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Point-Counterpoints on the Conservation of Big-Leaf Mahogany

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Point-Counterpoints on the Conservation of Big-Leaf Mahogany

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Abstract

The objective of this publication is to draw attention to research relevant to the evaluation of the conservation status of big-leaf mahogany and to clarify misconceptions concerning the species and its place in tropical forests. Many of these misconceptions have clouded the debate regarding the possible listing of big-leaf mahogany in Appendix II of the Convention for the International Trade of Endangered Species (CITES). Available data are used to address 14 point-counterpoint issues surrounding the controversy about the ecology and management of big-leaf mahogany. In addition, four critical questions regarding the issues of genetic erosion and conservation of genetic variation of big-leaf mahogany throughout its range are examined. Worst-case scenarios of the big-leaf mahogany situation in tropical America are examined and science-based conservation strategies are outlined.

Introduction

The status of big-leaf mahogany, one of the most valuable and best known tropical timbers, has been the subject of global attention over the past decade. The importance and scope of the debate, centered on the possible listing of the species in Appendix II of the Convention on the International Trade of Endangered Species (CITES), transcends the natural boundaries of the species range. The outcome of the big-leaf mahogany debate will affect the international trade of all timber species—whether they are endangered or not, or whether their origin is tropical, temperate, or boreal. Moreover, in reference to public opinion, the big-leaf mahogany issue is framed within the debate concerning the overall condition of tropical forests, their biodiversity, and the allowable level of human intervention in natural ecosystems. Given the importance of the big-leaf mahogany issue, it is imperative to consider the best scientific information available so that policy formulation is informed.

Leafless young adult tree in south Para, Brazil, with fruit capsules. (Photo by Jimmy Grogan)

Participants in the debate about the conservation of mahogany represent a broad spectrum of society, both in terms of geography and in their professional interests. The debate is global in terms of geography and in that the professional interest of participants spans from that of the general public to highly specialized scientists. While there have been several syntheses regarding the conservation of big-leaf mahogany (Lamb 1966, Hartshorn 1992, MacLellan 1996, Bauer and Francis 1998, and Mayhew and Newton 1998), many of the points of disagreement continue unresolved because there has been no attempt to sort available facts from opinions or hypotheses. As a result, progress is slow. The debate is hindered by the persistence of unsubstantiated positions or the presentation of "facts" that are either untested hypotheses or points of view whose truthfulness rest on hidden or unspecified assumptions. The resulting confusion has negative consequences to the formulation of policy because policymakers find themselves unable to differentiate opinion from scientific understanding.

The objective of this report is to draw attention to research relevant to the evaluation of the ecology and management of big-leaf mahogany and to clarify misconceptions that have clouded the debate about this species and the tropical forests to which it belongs. The discussion is framed with a point-counterpoint approach to draw attention to the polarity of that debate and to clarify the issues.

Tropical Forests

Point: All tropical forests are rain forests.

Counterpoint: Most tropical forests are seasonal and dry.

Tropical forests constitute about half of the world's forests (dividing 1.76 billion hectares of tropical forests [fig. 1] by 3.44 billion hectares of world forests [FAO 1995] = 51 percent). Tropical forests are diverse not only in species composition but also in the number of species associations. There are more forested lifezones (*sensu* Holdridge 1967) in the tropics than in the temperate and boreal latitudes combined (table 1). Because the lowland tropics have a narrow temperature range, lowland tropical forests are more adequately classified according to annual rainfall: 500 to 1,000 millimeters for dry forests, 1,000 to 2,000 millimeters for moist forests, 2,000 to 4,000 millimeters for wet forests, and more than 4,000 millimeters for rain forests (Holdridge 1967). Most of the tropical forest lands are classified as dry forests, followed in area by moist forests (table 1). Wet and rain forests cover the least area.

Big-leaf mahogany is mostly a lowland dry forest species, although it also grows in moist forests and at

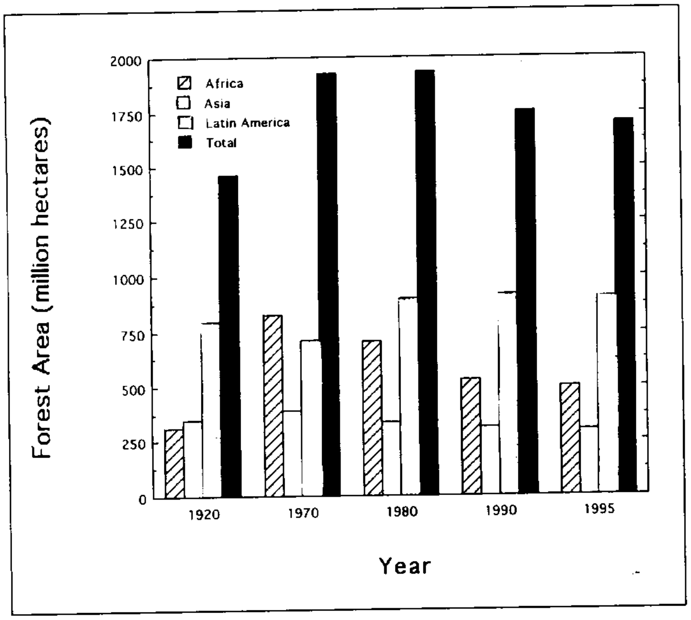

Figure 1. Estimates of the area of tropical forests. Sources of data are: 1920's—Zon and Sparhawk 1923; 1970's—Persson 1974; 1980's—FAO/UNEP 1982; 1990—FAO 1993a; and 1995—FAO 1997.

elevations of up to 1,400 meters above sea level (Lamb 1966). Its large natural distribution (some 200 million hectares) and growth in plantations span several lifezones, from tropical and subtropical dry, to tropical and subtropical moist, to wet forest. Big-leaf mahogany does not, however, grow well in more humid lifezones, such as subtropical lower montane wet forests, nor in tropical or subtropical rain forest lifezones.

Deforestation

Point: Forestry activities cause deforestation in the tropics.

Counterpoint: Forestry activities account for a small proportion of tropical deforestation.

The rate of tropical deforestation has been estimated to be between 0.6 percent per year from 1981 to 1985, and 0.8 percent per year from 1981 to 1990 (FAO 1993a). Estimates of the area of tropical forests since the 1920's (fig. 1) show a fairly constant area for Asia and Latin America, a rise followed by a decline in Africa, and a similar pattern for the whole region. Apparently the estimated area of tropical forests in 1995 was either the same as or higher than that estimated in the 1920's. The uncertainty in these estimates is high given the large area, its inaccessibility, and the poor state of knowledge about the tropics.

The rate of deforestation in the tropics is influenced by climatic condition, topography, and social factors. In general, rain and wet tropical forests experience lower deforestation rates than moist and dry ones; flat lands are deforested before steep lands; and agriculturally based economies are more likely to cause deforestation than those based on fossil fuels.

Kaimowitz and Angelsen (1998) reviewed 150 models of tropical deforestation and concluded that deforestation tends to increase when forests are readily accessible, agricultural and timber prices are high (with agricultural prices being a stronger determinant than timber prices), rural wages are low, and opportunities for long-distance trade of agricultural products are high. Most tropical deforestation occurs to compensate for the degradation of agricultural lands (Dale et al. 1993). Forestry activities account for a small proportion of the total deforestation in the tropics (Kaimowitz and Angelsen 1998), which means that even total cessation of international trade in forest products would solve at best only a small proportion of the deforestation problem. The indirect effects of roads is discussed below in the logging section.

Because the causal forces underlying deforestation are complex, it is impossible to extrapolate pantropical or even country-level deforestation rates to the habitat of a particular species such as big-leaf mahogany. In fact, countries with the largest fraction of big-leaf mahogany habitats are those with some of the lowest rates of deforestation among range countries (table 2). But such facts do not help explain land-use trends within the range of big-leaf mahogany. Specific studies at the proper spatial scales are needed to support any conclusions about the relationship between the status of big-leaf mahogany and the rates of deforestation in the tropics. For this reason, Kaimowitz and Angelsen (1998) recommended that future research on deforestation focus on the household and regional scales instead of the national and global. Such a focus allows better understanding of the proximate causes of deforestation.

Point: Deforestation is irreversible.

Counterpoint: Tropical forests can be restored in deforested areas.

Tropical deforestation is not irreversible. In the absence of further human activity, secondary forests develop in most areas previously deforested and used for purposes other than forests (Brown and Lugo 1990). The reforestation of abandoned pastures, agricultural fields, and even cities, such as those of the Maya, is a natural process mediated by animal seed dispersers—that is, birds, mammals, and insects. Most of the Central American range of big-leaf mahogany was deforested for a millennium by the Maya (Lamb 1966). Mature secondary forests with large big-leaf mahogany trees now are found in the region.

Similarly, secondary forests now occur in the State of Pará, Brazil, where the construction of the transamazonian highway in the 1970's resulted in a deforestation event that appeared in satellite images as a "fishbone pattern" with the main road running through the center and perpendicular deforested strips on both sides of the road. These satellite images were used to justify proposing

Table 1. Number of lifezones in the major geographic regions and climatic zones of the world (Lugo and Brown 1992) and area of tropical lands classified according to lifezones (Brown and Lugo 1982). Area of the tropical lifezones in parentheses, in million hectares.

Lifezone	*Geographic Region*			
Category	*Tropics*	*Temperate*	*Boreal*	*Total*
Dry	33 (1,887)	16	3	52
Moist	11 (1,582)	7	2	20
Wet/rain	22 (642)	14	4	40
Total	**66 (4,111)**	**37**	**9**	**112**
Forested	33	16	3	52

Table 2. Rate of deforestation (1980 to 1990) in countries where big-leaf mahogany grows naturally (FAO 1993a).

Country	*Deforestation (percent per year)*
Belize	0.2
Bolivia*	1.2
Brazil*	0.6
Colombia	0.7
Costa Rica	2.9
Ecuador	1.8
Guatemala	1.7
Honduras	2.1
Mexico*	1.3
Nicaragua	1.9
Panama	1.9
Peru*	0.4
Venezuela	1.2

*Countries that together comprise 90 percent of the forest area containing big-leaf mahogany.

the listing of big-leaf mahogany in CITES (Amendment to Appendix II, Tenth Meeting of the Conference of the Parties, Harare, Zimbabwe, 1997), based on the argument that such deforestation was somehow related to the international trade of the species. Today, the landscape has changed, and the deforested fishbone pattern is covered by vigorous secondary forests in those areas abandoned by humans (Tucker et al. 1998, Morán and Brondizio 1998). Morán et al. (1996) found that the rate of establishment of secondary forests along the transamazonian highway was twice as high as the current rate of deforestation. Big-leaf mahogany benefits from the regeneration and spread of secondary forests because it thrives in open areas, in secondary forests, or at the interface between abandoned pastures and secondary forests (Gerhardt 1994, 1996).

Tropical Timbers

Point: Tropical countries produce mostly wood products for local consumption and for export markets, where they compete with U.S. timber production.

Counterpoint: Most tropical countries are net wood importers, and most of their wood production is for fuelwood and charcoal for local consumption; exports of wood products from the neotropics are not significant and do not compete with U.S. products.

