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Growth response by big-leaf mahogany (*Swietenia macrophylla*) advance seedling regeneration to overhead canopy release in southeast Pará, Brazil

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Abstract

Big-leaf mahogany (*Swietenia macrophylla*) is a valuable neotropical timber species whose seedling survival and growth dynamics in natural forests are poorly understood. To document regeneration dynamics of mahogany in seasonal transitional evergreen forests of southeast Pará, Brazil, we followed naturally established seedlings in the forest understory and in experimental canopy gaps. We found that only 1–2% of seedlings in the forest understory survived 8 years after germination; mean height growth was approximately 4 cm year^{-1} of height over this period, confirming mahogany's classification as a light demanding species. To test whether seedlings could survive and respond to canopy release after a period of suppression beneath competing secondary vegetation, we opened experimental canopy gaps above naturally established seedling regeneration in 2–3-year old logging gaps; seedlings were monitored at intervals through 80 months. Seedling survival probability and seedling growth rates demonstrated significant positive correlation with initial seeding height, canopy opening size, and seedling distance to gap edge. Of these factors, initial seedling height (indicating performance in logging gaps prior to experimental release) was the most important predictor of survival and growth response. More seedlings died during the first dry season beginning 6 months after canopy release than during any other census interval. Mean height growth rate of seedlings in gaps peaked at 126.1 ± 23.9 cm year^{-1} during the third-year census interval, declining afterwards as secondary vegetation overtook seedling crowns. Attack rates by the mahogany shootborer (*Hypsipyla grandella*) were low amidst dense secondary vegetation that grew up after canopy opening. These results indicate that (1) advance regeneration experiencing early vigorous growth beneath disturbed canopies in logging gaps may respond to subsequent overhead canopy release, and (2) response vigor may depend on vigor of initial seedling growth.

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Resumo

O mogno (*Swietenia macrophylla*) é uma valiosa espécie madeireira da América tropical cuja dinâmica de crescimento e sobrevivência das plântulas é pouco entendida. Para documentar as dinâmicas de regeneração do mogno em florestas de transição no sudeste do Pará, Brasil, fizemos o acompanhamento das plântulas estabelecidas naturalmente no sub-bosque e em clareiras experimentais no dossel da floresta. Encontramos que oito anos após a germinação somente 1% – 2% de plântulas no sub-bosque da floresta haviam sobrevivido; o crescimento médio em altura foi de aproximadamente 4 cm ano^{-1} durante este período, confirmando o mogno como uma espécie demandante de luz. Para testar se as plântulas poderiam sobreviver e responder à liberação do dossel após um período de supressão sob a vegetação secundária competidora, abrimos clareiras experimentais sobre a regeneração de plântulas naturalmente estabelecidas em clareiras de exploração de dois a três anos. As plântulas foram monitoradas em vários momentos durante 80 meses. A probabilidade de sobrevivência de plântulas e suas taxas de crescimento demonstraram correlação positiva significativa com a altura inicial da plântula, tamanho da abertura da clareira e distância da plântula até a borda da clareira. Desses fatores, a altura inicial da plântula (indicando desempenho nas clareiras de exploração antes da liberação experimental) foi o mais importante para predizer a resposta em termos de sobrevivência e crescimento. A maior mortalidade de plântulas ocorreu durante a primeira estação seca que começou seis meses após a liberação do dossel do que durante qualquer outro intervalo de censo. A taxa média de crescimento em altura de plântulas nas clareiras chegou ao pico de 126.1 ± 23.9 cm ano^{-1} durante o terceiro ano de intervalo de censo, declinando posteriormente quando a vegetação secundária encobriu as copas das plântulas. As taxas de ataque da broca do ponteiro do mogno (*Hypsipyla grandella*) foram baixas no meio da vegetação secundária densa que cresceu após a abertura do dossel. Esses resultados indicam que: (1) a regeneração avançada que teve inicialmente um crescimento vigoroso sob as copas que sofreram distúrbios nas clareiras de exploração pode reagir à liberação subseqüente do dossel acima; e (2) o vigor da resposta pode depender do vigor de crescimento inicial da plântula.

Keywords: Amazon; Disturbance; Forest management; Light; Seasonal evergreen forest

1. Introduction

Big-leaf mahogany (*Swietenia macrophylla*, Meliaceae) is a highly valuable neotropical timber species achieving highest densities in seasonal forests receiving 1000–2000 mm of annual rainfall. Logged commercially since the 17th century (Lamb, 1966), in 2002 mahogany became the first widely traded timber species to be listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Blundell, 2004). Mahogany's Appendix II listing addressed concern over the sustainability of industrial harvest practices, which typically remove up to 95% 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). Because Appendix II listing requires exporting nations to verify that timber supplies originate from sustainably managed forests (Rodan and Blundell, 2003), thorough understanding of mahogany population dynamics is necessary in order to transform current predatory logging practices into sustainable forest management. Yet mahogany's regeneration dynamics in natural forests are poorly understood, in contrast to extensive knowledge about seedling establishment and growth in plantations (Mayhew and Newton, 1998).

