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"Meeting of the Working Group on Mahogany"

"Synthesis of mahogany natural history and management in the American tropics"

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Elaborated by Independent Consultants. Views presented here do not represent the official position of the Brazilian Government.

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SUMMARY

Mahogany (*Swietenia macrophylla* King) is the most valuable timber species in the American tropics. The majority of the mahogany sold in international markets originates from natural forest stands where extraction is conducted in an unsustainable manner. As a result, natural populations of mahogany have been drastically reduced throughout its range. There is a concern that logging activities threaten the existence of mahogany, with growing pressure to add mahogany to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITIES). Brazil and Bolivia have been at the center of this debate because they are the major suppliers of mahogany to the international market and because they retain the majority of the natural stocks of this species.

In this paper we present an overview of the life history of mahogany (its range, distribution patterns, population structures, regeneration, and growth) and genetic implications of mahogany extraction. We also present preliminary findings from a long-term study of mahogany ecology, genetic structure, and management in southern Pará. These results indicate encouraging potential for the management of mahogany in natural forests.

INTRODUCTION

1. Mahogany (*Swietenia macrophylla* King) is by far the most valuable timber species in tropical America, selling for approximately $1100 per cubic meter of export-grade sawn boards in 1998. *S. macrophylla* (referred to simply as "mahogany" throughout the remainder of this paper) is prized for its attractive color, durability, dimensional stability, and workability; it is used for decorative woodwork, furniture, door and window frames, shingles, beams and veneer (Lamb 1966, Veríssimo *et al.* 1995).

2. Mahogany has been extracted for almost 500 years from Mexico and Central America. In the Brazilian Amazon, significant commercialization of this species did not begin until the 1960s with the extension of highways into the southern Amazon Basin. Declines in mahogany supplies from Central America and Mexico has meant that demand for this species has been high in Bolivian and Brazilian Amazon in the last three decades (Rodan *et al.* 1992, Veríssimo *et al.* 1995).

3. Mahogany is currently being harvested throughout its natural range—from Mexico south through Central America in a a continous arc to the southern Amazon Basin in Bolivia and Brazil—from primary forests. As result, severe depletion of natural stands is evident in Central America and the eastern Brazilian Amazon (Rodan *et al.* 1992, Veríssimo *et al.* 1995). Very few plantations of mahogany have been successfully established in areas where this species is native due to attacks by the shoot-boring moth, *Hypsipyla grandella* Zeller (Rodan *et al.* 1992).

4. In Brazil, forest tracts containing mahogany are frequently localized using small airplanes: pilots search for mahogany in low-lying terrain, distinguishing it from other species by its large, shimmering, light-green

crown. Reconnaissance and tree felling typically occur during the rainy season; boles are extracted and transported to sawmills during the dry season. After trees are felled, bulldozers open roads and log landings. Logs are then transported up to several hundred kilometers to sawmills on roads built by logging companies. Approximately 60% of processed mahogany is exported to external markets, principally to the United States and the United Kingdom. The remainder is trucked to the south of Brazil for domestic consumption (Veríssimo & Lima 1998).

5. There is now concern that mahogany is threatened by unregulated logging activities (Rodan *et al.* 1992). Indeed, two relatives of generic mahogany, *Swietenia. mahagoni* and *S. humilis*, are now listed in Appendix II of CITIES (Rodan *et al.* 1992). There is now growing pressure to also add mahogany to Appendix II. This would mean that mahogany could only enter international markets after producer country governments determine that trade will not lead to significant population reductions. Listing mahogany might also reduce mahogany export quotas, increase prices, assist range states' efforts to manage the species, help distinguish legal from illegal timber, and provide incentives to manage supplies for the long term (NRDC 1994, Veríssimo *et al.* 1995). Brazil and Bolivia have been at the center of this debate because they are the major suppliers of mahogany for the international market and because they retain the majority of natural stocks of this species (Veríssimo *et al.* 1995).

6. This paper has three objectives. First, we present an overview of mahogany life history. Second, we discuss genetic issues. Finally, we consider progress from an on-going forest research project and potential for sustainable management of mahogany in the Brazilian Amazon.

MAHOGANY LIFE HISTORY

7. **Range.** Mahogany's range stretches in a continuous belt from Veracruz, México at 23^{O} N of the equator down along the Central American Atlantic coastal strip into South America, where it continues in a broad southeasterly arc from Venezuela through the Colombian, Ecuadorian, Peruvian, Bolivian and Brazilian Amazon regions to points as far as 18^{O} S (Lamb 1966, Pennington *et al.* 1981). Its distribution generally corresponds to forest classified by Holdrige (1967) as "tropical dry", with annual temperature averages of $>24^{O}$ C, 1000-2000 mm annual precipitation, and a year-round rainfall to evapotranspiration ratio of 1.0-2.0. It is also found in tropical moist and subtropical zones (Lamb 1966, Whitmore 1983). Mahogany grows at elevations ranging from 0-1400 m, from floodplains to mountain ridges, on a wide variety of soils—derived from alluvial, volcanic, metamorphic, and calcareous materials—and soil conditions—deep, shallow, acid, alkaline, well-drained, and gleyed. The composition and structure of associated forests are similarly diverse across its range (Oliphant 1928, Stevenson 1928, Williams 1931, Lamb 1966, Negreros-Castillo 1991, Snook 1993, Gullison *et al.* 1966). In Brazil, mahogany can be found in the floodplains of the western Amazon Basin (Acre, Amazonas), on a rolling landscape in rich red clay soils (Rondônia), on relatively flat terrain in the nutrient poor sands and clays derived from the Precambrian Brazilian Shield (Pará, Mato Grosso), to the tops of granitic inselbergs (southeast Pará), and in mountains to elevations above 700 m (southwest Para's Serras do Cachimbo).

