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Factors Limiting Post-logging Seedling Regeneration by Big-leaf Mahogany (*Swietenia macrophylla*) in Southeastern Amazonia, Brazil, and Implications for Sustainable Management[1]

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ABSTRACT

Post-logging seedling regeneration density by big-leaf mahogany (*Swietenia macrophylla*), a nonpioneer light-demanding timber species, is generally reported to be low to nonexistent. To investigate factors limiting seedling density following logging within the study region, we quantified seed production rates, germinability, dispersal patterns, and seed fates on the forest floor through germination and the first seedling growing season in southeastern Amazonia, Brazil. Fruit production rates were low by three logged and one unlogged populations compared to reports from other regions. Commercial-sized trees (>60 cm diameter) were more fecund than noncommercial trees (30–60 cm diameter) at two sites, averaging 14.5 *vs.* 3.9 fruits/tree/year, respectively, at Marajoara, a logged site, over 8 yr. Fruit capsules contained an average of 60.3 seeds/fruit, 70 percent of which appeared viable by visual inspection. Sixty-seven to 72 percent of apparently viable seeds germinated in nursery beds 2.5 mo after the dispersal period, when wet season rains began. Dry season winds blew most seeds west-northwest of parent trees, with median dispersal distances of 28 and 9 m on west and east sides of parent trees, respectively. Nearly 100 percent of seeds fell within an area of 0.91 ha. On the forest floor beneath closed canopies, mammals, invertebrates, and fungal pathogens killed 40 percent of apparently viable seeds, while 36 percent germinated. Nine months after seedling establishment—midway through the first logging season following seed dispersal—14 percent of outplanted seeds survived as seedlings, representing 5.8 seeds/fruit. We conclude that seedlings are likely to survive in logging gaps at appreciable densities only in rare cases where previous year fruit production rates by logged trees were high (4–12.5% of commercial-sized trees/year at Marajoara) and where tree crowns were felled in west or northwest directions.

RESUMO

A densidade de regeneração de plântulas de mogno (*Swietenia macrophylla*), uma espécie não pioneira mas demandante de luz, após exploração madeireira é geralmente reportada como de baixa a não-existente. Para investigar fatores que podem limitar a densidade de plântulas após exploração madeireira, quantificou-se as taxas de produção de sementes, a germinabilidade, os padrões de dispersão e o destino das sementes no chão florestal desde a germinação e no primeiro período de crescimento das plântulas no sudeste do Pará, Brasil. Foram verificadas taxas baixas de produção de frutos em três populações exploradas e em uma população não explorada comparado com produção de populações em outras regiões. Em Marajoara, uma área explorada, observou-se que as árvores com tamanho comercial (com diâmetros >60 cm) eram mais fecundas que aquelas com tamanho não comercial (com diâmetros de 30–60 cm), produzindo uma média de 14.5 *vs.* 3.9 frutos/ano/árvore respectivamente durante oito anos de observação. Através de inspeção visual, verificou-se que 70 por cento das 60, 3 sementes/fruto eram aparentemente viáveis. Destas, 67 a 72 por cento germinaram nos viveiros, 2.5 meses após o período de dispersão, quando começou a estação de chuvas. Os ventos da estação seca levaram a maioria das sementes na direção oeste-noroeste das árvores mães, com distâncias medianas de 9 e 28 metros nos lados leste e oeste respectivamente. Aproximadamente 100 por cento das sementes caíram dentro de uma área de 0.91 hectare. No chão florestal, embaixo do dossel fechado, mamais, invertebrados e patógenos fúngicos mataram 40 por cento das sementes aparentemente viáveis enquanto 36 por cento germinaram. Nove meses após o estabelecimento das plântulas—no meio da primeira estação de exploração após a dispersão das sementes—14 por cento das sementes transplantadas sobreviveram como plântulas. Concluiu-se que as plântulas são mais prováveis de sobreviver nas clareiras de exploração em densidades consideráveis somente em casos raros onde as taxas de produção de frutos do ano anterior foram altas (4% a 12.5% de árvores/ano em Marajoara) e onde as copas das árvores foram derrubadas na direção oeste ou noroeste.

Key words: Amazon; dispersal; fecundity; forest management; fungal pathogens; germination; mahogany; predation; seasonal evergreen forest; *Swietenia macrophylla.*

Logging practices in species-rich tropical forests typically resemble mining operations at the species level (Gomez-Pompa 1989, Johnson & Cabarle 1993, Moad & Whitmore 1994, Schulze *et al.* 2005). Whether a single high-value timber species, a group of species, or a wider community is targeted for extraction, adult populations experience sudden and severe density reductions, often at large spatial scales (Uhl *et al.* 1991; Veríssimo *et al.* 1992, 1995). Post-logging species-level recovery—the possibility that timber production might be sustained through multiple cutting cycles or rotations—depends on growth and reproduction by surviving adults, juveniles, and seedling regeneration (Smith *et al.* 1997). Tree species typically thought to be most capable of renewing population structures following logging occupy opposite ends of the classic pioneer–climax successional dichotomy (Swaine & Whitmore 1988), pioneers germinating from the soil seed bank in newly opened canopy gaps and climax or primary forest species

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accelerating growth by abundant shade-tolerant seedlings and juveniles awaiting release beneath closed canopies (Brokaw 1987, Martini *et al.* 1994, Dalling *et al.* 1998, Dekker & de Graaf 2003). Unfortunately, many current high-value timber species are nonpioneer light demanders whose seedlings occur at low densities in the forest understory due to limited shade tolerance (Jones 1956, Lamprecht 1989, Gullison & Hubbell 1992, Medjibe & Hall 2002, Hall *et al.* 2003, Grogan *et al.* 2005, Schulze *et al.* 2005). Examples include the wind-dispersed mahoganies and related genera in the family Meliaceae (*Swietenia, Cedrela, Chukrasia, Entandrophragma, Khaya, Toona*) as well as *Amburana*, *Cedrelinga*, *Couratari, Dinizia, Hymenolobium,* and *Tabebuia*. Post-logging regeneration surveys frequently document regeneration failure by these species (Veríssimo *et al.* 1995, Gullison *et al.* 1996, Dickinson & Whigham 1999, Mostacedo & Fredericksen 1999, Fredericksen & Mostacedo 2000, Grogan *et al.* 2003b, Schulze 2003).

Reproductive phases of species' life history must be well understood in order to adjust logging and silvicultural practices to promote regeneration success (Guariguata & Pinard 1998). How many seeds can a tree of a given stem or crown size be expected to produce in a given year? When, to what distance, and in what density pattern are seeds likely to disperse? When do seeds germinate, how germinable are they, and what are their principal mortality agents? At what densities are seedlings likely to establish? Answers to these questions can inform forest managers about what to expect in terms of advance regeneration densities at the time of logging and suggest why some silvicultural interventions designed to increase seedling densities and promote seedling growth rates may be more effective than others.