Mahogany is commonly believed to rely on catastrophic disturbances such as hurricanes, fires, and floods for successful recruitment by seedlings into juvenile and adult size classes, implying rapid growth over prolonged periods in large, persistent canopy gaps (Lamb, 1966; Snook, 1996, 2003; Gullison et al., 1996, 2003). Evidence supporting the catastrophic disturbance paradigm is largely inferential, based on observations of adult population structures and spatial distribution patterns. Aside from Gullison et al.'s (2003) demonstration that mahogany seedlings may survive flooding events and grow vigorously following canopy dieback, biological pathways providing for recruitment and stand replacement following large-scale disturbance remain unelucidated (Brown et al., 2003; Grogan et al., 2003a).

Mahogany seeds are relatively large (mean 0.347 g dry weight, Grogan, unpublished data), recalcitrant,

and wind dispersed. They germinate readily in both closed forest and in gaps following moisture imbibition soon after the onset of wet season rains (Gerhardt, 1996; Morris et al., 2000). Mahogany seedlings are heliophilic, requiring elevated light levels for optimal early growth; they may also be capable of tolerating suppression in the forest understory (Smith, 1942; Lamb, 1966; Gullison and Hubbell, 1992), though to what degree is unknown because survival by natural seedling regeneration has not been monitored over time in known light conditions. Suppressed 3 m tall saplings have been observed to persist and even slowly add height increment for many years under high shade (Lamb, 1966). Light response curves for mahogany seedlings grown in sun conditions demonstrate saturated photosynthetic response at photon flux densities $>750\ \mu mol\ m^{-1}\ s^{-1}$, or roughly 38% of full sunlight (Ramos and Grace, 1990), suggesting that increasing gap size beyond that necessary to achieve this irradiance level may yield little further advantage to seedling growth rates.

Two recruitment scenarios are suggested by these life history traits: seed germination in the forest understory with accelerated height growth following canopy release (disturbance opening growing space), or seed dispersal into canopy gaps at the time of or following disturbance with germination and early seedling growth there.

Large seed size and ability to germinate in the forest understory suggest the first recruitment scenario, which requires that advance seedling regeneration is able to survive suppression beneath closed forest canopies and that seedlings are capable of responding to suddenly elevated light levels with accelerated height growth. However, mahogany seedling densities and growth rates in closed forest are typically reported to be low. In the Bolivian Amazon, Gullison and Hubbell (1992) found up to 300 seedlings ha^{-1} in closed forest in the immediate vicinity of adult trees, with height increment averaging 7.4 cm $year^{-1}$. No long-term seedling banks were observed to accumulate; the authors estimated that seedlings could survive at most 6 years under closed canopy conditions. In Brazil, Grogan et al. (2003b) reported 53–77 seedlings ha^{-1} in closed forest to 40 m distance of adult trees where seedlings were found, though most trees had no regeneration in their immediate vicinity. In Belize, Stevenson (1927) recorded growth response by seedlings suppressed in gaps near mahogany seed trees of up to 60 cm within 3 weeks of release from shade. Experimental data demonstrating response by understory seedlings to canopy release have not appeared in the literature.

The second recruitment scenario – post-disturbance germination and growth in gaps – requires that seeds are available for dispersal at the time of disturbance or later through adult survival and reproduction, and that seedlings can establish and grow in canopy gaps. Lamb (1966) and Snook (1996, 2003) report that mahogany trees survive hurricane winds and subsequent fires in Central America better than most tree species; Gullison et al. (2003) found that mahogany survives flooding in lowland Bolivia at higher rates than other species. In Belize, Stevenson (1927) observed open gaps near mahogany seed trees dense with seedlings, with no regeneration in adjacent shaded forest understory. Gullison et al. (1996) found that seedlings in gaps grew at higher rates (14.7 cm $year^{-1}$) than seedlings in the forest understory. However, empirical evidence of post-catastrophic disturbance recruitment by naturally established seedlings in persistent gaps has not been presented in the literature.

Here we describe mahogany seedling population dynamics and response to canopy opening in a seasonal forest in southeast Pará, Brazil. For nearly 8 years we monitored survival and height growth of naturally established seedlings in the shaded forest understory and in experimental gaps created above clusters of advance regeneration. We also report incidence of mahogany shootborer (*Hypsipyla grandella* Zell., Lepidoptera: Pyralidae) attack. The shootborer is a nocturnal moth whose larval instars consume expanding apical meristems during periodic growth phases, crippling height growth and sometimes killing the seedling (Newton et al., 1993).

Questions we address include: how long can naturally established seedlings survive beneath closed canopies in the forest understory? How well do they grow there? Can advance seedling regeneration survive and respond to sudden overhead light exposure with accelerated height growth? If so, do survival and height growth rates vary by initial seedling size? by canopy opening size? by location within newly opened gaps? Assuming equivalent age among different-sized individuals in logging gaps, reduced survival and

growth response by smaller individuals following canopy release would indicate that response potential correlates positively with early seedling growth rate (in this case, seedling growth during 2–3 years in logging gaps). We conclude by discussing implications of results reported here for forest management practices designed to accelerate growth by advance seedling regeneration in the forest understory.

2. Methods

2.1. Study region and site

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 monthly temperatures ranging between 25 and 27 °C (Holdridge, 1967; Salati and Marques, 1984). Annual precipitation between 1995 and 2001 ranged from 1636 to 2170 mm, with >90% falling between November and May. In some years no rain fell for 3–4 months during the dry season (Grogan, 2001).

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. Marajoara was selectively logged for mahogany plus 5–7 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 (Grogan et al., 2003a).