8. **Distribution at the landscape scale.** Mature mahogany trees are typically found scattered through the forest matrix at densities of less than one tree per hectare. These tend to grow in aggregations of several tens to hundreds of mature stems, often with expanses of "empty" forest many kilometers in breadth separating aggregations. In the Petén district of northern Guatemala densities of 12/ha are found over large areas. Nearly pure stands of limited extent—a few hectares—with densities up to 50-70/ha have been reported from Panama, Nicaragua, Guatemala, Belize, and Mexico (Lamb 1966). Early European settlers in Central America associated mahogany with coastal riverways on the Atlantic seaboard of British Honduras (now Belize); its proximity to flowing water facilitated exploitation and export to the point of local exhaustion (Swabey 1941, Lamb 1966). From the same region Stevenson (1927) and Stevenson (1928) reported that, moving into interfluvial and upland ecosystems, mahogany characteristically grows in transition zones where different vegetative communities grade into each other, on soils with medium to good drainage. Descriptions from south America emphasize mahogany's association with river floodplains in the upper reaches of the western Amazon Basin. Williams (1931), Hoy (1946), Irmay (1949), Lamb (1966), White (1978), and Gullison & Hubbell (1992a, b) described its tendency to grow on drier, firmer soils slightly above seasonally inundated floodplains, where floods occur infrequently. Gullison *et al.* (1996), working in the floodplains of lowland Bolivia, reported that mahogany occurs in forest areas up to several hundred hectares in size, with 0.1-0.2 merchantable (>80 cm diameter at breast height, or dbh) trees/ha and similar densities of sub-merchantable stems. Outside these areas mahogany may not reappear for distances up to 10 km. Moving away from floodplain forests, Veríssimo *et al.* (1995) observed a similar pattern in the *terra firme* forests of south Pará, where mahogany tends to grow in low areas in the vicinity of rivers. In general, drier, more disturbance-prone areas tend to have higher stockings than wetter, more stable environments (Lamb 1966).

9. **Population structure.** Reported population structures of mahogany within aggregations or local areas containing merchantable trees are consistently described by bell-shaped curves attributed to even-aged cohorts (from Venezuela, Finol 1941; from Bolívia, Gullison & Hubbell 1992b; from Mexico, Snook 1993). That is, most mahoganies within a given area tend to be approximately the same size, implying that they established as seedlings at more or less the same time after some common disturbance event opened growing space across large areas (Lamb 1966, Snook 1993, Gullison *et al.* 1996). Large numbers of pole-sized individuals that would indicate steady recruitment into larger (that is, merchantable) size classes have not been documented, and indeed, post-logging inventories of logged stems (Veríssimo *et al.* 1995) and interviews with tree spotters who locate trees for felling in closed forests suggest that smaller size classes are generally poorly represented within stands.

10. **Adult morphology.** Mahogany is an upper canopy or emergent tree that attains heights up to 70 m and diameters as large as 3.5 m on moist, well-drained, fertile sites (Lamb 1966, Pennington & Sarukhán 1968). Mature crowns are typically 10-20 m in diameter but may spread as broadly as 40 m across; they tend to be irregular in shape and comprised of a few large branches (Lamb 1966, Snook 1993, Gullison *et al.* 1996). Clear boles are often 20-25 m in height, and in Central America are cloaked in thick, deeply furrowed, nearly black bark which provides excellent fire resistance (Lamb 1966, Chudnoff 1979). Leaves are pinnately compound, dark, and glossy, lending the crown a distinctive glistening sheen that tree-spotters use to identify the crowns from the

ground or small planes. In Central America leaves turn crimson before dropping during the dry season. The period of deciduousness ranges from days to months depending on local weather patterns and soil moisture relations (Swabey 1941, Pennington & Sarukhan 1968, Pennington *et al.* 1981, Whitmore 1983).

11. **Reproductive biology**. Age and size at first flowering and fruiting appears to depend on the crown achieving some minimal level of canopy dominance (Gullison *et al.* 1996). Sexual maturity at 12 years has been observed in plantations with open-grown trees (Lamb 1966), but in natural forest reproduction is likely delayed by intense vertical competition for canopy dominance. Flowering occurs after leaf-fall during the early to mid dry season, slightly after flushes of new leaves. Mahogany is monoecious, with axillary panicles of small (<1 cm across), pale green, fragrant flowers that appear perfect but which are functionally either male or female. Bees and moths commonly pollinate trees of the mahogany family, the Meliaceae, but which species, if any, serve mahogany is unknown (Styles & Khosla 1976).

