GROWTH OF BIG-LEAF MAHOGANY (*SWIETENIA MACROPHYLLA*) IN NATURAL FORESTS IN BELIZE

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SHONO, K. & SNOOK, L. K. 2006. **Growth of big-leaf mahogany (*Swietenia macrophylla*) in natural forests in Belize**. The annual diameter measurements (four years) of 75 big-leaf mahogany (*Swietenia macrophylla*) trees in natural forests in northwestern Belize were analysed to determine growth rates. Mean diameter increment exceeded 1 cm year^{-1}, with slightly higher growth rates in trees > 50 cm dbh. Inter-individual variation in growth rates was significant, with the fastest-growing individuals growing at rates greater than 2 cm year^{-1}. Inter-annual variation in growth rates was also significant. The diameter growth of 1.21 ± 0.1 cm during a wetter year (1456 mm) exceeded by 75% the diameter growth of 0.69 ± 0.1 cm during a drier year (1181 mm). The study revealed that mahogany trees as small as 23 cm dbh that were left standing after harvests could be expected to attain the commercial diameter of 60 cm in the 40 years between cutting cycles.

Keywords: Natural forest management, silviculture, sustainability, tropical moist forest, volume

SHONO, K. & SNOOK, L. K. 2006. **Pertumbuhan mahogani berdaun besar (*Swietenia macrophylla*) di dalam hutan semula jadi di Belize**. Data diameter tahunan (empat tahun) bagi 75 pokok mahogani berdaun besar (*Swietenia macrophylla*) yang tumbuh di dalam hutan semula jadi di bahagian barat laut Belize dianalisis untuk mengkaji kadar tumbesarannya. Pertambahan min diameter melebihi 1 cm setahun dengan pokok-pokok > 50 cm dbh merekodkan kadar pertumbuhan yang lebih sedikit. Variasi kadar pertumbuhan antara individu adalah bererti. Pokok yang tumbuh paling cepat tumbuh pada kadar melebihi 2 cm setahun. Variasi kadar pertumbuhan antara tahun juga bererti. Diameter pokok (1.21 ± 0.1 cm) pada tahun yang lembap (1456 mm hujan) melebihi pertumbuhan (0.69 ± 0.1 cm) pada tahun yang kering (1181 mm hujan) sebanyak 75%. Kajian ini menunjukkan bahawa pokok mahogani sekecil 23 cm dbh jika dibiarkan selepas tebangan boleh mencapai diameter komersial iaitu 60 cm dalam masa 40 tahun antara pusingan tebangan.

Introduction

Big-leaf or Honduras mahogany (*Swietenia macrophylla*) is a species of majestic proportions, sometimes exceeding 45 m in height, 25 m to the first branch and 1.8 m in diameter (Weaver & Sabido 1997). Highly valued for its attractive reddish colour and superior physical characteristics, mahogany has been for centuries the most commercially valuable timber species in the Neotropics (Lamb 1966, Weaver & Sabido 1997, Snook 1998). The natural range of mahogany is extensive, extending from Mexico to the southern Amazon basin of Brazil, Bolivia and Peru (Lamb 1966), but many former mahogany forests have been converted to other uses and mahogany has been depleted from many remaining forests. In Mesoamerica, the area of natural forest containing important populations of mahogany has been reduced to one-third of the area described by Lamb (1966) [Navarro *et al.* 2003]. The depletion of mahogany populations has led to concern for the future of the species and its commercial trade. In 2002, big-leaf mahogany was listed on Appendix II of the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora).

Mahogany timber for the international trade is still obtained, as it has been for centuries, from natural forests in Latin America (Blundell & Gullison 2003) because efforts to produce the timber in plantations in its native range have been considered unsuccessful due to the attack by *Hypsipyla grandella* shoot borer (Newton *et al.* 1993, Mayhew & Newton 1998). Mahogany harvests from natural forests are typically managed according to polycyclic systems (Gullison *et al.* 1996, Weaver & Sabido 1997, Snook 1998, Grogan 2001), by which removal of selected trees is conducted in a continuous

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series of felling cycles that are shorter than the time it takes the trees to reach harvest size (Whitmore 1998). This system will provide for sustained yields if harvested trees are replaced by the growth of existing residual trees and sufficient regeneration is established in each annual cutting area, either naturally or artificially (Snook 2003).

