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Big-leaf mahogany (*Swietenia macrophylla*) seedling survival and growth across a topographic gradient in southeast Pará, Brazil

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Abstract

Adult populations of big-leaf mahogany (*Swietenia macrophylla*) occur in aggregations along seasonal streams in transitional evergreen forests of southeast Pará, Brazil. To test whether variable seedling survival and growth across topography may underlie this observed distribution pattern, we planted nursery-grown seedlings in the forest understory and in artificial gaps at opposite ends of a slope gradient where mahogany occurs (low-ground hydromorphic soils) and does not occur (high-ground dystrophic soils). At both positions seedling survival and growth were significantly greater through 42 months in gaps than in adjacent forest understories, though mean understory survival exceeded that in gaps through the first growing season. Mean seedling growth in gaps on low ground was significantly greater than growth in gaps on high ground. Under nursery conditions (well watered, 70% full sun light), growth of seedlings planted in soils from low ground was significantly higher than that of seedlings planted in soils from high ground, indicating that differences in soil nutrient status, particularly Ca and Mg, may account for results in the outplanting experiment. Ca + Mg nutrient supplement accelerated growth rates of nursery seedlings planted in high-ground soils relative to growth rates of seedlings planted in low-ground soils, nullifying significant differences between controls. Soil differentiation across topographic relief with consequent gradients in soil nutrient status complements canopy disturbance regimes (increased light levels) in shaping adult distribution patterns and population structures. This implies that recruitment success under natural and artificial regeneration management practices may vary as a function of both gap size and soil fertility.

Resumo

Populações adultas de mogno (*Swietenia macrophylla*) ocorrem em agregações ao longo dos riachos sazonais em florestas perenes de transição no sudeste do Pará, Brasil. Para testar se as taxas variáveis de sobrevivência e crescimento das mudas ao longo da topografia podem ser a base desse padrão de distribuição observado, plantamos mudas crescidas em viveiros no sub-bosque da floresta e em clareiras artificiais em terrenos que estão nos extremos de um gradiente de inclinação onde o mogno ocorre (solos hidromórficos em terrenos baixos) e não ocorre (solos distróficos em terrenos altos). Nos dois extremos desse gradiente, a sobrevivência e o crescimento das mudas, durante 42 meses, foram significativamente maiores nas clareiras do que no sub-bosque da floresta adjacente, ainda que a taxa média de sobrevivência no sub-bosque da floresta tenha excedido a taxa de sobrevivência nas clareiras durante o primeiro período de crescimento. O crescimento médio das mudas nas clareiras

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no terreno baixo foi significativamente maior do que nas clareiras no terreno alto. Nas condições de um viveiro (bom aguamento, 70% de máxima luz solar), o crescimento das mudas plantadas nos solos provenientes do terreno baixo foi significativamente major do que o crescimento das mudas plantadas nos solos provenientes do terreno alto, indicando que as diferenças nas condições de nutrientes no solo, particularmente Ca e Mg, podem ser responsáveis pelos resultados do experimento com o plantio de mudas. A adição dos nutrientes Ca + Mg acelerou as taxas de crescimento das mudas de viveiro plantadas no terreno alto em relação às taxas de crescimento das mudas plantadas no terreno baixo, anulando as diferenças significativas entre as parcelas controle. A diferenciação no solo encontrada ao longo do relevo topográfico com conseqüentes gradientes de condições do solo complementa os regimes de distúrbio no dossel (níveis de iluminação aumentados) em condicionar padrões de distribuição de árvores adultas e estruturas de populações. Isto significa que o grau de sucesso do recrutamento sob práticas de manejo de regeneração natural e artificial pode variar como uma função tanto do tamanho da clareira como da fertilidade do solo.

Keywords: Amazon; Ca; Canopy openings; Disturbance; Forest management; Light; Mg; Regeneration; Soil nutrients

1. Introduction

In southeastern Pará State, Brazil, along the southern rim of Amazonia where closed forests grade into *cerrado* (savanna) vegetation, big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae) occurs in aggregations tracing seasonal streams draining the Brazilian Shield, a Precambrian landscape (Pires and Prance, 1985; Clapperton, 1993; Veríssimo et al., 1995; Grogan, 2001). These populations, distinct from now-extirpated riverine populations and from highly fragmented *inselberg* (island mountain) hill populations (Grogan, 2001), supplied the bulk of Brazilian mahogany production from the opening of this vast region in the early 1970s until commercial stocks were exhausted in the mid-1990s (Veríssimo et al., 1995; Grogan et al., 2002). On the nearly flat seasonal landscape, where topographic relief typically rises 5–15 m across slopes hundreds of meters broad, mahogany's distribution pattern demonstrates strong positive correlation with ephemeral seepageways, streambanks, and low ground immediately adjacent (Grogan, 2001; Baima, 2001). Even though topographic relief is slight, soil differentiation across it is highly predictable. Low ground is characterized by hydromorphic sandy soils that may experience impeded drainage during the rainy season; well-drained sandy loam or sandy clay dystrophic soils characterize high ground where vertical relief exceeds 5 m (see Askew et al. (1971) and Ratter et al. (1973, 1978)) and where adult mahogany trees rarely occur.

Recent studies of natural mahogany populations in Mexico's Yucatan Peninsula (Snook, 1993) and in Bolivian floodplain forests (Gullison et al., 1996) attribute even- or multi-aged adult population structures to pulsed recruitment after large-scale disturbance events such as hurricanes, fires, and floods. The causal mechanism is said to be prolonged juvenile plant exposure to elevated irradiance levels following massive canopy disturbance, whether top-down in the case of hurricanes or bottom-up in the case of fires and flooding (Snook, 2003; Gullison et al., 2003). A light-demanding species with wind-dispersed orthodox seeds and no appreciable seedling bank in the forest understory (Lamb, 1966; Gullison and Hubbell, 1992), mahogany apparently requires a rare confluence of events—seed or seedling availability immediately following disturbance at large spatial scale—for successful regeneration. Management recommendations derived from these studies include mimicking natural disturbance regimes to encourage natural regeneration after logging, i.e., intensive interventions that could include high-volume timber extraction at local scales (Snook, 1996, 2003; Gullison et al., 1996).

In transitional forests of southeast Pará, large-scale catastrophic disturbances similar to hurricanes, fires, and floods have not been documented. Downburst blowdowns associated with convective air columns are rare in Amazonia and occur mostly in the central-west region (Nelson et al., 1994). Local dominance by the fire-tolerant invasive palm babaçu (*Attalea speciosa*) suggests that fire associated with severe El Niño Southern Oscillation events may play a role in shaping forest structure and composition (Anderson et al., 1991; Ortlieb and Macharé, 1992, in Nelson,

1994). Liana forests west of this region in the Xingu River basin include fire-resistant trees and are thought to result from indigenous swidden fires (Balée and Campbell, 1990). Flooding along seasonal streams is a highly localized and ephemeral event on this landscape.

