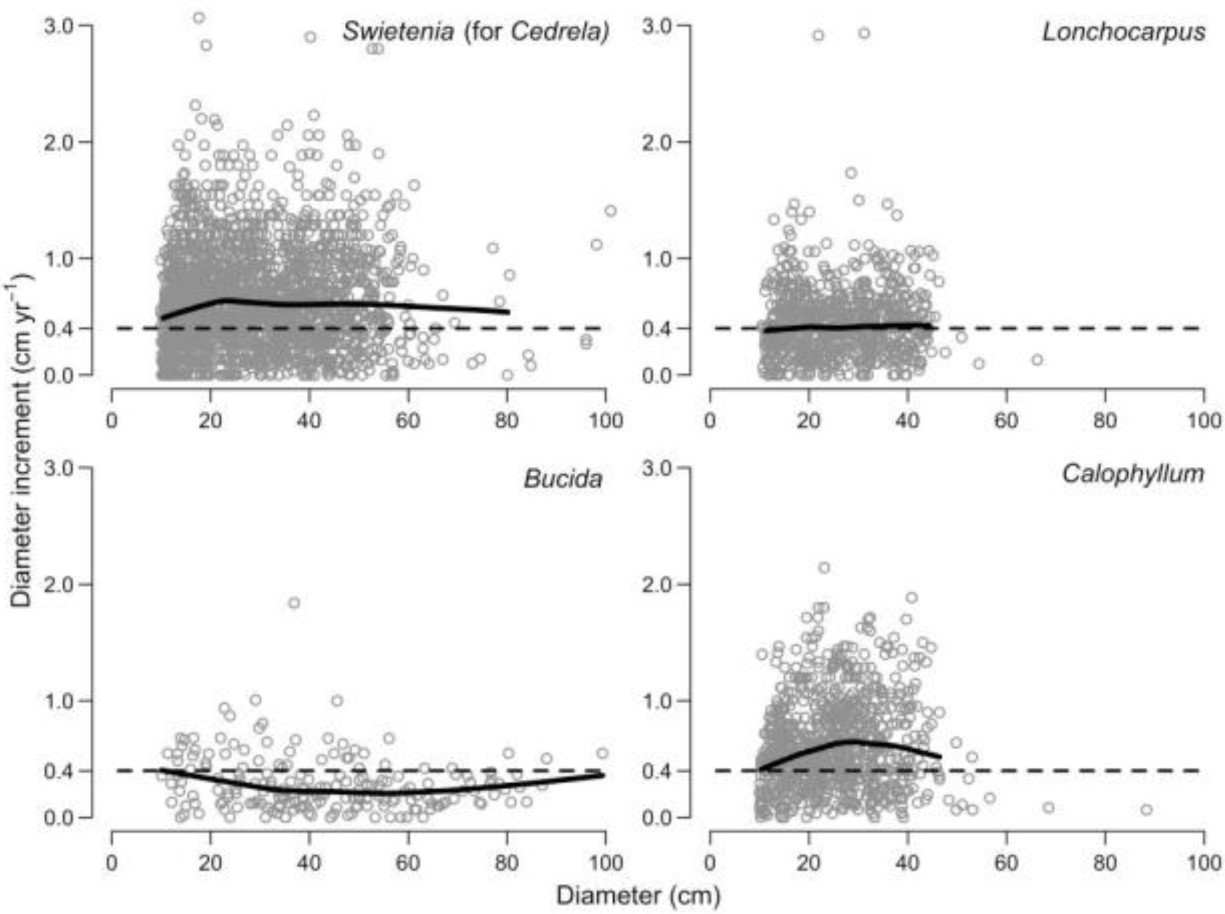
Data obtained for this study describing demographic rates of *Cedrela*, *Lonchocarpus*, *Bucida* and *Calophyllum* were restricted to diameter growth data from MUZ permanent plots. Empirical information regarding mortality, seed production, dispersal, germination, seedling establishment, and early plant growth was not found. This lack of dynamic information, especially for juvenile stems < 30 cm diameter, means that we cannot project population recovery by *Cedrela* and lesser-known species beyond a single cutting cycle, that is, beyond the second harvest.

The MBR permanent plots whose data was analyzed for this study did not have *Cedrela* individuals represented within them. Given this complete lack of diameter increment data, we substituted *Swietenia* permanent plot data for this species. *Cedrela* and *Swietenia* are closely related species in the family Meliaceae with similar growth requirements; a small sample of *Cedrela* trees > 10 cm diameter in Brazil demonstrated median growth rates roughly equivalent to mahogany over an 18-year period (Grogan & Schulze *unpublished data*).

Diameter growth data for these species from permanent plots are largely limited to sub-commercial trees 30–60 cm diameter. We synthesize this data to generate size-class dependent growth rates for modeling purposes (**Fig. 5**). Median annual growth by *Lonchocarpus* trees 10–50 cm diameter was approximately 0.4 cm year^{-1} across this size range, equivalent to the growth rate used to calculate cutting intensity. *Bucida* grew 0.4 cm year^{-1} or less over a size range of 10–100 cm diameter, with the lowest growth rates by trees 40–60 cm diameter. *Calophyllum* grew 0.4 cm year^{-1} or more over a narrower size range, from 10–45 cm diameter, peaking between 25–35 cm diameter.

An annual mortality rate of 1% was applied across stem size classes to *Cedrela* and the three lesser-known timber species, based on a large body of published research.

Fig. 5. *Observed diameter increment rates (cm year^{-1}) for* Cedrela *and three lesser-known timber species pooled from 5 of 11 forest concessions in the MUZ. Diameter increment rates for* Swietenia *from MUZ concessions are shown for* Cedrela *in the absence of MUZ data for* Cedrela*. Dark points indicate observed values and light points indicate extrapolated values. Solid black and grey lines indicate Lowess smoothers through the observed and full growth datasets, respectively. Dashed black lines indicate the 0.4 cm year^{-1} median diameter increment assumed by the cutting intensity formula.*



3.3 Modeling tree species populations in response to harvesting

3.3.1 Modeling *Swietenia* populations: the R model

The model used for simulating *Swietenia* population response to harvests is a non-spatial individual tree-based model constructed in the R programming language by Matthew Landis (Grogan & Landis 2009, Free et al. 2014, Grogan et al. 2014). As described above, the model's static and dynamic algorithms for simulating population growth through time are derived from mahogany populations under study in Brazil since 1995. Petén-specific management parameters (MDCL, cutting cycle, and cutting intensity) were incorporated into the model.

The R model was adapted to the spatially explicit NetLogo programming environment by Christopher Free. The NetLogo model offers a user-friendly menu-driven interface that allows forest managers to upload population data describing local conditions; it can also automate repeated simulations in order to generate median values for given management scenarios (http://www.swietking.org/model-applet.html). The two models generate identical median values over repeated simulations, but the R model has considerably greater computing power and therefore is the model used to generate results reported in this study.

Combining dynamic rates from Brazil for all phases of mahogany's life cycle with complete population structures available through commercial census and field transect data from MUZ concessions allows population response to harvests to be simulated into the future over multiple cutting cycles, using the management parameters applied by CONAP and concessionaires. In the current analysis we simulate four harvests over three cutting cycles for mahogany, or 75–120 years into the future depending on cutting cycle length (25–40 years) for a given POAF.

We corroborated outcomes generated by the R model based on Brazil data by also simulating Petén *Swietenia* populations using the lesser-known species model as described below (**section 3.3.4**). In this second modeling scenario, *Swietenia* diameter growth data from the MBR permanent plots and an annual 1% mortality rate replaced Brazil growth and mortality data.

3.3.2 Building initial *Swietenia* populations

The abundance of *Swietenia* trees < 30 cm diameter in each POAF was estimated from the density size structure of seedlings, saplings, and pole-sized trees observed in strip transect surveys. Diameters were selected uniformly from the 1- and 5-cm diameter size-class distributions generated by the 0.1-ha and 1-ha transect surveys, respectively. All trees < 30 cm diameter were assumed to be potential future crop trees, i.e., they will maintain sufficient bole quality for harvest.

For modeling purposes, trees > 2.5 to 30 cm diameter were combined with commercial census trees > 30 cm diameter to create the initial (or 'past') population for each POAF. We used 2.5 cm as a minimum diameter for inclusion in population simulations because the model assumes that only plants in gaps can survive and grow, and we lack detailed information regarding growing conditions for each individual seedling (or for the many additional seedlings that each sampled plant represents in the larger POAF area). Recalling that 2005/2006 POAFs were sampled in 2014, we assume that saplings < 2.5 cm diameter and especially seedlings < 1.5 m height 8–9 years after logging have been suppressed by competing vegetation and have low probability of recruiting to commercial size unless managed through silvicultural interventions (Grogan et al. 2003b, 2005).

There were 96 *Swietenia* trees in POAF commercial censuses with missing diameter data. Diameters for these trees were assigned by selecting randomly from the diameter distribution of other trees included in censuses. This allowed diameters to be designated without changing the shape of the observed distribution.

In POAF censuses, trees are classified into the following categories: commercial, retained, future crop, useless, seed tree, logged, salvaged, decrepit, protected, or none/unknown. Rules described in **Table 3** were used to reclassify all trees into four categories that better describe a tree's status at the time of first harvest: logged, salvaged, future crop, or useless. Only trees classified as logged or future crop were considered in the calculation of cutting intensity as described in **section 3.3.3** below. In subsequent harvests, only trees classified as future crop were considered in the calculation of cutting intensity.

3.3.3 Simulating *Swietenia* population dynamics and harvest outcomes

The *Swietenia* population model grows, kills, and reproduces trees on annual time steps based on regression equations as detailed above. The model includes functions for creating canopy gaps from both natural disturbances and logging and assumes that seed germination and seedling establishment only occur within such gaps. Trees are harvested based on minimum diameter cutting limits which vary among concessions (55 or 60 cm diameter), and then grown during the subsequent cutting cycle (25, 30 or 40 years; **Table 7**) until the second harvest. Trees designated as 'logged' and 'salvaged' in the 2006/2006 POAF data are removed from the population in year 0. These trees are given a 50% chance of fruiting before being harvested based on the timing of dry season logging operations, which begin before seed dispersal initiates and terminate well after seed dispersal is complete. Treefall gaps associated with the harvest of logged trees contribute towards the total gap area available for regeneration.

As described in **section 2.3.3**, in Petén the minimum diameter cutting limit and cutting cycle interact to determine the cutting intensity. Cutting intensity for commercial-sized trees < 90 cm diameter is calculated as the proportion of the summed basal area of trees expected to reach commercial size by the next harvest (during one cutting cycle) to the summed basal area of commercial-sized trees < 90 cm diameter at the present harvest:

$$Cutting\ intensity = \sum BA_{Thresh-DMC} / \sum BA_{DMC-90cm}$$

This calculation assumes an average annual diameter increment of 0.4 cm year^{-1} for all sub-commercial *Swietenia* trees. This allows calculation of a diameter threshold over which all trees are assumed to reach commercial size by the next harvest. The diameter threshold is calculated using the following equation:

$$Diameter\ threshhold\ (cm)\ = MCD - 0.4\ cm\ yr^{-1} \times cutting\ cycle\ length\ (yrs)$$

The cutting intensity represents the proportion of the summed basal area of commercial-sized trees < 90 cm diameter that can be logged in the present harvest. Thus, the 'target basal area' to log in the current harvest is equivalent to the basal area expected to replace logged trees in the next harvest. The model was adjusted to include this calculation; it randomly selects trees to log until the selection of an additional tree would cause the target basal area (cutting intensity) to be exceeded.

For trees > 90 cm diameter, the model assumes that managers will always harvest 65% of the basal area available (the maximum permitted) in this size class, and randomly selects trees to log until the selection of an additional tree would cause the target basal area (cutting intensity) to be exceeded. For the initial known harvest (2005/2006), we calculated the actual cutting intensity of commercial-sized trees < 90 cm and > 90 cm diameter according to POAF inventories, and compared these values to 'mathematically correct' cutting intensities as described above.

