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Survival, growth and reproduction by big-leaf mahogany (*Swietenia macrophylla*) in open clearing vs. forested conditions in Brazil

James Grogan · Mark Schulze · Jurandir Galvão

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Abstract Big-leaf mahogany (*Swietenia macrophylla*) trees are often retained in agricultural fields and pastures for seed and timber production after selective logging and forest clearing in the Brazilian Amazon. At a forest management site in southeast Pará, we censused trees growing scattered across a large open clearing after forest removal and in heavily disturbed forest after selective logging and canopy thinning for survival, stem diameter growth, fruit production, and date of dry season flowering initiation annually during 1997–2003. Trees in the open clearing died at faster rates, grew more slowly, produced fewer fruit, and initiated flowering earlier, on average, than trees in logged and thinned forest during this period. The principal cause of mortality and stem damage in both environments was dry season groundfires. Mahogany trees in logged and thinned forest at the study site grew faster than mahogany trees at a selectively logged but otherwise

J. Grogan (✉)
Yale University School of Forestry & Environmental Studies, 360 Prospect Street, New Haven, CT 06511, USA
e-mail: james.grogan@yale.edu; jgrogan@crocker.com

J. Grogan
Instituto do Homem e Meio Ambiente da Amazônia (IMAZON), Rua Domingos Marreiros, 2020, Bairro Fátima, Belém, PA 66060-160, Brazil

M. Schulze
H.J. Andrews Experimental Forest & Oregon State University, PO Box 300, Blue River, OR 97413, USA
e-mail: mark.schulze@oregonstate.edu

M. Schulze
Instituto Floresta Tropical (IFT), Caixa Postal 13077, Belém, PA 66040-970, Brazil

M. Schulze
School of Forest Resources & Conservation, University of Florida, PO Box 110760, Gainesville, FL 32611, USA
e-mail: mds11@ufl.edu

J. Galvão
Tauari/Capanema, Pará, Brazil

undisturbed closed-canopy forest site in this region during the same period. This was likely due to vine elimination by groundfires, increased crown exposure after canopy thinning, and soil nutrient inputs due to groundfires. Without effective regulation and control of anthropogenic fires, attempts to manage remnant mahogany trees for future timber yields or to restore commercially viable populations in this region may prove futile.

Keywords Agricultural-landscape trees · Crown liberation · Fire-induced mortality · Fruit production · Isolated trees · Shelterwood

Introduction

After tropical forests are logged and cleared for agriculture or pasture establishment, can trees yielding timber or non-timber forest products be usefully retained in open fields for continued production? Across Brazil's southeastern Amazon, extensive forest conversion to agriculture and pasture has occurred since the early 1970s following selective extraction of big-leaf mahogany (*Swietenia macrophylla*, Meliaceae) and secondary timber species (Schmink and Wood 1992; Grogan et al. 2002). We have often observed small-holder agriculturists in this region retain remnant or sub-commercial mahogany trees—those missed by loggers or too small for transport to mill (Veríssimo et al. 1995)—in open fields after forest clearing. Ranchers with large holdings sometimes retain heavily logged forest 'preserves' containing small mahogany trees. Both stakeholders typically refer to these trees as 'capital' for future generations, envisioning substantial financial returns from sawn timber after decades of growth and seed production.

However, in open fields, trees previously growing within a forest's structural matrix suddenly find themselves exposed to full sun, wind, and annual or supra-annual anthropogenic groundfires. Depending on a species' life history and physiology, surviving individuals may accelerate growth rates in response to such radically altered growing conditions (e.g., pioneer species *sensu* Swaine and Whitmore 1988), or growth rates may slow as crowns formed under shaded conditions die back in full sun. Even trees growing in primary forest near the edge of large pastoral or agricultural fields experience accelerated mortality rates during the years following clearing; Laurance et al. (2006) demonstrated this effect reaching up to 100 m into intact forest. Logged forests may also be subject to frequent burns on seasonally dry landscapes (Holdsworth and Uhl 1997; Cochrane et al. 1999; Cochrane and Schulze 1999).