Other studies indicate that distribution patterns and population dynamics of mahogany in natural forests could also be influenced by differential growth response attributable to differences in soil nutrient status. In Puerto Rico, outside mahogany's natural range, Ewel (1963) reported that height growth in Puerto Rican plantations correlates positively with depth of the nutrient-rich A1 surface horizon. Also in Puerto Rico, Weaver and Bauer (1986) inventoried 18-year-old mahogany plantations in the Rio Chiquito area on deep, acidic, clay soils, across a 170 m topographic gradient. They found that growth was best at slope bottoms and the poorest along ridgetops. It is unclear whether this difference arose as a function of drainage, nutrient status, or some other factor. In Belize, A. Lamb (1945) in Lamb (1966) recorded higher diameter increment rates by adult trees over an 8-year period on more fertile soil types. Sombroek and Sampaio (1962) reported from Brazil that in the transition zones of the lower Araguaia River basin within the present study region, mahogany occurred most commonly in areas with poor drainage on yellow podzols (ultisols) with high base saturation and exchangeable bases.

In this study we examined the roles that abiotic factors may play in mahogany regeneration ecology leading to recruitment success or failure. Expecting to see seedling growth response in gaps under increased irradiance, we also asked: could differences in soil textural properties and chemical status contribute to observed non-random adult distribution patterns on this landscape? Focusing on early seedling survival and growth as one of the most critical life phases for woody plants (Grubb, 1977; Harper, 1977), our objectives were to test for differences in mahogany seedling survival and growth rates among two forest cover types (gap vs. understory) and two topographic/edaphic positions (high-ground dystrophic soil where adult trees are rare vs. low-ground hydromorphic soil where adult trees are common) through outplanting and nursery experiments. Based on measured differences in soil chemical status between topographic/edaphic positions, we also tested for differences in seedling growth rates in response to Ca + Mg nutrient supplement in a nursery experiment.

2. Methods

2.1. Study region and site

The study region, which marks the easternmost extension of mahogany's natural range, is located between 6.5–8°S and 49.5–52°W, 750 km south of the coastal city of Belém (Grogan et al., 2003). 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.

The study site is a forest industry-owned management area called Marajoara, located at 7°50′S, 50°16′W, 34 km on a straight line northwest of Redenção. Marajoara was selectively logged for mahogany and 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. Soil distribution patterns at Marajoara follow predictable sequences across topographic relief: gray or bleached-white sandy profiles (eutrophic podzols, spodosols) predominate on low ground adjacent to the lowest order seasonal streams, while brown, yellow, or red-yellow soils (red-yellow latosols, oxisols; yellow podzols, ultisols) with higher clay content are found at higher elevations, often mixed with lateritic gravel. Transitions between these conditions appear gradual at the soil surface but may be abrupt belowground. Boulder-sized lateritic or ironstone concretions are common on higher ground, especially at mid-slope, as are granitic outcrops. Forests are predominately evergreen with a deciduous component. Differentiation in structure and composition is noticeable across gentle slopes. Low-ground forests tend to have irregular, low canopies punctuated by occasional emergents like mahogany; the understory is characterized by multi-stemmed açaí (*Euterpe edulis*, Palmae), babaçu (*A. speciosa*, Palmae), or bamboo thickets. High-ground forests tend to have more regular,

taller canopies and more open understory conditions in deeper shade.

2.2. Seedling outplanting experiment

Canopy opening and experimental design. At the beginning of the 1996–1997 rainy season, eight artificial canopy gaps 20 m in diameter were opened at high- and low-ground positions, four gaps at each position, at the top and bottom of a slope rising 6.5 m (vertical) across a horizontal distance of approximately 200 m. Loggers had harvested mahogany (low ground) and secondary timber species (high ground) from this area in 1993, but sufficient contiguous unlogged area remained to avoid working in logging gaps and skid trails. Gaps at each slope position were located based on two criteria: their centers were spaced at least 65 m apart to avoid interactions in light environments between adjacent gaps and the overstory to be felled contained no trees >30 cm dbh, to avoid compromising gap edges by large falling crowns. Within a circle 20 m diameter all vegetation was cut at ground level by machete or chainsaw and removed from the gap (retention of leaf litter and fine woody debris on the ground meant that little soil surface was exposed during this operation). After clearing, ground-level and overhead dimensions of each gap were measured by distance tape from gap centers in eight directions at 45° intervals, with overhead edges defined as beginning 2 m above the forest floor (Brokaw, 1982). Five square seedling plots 120 cm on a side were demarcated within each gap center (Fig. 1), with exact locations adjusted to avoid planting seedlings on mounds or near stumps. Seedlings were planted at 40 cm spacing in five nine-seedling plots per site ($n = 45$). Five seedling plots in the same spatial pattern were demarcated beneath intact forest canopy near each gap. The nearest understory plot was located 35 m from the gap center in a randomly chosen direction. Vegetation <2 cm dbh was removed from within each forest plot to reduce microhabitat variability at the seedling level.

Hydrology and soil measurements. Weekly measurements of depth to water were made in PVC-lined 10 cm diameter wells augered to the water table at high- and low-ground positions at the study site in

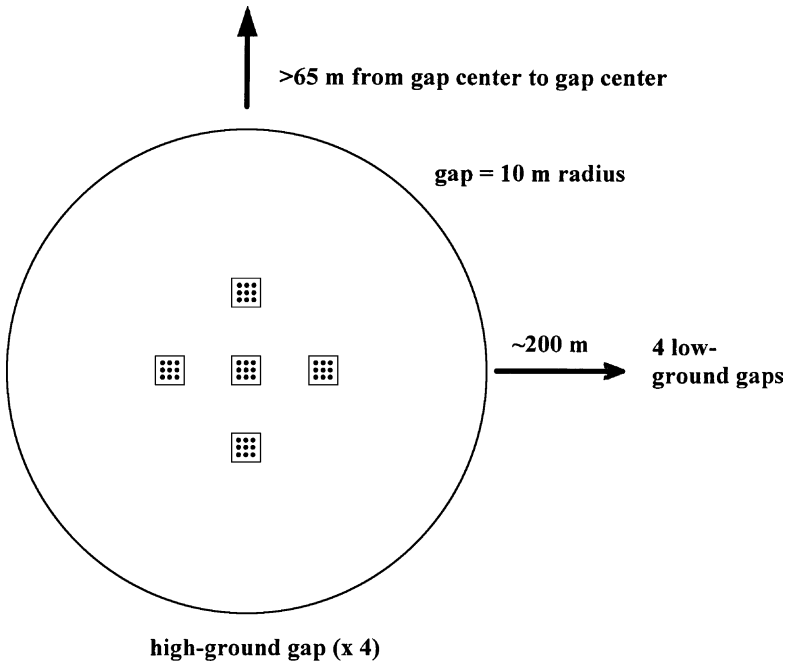

Fig. 1. Schematic illustration showing experimental design of the seedling outplanting experiment. Each of the eight 20 m diameter artificial gaps (large circle) had five plots set 2 m apart in the gap center (squares), each with nine seedlings planted at 40 cm spacing (dots).

September 1996, near the end of that year's dry season. Measurements were taken throughout the 42-month study period.

Soil samples for texture and chemical analysis were collected from four sites at Marajoara where low-ground sandy soils grade into finer-textured soils across slopes 200–400 m broad, including the slope where the outplanting experiment was installed. At each site high-ground sampling positions lay 5–8 m above low-ground positions. At respective positions within the four sites, soils were sampled to successive depths (0–10, 10–30, 30–60, and 60–100 cm) in four augered holes set 20 m apart. Samples were composited proportionally by depth, air dried, and sifted to remove the >2 mm component. The Munsell Color Chart was used to determine colors (wet) while in the field. Texture was analyzed using the Bouyoucos hydrometer method (Gee and Bauder, 1986), and matric potential (water retention curves) was determined using the pressure plate method (Klute, 1986; Vogt and Tilley, 1998) at the Yale University Soil Laboratory.