Wood is of critical importance to tropical countries, particularly fuelwood and charcoal used for heating and cooking in regions where fossil fuels are either unavailable or too expensive. Wood energy accounts for 58, 17, and 8 percent of the total energy consumption in the African, Asian, and American tropics, respectively (Masson 1983). Because of this need, the tropics as a whole are a net importer of timber and have a fuelwood deficit (Lyke and Brooks 1995). The tropics are responsible for a small fraction of the world's industrial roundwood production, but they produce the largest amount of fuelwood and charcoal in the world (fig. 2). However, even when fuelwood consumption per capita is included in the total, the annual consumption of wood by developing countries is lower than the world average and lower than that of the United States and other developed countries (fig. 3).

Tropical forests contain more tree species per unit area than any other forest type in the world, but that diversity of species has not been commercialized. Very few tropical species enter local markets and fewer still enter international markets. Yeom (1984) found that in Malaysia, the most prominent timber producing country in the tropics, there are about 3,000 common tree species, of which 677 are thought to have commercial value. Of these, 408 are actually used commercially. In Asia and South and Central America, fewer than 15 species account for most of the lumber trade.

The volume of tropical woods that enters the domestic and international markets is a small fraction of the standing wood volume in the forest (fig. 4). Species with market potential but which are not recognized by markets are designated as "lesser known species." Many argue that for tropical forestry conservation to be effective, these lesser known species need to be commercialized (Yeom 1984, Lugo 1987, Gullison and Hardner 1993). The use of lesser known species could relieve pressure on the few commercial species now recognized and provide economic incentives for better management and conservation of tropical forests (Browder et al. 1996).

Trade Situation

Point: International trade of big-leaf mahogany causes deforestation; by reducing trade, tropical deforestation is abated.

Counterpoint: Deforestation in the range of big-leaf mahogany is caused by complex socioeconomic factors rather than by international trade of the species; reduction of trade through nonmarket restrictions may, in fact, exacerbate deforestation by devaluing forests.

The known trade of big-leaf mahogany between 1850 and 1996 oscillated between 70,000 and 140,000 cubic meters per year, with occasional peaks and valleys beyond this range (for example, a 320,500-cubic-meter peak in 1987) (fig. 5). Importation to the United States between the 1910's and 1996 ranged from 30,000 to 320,500 cubic meters per year. This level of trade does not show a significant increasing trend. In fact, imports in the early 1950's were similar to the average of the 1990's. Imports to the United Sates are mostly from South

Recently germinated seedling in closed forest with simple leaves. (Photo by Jimmy Grogan)

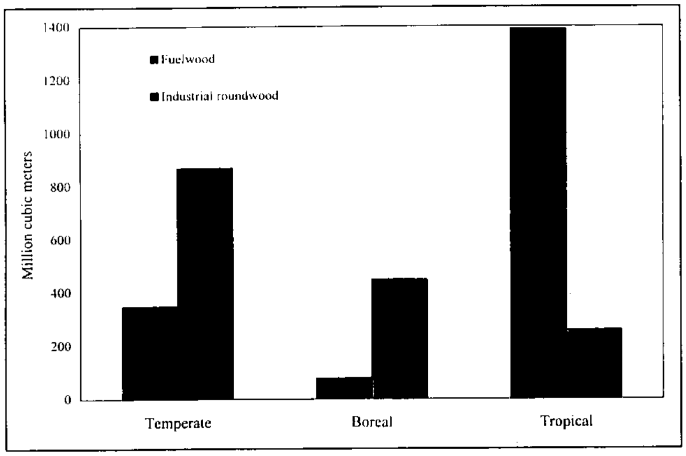

Figure 2. *Annual world production of industrial roundwood and fuelwood by latitudinal region (Lyke and Brooks 1995).*

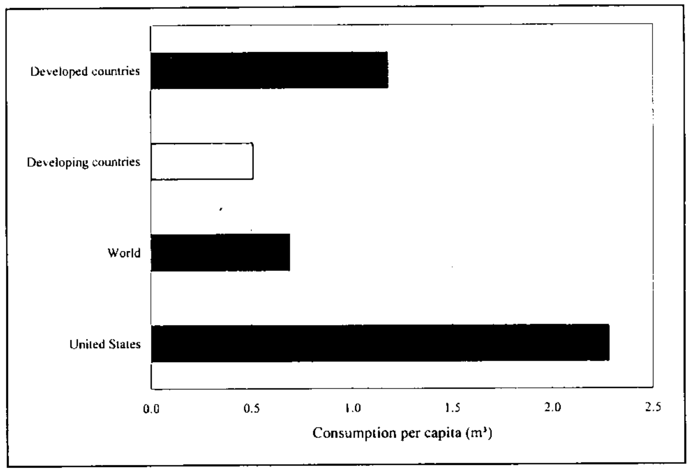

Figure 3. *Wood consumption by region of the world (Lyke and Brooks 1995).*

America. Mahogany exports from Central America in the 1990's were about 10 percent of the total mahogany imports to the United States (fig. 6). Trade exports from Pará, Brazil, show a recent decline associated with internal control measures (fig. 7).

The United States imported 4 percent of all tropical timber products traded in 1989 (Smith et al. 1995). The most important tropical timber species used commercially that year by the United States was big-leaf mahogany (Smith et al. 1995). Of the importation of tropical timber products to the United States in 1993, big-leaf mahogany accounted for 57 and 59 percent by volume and value, respectively. Big-leaf mahogany wood is imported to the United States in two grade levels for various end-uses by industries that include furniture manufacturers, level manufacturers, foundry industries, door manufacturers, and architectural manufacturers (Smith et al. 1995).

International trade is not a major factor in the deforestation process in Central and South America because the amount of wood involved is so small that its effects at the local scale are not significant. The total global trade in tropical timber products represents only 4 percent of the volume of tropical forest cut (Smith et al. 1995). The volume of big-leaf mahogany wood in international trade is less than 1 percent of estimated big-leaf mahogany stocks (assume a trade of 320,500 cubic meters [highest value in fig. 5] divided by stocks of about 35 million cubic meters [Figueroa Colón 1994] = 0.92 percent of stocks in trade). This volume is so small that the global demand could be satisfied with 70,000 hectares of slow-growing plantations (box 1). Moreover, the extraction of big-leaf mahogany causes very little disturbance to forests (see below).

Big-leaf mahogany habitat has been reduced in large sectors of its range for reasons other than forestry activities. Land-use change in the tropics responds to economic, political, cultural, and other factors that are weakly influenced by international trade or the effects of logging of particular species (Kaimowitz and Angelsen 1998). In the mahogany debate, it is often pointed out that the loss of habitat for big-leaf mahogany is analogous to the loss of habitat that occurred in the Caribbean for small-leaf mahogany (Amendment to Appendix II, Tenth Meeting of the Conference of the Parties, Harare, Zimbabwe, 1997). However, the socioeconomic, ecological, and geographic conditions that led to the

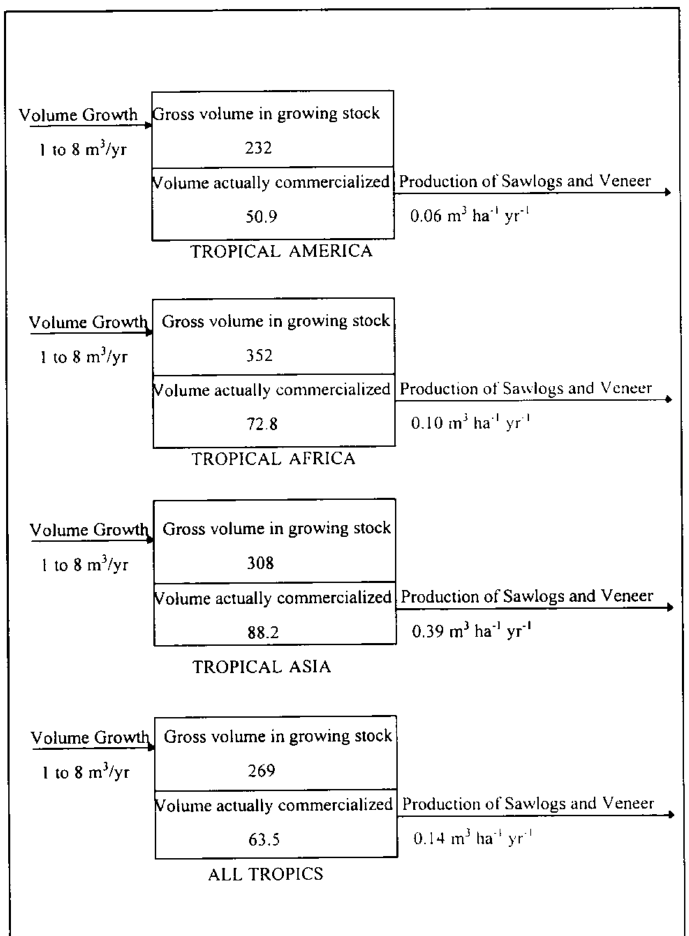

Figure 4. *Gross volume in growing stock and volume actually commercialized (cubic meters per year), and rate of volume growth and production of sawlogs and veneer (cubic meters per hectare per year) between 1976 and 1979, in productive closed tropical forests (FAO/UNEP 1982). Data are for overbark volume of trees greater than 10 centimeters in diameter at breast height.*

reduction of small-leaf mahogany habitat in the Caribbean islands are not the same as those impacting big-leaf mahogany in continental lands. For example, the human population density in Caribbean islands is between 10 and 100 times higher than that of countries within the natural distribution of big-leaf mahogany (Lugo et al. 1981). Each mahogany species grows in unique natural and anthropogenic environments. Today, both species grow and regenerate without difficulty where forests remain in South and Central America and the Caribbean. Efforts to protect big-leaf mahogany habitat could be more effective if the social forces that determine land-use change and forest management were addressed directly, with extensive local participation.

Logging for Big-leaf Mahogany

Point: Logging for big-leaf mahogany is destructive of biodiversity.

Counterpoint: Logging for big-leaf mahogany is compatible with conserving biodiversity.

Logging for big-leaf mahogany has very little potential to cause impact on forests (table 3). In Belize, logging for big-leaf mahogany did not change species composition, had minimal effects on bird communities, and was compatible with the regeneration of tree species of secondary economic importance (Whitman et al. 1994). In fact, of 26 avian guilds tested, none had more species in the unlogged than the logged forest, but four had more species in the logged than the unlogged forest (Whitman et al. 1998). Whitman et al. (1997) compared forest damage caused by big-leaf mahogany logging with forest damage caused by other types of logging and by natural disturbances (hurricanes and tree-fall gaps). They concluded that logging for big-leaf mahogany, which removes a few trees at a time, was less disruptive of forests than other types of logging; was "trivial" in comparison with hurricane damage; and was of lower density on the landscape than natural tree-fall gaps. Forest regeneration and turnover due to big-leaf mahogany logging was well within the normal range of forests subjected to natural disturbances.