Finally, the model estimates roundwood volumes using a single-entry equation from Kometter (2011) based on a large sample of *Swietenia* trees in Guatemala:

$$V = -5.298 + 0.126 * D$$

where V = volume (m^3) and D = diameter (cm) at 1.3 m height on the bole or at the height measured if buttresses exceeded this height. Note that volume estimates are also provided in the 2005/2006 commercial census data, but we recalculated volume using this equation to ensure comparability with future harvests. All POAF populations were simulated 100 times over three cutting cycles plus 10 years, that is, for 100 years in concessions where 30-year cutting cycles are anticipated. Reported outcomes represent median values from repeated simulations.

3.4 Modeling *Cedrela* + three lesser-known timber species populations

The model used to evaluate potential post-harvest recovery by *Cedrela* and three lesser-known timber species during one cutting cycle was similar to the one used to simulate population response by *Swietenia* and associated rare timber species in recent articles published in the scientific journal *Forest Ecology and Management* (Grogan et al. 2008, Schulze et al. 2008).

Initial population structures were constructed in the same way as described above for mahogany. After harvests in year 0 according to minimum diameter cutting rules which vary by concession (**Table 8**), the model grows sub-commercial and surviving commercial trees during the first cutting cycle (25–40 years) by randomly assigning, on a year-to-year basis, diameter growth rates drawn from a distribution of observed diameter growth rates for a given 5-cm size class from permanent plot data in the MUZ. For example, in year one a 32-cm tree will be assigned a growth rate observed for a conspecific tree in a permanent plot that was 30–35 cm diameter; this will be repeated, drawing from the same pool of observed growth rates, in year two and so forth. The model applies a background mortality rate of 1% to all trees throughout the cutting cycle. At the end of one cutting cycle, trees are logged according to the cutting intensity rules described above for the *Swietenia* model. Each species population was simulated 100 times and results reported below represent median values.

For comparative purposes, mahogany was re-analyzed using this lesser-known species model, based on diameter growth rates in MBR permanent plots and an annual mortality rate of 1% for trees of all sizes. The initial populations used in this analysis were identical to those in the R population model.

4 RESULTS: *SWIETENIA*

4.1 Population structures from commercial census data

Commercial census data for sub-commercial trees 30–60 cm diameter and for commercial trees > 60 cm diameter in 2005/2006 POAFs are combined in **Tables 8–10** and **Annex 1**; data for 2015 POAFs were unavailable at the time of analysis. Among 2005/2006 POAFs, the average density of *Swietenia* trees > 30 cm diameter was 225 trees per 100 ha (range: 104–439 at Árbol Verde 2006 and Uaxactún 2006, respectively; **Tables 8–9**). The average density of commercial-sized trees > 60 cm diameter was 81 trees per 100 ha (range: 20–138 at Árbol Verde 2006 and Río Chanchich 2006, respectively), noting that the minimum commercial density was 55 cm diameter at AFICC, Carmelita, and Paxbán. The average density of large trees > 90 cm diameter was 17 trees per 100 ha (range: 3–50 at Árbol Verde 2006 and Río Chanchich 2006, respectively).

Size class frequency distributions by 5-cm diameter increments are shown in **Table 10** and **Annex 1**, presented in number of stems per 100 ha. Visual inspection of charts in **Annex 1** offers two rapid indicators of whether future harvests will have higher or lower volumes relative to initial harvests. First, are sub-commercial trees abundant compared to commercial trees, i.e., is the frequency curve weighted towards small trees (for example, see Árbol Verde 2006), is the curve relatively flat (AFICC 2005), or is it weighted towards larger trees (Río Chanchich 2005)? The shape of the frequency curve influences the second visual indicator: what was the first cutting intensity, that is, how many commercial-sized trees were left in the forest (see light vs. dark gray bars)? For 'sustainability' purposes, cutting intensity can be high where sub-commercial trees are abundant compared to commercial trees, because sub-commercial trees are expected to recruit to commercial size during the first and subsequent cutting cycles. However, cutting intensity should be restricted when sub-commercial trees occur at low densities relative to commercial size classes because fewer individuals are available to replace today's harvested trees.

4.2 Population structures from transect surveys

Transect surveys in 2005/2006/2015 POAFs yielded a wide range of estimated densities of seedlings, saplings, small poles, and pole-sized trees (**Tables 11–14**, **Annexes 2–3**). While our sampling intensity was relatively low (1%-area coverage for poles, 0.1%-area coverage for seedlings and saplings) and we do not expect uniform spatial distributions of *Swietenia* regeneration throughout a given POAF, systematically located strip transects correct for patchy occurrence by pooling areas where plants occur at high, intermediate, and low densities.

Swietenia seedlings (*brinzales* < 1.5 m height) were present at relatively high densities in nearly all POAFs, averaging 5010 per 100 ha within 2005/2006 POAFs and 3015 per 100 ha in 2015 POAFs (**Table 12**). This apparent difference in seedling densities between harvested (2005/2006) and unharvested POAFs was expected because forest canopy disturbance associated with logging should promote seedling establishment and persistence during the 8–9 years since logging. Zero seedlings were found at the Uaxactún 2005 and Yaloch 2015 POAFs, while the highest estimated seedling density was found at Yaloch 2006 (14,750 per 100 ha, **Table 11**). Seedling densities are presented in detail (see '0–1 cm') in **Table 13** and **Annex 2**.

Densities of saplings (*latizales bajos* > 1.5 m height to 5 cm diameter) should be lower than seedling densities because fewer individuals survive over time to attain larger size. While saplings < 5 cm diameter occurred at much lower densities than seedlings, they appeared in transects in sufficient numbers to generate robust POAF-level densities. Sapling densities averaged 750 per 100 ha in 2005/2006 POAFs compared to 209 per 100 ha in 2015 POAFs (**Table 12**). Again, different average densities between harvested and unharvested POAFs were expected for stems < 5 cm diameter, as many of these individuals likely established after logging in 2005/2006. Zero saplings were recorded in three 2005 POAFs and four 2015 POAFs; the highest recorded sapling density was 4000 per 100 ha at Carmelita 2006 (**Table 11**). Sapling densities are shown by 1-cm size class (see '1–5 cm') in **Table 13** and **Annex 2**.

Small poles (*latizales altos* 5–10 cm diameter) occurred at lower densities than saplings, averaging 47 per 100 ha in 2005/2006 POAFs compared to 21 per 100 ha in 2015 POAFs (**Table 12**). Higher average small-pole densities in harvested vs. unharvested POAFs were expected because *Swietenia* seedlings and saplings can grow to 5–10 cm diameter within 8–9 years under favorable conditions, especially in high light environments associated with logging gaps. Zero small poles were found in four 2005 POAFs, two 2006 POAFs, and four 2015 POAFs. The highest small pole density recorded was 300 per 100 ha at Uaxactún 2006 (**Table 11**). Small pole densities are presented (see '5–10 cm') in **Table 13** and **Annex 3**.

We expect differences between 2005/2006 vs. 2015 POAFs to disappear for pole-sized trees (*fustales* 10–30 cm diameter) because trees this large likely established prior to logging events 8–9 years before transects were installed. As well, collateral damages associated with low intensity logging should not significantly impact pole densities in 2005/2006 POAFs. Indeed, **Table 12** shows no difference among years for this size category, averaging 127 per 100 ha overall. Zero stems were found at Río Chanchich 2005 and Chosquitan 2006; the highest pole density was 400 per 100 ha at AFISAP 2015 (**Table 11**). Pole densities are detailed by 5-cm size class (see '10–30 cm') in **Table 14** and **Annex 3**. It is not surprising that average pole densities are higher than small pole and sapling densities because stems > 10 cm diameter typically have crowns in or approaching the forest canopy, at which point they may persist for decades even in a suppressed position. In other words, mortality rates should be low for this size class compared to smaller size classes.

Similar to commercial census data discussed in **section 4.1**, visual inspection of size class frequency distributions from transect surveys offers a rapid indication of whether future harvests will be robust or weak relative to initial harvests. We expect stems < 30 cm diameter to grow into sub-commercial and commercial size classes during second and third cutting cycles, providing part or most of third and fourth harvests. (As noted in **section 3.3.2**, the minimum stem diameter of interest for modeling *Swietenia* population recovery is 2.5 cm diameter – stems smaller than this are not included in initial population structures, for reasons given.) Where sapling densities > 2.5 cm diameter (**Table 12, Annex 2**) and pole densities of any size (**Table 13, Annex 3**) are high, we can expect robust recruitment into sub-commercial and commercial size classes over the coming decades. As an example, sapling densities in 2005/2006 Carmelita POAFs were extremely high compared to other concessions, in contrast with several concessions where zero saplings were found in this size range (e.g., AFICC 2005, Yaloch 2005/2006). We can likewise anticipate impacts on future harvests of highly variable pole densities.

In summary, seedlings, saplings, and poles are present at relatively high densities in nearly all POAFs, available for silvicultural intervention should forest managers choose to invest in management practices aimed at accelerating growth rates.

4.3 Modeling populations under current forest management parameters in the MUZ

Complete population structures for *Swietenia* > 2.5 cm diameter in 2005/2006 POAFs can be seen in **Annex 4**, where estimated densities of stems < 30 cm diameter (**section 4.2**) are combined with observed densities of stems > 30 cm diameter (**section 4.1**). (Complete population structures could not be constructed for 2015 POAFs because commercial census data were not available at the time of analysis.) These are the populations that the model harvested in year 0 according to what actually occurred in 2005/2006 (see light gray bars for harvested trees > 55 or 60 cm diameter). Populations are then grown during the first cutting cycle of 25–40 years, harvested a second time, and then grown and harvested for two additional cutting cycles. Additional forest management parameters incorporated into long-term model simulations include MDCL (**Table 7**) and cutting intensity (**section 3.3.3**).

4.3.1 *Swietenia* commercial densities during three cutting cycles

Outputs from model simulations of *Swietenia* populations in 2005/2005 POAFs can be seen in **Table 15** and **Annex 5**. There we see initial commercial density (for example, 50 commercial trees per 100 ha pre-harvest in AFICC 2005), the impact on commercial density of the first harvest (falling to 22 commercial trees per 100 ha post-harvest in AFICC 2005), commercial density recovery during the first cutting cycle until the time of the second harvest (to a median value of 40 commercial trees per 100 ha pre-second harvest in AFICC 2005), decline in density after the second harvest (to a median value of 27 commercial trees per 100 ha post-second harvest in AFICC 2005), and so forth through three cutting cycles and four harvests.

On average, given forest management parameters applied in 2005/2006 and anticipated during future harvests, model simulations indicate that *Swietenia* populations in concession POAFs will recover or exceed initial commercial densities during cutting cycles between successive harvests. The overall trajectory of commercial density simulations spanning three cutting cycles shown in **Annex 5** is positive or nearly so for eight out of eleven 2005 POAFs, and for nine out of eleven 2006 POAFs. On average, median commercial density of simulated populations recovered to 109% and 116% of initial commercial density at the time of second harvests in 2005/2006 POAFs, respectively; to 146% and 150% of initial commercial density at the time of third harvests, respectively; and to 149% and 156% of initial commercial density at the time of fourth harvests, respectively (**Table 16A**). These overall recovery rates are strongly influenced by extremely positive recovery at both Carmelita POAFs, as discussed below. However, even after removing Carmelita results from consideration, future commercial densities after one to three cutting cycles represented, on average, 101–145% of initial commercial densities (**Table 16B**).

Recovery or not of commercial density during cutting cycles between harvests is a direct consequence of the distribution and densities of sub-commercial trees, poles, and saplings. Where these individuals occur at relatively high densities compared to commercial trees, future harvests may be comparable to initial harvests as sub-commercial trees recruit to commercial size during the coming decades. By linking cutting intensity to assumed growth rates by sub-commercial trees, forest managers in the MUZ restrict harvests to sustainable levels in terms of commercial density where population structures are favorable.

To better understand relationships between population structure and simulation outcomes, **Annex 8** presents inventory and transect data together with model simulations for each POAF.