In this paper, we address these questions for big-leaf mahogany (*Swietenia macrophylla*) in southeastern Brazilian Amazonia. Mahogany is a highly valuable Neotropical timber species occurring from Mexico to Bolivia at highest densities in seasonal forests receiving 1000–2000 mm of annual rainfall. Logged commercially since the 17th century (Lamb 1966), mahogany was listed in 2002 on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora because of concerns over the sustainability of industrial harvest practices, which typically remove up to 95 percent of adult trees from primary forests without regard for seedling regeneration necessary for stand replacement (Rodan *et al.* 1992, Snook 1996, Zimmerman *et al.* 2001, Blundell 2004). Considered commercially extirpated across large portions of its natural range (Calvo & Rivera 2000, Grogan *et al.* 2002, Kometter *et al.* 2004), mahogany's exploitation pattern is typical for high-value, nonpioneer, light-demanding species across the tropics.

We quantify aspects of mahogany's reproductive and regeneration ecology at sites in southeastern Amazonia in order to explain poor post-logging regeneration patterns reported from this region. Veríssimo *et al.* (1995) found seedlings in only 31 percent of seventy 5 × 15 m plots centered around mahogany stumps in logging gaps 3–9 yr old. While Grogan *et al.* (2003b) found seedling regeneration in 65 percent of forty 2- to 3-yr-old logging gaps, more than four seedlings were found in only 10 percent of surveyed gaps. Grogan *et al.* (2005) reported that high-density seedling clusters in logging gaps suitable for silvicultural management were rare. We ask: to what degree might seed production rates, dispersal patterns, germinability, and or predation pressures shape regeneration patterns observed following logging in this region? We conclude by discussing management implications of these findings for mahogany and other high-value, nonpioneer, light-demanding timber species under similar threat of commercial extirpation across the tropics.

METHODS

Study species.—Aspects of mahogany's reproductive ecology have been described from a small number of natural forest sites across its range. Mahogany seeds are relatively large (mean 0.35 g dry weight), winged, and wind-dispersed. They are produced in woody capsules 7–24 cm in length, each containing up to 70 seeds (Pennington *et al.* 1981, Grogan 2001, Niembro 2002). Fecundity increases with stem size from approximately 30 cm diameter, with trees larger than 100 cm capable of producing up to 750 fruits in a single year (Gullison *et al.* 1996, Snook *et al.* 2005). Seed dispersal occurs during the dry season (Lamb 1966, Daubenmire 1972). Gullison *et al.* (1996) found average dispersal distances of 32–36 m around mature trees in Bolivia, with 80 m the maximum distance observed; these authors reported seed viability at the time of dispersal to be 63 percent of production. Seeds have no long-term dormancy mechanisms (Lamb 1966). Moisture availability associated with the onset of the rainy season triggers germination (Gerhardt 1996, Morris *et al.* 2000). Germination by apparently viable seeds generally exceeds 70 percent in nursery settings (Chinte 1952, Campbell de Araujo 1971, Morris *et al.* 2000, Grogan *et al.* 2003b) but decline under forest conditions (Gerhardt 1996, Negreros-Castillo *et al.* 2003, Van Rheenen *et al.* 2004). Seed predation by invertebrates and mammals, especially pacas and other forest rodents, has been widely reported (Stevenson 1927, Wolffsohn 1961, Lamb 1966, Gullison *et al.* 1996, Grogan *et al.* 2003b, T. Clements, pers. comm.).

Study region and sites.—The study region, which marks the easternmost extension of mahogany's natural range in Amazonia, is located between 6.5°–8°S and 49.5°–52°W, 750 km south of the coastal city of Belém in the state of Pará. Climate is tropical dry, with mean monthly temperatures ranging between 25°C and 27°C (Holdridge 1967, Salati & Marques 1984). Annual precipitation during 1995–2001 at the primary study site, described below, ranged from 1636 to 2170 mm, with more than 90 percent falling between November and May. In some years no rain fell for 3–4 mo during the dry season.

The study site is a forest industry-owned management area called Marajoara, located at 7°50′S, 50°16′W, 34 km northwest of Redenção. The forest at Marajoara is dominated by evergreen trees intermixed with deciduous species. The site was selectively logged for mahogany plus five to seven secondary timber species between 1992 and 1994. The 4100-ha tract of forest is surrounded by heavily logged and burned forest and pasture. Topographic relief is slight. All streams are seasonal within the principal research area of 2050 ha. Observations from three additional sites, similar physiographically and floristically to Marajoara, supplement fruit production data reported here: Corral Redondo located 15 km northeast of Marajoara, Agua Azul located 110 km northwest, and Pinkaití located 185 km west. Of these, Corral Redondo and Agua Azul were logged at higher intensity than Marajoara in the early 1990s, while Pinkaití is an unlogged site.

FRUIT PRODUCTION.—To quantify annual fruit production by adult mahogany trees, fruit capsules on trees larger than 30 cm diameter were counted by two separate observers with binoculars during annual stem diameter increment censuses from 1997 to 2004 at Marajoara and Corral Redondo, from 1997 to 2003 at Agua Azul, and in 1996, 1998, and 1999 at Pinkaití ($N = 248$, 51, 81, and 49, respectively). Mahogany's large woody fruit capsules are readily identifiable on the tree crown from the forest floor. At Marajoara, trees whose crowns had not yet shed substantial portions of senescent leaves at the time of stem diameter measurement were recounted later when crowns were bare or nearly so. At all sites, fruit counts were verified by collecting dehisced capsule pericarps (five/fruit) on the forest floor beneath fruiting trees and dividing the total number by five; the final count was the larger figure yielded by the two methods. Surviving commercial-sized trees (>60 cm diameter, the legal minimum diameter cutting limit in Brazil since 2003) at Marajoara were, on average, small compared to logged trees; only 8 of 57 trees in this size class exceeded 90 cm diameter. At Corral Redondo, only one tree larger than 90 cm diameter survived among 14 commercial-sized trees. By contrast, the unlogged population at Pinkaití included 17 trees larger than 90 cm diameter among 31 commercial-sized trees.

SEED VIABILITY AND GERMINABILITY.—To estimate the number of viable seeds produced per fruit, 121 fruits collected from logged trees in forest adjacent to Corral Redondo were measured for length, sun-dried to dehiscence, and dissected, separating well-formed seeds from those clearly without embryos. Fruit capsules ranged from 9 to 19 cm in length. To verify that apparently viable seeds contained embryos, winged hulls were removed from seeds from 18 fruits. To determine percent seed germinability per fruit, apparently viable seeds from 18 fruit capsules ranging in size from 10 to 18 cm in length were planted in a raised nursery bed filled with well-drained sandy soil. Because previous seed dissections had demonstrated significant positive correlation between fruit capsule length and seed fresh weight (Grogan 2001), we noted fruit capsule length to test whether seed size would affect germinability as reported by Chinte (1952) and Niembro (2002). The bed was sheltered at 2 m height by doubled 30 percent shade cloth spread wide enough overhead to block direct sun. Seeds were planted to 1 cm depth, wings attached, segregated by fruit capsule. Planting occurred in early October, 2.5 mo after fruit were collected from logged trees, at the beginning of the 1997 rainy season. The planting bed was watered daily or as necessary to maintain moist surface conditions. New germinants were censused at 2-d intervals for 30 d as hypocotyls emerged above the soil surface. We also planted apparently viable seeds from 23 fruit capsules of intermediate length (15 cm), unsegregated by fruit, and censused new germinants as above.