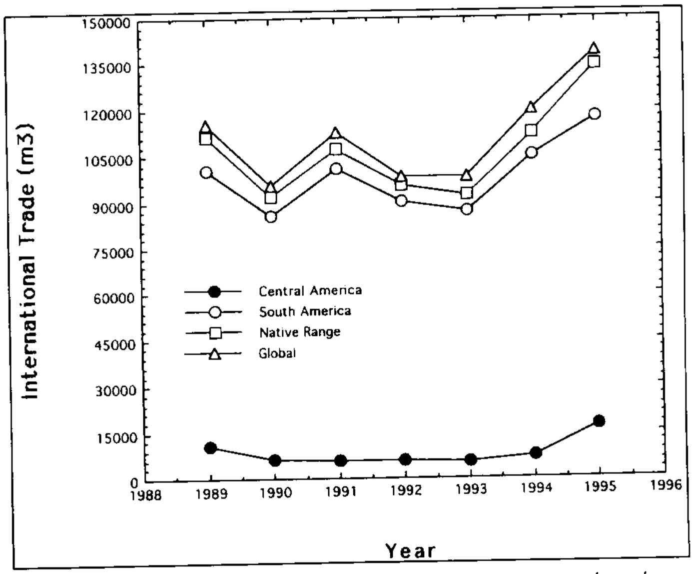

Figure 6. *International trade of mahogany from Central and South America (U.S. Department of Commerce, Bureau of the Census, Foreign Trade Division, Trade Data Inquiries and Controls Section, Washington, D.C.).*

Gullison and Hardner (1993) also found a low level of damage in big-leaf mahogany stands as a result of logging (4.4 percent of area damaged). However, a modeling exercise indicated that even this low level of damage could be reduced further through better road design and location. Lugo and Gucinski (personal communication) outlined an ecological approach for evaluating road alignment, design, operation, maintenance, and decommissioning in rural areas. Such an approach is needed because roads have many potential effects on ecosystems and land use, and dedicated management approaches are required to minimize their effects (Bruijnzeel and Critchley 1994). For example, roads are used in many tropical

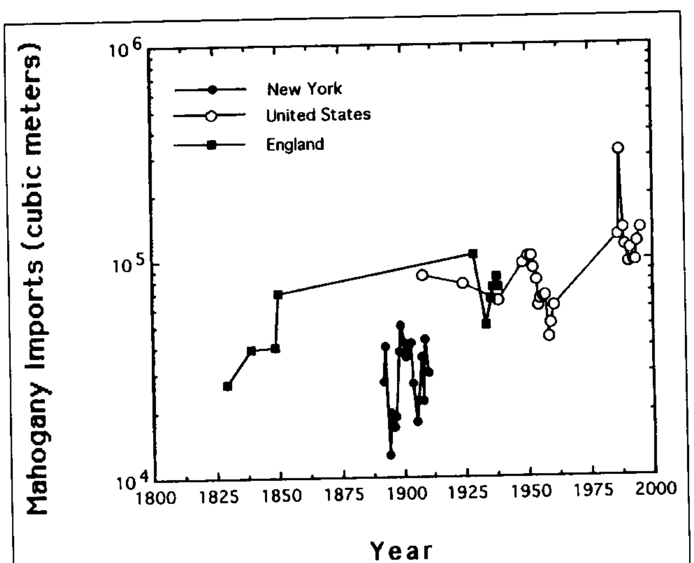

Figure 5. *Long-term record of international trade of mahogany, including the United States and England (Lugo and Fu 1998).*

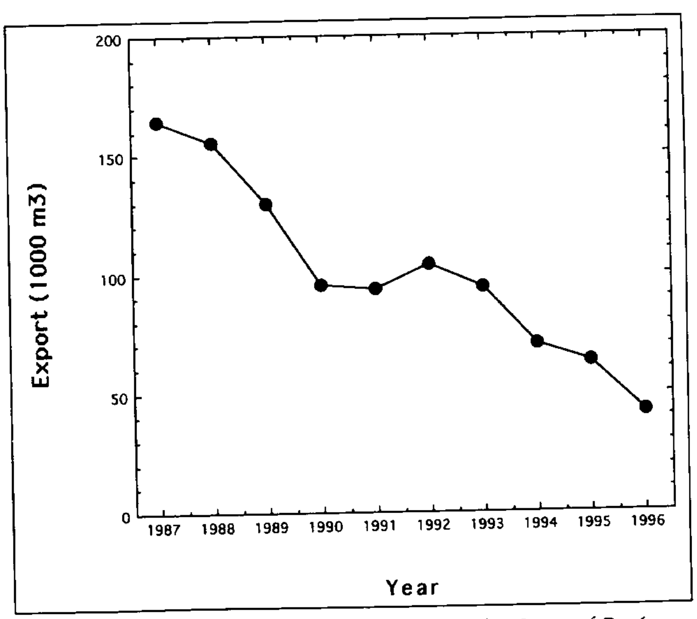

Figure 7. *Trade of big-leaf mahogany from the State of Pará, Brazil, between 1987 and 1996 (Gasparetto 1998).*

Box 1. Plantations Can Satisfy the Known Demand for Mahogany Wood

The global area of mahogany plantations is 150,000 hectares. The wood yield of these plantations ranges from 6 to 22 cubic meters per hectare per year (Figueroa Colón 1994, Tillier 1995, Lugo and Fu 1998). These yields cover plantations up to 50 years old in Puerto Rico, Martinique, Indonesia, and the Philippines.

- In 1995, mahogany imports to the United States were 116,387 cubic meters in rough volume, plus 22,503 cubic meters of dressed volume for a total of 138,890 cubic meters.
- Assume that for each cubic meter reported, two were lost, wasted, or not reported; thus, the total was 416,670 cubic meters. Contente de Barros et al. (1992) estimated a demand of 500,000 cubic meters per year for all mahogany uses in Brazil (box 4).
- Assume that mahogany plantations produce (minimally) 6 cubic meters per hectare per year
- The area required to satisfy the annual export of mahogany would be 416,670 ÷ 6.0 = 69,445 hectares, or about 70,000 hectares.
- The present area of mahogany plantations (150,000 hectares, from table 10) could produce twice the estimated volume in international trade. Moreover, plantations also minimize waste.

This estimate serves only to illustrate the potential of plantations and is not an indicator of the reality, because many of the mahogany plantations are not at rotation age or not dedicated to international trade.

For those who worry about the ecological effects of plantations, mahogany plantations have been shown to exhibit ecological characteristics similar to those of secondary forests of similar age (Lugo 1992, Lugo and Fu in press).

Saplings growing in forest shade develop flattened, surpressed crowns. Here a canopy gap has been opened above surpressed saplings in south Para, Brazil, to test their ability to respond to increased light. (Photo by Jimmy Grogan)

locations to gain access to resources and to abandon overexploited areas. These human population movements have complex social causes and conflicting rationales (Schmink 1987). Their solution rests on socioeconomic and political actions outside the realm of forestry.

Management Situation

Point: Active forest management is not an alternative to big-leaf mahogany conservation.

Counterpoint: Active forest management is the best alternative to big-leaf mahogany conservation.

Active forest management is not considered by many as an alternative to the conservation of big-leaf mahogany for a variety of reasons. These include (1) outright objections to any level of tree harvesting and forest management, (2) a focus on past management failures as evidence that management does not work, (3) a belief in preservation of remaining mature forest stands as the first option for conservation, and (4) the focus on the obstacles to sound forest management, such as insect depredation, perceived poor regeneration of the species, potential loss of genetic diversity, social pathologies, and so forth.

Little can be done here about the first point, which is a matter of beliefs and not of science. The second point is based on a grim reality in the tropics: tropical forests, including big-leaf mahogany stands, are not actively managed, nor are they treated commensurate with their importance and value. For example, after assessing the situation of tropical forest management in the neotropics, FAO (1993b, p. 133) concluded:

> *... readers will have to agree that notwithstanding all the numerous research and development projects undertaken here and there in Latin America, in most of the countries tropical forest management exists only in theory, and has practically never been put in practice in the field, though governments require submission of a forest management plan before issuing a logging permit.*

Regardless of this discouraging situation, it is precisely for the importance and value of tropical forests that one cannot accept past failures as a reason for not doing what needs to be done. To give up

Table 3. Percent of area or plants impacted by big-leaf mahogany logging activities for other species in Belize in comparison with other types of logging activities elsewhere in the neotropics (Whitman et al. 1997).

	Area Impacted (percent)	
Activity	*Mahogany*	*Other Neotropical Areas*
Direct effect of logging	12.9	18.3
Canopy cover removal	2.0	43.7
Soil compaction	3.8	no data
Trees damaged	4.8	64
Saplings damaged	1.9	no data

on the opportunity to manage tropical forests based on available scientific information is tantamount to allowing random forces to degrade and decimate the resource and to forfeit our stewardship responsibility over most of the global biodiversity. The condition of most tropical forestry today is analogous to that of the United States at the turn of the century, which empowered the Forest Service to protect and restore forests throughout the country. There is no known reason why tropical countries cannot conserve their forests sustainably if they decide to do so. However, recognizing the many values of forests, including their commercial value, is a necessary prerequisite to justifying government interest in tropical forests. If forests are perceived as not having value, the incentive for management and protection is lost, and large-scale land conversion to other uses will ensue.

Point three is not incompatible with active management. In fact, the conservation of genetic diversity and forest stands in a variety of states, including those preserved in protected areas, is an essential ingredient of sustainable forest management. However, the neotropical region has already dedicated a greater percentage of its land area to preserves than is typical for countries such as the United States. Mares (1986) reported that South America has three times more land area in preserves than the United States. In relative terms, 25 percent more of the land in South America is preserved than in the United States. The call for more preserves as a solution to land use or forest management issues in the neotropics requires careful consideration to the issues raised by Mares, who showed that the establishment of protected areas in the neotropics is not a simple matter. Mitigating circumstances to objections raised under point four are addressed here.

Branch with recently flushed leaves and axillary inflorescences, which flower for 2-4 weeks. (Photo by Jimmy Grogan)

Point: The silviculture of big-leaf mahogany forests is not sustainable because there are many impediments to management.

Counterpoint: Impediments to management of big-leaf mahogany can be resolved; however, determining whether sustainable management of the species is or is not attainable requires a sophisticated level of analysis.

In general, big-leaf mahogany can be managed successfully because the species has biological characteristics that predispose it to management (Lamb 1966), its silviculture is reasonably well understood (Lamb 1966, Mayhew and Newton 1998), and there have been many examples of successes with the species that can be followed. When big-leaf mahogany is managed poorly or not managed at all, failures do occur. There are many examples of past management failures that can provide insight for development of sustainable management guidelines.

Seed Production and Germination

Big-leaf mahogany is a prolific seed producer. As trees get larger (greater than 80 centimeters in diameter at breast height) and older, absolute seed production increases proportionally (Gullison et al. 1996, Camara and Snook 1998). However, mahogany trees can produce seed as early as age 12 (Lamb 1966). In a study in Mexico, Camara and Snook (1998) found that fruit production per unit of canopy area was not significantly different in trees ranging from 15 to 115 centimeters in diameter. Gullison et al. (1996) found the most fecund trees producing as many as 600 capsules per tree, with about 33,000 seeds in a year. These data justify the need to allow a few large trees to remain standing for seed production and regeneration purposes after logging operations. The collection, processing, and germination of big-leaf mahogany seeds all are well understood (Samaniego et al. 1995 a, b).