Despite its commercial importance, neither the ecology nor the management options for sustainable production and harvesting of mahogany are sufficiently known. This research examined the growth of mahogany trees in a natural production forest and evaluated the implications of growth rates for sustainability. The study was conducted as part of a major on-going research project on sustainable mahogany silviculture, of which the primary objective was to determine how best to ensure mahogany regeneration (Brokaw *et al.* 1998).

Materials and methods

Study site

This study was carried out near the Hill Bank Research Station (88° 42' W, 17° 36' N) in the Rio Bravo Conservation and Management Area (RBCMA) in Orange Walk district, northwestern Belize (Figure 1). The area is classified as the Subtropical Moist Life Zone, according to the Holdridge classification system (Programme for Belize 1996). The seasonal tropical forest of the RBCMA includes over 240 tree species, with an average canopy height of 20–25 m (Brokaw & Mallory 1993, cited by Programme for Belize 1996). In the study area, the forest is dominated by *Pouteria reticulata,*
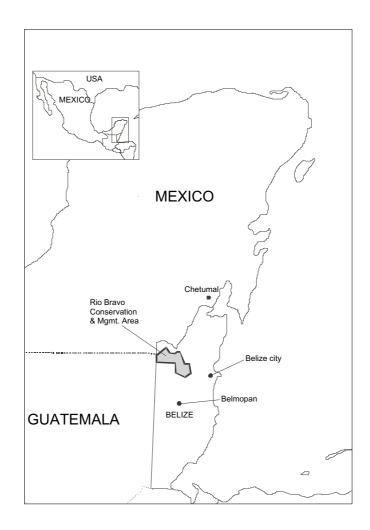

Figure 1   Mahogany growth in Belize

Aspidosperma cruenta, Manilkara chicle, Ampelocera hottlei, Terminalia amazonia and the palms *Sabal mauritiiformis* and *Attalea cohune* (Weaver & Sabido 1997, Whitman *et al.* 1997, Brokaw *et al.* 1998). Annual rainfall in the area is approximately 1600 mm, but total annual precipitation and seasonal distributions of rainfall vary widely from year to year (Whitman *et al.* 1997). There is a three-month dry season from February till April, typically including drought conditions in April and early May. Highest rainfall occurs in June and October. Occasional prolonged dry seasons and hurricanes affect the Belizean forests. Alluvial, calcareous soils found in the area are derived from porous limestone and are moderately deep and well drained, with a slightly acidic to slightly alkaline reaction (Programme for Belize 1996, Weaver & Sabido 1997). Topography of the region is mostly flat.

The 260 000-acre RBCMA is managed by a Belizean non-profit organization, the Programme for Belize, for the combined purposes of biodiversity conservation, education, tourism, and research in ecology, archaeology and forest management. The RBCMA was formerly part of a logging concession and logged for mahogany from the mid 19th century till 1982. The core of the reserve was created with a land grant by Coca-Cola Foods to the Massachusetts Audubon Society in 1989. Today, the RBCMA is the largest private reserve in Belize, covering 4% of the land area of the country (Programme for Belize 1996). Approximately 80% of the RBCMA is managed as a strict nature reserve, while 20% is designated as a surrounding buffer zone where timber harvesting and complementary forestry research are carried out. The production forest is divided into multiple compartments and managed on a 40-year felling cycle with a 60-cm minimum cutting diameter. Harvests are carried out on compartments totalling $\frac{1}{40}$ th of the production forest area each year and trees over the minimum diameter limit are extracted at each harvest. Trees smaller than the minimum cutting diameter are left in the forest to grow to harvest size in the interval between felling cycles.

Data collection

This study analysed diameter measurements obtained yearly between 1999 and 2003 on permanently marked mahogany seed trees. The trees are located in two 100-ha logging compartments: Punta Gorda (PG-01), to the north-west of Hill Bank Research Station and West Botes (WB-20), south-east of the research station. Before the commercial logging of PG-01 in 1997, 20 seed trees were selected from the population of mahogany trees in the compartment using a GIS map of all commercial timber trees to determine which potential mahogany seed tree would have the most trees of other species extracted from its defined downwind regeneration area. Then the harvest was carried out, leaving the 20 mahogany seed trees. A total of 183 trees of 15 species were removed from the 100-ha compartment (Robinson 1998). Commercial logging was conducted in WB-20 in 1998. In 1999 and 2000, additional trees were added to the original set of 20 seed trees in order to ensure that seed production was sampled for all mahogany trees that might shed seed on experimentally treated regeneration areas. Data were obtained from 31 seed trees in 1999 and from 75 seed trees starting in 2000. Seventeen of the seed trees were located in WB-20 and 58 were in PG-01.