2.2. Seedling regeneration in the forest understory

In December 1995, newly germinated naturally established seedlings were tagged in the forest understory to 30 m distance from eight parent trees. Parent trees were selected on the basis of seedling availability, ranged from 38 to 146 cm diameter, and were scattered within an area of approximately 200 ha representative of the forest environment at Marajoara. The total number of seedlings included in the study was 1925. Mean background incident light levels at the forest floor in this forest are high by tropical standards, with average Global Site Factor (GSF) values of 0.081 ± 0.012 (±standard error) or ∼8% of incident light (Grogan et al., 2003a). Seedlings were recensused monthly for survival and status through 4 years, and at longer intervals after that until 93 months (August 2003), noting cause of death where apparent and incidence of predation. Seedling heights were measured from the root collar to the apical tip of the primary stem after 24, 35, 45, and 93 months. Results are reported as mean percent survival and mean height increment among eight sites through 93 months.

2.3. Canopy release experiment

2.3.1. Site selection

In December 1996 we created experimental gaps at nine sites where densities of naturally established mahogany advance seedling regeneration were known to be high. Sites were selected within an area of approximately 1000 ha. All sites were on low ground with sandy, hydromorphic soils. Grogan et al. (2003a) demonstrated higher seedling growth rates in these soils than in dystrophic soils on high ground at Marajoara, indicating that soil nutrient status may complement canopy disturbance regimes in shaping adult distribution patterns and population structures. Seven of the nine sites were 2–3-year old logging gaps where seedlings had established in the immediate vicinity of commercial-sized mahogany trees either prior to or immediately following felling and stem removal; we surmise this because loggers removed seed trees from areas within dispersal distance surrounding these gaps (Table 1A). No subsequent interventions had occurred at these sites until the beginning of this experiment. Two sites had substantially different histories and are treated separately. One of these was a 3-year old logging gap bisected along its long axis by a permanent forest road that prevented vegetation regrowth and maintained artificially high light levels through the gap center (the ''road gap''); seedlings in this gap were, on average, taller than seedlings in other logging gaps (Table 1B). The other site was unlogged prior to gap creation where seedlings one or more years old survived after establishing in the forest understory surrounding a live mahogany tree in intact forest (the ''seed tree gap''); seedlings in this gap were, on average, shorter than seedlings in other logging gaps (Table 1C).

Table 1
Site, light environment, and seedling information

	A							B	C
Site characteristics									
Canopy opening area (m^2)	824	315	565	597	278	241	432	1015	1106
Global Site Factor (GSF)	0.841	0.664	0.786	0.733	0.611	0.431	0.652	0.778	0.663
Years since logging[a]	3	3	3	3	2	2	2	3	–
Logged dbh (cm)[b]	75	42	85	81	71	71	115	105	74
Nearest surviving seed tree (m)[c]	90-NE	50-S	150-NE	110-NE	40-W	15-N	45-W	140-E	–
Seed tree dbh/maximum fruit produced[d]	37/9	37/9	29/8	65/109	34/6	34/6	56/22	42/6	74/142
Experimental results									
Start no. of seedlings	32	17	29	41	73	54	19	59	34
Start median height (cm)	39	45	40	52	37	36	50	94	24
Start range of heights (cm)[e]	18–153	28–78	17–169	27–162	18–151	22–152	30–148	33–750	15–36
Maximum 80-months height increment (cm)[f]	1050	850	900	950	775	600	950	750	185
Shootborer incidence (%)[g]	3.1	–	35.9	12.2	2.7	1.9	10.5	28.8	–

A: seven sites logged 2 or 3 years before experiment start. B: the road gap, a logged site bisected by a permanent dirt track. C: the seed tree gap, an unlogged site where a mahogany seed tree was retained within the gap perimeter.

[a] At experiment's start.

[b] The dbh of logged mahogany tree within gap perimeter likely responsible for seedling regeneration (except C with seed tree).

[c] Distance in meters and direction of nearest surviving mahogany tree from gap center at time of experiment set-up.

[d] Nearest surviving mahogany tree dbh and maximum number of fruit it produced in any year from 1997 to 2003. One fruit contains ~42 viable seeds (Grogan, 2001).

[e] Shortest–tallest seedling at experiment's start.

[f] Maximum seedling height increment through 80 months.

[g] For all seedlings in each gap.

2.3.2. Canopy opening and measures

Canopy gaps were opened above seedling clusters in the early wet season of 1996–1997 by first cutting all understory vegetation <5 cm dbh (except mahogany seedlings) at ground level within the anticipated gap area by machete, and then directionally felling stems >5 cm dbh by chainsaw to create, as far as possible, circular overhead canopy gaps. Experimental gaps varied in size according to the area occupied by seedling clusters; canopy gap areas were mapped by compass and distance tape with overhead edges defined by vegetation ≥2 m above the forest floor (Brokaw, 1982). Gap light environments were quantified by taking hemispherical photographs at gap centers at 1 m height using a Canon A1 camera fitted with a fisheye lens and black and white Kodak Tri-X 400 asa film; at no site did surviving mahogany seedling crowns obstruct photographs. Photos were digitized and analyzed using HemiView software (Delta-T Devices Ltd., Cambridge, UK; Whitmore et al., 1993). The light index reported is Global Site Factor (GSF), which sums annual direct plus diffuse incident light based on the sun's overhead tracking position, expressed as a proportion of total above-canopy radiation.