Anyone working or traveling in the Brazilian Amazon has seen isolated Brazilnut trees (*Bertholletia excelsa*, Lecythidaceae) standing sentinel over open pasture and scrubby secondary forest where pastures have been abandoned. Protected by law, these trees are an example of Janzen's (1986) 'living dead', that is, without a reproductive future, because their pollinators, large-bodied euglossine bees, generally do not forage outside of closed primary and secondary forest canopies (Janzen 1971; Mori and Prance 1990; Brosi et al. 2008). The trees are frequently burned and scarred at their bases from recurrent dry season pasture fires, and may be felled by rainy season winds. Yet Brazilnut trees in pastures do produce fruit, albeit at reduced rates compared to forest trees. Do the hazards of open space, including impacts on pollinators, outweigh the benefits of reduced competition for light, growing space, and belowground resources?

Studies comparing performance of trees isolated in pastures with trees in continuous forest have tended to focus on reproductive success and genetic consequences of altered or disrupted pollinator movement. In Honduras, White et al. (1999, 2002) found that small generalist pollinators—bees and butterflies—dramatically expanded their range to transfer pollen between spatially isolated *Swietenia humilis* trees and trees in continuous forest. In their study, rates of seed production increased as disturbance intensity increased (measured by the degree of isolation resulting from forest clearing). In studies of other tropical species, isolated trees have been reported to experience increased flowering rates (White and Boshier 2000; Fuchs et al. 2003; Herrerías-Diego et al. 2006), but decreased outcrossing rates (Aldrich and Hamrick 1998; Fuchs et al. 2003; Hanson et al. 2008) and pollen reception (Rocha and Aguilar 2001). Compared to trees in continuous forest, fruit production by isolated trees may increase (Cascante et al. 2002), demonstrate no difference (Fuchs et al. 2003; Herrerías-Diego et al. 2006), or decline (Rocha and Aguilar 2001). Herrerías-Diego et al. (2006) observed accelerated flowering schedules by trees isolated in pastures, creating a temporal barrier to pollen exchange with forest trees and thus reducing the pool of potential seed parents. To our knowledge, studies comparing growth and mortality rates between trees growing in open clearing vs. forested conditions in the tropics have not been published.

In the early 1990s, new forest management regulations in Brazil required that timber supplies originate from managed forests registered with state and federal governments (Grogan et al. 2005b). In response, several logging companies specializing in mahogany extraction established management projects in southeast Pará (Veríssimo et al. 1995). At one of these sites, the Peracchi Management Project near the small agricultural town of Agua Azul southwest of Marabá, approximately 80% of 1,250 hectares of selectively logged forest had been cleared for mahogany plantation establishment when we first visited the site during the 1995 dry season. Mahogany trees <65 cm diameter had been retained in both open, pasture-like growing conditions and logged closed forest. During the next 2 years, the managing company thinned the remaining forest to promote growth and fruit production by surviving mahogany trees, and seedling establishment in the forest understory. However, plantation establishment in the cleared area stopped in 1996 due to a shortage of seedlings and resources for outplanting. Agricultural and pastoral groundfires originating outside the management area repeatedly swept across the cleared area and burned through the forest understory, killing nearly 100% of outplanted seedlings and encouraging establishment and spread of invasive pasture grasses. In spite of these fires, the remaining forest canopy survived relatively intact.

We returned annually to this site until 2003 to document survival, growth, fruit production, and reproductive phenology by mahogany trees split between open clearing and heavily disturbed forest growing conditions. In this paper we address the following questions: (1) Are sub-commercial mahogany trees fire-resistant in this region, as reported from Mexico and Central America (Snook 1996, 2003)? (2) Does tree performance differ between open clearing and heavily disturbed forest growing conditions? (3) Does tree growth and fruit production in logged and thinned forest differ from performance by trees in selectively logged but otherwise intact forest? We conclude by discussing management implications of these findings for both forest and non-forest managers.

