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Experimental establishment of big-leaf mahogany (*Swietenia macrophylla* King) seedlings on two soil types in native forest of Pará, Brazil

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Abstract

Research into the mechanisms underlying edaphic associations reported for many tropical forest tree species, including those in the Meliaceae, has paid little attention to the earliest post-dispersal life stages. We conducted a reciprocal sowing experiment to examine germination and establishment rates of big-leaf mahogany (*Swietenia macrophylla* King) during the first seedling growing season in two local edaphic habitats in southeastern Amazonia. In this region, adult populations are restricted primarily to low-ground soils associated with seasonal streams, but rarely are found on high-ground soils. Soil analyses revealed that low-ground soils at the study site were silty loams whereas high-ground soils were clays. High-ground soils were less acidic and more fertile than low-ground soils, especially with respect to total nitrogen, Mg, and sum of basic cations.

In October 2003, at 30 locations evenly split between the two soil types, we added 40 seeds to paired canopy gap and closed understory plots on low- and high-ground soils. Two months after sowing, no significant differences between the two soil types were found for the proportion of seeds: (1) ungerminated yet viable, (2) still germinating, (3) already established, or (4) surviving (variables 1, 2, and 3 combined). Nearly twice as many seedlings had established in the understory (43%) than in canopy gaps (24%), and overall survival was lower in canopy gaps than in the understory (46% vs. 58%, respectively). Seven months after sowing, survival was similar between gaps and understory; however, seedling recruitment on high-ground soils was nearly twice that on low-ground soils (38% vs. 20%, respectively; $P = 0.006$). Localised flooding in low-ground plots drowned seedlings at four locations (16 plots). Difference in seedling performance between soil types weakened when these flooded plots were discarded (corresponding recruitment was 38% vs. 27%, $P = 0.083$). On average, seedlings showed small differences in leaf damage, leaf numbers, and foliar conditions between edaphic habitats. As expected, seedlings had more leaves and greater between-census survival rates in canopy gaps compared to understory conditions. Collectively, we found little evidence of enhanced early post-dispersal performance on mahogany's preferred soil type in the region. Any ecological processes driving mahogany's association with low-ground forest soils presumably emerge beyond the first growing season.

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1. Introduction

Forest managers require a sound knowledge of the factors governing adult distributions of high-value Meliaceae timber species. Many tropical tree species are aggregated at local spatial scales (Condit et al., 2000), often in association with particular edaphic conditions (Davies et al., 1998; Clark et al., 1999; Webb and Peart, 2000; Thomas, 2003). Despite their frequency, the underlying mechanisms responsible for these aggregation patterns are not fully understood (Palmiotto et al., 2004; Baltzer et al., 2005). Such predictable, spatially biased distributions suggest that habitat differentiation might play an important role in promoting species co-existence in diverse tropical communities (Condit, 2003; Thomas, 2003). This may be especially the case for Meliaceae species consistently found on particular soil conditions or types across a substantial portion of their natural ranges (Lamb, 1966; Grogan et al., 2003; Hall et al., 2004).

A prime example is big-leaf mahogany (*Swietenia macrophylla* King). In the transitional forests of southeastern Amazonia, adult populations occur primarily on low-ground

hydromorphic soils associated with seasonal streams (Pires and Prance, 1985; Grogan et al., 2002, 2003). The idea that mahogany may respond directly to soil properties, and that soil distribution patterns possibly shape adult distributions at intermediate spatial scales (1–100 km^2), is not new. Evidence dating back to 1945 indicates that mahogany's growth rates are influenced by fertility and/or soil drainage (Lamb, 1966; references cited in Grogan et al., 2003). At the Marajoara forest in southeastern Pará, Brazil, where mahogany adults are rarely found in high-ground forests characterised by tall canopies and dystrophic soils (sandy to sandy clay and yellowish-brown), soil nutrient deficiencies (Ca and Mg) at high- compared to low-ground sites caused reduced seedling growth rates in canopy gaps (Grogan et al., 2003).

Our study site in southeastern Pará (Pinkaití) is home to a natural population of big-leaf mahogany, where since 2000 we have conducted research focused primarily on mahogany seed and seedling dynamics. Despite the proximity to Marajoara (ca. 180 km distant), Pinkaití harbours a different edaphic environment. Soil distribution patterns trace a gentle topography, much like at Marajoara, with stark visible soil transitions occurring over short distances of <1 km and across slight relief (<10 m). Here, however, red to dark red high-ground forest soils grade abruptly into yellow to yellow-grayish hydromorphic low-ground soils approaching seasonal streams. Changes in forest structure are similar to Marajoara, if not more pronounced. The abrupt soil zonation at Pinkaití, and the fact that very few mahogany adults are found on high-ground soils, prompted us to ask, why is mahogany excluded from high-ground forest soils?

Mahogany's edaphic association in Pará is a region-wide phenomenon. Hence, it is likely not driven by seed limitation, that is, the failure of enough seeds to reach suitable sites for seedling recruitment (Nathan and Muller-Landau, 2000). Instead, the association may reflect niche differentiation, which has long been hypothesized to promote species-coexistence in diverse communities (Grubb, 1977). Under this scenario, habitat-based performance differences drive ecological sorting among tree species following dispersal, whereby species gradually and eventually occupy those particular habitats where they are competitively superior, and in turn, are eliminated from sub-optimal habitats for regeneration (Ackerly, 2003). Hall et al. (2004) argued that relatively subtle variation in soil chemical properties across intermediate spatial scales in Central African forests can influence tree growth and distributions of co-occurring *Entandrophragma* spp. (Meliaceae). If this is the case for *S. macrophylla*, performance differences should emerge between mahogany individuals colonizing the different soil types at our site (Hall et al., 2004; Palmiotto et al., 2004; Russo et al., 2005).