2.3.3. Seedling measurements

Seedlings were mapped within canopy gaps, tagged, and measured at the time of canopy opening for total height from the root collar to the apical tip of the primary stem. Starting seedling numbers at each site ranged from 17 to 73 (Table 1); a total of 358 were included in the experiment, ranging in height from 17 to 750 cm at the time of canopy opening. Seedlings were recensused for survival 7 months after canopy opening, at the end of the first wet season; survival, total height, and mahogany shootborer incidence were recensused 11, 18, 22, 32, 46, 57, and 80 months after canopy opening. Vines and/or directly overtopping secondary vegetation were eliminated annually through 46 months by machete from individual seedlings in all experimental gaps but not from within larger gap areas. No further interventions occurred after 46 months.

2.4. Data analysis

Data from road and seed tree gaps (Table 1B and C) were excluded from all levels of analysis and are presented for comparative purposes. A groundfire that spotted into the study area from a nearby pasture burn in August 2000 eliminated all but two seedlings at one site, reducing site-level sample number to six from 57 months. Minimum significance was set at $\alpha = 0.05$ for all analyses.

In the release experiment, seedling survivorship was analyzed using a binary complementary log–log regression model. This approach involves fitting a linear regression model in which the dependent variable is $\log(-\log(1 - P_{it}))$, where P_{it} is the probability of death for individual i in the tth time interval. This approach is directly analogous to a proportional hazard model (i.e., Cox regression), but is more suitable when events are recorded on long intervals (e.g., yearly), resulting in many ties in survival time (Prentice and Gloeckler, 1978; Allison, 1982; Collett, 2003). Results are similar to a logistic regression model, but the complementary log–log model is preferred on theoretical grounds when deaths occur continuously and not just at discrete intervals (Allison, 1982). Explanatory variables included gap-level Global Site Factor (GSF), distance in m of each seedling from gap edge to gap center (EDGE), and height in cm of each seedling at the start of the experiment (HT_0). Seedling height was log-transformed to reduce skew. Analyses were performed using R Version 1.9.0 (R Development Core Team, 2004) and the 'car' library of Fox (2002).

Height growth of seedlings in the release experiment was analyzed with a linear mixed model, which accounts for temporal autocorrelation of repeated height measurements on individuals (Pinheiro and Bates, 2000). Time in months since release (TIME) was considered as a random effect nested within individual, also a random effect. Fixed effects were as specified in the survival analyses. Models were estimated using maximum likelihood in R Version 1.9.0 (R Development Core Team, 2004) and the 'nlme' library of Pinheiro and Bates (2000). Hypothesis tests on effects in the model were conducted using likelihood ratio tests formed by comparing (1) a full model including all possible interaction terms among the four main effects (TIME, $\log(HT_0)$, GSF, EDGE) with (2) a reduced model formed by deleting the term of interest and all related higher-order interactions (Venables and Ripley, 2002).

Because we found significant interactions between TIME and the main effects (see Section 3), we sought to examine the significance of main effects at each time point. We did this by performing separate multiple regressions for each census in which the response variable was growth increment since the previous census (cm year^{-1}) and explanatory variables were $\log(HT_0)$, GSF, and EDGE as in the two previous analyses.

3. Results

3.1. Natural seedling regeneration under closed canopy

Mean % seedling survival 1 year after germination surrounding eight adult trees was $33.2 \pm 7.4\%$ (Fig. 1A). Nearly 8 years after establishment in the forest understory, mean % survival was $1.3 \pm 0.7\%$ with 11 seedling survivors out of an original 1925 distributed among four of eight adult trees. The principal direct causes of seedling death during the first 4 years were dry season moisture stress, which accounted for a mean $21.1 \pm 1.7\%$ of mortality among sites; defoliation by larval caterpillars of the small nocturnal moth *Steniscadia poliophaea* (Noctuidae: Sarrothripinae), which consume flushing seedling leaves and stem dermal tissues ($20.0 \pm 5.1\%$; for description, see Grogan, 2001, Appendix B); and fungal pathogens or damping-off ($17.7 \pm 3.0\%$). Other mortality agents included insect predators, animals trampling seedling stems, branchfalls, and standing water in saturated soils. No seedling suffered attack by the mahogany shootborer.

Mean seedling height growth by site was 4.4 ± 0.5 cm year^{-1} after 4 years ($n = 84$ among eight sites) and 4.1 ± 1.2 cm year^{-1} after nearly 8 years ($n = 11$ among four sites; Fig. 1A). Light measurements were not taken for individual seedlings, but long-term survivors tended to be those growing where minor canopy disturbances created higher-than-average incident light levels at the forest floor (J. Grogan, pers. obs.).

