

## 9. Regeneration, Growth, and Sustainability of Mahogany in México's Yucatán Forests

Laura K. Snook

**Abstract.** Big-leaf mahogany was studied on nine mixed-species stands that became established naturally between 2 and 75 years ago after catastrophic disturbances (hurricane blowdown, fire, or bulldozer clearing). More than 50% of adult big-leaf mahogany trees had survived a severe hurricane, leaving 2.8 seed trees  $\text{ha}^{-1}$ . After fire, 29% to 100% of adult mahogany trees survived, leaving an average of 1.4 seed trees  $\text{ha}^{-1}$ . Thirty or more years later, postdisturbance mahogany trees were found at densities of 18  $\text{ha}^{-1}$  after fire, as compared to 6  $\text{ha}^{-1}$  after a hurricane. In mixed-species aggregations, mahogany trees grew at densities as great as 47 trees  $\text{ha}^{-1}$ , accounting for up to 10% of the individuals and 27% of the basal area. A chronosequence of post-fire stands 15 to 75 years old revealed annual diameter increments ranging from more than 1  $\text{cm yr}^{-1}$  between 15 and 30 years to 0.38  $\text{cm yr}^{-1}$  between 45 and 75 years. Assuming constant growth, a big-leaf mahogany requires 122 years, on average, to reach the 55-cm minimum cutting diameter, although the fastest-growing trees may do so in 82 years. The current selective harvesting system, based on a 25-year cutting cycle,

cannot be expected to ensure sustainable harvests of big-leaf mahogany because extraction exceeds growth and adequate regeneration conditions are not provided. Harvest rates should be reevaluated and efforts made to increase the harvest of other species and implement silvicultural treatments, or shifting agricultural systems should be integrated into the forest management regime to provide for the regeneration of this valuable shade-intolerant species.

**Keywords:** Big-leaf mahogany, *Swietenia macrophylla*, Silviculture, Disturbance, Hurricane, Fire, Sustainability, Natural regeneration, Growth, Community forestry

### Introduction

For centuries, the extraction of big-leaf mahogany timber has been one of the primary economic activities in the state of Quintana Roo, on México's Yucatán peninsula (Fig. 9.1). Harvests have been maintained over this long period as changes in extraction technology and markets continuously redefined the mahogany resource. Between the seventeenth century and the early 1900s, the successive replacement of manual labor by draft animals and a combination of narrow-gauge railroads and crawler tractors increased the forest resource from a fringe of less than 100 m to a band 60 km wide along the Río Hondo, the perimeter of the Laguna de Bacalar, and other bodies of water in the region, along which logs were floated to ships or processing plants (Chaloner and Fleming 1850; Mell 1917; Record 1924; Lamb 1966; Napier 1973; Konrad 1988). Since then, road building and rubber-tired skidders have permitted logging of big-leaf mahogany from almost every area of the forest (Villaseñor 1958; Medina et al. 1968; Snook 1998).

Changes in markets have also contributed to maintaining big-leaf mahogany harvests. Until the 1940s, only select mahogany trees were harvested for the international log export market (Medina 1948). Huge trees were left standing because they were imperfect. From the 1950s to the 1980s, many of these trees were harvested for a local veneer mill (Medina et al. 1968). Now that big-leaf mahogany timber is being sawn locally into boards, trees of lower quality and smaller diameters can be processed. These changes in markets and transformation technologies have redefined the mahogany resource so that trees left behind in earlier logging operations—



**Figure 9.1.** The study area on México's Yucatán peninsula.

because they were not considered commercial—are providing the bulk of today's harvests (Snook 1993, 1998).

The framework for sustaining mahogany harvests has changed significantly over the past decades. First, an untapped forest frontier no longer exists. Second, the ancient trees left behind in earlier eras have already been harvested from two-thirds of the 25 annual cutting areas of the 400,000 ha of community forest reserves in the state. These trees have accounted for much of the volume harvested during the past 16 years, providing a one-time windfall. The long-term economic viability of forestry in Quintana Roo depends on assuring sustainable mahogany harvests by providing for regeneration on each cutting area each year and balancing the rate of harvest with the rate of growth. This strategy requires an understanding of the patterns and processes of mahogany regeneration and growth in these forests and the design and implementation of silvicultural management systems based on this knowledge. This study set out to obtain this information and

propose silvicultural guidelines for sustaining mahogany harvests into the future.

### Big-Leaf Mahogany in the Forests of the Yucatán Peninsula

Big-leaf mahogany grows as a canopy emergent and can reach 70 m tall and 300 cm in diameter (Pennington and Sarukhan 1968). In the course of this study, trees 35 m tall and 150 cm in diameter were measured. Mahogany trees begin to flower and fruit at about 12 years old. Flowers are fragrant and apparently pollinated by as-yet-undefined insects. Fruits are hard capsules 12 to 18 cm long that mature in 10 to 12 months. Each fruit contains 40 to 50 seeds, 1 to 2 cm long with 6 to 7 cm wings; they are dispersed by the wind during the dry season, when adult mahogany trees are leafless (in Quintana Roo, March and April) (Lamb 1966; Pennington and Sarukhan 1968; Pennington et al. 1981). Mahogany seeds have been observed to land 60 m downwind (northwest and south) from a mother tree 30 m tall (Rodríguez et al. 1994), and they probably fly much farther (Alrasjid and Mangsrud 1973). In Quintana Roo, mahogany seeds germinate between June and October, once the rains begin (Negreros and Snook, unpublished data). Seeds do not maintain their viability from one year to the next (Lamb 1966; Parraguirre 1994; Morris et al. 2000). Observations from both Central and South America show that mahogany seedlings are almost never found in the understory (Finol 1964; Lamb 1966; Snook 1993; Gerhardt 1996) nor do they seem to survive in felling gaps (Stevenson 1927; Quevedo 1986; Veríssimo et al. 1995; Gullison et al. 1996).

Although big-leaf mahogany is more common in seasonal tropical forests like those of Quintana Roo than in any other forest type in México (Pennington and Sarukhan 1968), mahogany trees grow at an average density of only 1 commercial-sized ( $\geq 55$  cm diameter at breast height, dbh) tree per hectare (Lamb 1966; Medina et al. 1968) and up to 7 trees  $\text{ha}^{-1}$  of 15 cm or less dbh (Argüelles 1991; Flachsenberg 1993a) in a matrix of 200 to 400 other trees  $\text{ha}^{-1}$  ( $\geq 15$  cm dbh) of 60 or more different species (Argüelles 1991; Snook 1993). The most abundant species in these forests, growing at densities of 15 to 60 trees  $\text{ha}^{-1}$ , is sapodilla or chicozapote (*Manilkara zapota*), the source of the chicle latex used to make chewing gum (Medina et al. 1968; Argüelles 1991; Barrera de Jorgenson 1993, 1994; Flachsenberg 1993a), followed by breadnut or ramón (*Brosimum alicatum*), which may also be found at densities greater than 15 trees  $\text{ha}^{-1}$  ( $\geq 15$  cm dbh) (Argüelles 1991).

The forests of Quintana Roo are seasonal tropical forests with a dry season 5 to 7 months long with rainfall less than 100 mm  $\text{month}^{-1}$ . Seasonal forests of this type are the most extensive in Central America (Murphy and Lugo 1986). Annual rainfall in the big-leaf mahogany forests of central

Quintana Roo is 1200 to 1500  $\text{mm yr}^{-1}$ , and falls mostly between May and October (Secretaría de Agricultura y Recursos Hidráulicos in Snook 1993). During the dry season, which becomes most extreme in March and April, many tree species drop their leaves for a short time (Pennington and Sarukhan 1968; Snook 1993). Soils in the region are derived from limestone, and the topography is flat to slightly rolling.