For example, commercial density outcomes over four harvests for 2005/2006 AFICC POAFs are favorable, with density rising over time. Two reasons for this are shown in **Annex 8 panels B & D**, where we see, first, that sub-commercial trees (30–60 cm diameter) occur at high densities compared to commercial-sized trees; and second, that poles (10–30 cm diameter) are estimated to occur at quite high densities within both of these areas. Aside from poor representation in the smallest size classes, especially saplings (**panel A**), these are ideal population structures for medium and long-term management – so long as rules place limits on cutting intensities.

AFISAP 2006 predicts a flat commercial density recovery during the second cutting cycle from years 40–80 – why? Again **Annex 8 panels B & D** provide an explanation: transect surveys found relatively few stems < 30 cm diameter in this POAF, and these smaller trees are key to commercial population recovery during the second cutting cycle.

Model simulations predict rapid commercial density recovery and expansion during successive cutting cycles in both Carmelita POAFs. This happens because densities of sub-commercial trees from inventory data and of poles and saplings estimated from transect surveys are extremely high in both years. By contrast, at Río Chanchich, where trees < 30 cm diameter were scarce in both years, commercial densities fall over time. Again, this is a direct outcome of data from transect surveys indicating that *Swietenia* poles, saplings, and seedlings are scarce within 2005/2006 Río Chanchich POAFs. Note that this concession contained the area most heavily affected by Hurricane Richard in 2010, a possible contributor to this result.

4.3.2 *Swietenia* commercial volume production from four harvests

Outputs from model simulations of commercial roundwood production (volume in m^3 per 100 ha) during four harvests by *Swietenia* populations in 2005/2005 POAFs can be seen in **Table 17** and **Annex 6**. There we see actual harvested volumes during the first harvests in 2005/2006 (for example, 105 m^3 per 100 ha in AFICC 2005), the median simulated harvest volume at the time of second harvests following the first cutting cycle (69 m^3 per 100 ha in AFICC 2005 after 30 years), the median simulated harvest volume at the time of third harvests following the second cutting cycle (84 m^3 per 100 ha in AFICC 2005 after 60 years), the median simulated harvest volume at the time of fourth harvests following the third cutting cycle (96 m^3 per 100 ha in AFICC 2005 after 90 years), and the recovery rate each simulated harvest represents as a % of the initial observed harvest (66%, 80% & 91% from second, third, and fourth harvests compared to first harvests at AFICC 2005, respectively; **Table 17**).

On average, given forest management parameters applied in 2005/2006 and anticipated during future harvests, model simulations indicate that most *Swietenia* populations in concession POAFs will gradually recover initial commercial volumes during cutting cycles between successive harvests. In more than half of 2005/2006 POAFs we see a marked or slight decline in volume production during the second harvest but then gradual recovery during subsequent harvests (e.g., AFICC 2005/2006; **Annex 6**). The average roundwood production of simulated populations recovered to 83% and 81% of initial harvests during second harvests in 2005/2006 POAFs, respectively; to 119% and 97% of initial harvests during third harvests, respectively; and to 142% and 111% of initial harvests during fourth harvests, respectively (**Table 18**).

As expected, patterns of simulated roundwood production broadly resemble commercial density recovery within each POAF, but interpretation of recovery patterns for volume is more complex. Future roundwood production clearly depends on recruitment by sub-commercial and juvenile trees to commercial size. However, the main reason that second harvests were in most cases smaller than first harvests is that *actual* cutting intensities exceeded *target* cutting intensities calculated by the official formula in nearly all POAFs. This was due to adjustments requested by concessions and approved by CONAP (see **section 2.3.3**). This means that higher commercial volumes were removed from POAF-level populations than could be replaced by recruitment during the first cutting cycle. If initial harvest volumes in 2005/2006 had been closer to those anticipated by calculated cutting intensities, then second harvests after one cutting cycle would have more closely resembled initial harvests, and subsequent harvests (third, fourth) would have been more productive.

Other factors contributed to volume simulation outcomes. Both the degree to which commercial trees dominate populations numerically (that is, whether size class frequency distributions are weighted towards sub-commercial or commercial trees), and the intensity at which initial commercial populations are harvested, influence future outcomes for roundwood production. As an example, in AFISAP 2005, where the actual cutting intensity essentially equaled the calculated value, large numbers of juvenile and sub-commercial trees relative to commercial trees (**Annex 8 AFISAP 2005**) contributed to increasing volume production over time. But a sharp decline in second-harvest production in AFISAP 2006 in spite of a similar size class frequency distribution for sub-commercial and commercial trees was a consequence of too-high cutting intensity during the first harvest (**Annex 8 AFISAP 2006**). Remember that for harvests subsequent to the initial cut, the model assumes that managers follow the cutting intensity calculated as per **section 2.3.3** without approval of excess volume.

4.3.3 *Swietenia* cutting intensities during four harvests

Outputs from model calculations of *Swietenia* cutting intensities during four harvests in 2005/2006 POAFs can be seen in **Table 19** and **Annex 7**. There we see the *target* or calculated value as a % of commercial basal area (BA) during each harvest, and the *actual* or observed value during the first harvest, as derived from census data. For example, in AFICC 2005, the target cutting intensity was 31% of commercial basal area represented by trees 60–90 cm diameter, while the actual cutting intensity was 57%. Target cutting intensities calculated by the model for second, third, and fourth harvests in AFICC 2005 closely resembled the first-harvest target (30%, 30%, and 32%, respectively).

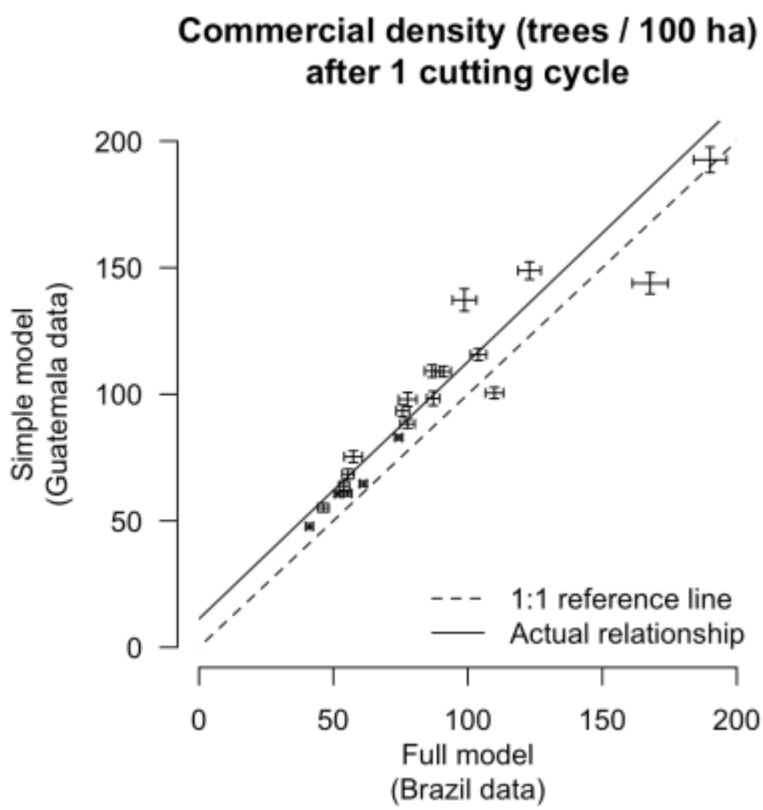
As noted in **section 4.3.2**, actual cutting intensities during the initial harvest exceeded target cutting intensities in nearly all POAFs, in some cases by margins approaching two times the target value. Target values averaged 47% and 52% in 2005 and 2006 POAFs, respectively, while actual harvests averaged 66% and 68%, respectively (**Table 20**). In most POAFs both 'small' commercial trees 60–90 cm diameter and 'large' commercial trees > 90 cm diameter appear to have been harvested at rates higher than calculated values during the first harvest.

While target and actual values were close in several POAFs (AFISAP 2005, Árbol Verde 2006, Carmelita 2005), only in Uaxactún 2005/2006 POAFs were actual values significantly lower than target values. These decisions led to consistent or growing simulated volume production over subsequent Uaxactún harvests and compensated for low densities of juvenile stems in the 2005 POAF.

4.4 *Swietenia* population response to harvest using the lesser-known species model

Simulated outcomes for *Swietenia* populations over one cutting cycle applying the lesser-known species model, which uses observed diameter growth rates from MBR permanent monitoring plots, were similar to simulated outcomes from the R model (**Annex 9**). At the POAF level the lesser-known species model predicted, on average, slightly faster recovery rates for commercial density than the R model (**Fig. 6**). One possible source of this difference is the mortality rate used by the respective models, which was lower in the lesser-known species model (assumed 1% $year^{-1}$ vs. observed 1.25% $year^{-1}$ from Brazil in the R model).

Fig. 6*. Comparison of commercial density recovery by* Swietenia *populations in 2005/2006 POAFs as predicted by the lesser-known species model using observed data from the MUZ vs. the R model using data from Brazil. The dotted line shows the trajectory of a one-to-one relationship; nearly all comparisons were near or above this line, demonstrating that the simpler model yields more optimistic outcomes.*



5 RESULTS: *CEDRELA, LONCHOCARPUS, BUCIDA* AND *CALOPHYLLUM*

5.1 Population structures from commercial censuses

Similar to *Swietenia*, commercial census data sources for sub-commercial trees (30 cm–MDCL) and for commercial trees (> MDCL) are combined in **Tables 21–23** and **Annex 10A–D**. Again, commercial census data for 2015 POAFs were unavailable at the time of analysis and cannot be presented here.

Cedrela occurred at very low densities in concession POAFs compared to *Swietenia*, with almost no density correlation between 2005/2006 POAFs within concessions. This indicates highly patchy or variable density on the MUZ landscape at large, noting *Cedrela*'s local preference for steep, rocky terrain. Among 2005/2006 POAFs, the average density of *Cedrela* trees > 30 cm diameter was 15 trees per 100 ha (range: 0–79; **Tables 21–22**). The average density of commercial-sized trees > 60 cm diameter was 5 trees per 100 ha (range: 0–22), noting that the MDCL was 55 cm diameter at AFICC and Carmelita. The average density of trees > 90 cm diameter was only 1 tree per 100 ha (range: 0–4). Again, this indicates not that *Cedrela* does not attain large stature within the MUZ but rather that the low-lying, relatively flat terrain that prevails across the 'effective area' of most 2005/2006 POAFs is unfavorable to *Cedrela* establishment and growth.

Cedrela's variable density can be seen in **Annex 10A**, where inventory data are shown as size class frequency distributions in each 2005/2006 POAF (see also **Table 23**). Occurring at low densities in most POAFs, we see relatively high-density populations dominated by sub-commercial trees compared to commercial size classes in Árbol Verde 2006, La Gloria 2006, and Uaxactún 2005. These population structures anticipate robust commercial recovery during 25- to 40-year cutting cycles before second harvests.

Lonchocarpus occurred at generally higher densities than *Cedrela* but still at lower densities than *Swietenia*. Landscape-scale variability in density was high. Among 2005/2006 POAFs, the average density of *Lonchocarpus* trees > 30 cm diameter was 39 trees per 100 ha (range: 7–200; **Tables 21–22**). The average density of trees > 60 cm diameter was 7 trees per 100 ha (range: 1–29), noting that the MDCLfor *Lonchocarpus* ranged from 45–60 cm among concessions (**Table 7**). Very few *Lonchocarpus* trees > 90 cm diameter werefound in any POAF (range: 0–2 per 100 ha), confirming that this is a medium-statured timber species in terms of stem diameter in the MUZ. **Table 23** and **Annex 10B** present size class frequency distributions for *Lonchocarpus* from inventory data in each POAF.

Bucida occurred at densities comparable to *Lonchocarpus*. Among 2005/2006 POAFs, the average density of *Bucida* trees > 30 cm diameter was 30 trees per 100 ha (range: 0–101; **Tables 21–22**). The average density of trees > 60 cm diameter was 17 trees per 100 ha (range: 0–71); like *Lonchocarpus*, the MDCL for *Bucida* ranged from 45–60 cm among concessions (**Table 7**). Like *Cedrela*, the average density of large *Bucida* trees > 90 cm diameter was 1 tree per 100 ha (range: 0–5). **Table 23** and **Annex 10C** present size class frequency distributions for *Bucida* from inventory data in each POAF.