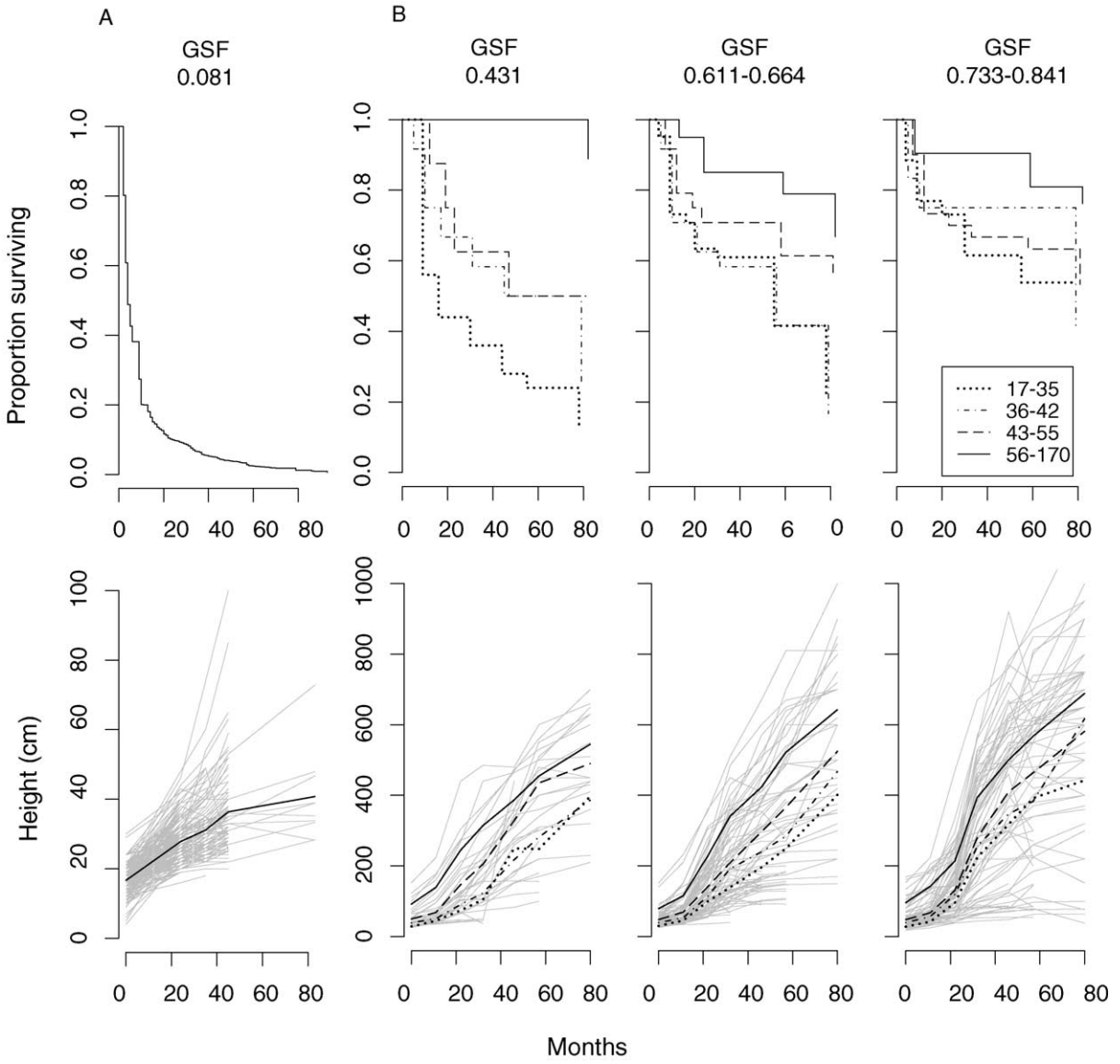

Fig. 1. Performance by naturally occurring mahogany seedlings in the forest understory surrounding eight adult mahogany trees (A) and in different-sized canopy gaps following release (B). Upper panels show Kaplan–Meier survival curves; bottom panels show height of seedlings over the observation periods. In (A), Global Site Factor (GSF) is a mean value for low-ground forest from Grogan et al. (2003a). Survival curve is for 1995 cohort, $n = 1925$, censused over 93 months. In the bottom panel, the heavy line shows average seedling heights at four measurement periods, light lines show height growth patterns of individual seedlings. In (B), seven experimental gaps with similar history are grouped by GSF value, representing one, three, and three gaps from smallest to large values, respectively. Survival curves are for four different classes of height at time 0 (indicated on legend in column 4, in cm). Heavy lines in bottom panels show average heights within classes of initial height, symbols as in upper panels; light lines show height growth patterns of individual seedlings. Note that GSF and size classes in (B) are illustrative only; statistical tests incorporated both as continuous variables. See Table 2 (survival) and Table 3 (growth). Note also axis change in bottom panels between (A) and (B).

3.2. Canopy openings: light environment

Nine experimental canopy gaps ranged in size from 241 to 1106 m^2 (Table 1). GSF values calculated from hemispherical photographs taken at gap centers ranged from 0.431 to 0.841. The largest canopy gaps did not have the highest GSF values due to irregular configurations. The road gap was elongate in shape and bounded along its southern edge by emergent *Ceiba pentandra* (Bombacaceae) and *Sterculia pruriens* (Sterculiaceae) trees (Table 1B), while the seed tree gap retained a 28 m tall mahogany tree within its perimeter (Table 1C). For seven canopy gap sites with similar configuration and history, linear regression analysis of GSF value versus gap area (m^2) demonstrated significant linear correlation ($P = 0.0103$, $R^2 = 0.762$). The road and seed tree gaps had GSF values within the range of other sites (0.778 and 0.663, respectively).