SEED DISPERSAL.—The timing of fruit dehiscence and seed dispersal was monitored by censusing 350 fruits mapped on the crowns of 13 trees at Marajoara at 10-d intervals through the 1997 dry season. Direction and distance of seed dispersal was quantified in 6°-wide wedge transects radiating in six directions from the bases of six trees maturing more than 40 fruits. Sampled trees were located at least 300 m from each other to avoid overlapping seed dispersal shadows. Trees were censused in the mid dry season (July) of 1997, when most seeds were dispersed but ground litter had not yet built appreciably from forest-level leaf shedding. Transect directions were chosen randomly within successive 60° arcs (NE = 0–60°, E = 60–120°, etc.) and extended to 75 m. Teams of five people swept sampling areas at least twice, moving all leaf litter with pronged sticks after searching the litter surface. The large size and distinctive cinnamon-orange sheen of mahogany seeds make them relatively easy to find even in thick litter. Knowing that prevailing dry season winds arrived out of the east-southeast, east-side transects (NE, E, SE) were extended only to 50 m after no seeds were found beyond 34 m at the first fruiting tree on the east side. This sampling strategy was validated when only nine seeds were found beyond 34 m among five other trees. West-arc (240–300°) transects were extended to 100 m at each tree to determine whether dispersal distance continued appreciably beyond 75 m in the direction in which most seeds were found. The search area covered 1505 m^2 at each tree.

SEED FATES ON THE FOREST FLOOR.—To document seed survival and mortality agents during germination and seedling establishment phases, we planted apparently viable seeds around heavily fruiting mahogany trees (>40 fruits) during the 1997 dry season at Marajoara. Twenty planting locations were located at random distances and directions to 20 m on the west sides (180°–360°) of each of nine trees distributed within 1350 ha at Marajoara. Heavily fruiting trees were chosen to exclude the possibility that nonfruiting trees might not attract mammal and invertebrate seed predators. Ten planting locations at each tree were enclosed in chicken-wire (1-cm mesh size) cages 60 cm on a side and 50 cm tall, to exclude mammal seed predators, while 10 planting locations without caging served as controls. Nine winged seeds collected from fruiting trees at Marajoara were planted in a 3 × 3 grid at 20-cm intervals at each planting location, dropping seeds onto leaf litter already in place. To help relocate seeds during recensuses, we planted each within 5 cm of a nail sunk into the ground whose head protruded above the soil surface. At each tree, 10 mammal exclusion plots contained nine seeds each, with the same number planted in uncaged plots. The experiment total was 9 trees × 180 seeds = 1620 seeds.

To test the effect of parent tree proximity on seed fates during germination and seedling establishment, we located six planting locations in random directions at 10, 25, and 50 m distance on the west side of these same nine trees plus one additional tree. Nine seeds were planted per location without cage protection as above. At each of 10 trees, six plots × nine seeds were planted at three distances for a total of 162 seeds/tree and 1620 total. To observe seed fates in treefall gaps, 10 planting locations were randomly selected in 1-yr-old artificial canopy gaps located less than 25 m from three of these parent trees. Gaps were 100–150 m^2 in area. Nine seeds were planted per location without cage protection as above for a total of 270 seeds.

After outplanting on July 20 during the mid dry season when most seeds had naturally dispersed, all plots were recensused for seed survival, fate, and germination at 2-wk intervals until the first week of December, a period covering 19 wk. Seed-level effects of mammal vs. invertebrate predators were clearly distinguishable based on experience from previous seed outplanting experiments (Grogan 2001). We considered missing seeds to have been removed by mammal predators given seed size and bulk (5–12 cm long with wing, 0.37 g mean fresh weight). The possibility that seeds were cached elsewhere cannot be ruled out but was considered unlikely due to rapid germination once wet season rains begin. Assessment of seed mortality due to fungal pathogens was also based on experience from previous seed outplanting experiments. Established seedlings were censused for survival during the following year's dry season in August 1998, 9 mo after establishment.

DATA ANALYSIS.—Differences in mean annual fruit production between diameter size classes (30–60 cm pre-commercial, >60 cm commercial) by site were tested using Tukey's studentized *t*-tests (JMP 5.1, SAS Institute, Cary, NC). Linear regression models plotting total number of seeds/fruit, number of apparently viable seeds/fruit, and germination percent/fruit vs. fruit capsule length tested fruit size effects. Differences in seed fate and seedling survival between caged exclosures and uncaged controls in the outplanting experiment were tested using Tukey's studentized *t*-tests. One-way analysis of variance (ANOVA) of means was used to detect differences in seed fate and seedling survival among distance treatments. Tukey's studentized *t*-tests compared means among treatments where ANOVA models were significant. Seed fate and seedling survival data were arcsine transformed for analyses.

RESULTS

FRUIT PRODUCTION.—Mean annual fruit production by trees larger than 60 cm diameter during 8 yr at Marajoara was significantly higher than by trees 30–60 cm diameter (Table 1). Maximum mean values exceeded 100 fruits/yr by only two trees, both larger than 60 cm diameter. Low median production values for both size classes indicate disproportionate contribution to total production by a subset of trees. In any given year, few trees in either size class produced large fruit crops at Marajoara. During the heaviest fruiting year (2000), 26.3 percent of trees larger than 60 cm diameter produced 25 fruits or more, while 8.8 percent trees of this size produced 100 fruits or more (Fig. 1). The percentage of commercial-sized trees producing 25 fruits or more averaged 12.5 ± 3.1 per yr (throughout the text, ± values signify one standard error), while 3.2 ± 0.8 percent of sub-commercial trees produced this number of fruits/year (Fig. 1).

No significant difference in fruit production by size class was observed at Corral Redondo and Agua Azul, where few trees larger than 60 cm diameter survived logging (Table 1). Consistently low median values indicate disproportionate contribution to total fruit crop by a subset of trees, similar to the pattern observed at Marajoara. The unlogged population at Pinkaití included 17 trees larger than 90 cm diameter, yet was the least productive by most measures, albeit over only 3 yr of observation. There, only 2 of 31 commercial-sized trees produced 100 or more fruit in any year.