However, an additional question is relevant: at what life history stage(s) do these performance differences predominate? Grogan et al. (2003) observed seedling growth in gaps and the forest understory in both soil habitats at their site. Different soil types may also affect earlier developmental stages such as post-dispersal mortality or seedling establishment. Ultimately,

rigorous tests of the mechanisms driving apparent edaphic specialisations must consider the possibility of differences in growth and survival rates at more than one life history stage, ideally through reciprocal transplant experiments such as Grogan et al. (2003) under natural field conditions (Webb and Peart, 2000).

Noticeably absent from the literature for both *S. macrophylla* and other high-value Meliaceae are reciprocal seed addition experiments conducted in different edaphic habitats. Differences in seed germination and seedling establishment rates may be directly influenced by the soils themselves (Kozlowski, 2002) and environmental factors associated with them. Seed and seedling predation may also vary along environmental gradients (Louda, 1989) and can play a role in promoting habitat specialisation across edaphic zones (Fine et al., 2004). For example, interactions between natural enemies and soil types can arise through either habitat-mediated differences in predator pressure or, in the case of herbivores, phenotypic variation in plant defenses and tolerance to damage driven by resource inequalities between soil habitats (Coley et al., 1985; Boege and Dirzo, 2005).

Better knowledge of seed and seedling ecology has important practical implications for post-logging regeneration treatments of high-value tree species (Guariguata, 2000; Makana and Thomas, 2005). However, tropical forestry has largely neglected the seed and seedling ecology of timber tree species, and mahogany is no exception (Hall, 1996). In this respect, understanding how regional-level variation in soil properties translates into patterns of growth and recruitment is fundamental for management in any context. If forest management is to include natural regeneration, establishing mahogany on inferior soil types is undesirable because it will likely require efforts targeted specifically at the mechanism(s) impeding recruitment associated with sub-optimal soil types. Conversely, such exclusionary mechanisms may be circumvented through silvicultural intervention once elucidated.

In this study, we use the reciprocal framework to examine soil type-specific post-dispersal seed survival and seedling establishment, which are widely considered to be the life stages most vulnerable to mortality in trees (Harper, 1977). First we asked, do the soil types (and their attributes) at Pinkaití mirror those reported by Grogan et al. (2003) elsewhere in southeastern Pará? Secondly, are there performance differences by seeds and seedlings on the two soil types through the first growing season? Specifically, we test the hypothesis that mahogany's concentrated distribution on low-ground soils at the study site is caused by higher germination or seedling establishment and recruitment rates compared to high-ground soils. In addition, we conducted the reciprocal experiment in two light microhabitats (understory vs. canopy gaps) at both the low- and high-ground sites and quantified percent leaf damage and foliar condition of seedling recruits to examine possible habitat-mediated differences in herbivory. Because natural enemies may reduce establishment near adult mahogany trees (Norghauer et al., 2006a), we intentionally positioned our seed plots far from adult seed shadows.

2. Study species

Big-leaf mahogany is a long-lived, fast-growing, deciduous canopy emergent that can attain heights of up to 70 m and diameters of 3.5 m (Lamb, 1966). It is recognised as a non-pioneer, light-demanding tree species (Grogan et al., 2002). Its distribution in the Pinkaití reserve, similar to elsewhere in southern Pará, is concentrated near seasonal streams on low-ground hydromorphic soils that are yellow-greyish in colour (hereafter, 'low-ground soils'; Grogan et al., 2003). Within a mapped core area of c. 600 ha in the reserve, less than 2% of mahogany trees ≥30 cm diameter were found in high-ground forests distinguished by dark reddish soils (hereafter, 'high-ground soils'). Mahogany's winged seeds are dispersed by wind in the dry season (June–August) and form a predictable seed shadow: approximately 50% of all seeds fall within 30 m of the parent (and up to 75% within 50 m) mostly to the west and northwest of parent crowns, the direction in which long distance dispersal events (>60 m) are restricted (Grogan and Galvão, 2006; Norghauer, unpublished data). These winged seeds are copper-coloured and relatively large, 5–13 cm in length. They are highly tolerant of desiccation and lie dormant until the onset of wet season rains triggers germination. Under suitable growing conditions, new mahogany seedlings typically set a tap-root that can range in depth from 9.9 to 21.0 cm ($N = 18$ seedlings) that is positively correlated with seed mass (Norghauer, unpublished data). In this region of Pará, mahogany is preyed upon by a nocturnal specialist moth, *Steniscadia poliophaea* Hampson (Noctuidae: Sarrothripinae), whose caterpillars attack meristematic stem and leaf tissues of newly germinated seedlings (Grogan, 2001; Grogan et al., 2003; Grogan and Galvão, 2006).

3. Methods

3.1. Study site

The field experiment was carried out at the Kayapó Centre for Ecological Studies (Pinkaití), a biological research station and forest reserve located in the Kayapó Indigenous Area (KIA) in the state of Pará, Brazil ($7°46'14''$S; $51°57'43''$W). The KIA is situated in a transitional zone at the southeastern limits of the Amazon Basin where closed evergreen forests grade into *cerrado* (savannah) vegetation. The reserve consists of c. 8000 ha of mostly lowland tropical forest surrounded by a large area of continuous forest, most portions of which were selectively logged for mahogany during 1989–2001. Elevation is 200–450 m above sea level (Salm, 2004). Annual rainfall in this region ranges from 1600–2100 mm; a severe 3–4 months dry season prevails from late May to early September when monthly rainfall is <50 mm and >100 rainless days may occur (Zimmerman et al., 2001; Grogan et al., 2003). Forest in the region is a mosaic of different vegetation types, including areas of vine forest and mixed palm forest (Pires and Prance, 1985). Brazilnut trees, *Bertholletia excelsa* (Lecythidaceae) and *Cenostigma tocantium* (Caesalpinoideae) are relatively common on high-ground soils (Salm, 2004), whereas mahogany is

relatively common on low-ground soils in riparian areas. The density of mahogany trees >20 cm diameter in high-ground forests is <0.05 ha^{-1}, whereas in low-ground forests mahogany density ranges from 0 up to 7 trees ha^{-1}. Topographic relief is slight between high- and low-ground forests, ranging <10 m between sites selected for this experiment.