For millennia, the forests of Quintana Roo have been affected by a spectrum of drastic natural and human-caused disturbances. Almost every year, in August or September tropical cyclones or hurricanes (Wilson 1980; Escobar 1981) bring heavy rains and winds as high as 300  $\text{km h}^{-1}$  from the south, southeast, or east (Jauregui et al. 1980; Whigham et al. 1991). Hurricanes usually measure about 600 km in diameter (Jauregui et al. 1980; Wilson 1980). Periodically, they defoliate or knock down thousands of hectares of forest, as in 1942, 1955 ('Janet'), 1974 ('Carmen'), 1988 ('Gilbert'), and 1995 ('Opal' and 'Roxanne') (Medina 1948; Miranda 1958; Lindo et al. 1967 in Johnson and Chaffey 1973; Escobar 1981; López-Portillo et al. 1990; García et al. 1992; author's observations). The effects of a sixteenth-century hurricane on the Yucatán forests were described as follows: "There came a storm that grew into a hurricane. The storm blew down all the high trees. The land was left so treeless that those of today look as if planted together and thus all grown of one size. To look at the country from heights, it looks as if all trimmed with a pair of shears" (de Landa 1566).

Forest fires have also been frequent in Quintana Roo. During particularly dry years, forest fires have been caused by lightning (Wolffsohn 1967), but more typically they spread from shifting agricultural fields. Extensive fires are typical in the years after hurricanes, when fallen foliage, branches, and trees provide abundant fuel, and may burn hundreds of thousands of hectares of forest. Forest fires were extensive in the posthurricane years 1945, 1975, and 1990 (Lamb 1966; Pérez 1980; López-Portillo et al. 1990; Whigham et al. 1991; García et al. 1992).

Shifting agriculture has been practiced in the forests of Quintana Roo since at least 2000 B.C., when the early Maya became established there (Hammond 1982). In this system, patches of forest of 0.5 to 3 ha or more (Murphy 1990) are cleared and burned, planted, and cultivated for 1 or more years, then abandoned and recolonized by forest species. In today's forest, the density of crumbling pyramids and other Mayan structures, currently overgrown by trees, reveals that much of today's forest grew up on abandoned agricultural lands and urban centers after the collapse of the Mayan empire. The process of depopulation began about 900 years ago and continued through the period of Spanish conquest and the establishment of Mexican control (de Landa 1566; Gates 1937; Hammond 1982; Edwards 1986). More recent additions to the disturbance regime in Quintana Roo are felling gaps, skid trails, and log yards opened by bulldozers, produced by commercial timber harvesting.

## Methods

The frequency and range of disturbances that affect the forests of Quintana Roo make it an ideal setting for studying the processes of forest regeneration and growth. Historical events have established a variety of “natural experiments” (Diamond 1986), where different kinds of catastrophic disturbance, or treatments, have taken place in the past, giving rise to new forest stands. Because of the frequency of disturbance, a chronosequence could be identified of stands that became established at different times in the past after the same kind of disturbance. By comparing the sizes of trees at different stages along the chronosequence, their development and growth over time could be analyzed.

To determine the ages of trees not known to produce annual growth rings, it was necessary to know the ages of sample stands. Fortunately, the forests of Quintana Roo have been and continue to be inhabited and used by chicle tappers, mahogany loggers, and hunters who remember what has happened in the past on different parts of their forests. In response to questions, they described and led me to stands where they knew what kind of disturbance had occurred, and when. I confirmed stand histories by evaluating site evidence (Lorimer 1985). On stands affected in the past by fire, I found fire scars on some standing trees and charred trunks on the ground; on posthurricane stands, evidence included broken branches and stems, sometimes resprouted, and the remains of uprooted trees; old log yards had scattered sawn-off hollow logs that had been cut off and left behind when log trucks were loaded.

To avoid confusing the effects of time with the effects of soil, sample stands were selected for study only if they were growing on the red soils known in the Mayan classification as “kankab,” described as chromic cambisols in the Food and Agriculture Organization system (Flachsenberg 1993a). These soils cover 52% of the 20,000-ha forest reserve of the community of Noh Bec (Argüelles 1991), where the study was carried out (see Fig. 9.1). Nine stands were sampled, ranging in age from 2 to 75 years since the most recent catastrophic disturbance and regeneration event (Table 9.1).

### Data Collection

Two sampling systems were used. In each stand of more than 1 ha, one or more transects of 1 km by 10 m or 20 m wide (depending on stand age and tree size and visibility) were established using a compass and tape. Within these transects, all big-leaf mahogany trees were measured and evidence of damage noted. Where mahogany trees had already been harvested, their stumps were measured and a formula relating stump diameter to diameter at breast height (dbh) on standing trees was used to determine their diameters. In all stands, plots were established to include mahogany trees and

**Table 9.1.** Age, Disturbance History and Estimated Area of Sample Stands, and Sampling Method Used in Each Stand

Age	Sample Stands		Sampling Method		
	Certainty <sup>a</sup>	Disturbance	Area (ha)	Plot Size (m)	Transects (ha)
2	C	Bulldozer <sup>b</sup>	1	9	—
8	C	Bulldozer <sup>c</sup>	<1/2	25	—
15	C	Bulldozer <sup>c</sup>	<1/2	25	—
15	E	Bulldozer <sup>d</sup>	<1/2	25	—
15	C	Fire	200	25	1
30	C	Fire	200	314	1
34	C	Hurricane	>200	314	4
45	C	Fire	>200	1000	3
75	NC	Fire	200	1000	4

<sup>a</sup> C, age and history confirmed independently by more than one informant; NC, age obtained from only one informant; E, age estimated.

<sup>b</sup> Clearing established as a helicopter landing pad.

<sup>c</sup> Log yard.

<sup>d</sup> Road edge.

their associates. Plot size varied with stand age and tree size, so that each plot contained about 40 trees (Table 9.1). Within each plot, all trees larger than a minimum size (2 m tall in stands up to 15 years old; 15 cm dbh in older stands) were identified, and their diameters and heights measured. In addition, any damage to the stem or the crown and its probable cause were recorded.

During the first field season, increment cores were collected from big-leaf mahogany trees on plots to see whether ring numbers correlated with historical data. Ten cross-sectional slabs were also cut from mahogany stumps of known age in a thinned plantation. In a confirmation of previous observations (Rodríguez 1944; Medina et al. 1968), initial counts showed that the number of rings did not correspond to the age of the stand or the plantation, nor did ring numbers correspond among neighboring trees. As a result, no further samples were collected.

### Data Analysis

Neither hurricanes nor fires destroyed all trees in the affected area. To analyze the patterns of regeneration and growth required differentiating two cohorts of trees in each stand: those that had survived the stand-initiating disturbance, and those that became established afterward. The ages of the latter group could be assumed to correspond closely to the number of years since the disturbance; those of the former group could not be determined. A tree was considered to have survived the stand-initiating disturbance if it was damaged in a way that corresponded to that type of disturbance and if it was larger than other trees in the stand (Lorimer 1985).



In stands affected by fire, damage to surviving trees consisted of fire scars at the base. Trees that had survived a hurricane were likely to have bent stems or broken branches, which might have resprouted. Unlike fires, which typically destroy smaller individuals, hurricanes are more likely to damage canopy trees. Because small trees and saplings in the understory typically escape wind damage, these trees were compared to conspecifics of known age to determine whether they were survivors. In cases of doubt, they were included in the postdisturbance cohort. Data were analyzed by using Systat and Sygraph (Wilkinson 1988).

## Results and Discussion

### The Survival of Big-Leaf Mahogany After Fire and Hurricane

Big-leaf mahogany trees and stumps found in transects through the different stands were classified, based on their sizes and evidence of damage, into three categories: those that died as a consequence of the disturbance (mortality); those that survived the disturbance (survivors); and those that became established after the disturbance (regeneration). Some trees may have been entirely destroyed by fire, leaving no evidence, although mature mahogany trees are considered extremely fire resistant when alive, as is their timber (Chaloner and Fleming 1850: 53).