TABLE 1. *Annual fruit production by mahogany trees at four sites in southeast Pará, Brazil. Max mean indicates the highest annual mean by an individual tree; $\geq$25 Fruits/yr indicates the percent of trees averaging this rate of fruit production over the observation period. Letters beside mean (SE) values indicate significant difference between diameter size classes by site, $\alpha = 0.05$ ($a > b$). Observation periods: *1997–2004, **1997–2003, ***1996, 1998–1999.*

		Location			
Diameter		Marajoara*	Corral Redondo*	Agua Azul**	Pinkaití***
30–60 cm	Mean (SE)	3.9 (0.4) b	7.2 (1.8) a	7.3 (1.1) a	0.7 (0.4) b
	Median	1.9	3.3	3.6	0
	Max mean	40	60	50	5
	$\geq$25 Fruits/yr	1.6%	2.7%	7.8%	0%
	N	191	37	77	18
>60 cm	Mean (SE)	14.5 (3.0) a	10.7 (2.5) a	4.9 (1.5) a	6.5 (2.0) a
	Median	6.3	7.4	6.2	2.3
	Max mean	108	32	7	50
	$\geq$25 Fruits/yr	17.5%	14.3%	0%	3.2%
	N	57	14	4	31

Maximum 1-yr production by individual trees during the observation period was 340, 230, 215, and 130 fruits at Marajoara, Corral Redondo, Agua Azul, and Pinkaití, respectively.

SEED VIABILITY AND GERMINABILITY.—Fruit capsules contained 60.3 ± 0.2 seeds/fruit, with 17.9 ± 0.5 of these malformed or empty, for an average 42.4 ± 0.5 seeds/fruit or 70.3 percent viable by visual inspection without removal of winged hulls. No significant correlation was seen between total number of seeds/fruit or number of viable seeds/fruit and fruit capsule length ($R^2 = 0.009$ and 0.071, respectively, $N = 121$). Seed dissections from 18 fruits revealed that 11.3 percent of seeds judged viable by visual inspection were in fact dead or empty (4.8 ± 1.2 seeds/fruit). That is, per fruit seed viability was 37.6, or 62.4 percent.

Eighteen fruit capsules 10–18 cm long contained 40.2 ± 1.7 viable seeds by visual inspection. Nursery-bed germination by these seeds, planted 2.5 mo after the dispersal period concurrent with rainy season onset, averaged 66.8 ± 6.0 percent per fruit, or 28.3 of 37.6 viable seeds. A significant positive relationship existed between fruit capsule length (proxy for mean seed size, Grogan 2001) and germination percent ($P = 0.043$, $R^2 = 0.23$, df = 17). Overall germination by seeds from fruit capsules of intermediate length (15 cm) was 72.1 percent, within the range predicted by the

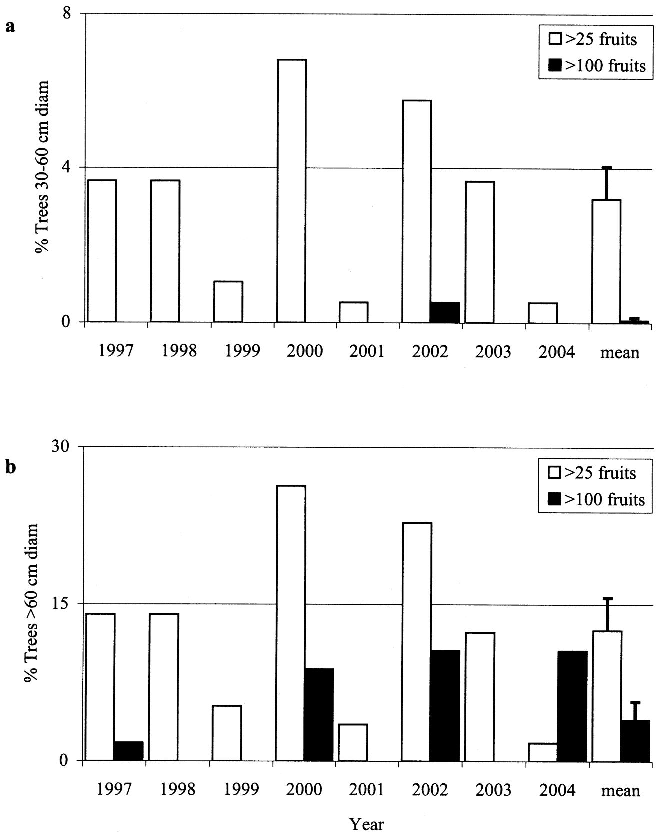

FIGURE 1. Fruit production at Marajoara, percent trees producing ≥25 and ≥100 fruits during each year from 1997 to 2004. (a) Trees 30–60 cm diameter. (b) Trees >60 cm diameter. Error bars for mean values indicate one standard error. Note different y-axis scales between figures.

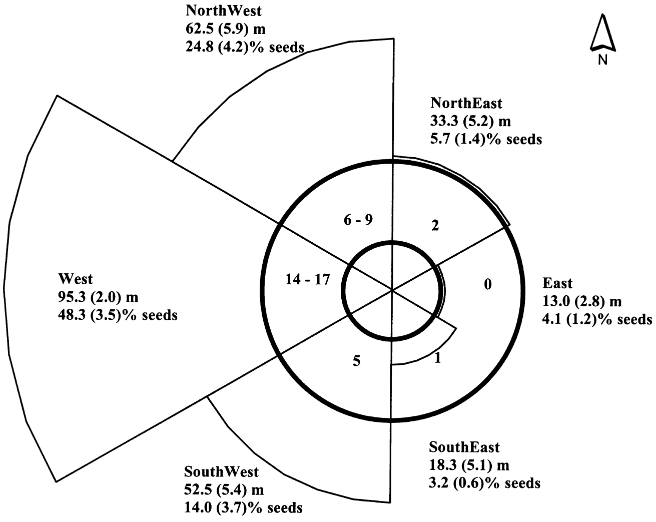

FIGURE 2. Sixty-degree arcs showing mean dispersal distance (±SE) among six parent trees to which 100 percent of seeds were found, and mean percent (±SE) of total seeds dispersed by arc. Parent trees stand at the intersection point. Bold circles drawn at 12- and 32-m radii indicate the area within which mahogany crowns are expected to fall during logging. Numbers within the crown-fall area in each arc indicate expected number(s) of seedlings 9 mo after germination within an area equivalent to an average-sized logging gap (289 m^2), assuming seed dispersal from 25 fruit capsules during the year before logging and 5.8 seedling survivors per fruit. Seedling numbers do not account for mortality during gap formation (tree felling). No seedlings are expected in the area of a logging gap located in the East arc at this level of fruit production due to limited seed dispersal distance (13 m = mean maximum observed).

regression equation for fruit capsule length vs. germination percent ($Y = -0.0764 + 0.054 \times \text{length}$).

SEED DISPERSAL.—Seven of 13 observed trees at Marajoara dehisced one or a few fruit capsules early in the dry season, while crowns still retained most old foliage. This behavior was common among the wider population at Marajoara, and some of these early dispersing seeds germinated in the forest understory still damp from the recently ended rainy season. Remaining fruit capsules dehisced as crowns approached complete deciduousness midway through the dry season. Most seeds dispersed within 2–3 wk after exposure to dry season winds.