Calophyllum occurred at densities roughly one-quarter to one-half as high as *Swietenia*. Among 2005/2006 POAFs, the average density of *Calophyllum* trees > 30 cm diameter was 87 trees per 100 ha (range: 0–549; **Tables 21–22**). The average density of trees > 60 cm diameter was 14 per 100 ha (range: 0–73); again, the MDCL for *Calophyllum* ranged from 45–60 cm among concessions (**Table 7**). Like *Lonchocarpus*, very few *Calophyllum* trees > 90 cm diameter were found in any POAFs (range: 0–1 per 100 ha; **Table 23**), confirming that this is a medium-statured timber species in terms of stem diameter within the MUZ. **Table 23** and **Annex 10D** present size class frequency distributions for *Calophyllum* from inventory data in each POAF.

5.2 Population structures from transect surveys

Transect survey data for *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* in 2005/2006/2015 POAFs are presented in **Tables 24–27** and **Annexes 11A–D & 12A–D**.

Like size classes > 30 cm diameter, estimated densities of *Cedrela* seedlings, saplings, and poles were extremely low in MBR concessions. No seedlings or saplings were found in 14 of 22 2005/2006 POAFs, or in 7 of 11 2015 POAFs (**Table 24**, **Annex 11A**). Average estimated densities in logged 2005/2006 POAFs were 38 seedlings and 36 saplings per 100 ha (**Table 25**); at these densities, essentially no *Cedrela* regeneration exists across much of this landscape. No clear post-logging establishment response comparable to *Swietenia*'s was seen, though average sapling densities in 2015 POAFs were roughly one-third the densities in 2005/2006 POAFs (**Table 25**). Seedling and sapling densities were highest in two POAFs with relatively high sub-commercial and commercial densities, that is, Árbol Verde 2006 and La Gloria 2006, demonstrating the importance of seed source to seedling establishment.

As expected, high densities of seedlings and saplings were found in transects for the shade tolerant species *Lonchocarpus* and *Calophyllum* (**Table25**; **Annexes 11B & D / 12B & D**). Again, estimated densities were highly variable from one POAF to another and between years. Exceptionally high seedling densities of both species indicate either that seedlings establish and die at high rates or that they establish and persist in deep shade with only rare opportunities to grow into larger size classes. While relatively few *Lonchocarpus* seedlings and saplings appear to persist to pole size, *Calophyllum* poles occurred at quite high densities, averaging 327 per 100 ha in 2005/2006 POAFs. These pole-sized trees could be targeted for silvicultural interventions to provide harvests after two or more cutting cycles.

Bucida presents an intermediate scenario for juvenile stems between *Cedrela*'s scarcity and *Lonchocarpus* and *Calophyllum*'s super abundance. Transect data indicate steady though patchy seedling establishment and persistence through sapling and pole size classes (**Annexes 11C & 12C**). That is, small pole and pole size classes occur at relatively high densities compared to sapling densities (**Tables 24–25**).

5.3 Modeling populations under current forest management parameters in the MBR

Complete population structures for *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* in 2005/2006 POAFs can be seen in **Annex 13A–D**, where estimated densities of stems < 30 cm diameter are combined with observed densities of stems > 30 cm diameter (or estimated from 5-year plan data). These are the populations which the lesser-known species model harvests in year 0 according to what actually occurred in the field in 2005 and 2006 (see light gray bars for harvested trees). Populations are grown during the first cutting cycle of 25–40 years and then harvested a second time. Forest management parameters incorporated into model simulations include MDCL (**Table 7**) and cutting intensity.

5.3.1 Commercial densities during one cutting cycle

Outputs from model simulations of *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* populations in 2005/2005 POAFs can be seen in **Table 28** and **Annex 14A–D**. There we see starting commercial density (for example, for *Cedrela* in **Annex 14A**, 6 commercial trees per 100 ha pre-harvest in AFICC 2005), the impact on commercial density of the first harvest (for *Cedrela*, falling to 2 commercial trees per 100 ha post-harvest in AFICC 2005), and commercial density recovery during the first cutting cycle until the time of the second harvest (for *Cedrela*, to a median value of ~6 commercial trees per 100 ha pre-second harvest in AFICC 2005).

On average, given forest management parameters applied in 2005/2006, model simulations indicate that *Cedrela* populations in concession POAFs will recover initial commercial densities during the cutting cycle between first and second harvests. The average commercial density of simulated populations recovered to 106% and 140% of initial commercial density at the time of second harvests in 2005/2006 POAFs, respectively, with relatively low variation in recovery rate among POAFs (**Tables 28 & 29**). We can understand this outcome by looking at population structures 30–60 cm diameter: *Cedrela* populations consistently demonstrate relatively high sub-commercial tree densities compared to commercial size classes, and in some cases sub-commercial trees occur at very high densities (see Árbol Verde 2006, La Gloria 2006; **Annexes 10A & 17A**). Growth by these sub-commercial trees drives commercial density recovery.

Simulated commercial density recovery between harvests by *Lonchocarpus* populations was more robust than for *Cedrela*, averaging 208% and 234% of first-harvest densities at the time of second harvests in 2005/2006 POAFs, respectively (**Tables 28 & 29**). However, these averages may be artificially high due to our reliance on 5-year plan inventory data to generate missing sub-commercial trees for populations in seven POAFs (**Table 4**): in five out of seven of these, 5-year plan data created extremely skewed population structures weighted towards sub-commercial trees, leading to rapid commercial density recovery. When we exclude these seven POAFs from consideration, simulated commercial density recovery by *Lonchocarpus* at the time of second harvests averaged 107% and 128% of initial commercial densities in 2005/2006 POAFs, respectively, almost identical to *Cedrela* (noting that *Cedrela* sub-commercial populations were observed in all POAFs rather than estimated from 5-year plans).

Of the four secondary timber species, *Bucida* occurred at the highest commercial densities but also exhibited the most patchy spatial occurrence, being absent or nearly so in six of 22 POAFs (**Table 4**). Where it did occur, recovery at the time of second harvests averaged 113% and 97% of first-harvest densities in 2005/2006 POAFs, respectively (**Tables 28 & 29**). Again these averages were heavily influenced by 5-year plan data: removing from consideration eight POAF populations whose sub-commercial densities were extrapolated from this data, average commercial density recovery among POAFs declined to 56% and 50% in 2005/2006 POAFs, respectively.

A similar pattern held for *Calophyllum*: commercial density recovery between harvests averaged 189% and 135% in 2005/2006 POAFs, respectively (**Tables 28 & 29**), but 5-year plan data from six POAFs skewed these results. Excluding 5-year plan data from consideration we find that commercial densities of *Calophyllum* recovered to 156% and 104% of 2005/2006 first-harvest densities, respectively, at the time of second harvests.

5.3.2 Commercial volume production from two harvests

Outputs from model simulations of commercial roundwood production (volume in m^3 per 100 ha) during two harvests by *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* populations in 2005/2006 POAFs can be seen in **Table 30** and **Annex 15A–D**. There we see actual harvested volumes during the first harvests (for example, for *Cedrela* in **Annex 15A**, 11 m^3 per 100 ha in AFICC 2005), the median simulated harvest volume at the time of second harvests (for *Cedrela*, ~3 m^3 per 100 ha in AFICC 2005 after 30 years), and the recovery rate that each simulated harvest represents as a percentage of the initial observed harvest (for *Cedrela*, 33% from the second harvest compared to the first harvest in AFICC 2005).

On average, given forest management parameters applied in 2005/2006 and anticipated during the second harvest, model simulations indicate that most *Cedrela* populations in concession POAFs will decline precipitously in terms of commercial volume production between successive harvests (14% and 46% recovery as a percentage of first harvests in 2005/2006 POAFs, respectively; **Table 31**).

Similar outcomes can be seen for *Lonchocarpus*, *Bucida*, and *Calophyllum*: on average, in spite of strong recovery by commercial size classes during the first cutting cycle, timber volume production is expected to decline in most POAFs after one cutting cycle. For *Lonchocarpus*, average percent recovery rates during second harvests are expected to represent 86% and 84% of first-harvest production rates among 2005/2006 POAFs, respectively. These average percentage recovery rates are inflated by extremely favorable harvests in a small number of POAFs: overall average production falls from 18.9 m^3 per 100 ha during first harvests in 2005 POAFs to 10.6 m^3 per 100 ha during second harvests, representing 56% of the first-harvest average (**Table 31**); corresponding values for 2006 POAFs were 23.9/15.9/66%. For *Bucida*, average percent recovery rates during second harvests are expected to represent 49% and 46% of first-harvest production rates in 2005 and 2006 POAFs, respectively. For *Calophyllum*, average percent recovery rates during second harvests are expected to represent 112% and 56% of first-harvest production rates in 2005 and 2006 POAFs, respectively.

Outcomes for species populations based on five-year plan data may have artificially inflated these recovery rates. Adjusted average % recovery rates for timber production were, on average, lower after removing these populations, especially for *Bucida* (**Table 31**).

5.3.3 Cutting intensities during two harvests

Outputs from model calculations of cutting intensities for *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* during two harvests in 2005/2005 POAFs can be seen in **Tables 32 & 33** and **Annex 16A–D**. There we see the *target* or calculated value as a % of commercial basal area during each harvest, and the *actual* or observed value during the first harvest derived from inventory data. For example, for *Cedrela* in AFICC 2005 (**Annex 16A**), the target cutting intensity was 51% of commercial basal area while the actual cutting intensity was 76%. The model calculates a target cutting intensity for *Cedrela* during the second harvest in AFICC 2005 of 11% (**Table 32**). Note that we are currently repeating this analysis due to problems with source data coding from four concessions identified during review of the first draft of this report; actual calculated CI figures in this section are therefore likely to change, although we do not anticipate the overall picture being significantly different.

Target first-harvest cutting intensities for *Cedrela* averaged 47% and 54% of commercial basal area in 2005/2006 POAFs, respectively; actual cutting intensities averaged 67% and 57%, or an average adjusted increase of 43% and 6% in respective years (**Table 33**). The actual cutting intensity exceeded the target cutting intensity in 16 of 20 POAFs where *Cedrela* was harvested during these two years; actual cutting intensity appears to have exceeded 80% in 3 of 20 POAFs. The model calculated average target cutting intensities much lower during second harvests than during first harvests, averaging 13% and 36% in 2005/2006 POAFs, respectively.

Target first-harvest cutting intensities for *Lonchocarpus* averaged 65% and 73% of commercial basal area in 2005/2006 POAFs, respectively; actual cutting intensities averaged 76% and 83%, or an average adjusted increase of 17% and 14% in respective years (**Table 33**). The actual cutting intensity exceeded the target cutting intensity in 16 of 21 POAFs where *Lonchocarpus* was harvested during these two years; actual cutting intensity appears to have exceeded 80% in 15 of 21 POAFs. Expected average target cutting intensities during second harvests were lower than during first harvests, averaging 44% and 53% in 2005/2006 POAFs, respectively.

Target first-harvest cutting intensities for *Bucida* averaged 53% and 56% of commercial basal area in 2005/2006 POAFs, respectively; actual cutting intensities averaged 80% and 78%, or an average adjusted increase of 53% and 39% in respective years (**Table 33**). The actual cutting intensity exceeded the target cutting intensity in 13 of 15 POAFs where *Bucida* was harvested during these two years; actual cutting intensity appears to have exceeded 80% in 11 of 15 POAFs. Expected average target cutting intensities during second harvests were lower than during first harvests in 2005 POAFs (48%) but higher in 2006 POAFs (63%).

Target first-harvest cutting intensities for *Calophyllum* averaged 70% and 62% of commercial basal area in 2005/2006 POAFs, respectively; actual cutting intensities averaged 82% and 86%, or an average adjusted increase of 17% and 39% in respective years (**Table 33**). The actual cutting intensity exceeded the target cutting intensity in 17 of 19 POAFs where *Calophyllum* was harvested during these two years; actual cutting intensity appears to have exceeded 80%)in 16 of 19 POAFs. Expected average target cutting intensities during second harvests were identical to first harvests.