After the hurricane of 1955, adult mahogany trees survived at an average density of 2.8 trees  $\text{ha}^{-1}$ , a rate of survival greater than 50% (Table 9.2). These results are similar to Lamb's observation (1966: 111) that 6 years after the hurricane of 1942 in Belize, 3 mahogany trees  $\text{ha}^{-1}$  survived. Mahogany is wind resistant because of its strong, flexible wood (Kukachka 1959), its buttresses, and its few, heavy branches (Snook 1993). In transects through burned areas, surviving adult mahogany trees were found at a density of 0.5 to 2.0  $\text{ha}^{-1}$ , representing 29% to 100% survivorship (Table 9.2). Mature individuals have thick bark and survive fire well, but large trees with fire scars were observed. The lower density and percentage of surviving mahogany trees in older stands may indicate that some survivors had died in the subsequent years, perhaps after having suffered damage. Because mahogany seeds are not viable beyond one rainy season and mahogany seedlings are typically rare or absent from the understory seedling bank, the survival of mature mahogany trees through fires and hurricanes is necessary to ensure colonization of open areas after such disturbances.

### Natural Regeneration of Big-Leaf Mahogany After Disturbance

The density of big-leaf mahogany trees that became established after fire and hurricane (Table 9.2) revealed two phenomena. First, the density of mahogany trees on the 15-year-old postfire stand was more than eight times the density in stands 30 years and older. The lower density of mahogany

**Table 9.2.** Density ( $\text{ha}^{-1}$ ) of Adult Mahogany Trees That Died or Survived After a Hurricane or a Fire, and Percentage Surviving; and Density ( $\text{ha}^{-1}$ ) of Mahogany Regeneration Established After the Disturbance

Disturbance	Time Since Disturbance	Mortality (number)	Trees Surviving (number)	Surviving (percentage)	Postdisturbance Big-Leaf Mahogany Regeneration <sup>a</sup> (number)
Fire	15	0	2.0	100	133
Fire	30	3.0	2.0	40	22
Fire	45	1.2	1.1	48	15
Fire	75	1.2	0.5	29	16
Hurricane	34	2.5	2.8	53	6.3

<sup>a</sup> Densities were determined from transects through sample stands.

trees on older stands probably reflected the process of self-thinning or stem exclusion, natural mortality in proportion to the increase in size of each individual (Westoby 1984; Oliver and Larson 1990). Second, the average density of postdisturbance mahoganies that became established after fire was three times higher (18  $\text{ha}^{-1}$ ) than the number that became established after a hurricane (6  $\text{ha}^{-1}$ ), although the density of surviving adult seed trees was twice as high after hurricane (2.8  $\text{ha}^{-1}$ ) as after fire (1.4  $\text{ha}^{-1}$ ). This finding indicated that the conditions for mahogany establishment were more favorable or more extensive, or both, after a fire had destroyed all seedlings and most adult trees, than after a hurricane, which produces a series of treefall gaps (Whigham et al. 1991). Opportunities were limited for mahogany seedlings to become established among the understory trees and juvenile stages of other species that typically survive disturbances such as hurricanes and logging that create canopy gaps. On stands more than 30 years old, other tree species were found at densities averaging 7,000 sapling-sized individuals  $\text{ha}^{-1}$  (>2 m tall and <15 cm dbh) and more than 110,000 seedlings  $\text{ha}^{-1}$  (<2 m tall) (Snook 1993).

Among the younger stands that became established after clearing or fire, big-leaf mahogany trees were found at densities greater than 1000  $\text{ha}^{-1}$  (Table 9.3). The highest density of mahogany trees, equivalent to 5600  $\text{ha}^{-1}$ , was found along the edge of a logging road, where the soil was mounded up. Mahogany trees averaged 5 m tall, and some reached 7 m. They were the most abundant species, accounting for 38% of all individuals. These patterns paralleled observations made by Wolffsohn (1961) in Belize, where he noted that mahogany regenerated most abundantly on areas cleared by fire, agriculture, or machinery.

In stands 30 years old or older, big-leaf mahogany trees represented up to 10% of the trees and 27% of the basal area in the mixed-species aggregations where they were growing (Table 9.3). Within these aggregations of 200 to 400 individuals  $\text{ha}^{-1}$  of about 40 tree species, postdisturbance

**Table 9.3.** Density on Plots of Mahogany Trees in Mixed-Species Aggregations Established After Disturbance

Stand	Age (years)	Big-Leaf Mahogany (trees ha <sup>-1</sup> )	Mahogany		
			As a Percentage of All Trees	Basal Area (BA)	
				Mahogany (m <sup>2</sup> ha <sup>-1</sup> )	Mahogany (percentage of total BA <sup>a</sup> )
Landing pad	2	1400	11	—	—
Log yard	8	4200	23	—	—
Log yard	15	2000	21	—	—
Road edge	15	5600	38	—	—
Fire	15	1700	16	—	—
Fire	30	32	6	2.2	7
Hurricane	34	37	8	2.5	7
Fire	45	47	10	4.7	18
Fire	75	43	10	7.4	27

<sup>a</sup> For trees ≥15-cm diameter.

mahogany trees were found at a density equivalent to 32 to 47 individuals ha<sup>-1</sup>. In the 75-year-old stand, the crowns of the 42 mahogany trees ha<sup>-1</sup> were close to touching each other, creating a supercanopy over the main canopy. As stand age increased, mahogany represented a progressively higher proportion of stand basal area because it grows more rapidly than almost all associated tree species (Snook 1993).

### Mahogany Growth in Mixed-Species Stands

Big-leaf mahogany growth rates were found to change with tree age (Table 9.4). The most rapid growth, exceeding 1 cm dbh yr<sup>-1</sup>, was observed in trees between 15 and 30 years old. The diameter increment of mahogany determined by comparing the size of trees on the 30-year-old stand with those on the 45-year-old stand (0.44 cm yr<sup>-1</sup>) was almost identical to the increment of 0.43 cm yr<sup>-1</sup> calculated by Juárez (1988) on the basis of three remeasurements at 5-year intervals of mahogany trees between 25 and 35 cm dbh, and corresponds to the average growth rate determined from two subsequent remeasurements of mahogany trees in Noh Bec (Whigham et al. 1998).

**Table 9.4.** Average Diameters and Periodic Annual Increments (PAI) of Mahogany Trees Established After Fire in Stands of Known Age<sup>a</sup>

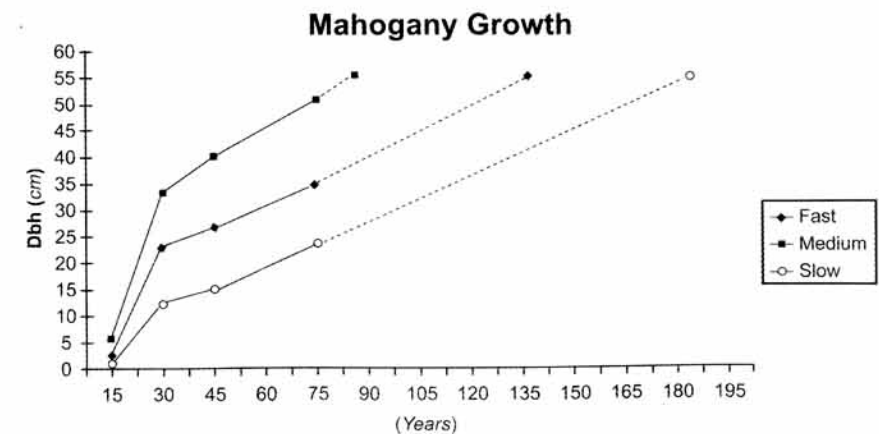
Age (years)	15	30	45	75
dbh + SE (cm)	3.1 ± 0.2	19.4 ± 2.8	25.9 ± 2.3	37.2 ± 1.4
PAI (cm yr <sup>-1</sup> ) <sup>a</sup>	0.20	1.09	0.44	0.38
n (trees) <sup>b</sup>	131	18	30	74