3.3. Seedling survival in canopy gaps

Mean % seedling survival during the first year in seven gaps with similar histories (Table 1A) was $77.9 \pm 1.8\%$. More seedlings died during the first year's dry season beginning 6 months after experiment onset than during any other sampling period; this first year's dry season was unexceptional compared to subsequent years in terms of onset, duration or total precipitation. Mean % seedling survival 80 months after canopy release was $43.8 \pm 5.2\%$, contrasting markedly with long-term survival by seedlings in the forest understory (Section 3.1).

Survival analysis for seedlings in seven gaps with similar histories demonstrated strong effects of initial seedling height as well as gap GSF level (Fig. 1B; Table 2 indicates significance patterns). Survival probability throughout the experiment was greatest for large seedlings and least for small seedlings, though this difference declined in gaps with greater GSF values (significant $\log(HT_0) \times GSF$ interaction; Table 2). Seedling distance to gap edge demonstrated positive but non-significant correlation at $\alpha = 0.05$ (Table 2).

Survival patterns in the two anomalous gaps were consistent with these results. In the road gap (Table 1B), seedlings were, on average, larger than those in other gaps and demonstrated the highest observed survival rate over the course of the experiment (61.0%). In the seed tree gap, which had no initial canopy disturbance associated with logging (Table 1C), seedlings were smallest and survived at the lowest observed rates in the experiment, 2.9% through 80 months; 59% of seedlings in this gap died during the first year's dry season.

Table 2
Binary complementary log–log regression model for survival of naturally established mahogany seedlings following release in experimental gaps

Effect[a]	β (S.E.)	Z	P
$\log(HT_0)$	−6.04 (2.17)	−2.79	**0.00533**
GSF	−31.92 (10.68)	−2.99	**0.0028**
EDGE	−2.65 (1.91)	−1.39	0.164
$\log(HT_0) \times GSF$	8.14 (2.98)	2.73	**0.00636**
$\log(HT_0) \times EDGE$	0.65 (0.53)	1.23	0.218
$GSF \times EDGE$	4.52 (2.69)	1.68	0.094
$\log(HT_0) \times GSF \times EDGE$	−1.14 (0.74)	−1.54	0.123

Main effects include TIME (coded as dummy variables for each census), log(initial seedling height (HT_0)), Global Site Factor for the gap, and seedling distance from the edge of the gap towards the center (EDGE). The β's are the model coefficients, with standard errors in parentheses. The Z values and associated probabilities test whether the coefficients significantly differ from zero. Bold type indicates $P < 0.05$. See Fig. 1B.

[a] For clarity, the separate coefficients of the time effect are not shown, but the overall likelihood ratio test for the time effect was highly significant ($\chi^2 = 82.2$ on 7 d.f., $P < 0.0001$).

3.4. Seedling height increment in canopy gaps

Mean seedling height increment during the first year after canopy opening in seven gaps with similar histories was 24.6 ± 3.6 cm $year^{-1}$. Mean annual height increment peaked at 126.1 ± 23.9 cm $year^{-1}$ during the interval between 22 and 32 months but declined afterwards to 59.1 ± 18.1 cm $year^{-1}$ during the period from 57 to 80 months. Maximum individual seedling height growth within gaps over the total 80 months ranged from 185 to 1050 cm, or 28 to 158 cm $year^{-1}$ (Table 1). Seedling growth rates recorded in canopy gaps contrasted markedly with those recorded for seedlings in the forest understory (Section 3.1).

As in the survival analysis, both the initial size of seedlings and GSF had a large impact on their long-term growth rates (Fig. 1B). Large seedlings tended to grow faster, increasing their height disproportionately over the course of the experiment (significant

Table 3
Effect tests for a linear mixed model of stem height growth over time for naturally occurring mahogany seedlings

Effect	Likelihood ratio	d.f.	P
TIME	258.81	8	**<0.0001**
log(HT_0)	189.55	8	**<0.0001**
GSF	13.07	8	0.1094
EDGE	7.53	8	0.4803
TIME × log(HT_0)	21.30	6	**0.0016**
TIME × GSF	14.90	6	**0.0211**
TIME × EDGE	11.73	6	0.0683
log(HT_0) × GSF	8.04	6	0.2351
log(HT_0) × EDGE	7.50	6	0.2772
GSF × EDGE	6.66	6	0.3536

Main effects as in Table 2. Significance of terms was determined by comparing the log-likelihoods of a full model (including all possible interactions) with a reduced model created by deleting the term of interest and all related higher-order interactions. For clarity, no third order and above interactions are shown; none approached significance. Bold type indicates $P < 0.05$. See Fig. 1B.

TIME × log(HT_0) interaction; Table 3). Growth also tended to be highest in large gaps, especially between 22 and 46 months (significant TIME × GSF interaction; Table 3). Seedling crowns were largely overtaken by competing vegetation by 46 months.

Separate multiple regressions of seedling growth rates between sampling intervals confirmed that the effects of log(HT_0) and GSF varied through time and provided further detail on temporal patterns. At 11 months after gap creation, the model accounted for 30.2% of variation (R^2 value) (Table 4). Initial seedling height contributed significantly to the model during all sampling periods except between 32 and 46 months. GSF and seedling distance to edge contributed significantly to the model during the interval from 22 to 32 months, the period during which mean seedling increment rates and model R^2 value were highest. Non-significant values and low model R^2 at 46 months were likely due to the timing of that recensus during the early wet season of 2000: flushing by seedling apical meristems at the wet season's onset was not highly synchronous, meaning that some seedling heights included new flush lengths while others did not. The 46-month census was the only one with this timing issue.