Target first-harvest cutting intensities for *Lonchocarpus* and *Calophyllum* were high compared to *Swietenia* and *Cedrela*, while *Bucida* was intermediate between the two categories. This is because sub-commercial densities of *Lonchocarpus* and *Calophyllum* tend to be higher relative to commercial densities, to no small degree because these are medium-statured species compared to *Swietenia* and *Cedrela* (again, with *Bucida* being intermediate between the two categories). If sub-commercial size classes are abundant compared to commercial size classes, calculated cutting intensities will also be high.

6 DISCUSSION

In this report we address the question: are current forest management practices in the MBR sustainable? We assume that 'sustainable' means 'sustained timber yield over multiple harvests' by the five timber species that currently generate the majority of income from forest concessions in this region. We apply the best available empirical knowledge to this question through use of life history-based models to simulate population dynamics of both observed and estimated species' population structures in 2005 and 2006 POAFs in 11 concessions representing most of the production forests of the Multiple Use Zone of the Maya Biosphere REserve. Overall, simulation outcomes indicate that management practices are well matched to species' population structures and dynamics. Below we discuss in more detail the nuances and implications of these findings, issues to consider for future forest management in the MBR, and certain limits of the modeling approach.

6.1 *Swietenia*

This report emphasizes outcomes for *Swietenia* because this species generates the lion's share of revenue from MUZ forests compared to all other timber species combined, as *Swietenia* does wherever it occurs. To no small degree, the future of natural forest management on this landscape depends on the sustainability or not of mahogany harvests.

Simulation outcomes for *Swietenia* populations in MUZ POAFs using the R model and the simpler lesser-known species model were in close agreement over the course of a single cutting cycle and two harvests. While simulations indicate a range of future-harvest outcomes both positive and negative, in most cases current forest management practices appear sustainable over the long term. This is a truly remarkable result considering the history of mahogany's exploitation across its vast Central and South American range, throughout which it has largely been treated as a non-renewable resource best suited for small-scale and industrial mining until populations reach a point approaching commercial extinction.

The positive outcomes in the MBR derive from two main sources: extremely favorable population densities and structures across much of the MUZ landscape, as detailed in **sections 4.1.1** and **4.1.2**, and a method for calculating cutting intensity that is based on biological reality rather than on short-term financial exigency. With exceptions as noted, *Swietenia* population structures in this region are generally weighted towards sub-commercial and juvenile (< 30 cm diameter) size classes, meaning that future commercial populations are already in place in the forest at the time of first harvest. Basing allowable cutting intensities on expected growth and recruitment by inventoried populations of sub-commercial trees is both intuitively obvious and exceptionally rare in the world of tropical forest management.

To understand just how remarkable the Guatemalan forest management scenario for *Swietenia* is, let us briefly consider how things work in Brazil, where the vast majority of natural forest mahogany populations originally occurred (Grogan et al. 2010). There, forest management parameters include: an MDCL of 60 cm, the same as most concessions in the MUZ; a minimum retention rate of 20% of commercial-sized trees; a landscape-scale minimum retention density of 5 commercial-sized trees per 100 ha; and cutting cycles of 25–30 years. Under these rules, *Swietenia* populations in Brazil cannot recover initial densities during cutting cycles between harvests, and timber production during future harvests falls precipitously (**Fig. 7**; Grogan et al. 2014). Indeed, when Brazilian mahogany populations are logged repeatedly at 80% intensity, only the minimum retention density rule of 5 commercial-sized trees per 100 ha prevents their complete commercial extirpation. Part of the problem for Brazilian populations is that population structures tend to be weighted more towards commercial size classes than MUZ populations, meaning that recruitment to commercial size by sub-commercial trees is relatively slow because there are fewer individuals available to replace harvested trees. But the main source of these outcomes is a one-size-fits-all-populations rule for cutting intensity that bears no relation to biological reality.

This study's transect data for *Swietenia* seedlings, saplings, and poles provides abundant support for future harvest scenarios. Transect data from harvested 2005/2006 POAFs present, on average, higher densities of juvenile stems than from 'undisturbed' or 'natural' 2015 POAFs. This means that most regeneration encountered in logged POAFs dates to the harvest event or earlier because removing commercial trees reduces the availability of seeds in subsequent years. The higher comparative densities in logged forest disappear in larger size classes (pole-sized stems > 10 cm diameter and larger) because these individuals originated before harvests in 2005 and 2006. This means that, first, logging apparently encourages higher densities of mahogany regeneration because the disturbance, which opens canopy gaps and ground-level growing space, encourages seedling establishment and early growth; and second, these higher seedling and sapling densities are available for application of silvicultural practices intended to accelerate growth rates should the forest industry and forest communities choose to invest in these practices.

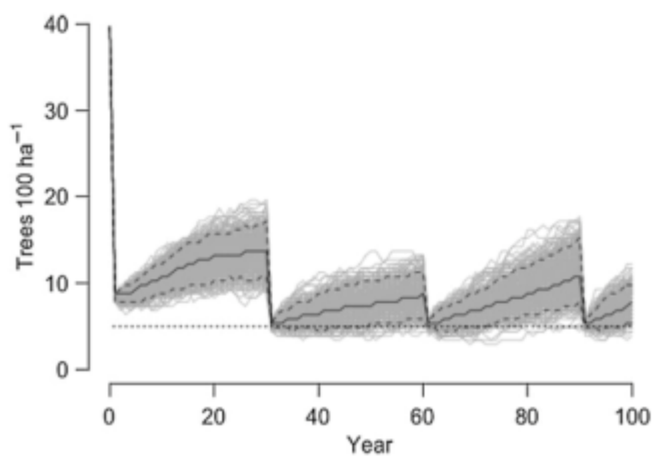


Fig. 7. Swietenia *simulated population recovery after harvests during 30-year cutting cycles in Brazil under current legal forest management parameters. See legend for full explanation. From Grogan et al. 2014, Fig. 4.*

Fig. 4. Simulations of mahogany population dynamics in south-east Pará, Brazil under current legal harvest regulations: 60 cm ninimum diameter cutting limit (MDCL), minimum 20% com-nercial-sized tree retention rate, 5 trees 100 ha^{-1} minimum post-arvest commercial population density, and (25- to) 30-year cut-ng cycles. There were 39·7 commercial-sized trees 100 ha^{-1} in ear 0. Grey lines indicate 500 replicate runs, the solid black line ndicates the median value, black dashed lines indicate 5th and 5th percentiles, and the horizontal dotted line indicates the mini-num post-harvest commercial density. Median recovered popula-ion densities in years 30, 60 and 90 before successive harvests ere 13·7, 8·8 and 11·3 trees 100 ha^{-1}.

6.2 *Cedrela* + three lesser-known timber species

Simulation outcomes for *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* were highly variable, and generally positive in terms of commercial density recovery during the first cutting cycle, but less optimistic with regards to timber production at the time of second harvest (explanation for this difference is discussed more in **section 6.3**). All four of these species occur at lower commercial densities than *Swietenia*, especially *Cedrela.* Also, all four species, especially *Bucida*, are more spatially patchy at the landscape scale, possibly related to more specialized habitat or site requirements for seedling establishment, growth, and recruitment. Combined with their lower economic value, these issues make it challenging for forest managers to adequately quantify their population structures and the vital demographic rates (annual growth, mortality, seed production, etc.) which will ultimately determine future harvest outcomes.

The 5-year Plan inventory data proved markedly inadequate for use in simulating population responses to harvests: most populations with only 5-year plan data available for sub-commercial trees demonstrated explosive commercial density recovery during a single cutting cycle, suggesting that these data, while perhaps applicable in some cases, are broadly inadequate for simulation purposes. 100%-area inventories for sub-commercial and commercial trees have been proven again and again to be cost-effective in tropical forest management.

6.3 Implications for current management practices in the MBR MUZ

6.3.1 Cutting intensity

The rate of recovery by commercial timber species following one or more harvests depends a great deal on cutting intensities and the assumptions that underpin them. Under Guatemalan regulations, cutting intensities in MUZ concessions for all five species considered here ostensibly depend on recruitment rates by sub-commercial trees into commercial size classes, and this remarkably rigorous practice should guarantee sustained timber yields over multiple harvests. However, two issues must be resolved for harvest rates to be in equilibrium with species' population dynamics. First, the formula for calculating cutting intensity should represent growth and mortality rates by sub-commercial trees of each species as accurately as possible. And second, assuming that cutting intensity calculations approximate reality reasonably well, forest managers and CONAP must limit harvests to levels that can be recovered during successive cutting cycles – that is, *actual* cutting intensities should equal *targeted* values calculated based on the formula.

Cutting intensity for all five species is currently calculated assuming the same median diameter growth rate (0.4 cm $year^{-1}$) for trees of all sizes in each POAF. Whether the current formula is the best solution to a very complex problem is an open question. For a given species, diameter growth rates may vary markedly as a function of stem size (diameter), recent growth history, degree of crown vine coverage, crown status, and recent fruiting history, to name just a few variables (Grogan & Landis 2009). Further, it is clear that populations of a given species may vary in diameter growth rates at local and regional scales. Also, the formula does not account for mortality that inevitably slows recruitment by sub-commercial trees over decadal timeframes.

The *Swietenia* model used in this study grows sub-commercial trees at a median rate of 0.66 cm $year^{-1}$, slightly faster than pooled data from MUZ permanent plots which yield a median rate of 0.60 cm $year^{-1}$ (**Fig. 5**). If trees on average grow faster than the cutting intensity formula

(0.4 cm $year^{-1}$) assumes – in mahogany's case, roughly 50% faster – then recruitment into commercial size classes should occur at higher rates than the formula currently calculates, and the current method likely underestimates sustainable harvest rates. On the other hand, two factors may lead CONAP and concessionaires to overestimate their sustainable yields: first, the cutting intensity formula does not account for mortality; and second, in most 2005/2006 POAFs at least, actual harvest rates exceeded target harvest rates, in many cases by large margins. (Note that both the *Swietenia* and lesser-known species models account for mortality.)

In the modeling results, most *Swietenia* POAF populations demonstrated stable or growing commercial densities at the time of second harvests, but depressed second-harvest volume production. This was because median growth rates by sub-commercial trees exceeded the 0.4 cm $year^{-1}$ assumed by the cutting intensity formula, while actual cutting intensities during observed first harvests exceeded target cutting intensities, in some cases by a factor of two or more (**Tables 16 & 18**). By exceeding target cutting intensities in 2005 and 2006, forest managers established artificially high initial volume production levels with implications for the definition of 'sustained yield'. That simulated population densities and volume production recovered during third and fourth harvests in most POAFs is due at least partially to the fact that the model restricted those harvest levels to the calculated target cutting intensities, with no adjustments allowed.

Similarly for the other four species, differences between observed median growth rates and the assumed median growth rate of 0.4 cm $year^{-1}$ by sub-commercial trees may impact population and timber production recovery. For *Cedrela*, our assumption that median growth rates are equivalent to *Swietenia* introduces significant uncertainty into results reported here (**Fig. 6**). Observed growth rates by *Lonchocarpus* within the MUZ monitoring parcels conform almost exactly to the assumed median growth rate. Observed growth rates by *Bucida,* however, are less than 0.4 cm $year^{-1}$, meaning the cutting intensity formula likely overestimates sustainable harvests by overestimating recruitment rates between harvests. Like *Swietenia*, observed median growth rates by sub-commercial *Calophyllum* trees exceed the assumed rate.

Why do population densities of the four lesser-known species recover or even increase, as reported above, while timber production during second harvests by the same populations declines? The primary reason for these outcomes is that adjusted cutting intensities permitted by CONAP exceeded calculated target cutting intensities in most POAFs for all four species during 2005 and 2006. Harvesting a higher proportion of commercial basal area than the pool of sub-commercial trees can be expected to replace establishes an artificially high initial timber production level that future commercial trees cannot maintain, guaranteeing a decline in second-harvest production. On the other hand, exceeding the target cutting intensity has little impact on the rate of population recovery besides depressing densities of commercial size classes at the time of harvest. As well, first harvests typically enjoy a 'nature's bonus' meaning that commercial-sized trees are larger, on average, at the time of harvest than the pool of trees in the second harvest which will be dominated by recruits that reach commercial size during the intervening cutting cycle.