Seedlings

Big-leaf mahogany seedlings have a high-light adaptation but can also grow and survive in the shade (Medina et al. in press). High leaf structural plasticity (in terms of leaf area, specific leaf area, nutrient uptake and allocation, and leaf sap osmolality) allows seedlings to grow in a wide range of light conditions. Maximum growth is in intermediate light. Transplanted seedlings survive in pastures and inside the canopy of deciduous and semievergreen secondary forests (Gerhardt 1994). Seedlings appear to be rather insensitive to large microsite variations in secondary vegetation (Gerhardt 1996), but canopy opening enhances seedling growth (Bauer 1987, Whitman et al. 1974 and 1977). Seedlings also grow well inside the canopy of big-leaf mahogany plantations (Lugo and Fu in press, Wadsworth et al. in press, Wang and Scatena in press).

Mahogany inflorescence with open flowers. Flowers are ~ 1 cm across and sharply scented. (Photo by Jimmy Grogan)

Big-leaf mahogany seedlings are large, and seedling size is important for seedling survival. Larger seedlings have better drought survival than smaller ones. Line plantings of big-leaf mahogany are more successful when large seedlings are used (Weaver and Bauer 1986).

Drought is a major cause of seedling mortality (Gerhardt 1994). Seedling mortality can be high when first subjected to drought, but decreases in the same cohort with subsequent drought events. Seedlings develop deep roots and a high root-to-shoot ratio. Seedling survival is also enhanced by reduced competition (Gerhardt 1994, Wang and Scatena in press).

Regeneration

Point: Big-leaf mahogany has low capacity for regeneration.

Counterpoint: Big-leaf mahogany has a high capacity for regeneration.

The source of the confusion about the poor regeneration of big-leaf mahogany is its poor regeneration under closed canopies. Many studies have shown that logging for big-leaf mahogany does

Two-year-old saplings approaching 5 m tall in growth experiments in south Para, Brazil. (Photo by Jimmy Grogan)

not disturb forests sufficiently to open the canopy to the degree required for big-leaf mahogany regeneration (Gullison and Hardner 1993, Whitman et al. 1994, 1997; but see Grogan et al. in press). As a result, regeneration after low-impact logging is poor. However, areas treated silviculturally with larger openings support increased big-leaf mahogany regeneration. Possible silvicultural solutions to the big-leaf mahogany regeneration in logged stands include establishing the species in line plantings or stimulating the harvest of lesser known species so that the percentage of the canopy opened after logging increases to thresholds that favor the regeneration of big-leaf mahogany and other high-light-adapted tree species.

The regeneration of big-leaf mahogany is dependent on site conditions. Under natural conditions, big-leaf mahogany regeneration is associated with large-scale and infrequent disturbances such as hurricanes (Snook 1993), fires (Snook 1993), floods (Gullison et al. 1996), and shifting agriculture (Negreros Castillo and Mize 1993), as well as small-scale events such as windthrows and canopy gap openings (Lamb 1966). Negreros Castillo and Mize (1993) point out that regeneration of big-leaf mahogany is usually delayed a few years after a catastrophic event. Numerous studies of regeneration show variability in the response of the species. While the conditions for natural regeneration of big-leaf mahogany are not under dispute, there is concern about the lack of regeneration after logging or poor silvicultural practices. However, several studies document the conditions necessary for big-leaf mahogany regeneration after human alteration of forests.

Ramos and del Amo (1992) studied big-leaf mahogany regeneration in enrichment plantings of secondary forests in Veracruz, Mexico. Results were based on 8-year-old plantings at different levels of canopy opening (17, 37, and 68 percent light transmission). Big-leaf mahogany grew best at 68 percent light transmission and least at 17 percent, and it survived best at 34 and least at 17 percent light transmission. Big-leaf mahogany had positive growth and survival at all light treatments. Noncommercial tree species had better growth than commercial species, but that did not affect the eventual success of big-leaf mahogany. Similar results were obtained in Belize, where big-leaf mahogany grew and survived when the canopy was opened by road and skid-trail establishment during logging operations (Whitman et al. 1994).

In Quintana Roo, Mexico, a large-scale study of forest regeneration in canopy openings that ranged from 0 to 55 percent canopy removal showed that some canopy opening was necessary for the regeneration of commercial the species, including big-leaf mahogany (Negreros Castillo and Mize 1993). However, the species composition of the forest was not affected by these levels of canopy opening. Light-demanding commercial species such as big-leaf mahogany increased in abundance with increased canopy opening. More noncommercial species regenerated than did commercial species (49.5 percent as opposed to 7.6 percent of 146,000 seedlings per hectare were noncommercial and commercial species, respectively), but the regeneration of commercial species, including big-leaf mahogany, was sufficient to ensure a future crop. Negreros Castillo (1991) listed specific management options for managing big-leaf mahogany in Quintana Roo.

Diameter distribution data from Bolivia illustrate two aspects of the regeneration behavior of big-leaf mahogany (fig. 8). The diameter distribution of a mature stand at the Chimanes forest in Beni shows a low tree density (less than one tree per hectare in all categories), a large range of diameter classes (from 2.5 to more than 150 centimeters), and more trees in the greater than 40-centimeter diameter classes than the 2.5-, 10- or 20-centimeter diameter classes. However, there were more trees in the 2.5- to 20-centimeter diameter classes than in the greater than 40-centimeter diameter classes. In spite of the relative abundance of small-diameter class trees, data such as these were used to signal concern about the lack of regeneration under closed canopy. Also, these results have been used to point out the danger of losing a whole population when the large-diameter trees are harvested and young trees are not available to replace them. This concern is particularly relevant when the data are segregated on a site-by-site basis, and some sites appear with almost no small-diameter class individuals.

Figure 8 also shows the diameter distribution in an 8-year-old, previously logged secondary forest in the Cinma Forest Concession at Bajo Paragua Forest Reserve in Bolivia. Here, the diameter distribution of big-leaf mahogany shows the same pattern of size-class distribution

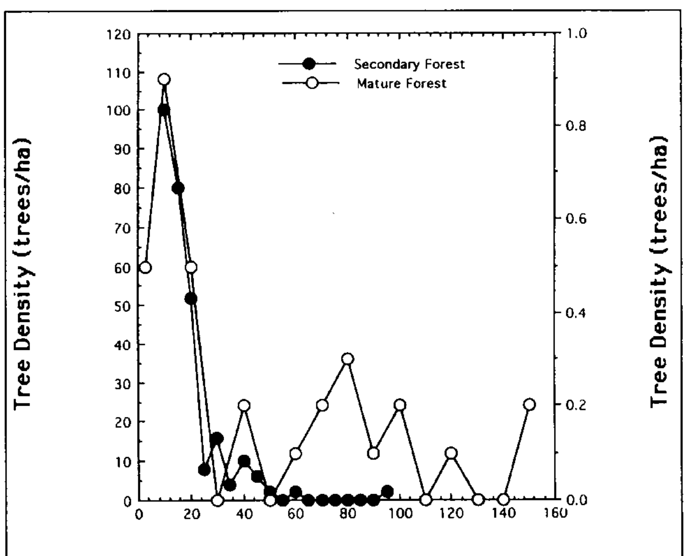

Figure 8. *Diameter distribution of a mature and a young big-leaf mahogany forest stand in Bolivia. Data for the mature stand are for the Chimanes Forest in Beni (Gullison et al. 1996); young forest data are for Bajo Paragua Forest Reserve, Cinma Forest Concession (Bascopé et al. 1995). The Chimanes forest histogram is based on an inventory of 50 hectares, while the Bajo Paragua histogram is based on a 0.5-hectare inventory. The differences in tree density values require two different scales for the same parameter.*

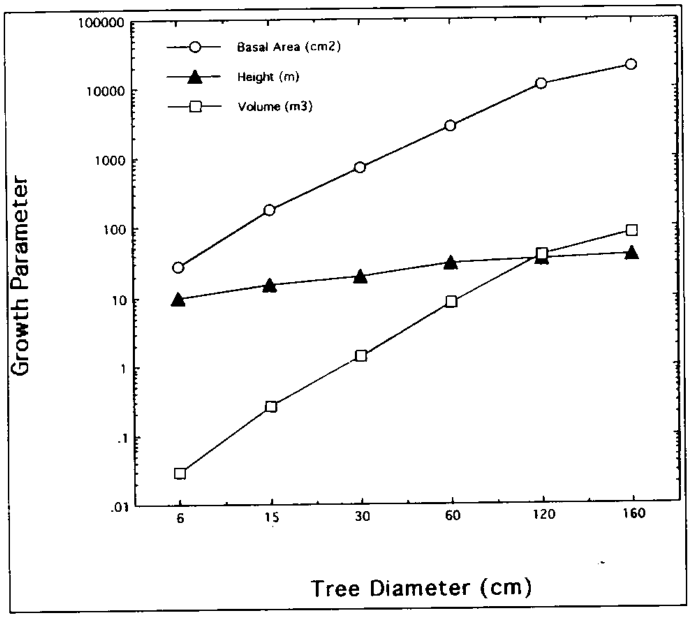

Figure 9. *Tree growth parameters over a range of tree diameters in Bolivia. Data are for the Chimanes Forest (Gullison et al. 1996).*

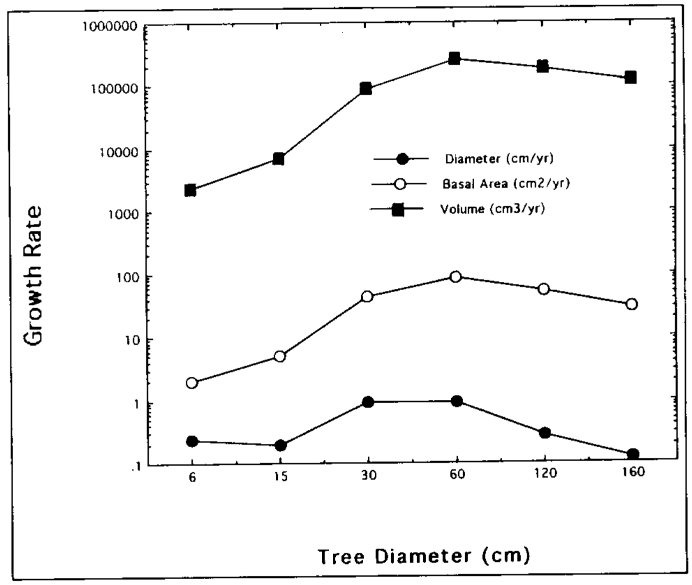

Figure 10. *Rate of tree growth over a range of tree diameters of big-leaf mahogany in Bolivia. Data are for the Chimanes Forest (Gullison et al. 1996).*