12. **Fruits**. Fruits are fist-sized woody five-valved capsules held upright above the crown, containing a five-winged receptacle with seeds stacked in two rows within each cell. Fruits mature through the rainy season and dehisce the following dry season before flowering re-initiates, releasing 45-60 winged seeds (Record & Hess 1947, Pennington & Styles 1975, Pennington *et al.* 1981, Whitmore 1983). Gullison et al (1996) observed that fecundity rises gradually with dbh size class, peaking at 130 cm; one individual this size produced 600 fruit capsules in a single year, or approximately 33,000 seeds. Fruiting intensity may vary considerably from year to year. Fluctuations associated with post-disturbances conditions, atypical seasonality, and sudden resource availability have been reported (Lamb 1966, Snook 1993, Gullison *et al.* 1996). Interviews with loggers and Kayapó Indians in southern Pará indicate that fruiting intensity varies considerably from year to year both within and among locations across the region (Grogan *et al.* in press).

13. **Seeds**. Seeds are winged, 6-13 cm long by 1-2.5 cm wide, and wind (or gravity) dispersed. Their geometric stacking within the fruit capsule leads to predictable variation in size, with the largest seeds exhibiting the highest germination rates and producing the largest seedlings (Chinte 1952). They are attached to the capsule receptacle by a thin funiculus near the apex of the wing, and require some degree of turbulence to dislodge them after detachment of the pericarp. Seeds are quite dry at the time of dispersal, with 6.3 + or –0.3% wet to dry weight ratio. Dry weights of seed (without the wing) collected form a mountainous region is southwest Pará average 0.418 g +- 0.123 g (N=150). Variation in seed weight by provenance has been reported, with seeds from Nicaragua, Venezuela, and Peru heavier than seeds from Belize, Mexico and Costa Rica (Lamb 1966, Whitmore and Hinojosa 1977, Whitmore 1983, Snook 1993). Whether these differences are related to genetic differences among populations or simply site conditions at points of collection is unknown.

14. **Seed Dispersal.** Seedfall occurs through the mid to late dry season. Little is known about its duration and pattern within and among trees in a given area. The seed rain forms a characteristic parabolic shape downwind of the fruiting tree. Dispersal distances may be augmented where strong winds are common. In

Mexico's Yucatan Peninsula, where hurricanes strike regularly, Snook (1993) reported a 3-hectare funnel-shaped seed shadow to the leeward of a single mature stem, while Lamb (1966) gave downwind dispersal area estimates of four hectares. Gullison *et al.* (1996) reported median dispersal distances of 32-36 m around mature trees in Bolivia, with 80 m the maximum distance observed, producing a 2-hectare seed shadow. In south Pará, seeds have been seen to disperse beyond 100 m from parent trees, carried by strong late dry season winds (Grogan *et al.* in press).

15. Water is also thought to be an important dispersal mechanism (Lamb 1966, Gullison & Hubbell 1992a). In Bolivia, where mahogany is commonly found along abandoned river courses and where establishment is thought to occur after large flooding events, seeds have been shown to float well and to retain germinability after 10 days of soaking (Gullison, pers. comm.). Early rainy season flooding observed in south Pará could carry ungerminated seeds considerable distances downstream.

16. **G[illegible]ination**. Seed viability at the time of dispersal is commonly >90% (Rodriguez & Barrio 1979 in Snook 19[illegible] Seeds have no long-term dormancy mechanisms, but can survive 4-6 months in the field under dry conditions (Rodriguez *et al.* 1992 in Snook 1993, Gullison *et al.* 1996) and up to 10 months when dried and c[illegible]d (Rodriguez & Barrio 1970 in Snook 1993). Germination is hypogeal and generally begins within 10 days of sowing in plantations, continuing for three weeks afterwards, with an average time between planting and total germination of 28 days (Marrero 1949, Lamb 1966, Alvarenga & Flores 1988). Moisture availability associated with the onset of the rainy season triggers germination, though the precise mechanism remains unclear (Lamb 1966). Water imbibition by the seed requires prolonged dampness; earliest germination in closed forest occurs at microsites where moisture is retained during the first fitful weeks of the rainy season (e.g., under thick litter). If the first rains are separated by a "mini-drought" several weeks long, seeds germinate in cohorts within a single tree's seed shadow (Grogan 1996). Germination under closed canopies in semi-evergreen forests has been reported at rates between 35-60%, with moisture apparently triggering response (Gerhardt 1996). Germination has been said to require generous light corresponding to mid-sized to large canopy gaps (Bascope *et al.* 1957 in Whitmore 1992), but seedlings are commonly encountered in moderate shade near adult stems (Stevenson 1927, Gullison & Hubbell 1992b). Wolffsohn (1961) and Snook (1993) observed that exposed mineral soil or thin litter present the best substrates for root establishment.