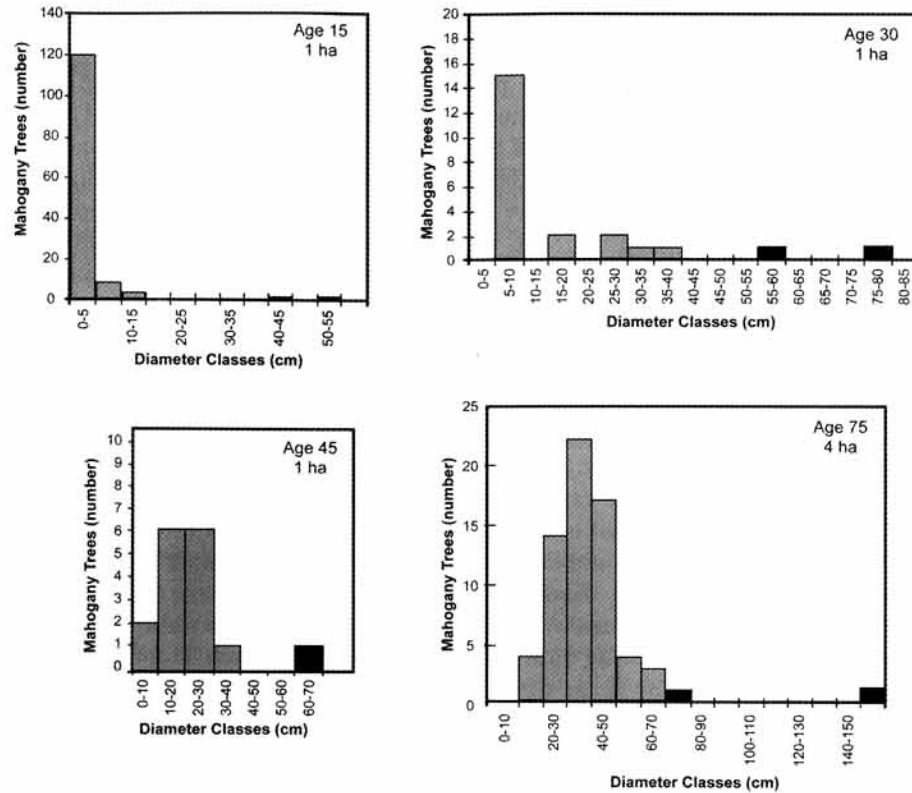
<sup>a</sup> PAI = (dbh t<sub>2</sub> - dbh t<sub>1</sub>)/(t<sub>2</sub> - t<sub>1</sub>).

<sup>b</sup> n, number of trees measured in each age-class.

The average diameter of big-leaf mahogany trees in the oldest sample stand was 37 cm, considerably less than the legal cutting limit of 55 cm. To estimate the time required for a mahogany to reach a diameter of 55 cm, a formula was derived from the periodic annual increments (PAI) of mahogany trees of known age. If the oldest stand was 75 years old, and if mahogany continued to grow in the future at the same annual rate of diameter growth as it did between 45 and 75 years, the time required for an average mahogany tree to reach a larger diameter can be calculated by using the following formula, derived from the data in Table 9.4: year = [(diameter - 25.9)/0.38] + 45. If these suppositions are true, a mahogany tree growing at an average rate in these forests would reach the diameter limit of 55 cm in 122 years. This growth rate means that the trees harvested during the course of this study, which averaged more than 80 cm dbh, became established about 200 years earlier, and that the largest trees measured were about 350 years old.

Some trees grow more rapidly than the average and others grow more slowly. When big-leaf mahogany age-cohorts were divided into thirds by diameter, cumulative annual increments ranged from 0.32 cm yr<sup>-1</sup> to age 75, for the slowest-growing third, to 0.67 cm yr<sup>-1</sup> to age 75, for the fastest-growing third. If these trees were to continue growing at the same rate into the future, the fast-growing 33% could be expected to reach 55 cm at about 82 years (Fig. 9.2). The range of diameters between fast- and slow-growing individuals in a single age-cohort explains how Olmsted and Álvarez (Plan Piloto Forestal 1987) found that 2 of the 57 mahogany trees ha<sup>-1</sup> growing in a log yard (<4% of the total), had reached 55 cm diameter at age 34. The average diameter of the mahogany trees they measured on that stand was

**Figure 9.2.** Diameters of mahogany trees at different ages, subdivided into thirds by size/growth rate, derived from trees on stands of known age and extrapolated to 55-cm diameter.



**Figure 9.3.** Mahogany trees by diameter class in four essentially single-cohort stands established after fire. *Black bars* represent trees that survived the stand-initiating fire.

25.4 cm, a size that falls on the average for that age as determined in this study (Table 9.4).

The diameter-class frequency distribution of big-leaf mahogany in the stands sampled reflects this variation in growth rates, changing from an inverse J-shaped curve, as faster-growing individuals move out of the sapling class, to a bell-shaped curve (Fig. 9.3). This growth pattern is typical of even-aged cohorts (Oliver and Larson 1990) and has been described for mahogany stands elsewhere (Finol 1964; Gullison and Hubbell 1992).

### Conclusions and Implications for Sustainable Silviculture

In the tropical forests of Quintana Roo, the regeneration strategy of big-leaf mahogany is characterized by the capacity of adult trees to survive hurricanes and fires that periodically destroy most other trees; the production, by those survivors, of winged seeds capable of dispersing by wind to those

recently opened areas; the capacity of mahogany seedlings to become established in open clearings; and the capacity of mahogany to develop and grow in essentially single-cohort mixed-species stands. In postdisturbance aggregations, mahogany trees more than 30 cm dbh can be found at densities approaching 50 trees ha<sup>-1</sup>. Data from this study suggest that, although the fastest-growing mahogany trees may reach 55 cm dbh in about 82 years, two-thirds of the trees will take well over a century, and some closer to two (see Fig. 9.2).

How do these ecological parameters of big-leaf mahogany regeneration and growth relate to current forest management, and what do they imply for sustaining future mahogany harvests? In Quintana Roo, 46 forest ejidos<sup>1</sup> control a total of nearly 400,000 ha of commercial forest in blocks that range from 1,000 to 30,000 ha per ejido (Argüelles 1993). The forest management plan for each ejido is designed to assure continuous yields from its particular forest by controlling the rate and spatial distribution of harvesting, based on a polycyclic system with a 25-year cutting cycle and a minimum diameter limit of 55 cm. Whatever the size of the ejido forest or the standing volume of commercial-sized mahogany trees calculated from forest inventories, these figures are divided by 25 to determine how much area and how much volume can be harvested each year. All mahogany trees larger than the minimum diameter are harvested from 1 of the 25 cutting areas each year. Harvests on a particular area are scheduled to recur at 25-year intervals.

### Sustaining Yields from Existing Trees

For each of the first 25 years of the cutting cycle, 1/25 of the existing stock of big-leaf mahogany trees larger than the diameter limit is harvested. According to current harvesting guidelines, all these trees will be logged during the first cutting cycle, although many of the largest have been felled and left in the woods because of poor wood quality (Argüelles 1991; author's observations). If inventories of trees in commercial size-classes accurately described the trees on the whole forest reserve of each ejido, this selective, diameter-limit harvesting system could be expected to assure continuous and relatively constant yields of timber over the 25 years of the first cutting cycle (of which 9 years remained in 2001). Where inventories do not cover the full forest reserve, however, annual harvests do not reflect timber availability on the whole forest, or over the whole cutting cycle. This discrepancy has led to unexpected fluctuations in timber availability from one cutting area, and one year, to the next.

Beginning with the second cutting cycle, in year 26 (2010), the forest reserve will be cut over again, one parcel each year. No gigantic big-leaf mahogany trees, centuries old, will remain; thus, the trees harvested on this second cut will be those currently in the 35- to 54-cm size-classes, the so-

<sup>1</sup> An ejido is a communal landgrant and its residents.



called reserve. During the 25 years of the first cutting cycle, they are expected to have grown to commercial diameters. The third cutting cycle, beginning in year 51, will cut over the 25 annual cutting areas, one by one, for the third time. Harvesting will focus on trees currently in the 15- to 34-cm size-classes, the so-called recruits, or repoblado, which will have had 50 years to grow into commercial size-classes (Argüelles 1991).