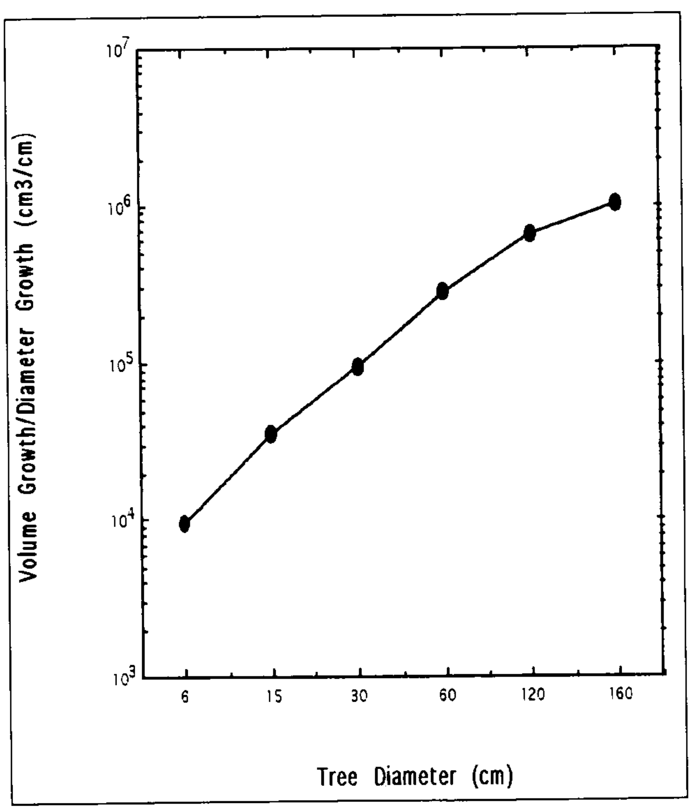

Figure 11. *The ratio of volume growth to diameter growth over a range of tree diameters of big-leaf mahogany trees in Bolivia. Data are for the Chimanes Forest (Gullison et al. 1996).*

as the mature forest, except that large-diameter trees are missing and total tree density is 100 times higher than in the mature forest. This type of big-leaf mahogany size-class distribution is less known because the focus of ecological research so far has been on mature forests and not young forests where big-leaf mahogany regenerates copiously. Both situations need to be taken into consideration to get a clear understanding of big-leaf mahogany regeneration. Like most species with low populations of adult trees, big-leaf mahogany regenerates in patches over the landscape where conditions favorable for regeneration occur. For this reason, one cannot expect regeneration to always occur below mature canopies. Instead, it will occur throughout the range when and where canopy gaps develop in response to local disturbances, either natural or silvicultural.

Tree Growth

Point: Large big-leaf mahogany trees grow very little if at all.

Counterpoint: Absolute tree growth increases with size and canopy dominance, but the diameter growth rate decreases.

The absolute growth rate of big-leaf mahogany trees increases with size. There is a misconception that large trees have a reduced growth rate because diameter growth slows down with increasing tree diameter or because energy is used for reproduction rather than growth. However, growth of a tree is better reflected in biomass or volume increments. Tree diameter is an indicator of a linear dimension of growth (that is, the girth of the tree). Trees also grow in height and deposit biomass as a function of the cross-section of the tree (its basal area) and its height. In the examples in fig. 9, all the dimensions of tree growth are shown in relation to tree diameter, using data from Gullison et al. (1996). The growth rate expressed in diameter increment reaches a peak early in the life of the tree and decreases with size (fig. 10). However, both cross-sectional growth (basal area) and volume growth remain at a high rate throughout the period of measurement.

Figure 11 shows that the volume-to-diameter ratio

Mahogany typically forms large buttresses, requiring that growth measurements be taken well up the lower stem. This tree is 1.8 m diameter at 5.5 m height. (Photo by Jimmy Grogan)

continues to increase as the diameter of the tree increases. As trees become larger, even if their diameter growth decreases, each unit of diameter increment adds an increasing amount of wood volume (and biomass) to the tree. The tree produces more woody biomass as it gets bigger, mainly because it occupies the forest canopy and is exposed to more direct sunlight and resources (thus increasing its photosynthetic output). This in turn allows it to increase its reproductive output, as observed by Gullison et al. (1996), and exert dominance over the stand. The same tree growth behavior is inherent in the chronosequence data in Snook (1993).

The Shoot Borer

Point: Big-leaf mahogany plantations and other silvicultural techniques will fail because of shoot borer infestation.

Counterpoint: Techniques are available to mitigate the effects of shoot borers on big-leaf mahogany.

The shoot borer *(Hypsipyla grandella)* is a moth whose larvae burrow into the meristems of the mahogany, causing branching, forking, and deformation of trees (Newton et al. 1993). In some cases, it also reduces growth rate and can even cause mortality when infestation is extreme.

The shoot borer can be a problem if not managed correctly, but there are effective means to mitigate its effects. Experience in Puerto Rico shows that on appropriate sites, the shoot borer has no long-term impact on growth or wood quality and is not crippling to the establishment of big-leaf mahogany plantations which today comprise some 150,000 hectares in the world (Pandey, in press). Browder et al. (1996) examined the characteristics of nine plantings of big-leaf mahogany in Rondonia, Brazil, and found 100 percent seedling infestation by the shoot borer. However, the plantings were performing satisfactorily, with low mortality, high growth rates, short time-intervals to reach 1.5 cubic meters per tree, and high economic profitability.

Weaver and Bauer (1986) assessed shoot borer damage and the growth rates of big-leaf mahogany plantings in Puerto Rico. They found no correlation between shoot borer damage and seedling crown class, the basal area of trees surrounding seedlings, or topographic position. Three of the plantings had shoot borer damage in 58, 11, and 18 percent of the trees. However, the survival, growth rate, and volume and biomass yield of the plantings were in the high range for plantations (14.6 cubic meters per hectare per year and 8.5 metric tons per hectare per year aboveground), and responded to factors such as topographic position of trees and light availability to tree canopies. Newton et al. (1993) review other successful examples of silvicultural treatment that mitigate the effects of shoot borers. Ward and Lugo (in press) found that for big-leaf mahogany, 92.8 percent of the variation in shoot borer attack was due to large- and small-scale environmental effects rather than intrinsic susceptibility of individuals.

Methods are available to silviculturally reduce shoot borer damage to big-leaf mahogany trees, even under block plantation conditions (table 4). The strategy is to optimize the vigor and growth rate of the trees at all stages of their development so that they are less susceptible to infestation or, if infected, that they are more capable of overcoming the effects of the borer. Chemicals and other means can be used at key stages of the life cycle to combat shoot borers (Newton et al. 1993, Ikeda et al. 1994, Howard 1995). Such combinations of silvicultural treatments coupled with selection of vigorous planting stock are at the core of the integrated methods of shoot borer management recommended by Newton et al. (1993).

Genetic Situation

Point: Big- and small-leaf mahogany and pacific mahogany suffer from genetic erosion.

Counterpoint: There is no evidence for or against genetic erosion in any of the three species.

> *In the case of some species such as* S. mahagoni *and* S. humilis, *it is no longer easy to find large, straight trees; it is more common to find small and genetically miss-shaped trees. The case of* S. mahagoni *is perhaps one of the most evident examples of genetic erosion in a tropical forest species* (Patiño Valera 1997, p. 1).

Statements such as the one by Patiño Valera are common in the mahogany literature. In one example, Rodan et al. (1992) included a photo of "a genetically eroded small-leaf mahogany tree." The origin of

Table 4. Management strategies for big-leaf mahogany in Puerto Rico (Weaver and Bauer 1986).

Nursery

- Control shoot borer infestation chemically.
- Provide seedlings with appropriate shade.

Outplanting and Tending

- Orient planting lines east to west within the forest to maximize sunlight.
- At the time of line-clearing, poison all large overstory trees shading the lines.
- Lift the seedlings when about 1 meter tall, using the larger size classes on lower slopes and bottomlands.
- Cut all *Zyzygium jambos* trees, poison stumps, and cut back sprouts, or do not plant beneath this species.
- Space lines 11 meters apart and trees within the lines at 2.5 meters apart.
- Follow established line-planting guidelines in Lamb (1968).
- Within 1 year of outplanting, reduce all surrounding basal area to under 15 square meters per hectare.
- Experiment both in the field and the nursery to improve rules for big-leaf mahogany management.

Table 5. Ratio of three parameters (density, basal area, and volume) of big-leaf mahogany trees less than 15 centimeters in diameter at breast height to those of big-leaf mahogany trees greater than 50 centimeters in diameter at breast height in various ejidos located in southern Quintana Roo, Mexico (Patiño Valera 1997).

Ejido	*Tree Density*	*Basal Area*	*Volume*
Caobas	6.85	1.96	2.21
Plan de la Noria	72.25	11.00	14.62
Divorciados	10.38	2.97	3.49
Manuel Avila Camacho	7.44	2.48	2.61
Petcacab	7.26	2.33	2.68
Nohbec	5.32	1.72	1.83
Tres Garantías	9.18	2.24	2.60
Botes	11.84	3.25	3.90
Average	9.13	2.48	2.79

these statements was an assertion by Styles and Khosla (1976), repeated by Styles (1981) in the monograph of the Meliaceae, the family to which big-leaf mahogany belongs. Forest Service colleagues have observed vigorous, large-diameter, straight-bole, small-leaf mahogany trees in extensive forest stands in the Dominican Republic and elsewhere in the Caribbean where natural forest stands are allowed to mature.

The causes of genetic erosion in big-leaf mahogany are attributed to logging, deforestation, and international trade. The scientific evidence in support of the statements by Styles (1981), Rodan et al. (1992), Rodan and Campbell (1996), Patiño Valera (1997), and others that repeat them has not been substantiated (Newton et al. 1996). Genetic research on tropical trees is rudimentary, whereas demonstration of genetic erosion requires considerable documentation. To properly explain the issue, it is necessary to review some concepts of genetics and the state of empirical science with respect to tropical trees in general and big-leaf mahogany specifically.

Genetic erosion refers to the loss of genetic variation in a species. The conservation of genetic resources is important because the genetic code contains the information that allows living organisms to cope with their environments. The reduction of populations and the extinction of species are events that reduce the overall genetic stock of the biosphere. The main threats to loss of genetic diversity in forests are deforestation and forest fragmentation, because these processes reduce and isolate populations (Alvarez Buylla et al. 1996). However, the information on the genetic resources of tropical tree species is so scarce that it is difficult to assess the relative progress and magnitude of these factors and the general resilience of genetic systems.

A confounding factor to conservation efforts is the low population density (rarity) of tropical tree species (Bawa and Ashton 1991). Because most tropical tree species are rare (that is, their abundance is less than one adult per hectare), Alvarez Buylla et al. (1996) considered rarity and high species diversity as the greatest challenges of tropical forest conservation. They also point out that most demographic and genetic studies have been conducted on species that are abundant rather than rare. Do rare tropical tree species have mechanisms for maintaining genetic diversity in spite of their rarity and fragmented distributions? Could historical fragmentation of tropical forests pre-adapt species for dealing with some level of modern fragmentation (Moritz et al. 1997)? Research is needed on the group of species to which many tropical trees belong—long-lived and rare species and/or long-lived and fragmented.

Patiño Valera (1997) suggested that big-leaf mahogany can be considered a model for understanding the overall behavior of rare species. However, he points out that in the case of big-leaf mahogany, rarity applies only in terms of adults, as the density of trees smaller than 15 centimeters, as well as their contribution to stand basal area and volume, is usually higher than that of adult trees, particularly in secondary forests (table 5). If so, rarity may be a natural state for big-leaf mahogany in mature forests, one which gives it an advantage in escaping or minimizing the effects of natural enemies, such as the shoot borer.

Research offers powerful new tools for understanding the genetic resources of populations and species. These include the use of molecular markers (Parker et al. 1998) and demographic models (Alvarez Buylla et al. 1996, Clark and Clark 1992). Maximum analytical power is attained when both techniques are used in tandem (Alvarez Buylla et al. 1996) because the interpretation of molecular marker data is greatly improved when done in the context of life history traits. Modeling of both genetic and demographic data further enhances the interpretation of the ecological and genetic behavior of populations.