3.2. Soil sampling and analyses

We collected soil samples at 0–10, 10–30, and 30–60 cm depths at four augered holes spaced 20 m apart in a square at four sites in each of the two soil types. Sampling locations were parallel to a major seasonal stream and spaced c. 350 m apart. Soil samples were air dried and then thoroughly mixed at the site level to generate 24 composite samples for chemical analyses. Due to limited funds, textural analyses were restricted to the 10–30 cm depth only; this choice was made because at the time of experiment establishment we intended to follow seedlings into the second growing season, at which time roots would presumably have reached this depth or deeper. To generate water retention curves for each soil type, an aluminium core ring was used to laterally penetrate the soil profile close to each augered hole at a depth of 10–15 cm. Upon removal, these rings were sealed in plastic wrap and stored in plastic bags to prevent moisture loss. The composite soil samples and intact soil core rings were later analysed at the Centro de Solos e Recursos Ambientais of the Instituto Agronomico in Campinas, SP, Brazil.

Textural analyses of eight composite samples were conducted following de Camargo et al. (1986); chemical analyses of 24 composite samples (three depth ranges) followed van Raij et al. (2001). Specifically, pH was determined in CaCl$_2$ solution (0.01 mol L^{-1}) using a soil–solution ratio of 1:25. Soil organic matter (OM) content was estimated using a modification of the Walkley–Black procedure that involved oxidation of organic C with dichromate in an acidic medium; a spectrometric procedure was used to determine Cr(III). The results presented here for organic C were obtained by dividing OM by 1.72. Total nitrogen content was determined using the Kjeldahl method, digesting the soil sample in sulphuric acid using K$_2$SO$_4$, CuSO$_4$, and Se. The resulting clear digest solution was distilled with NaOH and titrated with H$_2$SO$_4$ (standardised). Although total N does not represent nitrogen immediately available for plant uptake, this measure does provide a reliable indication of the size of the available and potentially mineralizable nitrogen pool in the soil. Extractable P was equivalent to ion exchange resin extracted P (van Raij et al., 1986). Similarly, exchangeable Ca, Mg, and K were extracted with ion exchange resins detailed in van Raij et al. (1986). The cation exchange capacity (CEC) was the sum of Ca, Mg, K, and H + Al; Na was not included because it is negligible in Brazilian soils (Cantarella, personal communication). Apart from total N and pH, chemical properties of soils were expressed in volumetric units (mmolc/dm^3) because these better represent nutrient availability in the root zone compared to g kg^{-1} units; under natural conditions, plant roots obtain nutrients from a volume of soil regardless of the soil's weight

per unit volume. Soil matric potentials were generated for 10–15 cm depth from two of four core ring samples collected at each site using a pressure plate membrane apparatus.

To facilitate better comparison with soil results reported in Grogan et al. (2003), we converted volumetric measures of nutrient availability to measures based on the dry weight of oven-dried soils (cmolc kg^{-1}). We divided observed values by the mean bulk densities obtained for sampling locations from the core rings collected for water retention analyses. The results of statistical tests comparing soil nutrients between soil types at given depths were identical to those obtained from volumetric units.

3.3. Experimental design for seed additions

We used a replicated, randomized block design to examine the main and interactive effects of soil type and canopy cover (microhabitat). The unit of replication was a 2 m × 2 m plot. We placed 10 seeds in each 1 m × 1 m quadrat in the plot for a total of 40 seeds per plot. This density approximated high levels of seed deposition observed at the base of large fecund adult trees and where seed shadows overlapped between adults. We avoided placing plots under large palms due to possible mortality from falling leaves, and plots were not weeded during this short-term study. Collected seeds were stored in cardboard boxes and kept dry at our base camp from August 2003 to time of seed additions (∼3 months). This storage period was equivalent to the interval between dry season dispersal and early wet season germination in the forest, and should not have affected germinability or rates.

Each block consisted of two plots, one in the centre of a recently formed canopy gap and another in closed-canopy forest, established 40–60 m from the gap edge on a random compass bearing. The final position of understory plots was adjusted to be at least 20 m from the edge of any other recent canopy gap as defined by Brokaw (1982). All gaps used in this study were naturally formed and ranged in size from 25 to 400 m^2. In order to emulate dispersal under natural conditions encountered between edaphic habitats, the gaps were not manipulated in any way (i.e., there was no clearing or weeding of vegetation). We established 30 such blocks, split equally between the two soil types. All 30 gap locations were at least 125 m apart and mean (± 1S.E.) nearest neighbour distance was 233 ± 17.9 m. All gap and understory locations were ≥45 m from adult mahogany trees. Seeds were added in the early wet season (first 2 weeks of October 2003) and plots were revisited in mid-December 2003 (2 months post-seed addition) and again at the end of the wet season in mid-May 2004 (7 months post-seed addition).

At the December census, we counted the number of seeds that were ungerminated yet viable (defined by no visible radicle emergence and a firm seed hull), still in the process of germinating, or already established (defined as first 3–4 leaves fully expanded and darkened). We were unable to revisit one block in the low-ground soil type; hence, the total number of seeds from plots assessed at this time was 2320 and not 2400. At the May census, we counted the number of established

seedlings and the number of leaf nodes and extant leaves and/or leaflets for each, considering leaf/leaflet number the best measure of plant size and vigour during this first growing season (Bunker and Carson, 2005).