A total of 2209 seeds were recovered in randomly stratified 10 percent-area wedge transects around six trees. Dispersal patterns were similar among trees: 63–80 percent of seeds landed within two west-northwest arcs (240–360°) at individual trees, while relatively few seeds fell on the east side (0–180°) of parent trees, ranging from 7 to 19 percent of totals at each tree. This was not unexpected given east-southeast prevailing winds during the dry season at Marajoara. On average, nearly 50 percent of all recovered seeds landed in a single arc on the west side (240–300°; Fig. 2). West of parent trees, 50 percent of seeds dispersed within 28 m; east of parent trees, the median dispersal distance fell to 9 m. Averaging distances among sampled trees to which successive quartiles of the 1997 seed crop dispersed, 50 percent of all seeds fell within 0.12 ha of parent trees, while nearly 100 percent fell within 0.91 ha in a broadly parabolic shape weighted west-northwest (Fig. 2). Some small number of seeds colonized an area beyond the sampled distances to at least 250 m on the west side of parent trees based on occasional sightings of seeds on the ground at Marajoara with no parent tree within this distance.

SEED FATES ON THE FOREST FLOOR.—Weather through the observation period was dry at the time of outplanting in mid July 1997, wet for 2 wk in late September and early October (172 mm of rainfall in 12 d), and then dry again with rare light rains through late November. That is, outplanted seeds were first watered in the field at the same time as seeds of identical age were planted in the nursery germination experiment.

Seed losses to foraging mammal predators in uncaged plots within 20 m of parent trees averaged 14.3 ± 2.9 percent of outplanted seeds among nine trees over the 19-wk observation period (Fig. 3a). We observed agoutis (*Dasyprocta agouti*), pacas (*Agouti paca*), and rabbits (*Sylvilagus brasiliensis*) foraging for seeds. Spiny

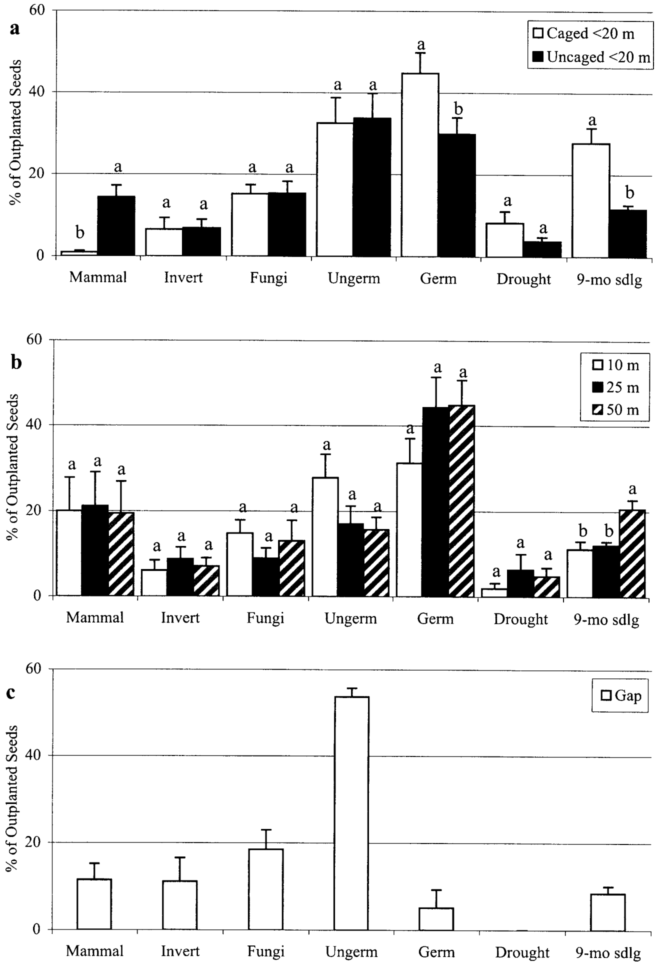

FIGURE 3. Seed fates on the forest floor and seedling survival 9 mo after establishment as mean percent of outplanted seeds among planting sites (parent trees). Mammal, invert(ebrate), and fungi indicate pre-germination mortality agents. Ungerm and germ indicate ungerminated and germinated seeds at the end of the 19-wk observation period. Drought refers to seedling deaths attributable to drought after germination but before establishment; 9-mo sdlg indicates seedling survivors 9 mo after establishment. (a) Caged exclosures vs. uncaged controls <20 m from nine parent trees. (b) Distance treatments (10, 25, and 50 m) from 10 parent trees, uncaged plots. (c) Artificial canopy gaps at three parent trees, uncaged plots. Error bars show one standard error. Letters indicate significant difference between or among treatments by seed fate category, $\alpha = 0.05$ (a > b). Gap results are shown for comparative purposes.

rats (*Proechimys* sp., T. Clements, pers. obs.) may also have contributed to seed losses. Chicken-wire exclosures protected seeds from mammal predators. Rare seed losses from within exclosures indicate that at least one mammal predator may have been capable of scaling chicken-wire to 50 cm height. Most seed mortality attributable to mammals occurred during the first month of observation, before dry season leaf litter from the shedding forest canopy obscured seeds from ground foragers. Mammal predation in uncaged plots ranged from 4.4 to 32.2 percent among trees. Invertebrate predators—a broad category including ants, termites, beetles, nematodes, and snails—killed approximately half as many seeds as mammals, while mortality due to fungal pathogens was approximately equal to that caused by mammals.

Heavy rains beginning 9 wk after outplanting triggered widespread germination by surviving seeds. The 19-wk germination percentage by seeds in caged plots significantly exceeded that by uncaged seeds (44.9 ± 5.0% vs. 29.9 ± 4.1% of outplanted seeds, respectively; Fig. 3a), with the difference partially attributable to seeds avoiding mammal predators. The dry season's return after 2 wk of wet weather proved lethal to some recent germinants: 8.2 ± 2.8 percent of outplanted seeds germinated within cage exclosures but dried out before establishing as seedlings, compared to 3.7 ± 1.0 percent in uncaged plots. This difference can be attributed to accelerated germination within exclosures where leaf litter accumulated excessively, creating moisture-retaining microsites that promoted germination but failed to protect new germinants from the returning drought.

Nine months after the last seed census, midway through the 1998 dry season, seedling survival within cage exclosures (27.8 ± 3.7% of seeds planted 13 mo earlier) significantly exceeded that in uncaged plots by almost three to one (Fig. 3a). In many cases exclosure plots resembled green oases amid thinner surrounding understory vegetation; by excluding mammals and retaining moisture in deeper leaf litter, caged plots reduced mortality by mahogany seedlings and other plant species. In control plots without wire cages, 11.5 ± 1.0 percent of outplanted seeds survived as seedlings.