6.3.2 Minimum diameter cutting limit (MDCL)

CONAP permits forest managers in MBR concessions flexibility in determining MDCL for each timber species, which can change from year to year (**Table 7**). This is an unusual and laudable arrangement compared to standard practice across the tropics, where 'one-size-fits-all' rules more typically determine MDCL for broad classes of timber. For canopy-emergent species like *Swietenia* and *Cedrela* that have significant proportions of sapwood until they reach larger size, an MDCL of 60 cm (occasionally 55 cm) balances the imperative to maximize productivity versus the diminishing proportion of heartwood from smaller trees. Smaller MDCL for the other three lesser-known species is warranted because these do not typically grow as large, with fewer trees > 60 cm diameter relative to those smaller than this size. Trees as small as 45 cm of all three species presumably yield reasonable quantities of commercial heartwood.

How low can or should MDCL go? For *Swietenia*, lowering MDCL below 60 cm diameter introduces a trade-off in reproductive capacity: trees smaller than this size have not yet attained adult reproductive stature, that is, seed production by trees smaller than this size is low, on average, compared to larger adults (Gullison et al. 1996, Snook et al. 2005, Grogan & Galvão 2006a). Since natural forest management relies for future harvests on natural regeneration, reducing reproductive capacity can lead to reduced recruitment by juvenile trees to commercial size, diminishing future harvests.

6.3.3 Cutting cycle

Allowing populations longer recovery times between harvests leads to higher commercial density and timber production rates over an equivalent number of cutting cycles. For *Swietenia*, 40-year cutting cycles yielded higher rates of commercial density recovery over the course of three cutting cycles than 30- or 25-year cutting cycles. However, we did not test here whether total production differs depending on cutting cycle length over equivalent timeframes: for example, whether production from three 40-year cutting cycles will be similar to production from four 30-year cutting cycles from a given concession. This is a question that the R model for *Swietenia* could usefully address in a future analysis.

An important issue for concession owners in the MUZ is the disconnect between concession contract periods and the explicit expectation that forest management practices be sustainable. Current contracts run for 25 years and the power to renew them lies with CONAP; the Guatemalan congress also has the power to revoke concessions at any time. Thus concessionaires have no certainly as to whether they will manage the forest beyond a single cutting cycle. This places a burden of 'best behavior' on concession managers who have no guarantee that they will reap the future benefits of today's management practices, and reduces incentives to invest in silvicultural interventions that could increase population density and/or promote tree growth and seed dispersal.

6.3.4 Regeneration

The transect surveys installed during May–June 2014 generated empirical data for seedlings, saplings, and pole-sized trees that was crucial for modeling *Swietenia*'s population response to repeated harvests (**Tables 11–14**, **24–27**).

For *Swietenia* in particular, seedling, sapling and pole densities were relatively high in many POAFs, and rarely absent altogether. Generally higher seedling and sapling densities in harvested 2005/2006 POAFs compared to unharvested 2015 POAFs indicates that forest canopy disturbance associated with logging may assist post-harvest establishment and growth. Both *Bucida* and *Calophyllum* apparently experience similar post-harvest boosts in seedling and sapling densities. However, we cannot say to what degree elevated seedling and sapling densities can be attributed to disturbance associated with logging, nor whether more intensive harvests would further stimulate seedling establishment and survival. Harvest intensities in the MUZ are currently relatively low, generally < 3 m^3 ha^{-1}. At this landscape-scale intensity, post-harvest impacts on *Swietenia* seedling densities will be mainly attributable to the felling and extraction of mahogany trees, not to the removal of other species that may or may not occur nearby.

High densities of natural regeneration do not guarantee that future timber harvests will equal or exceed today's. Seedlings established in the forest understory and in natural and logging gaps will survive and grow at rates reflecting their ability to tolerate and exploit growing conditions that change constantly through time; nearly 100% will die without assistance. In *Swietenia*'s case, seedlings and saplings will tend to occur in patches at small local scales, perhaps tracinga single tree's seed shadow during a harvest year when a gap opened for colonization. To promote higher regeneration rates, these patches could be located and maintained open to encourage extended growth by mahogany seedlings, much as enrichment gaps must be kept open for years after outplanting seedlings. On the other hand, enrichment plantings guarantee establishment of healthy nursery-grown seedlings (unless seeds are broadcast-sown) at known locations which can be easily re-located for tending during the decade or decades after harvests. There are significant costs and benefits associated with both management strategies.

6.3.5 Assessing population structures for production potential

Examining population structures by stem size classes, from seedlings to commercial-sized adult trees, provides an empirical basis for evaluating the potential timber yield of a given species over multiple cutting cycles. The proportion of stems in sub-commercial compared to commercial size classes determines the intensity at which commercial trees can be exploited during the first harvest; second and third harvest rates will be determined by successively smaller size classes down to today's seedlings and saplings in forest gaps and the forest understory. This logic allows us to interpret patterns in POAF-level density recovery and timber production by *Swietenia* populations over multiple cutting cycles (**Annex 8**). Without a reasonable understanding of complete population structure within a given area, our understanding of the future consequences of today's management decisions remains quite limited. For example, the fieldwork conducted for this study was necessary because data collected by concessionaires – whether for POAFs, 5-year Plans or Management Plans – does not include sampling of individuals < 30 cm diameter. The 0.1%-area sample for seedlings and saplings may not have captured a fully accurate picture of early regeneration; results showing very high or low densities in certain POAFs may also reflect artifacts of transect locations or field conditions during a particular day of fieldwork.

At present, we cannot distill this analysis to a simple formula or fixed numerical ratios for any species, including *Swietenia,* in order to provide a quantitative indicator of 'healthy' population structure. This is a topic ripe for further inquiry and development; the large pool of high-quality data from this study offers an excellent place to start.

6.3.6 Spatial distribution of species populations on the MUZ landscape

Results from this study are 'spatially blind', meaning that population densities are considered constant on a per unit area basis. In reality, species populations commonly demonstrate patterns in their spatial distributions, often related to physiographic features such as topography and or soil type. Concession forest managers are generally knowledgeable about such patterns on a species-by-species basis, and during an initial validation workshop they asked whether we had considered these patterns in our analysis. While beyond the scope of our immediate objective, commercial census data from MUZ concessions includes spatial locations of all inventoried trees, offering a potentially rich resource for inquiry into production implications of species' distribution patterns.

A second spatial issue concerns the role that protected areas play in the conservation of species' ecological and genetic integrity during the coming years. Protected areas may include buffer zones adjacent to archaeological features (un-excavated Mayan mounds are common on this landscape), seasonal or aseasonal streams, areas where topographic relief is too steep or too swampy to move heavy equipment across, or areas where harvest operations would create excessive erosion. Protected areas accounted for 0–46% of individual POAF areas considered here, representing 13% and 14% of summed POAF areas in 2005 and 2006, respectively. The degree to which these non-loggable areas provide refuge for species populations will depend on many factors, including: the shape, extent, and connectedness of protected areas within a given POAF; whether a species demonstrates positive or negative affinity to a given type of protected area (streamside, steep slope, etc.); and the degree to which harvest operations honor the spatial integrity of designated protected areas during first and repeated harvests.

6.4 Caveats associated with modeling population dynamics

Results from model simulations reported here represent predicted future outcomes of current forest management practices in the MUZ, based on the most up-to-date knowledge, data, and assumptions available regarding *Swietenia* and four associated timber species. Because we cannot say with certainty what will happen in the future, it is important that we view these results with caution for several reasons.

1) *The modeling approach*: Models perform only as well as their data-based algorithms describe reality. In fact, forest ecosystems, including the hundreds of tree species that form the super-structure of tropical forests, are so complex that modeling exercises such as these require extreme simplification of reality. However, a great deal of empirical knowledge about *Swietenia* has accumulated in recent years from research in Mexico, Belize, Guatemala, Bolivia, and Brazil, and the R model used in this study provides the best available interpretation of our current understanding of mahogany life history. We are confident that the R model for *Swietenia* performs extremely well over two to four decades, a timeframe comparable to the temporal depth of the Brazilian data; uncertainty associated with model outcomes increases beyond this time horizon. In turn we attach higher uncertainty to the second modeling scenario, the lesser-known species model which is based solely on limited growth data and a fixed mortality rate.

2) *Source data for model algorithms*: Simulation outcomes for *Swietenia* population dynamics in the MUZ are based on growth, mortality, and reproductive rates from populations in Brazil. How confident are we that these crucial rates are transferable from Brazil to Guatemala? Data presented in **Table 6** and in **section 4.3.1** indicate that population-level growth and mortality rates are both highly variable and consistent in that variability from region to region and locality to locality where *Swietenia* occurs. Variability is the rule, not the exception, with local rates dependent on site factors and stochastic disturbance regimes too complex for any model to fully

describe. The mahogany growth function from Brazil almost perfectly matches growth data from MUZ concessions (**Fig. 5**); data from other sites in the Maya Rainforest and Central and South America indicate a range of growth rates encompassing those from MUZ permanent plots (**Table 6**).

It is also worth noting here the importance of consistent and highly precise growth measurements. The growth data obtained from permanent monitoring parcels showed a marked difference between the La Gloria parcel and plots in community concessions. Understanding whether this is an actual phenomenon or an artifact of data collection would be useful to adjusting CONAP's growth data assumptions.

3) *Model limitations*: Simulated Brazilian *Swietenia* populations increase gradually in density over time in the absence of logging, that is, the model is poorly constrained by observed static and dynamic rates (Grogan et al. 2014). We do not know whether this expansion is realistic, and if it is not, we cannot identify which rate(s) used by the model is responsible for population expansion. However, while this situation is problematic for populations in Brazil which occur at very low landscape-scale densities, these population growth rates may in fact be more realistic for Petén mahogany populations which occur at much higher densities.

4) *Stochastic factors*: Unforeseen forces may impact these predicted future outcomes, including hurricanes, fires, changes in markets or land use, political or economic instability, or social change in the coming years and decades. Hurricane Richard, for example, which came far inland in 2010 and left swaths of extensive forest blowdown and associated damage on the eastern edge of the MUZ, appears to have negatively affected model projections for at least one concession. These natural and anthropogenic forces could be large enough to impose significant and unforeseen changes on the current status quo in the MUZ, both in terms of the forest and of the socio-economic structures driving natural resource management on this landscape.

7 CONCLUSIONS

Based on results presented here and bearing associated caveats in mind, forest management practices in the Maya Biosphere Reserve Multiple Use Zone represent state-of-the-art best-practices for species-level management in tropical forests. 100%-area inventories for commercial and sub-commercial trees, coupled with planned harvest operations that reduce damages to residual stems, are increasingly standard practice in species-rich forests across the tropics. But determining and actually implementing cutting intensities based on species biology represents a genuine advance towards sustained yield timber production that deserves recognition and replication in other regions. In the specific conclusions listed below we assign relative degrees of certainty to key outcomes in order to reflect the quality and quantity of data available for each analysis.

7.1 *Swietenia*

- With a high degree of certainty, *Swietenia* populations will recover pre-harvest commercial densities during the first cutting cycle between harvests, on average, and this outcome appears sustainable over repeated harvests under current forest management practices in the MUZ.

- Recovery of commercial volume production will lag behind tree density recovery during the first cutting cycle, leading to smaller second harvests, on average. Timber production should recover to initial harvest levels or higher during third and fourth harvests, assuming that cutting intensity calculations are applied without significant adjustments.

- Two interrelated current management parameters drive these outcomes: 1) the median growth rate (0.4 cm $year^{-1}$) assumed by CONAP for sub-commercial trees which, if too low, represents a constraint on harvest yields; and on the other hand 2) adjustments to target cutting intensities, in nearly all cases allowing higher yields than anticipated by observed distributions of commercial and sub-commercial trees. These adjustments establish artificially high first-harvest production levels that cannot be achieved during second harvests.