For each extant leaf, we quantified leaf damage by measuring the total percentage of missing or obscured photosynthetic leaf area (visually estimated to the nearest 5%, with 1% assigned to leaves with ≤1% herbivory). All herbivory measurements were made by one observer (JMN). Visual estimates of percent damage were close to the actual damage measured with a transparent plastic grid (linear regression, $P < 0.0001$, $r^2 = 0.95$, $N = 45$ leaves). We included damage caused by insects and by leaf fungal pathogens, as well as areas colonized by epiphylls because these are known to reduce leaf photosynthetic capacity, which may be critical in the light-limited understory (Coley and Kursar, 1996). Following Blundell and Peart (1998), we also employed mean percent tissue retention over all nodes as a measure of foliar condition because absent leaves on seedlings may indicate cryptic herbivore effects.

3.4. Data analyses

We used analyses of variance (PROC MIXED in SAS v.8.2, Cary, NC, USA) to examine the interactive effects of soil type and microhabitat. Because we selected a subset of existing gaps, the block term was nested within soil type and designated as a random factor, whereas soil type, microhabitat, and their interaction term were designated as fixed factors (Littell et al., 1996). Performance at 2 months (December) was assessed using the following four variables: (1) proportion of seeds ungerminated yet viable, (2) proportion of seeds germinating, (3) proportion of seeds established, and (4) proportion seeds surviving (i.e., sum of 1–3). We included the latter variable to account for pre-germination seed losses that may have occurred owing to insects, pathogens, and/or rodents (Gullison et al., 1996; Grogan and Galvão, 2006; Norghauer et al., 2006a). Performance at 7 months (May) was based on the proportion of seeds surviving to seedling stage (hereafter, 'seedling recruitment') and proportion of seeds alive at 2 months that survived to 7 months (hereafter, 'seedling survival rate'), plus three foliage-related variables: number of leaves, percent herbivory, and foliar condition of extant seedlings. All variables were arcsine transformed except the foliage-related variables, which were log-transformed, to satisfy assumptions of normality and equal variance as confirmed by a visual examination of model residuals.

4. Results

4.1. Soil properties

On average, high-ground soils had almost twice as much clay but only half the silt content of low-ground soils (Table 1). Low-ground soils were finer textured silty loams, whereas high-ground soils ranged from clay to clay loam among the four locations (Brady and Wiel, 1996). High-ground soils displayed

Table 1

Texture analysis of high-ground and low-ground soil types found at the Pinkaití forest reserve, Pará, Brazil[a]

High-ground soils				Low-ground soils			
Sand (%)	Silt (%)	Clay (%)	Munsell colour designation	Sand (%)	Silt (%)	Clay (%)	Munsell colour designation
15	35	50	Dusky red	15	63	23	White-pale yellow
16	31	53	Dark red	18	55	28	Yellow
36	29	35	Dark red	19	59	23	White-light grey
28	32	40	Red	26	50	24	Yellow
24 (9.8)a	32 (2.3)b	44 (8.3)a		19 (4.8)a	56 (5.5)a	24 (2.4)b	

[a] Values given are for the eight sampling locations followed by their means in the bottom row with 1S.E. in parentheses. Different lower-case letters indicate significant differences in sand, silt and clay contents at equivalent depths between the two soil types (a > b) and were tested using the Wilcoxon–Kruskal–Wallis test ($\alpha = 0.05$).

greater variability in sand and clay content than low-ground soils, but in both soil types sand content was lowest among the three principle soil components. High-ground soils were dark red to red; low-ground soils were yellow to white-light grey.

The striking inversion in silt and clay contents between the two soil types likely influenced many of their respective chemical properties (Brady and Wiel, 1996). High-ground forest soils were slightly less acidic but more fertile than low-ground soils, especially in terms of organic C, total N, available Mg concentrations, and sum of base cations (Table 2). Levels of extractable P and K were similar between soil types, and, although not statistically significant at $\alpha = 0.05$, Ca concentrations on high ground soils exceeded that on low-ground soils, particularly in the seedling rooting zone (0–10 and 10–30 cm depths, $P = 0.081$ and 0.083, respectively, Kruskal–Wallis tests). Despite the textural differences between soil types, they had virtually identical water retention curves. At the wilting point (-1500 kPa), low-ground soils held slightly more water than high-ground soils (means $\pm$ 1S.E., $n = 4$: low-ground, 0.197 ± 0.008 H$_2$O m^3 m^{-3}; high-ground, 0.185 ± 0.019 H$_2$O m^3 m^{-3}).

Table 2

Mean chemical properties ($\pm$ 1S.E.) of high- and low-ground soil types at the Pinkaití forest reserve, Pará, Brazil ($n = 4$ per topographic position)