The pH and macro-nutrients were analyzed at the University of Georgia, Athens Soil Laboratory. Soil pH in water was measured using a calomel electrode; exchangeable cations and extractable P were measured by double-acid extraction, with solutions analyzed on a Perkin-Elmer 560 atomic absorption spectrometer (Nelson et al., 1953; Perkins, 1970). Total N was determined by digestion prepared with ammonical nitrogen/BD acid and analyzed on a Technicon Auto-Analyzer II.

Soil moisture status was monitored gravimetrically as % dry weight from October 1996 to November 1997, monthly during the rainy season and every 2 weeks from the late rainy season (April 1997) through the dry season. Samples were collected at two depths (10–15 and 35–40 cm) under closed forest canopies and from gap centers at high- and low-ground positions. Through the rainy season a single sample was collected from each depth at each location; during the dry season two samples were collected from each depth at each location, and average % dry weights are reported. Samples were dried at 55–60 °C for 24–48 h. Wet and dry weights were recorded to the nearest 0.01 g. This temperature and duration were shown to be sufficient for gravimetric determinations by re-drying (24 h at 105 °C) and re-weighing a subset of samples at the Yale University Soil Laboratory.

Light environment. Light environments in gap and understory plots were quantified by taking hemispherical canopy photographs at 1 m height above seedling plot centers with a Canon A1 camera fitted with a fisheye lens, using black and white Kodak Tri-X 400 asa film. Photos were digitized and analyzed using HemiView software (Delta-T Devices, 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.

Nursery and seedling outplanting. In a nursery, mahogany seeds were planted in black polyvinyl bags 12 cm (diameter) × 30 cm (deep), filled with uniformly mixed high-ground or low-ground soil from the experiment site. Seedling bags were grouped by soil type under 30% shade cloth. Seeds germinated between mid-November and early December 1996. Seedlings were randomly chosen and transplanted into gap and forest plots during the first week of February 1997; seedlings were planted with rooting soils by removing nursery bags and slipping intact moist soil cores weighing ∼3.5 kg into prepared holes. A total of 720 seedlings were outplanted.

Seedling measurements and maintenance. At the time of outplanting, seedlings were measured for height from the root collar to the apical tip and for the number of leaves. To reduce metabolic stress associated with sudden exposure to intense sunlight in gap centers, all but the three largest leaves were clipped from each seedling; seedlings planted in the forest understory were treated identically. Seedlings were recensused during successive dry seasons until July 2000, at 7, 20, 30, and 42 months after outplanting. Variables measured included: height and diameter 20 cm above the root collar (to avoid asymmetrical stem growth at the root collar) at 20, 30, and 42 months after planting, and leaf number at 20 and 30 months.

Aboveground competing vegetation in the eight gaps was periodically cut back to the edges of each gap, and within the boundaries of forest understory seedling plots, restoring approximate starting light conditions. As well, an insecticide (Agril-320, *n*-dodecylbenzene sodium sulfate) was applied to all seedlings two to three times during each rainy season to control larval caterpillars of the nocturnal moth *Steniscadia poliophaea* Hampson (Noctuidae:

Sarrothripinae), which preferentially feed on newly flushed mahogany leaves and leaflets and can defoliate and kill seedlings and saplings (see Grogan (2001), Appendix B).

2.3. Nutrient supplement experiment

To test the effects of Ca + Mg nutrient supplement on seedling height growth, we transported soils to the nursery from high- and low-ground positions at the study site and from one other slope gradient located 3 km away at Marajoara. For each of the two soil types from respective sampling sites, half was supplemented with 39% Ca and 5% Mg mixed at 3 kg/m^3, and the other half was left untreated. Forty seeds were planted in polyvinyl bags (12 cm (diameter) × 30 cm (deep)) in each sampling site/soil type/nutrient supplement treatment, or 320 total ($40 \times 2 \times 2 \times 2$) under 30% shade cloth. Seedling heights were recorded 8 months after planting and are reported as means by soil type/nutrient supplement treatment.

2.4. Analysis of data

Two-way analysis of variance (ANOVA) of means was used to detect differences in seedling survivorship, height growth from the time of outplanting, diameter growth, and leaf number among treatments in the outplanting experiment (PROC GLM, SAS Institute, Cary, NC). Survivorship data were arcsin transformed for analysis, while all other data were log transformed. Tukey's studentized *t*-tests compared means among treatments where ANOVA models were significant. ANOVA and Tukey's studentized *t*-tests were used to test for difference among and between treatments in the nursery seedling experiment. Differences in gap area (m^2) within and between slope positions were tested using unpaired *t*-tests (PROC TTEST). Linear regression models plotting seedling height growth by plot vs. plot-level GSF value tested growth response within gap treatments. Minimum significance was set at $\alpha = 0.05$ unless otherwise specified.

Although four gaps were created at each slope position in the outplanting experiment, they cannot be called true replicates if the objective was to test survival and growth between positions—to do so, single gaps should have been opened at opposite ends of four different slope gradients (Hurlbert, 1984). This was not possible due to logistical constraints at the study site. The apparent power of the two-way ANOVA was therefore greater than its actual power. However, differences in the nature and properties of soils between slope positions were consistent among four slope gradients described in Grogan (2001), and we expect that different growth rates between positions demonstrated in this experiment would be repeated at other sites.

3. Results

3.1. Hydrology, soil texture, and chemical status

The water table rose to perch at or near the soil surface at the low-ground topographic position for most of the 1997 rainy season; at the high-ground position it rose to within 2 m of the soil surface (Fig. 2). From this across-slope tilted position the water table receded steadily through the dry season to re-establish an essentially flat deep-soil water table by the onset of the following year's rainy season. This annual cycle was repeated during subsequent years (Grogan, 2001).

Soils at the high-ground position were increasingly finer textured at depth and well drained compared to soils at slope bottoms. Textural designations ranged from sand to sandy clay on high ground vs. sand to sandy loam on low ground. Munsell soil colors ranged from yellowish-brown in the surface horizon to red at depth on high ground vs. (grayish) brown to pale brown or gray at depth on low ground. High-ground soils were mixed with a 5–10 cm layer of lateritic and quartz gravel at variable depths to 1 m, while a 5 cm layer of quartz gravel appeared at ∼1 m depth in low-ground profiles.