17. **Seed Predation**. Seed predation begins on the tree, where macaws and parrots feed on fruit capsules. Ground feeding animals, especially pacas and other forest rodents, are known to eat seeds on the ground (Lamb 1966). Insect predation of dispersed seeds has been cited by Wolffsohn (1961) as a probable important mechanism regulation Central America populations, while Gullison *et al.* (1996) attributed post-dispersal seed mortality to insects and fungus. Seeds are highly astringent, suggesting that protective secondary compounds may be an important defense mechanism. Whether this protection extends to seedlings is unknown.

18. Seedling Establishment. Seedling regeneration after logging is generally reported as poor to non-existent. Stevenson (1927) described large areas of "primary association" forest on moist, well-drained sites in Belize as having little or no regeneration after logging. Stevenson noted that, where occurring, initial high seedling densities around exposed stumps declined rapidly in competition with advance regeneration of other species, often fading to zero within one year. Quevedo (1986), working in Bolivia, encountered regeneration in three-year-old logging gaps created by mahogany extraction, but not in nine-year-old gaps. Gullison and Hubbell (1992) found an average of 48 seedling in 18 treefall gaps created by recent mahogany extraction in Bolivia. However, in the same study area, Gullison *et al.* (1996) found regeneration attributable to release by or recruitment after logging in only two of 28 gaps 18-20 years old. In south Pará, Brazil, Veríssimo *et al.* (1995) found regeneration in 31% of 70 plots centered around stumps in logging gaps three to nine years old. High correlation with remnant seed trees indicated that many of these seedlings germinated after extraction. Grogan *et al.* (in press) found regeneration in 65% of 40 single treefall gaps created by logging two to three years prior to sampling. Lamb (1966) stated that on favorable sites, that is, where soil moisture and drainage are good, mahogany fares poorly in competition with advance regeneration except after large-scale disturbances.

19. Growth. Little is known about physiological processes governing mahogany growth. As a deciduous species with considerable variation in leaf size and texture according to site, mahogany both avoids and tolerates water stress (Lamb 1966). Nutrient translocation apparently occurs shortly before leaf shedding, as evidenced by the change in crown color from deep green to crimson (at least in Central America; this has not been reported from South America). Since flowering and leaf flushing occur before the end of dry season, carbohydrates and water either must be accumulated and stored within the tree, most likely in the roots, during the rainy season; or assimilation must continue through the dry season through roots tapping deep soil water. Wood color and the astringent properties of sap and seeds attest to a high rate of investment in secondary compounds for anti-fungal and -herbivory purposes, a trait common in the Meliaceae (Lamb 1966, Pennington *et al.* 1981, Loehle 1988).

20. Some discrepancy exists in the literature regarding optimal seedling growing conditions. Seedlings in natural forests have been said to be drought sensitive and intolerant of full sun (Stevenson 1927). On the other hand, seedlings have been reported to be intolerant of deep shade, though they may persist in medium light (Smith 1942). Ramos & Grace (1990) found that seedlings grown in high light conditions approached light saturation—that is, maximal photosynthetic response—at approximately 50% of full sun, suggesting that mahogany is physiologically equipped for high light environments associated with canopy gaps but not necessarily full sun. Stevenson (1927) observed open gaps near seed trees dense with mahogany seedlings, with no regeneration in adjacent shaded understory. Gullison & Hubbell (1992b) described seedlings as heliophilic, requiring generous light for growth. Though they documented seedling densities of 300/ha around reproductive adults, no long-term seedling banks were observed to accumulate. They estimated that seedlings could survive at most six years under closed canopy conditions. Grogan *et al.* (in press) found seedling densities up to 240/0.5 ha in areas immediately adjacent to parent trees, though most trees had little to no regeneration. They reported 18% survivorship by naturally established seedlings in closed forest after 10 months, and 28% survivorship for planted seedlings.

21. Experimental studies following survival and growth of mahogany seedlings in Mexico and Costa Rica confirm its preference for high light environments at an early age. Ramos & Del Amo (1992) found in a 7-year study in moist forest near Veracruz, Mexico that height growth correlates positively with degree of canopy opening, though survival rates were highest at intermediate levels. Working in dry forest in northwestern Costa Rica, Gerhardt (1993) found that survival rates increase with irradiance levels; after three years of growth, saplings were taller on average in pasture environments compared to secondary forests. Mortality due to predation was higher in forests.

22. Lamb (1966) reported that seedlings grow approximately 15 cm in height in the first six months under forest conditions, while growth in nurseries over the same period averages 1 m. Gullison & Hubbell (1992) recorded growth rates for established seedlings under closed canopy of 7.4 cm/yr.; in gaps, growth rates increased to 14.7 cm/yr., with maxima of 100 cm/yr. Stevenson (1927) observed seedling growth responses up to 60 cm within three weeks of release from shade. Branching generally occurs after the stem is >2 cm dbh and several meters tall (Snook 1993). Suppressed 3-m tall saplings can persist and even slowly add height increments for many years under high shade (Lamb 1966). Snook (1993) found that the fastest diameter growth rates for mahogany occur between the ages of 15-30. Gullison and Hubbell (1992) determined that the fastest growth rates occur for 20-80 cm dbh size classes. No information is available regarding the ability of seedlings, saplings, and poles to respond to canopy release.