The abundance and proportion of different age-classes of big-leaf mahogany on any area is a function of the timing and characteristics of catastrophic disturbances in the past. In some areas, the number of trees currently in precommercial size-classes may be greater than the number in commercial size-classes. Trees in these categories, however, may be fast-growing young trees or slow-growing older trees. Based on extrapolations in Figure 9.2, most trees 45 cm in diameter today can be expected to attain 55 cm in 25 years, but even the fastest-growing trees that measure 35 cm dbh today could not be expected to attain 55 cm in 25 years. Additional data on growth are needed, but both minimum diameters and total volumes of harvests in the second and third cutting cycles are likely to be lower than expected. The 25-year cutting cycle used in Quintana Roo was not derived from growth data but from the 25-year duration of the forest concession granted to a veneer company in the 1950s (Rodríguez 1944; Medina et al. 1968; Snook 1998). Across the border in Belize, where forests are very similar but may benefit in some areas from deeper soils and more rainfall, mahogany forests are managed on a 40-year cutting cycle.

### Sustaining Yields from New Trees

The long-term sustainability of big-leaf mahogany harvests, beyond the 75 years of the first three cutting cycles that focus on existing trees, depends on establishing mahogany regeneration on each parcel after each harvest. Regeneration requires seeds or seedlings and a favorable environment for their survival and growth. Opportunities for regeneration depend on the ecological requirements of the species, the calendar and characteristics of harvesting operations, and the design and implementation of silvicultural techniques.

The practices of big-leaf mahogany logging in Quintana Roo are defined by both ecological and economic parameters. A key ecological factor is the fact that commercial-sized mahogany trees grow at relatively low densities in stands comprising hundreds of individuals of dozens of other species (Argüelles 1991; Snook 1993). The economic context for logging is that mahogany is by far the most valuable species, with unlimited market demand. Few associated species have commercial value, and those that do have limited demand and low value (Flachsenberg 1993b). As a consequence of these combined factors, mahogany is selectively logged while associated species are left standing. Although mahogany typically regenerates in clearings produced by the destruction of trees of other species, selec-

tive harvesting of mahogany inverts those conditions. This practice short-circuits the regeneration ecology of mahogany in two ways: by reducing the availability of mahogany seed, and by perpetuating conditions unfavorable to the establishment and growth of mahogany seedlings.

Because big-leaf mahogany seeds do not retain their viability beyond one season (Lamb 1966; Rodríguez Pacheco and Barrio 1979; Parraguire 1994), natural regeneration requires that seed sources be retained within dispersal distance of an appropriate clearing. The current harvesting schedule, in which mahogonies are felled during January and February, just before their seeds are dispersed (March–April), does not permit the seeds from harvested trees to contribute to natural regeneration. Furthermore, if the less-valuable species are harvested, they are normally felled and extracted after mahogany, and after the period of mahogany seed dispersal. This schedule means that mahogany seeds are not able to colonize felling gaps during that year. Because mahogany regenerates in essentially even-aged aggregations, in old stands all or nearly all mahogany trees have attained commercial size. In such stands, diameter-limit harvesting can deplete seed sources over a large area. If some precommercial trees in smaller-diameter classes remain, they could serve as seed sources, although their rate of seed production is a fraction of that of trees greater than 75 cm (Gullison et al. 1996; Camara and Snook 1998).

The lack of seeds can be overcome, at some cost, by sowing or planting. A more difficult challenge is the fact that postharvest conditions are inhospitable for the survival of mahogany seedlings because of their intolerance of shade and competition. Selectively harvesting big-leaf mahogany creates relatively minor effects on the forest and was calculated to reduce canopy cover by only 2% (Whitman et al. 1997); this represents a problem for a species that typically regenerates after catastrophic disturbance and requires direct sunlight to grow. The selective harvest of mahogany trees in Quintana Roo produces an average of one treefall gap  $\text{ha}^{-1}$  that is 10 m or less to 20 m in diameter, plus skid trails less than 5 m wide and a few 0.2- to 1-ha log yards per cutting area (Argüelles 1991). In one evaluation, only 3.6% of a cutting area was calculated to have been disturbed by mahogany harvesting, and none of that area was considered favorable for regeneration. When more species were extracted, 5.4% of the area was affected, leaving 1.8% of the cutting area in a condition considered favorable for regeneration (Flachsenberg 1993a). Although log yards provide a favorable environment for mahogany regeneration, they cover only 0.5% to 5% of each cutting area (Snook 1993; Argüelles 1991), so even locating log yards near mahogany seed trees will not be adequate to sustain the forest's potential for mahogany production.

Given the practices and calendar of harvesting and the characteristic stand structures and regeneration dynamics of big-leaf mahogany, natural regeneration will not be sufficient to sustain mahogany in these forests. Silvicultural management is necessary. To date, the only silvicultural activ-



ities have consisted of planting to compensate for the lack of mahogany seed sources. Seeds are collected from felled or standing mahoganies, sown in nurseries, and the seedlings transplanted into felling gaps, skid trails, and log yards. An evaluation of plantings 1 to 3 years later, however, showed that only 22% of mahogany seedlings had survived, in part because of poor seedling quality and poor planting technique (Negreros 1995), but probably also because of competition from other species in both the overstory and understory. An evaluation of plantings in log yards showed a survivorship of 25% to 75% after 5 to 6 years, and the stocking of survivors was considered adequate (Synnott 1995).

### Sustaining Big-Leaf Mahogany Harvests Through Silvicultural Management

If the objective of forest management in Quintana Roo is to sustain yields of big-leaf mahogany over time, current practices must be modified to take into account what is known about the growth and regeneration of this species. In the short term, the 25-year cutting cycle and its implicit 75-year rotation must be recognized as shorter than the time required for mahogany trees to grow to the 55-cm commercial diameter. Diameter limits and annual harvests should be reevaluated so that harvests are balanced with the rate of growth. Because most logs are now being sawn into boards rather than peeled for veneer, trees could be processed at 40 cm rather than 55 cm dbh, and they could be harvested at about 80 years. Even if trees were harvested younger and smaller, however, harvesting smaller trees would yield lower annual harvest volumes. This reduction would have important economic implications for the ejidos that depend on mahogany harvests for a significant portion of their income.

Furthermore, sawing yields the lowest return per unit of timber processed. The relatively small scale of ejido forestry operations represents a significant constraint to making adjustments to increase the value of each meter harvested. Volumes of big-leaf mahogany per ejido ( $0\text{--}1588\text{ m}^3\text{ yr}^{-1}$ ) (Flachsenberg 1993b) are typically too low to provide a constant supply of logs to any kind of transformation industry, and at that scale it is not economical to invest in the technology necessary to transform mahogany into the products with the highest value per unit of volume.

Over the longer term, efforts to sustain or enhance big-leaf mahogany production will have to focus on improving the opportunities and conditions for establishing mahogany regeneration by increasing the number of openings created by harvesting and reducing competition for mahogany seedlings. At a minimum, however, two relatively minor modifications in the calendar of harvesting could enhance the potential for natural regeneration of mahogany: harvesting mahogany after its seeds are dispersed and harvesting other species first, before mahogany seeds fall. These changes would require that mahogany be harvested between April and the begin-

ning of the rains in June or July, and it would delay the influx into ejido economies of capital from early mahogany sales. It would also require that markets be further developed for species other than mahogany. In addition to providing a greater range of silvicultural options, however, this strategy would greatly increase the yield from each hectare. Incorporating into the management plan the harvesting of other products including railroad ties and poles and thatch for construction (Murphy 1990, 1994) would also enhance regeneration opportunities. These currently haphazard activities could be concentrated in time (before mahogany seeds fall) and space (each year's cutting area) to maximize the openings available for mahogany regeneration and minimize competition for seedlings from midcanopy and understory species.