Soil matric potentials sorted predictably according to texture, with high-ground profiles securing more water against gravity at the permanent wilting point (−15 bars) than coarser profiles at the low-ground positions (7–13% dry weight by high-ground soils vs. 2–6% by low-ground soils). These values conformed well to observed field values (Fig. 3). By gravimetric moisture content, gap soils were drier than forest understory soils at the high-ground position, with coarser soils at 10–15 cm securing less moisture against gravity than finer-textured soils at

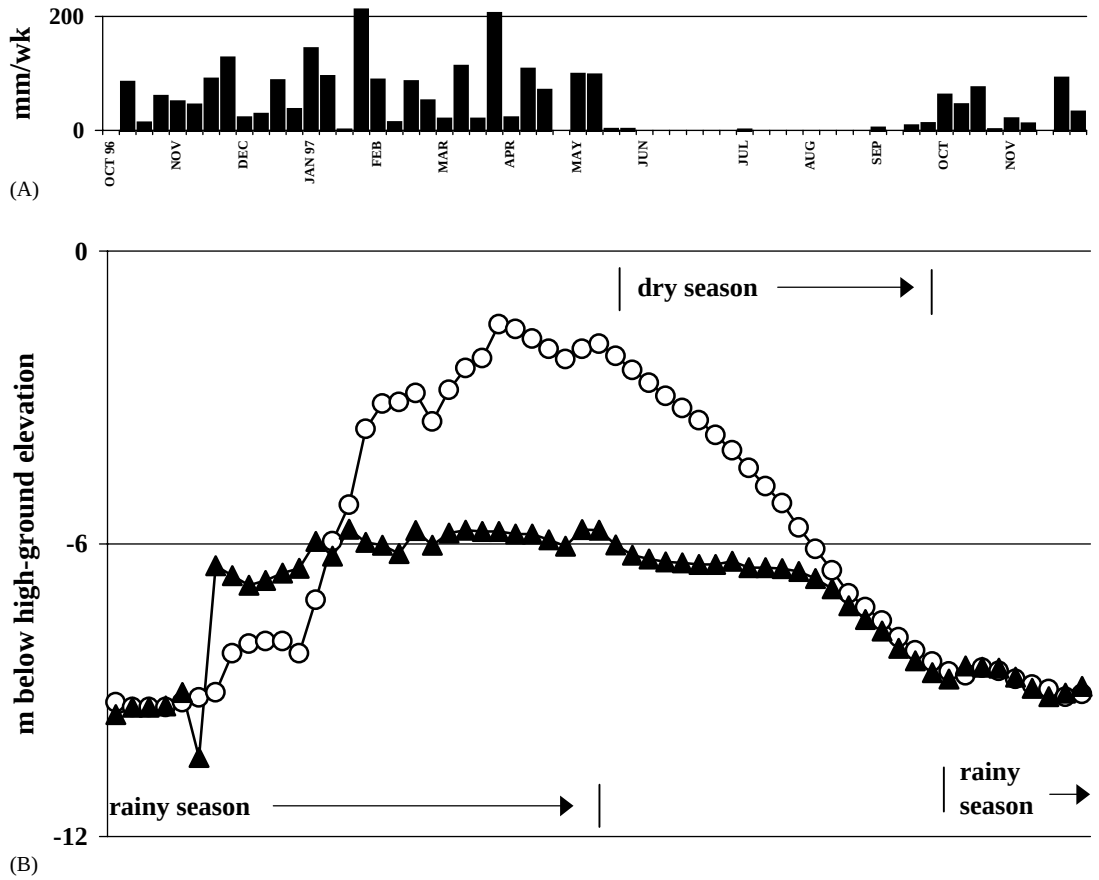

Fig. 2. Weekly precipitation totals in mm (A) and depth to the water table in meters at high- (○) and low-ground (▲) topographic positions (B), October 1996–November 1997. Zero meter corresponds to the soil surface elevation at the high-ground well position, which lay 5.5 m above the low-ground well position. This pattern was repeated annually through the 42-month observation period.

35–40 cm depth. Evaporative losses due to increased insolation in gaps likely caused this difference. This pattern was not repeated in the low-ground gap and adjacent forest understory. There, gap soils retained more moisture than forest soils until the mid-dry season, especially at 10–15 cm depth. This difference was likely due to persistent lateral subsurface drainage across the slope gradient as the water table subsided through the dry season, with reduced transpirational demand after removal of aboveground vegetation.

High-ground soils were significantly more acidic and had significantly higher % C and % N levels below 30 cm depth (Table 1). While levels of extractable P and exchangeable Ca^{++} and Mg^{++} were on average higher in low-ground soils, variability among low-ground samples rendered some comparisons by depth non-significant at $\alpha = 0.05$. Even so, Ca^{++} and Mg^{++} were particularly elevated at low-ground positions. Levels of exchangeable acids were significantly higher throughout high-ground soil profiles, while the reverse was true for % base saturation.

3.2. Light environment

Artificial gaps were intended to cover 314 m^2 at ground level (10 m radius), and mean gap size was close to the target size, with no significant difference between high and low ground (Table 2). However, mean overhead canopy opening size was significantly larger for gaps at low-ground positions, averaging

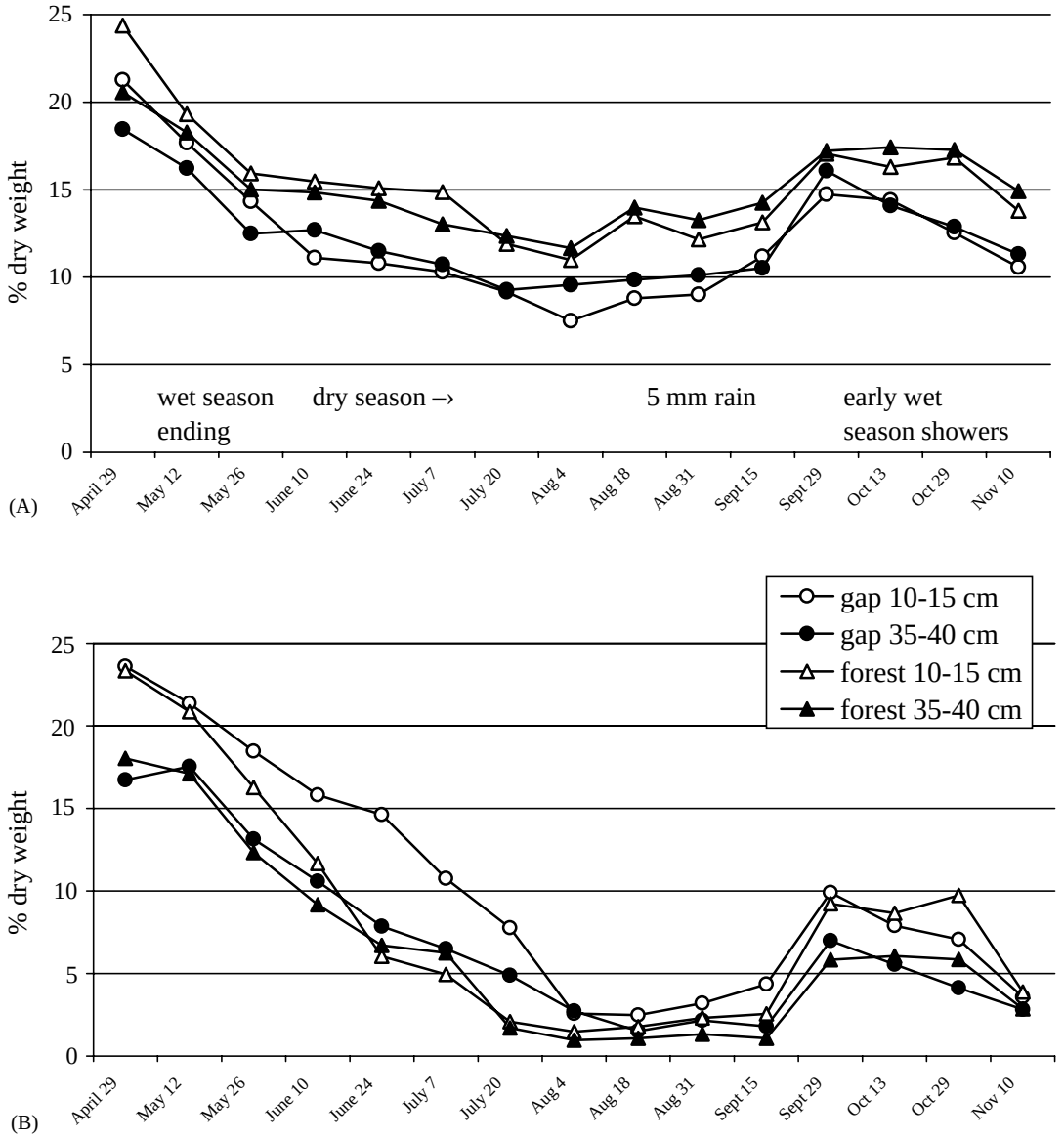

Fig. 3. Seasonal changes in gravimetric soil moisture as % dry weight, 10–15 and 35–40 cm depths, from the late rainy season through the dry season and early rainy season 1997, for (A) high-ground gap center + forest understory; (B) low-ground gap center + forest understory. Legend in (B) applies to both charts.