Diameter measurements were taken with a diameter tape each year in May or June at either 1.3 m or 20 cm above the buttress. Measurement of heights were indicated with paint marks, but some trees had multiple paint lines on them, meaning that not all diameter measurements were taken at the same height. However, the height of each diameter measurement was recorded, and in some years, measurements were taken at all paint marks as well as at the standard height of 1.3 m. This permitted comparison of pairs of diameter measurements taken at the same heights. Heights of trees were calculated from clinometer readings taken from distances measured with a surveyor's tape. In order to estimate the canopy projection area, the shortest and longest diameters between points at the edge of each tree crown were measured with a surveyor's tape.

Monthly rainfall data was obtained from the Belize Meteorological Service, Tower Hill meteorological station, 48 km north of the study site (88° 34' W, 18° 02' N). Annual rainfall for each year was calculated by summing monthly rainfall between May and April.

Data analysis

Annual diameter increments were calculated by subtracting from each year's diameter measurement the diameter measurement of the previous year, taken at the same height. Diameter measurements from the year 2000 were not used in this analysis because they lacked corresponding height measurements for each diameter measurement. In order to include this period, we assumed equal rates of annual diameter growth between 1999–2000 and 2000–2001 and divided by two the diameter increment between 1999 and 2001. These average increments were used to calculate mean annual growth of each tree, but not for year-to-year comparisons. Dbh measurements were also used to calculate basal area and volume of the sample trees each year and their annual increments. A single-tree volume equation derived from plantation-grown mahogany in Sri Lanka was used for calculation of tree volume (Mayhew & Newton 1998: Volume = $0.056 - 0.01421$ Diameter $+ 0.001036$ Diameter ^{2}). This formula represents the over-bark volume of the main stem to a 10-cm-top diameter, or to the last 2 m log, excluding the branches. Mahogany trees in plantations typically exhibit diameter growths that exceed 1 cm year^{-1} during the early years (Lamb 1966, Mayhew & Newton 1998), and are generally managed on a rotation of 25 till 35 years. Allometric relationship between diameter and volume may be slightly different for mahogany trees growing in natural forests compared with plantation mahogany. However, this did not bias our results since our main interest was in examining volume increments rather than absolute volume.

SAS® software version 8.02 (1999–2001) was used for statistical analyses of the data. Regression analyses were performed to evaluate relationships between diameters and parameters of growth and a one-way analysis of variance (ANOVA) was used to compare annual growth rates between the two years for which annual measurements were available (i.e. 2001–2002 and 2002–2003).

Results

Figure 2 shows that the size distribution is not balanced. This reflected that the initial cohort of seed trees was obtained from among mahogany trees of commercial size (i.e. > 60 cm). Subsequent sample trees were selected according to their location with respect to experimental treatment areas, so they represent a broader spectrum of diameters.

Mean height of sample trees included in the study was 21.2 m and mean canopy projection area was 97.3 m^2. Both the height and canopy projection area were positively correlated with diameter (R^2 values of 0.43 and 0.64 respectively), and dbh was shown to be a statistically significant predictor of both (p < 0.001). Mean height–diameter ratio for the entire sample was 45.07 ± 1.26.

Diameter increments were highly variable among the individuals in different size classes (Figure 3). Regression analysis revealed that diameter and annual diameter increments were not well correlated (R^2 = 0.11), although dbh was a statistically significant predictor of annual diameter increment (p = 0.005). The overall mean annual diameter increment was 1.01 ± 0.10 cm year^{-1}. Differences in growth rates among diameter classes were not statistically different (Tukey's Honestly Significant Difference test, p < 0.05), and diameter class was not a significant predictor of annual diameter growth (p = 0.071). Absolute annual increments in basal area increased from one size class to the next, culminating in 157.28 cm^2 of annual basal area growth in the largest diameter class (Table 1). Absolute annual volume growth also increased from 0.0317 m^3 in the smallest diameter class to 0.1945 m^3 in the largest diameter class (Table 1). Annual per cent volume growth, however, decreased with increase in size.