23. Growth data from natural forests, secondary forest enrichment plantings, and plantations are listed in Table 1 (p. 19). While both diameter and height increments vary dramatically due to site and provenance differences, it is clear from the data that mahogany is capable of rapid growth. Rates in forest settings tend to run lower than in plantations, though Lamb's (1966) 0.14 -0.36 cm/yr and Gullison *et al.*'s (1996) 0.36- 0.9 cm/yr estimates for dbh growth are measures of narrow periodic increments rather than mean annual increments for trees of known age. With few exceptions diameter growth in plantations exceeded 1 cm/yr, attaining rates as high as 3 cm/yr in Martinique (Marie 1949). Height growth generally exceeds 1 m/yr in plantations, with some seedlings in Costa Rica reaching 5 m by the end of one year (Newton 1992). Estimates for the time required for trees to grow to merchantable size vary from Snook's (1993) 122 years for 55 cm dbh trees in Quintana Roo, Mexico, to Gullison & Hubbell's (1992a) 105 years for 80 cm dbh trees in Bolivia (with a range of 52-148 years). Lamb (1966) estimated a rotation period of 40-50 years for 58 cm dbh trees grown on plantations in Belize.

24. While early growth of mahogany may be robust, successful maturation to merchantable size in plantations is hampered by the shoot-boring moth, *Hypsipyla grandella* Zell, which lays its eggs on the expanding apical meristem of flushing seedlings and saplings (Holdridge & Morrero 1940, Martorell 1943, Félix de Barros & Brandi 1975, Weaver & Bauer 1986). Larval caterpillars hatch and burrow into the growing apical tip, feeding on the new plant tissues and eventually disabling the leader. This in turn causes sprouting with consequent stem deformation (Lamb 1966, Yamazaki *et al.* 1992, Newton *et al.* 1993). Plantations managers have long been

aware that planting at low densities in secondary vegetation reduces attack rates (Stevenson 1927, Marshall 1939, Swabey 1941, Marie 1949, Yared & Carpanezzi 1981). Even so, the shoot-borer remains the principal obstacle to successful plantation management across mahogany's natural range. Little is known about the shoot-borer's role in regulating mahogany populations in natural forests.

25. **Disturbance and development in stands.** As an emergent tree found at low densities with few or no seedlings establishing under closed canopy conditions, and capable of rapid growth in high light environments, mahogany regeneration in natural forests is apparently associated with large gaps produced by large-scale disturbance events (Snook 1993), leading to its classification as a pioneer, early successional, or large-gap specialist (Budowski 1965, Denslow 1987, Swaine & Whitmore 1988). Disturbance scenarios known to favor mahogany include hurricanes, fires, floods, agricultural clearings, abandoned loading yards and roadsides associated with timber extraction, and treefall gaps (Wolffsohn 1961, Lamb 1966, Snook 1993, Gullison *et al.* 1996).

26. The forests of Belize, Guatemala and Mexico are regularly disturbed by hurricanes, which damage canopies from the top down, releasing advance regeneration and allowing invasion of secondary species over large areas (Lamb 1966, Smith 1986). With *Cedrela odorata*, mahogany survives hurricane winds better than any other species in Belize (Lamb 1966, Wolffsohn 1967); Snook (1993) and Francis (1991) found similar behavior in Mexico and Puerto Rico, respectively (the latter for *S. mahagoni*; but see Wadsworth & Englerth 1959 on mahogany's susceptibility to high winds in Puerto Rico). Lamb (1966) noted that light conditions in hurricane-damaged forests were suitable for mahogany regeneration, and concluded that seedlings growing vigorously after the 1942 hurricane in Belize began as advance regeneration. Snook (1992, 1993) described a 34-year-old post-hurricane stand with two broad size-classes, the larger stems representing a cohort that established after some large-scale disturbance in the distant past, and the smaller stems representing a cohort that established after the 1955 hurricane. Suppressed mahoganies indicated that lateral canopy closure by trees surviving the hurricane may occur rapidly enough to prevent mahogany from attaining canopy dominance. She demonstrated that mahogany may established successfully after hurricanes and fires occurring at intervals decades to centuries wide, and concluded that single-treefall gaps created by selective extraction of widely spaced adult trees present insufficient (being too small) or inappropriate (lacking soil disturbance) growing conditions for mahogany regeneration.

27. Gullison & Hubbell (1992a, b) concluded that mahogany regenerates under open canopies created by forest dieback after rare large-scale flooding events kill overstory trees through prolonged submergence and silt deposition. Large stems growing above erosion gullies on high terraces indicate a single massive disturbance event in the distant past that released a single cohort. In both scenarios, the presence of bare soil, good drainage, and persistent canopy opening substantiate the view that mahogany requires large-scale disturbance for successful recruitment.