281 m^2 compared to 158 m^2 at high-ground positions (t-value $= 4.475$, d.f. $= 6$, $P = 0.0042$). This outcome arose from forest structural differences between the two slope positions: the high-ground forest was more vertically oriented and had denser, more evenly distributed mid- and overstory canopies than the low-ground forest. Canopy irregularity at the slope bottom, combined with heavier canopy vine loading, meant that the crown of a given overstory tree was more likely to be bordered by open space or linked by vines to other tree crowns than at the slope top, creating larger gaps, on average, when felled.

Table 1
Soil chemical properties, comparing high- vs. low-ground positions[a]

Sample depth (cm)	Topographic position			
	High ground	Low ground	High ground	Low ground
	pH, water		Ca, cmolc/kg	
0–10	4.35 (0.077) b	4.98 (0.090) a	0.138 (0.045) b	1.167 (0.259) a
10–30	4.38 (0.082) b	5.11 (0.114) a	0.075 (0.019) a	0.730 (0.256) a
30–60	4.64 (0.054) b	5.43 (0.055) a	0.067 (0.009) a	0.239 (0.064) a
60–100	4.82 (0.072) b	5.72 (0.109) a	0.075 (0.017) b	0.310 (0.061) a
	% C, cmolc/kg		Mg, cmolc/kg	
0–10	0.981 (0.070) a	1.163 (0.132) a	0.104 (0.012) b	0.238 (0.025) a
10–30	0.653 (0.056) a	0.520 (0.089) a	0.042 (0.003) b	0.120 (0.017) a
30–60	0.410 (0.038) a	0.175 (0.023) b	0.032 (0.005) b	0.069 (0.009) a
60–100	0.278 (0.013) a	0.109 (0.011) b	0.037 (0.007) a	0.090 (0.027) a
	% N, cmolc/kg		Exch. acid, cmolc/kg	
0–10	0.078 (0.006) a	0.107 (0.011) a	0.936 (0.074) a	0.142 (0.037) b
10–30	0.054 (0.003) a	0.047 (0.009) a	0.910 (0.085) a	0.144 (0.046) b
30–60	0.029 (0.002) a	0.016 (0.002) b	0.888 (0.097) a	0.211 (0.152) b
60–100	0.020 (0.001) a	0.010 (0.001) b	0.600 (0.112) a	0.151 (0.132) b
	Ext. P[b], cmolc/kg		ECEC[c], cmolc/kg	
0–10	0.850 (0.075) a	2.840 (1.668) a	1.278 (0.107) a	1.643 (0.271) a
10–30	0.475 (0.063) a	0.810 (0.184) a	1.086 (0.064) a	1.027 (0.247) a
30–60	0.340 (0.207) a	0.325 (0.053) a	1.017 (0.110) a	0.534 (0.215) a
60–100	0.080 (0.000) b	0.313 (0.046) a	0.746 (0.129) a	0.568 (0.090) a
	K, cmolc/kg		% base saturation[d]	
0–10	0.101 (0.012) a	0.097 (0.013) a	26.3 (3.47) b	90.3 (2.68) a
10–30	0.059 (0.005) a	0.033 (0.005) b	16.8 (3.32) b	83.0 (5.20) a
30–60	0.031 (0.006) a	0.016 (0.003) a	12.7 (0.76) b	72.9 (11.34) a
60–100	0.034 (0.007) a	0.017 (0.003) a	20.1 (2.08) b	80.0 (17.23) a

[a] Data are means of composited samples from four separate slope gradients, with standard errors in parentheses. Comparisons are of equivalent depths between positions (e.g., 0–10 cm vs. 0–10 cm). Letters qualitatively indicate significant differences ($a > b$) at the 5% level.
[b] Extractable P.
[c] Effective cation exchange capacity = sum of cations + exchangeable acid.
[d] % base saturation = sum of cations/ECEC.

Table 2
Light environments comparing high- vs. low-ground positions[a]

		Topographic position	
		High ground	Low ground
Gap opening (m^2)	Ground	337.0 (11.0) a	305.3 (8.5) a
	Overhead	158.3 (10.9) b	281.0 (25.2) a
GSF (1.0 = full sun)	Gap	0.528 (0.013) b	0.644 (0.042) a
	Forest	0.079 (0.004) a	0.081 (0.012) a

[a] Data are means for gap opening and GSF for four gaps and associated forest understories at respective topographic positions, with one standard error in parentheses. Comparisons are between positions; letters qualitatively indicate significant differences ($a > b$) at the 5% level.

These differences in overhead gap size led to differences in mean incident light as expressed by the GSF. Mean GSF values were significantly higher in low-ground gaps than in high-ground gaps (t-value = 2.678, d.f. = 6, $P = 0.0366$). Though mean GSF values for forest understory seedling plots were nearly identical between slope positions, within-position variability was higher in low-ground forests, again indicating greater canopy irregularity.

3.3. Outplanted seedlings

Mean % seedling survival in gaps after 42 months (61–64%) was significantly higher than in the forest