Seed fates in distance treatments (10, 25, and 50 m from 10 parent trees) were consistent with results from the mammal exclosure experiment. Higher germination percentages at greater distance were nonsignificant due to variability among trees (Fig. 3b). However, seedling survival 9 mo after the last seed census was significantly higher at 50 m distance (20.6 ± 2.1%) compared to 25 and 10 m (12.0 ± 0.9% and 11.1 ± 1.9%, respectively).

Gap plots dried quickly following heavy rains at the beginning of the wet season, preventing moisture imbibition triggering germination. Seed germination percentages in gaps were low after 19 wk compared to forest understory treatments (5.2 ± 4.1%; Fig. 3c). Yet 9-mo seedling survival in gaps approached that in uncaged forest understory treatments, indicating that seeds in gaps continued germinating after the 19-wk observation period, and that seedling survival in gaps may exceed survival in the forest understory (Grogan *et al.* 2003a, 2005).

Combining results from uncaged and nongap forest understory treatments, 35.5 ± 4.5 percent of outplanted seeds germinated among trees, or 15.1 of 60.3 total seeds/fruit; 13.6 ± 0.7 percent of outplanted seeds survived as seedlings in August 1998, representing 5.8 seeds/fruit.

DISCUSSION

Selective logging may depress seed production by surviving trees in tropical regions by lowering outcrossing rates among flowering adults occurring at sharply reduced densities (Murawski *et al.* 1994). On the other hand, tree species may fruit at smaller diameter size classes in logged vs. unlogged forest (Appanah & Manaf 1990), possibly due to greater light availability (Guariguata & Sáenz 2002) in combination with reduced intraspecific competition with dominant trees for pollinators. In Brazil's southeastern Amazon region, pre-commercial mahogany trees (30–60 cm diameter) were more productive at logged sites than at the single unlogged site, albeit over different observation periods (Table 1), indicating that logging could have a positive effect on fruit production by smaller diameter size classes. Commercial-sized mahogany trees (>60 cm diameter) surviving logging in this study produced relatively few fruits compared to trees of comparable size in intact populations studied in Bolivia (Gullison *et al.* 1996), Mexico (Snook *et al.* 2005), and western Amazonia (J. Grogan, pers. obs.). Three years of fruiting data from Pinkaití, the unlogged site, indicate that fruit production rates even by very large trees may be low in this region.

Germination percentages recorded in this study are compatible with germination exceeding 80 percent reported from some nursery studies (*e.g.*, Morris *et al.* 2000, Grogan *et al.* 2003b) because seeds planted in nursery settings are likely to be screened for large size, selecting for higher germinability; and because seed germinability in this study likely declined during the 2- to2.5-mo period between fruit dehiscence and water imbibition (Campbell de Araujo 1971, Niembro 2002).

A majority of seeds disperse to within a distance shorter than parent tree height. Dispersal patterns are extremely predictable within the study region due to persistent east-southeast winds during the dry season. In contrast, dispersal shadows reported for *Entandrophragma* in the Central Africa Republic—timber species with seeds and dispersal syndromes similar to mahogany—were not found to be strongly oriented by wind direction (Medjibe & Hall 2002).

Most seed losses to mammal predators occurred immediately following dispersal while seeds were exposed on top of forest floor leaf litter. As dry season leaf litter accumulated and shifted, seeds descended gradually to the soil surface, where most invertebrate predation occurred. Losses to fungal pathogens accelerated as seeds were soaked by the first seasonal rains, especially where leaf litter and soil surfaces dried out after repeated wetting—as, for example, in treefall gaps exposed to the sun. The identity of neighboring trees may also influence mortality due to fungal pathogens. In a separate experiment, we noted that mahogany seeds outplanted beneath tree species dropping fleshy fruits experienced up to 100 percent infection associated with rotting fruits.

Results from the seed outplanting experiment plus observations during other years at Marajoara indicate that the timing and intensity of the rainy season's onset may influence seed germination and seedling establishment patterns. During the 7-yr rainfall monitoring period at Marajoara, we observed three general patterns of rainy season onset. Early sustained onset (in 2000) may encourage early seed germination and reduce mortality from invertebrates, fungal pathogens, and, to lesser degree, mammals. False early onset of wet season rains followed by renewed drought (in 1995, 1997, and 1999) may kill many new germinants directly, as reported here, and prolong exposure by ungerminated seeds to mortality agents. The effect of delayed but sustained onset of rainfall (in 1996, 1998, and 2001) on seed fate probably represents an intermediate survival and establishment scenario for mahogany. That is, worst-case seasonal weather patterns for seedling establishment occurred during this study, and these conditions prevailed during 3 of 7 yr at Marajoara.

Significantly higher seedling survival 9 mo after establishment at 50 m distance from parent trees may be attributable to density-dependent effects associated with predation by larval caterpillars of the small nocturnal moth *Steniscadia poliophaea* (Noctuidae: Sarrothripinae), which consume flushing seedling leaves and stem dermal tissues (Grogan *et al.* 2005).

Information on mean seed dispersal distances and densities by 60° arc among surveyed parent trees can be combined with seedling survival data to estimate the number of seedlings likely present in the forest understory at the time of logging during the dry season following seedling establishment (5.8 seedlings/fruit). Trees producing 25 fruits during the previous year could be expected to have ~135 seedlings surviving scattered in a predictable pattern within ~1 ha weighted to the west side. Since an average crown gap caused by felling mahogany encompasses 289 ± 11 m^2 at Marajoara (Grogan *et al.* 2003b), and since the average commercial-sized tree crown falls 12–32 m from the tree base (Grogan 2001), the number of seedlings likely present on the ground within the projected perimeter of an average-sized crown gap ranges from 14 to 17 due west of parent trees to 0 due east under this fruit production scenario (Fig. 2); that is, expected post-logging seedling densities in treefall gaps decline sharply as felling direction shifts away from the west arc.

This analysis clarifies why post-logging surveys of mahogany seedling regeneration in crownfall gaps record, on average, low seedling densities (Veríssimo *et al.* 1995; Grogan *et al.* 2003b, 2005). Although seeds are highly germinable and seedlings, once established, persist at high rates through the first growing season, only one in approximately eight commercial-sized trees may produce 25 fruits or more during a given year. Our data further indicate that trees rarely produce large fruit crops in consecutive years. Only one in six randomly sampled logging gaps will occur in the west arc where seedling densities are expected to be highest. Additional factors limiting post-logging seedling regeneration include: some portion of the previous year's seedling cohort will die beneath the falling crown; seedlings suppressed in the forest understory during the first growing season may respond poorly or die following overhead canopy release, especially when release occurs in logging gaps created during southeastern Amazonia's severe dry season (Grogan *et al.* 2005); and loggers rarely respect the minimum diameter cutting limit for mahogany in Brazil (Grogan *et al.* 2002), meaning that randomly sampled logging gaps will include those created by felling pre-commercial trees of low fecundity (as small as 28 cm diameter at Marajoara).

Finally, the timing of the logging event may impact post-logging seedling densities. Mahogany trees are typically felled in remote forests from the late rainy season (March–April) through the dry season until the rainy season's return (October–November) renders access and log extraction impossible. Where trees are felled after seed dispersal, seedling densities in crownfall gaps may be augmented by post-logging germinants.