Sample depth (cm)	pH (CaCl$_2$)		Ca (mmolc/dm^3)	
	High-ground	Low-ground	High-ground	Low-ground
0–10	4.78 (0.28)a	4.25 (0.064)a	24.00 (8.54)a	11.50 (1.32)a
10–30	4.63 (0.23)a	4.10 (0.000)b	12.75 (4.01)a	5.75 (0.25)a
30–60	4.63 (0.20)a	4.13 (0.088)b	8.25 (2.39)a	6.00 (1.53)a
	Total N (g kg^{-1})		K (mmolc/dm^3)	
	High-ground	Low-ground	High-ground	Low-ground
0–10	1.87 (0.21)a	1.59 (0.092)a	1.30 (0.31)a	1.63 (0.32)a
10–30	1.19 (0.087)a	0.67 (0.064)b	1.08 (0.38)a	1.08 (0.11)a
30–60	0.62 (0.037)a	0.33 (0.11)b	0.68 (0.28)a	1.20 (0.21)a
	Organic C (g/dm^3)		Sum basic cations (mmolc/dm^3)	
	High-ground	Low-ground	High-ground	Low-ground
0–10	17.30 (1.6)a	12.5 (0.99)b	33.80 (9.67)a	15.88 (2.10)b
10–30	10.75 (0.69)a	4.94 (0.69)b	20.58 (5.14)a	8.58 (0.37)b
30–60	5.23 (0.53)a	2.71 (0.69)b	15.18 (3.16)a	9.20 (2.15)a
	P (mg/dm^3)		CEC (mmolc/dm^3)	
	High-ground	Low-ground	High-ground	Low-ground
0–10	5.00 (0.41)a	5.75 (0.48)a	76.90 (5.56)a	60.77 (2.02)a
10–30	2.25 (0.25)a	1.75 (0.25)a	66.70 (8.80)a	53.48 (2.99)a
30–60	1.25 (0.25)a	1.33 (0.33)a	56.98 (6.77)a	50.40 (1.98)a
	Mg (mmolc/dm^3)		% Base saturation	
	High-ground	Low-ground	High-ground	Low-ground
0–10	8.50 (1.32)a	2.75 (0.478)b	44.00 (10.70)a	26.25 (3.57)a
10–30	6.75 (1.38)a	1.75 (0.250)b	34.25 (10.50)a	16.25 (1.31)a
30–60	6.25 (0.946)a	2.00 (0.577)b	28.50 (7.77)a	18.33 (4.84)a

Significant differences between the two soil types at equivalent depths are indicated by different lower case letters (a > b) and were determined using Wilcoxon–Kruskal–Wallis tests ($\alpha = 0.05$).

4.2. Seed and seedling performance between soil types

At the first (2 months) census, mahogany seed performance on the two soil types appeared indistinguishable and independent of forest canopy cover (gap vs. understory). No significant differences were detected between soil types for all four response variables nor was there any significant interaction between soil type and microhabitat (Fig. 1).
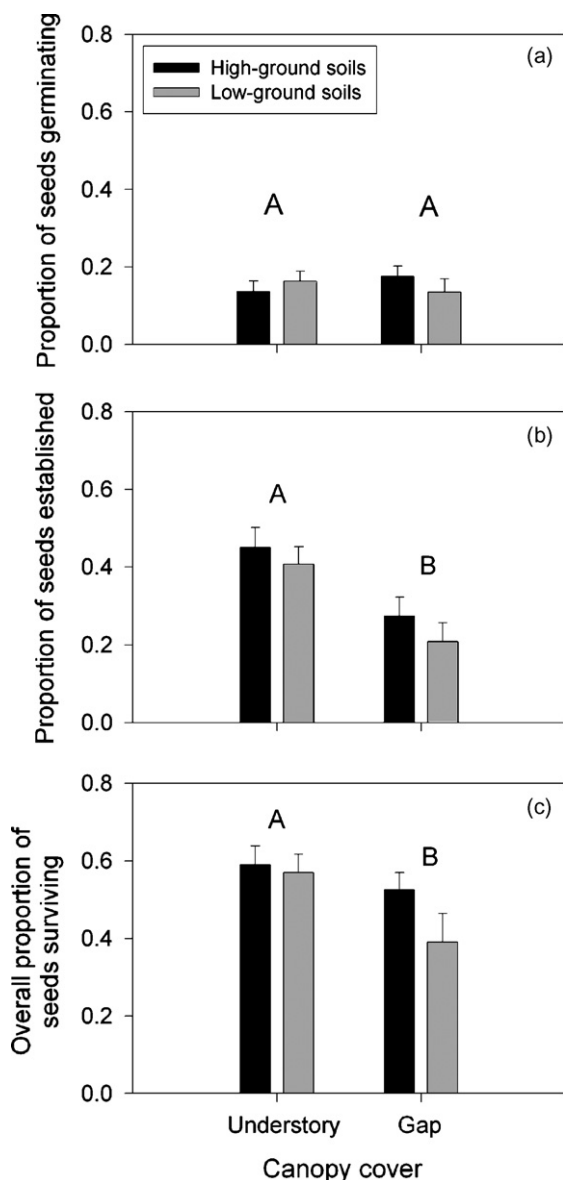

Fig. 1. The effect of soil types and light microhabitats 2 months after seed addition on (a) proportion of sown seeds germinating, (b) proportion of sown seeds established as seedlings, and (c) overall proportion of seeds surviving at the Pinkaití forest reserve, Pará, Brazil. Different upper-case letters indicate a significant main effect of canopy cover between understory vs. canopy gaps (pooled across soil types; A > B at $\alpha = 0.05$). Mixed two-factor ANOVA statistics for microhabitat are: (a) $F_{1,27} = 0.05$, $P = 0.822$; (b) $F_{1,27} = 18.82$, $P = 0.0002$; (c) $F_{1,27} = 5.88$, $P = 0.022$. Neither soil type nor the interaction term was significant for any of the three response variables (soil type, $Fs_{1,27} < 1.65$, $Ps > 0.21$; interaction term, $Fs_{1,27} < 1.52$, $Ps > 0.23$). Bars are means ± 1S.E..
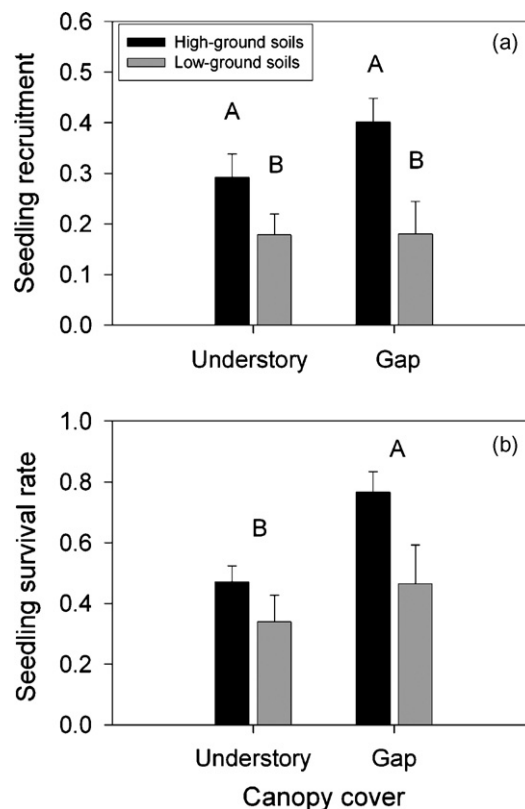