28. **Natural stocks**. Estimates of natural stocks of mahogany remain speculative. This is because there exist no national inventories of this species. A survey conducted by Figueroa (1994) provided qualitative estimates in some countries. In that study, remaining natural stocks varied from severely depleted (Costa Rica, Panamá, Peru, Guatemala) to moderately abundant (Belize). However, no overall status assessment was available for Ecuador, Colombia, or Venezuela. There was also a lack of accurate information on natural stocks of mahogany in Mexico, Bolivia, and Brazil.

29. In Brazil, an unpublished study by Barros *et al.* (1992) based on RADAMBRASIL data, estimated that natural stocks of mahogany in Brazil remain relatively abundant, totalling roughly 21 million cubic meters (5,7 millions trees). However, Veríssimo *et al.* (1992) argued that accurate data on remaining mahogany stocks are difficult to collect because of its clumped distribution pattern; thus all such estimates should be regarded with caution.

GENETICS

30. The issue of genetic erosion in mahogany has been a part of the literature for a number of years (Styles & Khosla 1976). High levels of extraction will reduce the size of a genetic population, and population genetic theory makes clear that this can lead to genetic drift, loss of alleles and genotypes, and changes in the mating system, especially increased inbreeding. There are efforts underway to document the genetics of mahogany, especially from the perspective of conservation biology. Published data are available from the Chimanes Forest, Beni, Bolivia (Loveless & Gullison 1998). They surveyed isozyme (protein) variation in four local populations of mahogany separated by up to 100 km. They found relatively high levels of genetic variation in these Bolivian populations, when compared to the variation detected in populations of other tropical tree species. Mean heterozygosity in the two best-sampled mahogany population was 0.22 (Loveless & Gullison, in prep), compared with 0.11 in a summary of 81 native tropical plant species (Loveless 1992). This means that individual mahogany populations contain considerable genetic variation, and thus have the potential for differentiation and local adaptation. The populations in Bolivia did not, however, show much genetic differentiation. This suggests that on the local scale, gene flow by pollen or seed dispersal is substantial. Local aggregations of adults which are part of an intact forest matrix are not genetically isolated, and have similar genetic makeup. On-going fragmentation of the landscape as a result of timber extraction and conversion of land to pasture (especially in Brazil) could, however, potentially interrupt gene flow and may act to promote genetic divergence between populations and genetic erosion within populations.

31. The potential for gene flow in mahogany is also shown by direct measurement of outcrossing using isozyme markers (Loveless & Gullison 1998). Analyses of progeny arrays showed complete outcrossing, despite the fact that mahogany is capable of self-pollination in plantation settings. Moreover, measures taken in one Bolivian population before and after isolation due to timber extraction showed a 15% increase in the level of inbreeding in the residual trees (Loveless & Gullison, in prep). This is probably due to restricted pollen flow and

mating between related individuals. Such increases in inbreeding in a species which historically outcrossed could have serious negative consequences for natural regeneration of mahogany from a small number of seed trees. This could include such phenomena as decreased germination, increased mortality, lower seedling fitness, or reduction in growth rate.

32. Genetic studies are now being undertaken in Brazilian populations. Maristerra Lemes (INPA, CENARGEN) is using microsatellite markers to characterize genetic structure in mahogany population from Acre, Rondônia, and southern Pará. M. D. Loveless (College of Wooster, USA) is using isozymes to measure genetic variation in these same populations. These data should be available within the next year. This will allow us to determine the degree to which populations of mahogany differ genetically through their Brazilian range, and the most effective means to achieve genetic conservation of this species in the face of harvesting pressure.

RESEARCH PROGRESS ON MAHOGANY: THE BRAZILIAN CASE

33. Effective management strategies for commercial timber species in natural forests can only be formulated when thorough knowledge of natural population dynamics has been obtained. That is, natural forests cannot be managed for present and future harvests if species-level understanding of life history strategies in the wild is lacking. How does the tree reproduce, survive, grow, and move about on the landscape ? Though the ecological information we have presented to this point may suggest otherwise, in fact relatively little is known about processes affecting population dynamics of mahogany in natural forests.

34. After over 400 years of commercial exploitation, only two field studies of natural populations have been undertaken to date, by Snook in Mexico and by Gullison *et al.* in Bolivia. While both studies indicate that mahogany may have adapted its regeneration strategy to catastrophic disturbances occurring at stochastic intervals at large spatial scales, it seems likely, given mahogany's vast range and the diverse conditions under which it grows, that its ecological amplitude may be broader than these studies suggest. Considering weather patterns, geological history, topography, soils, forest composition, and long-term disturbance history at study sites from south Pará to Bolivia to Mexico, the only common feature is presence of mahogany. If life history strategies differ from one site to another, it may be that management strategies may also require flexibility to suit the particulars of each site.