Materials and methods

Study species

Big-leaf mahogany is a canopy emergent species associated with seasonally dry tropical forests from Mexico to Bolivia (Lamb 1966). It is a soil generalist whose local distribution in the Brazilian Amazon commonly traces seasonal streams or rivers. Population densities are typically <1 adult tree ha^{-1} but may be locally higher (Baima 2001; Grogan et al. 2008). Mahogany is a fast-growing, light-demanding late successional species requiring canopy disturbance opening persistent growing space for optimal early growth and recruitment to juvenile and adult size classes (Lamb 1966; Grogan et al. 2005a). Commercial populations of mahogany have been extirpated across much of their natural range in South America since industrial exploitation began after the turn of the nineteenth Century (Grogan et al. 2002, 2010; Kometter et al. 2004). Trees at this study's principal research site survived two episodes of selective logging in the mid 1980s and early 1990s that eliminated all mahogany stems >65 cm diameter.

Study sites

The principal study site ('Agua Azul') is a 1,250-ha reforestation and management project owned during the study period by Peracchi Ltda, a logging company specializing in mahogany extraction. Agua Azul is located in southeast Pará state, nine km south of state highway PA-279 midway between Xinguara and Tucumã (S 6°51′, W 50°31′). Climate is tropical dry. Annual precipitation during 1995–2001 averaged 1859 mm at a research site 110 km southeast of Agua Azul ('Marajoara', S 7°50′, W 50°16′), with more than 90% falling between November and May (Grogan and Galvão 2006b). Topographic relief within the study area at Agua Azul is slight, with terrain rising <10 m from seasonally dry first- and second-order streambeds across barely perceptible slopes. Soils are sandy gray or white eutrophic podsols throughout. Mahogany occurs at highest densities on the banks of or in flat areas adjacent to seasonal streams. The forest is dominated by evergreen trees intermixed with deciduous species.

Agua Azul consists of adjacent cleared and forested areas covering roughly 1,000 and 250 ha, respectively. Nursery-grown mahogany seedlings were outplanted by the managing company from 1994–1996 into bulldozed flats between hedgerows spaced ~100 m apart in the large open clearing. Extensive cleared areas were also planted in pasture grasses due to chronic shortages of mahogany seedlings, though the site was not grazed during the study period. Forested areas, occurring in two discrete patches bisected by the open clearing (Fig. 1), were subjected to heavy under- and overstory thinning in 1995 and 1997, respectively, approximating a combined shelterwood plus crown liberation treatment for surviving mahogany trees. The resulting forest canopy is open and highly irregular. Both open clearing and logged and thinned forest areas are fire-prone during the dry season. Fires burned faster, hotter, and more extensively in the pasture-like open clearing compared to fires in the forest understory, where partial canopy cover and uneven distribution of leaf litter and woody fuels prevented 100%-area burns (Cochrane et al. 1999; Cochrane and Schulze 1999). Agua Azul is surrounded by heavily logged forest, pasture, and small-holder agricultural fields. Groundfires spotting in from neighboring pastoral and agricultural burns swept across the site in alternate years from 1995; fires may have occurred before our arrival but could not be confirmed by nursery crews.

Data from one additional forest management site in this region are presented for comparative purposes. The landscape at Marajoara is similar physiographically to Agua Azul, with slight topographic relief, gray to white sandy eutrophic podsols across most of the landscape, and mahogany trees clustered along seasonal streams (Grogan et al. 2005a; Grogan and Galvão 2006b). Marajoara was selectively logged for mahogany during 1992–1994; no further canopy (crown liberation) or understory disturbances were introduced there except on a limited experimental basis (Grogan and Landis 2009).

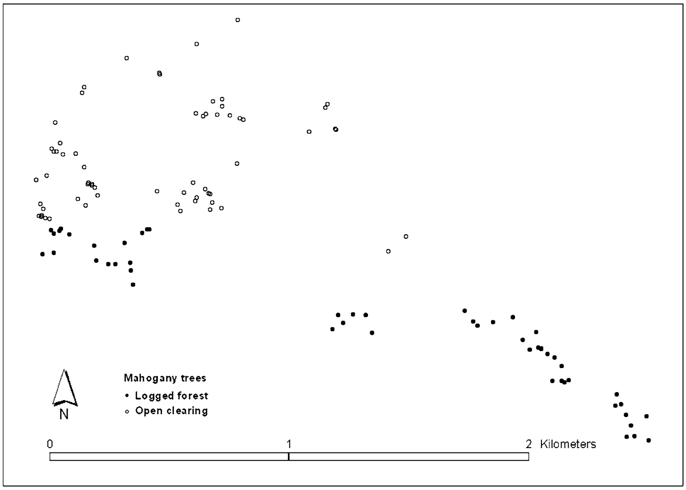

Fig. 1 Map of the Agua Azul study site showing proximal locations of trees in the open clearing (*open circles*) and trees in logged and thinned forest (*closed circles*)