Fig. 2. The effect of soil types and light microhabitats 7 months after seed addition on (a) proportion of sown seeds surviving to seedling stage (seedling recruitment), and (b) proportion of live seeds at the 2-month census that survived to the 7-month census. Different upper-case letters indicate a significant main effect in soil type between high- and low-ground soils (pooled across microhabitat), and canopy cover between understory vs. canopy gaps (pooled across soil types, A > B at $\alpha = 0.05$). Mixed two-factor ANOVA statistics are: (a) soil type: $F_{1,28} = 8.85$, $P = 0.006$; microhabitat: $F_{1,28} = 1.71$, $P = 0.20$; (b) soil type: $F_{1,24.3} = 3.35$, $P = 0.80$; microhabitat: $F_{1,23.9} = 11.57$, $P = 0.0024$. The interaction term was not significant for both response variables ($Fs < 1.53$, $Ps > 0.23$). Bars are means ± 1S.E.

At the second (7 months) census, recruitment patterns had changed. A highly significant effect of soil type emerged: almost twice as many seedling recruits were found on high-ground compared to low-ground soils, and this effect appeared to be independent of microhabitat (Fig. 2). The pronounced edaphic effect was due in part to zero recruitment at four of the blocks on low-ground soils (i.e., eight plots), which, judging by the heavily rusted wire stake flags, were submerged for prolonged periods under standing water that presumably killed any established seedlings between censuses. When these flooded plots were excluded from the analysis, the positive effect of the high-ground soil type on seedling recruitment weakened ($P = 0.083$) and the seedling survival rate became virtually indistinguishable between soil types. Seedlings growing in both soil types had similar numbers of leaves, leaf damage, and foliar condition (Fig. 3).

4.3. Seed and seedling performance between microhabitats

In contrast to soil type, canopy cover had a strong and statistically significant effect on seed and seedling performance
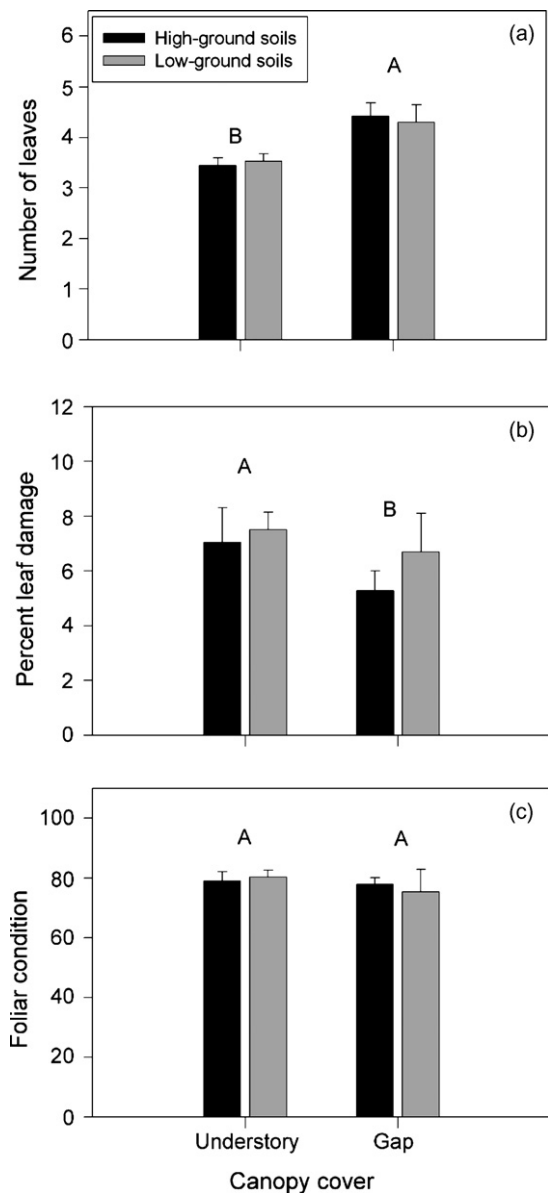
Fig. 3. The effect of soil types and light microhabitats 7 months after seed addition on (a) number of extant leaves, (b) percent leaf damage, and (c) foliar condition of seedling recruits. Different upper-case letters indicate a significant main effect of canopy cover between understory vs. canopy gaps (pooled across soil types; A > B at $\alpha = 0.05$). Mixed two-factor ANOVA statistics for microhabitat are: (a) $F_{1,45} = 9.41$, $P = 0.0036$; (b) $F_{1,28.1} = 1.55$, $P = 0.23$; (c) $F_{1,24.5} = 1.10$, $P = 0.31$. Neither the soil type main effect nor interaction was significant for any of the three response variables (soil type, $0.00 < Fs < 1.63$; $0.21 < Ps < 0.98$; interaction term, $Fs_{1,27} < 0.36$, $Ps > 0.93$). Bars are means ± 1 S.E.

at both censuses. Two months after outplanting, between 50% and 80% more seedlings were established in understory plots compared to canopy gaps (Fig. 1). Although the proportion of seeds still germinating was significantly higher in the understory than in canopy gaps, more ungerminated seeds were encountered in gaps than in the understory (main effect, ANOVA, $F_{1,54} = 22.35$, $P < 0.0001$) and a lower proportion of seeds were alive in some form or another in canopy gaps (Fig. 1). However, at the second census, the proportion of

seedling recruits was similar between the two microhabitats, and, as expected given relatively higher light availability in gaps, the seedling survival rate was higher in canopy gaps than in understory plots whether flooded plots were excluded or not (Fig. 2).