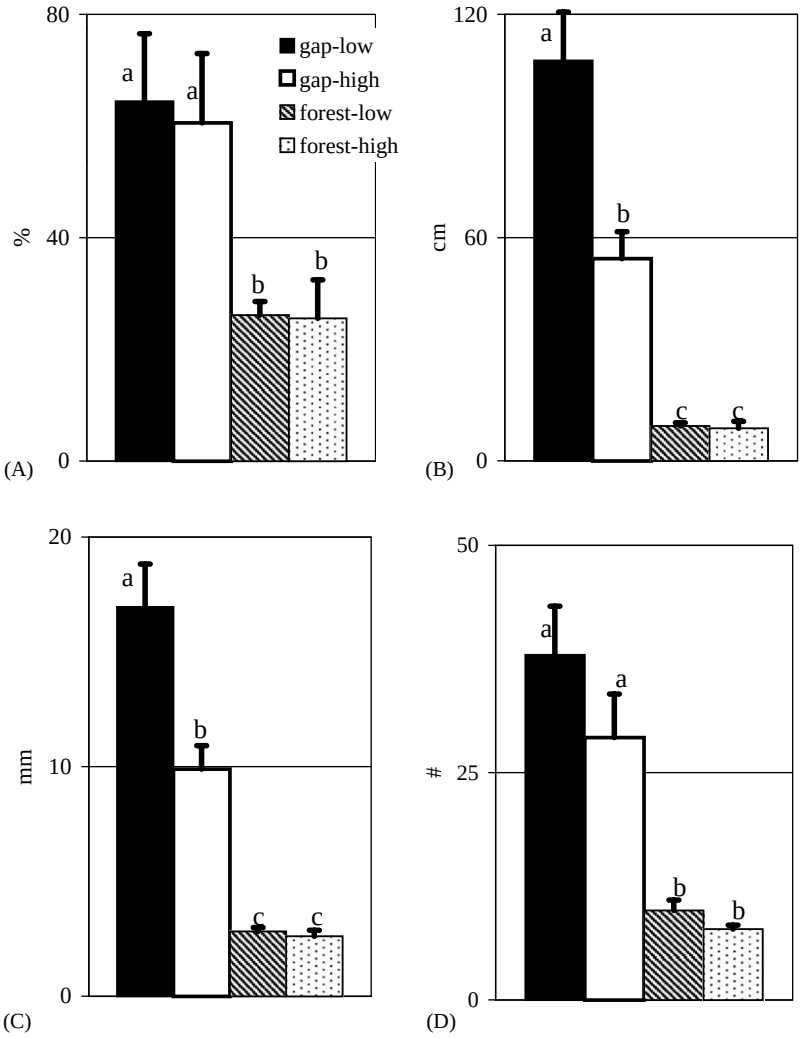

Fig. 4. Mean % seedling survival (A), height growth in cm (B), stem diameter in mm (C), and number of leaves (D) by light environment/topographic position treatments 42 months after outplanting (except (D), 30 months). Legend in (A) applies to all charts. Error bars show one standard error. Treatments not sharing the same letter within charts differ significantly at $P < 0.10$ in (A), and at $P < 0.05$ in (B–D).

understory (25%). Even though survivorship among gaps was highly variable, comparisons between gap and understory treatments yielded significant differences at $\alpha = 0.10$ (Fig. 4A). Mortality in gaps actually exceeded that in the forest understory during the first rainy (growing) season, but this trend's reversal grew more pronounced during subsequent years. Mortality attributed to moisture stress was more common in both gap and forest understory treatments at high-ground positions compared to at low-ground positions (Table 3). Although care was taken to avoid planting seedlings where microtopographic relief threatened partial flooding at low-ground positions during the rainy season, in a few cases seedling plots did flood out through some portion of the first rainy season (1996–1997), the heaviest in 5 years at Marajoara. Yet no seedling deaths were directly attributable to waterlogged soils.

Mean seedling height growth was significantly higher after 42 months in gaps than in the forest understory, with topographic position contributing

Table 3
Non-mortal events affecting outplanted seedlings through three growing (rainy) seasons, by treatment and events resulting in seedling deaths (gap and forest are light environments)

	Non-mortal events affecting outplanted seedlings				Events resulting in seedling death			
	Gap		Forest		Gap		Forest	
	High	Low	High	Low	High	Low	High	Low
Moisture stress	6	6	–	1	19	12	17	6
Broken[a]	8	2	2	4	1	5	9	3
Browsed[b]	6	10	1	1	–	6	1	2
Shootborer[c]	4	42	–	–	–	–	–	–
Indeterminate	–	–	–	–	29	37	75	98
Total	24	60	3	6	49	60	102	109

[a] Includes seedlings stepped on by animals and fallen upon by branches.
[b] By grasshoppers, crickets, and termites.
[c] Three of the 42 seedlings in low-ground gaps suffered shootborer attack during both the second and third rainy seasons.

to model significance (Table 4, Fig. 4B). That is, gap seedlings responded to increased light levels; seedlings in low-ground gaps responded more vigorously than seedlings in high-ground gaps. This disparity in height growth in gaps between slope positions emerged despite predations of the mahogany shootborer, which occurred almost exclusively in low-ground gaps (Table 3) and reduced mean heights in three of the four low-ground gaps by perhaps 50% based on growth rates observed in other experiments at Marajoara. In fact, significant differences in seedling heights among treatments were discernible at the time of outplanting. The source of significance in the two-way ANOVA for starting seedling height was slope position, derived from the two soil types used in the nursery: seedlings germinating in sandy loam soil transported to the nursery from the high-ground position were slightly but significantly shorter at the time of outplanting than seedlings germinating in sandy soils transported from the low-ground position ($F = 12.35, P = 0.0006$). Even though light environment's contribution to model significance equaled slope position's by 7 months after outplanting and far exceeded slope position's contribution by experiment's end, slope position nonetheless contributed significantly to seedling height growth through four rainy (growing) seasons.

In the forest understory, seedlings added height increment at both slope positions to attain 25–28 cm through 42 months (Fig. 4B). While mean height growth by low-ground seedlings slightly exceeded that by high-ground seedlings, differences were not significant.

Table 4
Variance ratios (F values) from ANOVAs of seedling survival, height growth (cm), stem diameter (mm), and leaf number (values are for observations after 42 months except leaf number (30 months))

	Seedling survival	Height growth	Stem diameter	Number of leaves
Model	4.57*	68.54***	96.34***	29.76***
Source				
Light environment	13.57**	195.26***	272.35***	85.98***
Topographic position	ns[a]	7.15*	10.92**	ns
Light × topography	ns	ns	5.75*	ns

[a] Not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Table 5
Seedling heights after 8 months and variance ratio from ANOVA of the nursery experiment (high and low are topographic positions)[a]

	Nutrient supplement				F value
	Ca + Mg		Control		
	High	Low	High	Low	
Seedling height (cm)	34.0 (0.64) a	31.5 (1.27) a	22.3 (1.56) b	29.0 (3.96) ab	10.52*

[a] Height values are means from two sites for each nutrient supplement/topographic position treatment. One standard deviation shown in parentheses; letters qualitatively indicate significant differences ($a > b$) at the 5% level.
* For F value $P < 0.05$.

Mean stem diameter and leaf number were significantly larger in gaps after 42 months (30 months for leaf number) than in the forest understory, with topographic position contributing to model significance for stem diameter but not for leaf number (Table 4, Fig. 4C and D). Noteworthy were differences in starting leaf numbers, which reflected differences in starting height: seedlings germinating in low-ground sandy soils were in all respects larger than seedlings germinating in high-ground soils.

3.4. Nutrient supplement experiment: height growth response to Ca + Mg

High- and low-ground soils transported to the nursery from two slope gradients were similar between respective positions in texture, color, and chemical status (Grogan, 2001). Without Ca + Mg supplement, mean seedling height in low-ground soils exceeded that in high-ground soils after 8 months at $\alpha = 0.05$, as expected from results in the outplanting experiment (Table 5). The Ca + Mg supplement led to significantly increased seedling height growth in high-ground soils characterized by low exchangeable cations and base saturation.