MANAGEMENT IMPLICATIONS

Logging mahogany without silvicultural interventions designed to increase seedling densities and growth rates leads to commercial extirpation except at rare sites where advance regeneration densities are consistently high (Stevenson 1927, Lamb 1966, Brown *et al.* 2003). If sustained-yield timber production of mahogany is a management objective, then forest managers must address reproductive and regeneration issues. This is true for similar nonpioneer light-demanding species across the tropics sharing reproductive and autecological traits with mahogany: wind dispersed, restricted seed shadows, germination in the forest understory, and shade-intolerant seedlings. While the particulars may vary—for example, mahogany seeds are larger and more germinable than most, though perhaps produced at lower rates—sudden removal of nearly all reproductive adults is catastrophic for future population structures of these high-value timber species.

Management systems emphasizing recruitment of natural regeneration into adult size classes must reconcile apparent contradictions between seed and seedling site requirements (Sork 1985, Ter Steege *et al.* 1994, Schupp 1995). Mahogany's germination and establishment rates are higher in closed forest than in gaps (Gerhardt 1996, Morris *et al.* 2000), but seedling survival and growth rates are higher where light levels are elevated (Gullison & Hubbell 1992; Grogan *et al.* 2003a, 2005).

Seed production rates by individual trees and by local populations must be monitored in order to know which trees warrant silvicultural intervention fostering seedling establishment, and in which years widescale interventions are feasible. If high seedling densities are desirable—*e.g.*, in a shelterwood system where further destructive canopy removal is anticipated—canopy thinning operations raising light levels at the forest floor should occur immediately following germination and seedling establishment. Within the study region this would require mid rainy season intervention that ideally would target second-tier commercial timber species. If lower seedling densities are acceptable—*e.g.*, if seedlings will be tended during the years following logging—canopy thinnings could occur before germination, with two options: pre-seed dispersal intervention with some degree of soil scarification eliminating advance regeneration of competing species and loosening soil (Fredericksen & Pariona 2002, Fredericksen & Putz 2003); or post-dispersal intervention at reduced intensity in order to lower seed mortality during treatment. These options would require either early or late dry season treatment targeting mahogany trees producing many fruits. Removal of second-tier timber species where economically viable could facilitate both options.

Without these silvicultural interventions, artificial regeneration, outplanting either seeds or seedlings into logging gaps and or logging patios where growing conditions are ideal for heliotropic seedlings (Negreros-Castillo *et al.* 2003, Snook & Negreros-Castillo 2004) will be necessary for sustained-yield production. To this end, the most highly fecund individuals in a population must be identified and retained to restock areas where natural and artificial regeneration fails.

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LITERATURE CITED

Appanah, S., and M. R. A. Manaf. 1990. Smaller trees can fruit in logged dipterocarp forests. J. Trop. For. Sci. 3: 80–87.

Blundell, A. G. 2004. A review of the CITES listing of big-leaf mahogany. Oryx 38: 1–7.

Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. J. Ecol. 75: 9–19.

Brown, N., S. Jennings, and T. Clements. 2003. The ecology, silviculture and biogeography of mahogany (*Swietenia macrophylla*): A review of the evidence. Perspect. Plant Ecol. Evol. Syst. 6: 37–49.

Calvo, J. C., and H. Rivera. 2000. The status of mahogany in Mesoamerica. Workshop executive summary, Tropical Science Center and Programa Ambiental Regional para Centroamérica/Central American Protected Areas System (PROARCA/CAPAS), San José, Costa Rica.

Campbell De Araujo, V. 1971. Sôbre a germinação do mogno (aguano) *Swietenia macrophylla* King. Acta Amazonica 1: 59–69.

Chinte, F. O. 1952. Trial plantings of large leaf mahogany in the Philippine Islands. Caribb. For. 13: 75–84.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79: 564–578.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J. Ecol. 60: 147–170.

Dekker, M., and N. R. De Graaf. 2003. Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. For. Ecol. Manage. 172: 183–190.

Dickinson, M. B., and D. F. Whigham. 1999. Regeneration of mahogany (*Swietenia macrophylla*) in the Yucatan. Int. For. J. 1: 35–39.

Fredericksen, T. S., and B. Mostacedo. 2000. Regeneration of timber species following selection logging in a Bolivian tropical dry forest. For. Ecol. Manage. 131: 47–55.

——, and W. Pariona. 2002. Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest. For. Ecol. Manage. 171: 223–230.

———, and F. E. Putz. 2003. Silvicultural intensification for tropical forest conservation. Biodivers. Conserv. 12: 1445–1453.

Gerhardt, K. 1996. Germination and development of sown mahogany (*Swietenia macrophylla* King) in secondary tropical dry forest habitats in Costa Rica. J. Trop. Ecol. 12: 275–289.

Gomez-Pompa, A. 1989. Tropical deforestation and Maya silviculture: An ecological paradox. Tulane Stud. Zool. Bot. 26: 19–37.

Grogan, J. 2001. Bigleaf mahogany (*Swietenia macrophylla* King) in southeast Pará, Brazil: A life history study with management guidelines for sustained production from natural forests. Ph.D. Dissertation, Yale University, New Haven, CT.

——, M. S. Ashton, and J. Galvão. 2003a. Big-leaf mahogany (*Swietenia macrophylla*) seedling survival and growth across a topographic gradient in southeast Pará, Brazil. For. Ecol. Manage. 186: 311–326.

——, P. Barreto, and A. Veríssimo. 2002. Mahogany in the Brazilian Amazon: ecology and perspectives on management, 58 pp. IMAZON, Belém, Pará, Brazil. Available in pdf format at http://www.imazon.org.br.

——, J. Galvão, L. Simões, and A. Veríssimo. 2003b. Regeneration of big-leaf mahogany in closed and logged forests of southeastern Pará, Brazil. *In* A. Lugo, J. C. Figueroa Colón, and M. Alayón (Eds.). Big-leaf mahogany: Genetics, ecology, and management, pp. 193–208. Springer-Verlag, New York, NY.

——, R. M. Landis, M. S. Ashton, and J. Galvão. 2005. Growth response by big-leaf mahogany (*Swietenia macrophylla*) advance seedling regeneration to overhead canopy release in southeast Pará, Brazil. For. Ecol. Manage. 204: 399–412.

Guariguata, M. R., and M. A. Pinard. 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: Implications for natural forest management. For. Ecol. Manage. 112: 87–99.

——, and G. P. Sáenz. 2002. Post-logging acorn production and oak regeneration in a tropical montane forest, Costa Rica. For. Ecol. Manage. 167: 285–293.

Gullison, R. E., and S. P. Hubbell. 1992. Regeneracion natural de la mara (*Swietenia macrophylla*) en el bosque Chimanes, Bolivia. Ecologia en Bolivia 19: 43–56.