Seedling recruits in gaps had significantly more leaves than in the shaded understory, but mean percent leaf damage was low (<8%) and foliar condition was high in both microhabitats (Fig. 3). Pooled across all experimental plots, seed establishment at the first census was 34%, while survival was 52% (or 779 and 1207 seeds, respectively, out of 2320). Based on visual identification of larval activity, attacks by the specialist mahogany herbivore, *S. poliophaea*, were rare, with only four seedlings damaged (100% defoliation in each case). The proportion of seeds surviving to the seedling stage at the second census was 26% (or 631 out of 2400 seeds) and increased to 30% when flooding plots were excluded (631 out of 2080 seeds).

5. Discussion

5.1. Soil properties and adult distribution of mahogany

Contrary to expectations, high-ground soils at Pinkaití were not nutrient impoverished, but rather clay-rich and slightly more fertile than low-ground soils. These patterns contrast with those described by Grogan et al. (2003) at Marajoara, 180 km east of Pinkaití, a site where high-ground soils were coarser in surface horizons and less fertile than low-ground soils, especially in terms of available Mg and Ca. At comparable depths (0–30 cm), in contrast to the pattern at Pinkaití, clay was a minor component (3–17%) while sand formed the major component (74–89%; Grogan, 2001, p. 96) at Marajoara. However, our converted estimates of Mg on low-ground soils, expressed by weight instead of volume (i.e., cmolc kg^{-1}), are within the range of Mg for low-ground soils at Marajoara. The fact that mahogany is essentially restricted to low-ground habitats at both sites, despite contrasting soil conditions, suggests that nutrients are not the major driver of adult distributions—at least not beyond some minimum threshold. Grogan et al. (2003) concluded that poor adult recruitment arose in part from nutrient deficiencies in Mg and Ca of high-ground soils compared to low-ground soils. Our data cast doubt on the generality of this hypothesis; it appears that some other mechanism(s) is driving the edaphic association for this species at Pinkaití.

Despite pronounced differences in soil properties between topographic positions at Pinkaití, we found little evidence to support the hypothesis that mahogany's soil association reflects enhanced post-dispersal performance through the first growing season on low- versus high-ground soils. In fact, recruitment by the end of the first growing season was slightly better on average at high-ground compared to low-ground sites, even when mortality associated with plot flooding was excluded. If anything, mahogany appeared to suffer a slight home-soil performance disadvantage in early post-dispersal phases.

Such a disadvantage on its 'preferred' low-ground habitat can arise in at least two ways: (1) if episodes of flooding wipe out newly germinated seedlings before the end of the first growing season, and (2) if natural enemies such as seed and seedling predators are density-responsive, or are simply more prevalent in low-ground than in high-ground forest.

Regarding the first possibility, the four flooded blocks were all relatively close to one another, suggesting that flooding is a highly localised phenomenon at Pinkaití. Such localised disturbances likely occur on very poorly drained soils and, based on limited experience at this site (dating from 2000), floods appear to occur at 4–5-year intervals when heavy rainfalls follow each other in close succession. The detrimental effects of flooding are presumably ontogenetically dependent, because it is known that adult mahogany groves can occur in swamps (Lamb, 1966). Small seedlings may succumb to inundation; however, once tall enough, they may gain a competitive advantage if standing waters eliminate shorter, heterospecific seedlings as well. Established mahogany seedlings have been shown to be favoured by episodic flooding in Bolivia, thereby enhancing the regeneration prospects of mahogany saplings (Gullison et al., 2003).

Regarding the second possibility, our experimental design was largely successful at excluding a key mahogany herbivore (*S. poliophaea*), enabling us to better isolate edaphic influences. This escape from predation, despite plot densities similar to those found <15 m from parent trees, was not surprising given that all plots were situated ≥45 m from the nearest adult and the fact that *S. poliophaea* predation is focused close to adults (Norghauer et al., 2006a). Although not quantified in this study, heavy predation by rodents seemed more common at low-ground (four gap plots with 100% predation) than high-ground soil locations (one gap plot moderately predated) and helped reduce the number of recruits. Because the forest on low-ground soils tends to have a lower canopy, indicating more frequent disturbance than at high-ground sites (Grogan et al., 2003), rodents that occasionally eat mahogany seeds may be on average more abundant there than in less-disturbed high-ground forest (Malcolm, 1995).

Our findings suggest that any ecological processes shaping mahogany's association with low-ground soils occur beyond the first growing season after seedlings are well established. This result is consistent with Webb and Peart (2000), who found fewer significant associations with soil types for seedlings versus adults for 45 abundant tree species in Borneo, suggesting that relatively high mortality between the seedling and adult stage occurs in 'suboptimal' habitats. Russo et al. (2005), also working in Borneo, studied growth rates and mortality of trees ≥1 cm diameter and found that species disappeared from the less-used soil type in successive diameter size classes faster than by chance alone. However, in a Mexican tropical dry forest, the occurrence of wild seedlings and saplings was explained more by soil properties than by canopy gaps, suggesting that soil-related specialisation occurred as early as the seedling stage (Vargas-Rodriguez et al., 2005). Hence, we cannot preclude the possibility beyond the first growing season; juveniles could exhibit performance differences associated with differences in soil properties at greater rooting depths (30–60 cm, see Table 2). For example, mahogany, which occurs on what appears to be a less favourable soil type, may be excluded from the better, high-ground soil by competition, especially below-ground (Goldberg, 1985).