Field methods

The Agua Azul sample consists of 115 mahogany trees from 10–65 cm diameter in a study area of 600 ha, split between the open clearing (63 trees in 350 ha) and logged and thinned forest (52 trees in 250 ha) areas. Trees were located, tagged, and mapped during the 1996 dry season. Most sample trees grow mixed by size class in clusters strung along the banks of or near seasonal streams. To protect trees from groundfires, aboveground vegetative regrowth was slashed and removed each dry season beginning in 1997 to a 3-m radius of tree stems in both growing conditions.

Trees were censused annually during the dry season (July–August) from 1997–2003 for survival, stem diameter increment ('growth'), fruit production, and crown leaf and reproductive phenology. Cause of death was noted where obvious. Annualized mortality rates were calculated according to Sheil et al. (1995):

$$m = 1 - (N_1/N_0)^{1/t}$$

where N_0 is the number of live stems at time 0 and N_1 is the number of survivors at time t. Mortality rates are presented for the period 1996–2002 because we obtained only partial access to the site (roughly half of the sample trees) in 2003 due to a change in ownership.

Tree diameters were measured 1.3 m above the ground or at least 60 cm above the reach of the highest buttress in 1997, and again 30 cm above this height. Aluminum nails were affixed 10 cm above the highest measurement plane on opposite sides of each tree to afford precise re-location of measurement heights each year. Annual diameter increment was calculated as the difference between current and previous year's measurements at a given height on the stem, averaged between the two measurements per tree. Diameter measurements were made by a single four-person field crew throughout the study period to reduce measurement error associated with unfamiliar field and tree conditions. Due to mortality and difficulties encountered during some years in relocating some trees, growth rates are analyzed for sub-sets of the full sample as noted in "Results".

To quantify annual fruit production, fruit capsules were counted within the crown of each mahogany tree by two separate observers with binoculars during annual diameter censuses. Mahogany's large woody fruit capsules (10–22 cm long) are readily identifiable on the tree crown from the ground during the mid to late dry season when crowns are leafless or nearly so. Fruit counts were verified by collecting dehisced capsule pericarps (five per fruit) beneath the crown area of fruiting trees and dividing the total number by five. The final count was the larger figure yielded by the two methods. Fruit capsule production data are reported for trees >30 cm diameter ($N = 41$ trees in the open clearing, 36 trees in logged and thinned forest). This is the stem size at which trees can generally be expected to be reproductively mature in this region (Grogan and Galvão 2006a).

To estimate the date of flowering onset by individual trees during each dry season, we applied a scoring system for crown leaf exchange and flowering developed at Marajoara (Grogan 2001). This system was derived from bi-weekly crown observations of 23 trees with leaf and flower traps during crown shedding, reflush, and flowering phases in 1997 and 1998. Crown observations were coupled with leaf counts and known flowering onset dates to refine a scoring system for crown phenology. Crown shedding and reflush phases were each divided into four sub-phases bridged by a bare-crown phase. During reflush, flowerbuds were observable from the second sub-phase forward. Observations were pooled to estimate the mean number of days to flowering onset represented by successive crown phases. The date of flowering onset by a given tree could then be estimated based on observed crown phenology on a given calendar date. The sample is restricted to trees >30 cm diameter for which crown phenology data were collected during each year from 1997–2000 (4 years; $N = 18$ trees in the open clearing, 20 trees in the logged and thinned forest; stem diameter distributions were approximately equivalent between the two growing conditions).