35. A long-term study of the ecology, genetic structure, and management of mahogany in south Pará was begun in 1995 by researchers from IMAZON, Yale University (USA), Pennsylvania State University (USA), Wooster College (USA) and INPA-CENARGEN. Fieldwork to date has identified three different distribution patterns of mature trees in this region: 1) Relatively high densities along the banks and in localized floodzones of the region's larger tributaries to major branches of the Amazon river; unfortunately these populations have probably been completely extirpated; 2) intermediate densities on low ground associated with seasonal streams, with few or no individuals occupying intervening high ground separating micro-watersheds; and 3) unknown

densities on dry slopes of scattered inselbergs (granitic outcrops). Sub-populations of adult mahogany have been censused for growth, seed production, and recruitment studies at four sites of type 2), in cooperation with the Brazilian timber industry (the SEMASA and Peracchi timber export companies).

36. Population structure and the natural disturbance regimes that may account for them appear to be rather more complex in south Pará than those reported elsewhere. At landscape scales, size-class distribution patterns approximate the bell-shaped curve described in Venezuela, Mexico, and Bolivia, indicating low recruitment rates into smaller adult size classes in recent years. However, an intensive mapping project at the principal research site, the Marajoara Management Project, indicates that size-class representation within a given micro-watershed—that is, among localized groups of trees—is typically broad, with pole-sized, vigorously growing individuals mixed with large, reproductive adults. Smaller trees are commonly seen growing into canopy gaps opened years or decades earlier by the deaths of different species of overstory trees. Coupling preliminary growth data showing a marked decline in periodic annual increment by trees >80 cm dbh (echoing findings by Gullison *et al.* 1996) with the observation that mortality rates appear relatively high for all size classes leads us to hypothesize that recruitment into adult size classes may be occurring at smaller spatial and narrower temporal scales than has been inferred from other studies. While rare forest-level blowdowns proposed by Nelson (1994) and region-wide fires occurring at centuries-wide intervals proposed by Meggers (1994) could initiate mahogany regeneration at landscape scales, it is probable that other processes also play a role in maintaining population levels in south Pará.

37. Experimental work examining seedling response to gradients of light, soil moisture, and soil nutrients has been designed to clarify these issues. Emphasis has also been placed on describing seed production cycles over many years, identifying pollination vectors, determining the impacts of selective extraction on the reproductive efforts of remnant trees, and comparing genetic structures of unlogged vs. logged sub-populations. Silvicultural treatments planned for the 1998 dry season will test hypotheses about mahogany's regeneration capacity under disturbance regimes of varying intensities, and about baseline forest development pathways that represent the competitive environment within which management strategies must be implemented.

EMERGING NATURAL FOREST MANAGEMENT RECOMMENDATIONS

38. As results from Grogan *et al.* research in south Pará become available over the next two years, the authors anticipate that empirically based formulas for silvicultural management of mahogany in natural forests will emerge. Again, site- or region-specific understanding of life history patterns must be placed within local or regional environmental contexts for these strategies to bear fruit, considering influences of climate, soils, hydrology, disturbance patterns, and competitive floristics. Essential components of successful management systems for sustainable harvests will likely include the following:

I. Modification of minimum-diameter cutting guidelines

39. Minimum-diameter guidelines for any natural population of timber tree represent a prescription for a simple high-grading of the resource. 'Reasons for modifying the practice include the following:

a. Fecundity—the ratio of seed production to stem size—rises sharply in trees >80 cm dbh, as shown by Gullison et al (1996) and preliminarily by Grogan *et al.* in south Pará. Removing the largest trees disproportionately removes potential available seeds for re-colonization of harvested sites.

b. Many larger trees have persisted long enough to develop hollow stems that make them worthless as timber. Yet these trees are invariably felled anyway, marked by tree spotters and cut by chainsaw operators who can tell by a simple tap on the trees stem whether it is "ocado" or not. These trees are felled either in hopes that some small portion of the upper bole can be salvaged, or because tree spotters and chainsaw operators are paid by the stem, regardless of whether it is eventually removed from the site or not.

40. Possible modifications of minimum-diameter cutting guidelines include the following:

a. Some proportion of large, emergent, healthy trees should be retained within the harvest area as seed sources for regeneration treatments.

b. All hollow trees, regardless of size, should be retained as seed sources for regeneration treatments. Even if still relatively small, these trees, worthless from a timber perspective, represent a valuable ecological resource insofar as they provide pollen—the population's genetic capital—for seed set by other members of the unharvested population.

II. Sub-population- (micro-watershed-) level management scale

41. Preliminary analysis of micro-watershed-level aggregations of mahogany in south Pará indicates some degree of continuous gap-phase recruitment of new individuals into the rank of adult populations, perhaps within larger cycles of landscape-scale-disturbance. This suggests that micro-watershed aggregations of trees represent the appropriate spatial scale for management planning. A managed extraction operation might proceed as follows:

a. A management area could be divided into component stream drainage systems, within each of which reside sub-populations of mahogany.

b. These sub-populations could be inventoried—"explored" as they are in practice—by size-class and spatial distribution of stems, a relatively fast and simple operation given the orienteering skills of typical woodsmen.

c. Selection of seed trees for retention, considering the distribution of non-commercial (hollow or diseased) stems. could then be made to maximize dispersal of seeds from retained mother trees to logged areas. This would shift extraction management toward a rational strategy, away from high-grading as currently practiced. Vigorous trees smaller than some minimum diameter – preferably <50 cm dbh—would be retained.