- Estimated densities of *Swietenia* pole-sized trees, saplings, and seedlings in nearly all POAFs are sufficiently high to anticipate population and timber production recovery during second and third cutting cycles. Logging appears to encourage seedling establishment and short-term post-harvest growth. Silvicultural treatments should target abundant advance regeneration to encourage survival, growth, and future timber yields.

7.2 *Cedrela*

- With a low degree of certainty, most *Cedrela* populations occurring at extremely low landscape-scale densities will recover pre-harvest commercial densities during the first cutting cycle, but volume production will be much lower during second harvests compared to first harvests.

• The low degree of certainty associated with *Cedrela* simulations can only be improved by acquiring empirical data describing size-related growth and mortality rates within the MBR. For example, little evidence exists supporting the use of 0.4 cm $year^{-1}$ as the median growth rate by sub-commercial trees to calculate cutting intensity.

• Predicted declines in volume production during second harvests are primarily due to adjustments to target cutting intensities which establish artificially high first-harvest production levels.

• Estimated landscape-scale densities of *Cedrela* pole-sized trees, saplings, and seedlings are very low overall and patchily distributed on the landscape, suggesting that repeated harvests may not be possible in many POAFs. To some degree this is related to the fact that the low-lying, relatively flat terrain characterizing most POAFs considered here is not *Cedrela*'s preferred habitat.

7.3 The lesser-known timber species *Lonchocarpus*, *Bucida*, and *Calophyllum*

• With an intermediate degree of certainty, most *Lonchocarpus*, *Bucida*, and *Calophyllum* populations will recover pre-harvest commercial densities during the first cutting cycle. Volume production will be lower, on average, during second harvests compared to first harvests, but the decline will not be as extreme as for *Cedrela*.

• Like *Swietenia* and *Cedrela*, predicted declines in volume production during second harvests are primarily due to adjustments to target cutting intensities which establish artificially high first-harvest production levels.

• Limited empirical evidence exists to support the use of 0.4 cm $year^{-1}$as the median growth rate by sub-commercial trees to calculate cutting intensity. Data from permanent plots in the MUZ indicate that this rate is approximately correct for *Lonchocarpus*, too high for *Bucida*, and too low for *Calophyllum*.

• Transect surveys indicate that pole-sized trees, saplings, and seedlings of *Lonchocarpus* and *Calophyllum* are consistently present in surveyed POAFs at relatively high densities, while *Bucida* occurs more patchily, similar to *Cedrela*. Silvicultural treatments should target abundant advance regeneration to encourage survival, growth, and future timber yields.

7.4 Current forest management practices in the MUZ

• The method for determining cutting intensity represents an important advance in natural forest management in the tropics, but should be improved both empirically and from a regulatory standpoint. Empirically, better understanding of diameter growth and mortality rates by sub-commercial size classes is required to refine the formula on a species-by-species basis. From a regulatory standpoint, less flexibility in granting exceptions (usually allowing higher actual vs. target harvest levels) will constrain harvests in 2015 and beyond to more sustainable levels.

- The data from permanent monitoring plots that has been collected until now is valuable but not sufficient to guide fully informed decision-making. Collection of species-level growth and mortality data from permanent monitoring plots should reflect the need for more accurate calculations of cutting intensity, and to consider adopting a calculation with size-class specific growth rates. Considerations are included in the Recommendations section below.

8 RECOMMENDATIONS

This study leads us to make the following recommendations for improving forest management practices in the MBR.

8.1 Improving data available for long-term forest management

1) **Improve knowledge of species' dynamic rates, especially size-dependent growth and mortality**. Better information about growth and mortality for all five species analyzed here would greatly improve understanding of management outcomes and how to calculate cutting intensity. Long-term studies of mortality and diameter growth rates by trees of all sizes are relatively inexpensive but require annual attention and consistent implementation.

Relevant questions include: Should units of observation (individual trees) be grouped by local or concession-wide populations? Are site differences for different populations of a given species (for example, soil type) sufficient to justify stratifying samples with the objective of creating multiple modeling platforms? What additional variables should be accounted for in dynamic rate studies (for example, patterns of seasonal and annual precipitation; crown canopy position and neighborhood density; crown vine coverage; patterns of fruit production)? How can data be shared and processed into useful mortality and growth algorithms for timber species in the MBR?

The existing long-term permanent monitoring plots in MBR concessions should be supplemented:

- More individuals of the target species should be monitored; for example, there were no *Cedrela* trees in the plots analyzed for this study.
- Measurements should continue to be done on an annual basis using standardized and rigorously controlled methodologies to ensure accuracy, with training for field personnel to address the many patterns and idiosyncrasies that live trees present in the field.
- The full range of size classes represented by a given species on the landscape, from seedling to large adult, should be included.
- Survival/mortality should be included as a standard annual observation.
- Quality control protocols should be incorporated to ensure that data quality matches the important role this data will play in determining sustainable harvest levels.

2) **Systematic sampling of juvenile stems (seedlings, saplings, poles) should be incorporated into annual management operations**. We cannot look further into the future than a single cutting cycle if we cannot quantify the size classes that will recruit to commercial size during third and fourth harvests, to consider the shortest long-term horizon.

The sampling effort in May–June 2014 that produced the data necessary for model simulations reported here was large (265 1-ha transects in 33 POAFs) and expensive, but only because POAFs across the entire MBR had to be surveyed in a short time using a new and seemingly elaborate field protocol. Incorporating transect surveys into standard operational protocols for 5-year plan or annual POAF preparation would make them less expensive – field crews could be smaller, transportation expenses would decline, logistics would be easier – and, over time, more efficient as sampling methods evolve. With the user-friendly NetLogo model available for simulating *Swietenia* population recovery following harvests under Guatemalan forest management parameters, data that quantifies juvenile densities could see immediate and profitable use by forest managers in the MBR.

3) **Improve knowledge of species' regeneration and recruitment requirements**. *Swietenia* regeneration ecology is fairly well understood: the R model used in this study incorporates empirical knowledge about seed production, dispersal, and germination, seedling establishment, and growth and mortality by seedlings, saplings, and poles. Similar knowledge about *Cedrela*, *Lonchocarpus*, *Bucida*, and *Calophyllum* must be acquired in order to be able to model population recovery beyond second harvests. Like studies of growth and mortality described above, regeneration studies could be relatively inexpensive, but they require consistent attention and implementation for results to be broadly applicable.

4) **Improve knowledge of the disturbance regime in the MBR multiple-use zone**. The *Swietenia* model used here assumed the creation of canopy gaps based on a combination of cutting intensity (that is, every felled tree produces a gap) and an algorithm from Brazilian data. It does not incorporate large-scale incidents such as storms or fires. Given the importance of light availability for *Swietenia* recruitment and growth, incorporating a more site-specific understanding of the disturbance regime into future modeling efforts would improve its accuracy. Another useful analysis would be to look at whether logging of lesser-known species in the POAF contributes significantly to opening more gaps that promote mahogany recruitment.

5) **Aggregate and harmonize as much census information as possible**. CONAP should follow up its work with concessions to standardize tree codes applied during commercial census and 5-year plans, to ensure databases that are uniform, comparable, combinable, and thus usable for analysis afterwards.

8.2 Improving forest management practices in the MBR

1) **Implement target cutting intensities more consistently**. Not unexpectedly, simulations indicate that harvests at higher cutting intensities than target rates lead to reduced commercial volumes during second harvests. CONAP's current practice of consistently approving extraction of extra volume from the non-recoverable basal area is likely to produce population declines over time. Adjustments should be approved with caution if at all, and be attached to requirements for silvicultural treatment that will accelerate the recuperation of basal area.

2) **Emphasize silvicultural practices designed to reduce mortality and increase growth rates by commercial, future crop, and juvenile trees**. As an example, pre- and post-harvest vine cutting to free crowns of commercial species is the single most effective way to reduce mortality and accelerate long-term diameter growth rates. For light demanding species, canopy 'release' over concentrated patches of regeneration could encourage growth and recruitment at reasonable expense; consistent attention to growing conditions during the first 10 years after seedling establishment may be sufficient to gain canopy passage for juvenile stems.

In contrast to *Swietenia*, *Cedrela* is simply rare and *Lonchocarpus,* while demonstrating high seedling density, appears to have limited ability to persist and grow through successive size classes. *Bucida* and *Calophyllum* appear to be the most likely to persist and grow once established, presenting more options for silvicultural practices aimed at reducing mortality and accelerating growth rates.

3) **Incorporate use of a tailored NetLogo model into management decision-making**. A variety of adjustments to the original NetLogo model were made by the team during the analytical phase of this study, including incorporation of the cutting intensity calculation used in the MBR and a modality that allows for simulations applying hypothetical cutting intensities to real POAF data. Further possible adjustments were suggested during the presentation of preliminary results, such as the use of basal area rather than tree density in result outputs. Additional improvements to further automate data preparation prior to input would likely also be necessary in order for less expert users to apply the tool without errors. Completely tailoring the NetLogo model to Petén is impossible at this time given the lack of information about necessary dynamic population parameters as described above; however, use of the model with the adjustments mentioned here would allow CONAP, regents, and concession managers to make more informed decisions regarding MDCL, cutting cycles, and particularly cutting intensity.

4) **Ensure that incentives for long-term management are in place by establishing concession contracts over multiple harvest cycles**. This study has demonstrated the strong influence of present-day decisions on the future forest. Higher cutting intensities during the first harvest have consequences. However, concessionaires currently lack strong incentives to collect additional long-term data, or to not request additional cutting intensity above recoverable base area, because there is no legal surety that their concession contracts will be extended beyond the first harvest. A legal model harmonized with long-term incentives would need to give concessionaires legal guarantee through multiple harvest cycles.

8.3 Improving forest management beyond the MBR

Disseminate the results of this study in a variety of venues. As we have mentioned above, the ecologically intuitive cutting intensity calculation is something rarely witnessed in tropical forest management. We are comfortable stating that the model of forest management in Petén is an example that should be recognized and replicated. Publications in Spanish, English, and French describing the practices used in the MBR and the results of this analysis should be disseminated in scientific, technical and public forums. Not least, the CITES Secretariat, Plants Committee, and Parties should be provided with this information and its relevance to making non-detriment findings for *Swietenia* and *Cedrela* populations.

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10 LIST OF ANNEXES

The companion document 'REPORT_Annexes.pdf' can be navigated by Annex number in Adobe Reader by activating the thumbnails feature in the upper left-hand corner of the opening page.

Annex 1. Inventory data for *Swietenia*

Inventory data from 2005/2006 POAFs for *Swietenia* trees > 30 cm diameter presented as number of trees by 5-cm diameter class per 100 ha (see **Table 10**). Note that y-axes are variable, ranging from 20–70 per 100 ha maxima. The first unlabeled bar on the x-axis shows trees 30–35 cm diameter; the '40' bar shows trees 35–40 cm diameter, etc. Light gray bars indicate harvested trees.

Annex 2. Transect data for *Swietenia*: seedlings & saplings

Transect data from 2005/2006 POAFs for *Swietenia* seedlings (*brinzales* < 150 cm height) and saplings (*latizales bajos* > 150 cm height < 5 cm diameter) presented as number of stems by 1-cm diameter class per 100 ha, from 0.1-ha transects (see **Table 13**). Note that y-axes are variable, ranging from 500–14000 per 100 ha maxima. '1' on the x-axis shows seedlings 0–1 cm diameter, that is, seedling heights have been converted to diameters. '2' combines seedlings with saplings in some cases; size classes 3–5 are all saplings.

Annex 3. Transect data for *Swietenia*: poles

Transect data from 2005/2006 POAFs for *Swietenia* small poles (*latizales altos* 5–10 cm diameter) and poles (*fustales* 10–30 cm diameter) presented as number of stems by 5-cm diameter class per 100 ha, from 1-ha transects (see **Table 14**). Note that y-axes are variable, ranging from 20–300 per 100 ha maxima. '5' on the x-axis shows small poles 5–10 cm diameter, '10' shows poles 10–15 cm diameter, etc.