Additional treatments would probably increase the success of regeneration. During the 1920s, in Belize, silvicultural practices that included the poisoning and girdling of undesirable species to open up the canopy and understory cleaning were implemented to encourage the establishment of big-leaf mahogany regeneration before logging and foster its subsequent development. These methods led to the establishment of about 100 mahogany seedlings  $\text{ha}^{-1}$  (Stevenson 1927). Although these treatments were abandoned during the depression (Johnson and Chaffey 1973), experiments with canopy opening, combined with understory cleaning, have been undertaken in Quintana Roo. Three years after treatment, mahogany seedlings of natural origin were found at a density of  $1000\text{ ha}^{-1}$  (Negreros and Mize 1994). These seedlings may require periodic cleanings to successfully compete with the sprouts of understory seedlings and saplings of other species.

Line plantings of big-leaf mahogany seedlings were widely established in the forests of Quintana Roo in the 1950s (Miranda 1958; Medina et al. 1968; Weaver 1987). They were apparently unsuccessful (Miranda 1958), probably because of canopy shade, root competition, and understory sprouts. Line planting of mahogany has been considered successful in Puerto Rico, however, where seedlings have been carefully tended (Bauer 1991).

More intensive silviculture would be required to duplicate the conditions that have favored the establishment of high-density stands of big-leaf mahogany in the past. Probably the most common disturbance pattern to have given rise to high-density mahogany stands in Quintana Roo has been hurricanes followed by fire. Very similar ecological conditions are produced by slash-and-burn agriculture, still the mainstay of the subsistence farmers who make up the rural and forest-dwelling population of Quintana Roo (Murphy 1990, 1994). The regeneration of mahogany and associated tree species was probably favored in the past by shifting agriculture, yet, ironically, the first step in organizing forestry in Quintana Roo was to create permanent forest reserves where agriculture is prohibited (Snook 1991). There were logical reasons for doing so: where population densities are high, fallow periods become so short that forests never regrow beyond a scrubby

stage, and significant logistical difficulties and risks can be incurred when agricultural activities and their associated fires take place in a commercial forest.

Nonetheless, farmers have noticed that where big-leaf mahogany seed trees occur nearby, seedlings become successfully established on their abandoned fields (huamils). Some farmers are reluctant to clear a fallow field where mahogany trees have regenerated. Currently, researchers are working with members of forest ejidos to establish experimental slash-and-burn fields where mahogany seeds are being sown along with corn, beans, and squash to evaluate the costs and success of this agrosilvicultural system. Experimental patch clear-cuts and mechanical clearings imitating log yards are also being established to permit a comparison of the relative costs and results of creating mahogany regeneration conditions by using these three intensive methods. These systems are expected to result in the establishment of even-aged, mixed-species stands with 50 to 100 mahogany trees  $\text{ha}^{-1}$  at the end of the rotation.

### **Beyond Big-Leaf Mahogany: Sustaining the Forest**

Maintaining future yields of big-leaf mahogany is only one rather simple criterion for determining the sustainability of forestry practices in the forests of Quintana Roo. The larger objectives of forest management in this area are to sustain both the forest-based economies of local communities and the forest itself, part of the Mayan forest ("Selva Maya"), the largest continuous block of tropical forest north of the Amazon basin. Although big-leaf mahogany is the most valuable timber species, for both economic and ecological reasons many other species should be taken into account in designing silvicultural management plans for these forests. For example, chicle latex provides half or more of some people's annual incomes, so a healthy population of productive chicle trees must be maintained. Many species that do not reach commercial diameters are used for building houses and for fencing (Snook 1993; Murphy 1990, 1994; Snook and Barrera de Jorgenson 1994). Several animal species are also important to the subsistence of local people. In the process of refining the forest management system, consideration should be given to the fact that sapodilla and breadnut fruits are major food sources for pacas and deer, two of the most important game species in the forest (Jorgenson 1993, 1994, 1998).

Even beyond their utilitarian values, in a tropical forest where little is known about pollination and dispersal, maintaining species diversity should be considered a safeguard for the future of many species. For example, it is not yet known what species pollinate big-leaf mahogany flowers and what other species these creatures may require to survive. Both food supplies and habitat needs for fauna should be considered. Intensive silviculture for the production of mahogany timber need not reduce the diversity of tree

species because patchy catastrophic disturbance events have sustained the existing mixture of species for centuries. The tree species associated with mahogany either regenerate successfully under the same open, cleared conditions as mahogany or in the kinds of small canopy gaps produced by logging and wind (Snook 1993), so if thought is given to maintaining the full spectrum of species, this can be achieved as part of a silvicultural regime designed to sustain mahogany harvests. Nonetheless, if more species are harvested, more knowledge is required to ensure that their populations are not depleted.

As part of the effort to sustain biodiversity, attention should also be paid to sustaining a mixture of ages and sizes of trees, including some ancient ones. If the current diameter-limit harvesting plan is followed, by the end of the first cutting cycle the age and size structure of the forest will have been altered significantly from what it has been over the past 800 years or more. Big-leaf mahogany trees attain larger sizes than other trees in this forest. The harvest of huge, old mahoganies is reducing the availability of nesting cavities for parrots and toucans, important seed dispersers and inhabitants of the forest.

Big-leaf mahogany has been an important product of the forests of Quintana Roo since the Maya used these large trees for making canoes (Hammond 1982). New knowledge of its regeneration ecology and growth rates can be integrated into silvicultural management plans to sustain its production into the future. Unusual opportunities for silvicultural management are provided by the diverse economies of the local forest communities. Shifting agricultural techniques used to produce the local staples of corn, beans, and squash mimic natural disturbance patterns. The fact that local people use a wide range of resources, from building poles and thatch to chicle latex and game, also provides a broader framework than a simple industrial timber economy for developing forest management plans. Silviculture in this region could integrate ecological understanding with local patterns of resource use, focusing on intensive management of small areas for multiple products produced in a mosaic of time and space. Because land is abundant, mahogany could conceivably be sustained, along with a mixture of other species, as part of the shifting agricultural system, in a mosaic of age structures that would simultaneously provide wildlife habitat, chicle supplies, and building materials. A diversified peasant economy may provide the best framework for a kind of silviculture that works with the complexities of these species-diverse tropical forests.

*Acknowledgments.* This study was carried out as a doctoral dissertation for Yale's School of Forestry and Environmental Studies, New Haven, CT, USA. Financial support was provided by a Fulbright Doctoral Dissertation grant from the U.S. Department of Education; the Charles A. Lindbergh Fund; the Tropical Resources Institute (TRI) of Yale's School of Forestry and Environmental Studies; and by the German-Mexican Forestry Agree-



ment of the German GTZ. Additional support was provided by México's National Institute for Research on Forestry, Agriculture and Animal Husbandry (INIFAP), through their San Felipe Bacalar Field Station, and México's former National Institute for Research on Biotic Resources (INIREB). Research was carried out in Noh Bec, Quintana Roo, México. I thank all those institutions, as well as the following people: Abel Rodríguez Tun, of Noh Bec, whose knowledge of the forest was crucial to every day of data collection during 13 months of fieldwork; Bernaldo Blanco and Francisco Tadeo of Noh Bec, who provided much of the historical information that allowed me to find my sample stands; and Javier Chavelas Polito of INIFAP, for his botanical knowledge and other support, and his family, for their hospitality. Thanks also to three anonymous reviewers for their helpful comments.