Genetic structure refers to the distribution of genetic variation in space and time (Nason et al. 1997). The breeding system is a principal factor in the organization of the genetic structure of a population. From the point of view of genetic diversity, outcrossing is a critical outcome of the breeding system of species such as big-leaf mahogany. Outcrossing allows not only gene exchange within a population, but also permits significant amounts of gene flow among populations. Outbreeding, long life cycles, and repeated reproduction encourage gene flow and appear to be important in distributing alleles widely within a species. This interpopulation migration repeatedly generates new genetic combinations, whose fate depends on local selective pressure. High genetic diversity (H_s) occurs in outcrossing species with large ranges, high fecundity, wind pollination, long generation times, and successional habitats (tables 6 and 7; Loveless and Hamrick 1984, Hamrick et al. 1991).

A review of the genetic diversity of tropical tree species concluded that gene flow among local populations of tropical trees is high and that

Table 6. Genetic diversity of tropical plants within populations (Hamrick et al. 1991).

Plant Group	*Genetic Diversity* (G_{st})
Six sites at Barro Colorado Island	0.022 to 0.090
Wind-pollinated species	0.10
Selfing species	0.51
Animal-pollinated species	0.21
Annual species	0.30
Long-lived woody perennials	0.08
Shorted-lived herbaceous	0.23

Table 7. Polymorphism (P) and heterozygosity (H) of plants (Hamrick et al. 1991).

Plant Group	*P*	*H*
All plants studied	34.2	0.11
All trees studied	50.0	0.15
Common tropical trees and shrubs	57–61	0.18–0.21
Uncommon species	42	0.14
Uncommon species minus strangler figs	34	0.12
Selfing species	no data	0.15
Wind-pollinated species	no data	0.07
Carapa guianensis (Hall et al. 1994)*	35	0.12

* Had an H_s (genetic diversity) of 0.35, an A_e (alleles per locus) of 1.18, and an outcrossing rate of 1.0

Box 2. Five Genetic Parameters and an Index of Genetic Diversity Among Populations Used To Evaluate Populations (Hamrick et al. 1991, Loveless and Gullison in press).

Genetic diversity is represented by the combined measures of P, A_e, and H_e.

P Genetic variation, or the percent polymorphic loci.

A Mean number of alleles per locus.

A_e Allelic diversity, or the effective number of alleles per locus.

H_e Gene diversity index (proportion of loci heterozygous per individual under Hardy-Weinberg expectations).

H_o Genotypes present in the population.

G_{st} The proportion of total genetic diversity residing between populations, that is, the degree to which populations are genetically different from each other. It ranges from 0.0, when all populations are identical, to 1.0, where populations are completely divergent.

geographically distant populations show, at most, moderate levels of genetic differentiation (Loveless 1992). Tropical trees possess many mechanisms to enhance or enforce outcrossing, including dioecy, protandry, heterostyly, and genetic self-incompatibility. Nason et al. (1997) report that 19 of 22 tropical tree species studied have an outcrossing rate greater than 80 percent.

Research on molecular markers (box 2) is now yielding a better understanding of the characteristics of tropical moist, wet, and rain forest trees that allow them to survive in spite of being rare and fragmented. Alvarez Buylla et al. (1996, p. 387) summarized the situation:

> *Population genetic models have shown that tropical rain forest trees: (a) possess high levels of genetic diversity, (b) maintain greater proportions of genetic variation within than among populations, (c) are predominantly outcrossed, and (d) have high levels of gene flow. These results suggest that tropical tree species may not be in immediate danger of extinction from genetic factors if actual conditions are maintained.*

Carapa guianensis, a tree belonging to the same family as big-leaf mahogany, had low polymorphism (35 percent) and low heterozygosity (0.12) in comparison to other tropical tree species (Hall et al. 1994). Only 4.6 percent of the total genetic variability could be attributed to population differentiation, even though populations were separated by as much as 70 kilometers. Some genetic difference was observed between pairs of compared populations. A high rate of outcrossing was also observed, although there was some evidence of nonrandom mating. High levels of gene flow are probably maintained by seed dispersal as well as synchronous flowering and high population density. Pollen dispersal distances in the tropics are also large (Nason et al. 1997).

Loveless and Gullison (in press) used molecular markers in a study of four big-leaf mahogany populations separated by as much as 100 kilometers and found (table 8): (1) that they differed little from each other—only 3 and 6 percent of the total genetic variation was unique to individual populations in this region; (2) the populations contained substantial levels of genetic variation and were completely outcrossed (outcrossing rates of 1.038 ± 0.024); (3) that pollen probably moves long distances in big-leaf mahogany populations; and (4) that gene diversity was similar to that of other tropical species from Panama. These results are in agreement with what has been discussed above for tropical trees in general.

Ward and Lugo (in press) analyzed 14 years of growth data for more than 2,000 trees in a study of 12 provenances of big-leaf mahogany and found: (1) that more

Table 8. Measures of genetic variation and population differentiation in big-leaf mahogany in comparison with other groups of plant species (Loveless and Gullison in press). Box 2 contains the definition of parameters: P = polymorphic loci, A_e = alleles per locus, H_e = gene diversity index, and G_{st} = genetic diversity.

Species or group of species	*P*	A_e	H_e	G_{st}
Long-lived woody perennials	0.50	no data	0.149	no data
Native woody tropical species	0.39	no data	0.109	0.109
Common trees on BCI*	0.61	no data	0.211	0.055
Rare trees on BCI*	0.42	no data	0.142	no data
Big-leaf mahogany (species)	0.83	1.37–1.34	0.21	0.063
Big-leaf mahogany (population)	0.67	1.35–1.34	0.20	0.063

* BCI is Barro Colorado Island, Panama.

phenotypic variation is attributable to environmental variance (79.2 percent), followed by genetic variance (10.8 percent) and genotype by environment interactions (8.2 percent); (2) most environmental variation occurred among rather than within plantation sites in Puerto Rico; (3) similar amounts of genetic variance occurred among and within populations; and (4) provenances became more genetically distinct as distances increased. The results of this study contrast with others based on localized populations because the study covered seeds from areas that ranged in separation between 160 and 1,600 kilometers. This work reveals broad geographic-level aspects of genetic variation in big-leaf mahogany and signals the need to consider species-wide genetic variation and performance in the assessment of the conservation status of big-leaf mahogany.

Newton et al. (1992) interpreted the naturally hybridized mahogany in Puerto Rico (Whitmore and Hinojosa 1977) as potentially negative because such hybridization could dilute the genome of both the big and small-leaf mahogany populations. However, Haig (1998) points out that hybridization of a population's genome can either benefit (increased genetic diversity, fitness, and adaptability) or injure (loss of genetic diversity, genetic assimilation, and outbreeding depression) the population. Molecular markers and life history research combined with quantitative traits information can sort out the positive or negative effects of mahogany hybridization.

Critical Questions Concerning Genetic Diversity

The genetic diversity issue is fundamental to understanding conservation problems such as those involving big-leaf mahogany. However, the use of genetic diversity information to influence policy or conservation actions requires scientific information and/or a clear statement of assumptions. For the tropics as a whole, there are no data to sustain a yes or no answer to questions about loss of genetic diversity as a result of logging, other management activities (Brown and Moran 1981), or forest fragmentation (Nason et al. 1997). One can make a case for either a yes or no answer for any scenario, but such arguments are based on assumptions that need to be clearly stated and understood. Ultimately, conditions on a case-by-case basis and better scientific understanding will lead to better answers to these questions.

How much of the observed variation in tree form and growth rate is due to genetic control as opposed to environmental control or to their interaction? Experience with loblolly pine (Roberts and Conkle 1984) suggests that the size and shape of trees is for the most part determined by the environment in which seeds germinate and grow. Progeny tests were planted from seeds of sitka spruce individuals from dominant, codominant, intermediate, and suppressed positions in the canopy. Results showed no significant difference in height performance among the various progeny when grown in controlled field conditions (Samuel and Johnstone 1979). Empirical evidence suggests that it is not possible to identify superior individuals from natural or plantation sources. This is due to the patchiness of the natural environment, which makes it difficult to predict what genetic combinations will perform best on a specific site. In fact, tree improvement programs throughout the world have claimed limited genetic gain (10 to 20 percent in changing gene frequencies) in the initial process from the wild or even in plantations. A special issue of the Canadian Journal of Forestry Research (27:395-446, 1997) contains a comprehensive discussion of genetic diversity issues in temperate commercial forest plantations.

Cornelius (1994) reviewed information on the heritability of the main traits of trees and found that only wood density resulted in heritability values above 0.4. Other traits, such as height, diameter, tree volume, straightness, morphological and structural characteristics, and branching resulted in consistently low heritability values (0.19 to 0.26). Cornelius concluded that obtaining "a reasonable level of genetic gain" requires only that plus trees reproduce with plus trees; "the problem of the tree breeder is to find them."

Data for heritability values of big-leaf mahogany are variable (table 9), but in general support Cornelius. The high heritability value for seedlings decreases as seedlings develop into trees. Ward and Lugo (in press) quantified the proportion of variance in growth performance that could be attributed to genetic variation as opposed to environment or their interaction. They found that by year 14 for big-leaf mahogany, 79.2 percent of the variance was due to environment, 10.8 percent was due to genetics, and 8.2 percent was due to interaction.

Does dysgenic selection occur in big-leaf mahogany? Dysgenic selection, known also as high-grading, is believed to have negative effects on genetic diversity as a result of the selective harvesting of the best formed and largest trees in a population. The argument for a yes answer is based on the assumptions that traits that lead to large size and desirable form are under genetic control and highly heritable; that after harvesting, there is no availability or regeneration of seeds with the traits that lead to large size and good form genome; and that the harvesting activity selects against the propagation of particular alleles. The argument for a no answer is based on the assumption of the low heritability of growth rate and tree form (table 9), the overriding effect of environmental control over the expression of growth rate (Ward and Lugo in press), and the possibility of regeneration and gene flow from these and other similar individuals into the population after harvesting.

Table 9. Median heritability for forest trees.

Trait or Trait Type	*Heritability*
Based on a review of 67 published papers (Cornelius 1994)	
Height	0.25
Diameter	0.19
Volume	0.18
Straightness	0.26
Morphological and structural	0.23
Specific gravity	0.48
Branching traits	0.24
Big-Leaf Mahogany	
Total height (Costa Rica)*	0.81
Root collar diameter*	0.47
Total height (Costa Rica)+	0.38
Total height (Trinidad)+	0.11

* Navarro (1997), after 8 months of growth.
+ Newton et al. (1996).

Newly flushed crown spanning 40 m of the large adult shown in the previous photo. Once mature, mahogany leaflets flutter in the slightest breeze, creating a characteristic shimmery look. (Photo by Jimmy Grogan)

Is genetic erosion occurring in big-leaf mahogany? The argument for a yes answer is based on assumptions that deforestation and fragmentation reduce the genetic diversity of big-leaf mahogany by (1) eliminating unique genetic material from those populations that are lost and (2) preventing gene flow among surviving populations. Surviving populations then become isolated and drift to extinction. The argument for a no answer is based on the assumption that, at the current level of use, surviving populations contain sufficient genetic diversity to restore the species' genetic resources, and that big-leaf mahogany has mechanisms of gene flow that can overcome some unknown degree of deforestation and fragmentation.