Growth rates varied considerably between years (Table 2). A one-way ANOVA confirmed that variation in growth between years was significant (p < 0.001), and that growth in 2001–2002 (rainfall 1456 mm) was significantly greater than growth in 2002–2003 (rainfall 1181 mm) (Tukey's HSD test, p < 0.05). Monthly rainfall data for the growing seasons studied and 18-year averages are shown in Table 3. Regression analysis further revealed that total annual precipitation was a significant predictor of annual growth (p < 0.001; R^2 = 0.18). Monthly temperatures were relatively constant over the years and did not have a significant influence on growth.
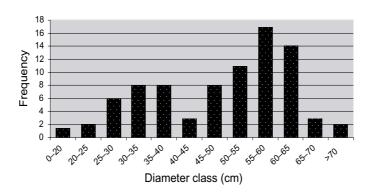
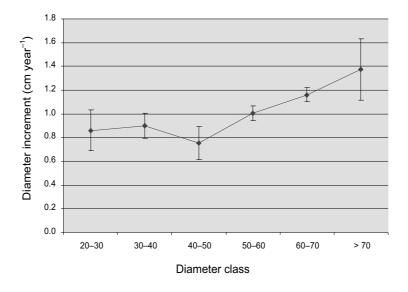**Figure 2**   Diameter distribution of sample mahogany trees

Figure 3   Annual diameter increment by diameter size class

Table 1   Annual mean diameter increment, basal area increment, volume increment and per cent growth by diameter class

Diameter class (cm)	n	Dbh increment (cm)	Basal area increment (cm^2)	Volume increment (m^3)	Volume growth (%)
20–30	6	0.86 ± 0.17	34.41 ± 7.16	0.0317 ± 0.0071	9.89 ± 1.91
30–40	14	0.90 ± 0.10	48.12 ± 5.56	0.0507 ± 0.0059	6.96 ± 0.86
40–50	8	0.75 ± 0.14	51.98 ± 8.93	0.0631 ± 0.0098	4.25 ± 0.88
50–60	24	1.00 ± 0.06	83.12 ± 5.28	0.1118 ± 0.0061	4.61 ± 0.31
60–70	20	1.16 ± 0.06	109.26 ± 5.56	0.1236 ± 0.0065	4.49 ± 0.24
> 70	3	1.38 ± 0.26	157.28 ± 29.18	0.1945 ± 0.0349	4.30 ± 0.84
Average	13	1.01 ± 0.10	79.29 ± 6.90	0.0983 ± 0.0078	5.37 ± 0.60

Table 2   Annual mean dbh increment, basal area increment, volume increment and per cent by year

Year	n	Dbh increment (cm)	Basal area increment (cm²)	Volume increment (m³)	Volume growth (%)
99–01	31	1.13 ± 0.09	99.99 ± 8.6	0.1139 ± 0.0100	5.11 ± 0.55
01–02	71	1.21 ± 0.07	93.13 ± 6.3	0.1083 ± 0.0076	6.69 ± 0.50
02–03	68	0.69 ± 0.05	55.47 ± 5.4	0.0691 ± 0.0064	3.63 ± 0.27
Average	57	1.01	79.29	0.0983	5.37

Values given for 99–01 are annual averages for the two-year period. Annual basal area and volume increments for year 99–01 were greater than the other years since the sample size in year 99–01 was smaller and larger trees accounted for a greater proportion of the sample.

Table 3   Monthly precipitation data (mm) from the Tower Hill station of the Belize Meteorological Service (88° 34' W, 18° 02' N with an elevation of 13 m)

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total
2002–2003	122	240	145	178	127	179	16.4	105	39.6	12	8.3	8.5	1181.2
2001–2002	267	122	149	441	175	121	40.2	49	27.1	46.5	18.6	0.3	1456.4
2000–2001	171	184	52.5	359	124	188	47	31.3	56.2	34.5	88.8	27.6	1362.6
1999–2000	7.7	209	258	185	202	200	93.8	42.8	29.2	13.5	75.6	22.3	1338.7
18-year avg.	99.1	203	192	206	171	189	102	77.4	76.8	33.7	28.8	45.9	1422.8

Discussion

Growth of mahogany

Growth has been found to vary with age (Snook 2003), size class (Gullison *et al.* 1996, Grogan 2001), rainfall (Whigham *et al.* 1998) and sites (Lamb 1966, Bird 1998). Biotic and abiotic factors such as size and position of the tree crown, competition from other plants, microsite differences in soil drainage and nutrient status, and genetic variation interact to influence diameter increments of individual trees, resulting in a wide inter-individual variability in growth rates. In Belize, Lamb (1966) measured diameters of 2202 trees eight years apart and reported mean annual diameter growth of 0.91 cm among mahogany trees growing on favourable sites, with fertile and well drained soils characterized by an abundance of cohune palms (*A. cohune*). Similar conditions were found in the compartments where this research was carried out. Grogan (2001) analysed three years of diameter measurements for 214 mahogany trees in Brazil and found that growth by the fastest-growing quartile in each size class exceeded 1 cm year^{-1} for nearly all size classes below 70 cm dbh.