III. Growth (volume increment) management

42. Annual volume increment for 10-cm size classes, monitored for ~550 trees across south Pará since November 1995, indicates wide variability within all size classes, as well as significant decrease in growth rates for trees >80 cm dbh. Variability in growth rate appears correlated with site (topographic position, subsurface hydrology, soil type) and degree of vine loading. Experimental vine cutting will be implemented in 1998 to assess the effectiveness of vine release as a silvicultural treatment. The drop-off in growth rate for trees >80 cm dbh is likely related to increased investment of photosynthetic resources into seed production, as suggested by Gullison *et al.* (1996). Possible consequences and implications from growth studies include the following:

a. Appropriate rotation lengths for polycyclic natural forest management systems should emerge once 5-10 years of growth data become available. That is, we should soon know how long, given specific site and competitive conditions, it takes for trees in the southeastern Brazilian Amazon to attain harvestable diameters, as calculated in Mexico by Snook (1993) and Bolivia by Gullison *et al.* (1996).

b. Silvicultural experiments examining growth response to vine cutting and canopy opening will indicate whether vine-loaded and or canopy crowded mahoganies in the smaller size classes can be cost-effectively released for growth or whether they should be harvested directly. Long-term flowering and seed production studies will strengthen the analysis. It may turn out that some trees are too thoroughly compromised by growing conditions to justify their retention for future harvests, regardless of size, and that further modification of minimum-size guidelines for harvest will promote culling of non-competitive, poorly growing, non-productive (in terms of flowers and seeds) trees.

IV. Regeneration strategies: promoting establishment of the next harvestable generation

43. The Grogan *et al.* studies in south Pará indicate the following for that region:

a. Seed dispersal occurs in the mid- to late dry season, creating "shadows" of seeds and, as the rainy season begins, seedlings which germinate to the downwind (generally western) side of adult trees.

b. Seed production, occurring annually at some level, may be pulsed in cycles 3-4 years wide.

c. Seeds germinate readily in closed forest as well as open gap environments.

d. Seedlings grow best in high light environments, though they may persist for years in closed forest.

e. Achieving optimal seedling performance may depend on identifying microsites within a disturbed landscape—growth "hotspots"—where long-term robust growth, if not survival, is assured.

44. Management implications include the following:

a. Felling should be timed so that trees come down after seeds are dispersed.

b. Some years are likely to be more favorable than others in terms of seed production, and therefore in terms of the likelihood of post-harvest seedling regeneration. Basic knowledge of seed production cycles at local or regional levels could enormously strengthen success rates of management for regeneration.

c. Trees should be felled with regeneration in mind. That is, where possible, canopy gaps should be opened downwind of adult trees. Where more than one tree will be removed at a single site, multiple-treefall gaps could be oriented to provide contiguous openings to maximize growing space for light-demanding seedlings. Though buttresses on adult trees often dictate felling direction, as well as the layout of logging roads and skid trails, even minimal planning of the felling operation could sharply increase prospects for successful recruitment of future trees.

d. Better understanding of seedling resource requirements—its growth relations to light, soil water, soil nutrients, and competing vegetation—will allow development of optimal strategies for artificial regeneration at sites where natural seed sources have been removed or are unavailable. It may be that microsite selection for seed planting proves more important than the quantity of seeds planted, raising the cost-effectiveness of artificial systems.

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Table 1. Mahogany growth rates

Mahogany diameter and height growth rates (mean annual increment)				
location	**site**	**age (years)**	**dbh (cm/yr)**	**height (m/yr)**
Belize	Forest	all ages	0.14 - 0.36	
Bolivia	Forest	all ages	0.26 - 0.9	
Bolivia	Forest	< 6		0.074 / 0.147
Mexico	Forest	15 - 75	0.2 - 0.65	
Mexico	Forest	15		0.34
Mexico	secondary forest	6.7	0.34 / 0.6	0.44 / 0.67
Costa Rica	secondary forest	3	0.30	
Costa Rica	abandoned pasture	3	0.70	
Mexico	abandoned logyard	34	0.74	
Puerto Rico	plantation	2	1.40	1.59
Belize	taungya	3	0.89	1.5 - 2.0
Brazil	plantation	4	1.26	1.36
Colombia	plantation	4.2	0.74	1.06
Puerto Rico	plantation	10	1.02	1.2 - 1.5
Belize	plantation	12	2.54	
Martinique	plantation	17	3.00	
Puerto Rico	plantation	18	1.40	1.00
Sri Lanka	plantation	22	1.77	
Puerto Rico	plantation	26	0.90	0.66
Puerto Rico	plantation	27	1.32	
Puerto Rico	mixed plantation	27	1.69	
India	plantation	38	1.47	0.68
Sri Lanka	plantation	50	1.16	
Costa Rica	plantation	1		1.0 - 5.0
Puerto Rico	plantation	7		1.20
Peru	plantation	7		1.63
Puerto Rico	plantation	8		0.70