——, S. N. Panfil, J. J. Strouse, and S. P. Hubbell. 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes Forest, Beni, Bolivia. Bot. J. Linn. Soc. 122: 9–34.

Hall, J. S., V. Medjibe, G. P. Berlyn, and M. S. Ashton. 2003. Seedling growth of three co-occurring *Entandrophragma* species (Meliaceae) under simulated light environments: Implications for forest management in central Africa. For. Ecol. Manage. 179: 135–144.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Johnson, N., and B. Cabarle. 1993. Surviving the cut: Natural forest management in the humid tropics. World Resources Institute, Washington, DC.

Jones, E. W. 1956. Ecological studies on the rain forest of southern Nigeria IV (continued). The plateau forest of the Okomu Forest Reserve Part II. The reproduction and history of the forest. J. Ecol. 44: 83–117.

Kometter, R. F., M. Martinez, A. G. Blundell, R. E. Gullison, M. K. Steininger, and R. E. Rice. 2004. Impacts of unsustainable mahogany logging in Bolivia and Peru. Ecol. Soc. 9. http://www.ecologyandsociety.org/vol9/iss1/art12.

Lamb, F. B. 1966. Mahogany of tropical America: Its ecology and management. University of Michigan Press, Ann Arbor, MI.

Lamprecht, H. 1989. Silviculture in the tropics: Tropical forest ecosystems and their tree species—possibilities and methods for their long-term utilization. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, West Germany.

Martini, A. M. Z., N. A. Rosa, and C. Uhl. 1994. An attempt to predict which Amazonian tree species may be threatened by logging activities. Environ. Conserv. 21: 152–162.

Medjibe, V., and J. S. Hall. 2002. Seed dispersal and its implications for silviculture of African mahogany (*Entandrophragma* spp.) in undisturbed forest in the Central African Republic. For. Ecol. Manage. 170: 249–257.

Moad, A. S., and J. L. Whitmore. 1994. Tropical forest management in the Asia-Pacific region. J. Sustainable For. 1: 25–63.

Morris, M. H., P. Negreros-Castillo, and C. Mize. 2000. Sowing date, shade, and irrigation affect big-leaf mahogany (*Swietenia macrophylla* King). For. Ecol. Manage. 132: 173–181.

Mostacedo, B. C., and T. S. Fredericksen. 1999. Regeneration status of important forest tree species in Bolivia: Assessment and recommendations. For. Ecol. Manage. 124: 263–273.

Murawski, D. A., R. Dayanandan, and K. S. Bawa. 1994. Outcrossing rates of two endemic *Shorea* species from Sri Lankan tropical rain forests. Biotropica 26: 23–29.

Negreros-Castillo, P., L. K. Snook, and C. W. Mize. 2003. Regenerating mahogany (*Swietenia macrophylla*) from seed in Quintana Roo, Mexico: The effects of sowing method and clearing treatment. For. Ecol. Manage. 183: 351–362.

Niembro, R. A. 2002. *Swietenia macrophylla* King. *In* J. A. Vozzo (Ed.). Tropical tree seed manual, US Department of Agriculture Handbook 721, pp. 722–725. USDA Forest Service, Washington, DC.

Pennington, T. D., B. T. Styles, and D. A. H. Taylor. 1981. Meliaceae. Flora Neotropica Monogr. 28: 1–472.

Rodan, B. D., A. Newton, and A. Veríssimo. 1992. Mahogany conservation: Status and policy initiatives. Environ. Conserv. 19: 331–342.

Salati, E., and J. Marques. 1984. Climatology of the Amazon region. *In* H. Sioli (Ed.). The Amazon: Limnology and landscape ecology of a mighty tropical river, pp. 85–126. Dr. W.J. Junk Publishers, Boston, MA.

Schulze, M. 2003. Ecology and behavior of nine timber tree species in Pará, Brazil: Links between species life history and forest conservation and management. Ph.D. Dissertation, Pennsylvania State University, University Park, PA.

——, E. Vidal, J. Grogan, J. Zweede, and D. Zarin. 2005. Madeiras nobres em perigo: práticas e leis atuais de manejo florestal não garantem a exploração sustentável de madeira. Ciência Hoje 214: 66–69.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. 82: 399–409.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The practice of silviculture: Applied forest ecology, 9th edition, 537 pp. John Wiley & Sons, Inc., New York, NY.

Snook, L. K. 1996. Catastrophic disturbance, logging and the ecology of mahogany (*Swietenia macrophylla* King): Grounds for listing a major tropical timber species in CITES. Bot. J. Linn. Soc. 122: 35–46.

——, L. Cámara-Cabrales, and M. J. Kelty. 2005. Six years of fruit production by mahogany trees (*Swietenia macrophylla* King): Patterns of variation and implications for sustainability. For. Ecol. Manage. 206: 221–235.

——, and P. Negreros-Castillo. 2004. Regenerating mahogany (*Swietenia macrophylla* King) on clearings in Mexico's Maya forest: The effects of clearing method and cleaning on seedling survival and growth. For. Ecol. Manage. 189: 143–160.

Sork, V. L. 1985. Germination response in a large-seeded neotropical tree species, *Gustavia superba* (Lecythidaceae). Biotropica 17: 130–136.

Stevenson, N. S. 1927. Silvicultural treatment of mahogany forests in British Honduras. Empire For. J. 6: 219–227.

Swaine, M. D., and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75: 81–86.

Ter Steege, H., C. Bokdam, M. Boland, J. Dobbelsteen, and I. Verburg. 1994. The effects of man made gaps on germination, early survival, and morphology of *Chlorocardium rodiei* seedlings in Guyana. J. Trop. Ecol. 10: 245–260.

UHL, C., A. VERÍSSIMO, M. M. MATTOS, Z. BRANDINO, AND I. C. G. VIEIRA. 1991. Social, economic, and ecological consequences of selective logging in an Amazon frontier: The case of Tailândia. For. Ecol. Manage. 46: 243–273.

VAN RHEENEN, H. M. P. J. B., R. G. A. BOOT, M. J. A. WERGER, AND M. U. ULLOA. 2004. Regeneration of timber trees in a logged tropical forest in north Bolivia. For. Ecol. Manage. 200: 39–48.

VERÍSSIMO, A., P. BARRETO, M. MATTOS, R. TARIFA, AND C. UHL. 1992. Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: The case of Paragominas. For. Ecol. Manage. 55: 169–199.

——, P. BARRETO, R. TARIFA, AND C. UHL. 1995. Extraction of a high-value natural resource in Amazonia: The case of mahogany. For. Ecol. Manage. 72: 39–60.

WOLFFSOHN, A. L. A. 1961. An experiment concerning mahogany germination. Empire For. Rev. 46: 71–72.

ZIMMERMAN, B., C. A. PERES, J. R. MALCOLM, AND T. TURNER. 2001. Conservation and development alliances with the Kayapó of south-eastern Amazonia, a tropical forest indigenous people. Environ. Conserv. 28: 10–22.