Growth rates of mahogany revealed in this study were greater overall than those reported from other studies of mahogany trees in natural forests. This variation may be due in part to differences in study methodology. Among the studies, sample sizes varied and samples were selected using different parameters. Some of the study sites had been logged and the intensity of logging varied. It is possible that growth of these mahogany trees was stimulated by the removal of other canopy trees. Logging on PG-01 only opened 2.4% of the canopy overall, but 6%, on average, of the seed shadow areas downwind of the mahogany seed trees (Robinson 1998). Subsequent silvicultural treatments on this compartment completely removed the vegetation on the quadrants downwind of 10 of the mahogany seed trees and girdled the residual trees downwind of another 5 seed trees. These

subsequent treatments may have also stimulated the growth of these seed trees, although comparisons of a limited number of trees that had vegetation removed from their neighbouring seed shadow areas and trees that did not reveal difference in growth rates. Bird (1998) found that mahogany trees in natural forest in Belize that were remeasured after three years had grown between 0.08 and 0.60 cm year^{-1}, depending on the site, but on paired plots where logging had taken place, growth rates ranged from 0.17 to 0.74 cm year^{-1}. Two of his six 4-ha sample plots were located at Hill Bank. On one of these, mahogany trees had grown an average of 0.08 cm year^{-1} on the unlogged treatment and 0.17 cm year^{-1} on the logged treatment and on the other, they had grown 0.34 cm year^{-1} on the unlogged treatment and 0.57 cm year^{-1} on the logged treatment.

Growth differences may also reflect differences in regional precipitation patterns and soil properties. In Para', Brazil, the highest density of mahogany trees was found in the most fertile soils adjacent to first-order streams and planted mahogany seedlings performed best on soils with high levels of exchangeable cations (Grogan *et al.* 2003). Climate and physical conditions in northwestern Belize, including calcareous soils with generally favourable nutrient status, seem to present optimal conditions for mahogany development in a natural forest formation. Additionally, the provenance of mahogany found in the region may be a fast-growing variety.

Implications for sustainability

Growth rates of mahogany trees by size class can be combined with data from complete stock surveys of the logging compartments to calculate annual production of mahogany from this area. Sustained yields of mahogany at the RBCMA are premised on a level of harvest that is balanced by the growth of residual trees left behind and the successful recruitment of new regeneration. The average growth rate of 0.93 cm year^{-1} derived from trees < 60 cm diameter suggests that mahogany trees as small as 23 cm in diameter can be expected to reach the 60 cm commercial diameter by the time of the next harvest 40 years later. Eighty years from the first harvest, in the third cutting cycle, the harvest will have to be made up primarily of new mahogany trees from regeneration that became established after the first harvest. Even under a conservative assumption that newly germinated seedlings will reach 20 cm dbh in 30 years, and that they can sustain a growth rate of 0.8 cm year^{-1} thereafter, new seedlings that become established in year 0 should provide the next generation of harvest trees by the third cutting cycle in year 80. However, naturally occurring mahogany seedlings and saplings are rare in the forest today (personal observation), so it seems that silvicultural techniques must be applied to favour the establishment of mahogany regeneration on each cutting area at each harvest.

Since mahogany is a light-demanding species that typically regenerates after catastrophic disturbances (Snook 1996), ensuring regeneration in a closed forest represents a challenge. Implementation of appropriate silvicultural treatments is required in order to provide the necessary conditions for recruitment and seedling growth—high light levels, and reduced above- and below-ground competition (Grogan *et al.* 2002, Snook & Negreros-Castillo 2004). Experiments have shown that mahogany seedlings grow best on clearings of 5000 m^2 or more, and that natural regeneration and growth of planted seedlings can be enhanced by clearing vegetation using methods that prevent sprouting such as burning (Snook 2003). It has also been demonstrated that treefall gaps do not provide favourable conditions for sustained growth of mahogany seedlings (Grogan *et al.* 2003), which explains the frequently reported lack of regeneration in logged forests in Belize and other regions (Snook 1996, Gullison *et al.* 1996, Grogan *et al.* 2003).

Acknowledgements

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