4. Discussion

A large body of literature describes the distribution of plant species and forest associations across topographic relief with associated soil catenas (e.g., Davis and Richards, 1934; Morison et al., 1948; Markham and Babbedge, 1979; Gartlan et al., 1986; Hubbell and Foster, 1986; Newbery et al., 1986; Basnet, 1992; Clark et al., 1995; Lieberman et al., 1996; Svenning, 1999), but experimental studies testing hypotheses about underlying causes of these patterns are rare. Ashton et al. (1995) found that differences in survival and growth among four species of the genus *Shorea* (Dipterocarpaceae) across topography in a Sri Lankan hill forest were related to gradients in soil moisture availability and light regimes, with species co-existence fostered by disturbance regimes. Ashton and Larson (1996) attributed differential growth rates among related *Quercus* species (Fagaceae) across a topographic sequence in the northeastern United States to differences in drought tolerance, germination, and establishment rates across the gap-forest understory light continuum. Palmiotto (1998) found that variability in soil texture and nutrient status occurring at small spatial scales influenced species demographic patterns in highly diverse hill forests in northern Sarawak, Malaysia through effects on seedling growth rates. Hall et al. (2003) related seedling performance of four sympatric *Entandrophragma* species (Meliaceae) under different soil fertility and moisture treatments to observed adult distribution patterns with respect to soils and moisture availability across topography.

Results reported here indicate that mahogany adult distribution patterns at Marajoara are disturbance related insofar as elevated light levels at ground level are necessary for vigorous seedling growth, regardless of topographic position and associated soil type. Indeed, seedling height growth rates were higher in larger 0.65 ha artificial clearings on low-ground soils in separate experiments at Marajoara (Grogan, 2001). Our experience creating artificial gaps suggests that differences in canopy structure between slope positions may favor light-demanding species like mahogany at low-ground topographic positions

by providing, on average, larger and therefore more persistent canopy openings.

Since overhead canopy openings in low-ground gaps were significantly larger than those at high-ground positions, could elevated light levels (GSF values) account for different mean growth rates rather than or in addition to soil type? If such were the case, we might expect to see within-treatment growth response across the range of GSF values represented by high- and low-ground light environments (0.48–0.59 and 0.54–0.77, respectively). Yet linear regression analysis of mean seedling height vs. GSF values within gaps demonstrated no significant response over the range of values recorded within treatments at any sampling point to 42 months. The scale of light differences between gaps at high- and low-ground positions in this experiment thus does not appear to have been great enough to cause measurable differences in seedling height growth.

Soil distribution patterns may also shape adult mahogany distribution patterns at Marajoara. In highly diverse forest communities, growth rates <50% of maximum rates as documented in high-ground gaps are likely insufficient for recruitment except under extreme conditions where resource limitations eliminate most competitors (see Tilman (1982) and Terborgh et al. (1997)). While no definitive statement can be made about which soil chemical properties contribute most to different growth rates between positions, exchangeable cations, especially Ca^{++} and Mg^{++}, were considerably elevated in low-ground sandy soils at Marajoara. That seedling height growth in high-ground soils treated with Ca + Mg supplement was equivalent to or even exceeded height growth in low-ground soils with or without supplements indicates the importance of these nutrients to early mahogany seedling performance. These highly mobile cations are likely being transported in soil water solution laterally across topographic relief, accumulating in low-ground soils. We suggest that conventional woodsmen's wisdom within this region, that the highest densities of merchantable mahogany trees can be found in the most fertile soils adjacent to first-order streams (*cabeceiras*), is related to nutrient accumulation in these areas, especially by Ca^{++} and Mg^{++}.

Though care was taken to avoid planting seedlings where decaying roots and tree stumps might provide nutrient boosts to growing seedlings, nevertheless some seedlings did apparently draw unequal advantage from decaying belowground materials. Indeed, the tallest sapling after 42 months grew within 1 m of a densely rooted bacaba stump (*Oenocarpus distichus*, Palmae) in a high-ground gap, although many low-ground gap seedlings would have exceeded this one in total height but for attack, sometimes repeated, by the mahogany shootborer. In many cases, exceptionally vigorous growth by one or a group of seedlings in gaps was correlated with the presence nearby of a stump, especially palm stumps. Microsite variability in belowground resources no doubt introduced considerable "noise" into survival and growth data.

These observations of individual seedlings in small artificial gaps may help to explain population structures characterized by mixed size classes of adult trees within micro-watershed-level aggregations at Marajoara and other study sites in southeast Pará. In particular, juvenile stems (10–30 cm dbh) are commonly observed growing vigorously into small canopy gaps or beneath intact overstory, based on diameter increment growth over many years (Grogan, 2001). We have even seen mahogany flower while overtopped by larger individuals of different species. These cases are anomalous according to the catastrophic disturbance paradigm (Snook, 1993; Gullison et al., 1996), under which successful recruitment requires massive and prolonged canopy disturbance. Small-scale canopy disturbances in combination with localized belowground nutrient hotspots may account for these trees, indicating that the current regeneration paradigm for mahogany, with its emphasis on elevated light regimes, may require regional modification with inclusion of other factors such as variation in soil fertility at local scales.

5. Management implications

These results indicate that mahogany growth rates and recruitment at Marajoara may be limited within high-ground zones characterized by relatively nutrient-impoverished soils. While management systems focusing on natural regeneration through retention of seed trees would ignore these zones due to limitations on seed dispersal (Smith et al., 1997), enrichment plantings should also avoid high-ground areas which mahogany rarely colonizes. The size of canopy gaps

necessary for successful recruitment by natural or outplanted seedlings (i.e., enrichment plantings) will likely vary according to soil fertility—where soils are nutrient-rich, especially with regards exchangeable cations, canopy gaps may be smaller. This principle will function at both meso scales (high vs. low ground) as well as at micro scales (within low ground). These results also have implications for management in plantations: poor growth rates commonly observed on high ground within the study region by seedlings planted in straight lines across vast deforested areas are likely due to soil nutrient deficiencies which can only be corrected by fertilizer inputs, especially liming.

Within the low-ground landscape, nutrient-rich zones are not randomly distributed. Areas adjacent to first-order streams where mahogany densities are the highest may be nutrient accumulation zones compared to flats flanking higher-order streams where soils are prone to extended periods of waterlogging. And at smaller scales within any gap or forest under- and story-plot, some planting sites—slightly raised, near nutrient "hotspots" like decaying stumps and logs—are readily identified as better than others. The most successful enrichment efforts will be those concentrating investment in areas where nutrient-rich soils are available to boost early seedling growth.

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References

Anderson, A.B., May, P.H., Balick, M.J., 1991. The Subsidy from Nature: Palm Forests, Peasantry, and Development on an Amazon Frontier. Columbia University Press, New York, NY, USA.

Ashton, P.M.S., Larson, B.C., 1996. Germination and seedling growth of *Quercus* (section Erythrobalanus) across openings in a mixed-deciduous forest of southern New England, USA. For. Ecol. Manage. 80, 81–94.

Ashton, P.M.S., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. J. Trop. Ecol. 11, 263–279.

Askew, G.P., Moffatt, D.J., Montgomery, R.F., Searl, P.L., 1971. Soils and soil moisture as factors influencing the distribution of the vegetation of the Serra do Roncador, Mato Grosso. In: Ferri, M.G. (Ed.), III Simpósio sôbre o Cerrado. Editôra de USP, São Paulo, SP, Brasil, pp. 150–160.

Baima, A.M.V., 2001. O Status de *Swietenia macrophylla* King (Mogno) em duas florestas exploradas no Estado do Pará: O caso de Marabá e Rio Maria. Master of Forest Science Thesis. FCAP, Belém, Pará, Brasil.

Balée, W., Campbell, D.G., 1990. Evidence for the successional status of liana forest (Xingu River Basin, Amazonian Brazil). Biotropica 22, 36–47.