Nason et al. (1997) reported that the neighborhood areas of individual tropical tree species may be on the order of tens to hundreds of hectares, which is larger than the sizes of forest fragments in many disturbed landscapes. Unfortunately, the fragmentation process and the response of plants and animals to fragmentation are too complex to properly assess their effects on genetic diversity (Laurance et al. 1997). Moritz et al. (1997) pointed out that animal populations, including pollinators and seed dispersers, in the wet tropics of Australia were exposed to a late Pleistocene fragmentation event that left a legacy on their genetic structure and diversity. Such a legacy has effects on the capacity of modern populations for coping with anthropogenic fragmentation and raises the possibility that at least some tropical species (that is, the rare ones such as big-leaf mahogany) might be preadapted to fragmentation.

Regardless of responses to the above questions, can the genetic situation of big-leaf mahogany be managed for the benefit of its conservation? Management actions can help mitigate threats to the genetic diversity of big-leaf mahogany. These actions include: (1) protection of genetic diversity through establishment of reserves that cover the range of ecological conditions faced by the species and (2) promoting gene flow and maintaining local genetic variation through silvicultural practices such as maintaining large seed trees in harvested areas, actively regenerating the species, and artificially exchanging seeds among populations. Conservation strategies for big-leaf mahogany and other tropical tree species require spatial and temporal considerations so that populations selected for protection include all of the biotic structures that contribute to the maintenance of the genetic structure.

The Sustainability Question

Point: Big-leaf mahogany cannot be managed sustainably.

Counterpoint: Big-leaf mahogany can be managed sustainably, but there are currently few attempts to manage big-leaf mahogany and little or no documentation that would lead to an assessment of sustainability.

"Forest sustainability is a concept for the desired condition of forest ecosystems all over the world. The essential aspects of sustainable forests differ tremendously, however, among peoples of the world" (Amaranthus 1997, abstract).

Amaranthus recommends defining sustainability to minimize conflict, confusion, and mistrust. He asks: "For what, where, whom, and how long are forest values being sustained?" Such questions are not being properly defined in the big-leaf mahogany debate; each participant generalizes and concludes about sustainability without properly quantifying outcomes or defining terminology and objectives.

Amaranthus recommends assessing sustainability at the landscape level and defining the processes, structures, and resources needed to meet many of society's objectives. Moreover, to ensure the success of any resource management issue, it is necessary to involve those social groups most immediately affected by changes in the resource base. This has been made clear within the northern part of the range of big-leaf mahogany in relation to the ejidos of Mexico and the many unique political, social, cultural, and economic aspects of their ownership arrangement (Thoms and Betters 1998). The same applies to indigenous cultures elsewhere in the range of big-leaf mahogany (Morán 1993, Redford and Padoch 1992, Schmink and Wood 1992). Even within the context of globalization, it is not wise to ignore local ownership of forest resources or to impose foreign values without adequate dialogue and justification.

While the sustainability argument is used prominently in MacLellan (1996), no such analysis accompanies the opinions expressed (c.f. Rodan and Campbell 1996, Snook 1996). The measures of sustainability are not defined, nor is the length of time expected for the time axis of what is being sustained defined, and no information is presented to define the rate of change of big-leaf mahogany population stocks. A recommendation was given by Veríssimo et al. (1997), who proposed the zoning of timber extraction as one means of sustaining forestry operations in the Brazilian Amazon. They reasoned that proper use of forest lands was an important first step toward sustaining forestry activities in the region.

A commonly used argument is that the short-term economics of forestry in the tropics favor rapid exploitation of timber, and that this alone prevents sustainability. Browder et al. (1996) examined 30 alternative scenarios of big-leaf mahogany production in Brazil. They found 21 of them to be financially viable. These scenarios included growing big-leaf mahogany in agroforestry systems and in plantations. Plantations were particularly attractive financially because of their high yields and high profitability. Browder et al. recommended establishing plantations outside the native range of the species to avoid the shoot borer and other natural constraints on the species.

Does sustainability by definition require a short-term market profit? Do below-cost sales in the United States make forestry activities unsustainable by definition? Can economically unsustainable activities in one sector of the economy be justified to achieve sustainability in another sector of the economy or society? Or alternatively, is market economics the wrong evaluation tool for sustainability because it does not value biodiversity as explicitly stated by Browder et al. (1996) in their analysis?

The only available long-term and large-scale data to evaluate the sustainability of big-leaf mahogany production are global trade data (fig. 5). These data, which reflect the whole range for the species, show no declining trend. However, declines are possible when particular sectors of the range of mahogany are considered. For example, trade data for Belize only show a decline over a portion of time, followed by partial recovery (fig. 12). But using these declines in isolation does not support a conclusion about sustainability because information on productivity is needed as well.

One could compare the level of trade with the yield of natural big-leaf mahogany populations and thus make a determination regarding the sustainability of the particular level of trade. To arrive at a yield per unit area for big-leaf mahogany in the wild, one needs repetitive measurements of all trees in plots of known area. Such data are not available. The next best option is to extrapolate individual tree growth data to an area basis. To do this, data on tree growth and tree density are needed.

Available tree growth data (Lamb 1966, Snook 1993, and Gullison et al. 1996) are based on diameter growth. Lamb measured 2,002 trees, Snook measured 161 trees, and Gullison et al. measured 117 trees. These measurements ranged from nearly zero to 1.6 centimeters per year. The study by Gullison et al. (1996) reported the whole range of values. Rates in all studies varied with tree age or tree size (figs. 9 and 10). For the purpose of this exercise, the average values reported by Snook (1993) and Gullison et al. (1996) were used as well as some low and high values to show the range of expected results. This results in a range of data within which the species likely functions (table 10).

Available tree density data for trees with breast-height diameters greater than 20 centimeters range from absent to more than 200 trees per hectare in secondary forests (fig. 8). However, most tree density data fluctuate between absent to about 10 trees per hectare, depending on the age of the stand and size class being considered.

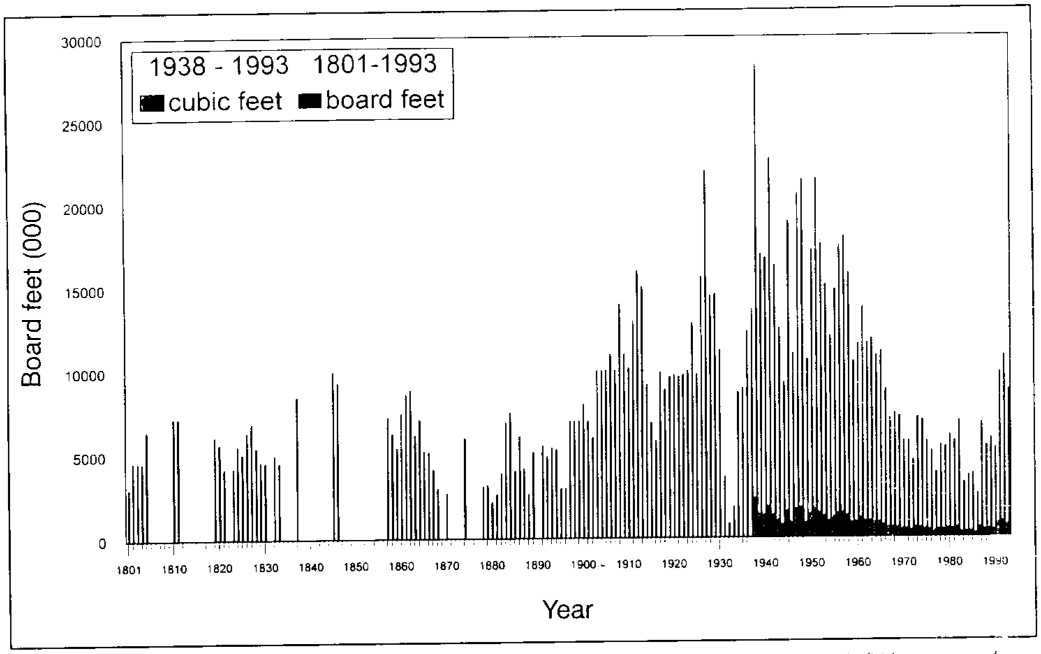

Figure 12. Chronology of big-leaf mahogany exports from Belize, 1801 to 1993 (Weaver and Sabido 1997).

Table 10. Calculation of yield rates from diameter growth data and different assumptions about tree density. The number in parentheses is the area of wild big-leaf mahogany habitat (rounded to the nearest million hectares) required to produce 416,670 cubic meters of wood in a year. Box 1 derives this value from the estimated volume in international trade.

Source and Representation of Data	*Volume Growth (cubic meters per tree per year)*	*Yield @ 0.1Stems per Hectare (cubic meters per hectare per year)*	*Yield @ 1.0 Stems per Hectare (cubic meters per hectare per year)*
Gullison et al. (1996)*			
50th percentile			
Mean (all trees)	0.11	0.011 (40)	0.11 (4)
Lowest (30-centimeter tree)	0.08	0.008 (52)	0.08 (5)
Highest (60-centimeter tree)	0.26	0.026 (16)	0.26 (2)
90th percentile (120-centimeter tree at 1.0-centimeter per year growth)	0.66	0.066 (6)	0.66 (1)
Snook 1993			
Average (all trees)	0.03	0.003 (139)	0.03 (14)
Trees age 28 to 34	0.05	0.005 (83)	0.05 (8)
Trees age 44	0.06	0.006 (69)	0.06 (7)

*Gullison et al. reported tree growth for a diameter range of 2.5 to 160+ centimeters. For each diameter class, diameter growth rate was reported from minimum to maximum rate and for the 10th, 50th, and 90th percentile. This report uses a range of values to show how yield estimates can vary depending on the diameter growth rate of trees.

Box 3. Area of Wild Big-Leaf Mahogany Habitat Needed To Satisfy the 1995 International Trade in the Species

- Assume a volume of 416,670 cubic meters per year is required to maintain current trade (box 1).
- Assume that the rate of wood production in the wild ranged from 0.006 to 0.066 cubic meters per hectare per year at a tree density of 0.1 trees per hectare, and from 0.06 to 0.66 cubic meters per hectare per year at a tree density of 1.0 trees per hectare (table 10).
- The area required to satisfy the annual export of mahogany would be 416,670/yield in table 10. This results in a range of 1 million to 140 million hectares of big-leaf mahogany habitat required to satisfy the wood volume in international trade. The most likely range of values is 4 million to 40 million hectares, based on the average of all trees at the 50th percentile growth rate values in Gullison et al. (1996).
- The area covered by wild big-leaf mahogany forest is about 200 million hectares. Thus, stocks of mahogany wood should be increasing in the wild.

Multiplying tree density data by tree growth rate results in yield per unit area:

(cubic meters per tree per year) (trees/hectare) = cubic meters per hectare per year

Table 10 has representative results based on tree growth data and two assumptions on tree density. Using the most conservative assumptions, it can be estimated that, at most, 140 million hectares of wild habitat can satisfy the known global trade of mahogany. The present area of wild big-leaf mahogany habitat is about 200 million hectares. Therefore, these data suggest that populations of big-leaf mahogany are at least not decreasing their wood volume as a result of harvesting activities for international trade (box 3).