### Literature Cited

- Alrasjid, H., and Mangsud. 1973. [Natural regeneration trials with mahogany (*Swietenia* spp.) in the Ngraho and Tonbo forest circles, East Java.] Laporan, Lembaga Penelitian Hutan 165, 25 p. *Forestry Abstracts* 36:190.
- Argüelles, S.L.A. 1991. *Plan de Manejo Forestal para el Bosque Tropical de la Empresa Ejidal Noh Bec*. Tesis, Ing. Agrónomo Esp. en Bosques, División de Ciencias Forestales, Universidad Autónoma de Chapingo, México.
- Argüelles, S.L.A. 1993. Conservación y manejo de selvas en el estado de Quintana Roo, México. In *Conservación y Manejo de Selva en el Estado de Quintana Roo, México*. Ponencia presentada en el I Congreso Forestal Centroamericano, III Congreso Forestal de Guatemala, Petén, Guatemala, 29 ag.–4 sept.
- Barrera de Jorgenson, A. 1993. *Chicle Extraction and Forest Conservation in Quintana Roo, México*. M.S. thesis, University of Florida, Gainesville, FL.
- Barrera de Jorgenson, A. 1994. La extracción de chicle y la conservación del chicozapote (*Manilkara zapota*) en las selvas de Quintana Roo. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*, eds. L. Snook and A. Barrera de Jorgenson, pp. 47–66. PROAFT/INIFAP/USAID/WWF-US. (Available from L. Snook.)
- Bauer, G.P. 1991. Line planting with mahogany (*Swietenia* spp): experiences in the Luquillo Experimental Forest, Puerto Rico, and opportunities in tropical America. Proceedings, Humid Tropical Lowlands Conference: Development Strategies and Natural Resource Management 5:45–64. DESFIL Project TRD/USAID and the U.S. Department of agriculture, Forest Service Tropical Forestry Program, Panama City, Panama, June 17–21, 1991.
- Camara, L., and Snook, L. 1998. Fruit and seed production by mahogany (*Swietenia macrophylla*) trees in the natural tropical forests of Quintana Roo, México. *Journal of the Tropical Resources Institute, Yale School of Forestry and Environmental Studies*, New Haven, CT, pp. 18–21.
- Chaloner, E., and Fleming. 1850. *The Mahogany Tree*. Rockliff and Son, Liverpool.
- de Landa, Fr. Diego. 1566/1937/1978. *Yucatán Before and After the Conquest*. Dover, New York.
- Diamond, J. 1986. Overview: Laboratory, field experiments and natural experiments. In *Community Ecology*, eds. J. Diamond and T.J. Case, p. 322. Harper & Row, New York.
- Edwards, C.R. 1986. The human impact on the forest in Quintana Roo, México. *Journal of Forest History* 30:120–127.
- Escobar, N.A. 1981. *Geografía General del Estado de Quintana Roo*. Fondo de Fomento Editorial del Gobierno del Estado de Quintana Roo, Chetumal.
- Finol, H. 1964. Silvicultural study of some commercial species in the university forest of Caimital, Barinas. *Revista Forestal Venezolana* 7(10/11):17–63.
- Flachsenberg, H. 1993a. Aspectos socioculturales, técnicos, económicos y financieros en el manejo del bosque tropical. In *Conservación y Manejo de Selva en el Estado de Quintana Roo, México*, pp. 1–27. Ponencia presentada en el I Congreso Forestal Centroamericano, III Congreso Forestal de Guatemala, Petén, Guatemala, 29 ag.–4 sept.
- Flachsenberg, H. 1993b. Descripción general. Unpublished internal report, Plan Piloto Forestal/Acuerto México-Alemania, Chetumal, Quintana Roo, México.
- García C., X., Rodríguez S., B., and Chavelas P., J. 1992. Regeneración natural en sitios afectados por el huracán Gilberto e incendios forestales en Quintana Roo. *Revista Ciencia Forestal en México* 17(72):75–99.
- Gates, H. 1937, 1978. Introduction. In *Yucatán Before and After the Conquest*, Fr. Diego de Landa, pp. 1–15. Dover, New York.
- Gerhardt, K. 1996. Germination and development of sown mahogany (*Swietenia macrophylla* King) in secondary tropical dry forest habitats in Costa Rica. *Journal of Tropical Ecology* 12:275–289.
- Gullison, R.E., and Hubbell, S. 1992. Regeneración natural de la mara (*Swietenia macrophylla*) en el bosque Chimanes, Bolivia. *Ecología en Bolivia* 19:43–56.
- Gullison, R.E., Panfil, S.N., Strouse, J.J., and Hubbell, S.P. 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes Forest, Beni, Bolivia. *Botanical Journal of the Linnean Society* 122:9–34.
- Hammond, N. 1982. *Ancient Maya Civilization*. Rutgers University Press, New Brunswick, New Jersey.
- Jauregui, E., Vidal, J., and Cruz, F. 1980. Los ciclones y tormentas tropicales en Quintana Roo durante el período 1871–1978. In *Quintana Roo: Problemática y Perspectiva*, pp. 47–64. Memorias del Simposio, Instituto de Geografía, UNAM & Centro de Investigaciones de Quintana Roo, Cancún, Quintana Roo, octubre de 1980.
- Johnson, M.S., and Chaffey, D.R. 1973. *An Inventory of Chiquibul Forest Reserve, Belize*. Land Resource Study 14. Foreign and Commonwealth Office, Overseas Development Administration, Land Resources Division, Surbiton, Surrey, England.
- Jorgenson, J.P. 1993. *Gardens, Wildlife Densities and Subsistence Hunting by Maya Indians in Quintana Roo, México*. Ph.D. dissertation, University of Florida, Gainesville, FL.
- Jorgenson, J.P. 1994. La cacería de subsistencia practicada por la gente Maya en Quintana Roo. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*, eds. L. Snook and A. Barrera de Jorgenson, pp. 19–46. PROAFT/INIFAP/USAID/WWF-US. (Available from L. Snook.)
- Jorgenson, J.P. 1998. The impact of hunting on wildlife in the Maya forest of México. In *Timber, Tourists and Temples: Conservation and Development in the Mayan Forest of México, Belize and Guatemala*, eds. R. Primack, D. Bray, H. Galletti, and I. Ponciano, pp. 179–194. Island Press, Washington, DC.
- Juárez B., C.J. 1988. *Análisis del Incremento Periódico de Caoba (Swietenia macrophylla King) y Cedro (Cedrela odorata) en un Relicto de Selva en el Estado de Campeche*. Tesis, Ing. Agrónomo Esp. en Bosques, División de Ciencias Forestales, Universidad Autónoma de Chapingo, Texcoco, México.
- Konrad, H.W. 1988. De la subsistencia forestal tropical a la producción para exportación: La industria chiclera y la transformación de la economía maya de Quintana Roo de 1890 a 1935. In *Etnohistoria e Historia de las Americas*.