Basnet, K., 1992. Effect of topography on the pattern of trees in tabonuco (*Dacryodes excelsa*) dominated rain forest in Puerto Rico. Biotropica 24, 31–42.

Brokaw, N.V.L., 1982. Treefalls: frequency, timing, and consequences. In: Leigh Jr., E.G., Rand, A.S., Windsor, D.M. (Eds.), The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, DC, USA, pp. 101–108.

Clapperton, C., 1993. Quaternary Geology and Geomorphology of South America. Elsevier, Amsterdam, The Netherlands.

Clark, D.A., Clark, D.B., Sandoval, R.M., Castro, M.V., 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology 76, 2581–2594.

Davis, T.A.W., Richards, P.W., 1934. The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest. Part II. J. Ecol. 22, 106–155.

Ewel, J.J., 1963. Height growth of bigleaf mahogany. Caribbean For. 24, 34–35.

Gartlan, J.S., Newbery, D.M., Thomas, D.W., Waterman, P.G., 1986. The influence of topography and soil phosphorous on the vegetation of Korup Forest Reserve, Cameroon. Vegetatio 65, 131–148.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Part I. Physical and Mineralogical Methods. Agronomy Monograph No. 9, 2nd ed. American Society of Agronomy/Soil Science Society of America, Madison, WI, USA, pp. 383–411.

Grogan, J.E., 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. Thesis. Yale University, New Haven, CT, USA.

Grogan, J., Barreto, P., Veríssimo, A., 2002. Mahogany in the Brazilian Amazon: Ecology and Perspectives on Management. Imazon, Belém, Pará, Brasil. http://www.imazon.org.br (pdf version).

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

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

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

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

Gullison, R.E., Vriesendorp, C., Lobo, A., 2003. Effects of large-scale flooding on regeneration of big-leaf mahogany in the Bolivian Amazon. In: Lugo, A., Figueroa Colón, J.C., Alayón, M. (Eds.), Big-leaf Mahogany: Genetics, Ecology, and Management. Springer, New York, NY, USA, pp. 209–236.

Hall, J.S., Ashton, P.M.S., Berlyn, G.P., 2003. Seedling performance of four sympatric *Entandrophragma* species (Meliaceae) under simulated fertility and moisture regimes of a central African rain forest. J. Trop. Ecol. 19, 55–66.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London, UK.

Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

Hubbell, S.P., Foster, R.B., 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper & Row, New York, NY, USA, pp. 314–329.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Klute, A., 1986. Water retention: laboratory methods. In: Klute, A. (Ed.), Methods of Soil Analysis. Part I. Physical and Mineralogical Methods. Agronomy Monograph No. 9, 2nd ed. American Society of Agronomy/Soil Science Society of America, Madison, WI, USA, pp. 635–662.

Lamb, F.B., 1966. Mahogany of Tropical America: Its Ecology and Management. University of Michigan, Ann Arbor, MI, USA.

Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J. Ecol. 84, 137–152.

Markham, R.H., Babbedge, A.J., 1979. Soil and vegetation catenas on the forest-savanna boundary in Ghana. Biotropica 11, 224–234.

Morison, C.G.T., Hoyle, A.C., Hope-Simpson, J.F., 1948. Tropical soil–vegetation catenas and mosaics: a study in the south-western part of the Anglo-Egyptian Sudan. J. Ecol. 36, 1–84.

Nelson, B.W., 1994. Natural forest disturbance and change in the Brazilian Amazon. Remote Sens. Rev. 10, 105–125.

Nelson, B.W., Kapos, V., Adams, J.B., Oliveira, W.J., Braun, O.P.G., Amaral, I.L., 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. Ecology 75, 853–858.

Nelson, W.L., Mehlich, A., Winters, E., 1953. The development, evaluation, and use of soil tests for phosphorus availability. In: Pierre, W.H., Norman, A.G. (Eds.), Soil and Fertilizer Phosphorus, vol. II, Agronomy, A Series of Monographs. Academic Press, New York, NY, USA, pp. 153–188.

Newbery, D.M., Gartlan, J.S., McKey, D.B., Waterman, P.G., 1986. The influence of drainage and soil phosphorous on the vegetation of Douala-Edea Forest Reserve, Cameroon. Vegetatio 65, 149–162.

Palmiotto, P.A., 1998. The role of specialization in nutrient-use efficiency as a mechanism driving species diversity in a tropical rain forest. Ph.D. Thesis. Yale University, New Haven, CT, USA.

Perkins, H.F., 1970. A rapid method of evaluating the zinc status of Coastal Plain soils. Commun. Soil Sci. Plant Anal. 1, 35–46.

Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon. In: Prance, G.T., Lovejoy, T.E. (Eds.), Key Environments: Amazonia. Pergamon Press, Oxford, UK, pp. 109–145.

Ratter, J.A., Richards, P.W., Argent, G., Gifford, D.R., 1973. Observations on the vegetation of northeastern Mato Grosso. I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. Philos. Trans. Roy. Soc. Lond. Ser. B 266, 449–492.

Ratter, J.A., Askew, G.P., Montgomery, R.F., Gifford, D.R., 1978. Observations on the vegetation of northeastern Mato Grosso. 2. Forest and soils of the Rio Suia-Missu area. Proc. Roy. Soc. Lond. Ser. B 203, 191–208.

Salati, E., Marques, J., 1984. Climatology of the Amazon region. In: Sioli, H. (Ed.), The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River. Dr. W.J. Junk Publishers, Boston, USA, pp. 85–126.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture: Applied Forest Ecology, 9th ed. Wiley, New York, NY, USA.

Snook, L.K., 1993. Stand dynamics of mahogany (*Swietenia macrophylla* King) and associated species after fire and hurricane in the tropical forests of the Yucatan Peninsula, Mexico. Ph.D. Thesis. Yale University, New Haven, CT, USA.

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.

Snook, L.K., 2003. Regeneration, growth, and sustainability of mahogany in México's Yucatán forests. In: Lugo, A., Figueroa

Colón, J.C., Alayón, M. (Eds.), Big-leaf Mahogany: Genetics, Ecology, and Management. Springer, New York, NY, USA, pp. 169–192.

Sombroek, W.G., Sampaio, J.B., 1962. Reconnaissance soil survey of the Araguaia mahogany area. FAO, Comissão de Solos, Belém, Pará, Brasil.

Svenning, J.-C., 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. J. Ecol. 87, 55–65.

Terborgh, J., Flores, C., Mueller, P., Davenport, L., 1997. Estimating the ages of successional stands of tropical trees from growth increments. J. Trop. Ecol. 14, 833–856.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ, USA.

Veríssimo, A., Barreto, P., Tarifa, R., Uhl, C., 1995. Extraction of a high-value natural resource in Amazonia: the case of mahogany. For. Ecol. Manage. 72, 39–60.

Vogt, D.J., Tilley, J.P., 1998. Laboratory Procedures for Soil and Plant Analysis (manual). Yale University School of Forestry and Environmental Studies, New Haven, CT, USA.

Weaver, P.L., Bauer, J., 1986. Growth, survival and shoot borer damage in mahogany plantings in the Luquillo Forest of Puerto Rico. Turrialba 36, 509–522.

Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy, D., Goodwin-Bailey, C.I., Gong, W.K., 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. J. Trop. Ecol. 9, 131–151.