There are alternative scenarios to evaluate the sustainability of big-leaf mahogany stocks (fig. 13). The decline scenarios, whether exponential, linear, or beyond a threshold of use, are worst-case scenarios. They assume no regeneration or tree growth after logging for big-leaf mahogany. For example, Contente de Barros et al. (1992) estimated that big-leaf mahogany stocks in Brazil would last between 32 and 42 years at the current level of logging if trees stopped growing and regenerating. The 32-year scenario, without articulating the assumptions, was used to illustrate the plight of big-leaf mahogany and justify its listing in Appendix II of CITES (Amendment to Appendix II, Tenth Meeting of the Conference of the Parties, Harare, Zimbabwe, 1997). When only the growth of the remaining stock is taken into consideration, one finds that, in spite of the logging pressure, the big-leaf mahogany stock would increase rather than decrease (box 4).

Tree growth, tree mortality, logging pressure, and regeneration in available land, plus the changes in available land and quality of big-leaf mahogany habitat, are factors that need to be taken into consideration to estimate the trend in big-leaf mahogany stocks over time. By estimating the trends for each of these elements, one can assess whether mahogany stocks are being sustained or not. Such an analysis would lead to "pulsed" models (fig. 13) with repetitive periods of use followed by periods of recovery. These models can lead to a decline, increase, or steady state of stocks, depending on the magnitude of the processes influencing the species. Regional or country-level management of levels of logging, replanting and caring, and land assigned to big-leaf mahogany can lead to pulses of net use or net gain of stocks and positive, negative, or neutral trends in the stocks of the species.

Only through several cycles of use and regeneration will it be possible to seriously assess whether the management of big-leaf mahogany is sustainable or not. The cycles can themselves be of different duration and magnitude. For example, it is known that the pre-Columbian Maya were responsible for a cycle of big-leaf mahogany use in Mesoamerica that spanned millennia (Lamb 1966) and which could be repeating itself today if recently deforested lands are regenerated to big-leaf mahogany. Shorter-term cycles can be implemented at local scales, such as with ejidos, using agroforestry systems or secondary forests or through even shorter plantation rotations.

Resilience of Big-leaf Mahogany Forests

Point: Big-leaf mahogany forests are fragile and need preservation.

Counterpoint: Big-leaf mahogany forests are resilient but vulnerable and need sound management and protection.

> *"Mahogany in Belize endured the Mayas for two millennia; Baymen loggers in the 17th and 19th centuries; colonial forest administrators, two world wars, and a depression in the 20th century; and hurricanes through the entire period."* (Weaver and Sabido 1997, p 1).

After all this history, Belize retains its big-leaf mahogany forests, albeit in a deteriorated state due to overharvesting and inadequate management. The volume of Belizian big-leaf mahogany exports over the period of

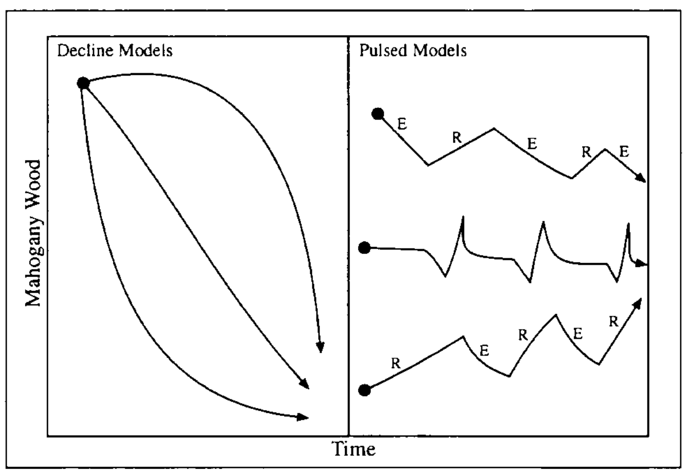

Figure 13. *Patterns of change in big-leaf mahogany wood stocks over time according to different models. Decline models include a steady decline, a rapid decline, and a slow decline with a threshold. Pulsed models can be ascending, descending, or steady state, which by definition means sustainability. Because there is no information on the time aspect of the pulses, it is nearly impossible to interpret trends as being part of one or another pattern of change. Recovery is R and exploitation is E.*

Box 4. Information About the Area of Natural Habitat, Magnitude of Timber Stocks, Demand for Big-Leaf Mahogany, and Duration of Stocks in the Brazilian Amazon.

These data are from Contente de Barros et al. (1992).

Habitat Area

- Area of natural occurrence: 152 million hectares.
- Area in indigenous lands: 34 million hectares.
- Area in reserves: 50 million hectares.

Volume per Unit Area

Explored volume	
at low tree density:	0.2 cubic meters per hectare
at normal tree density:	0.4 cubic meters per hectare
at high tree density:	0.6 cubic meters per hectare
Exploitable volume:	0.4152 cubic meters per hectare

Available Exploitable Stocks

Over the whole region:	59.59 million cubic meters
Over an area of 0.50 million km²:	20.94 million cubic meters or 5.7 million trees

Annual Demand for Timber

0.5 million cubic meters

Duration of Estimated Stocks Assuming No Tree Growth

- 42 years if stocks of 20.94 million cubic meters are exploited at a rate of 0.5 million cubic meters per year
  (20.94 ÷ 0.5 = 42 years).
- 32 years if stocks of 15.95 million cubic meters are exploited at a rate of 0.5 million cubic meters per year
  (15.95 ÷ 0.5 = 32 years).

Comment

When the "32-year" number is quoted, it is not mentioned that the estimate assumed no tree growth or regeneration, nor that it was based on one-third of the mahogany habitat, that is, 0.50 million square kilometers of a total of 1.5 million square kilometers. Only a small fraction of trees are cut each year (2 to 3 percent). All uncut trees continue to grow and regenerate, therefore preventing the exhaustion of the mahogany timber supply. It is obvious that these estimates of duration of stocks are worst-case scenarios, as pointed out by the authors. In fact, they indicated that the estimated time span of 32 to 42 years was sufficient to plant and harvest mahogany through a plantation cycle.

record (fig. 12) forms a classic natural resource exploitation curve between the late 1880's and 1980's. However, the level of export increased in the 1990's to about 10 million cubic meters per year. Living resources are vulnerable to the laws of market economics that set their value as a function of supply. In many instances, by the time the market recognizes scarcity and the value of the natural resource, the natural systems have been overexploited and either gone extinct, as with the passenger pigeon, or require long time periods to recover. Big-leaf mahogany is in no danger of extinction, but the stock of large trees in many parts of its range has been reduced by overexploitation. Time will be required to recover the stocks of large big-leaf mahogany trees in overexploited areas, and afterwards a new cycle of use will be possible.

In spite of the history of exploitation, there is sufficient big-leaf mahogany in Belize (table 4 in Weaver and Sabido 1997) so that, with appropriate forest management, the country can sustain a particular level of commercial export while conserving the biodiversity of forests. Weaver and Sabido (1997, p. 21) wrote: "Although mahogany has declined dramatically in both abundance and size during 300 years of exploitation in Belize, the species still grows in much of the country. Moreover, recent local measures have been adapted to protect mahogany and other important commercial species." The ability of big-leaf mahogany forests to recover from both natural and human disturbances is a measure of their resilience. This resilience is the best available asset as the world strives to conserve this magnificent species.

The traits of big-leaf mahogany that may provide it with resilience are copious production of seed, particularly during mast years; abundant seed germination; morphological and physiological plasticity of its seedlings toward light conditions; high genetic diversity; high level of outcrossing; high nutrient-use efficiency; long lifespan; resistance to drought and high wind speeds; and ability to dominate the crown of the tropical forest. These traits may give mahogany the capacity to overcome large-scale and infrequent natural disturbances and pre-adapt the species to human-impacted systems and to silvicultural manipulation.

Epilogue

A policy for the conservation of big-leaf mahogany requires the best information possible. The information reviewed here demonstrates the complexity of the big-leaf mahogany situation. It is easy to develop a worst-case scenario for the species and assume that such a scenario plays out throughout the range. This has been at the core of proposals for listing mahogany in Appendix II of CITES. The worst-case scenario includes the less than optimal management situation of the tropics; the high rates of tropical deforestation, whether related to big-leaf mahogany or not; and a big-leaf mahogany species assumed to be incapable of regeneration after logging, suffering genetic erosion because of the way it grows in clumps of similar size that are extirpated from the landscape, a species incapable of growing in plantations because the shoot borer overwhelms it and causes poor-form trees, and a species quickly losing space to changing land uses throughout its range.

Table 11. Area of big-leaf mahogany plantations in the world (Pandey, in press). Plantations in Martinique (Tillier 1995) and Puerto Rico (Lugo and Fu 1998) are not included.

County	*Area (hectares)*
Bangladesh	2,700
Benin	2,100
Cameroon	1,600
Dominica	250
Fiji	29,520
Guatemala	2,850
Indonesia	90,690
Jamaica	744
Nigeria	1,750
Philippines	9,120
Saint Vincent	200
Solomon Islands	4,350
Sri Lanka	3,840
Trinidad and Tobago	1,500
Total	**151,214**

The worst-case scenario ignores the vigorous regeneration of big-leaf mahogany under natural conditions of disturbance and its expansion in rapidly developing secondary forests throughout its range; 150,000 hectares of successful big-leaf mahogany plantations (table 11); a wealth of knowledge about how to manage the species, both under natural and artificial conditions; and the resilience of the species and its genetic structure, which may resist reductions in natural variability of the species, provided space for regeneration is available. The changing land uses in the tropics may favor the long-term regeneration of big-leaf mahogany because humans are creating agroforestry systems similar to those of the Maya where much of today's Central American big-leaf mahogany developed (Lamb 1966).

Because of its high commercial value, big-leaf mahogany is a tree species that challenges the will of tropical countries to manage their natural resources sustainably. All of the conditions for success are present, but it is not clear if the will to take charge of the situation is or is not available. International partnerships will aid in the effort to make the conservation of big-leaf mahogany a reality.

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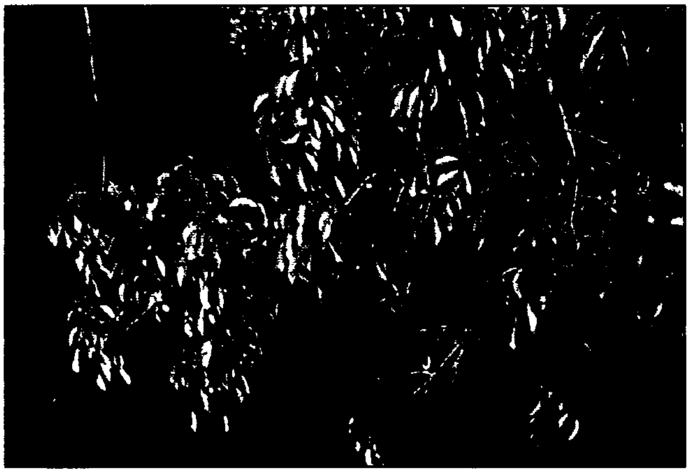

Flowering crown with seeds still attached to fruit columns, waiting for the next sharp wind to bear them off. (Photo by Jimmy Grogan)

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