Results from the two gaps with dissimilar histories were consistent with the effects of initial seedling height found here. Though initial mean seedling height was highest in the road gap (Table 1B), long-term growth response there did not exceed mean response rates in the seven logged gaps with similar history (65.2 cm year^{-1} versus 83.8 ± 8.9 cm year^{-1} through 80 months). This indicates that response rates observed in this experiment may approach maximum possible seedling growth rates for the site and documented light conditions. In the seed tree gap (Table 1C), the initially small seedlings there had the lowest growth rates during all sampling periods (27.8 cm year^{-1} through 80 months).

3.5. Mahogany shootborer incidence

The shootborer infested 11.1% of all seedlings in the experiment; 85% of these were >40 cm at

Table 4
Model R^2 and significance values for completely randomized three-factorial ANOVAs testing seedling height growth between successive census intervals (0–11 months, 11–22 months, etc.) against initial seedling height (log(HT_0)), Global Site Factor (GSF), and seedling distance to gap edge (EDGE)

Months	11	22	32	46	57	80
Model R^2	0.302	0.190	0.312	0.063	0.137	0.123
log(HT_0)	***	***	***	ns[a]	*	*
GSF	ns	ns	***	ns	ns	ns
EDGE	ns	ns	**	ns	ns	ns
log(HT_0) × GSF	*	ns	ns	ns	ns	ns
log(HT_0) × EDGE	ns	*	ns	ns	ns	*
GSF × EDGE	ns	ns	ns	ns	ns	ns
log(HT_0) × GSF × EDGE	ns	ns	ns	ns	ns	ns

[a] Non-significant at $\alpha = 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

experiment onset, and 27.5% of those attacked were infested on at least two separate occasions. Shootborer attack rates ranged from 0 to 35.9% of seedlings by gap and tended to be higher in larger gaps (Table 1). No shootborer attacks were recorded through 80 months in two gaps, including the unlogged site where seedling height response was poor. 52.9% of all attacks occurred during the first 2 years after canopy release, when seedling crowns were most exposed; no attacks occurred after 57 months, when seedling crowns were largely surrounded by competing secondary vegetation.

4. Discussion

Naturally established mahogany seedlings have survived 8 years to date in the forest understory beneath closed canopies surrounding adult trees in this study, albeit at very low rates and with negligible height increment compared to growth rates in partial sunlight as observed in this study's release experiment. These findings are consistent with predictions by Gullison and Hubbell (1992). As documented by Gerhardt (1996) in Costa Rica, dry season moisture stress accounted for more seedling deaths than any other cause. Relatively high incident light levels beneath low, irregular forest canopies at Marajoara may contribute to long-term survival in understory shade by seedlings generally understood to be light demanding (Stevenson, 1927; Lamb, 1966; Gullison and Hubbell, 1992). Mean forest understory GSF values at Marajoara of ~8% contrast with 0.8–3.8% transmission rates of total incident light at ground level reported from diverse forests by Chazdon and Fetcher (1984). As mean annual precipitation totals rise moving north and west into the Amazon Basin interior, taller, denser forest canopies casting deeper shade at ground level may increase seedling mortality rates, contributing to declining adult population densities observed moving from seasonal to aseasonal forests in Amazonia (Grogan et al., 2002; Brown et al., 2003).

Seedling clusters included in the canopy release experiment could have originated in three ways: as advance regeneration present in the forest understory at the time of logging in 1993–1994; from seeds either on the ground at the time of logging or dislodged from tree crowns when trees were felled; or from seeds dispersing into logging gaps during the years following logging. The third scenario is unlikely because the only surviving mahogany tree of sufficient fecundity near any of these gap sites was located 110 m northeast of the fourth gap listed in Table 1A, beyond seed dispersal range (Gullison et al., 1996; Grogan et al., 2003b). Whether originating as advance regeneration or from seed at the time of logging, we believe that seedlings in this study represent essentially single-aged cohorts establishing at the time of or shortly before the logging event. This is because natural regeneration established in the forest understory cannot survive prolonged suppression, nor can it grow vigorously enough to differentiate into mixed-size cohorts like those encountered at the start of this experiment (Fig. 1B). Shallow and flattened seedling crowns at the experiment's onset indicated that advance regeneration in 2- and 3-year old logging gaps were suppressed by closing overhead canopies and competing secondary vegetation.

Seedling mortality was low immediately following canopy release, at least through the first rainy season. During the first dry season following release, intense insolation in gaps combined with soil moisture deficits (Grogan et al., 2003a) to kill many seedlings, with survival probabilities correlating positively with initial seedling height. Smaller seedlings that had not experienced a period of rapid growth in logging gaps before release – particularly those one or more years old in the forest understory at the unlogged site – suffered highest mortality during the first dry season.

Surviving seedlings accelerated height growth rates through 32 months, after which growth rates declined to less than half of maximum rates observed in the experiment. Relatively low mean seedling growth rates during the first year indicates a period of re-acclimation to high irradiance levels following shade suppression (Strauss-Debenedetti and Bazzaz, 1991). Two factors may have extended vigorous growth through 3 years: relatively slow regrowth in gaps by secondary vegetation due to low-nutrient soils with seasonally extreme moisture conditions (Grogan et al., 2003a); and annual cleanings during the experiment's first 4 years freeing seedling crowns from vines and directly competing vegetation.