Annex 4. Population structures for modeling: *Swietenia*

Size class frequency distributions from 2005/2006 POAFs for *Swietenia* > 2.5 cm diameter by 5-cm diameter class per 100 ha, combining data from inventories (**Annex 1**) and transects (**Annexes 2 & 3**). Note that y-axes are variable, ranging from 20–2000 per 100 ha maxima. The first unlabeled bar on the x-axis shows trees 2.5–5 cm diameter; the '10' bar shows trees 5–10 cm diameter, etc. Light gray bars indicate trees harvested in 2005 and 2006.

Annex 5. Simulation outcomes: *Swietenia* commercial densities during three cutting cycles

Model outputs showing population recovery in 2005/2006 POAFs by commercial *Swietenia* trees (number per 100 ha) during simulations lasting three cutting cycles plus 10 years (see **Table 15**). Four harvests resulting in sharp population declines occur at intervals (years) corresponding to the cutting cycle indicated on the x-axis. The solid black line indicates the median density value of 100 simulations; dotted lines indicate 5% and 95% values; gray lines indicate values for individual simulations. DMC = minimum diameter cutting limit.

Annex 6. Simulation outcomes: *Swietenia* commercial volumes from four harvests

Model outputs showing roundwood production (volume in m^3) per 100 ha by commercial *Swietenia* trees from four harvests in 2005/2006 POAFs during simulations lasting three cutting cycles plus 10 years (see **Table 17**). Four harvests occur at intervals (years) corresponding to the cutting cycle indicated on the x-axis. The horizontal line in year 0 shows the observed harvest volume during the initial harvest. Box plots for subsequent harvests show median values (heavy black line), the interquartile range or 25^{th} to 75^{th} percentile values (IQR; box), 1.5 times the IQR (whiskers), and extreme values (open circles).

Annex 7. Simulation outcomes: *Swietenia* cutting intensities during four harvests

Model outputs showing cutting intensities (proportion of basal area as defined in the text; 0.6 on the y-axis = 60%) of commercial *Swietenia* trees during four harvests in 2005/2006 POAFs (see **Table 19**). Four harvests occur at intervals (years) corresponding to the cutting cycle indicated on the x-axis. In the first harvest at time 0, the black line indicates the target cutting intensity as determined by the assumed median growth rate for all stems (0.4 cm $year^{-1}$) and sub-commercial population density; the red line represents the actual cutting intensity. Box plots for subsequent harvests show median target values (heavy black line), the interquartile range or 25^{th} to 75^{th} percentile target values (IQR; box), 1.5 times the IQR (whiskers), and extreme target values (open circles).

Annex 8. Data synthesis pages for *Swietenia* populations in 2005/2006 POAFs

Model outputs for *Swietenia* in 2005/2006 POAFs; all density measures in number of stems per 100 ha. **(A)** Stem densities in 1-cm diameter size classes from 0.1-ha transect surveys for seedlings and saplings < 5 cm diameter. On the x-axis, '1' = stems 0–1 diameter, etc.; '1' stems are seedlings (brinzales) with height < 1.5 m. **(B)** Stem densities in 5-cm diameter size classes from 1-ha transect surveys for poles 5–30 cm diameter. On the x-axis, '10' = stems 5–10 cm diameter, '20' = stems 15–20 cm diameter, etc. **(C)** Stem densities in 5-cm diameter size classes from 100%-area POAF inventories for stems > 30 cm diameter. Light gray bars indicate harvested trees; x-axis as in B. **(D)** Initial population structures for model simulations combining A+B+C; minimum diameter included is 2.5 cm as explained in the text. Light gray bars as in C; x-axis as in B & C. **(E)** Commercial density over three cutting cycles plus 10 years, with sharp declines at intervals representing four harvests. Gray lines indicate 100 replicate runs, the solid black line indicates the median value, black dashed lines indicate 5^{th} & 95^{th} percentile values. **(F)** Estimated harvest volumes over three cutting cycles. Box plots show median values (heavy black line), the interquartile range of values (IQR; box), 1.5 times the IQR (whiskers), and extreme values (open circles). **(G)** Target cutting intensity for four harvests over three cutting cycles. In the first harvest at time 0, the black line indicates the target cutting intensity as determined by the assumed median growth rate for all stems (0.4 cm $year^{-1}$) and sub-commercial population density; the red line represents the actual cutting intensity. Box plots as in F. **(H)**

Density of trees per 100 ha in 5-cm diameter size classes anticipated during the final harvest. Light gray bars indicate harvested trees.

Annex 9. **Simulation outcomes: *Swietenia* commercial density recovery during one cutting cycle using the lesser-known species model**
Model outputs showing population recovery in 2005/2006 POAFs by commercial *Swietenia* trees (number per 100 ha) during simulations lasting one cutting cycle. Harvests occur at the beginning and end of the cutting cycle. The solid black line indicates the median density value of 100 simulations; gray lines indicate values for individual simulations.

Annex 10A–D. Inventory data for *Cedrela* + three secondary timber species

Inventory data from 2005/2006 POAFs for *Cedrela* (10A), *Lonchocarpus* (10B), *Bucida* (10C), and *Calophyllum* (10D) trees > 30 cm diameter presented as number of trees by 5-cm diameter class per 100 ha (see **Table 23**). Note that y-axes are variable. The first unlabeled bar on the x-axis shows trees 30–35 cm diameter; the '40' bar shows trees 35–40 cm diameter, etc. Light gray bars indicate harvested trees.

Annex 11A–D. Transect data for *Cedrela* + three secondary timber species: seedlings & saplings

Transect data in 2005/2006 POAFs for *Cedrela* (11A), *Lonchocarpus* (11B), *Bucida* (11C), and *Calophyllum* (11D) seedlings (*brinzales* < 150 cm height) and saplings (*latizales bajos* > 150 cm height < 5 cm diameter) presented as number of stems by 1-cm diameter class per 100 ha, from 0.1-ha transects (see **Table 26**). Note that y-axes are variable. '1' on the x-axis shows seedlings 0–1 cm diameter, that is, seedling heights have been converted to diameters. '2' combines seedlings with saplings in some cases; size classes 3–5 are all saplings.

Annex 12A–D. Transect data for *Cedrela* + three secondary timber species: poles

Transect data from 2005/2006 POAFs for *Cedrela* (12A), *Lonchocarpus* (12B), *Bucida* (12C), and *Calophyllum* (12D) small poles (*latizales altos* 5–10 cm diameter) and poles (*fustales* 10–30 cm diameter) presented as number of stems by 5-cm diameter class per 100 ha, from 1-ha transects (see **Table 27**). Note that y-axes are variable. '5' on the x-axis shows small poles 5–10 cm diameter, '10' shows poles 10–15 cm diameter, etc.

Annex 13A–D. Population structures for modeling: *Cedrela* + three secondary timber species

Size class frequency distributions from 2005/2006 POAFs for *Cedrela* (13A), *Lonchocarpus* (13B), *Bucida* (13C), and *Calophyllum* (13D) > 2.5 cm diameter by 5-cm diameter class per 100 ha, combining data from inventories (**Annex 10**) and transects (**Annexes 11 & 12**). Note that y-axes are variable. The first unlabeled bar on the x-axis shows trees 2.5–5 cm diameter; the '10' bar shows trees 5–10 cm diameter, etc. Light gray bars indicate trees harvested in 2005 and 2006. Blank panels indicate POAFs where 5-year plan data was unavailable to derive missing sub-commercial trees, or because populations occurred at densities too low for harvests.

Annex 14A–D. Simulation outcomes: *Cedrela* + three secondary timber species commercial densities during one cutting cycle

Model outputs showing population recovery in 2005/2006 POAFs by commercial *Cedrela* (14A), *Lonchocarpus* (14B), *Bucida* (14C), and *Calophyllum* (14D) trees (number per 100 ha) during simulations lasting one cutting cycle (**Table 28**). Harvests occur at the beginning and end of the cutting cycle. The solid black line indicates the median density value of 100 simulations; gray lines indicate values for individual simulations. Blank panels indicate POAFs where 5-year plan data was unavailable to derive missing sub-commercial trees, or because populations occurred at densities too low for harvests.

Annex 15A–D. Simulation outcomes: *Cedrela* + three secondary timber species commercial volumes from two harvests

Model outputs showing roundwood production (volume in m^3) per 100 ha by commercial *Cedrela* (15A), *Lonchocarpus* (15B), *Bucida* (15C), and *Calophyllum* (15D) trees from one observed and one simulated harvest in 2005/2006 POAFs (**Table 30**). Year marks on the x-axis indicate the cutting cycle length. The horizontal line in year 0 shows the observed harvest volume during the initial harvest. Box plots for the second harvests show median values (heavy black line), the interquartile range or 25^{th} to 75^{th} percentile values (IQR; box), 1.5 times the IQR (whiskers), and extreme values (open circles). Blank panels indicate POAFs where 5-year plan data was unavailable to derive missing sub-commercial trees, or because populations occurred at densities too low for harvests.

Annex 16A–D. Simulation outcomes: cutting intensities for *Cedrela* + three secondary timber species during two harvests

Model outputs showing cutting intensities (proportion of basal area as defined in the text; 0.6 on the y-axis = 60%) of commercial *Cedrela* (16A), *Lonchocarpus* (16B), *Bucida* (16C), and *Calophyllum* (16D) trees during two harvests in 2005/2006 POAFs (**Table 32**). Year marks on the x-axis indicate the cutting cycle length. The dotted line at 0.8 on the y-axis indicates the maximum allowable cutting intensity. In the first harvest at time 0, the black line indicates the target cutting intensity as determined by the assumed median growth rate for all stems (0.4 cm $year^{-1}$) and sub-commercial population density; the red line represents the actual cutting intensity. Box plots for subsequent harvests show median target values (heavy black line), the interquartile range or 25^{th} to 75^{th} percentile target values (IQR; box), 1.5 times the IQR (whiskers), and extreme target values (open circles). Blank panels indicate POAFs where 5-year plan data was unavailable to derive missing sub-commercial trees, or because populations occurred at densities too low for harvests.

Annex 17A–D. Data synthesis pages for *Cedrela* + three secondary timber species populations in 2005/2006 POAFs

Model outputs for *Cedrela* (17A), *Lonchocarpus* (17B), *Bucida* (17C), and *Calophyllum* (17D) in 2005/2006 POAFs; all density measures in number of stems per 100 ha. Blank panels indicate

POAFs where 5-year plan data was unavailable to derive missing sub-commercial trees, or because populations occurred at densities too low for harvests. **(A)** Stem densities in 1-cm diameter size classes from 0.1-ha transect surveys for seedlings and saplings < 5 cm diameter. On the x-axis, '1' = stems 0–1 diameter, etc.; '1' stems are seedlings (brinzales) with height < 1.5 m. **(B)** Stem densities in 5-cm diameter size classes from 1-ha transect surveys for poles 5–30 cm diameter. On the x-axis, '10' = stems 5–10 cm diameter, '20' = stems 15–20 cm diameter, etc. **(C)** Stem densities in 5-cm diameter size classes from 100%-area POAF inventories for stems > 30 cm diameter. Note that some frequency distributions are derived from 5-year plan data. Light gray bars indicate harvested trees; x-axis as in B. **(D)** Initial population structures for model simulations combining A+B+C; minimum diameter included is 2.5 cm. Light gray bars as in C; x-axis as in B & C. **(E)** Commercial density over one cutting cycle, with the sharp declines in year 0 showing the initial observed harvest. Gray lines indicate 100 replicate runs, the solid black line indicates the median value, black dashed lines indicate 5th & 95th percentile values. **(F)** Observed and estimated harvest volumes from the first and second harvests, respectively, in m^3 per 100 ha. The line in year 0 shows observed initial harvest volume; box plots for the second simulated harvest show median values (heavy black line), the interquartile range of values (IQR; box), 1.5 times the IQR (whiskers), and extreme values (open circles). **(G)** Cutting intensities during two harvests. The dotted line at 0.8 on the y-axis indicates the maximum allowable cutting intensity. In the first harvest at time 0, the black line indicates the target cutting intensity as determined by the assumed median growth rate for all stems (0.4 cm year^{-1}) and sub-commercial population density; the red line represents the actual cutting intensity. Box plots as in F.

11 TABLES

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12 ANNEXES

Separated due to file size. Please see separate document 'REPORT_Annexes'.