In this short-term experiment, we did not follow seedlings through the second growing season, leaving open the possibility that differences in seedling drought tolerance might emerge at a later time (Bunker and Carson, 2005). If high-ground soils secure water more tightly against plant uptake than low-ground soils, then seedlings growing there might be more susceptible to dry season mortality. However, our results suggest that water availability to seedling roots up to the wilting point (-1500 kPa) is similar between high- and low-ground soils. While this hypothesis remains to be tested, we anticipate negligible differences in drought tolerance between the two soil types (all else being equal). Seasonal variation in water table height across topography is likely despite the slight relief at Pinkaití (Grogan et al., 2003); if low-ground soils retain water longer into the dry-season because of a persistent higher water table, more water could be available to mahogany juveniles.

In a similar vein, another 'species-coexistence avenue' involves changes in ambient light levels across particular soil conditions, which often vary with topography (Condit, 2003). We found some evidence that canopy gap disturbance regimes differ between high- and low-ground sites at Pinkaití: at 5 of the 15 blocks on low-ground soils, a new treefall gap had formed within 10–25 m of an understory plot, whereas none had formed at any of the forest blocks on high-ground soils (Fisher's exact test, $P = 0.04$). In this case, richer high-ground soils may be poorer in light availability, perhaps below some threshold required by mahogany juveniles to reach the canopy and attain maturity. Conversely, while low-ground soils may be nutrient poor, forests sustained on these soils may yield higher rates of canopy disturbance and ambient light transmission, a factor which might be crucial for mahogany and other Meliaceae that are light-demanding (Grogan et al., 2005).

A related avenue is that greater herbivory levels in high-ground forests might drive intraspecific differences in early performance, possibly attributable to either an increase in herbivore pressure or phenotypic differences in plant resistance to attack (Coley et al., 1985; Boege and Dirzo, 2005). This hypothesis was not supported by our results insofar as we found similar foliar conditions in the two edaphic habitats. Thus, if a role for insect herbivores exists in promoting mahogany's edaphic specialisation, as recently demonstrated for other edaphically specialised Amazonian trees (Fine et al., 2004), it must emerge sometime later in the tree's life cycle. In this context, it is worth mentioning that Grogan et al. (2003) evaluated growth responses between their high- and low-ground positions in the absence of herbivory through periodic application of insecticide. A replication of their field experiment, wherein half the outplanted seedlings were protected from and the other half left exposed to *S. poliophaea* as well as the mahogany shootborer, *Hypsipyla grandella*, would certainly shed light on this question.

5.2. Canopy effects on early post-dispersal performance

Enhanced germination rates in the shade offset by enhanced survival and growth under a more open canopy agree with other studies to date (Gullison et al., 1996; Morris et al., 2000; Negreros-Castillo et al., 2003; Grogan et al., 2005; Grogan and Galvão, 2006). Slower germination rates in gaps were likely caused by the repeated drying of seeds caused by higher insolation. Similarly, establishment rates for two other Meliaceae species, *Khaya anthotheca* and *Entandrophragma utile*, were greater in the understory than in canopy gaps (Makana and Thomas, 2005). Following germination, the higher survival rate and larger size attained by seedlings in gaps corroborates the conventional view that mahogany seedlings require high insolation for early survival and vigorous growth, which is presumably critical for reaching the next growing season (Lamb, 1966; Gullison et al., 1996; Grogan and Galvão, 2006).

5.3. Management implications for mahogany

Although we found little evidence of barriers to successful germination and seedling establishment on high-ground soils, the dearth of adults found there means that reliance upon natural seeding alone to expand mahogany's local distribution and increase merchantable stocks will prove inadequate. Enrichment planting and manual seeding could increase advance regeneration densities in these 'unoccupied' forests on high-ground soils, and possibly avoid distance-dependent predators. However, insofar as high-ground forest soils appear 'sub-optimal' for eventual adult recruitment, intensive silvicultural interventions presumably would be required to increase light levels and facilitate adult recruitment. Until we know more about both natural disturbance frequencies and tree growth rates, and about how the performance of juveniles through sapling and pole stages on both soil types are impacted by natural enemies such as *S. poliophaea* and *H. grandella*, management and reforestation efforts should remain focused on regenerating mahogany in its optimal edaphic habitat; that is, low-ground soils near seasonal streams where adult recruitment occurs successfully.

Finally, although these results suggest that mahogany is strongly seed limited, simply increasing seed densities within its preferred habitat on low-ground soils might not necessarily translate into greater adult densities. In this region, mahogany juveniles are attacked by the specialized folivore *S. poliophaea* at the seedling stage (Grogan and Galvão, 2006; Norghauer et al., 2006b) and by the shootborer *H. grandella* at subsequent sapling stages (Grogan et al., 2005). *S. poliophaea* moths are capable of finding vigorously growing mahogany seedlings in gaps >50 m from adults; however, they concentrate attacks upon high-density germinants near adult trees, responding in both distance- and density-responsive ways. Thus, enrichment planting alone may not necessarily produce higher adult densities if attacks by these natural enemies are not mitigated in some way.

Future research should target mechanisms giving rise to performance differences during mahogany's juvenile phases beyond the first growing season (e.g., Grogan et al., 2003). Two fruitful avenues of investigation are soil-related differences in canopy disturbance regimes and associated interactions with natural enemies. A limitation of this study is that we may have missed fine-scale deviations in performance along major gradients both between and within soil types. We recommend that future studies quantify gradients in environmental heterogeneity a priori, especially light availability and soil properties, before adding seeds and/or planting seedlings. This creates a more powerful framework for interpreting and predicting abiotic effects on seedling performance (e.g., Kobe, 1999) and their consequences for adult distributions, which is crucial for successful management of mahogany and possibly other Meliaceae timber species as well.

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