The best indicator of survival and growth response proved to be seedling height at experiment's onset. In

other words, seedlings experiencing early vigorous growth – those growing tallest during 2 or 3 years after logging disturbance – were most likely to both survive and exploit subsequent canopy release. A small number of seedling survivors in the seed tree gap that had not benefited from a period of early rapid growth grew well during the years immediately following release, but were eventually suppressed beneath competing secondary vegetation. Growth rates were significantly faster in larger gaps; positive effect could also be seen for seedlings closer to gap centers rather than near gap edges, which closed faster. However, these effects were discernible only after seedling re-acclimation, and they faded after secondary vegetation re-occupied available growing space in gaps. We attribute low mahogany shootborer attack rates to cover afforded by dense secondary regrowth rendering seedling crowns difficult for nocturnal moths to locate (Newton et al., 1993).

Taken together, these results indicate that advance seedling regeneration established in the forest understory is capable of responding to canopy disturbance, especially when seedlings experience early vigorous growth. However, response ability may decline as the period of suppression lengthens, and seedlings establishing and growing one or more years in the forest understory may already suffer reduced response ability. These results support a growing body of research in temperate and tropical forests indicating the importance of early rapid growth rates to successful recruitment by light demanding species (Peet and Christensen, 1987; Brown, 1996; Terborgh et al., 1997; Ruel et al., 2000; Landis and Peart, in press). Natural recruitment scenarios best fitting these results are seed germination in the forest understory with canopy release during the first growing (wet) season, before prolonged shade suppression; and seed dispersal and seedling establishment in newly formed gaps with vigorous early growth.

The ability of seedlings to respond to canopy release after suppression suggests that mahogany may be capable of attaining the forest canopy through repeated release (Hartshorn, 1980; Foster and Brokaw, 1982; Canham and Marks, 1985; Clark and Clark, 1987) rather than requiring a single catastrophic disturbance event for successful recruitment. At Marajoara and other sites within the study region, diameter frequency distributions within aggregations of adult trees indicate episodic recruitment at smaller spatial scales than suggested by the catastrophic disturbance hypothesis (Baima, 2001; Grogan, 2001; Brown et al., 2003). Repeated canopy release after seedling establishment and early vigorous growth at favorable microsites (Grogan et al., 2003a) could represent an alternative recruitment pathway for mahogany within a large portion of its natural range.

5. Management implications

Clusters of advance seedling regeneration such as those described here are rare within the study region following logging, and restricted to low-ground hydromorphic soils where adult mahogany trees are concentrated (Veríssimo et al., 1995; Grogan et al., 2003a). Grogan et al. (2003b) found >4 seedlings at only three of 40 randomly chosen 2–3-year old logging gaps at Marajoara. The eight logging sites included in this experiment were the only known high-density seedling clusters associated with logging within a core study area of 1035 ha from which ~370 mahogany trees were harvested. This scarcity may derive from several factors including low annual seed production rates by reproductive adults (Grogan et al., 2003b); logging gaps opened before seed dispersal by some trees; many logging gaps opened upwind of dispersed seeds in a region where prevailing dry season winds blow east to west (Grogan, 2001); and poor survival in logging gaps by advance seedling regeneration growing one or more years in the forest understory before tree removal. Whatever the explanation, this scarcity of post-logging regeneration indicates that silvicultural practices fostering seedling establishment and growth must be implemented at the time of logging if long-term production of mahogany from natural forests is a management objective.

Current seedling size as a proxy for post-establishment growth rate represents the best gauge of release potential. Investment in canopy removal above advance mahogany seedling regeneration may be justified if seedling heights and site history indicate vigorous growth shortly after establishment. Clearly suppressed small seedlings in the forest understory likely do not warrant investment costs. Within the study region, our results indicate that mahogany seedlings may respond to relatively small canopy

manipulations ($<500\ m^2$), offering incentive for investment in forest management.

Seedlings that were tall at this experiment's outset, generally >4 m height, occasionally collapsed after canopy opening and cleaning at ground level, their crowns bending over to rest on the ground. These seedlings had invested disproportionately in vertical growth amidst competing vegetation in the race for canopy position after disturbance associated with logging, and lacked sufficient stem strength to stand alone once secondary regrowth had been cleared away. Bent-over crowns should be lopped off at 2–5 m height depending on stem diameter, and the stem propped up with a Y-necked stake – since these were the most vigorous individuals to begin with, they frequently sprout healthy new crowns. Better still, some competing vegetation should be retained to nurse tall, thin seedlings.

Annual removal of vines and directly overtopping secondary vegetation through 4 years of this experiment probably lowered mortality and increased mean height growth rates relative to unmanipulated gaps. Yet the fastest growing mahogany seedlings kept vertical pace with competing vegetation at all but the seed tree site, which had not been logged, indicating that less frequent post-release interventions may be possible under active forest management. Retention of dense secondary regrowth may benefit growing mahogany seedlings by providing protective cover against the mahogany shootborer; by encouraging rapid vertical growth with minimal branching until the overhead canopy is attained (Smith et al., 1997); and by preventing severely bent-over seedling crowns. Further experimentation at larger scales than reported here is needed to assess the costs and benefits of tending operations.

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