- Memorias, pp. 161–182. 45 Congreso Internacional de Americanistas. Ediciones Uniandes, Bogotá, Colombia.
- Kukachka, B.F. 1959. Mahogany (*Swietenia macrophylla* King) Meliaceae. Foreign Wood Series 2167. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI.
- Lamb, F.B. 1966. *Mahogany of Tropical America: Its Ecology and Management*. University of Michigan Press, Ann Arbor, MI.
- López-Portillo, J., Keyes, M.R., González, A., Cabrera, E.C., and Sánchez, O. 1990. Los incendios de Quintana Roo. Catástrofe ecológica o evento periódico? *Ciencia y Desarrollo* 16(91):13–57.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15:200–213.
- Medina, R.B. 1948. *La Explotación forestal en el territorio de Quintana Roo*. Tesis. Ing. Agrónomo Esp. en Bosques. Escuela Nacional de Agricultura, Chapingo, México.
- Medina, R.B., Cuevas, A.L., and de los Santos, M.V. 1968. Ajuste al proyecto de ordenación forestal. UIEF MIQRO, Chetumal, México.
- Mell, C.D. 1917. True mahogany. Bulletin 474. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Miranda, F. 1958. Estudios acerca de la vegetación. In *Los Recursos Naturales del Sureste y su Aprovechamiento*, ed. E. Beltran, pp. 213–272. Instituto Mexicano de Recursos Naturales Renovables, México City, México.
- Morris, M.H., Negreros-Castillo, P., and Mize, C. 2000. Sowing date, shade, and irrigation affect big-leaf mahogany (*Swietenia macrophylla* King). *Forest Ecology and Management* 132:173–181.
- Murphy, J. 1990. Indigenous forest use and development in the “Maya Zone” of Quintana Roo, México. Master’s paper, Graduate Program in Environmental Studies, York University, Ontario, Canada.
- Murphy, J. 1994. Aprovechamiento forestal y la agricultura de milpa en el ejido de X-Maben, Quintana Roo, México. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*, eds. L. Snook and A. Barrera de Jorgenson, pp. 3–18. PROAFT/INIFAP/USAID/WWF-US. (Available from L. Snook).
- Murphy, P.G., and Lugo, A.E. 1986. Ecology of a tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88.
- Napier, I.A. 1973. A brief history of the development of the hardwood industry in Belize. *Coedwigwr* 26:36–43.
- Negreros Castillo, P. 1995. Enrichment planting as a silvicultural technique for sustaining Honduras mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*) production: an evaluation of experiences in Quintana Roo, México. Paper presented at the conference Conservation and Community Development in the Selva Maya of Belize, Guatemala and México, Chetumal, Quintana Roo, November 8–11.
- Negreros, C.P., and Mize, C. 1994. El efecto de la abertura del dosel y eliminación del sotobosque sobre la regeneración natural de una selva de Quintana Roo. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo*, eds. L. Snook and A. Barrera de Jorgenson, pp. 107–126. INIFAP/PROAFT/AID/WWF-US, Mérida, México. (Available from L. Snook).
- Oliver, C.D., and Larson, B. 1990. *Forest Stand Dynamics*. Biological Resource Management Series. McGraw-Hill, New York.
- Parraguirre L., C. 1994. Germinación de las semillas de trece especies forestales comerciales de Quintana Roo. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*, eds. L. Snook and A. Barrera de Jorgenson, pp. 67–80. PROAFT/INIFAP/USAID/WWF-US. (Available from L. Snook).
- Pennington, T.D., and Sarukhan, J. 1968. *Árboles Tropicales de México*. INIF/FAO, México.
- Pennington, T.D., Styles, B.T., and Tayler, D.A.H. 1981. Meliaceae. *Flora Neotropica Monograph* 28:1–472.
- Pérez, V.G. 1980. El clima y los incendios forestales en Quintana Roo. In *Quintana Roo: Problemática y Perspectiva*, pp. 65–80. Memorias del Simposio, Instituto de Geografía, octubre de 1980. UNAM & Centro de Investigaciones de Quintana Roo, Cancun, Quintana Roo, Mexico.
- Plan Piloto Forestal. 1987. El Remate, Ejido Noh Bec. Unpublished internal document. Sociedad de Productores Forestales Ejidales de Quintana Roo, Chetumal, Quintana Roo, Mexico.
- Quevedo H., L. 1986. *Evaluación del Efecto de la Tala Selectiva Sobre la Renovación de un Bosque Humedo Subtropical en Santa Cruz, Bolivia*. Masters thesis, Universidad de Costa Rica, CATIE, Turrialba, Costa Rica.
- Record, S.J. 1924. *Timbers of Tropical America*. Yale University Press, New Haven, CT, pp. 348–356.
- Rodríguez C., R. 1944. *La Explotación de los Montes de Caoba en el Territorio de Quintana Roo*. Tesis. Ing. Agr. en Bosques. Escuela Nacional de Agricultura, Chapingo, México.
- Rodríguez S., B., Chavelas P., J., and García C., X. 1994. Dispersión de semillas y establecimiento de caoba (*Swietenia macrophylla*) después de un tratamiento mecánico del sitio. In *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*, eds. L. Snook and A. Barrera de Jorgenson, pp. 81–90. PROAFT/INIFAP/USAID/WWF-US. (Available from L. Snook.)
- Rodríguez y Pacheco, A.A., and Barrio Chavira, J.M. 1979. Desarrollo de caoba (*Swietenia macrophylla* King) en diferentes tipos de suelos. *Ciencia Forestal* 4(22):45–64.
- Snook, L.C. 1991. Opportunities and constraints for sustainable tropical forestry: lessons from the Plan Piloto Forestal, Quintana Roo, México. Proceedings, Humid Tropical Lowlands Conference: Development Strategies and Natural Resource Management 5:65–83. DESFIL Project, TRD/USAID and the U.S. Department of Agriculture, Forest Service Tropical Forestry Program, Panama City, Panama, June 17–21, 1991.
- Snook, L.K. 1993. *Stand Dynamics of Mahogany (Swietenia macrophylla) and Associated Species After Fire and Hurricane in the Tropical Forests of the Yucatán Peninsula, México*. Doctoral dissertation, Yale School of Forestry and Environmental Studies, New Haven, CT. (University Microfilms International 9317535, Ann Arbor, MI.)
- Snook, L.K. 1998. Sustaining harvests of mahogany from México’s Yucatán forests: past, present and future. In *Timber, Tourists and Temples: Conservation and Development in the Mayan Forest of México, Belize and Guatemala*, eds. R. Primack, D. Bray, H. Galletti, and I. Ponciano, pp. 61–80. Island Press, Washington, DC.
- Snook, L.K., and Barrera de Jorgenson, A., eds. 1994. *Madera, Chicle, Caza y Milpa: Contribuciones al Manejo Integral de las Selvas de Quintana Roo, México*. PROAFT/INIFAP/USAID/WWF-US, Mérida, México. (Copies available from L. Snook.)
- Stevenson, N.S. 1927. Silvicultural treatment of mahogany forests in British Honduras. *Empire Forestry Journal* 6:219–227.
- Synnott, T.J. 1995. Practices for sustainable silviculture at the Plan Piloto Forestal in Quintana Roo, México. Unpublished final report to the Biodiversity

- Support Program. Biodiversity Support Program, WWF/TNC/WRI, Washington, DC.
- Verissimo, A., Barreto, P., Tarifa, R., and Uhl, C. 1995. Extraction of a high-value natural resource in Amazonia: the case of mahogany. *Forest Ecology and Management* **72**(1):39–60.
- Villaseñor A., R. 1958. Los bosques y su explotación. In *Los Recursos Naturales del Sureste y su Aprovechamiento*, ed. E. Beltran, pp. 273–326. Instituto Mexicano de Recursos Naturales Renovables, México City, México.
- Weaver, P.L. 1987. Enrichment planting in tropical America. In *Management of the Forests of Tropical America: Prospects and Technologies*, eds. J. Figueroa, F. Wadsworth, and S. Branham, pp. 259–277. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Río Piedras, PR.
- Westoby, M. 1984. The self-thinning rule. *Advances in Ecological Research* **14**:167–225.
- Whigham, D.F., Olmsted, I., Cano, E.C., and Harmon, M.E. 1991. The impact of hurricane Gilbert on trees, litterfall and woody debris in a dry tropical forest in the northeastern Yucatán península. *Biotropica* **23**(4a):434–441.
- Whigham, D.F., Lynch, J.F., and Dickinson, M.B. 1998. Dynamics and ecology of natural and managed forests in Quintana Roo, México. In *Timber, Tourists and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala and México*, eds. R.B. Primack, D.B. Bray, H.A. Galletti, and I. Ponciano, pp. 267–281. Island Press, Washington, DC.
- Whitman, A., Brokaw, N.V.L., and Hagan, J.M. 1997. Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. *Forest Ecology and Management* **92**:87–96.
- Wilkinson, L. 1988. *Systat. The System for Statistics for the PC*. SPPSS, Inc., Chicago, IL.
- Wilson, E.M. 1980. Physical geography of the Yucatán península. In *Yucatán: A World Apart*, eds. E.H. Mosley and E.D. Terry. University of Alabama Press, Tuscaloosa, AL.
- Wolffsohn, A.L.A. 1961. An experiment concerning mahogany germination. *Empire Forestry Review* **40**(1):71–72.
- Wolffsohn, A.L.A. 1967. Post-hurricane forest fires in British Honduras. *Commonwealth Forestry Review* **46**:233–238.