For comparative purposes, we present survival, growth, and fruit production data for 305 mahogany trees 10–65 cm diameter censused annually over the same study period (1996–2002/2003) at Marajoara. Methods for data collection were identical between the two sites.

Data analyses

Pearson correlations were computed to assess the relationship between stem diameter and diameter growth rate. Differences in growth rates, fruit production rates, and estimated dates of flowering onset between open and forest trees at Agua Azul were tested using ANOVA. Minimum significance was set at $\alpha = 0.05$. All data analyses were performed using JMP 7 (SAS, Cary, NC).

Results

Mortality

Sample numbers for trees in the open clearing and trees in logged and thinned forest at Agua Azul were broadly equivalent across 10-cm size classes in 1996, with most trees between 30–50 cm diameter (Fig. 2). Trees in the open clearing died at accelerated rates compared to trees in logged and thinned forest during 1996–2002 (4.4 vs. 1.0% year^{-1}). The mortality rate by trees 10–65 cm diameter at the logged but otherwise undisturbed forest management site Marajoara was 1.2% year^{-1} over the same period. Under both

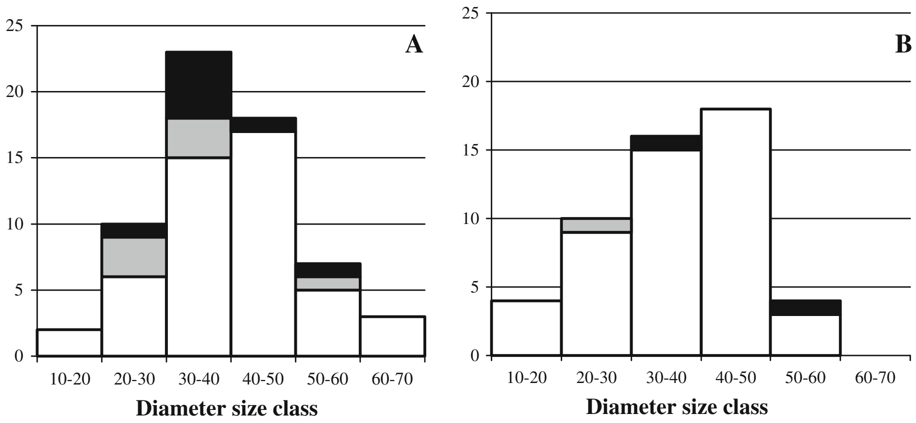

Fig. 2 Frequency distribution of trees at the Agua Azul study site by growing conditions (**a** trees in the open clearing, **b** trees in logged and thinned forest). Filled portions of *bar columns* indicate trees that died during the study period: *black* = directly or indirectly caused by fire, *gray* = other causes

growing conditions at Agua Azul, trees <30 cm diameter died at higher rates than trees >30 cm diameter (in the open clearing, 6.5 vs. 4.0% year^{-1}, respectively; in disturbed forest, 1.2 vs. 0.9% year^{-1}, respectively).

Fifteen of 18 observed deaths at Agua Azul occurred during the first 2 years of study. Over half of deaths (10 of 18) were attributable to groundfires, which killed both open and forest trees from the base of the stem up (Fig. 2). A third of deaths were windthrows with fire damage possibly a contributing factor. Impeded drainage between bulldozed hedgerows created waterlogged soils that killed one tree in the open clearing.

Diameter growth

No correlation was seen between stem diameter and diameter growth for trees with two or more years of increment data ($N = 97$, Pearson's $r = -0.0685$) at Agua Azul. Pooled growth rates by trees in the open clearing vs. trees in logged and thinned forest differed significantly during annual census intervals from 1997–2003 except 1998–1999, with forest trees growing faster, on average, than trees in the open clearing (Fig. 3). Long-term (5- or 6-year) diameter growth rates by trees in logged and thinned forest were significantly higher than growth rates by trees in the open clearing (0.86 ± 0.07 (SE) vs. 0.68 ± 0.06 cm year^{-1}, $P = 0.0208$). This relationship held only for adult trees (30–65 cm diameter); juvenile growth rates between forest and open trees did not differ statistically over this period (Table 1). Maximum observed growth rates for open trees exceeded those of forest trees for both size classes (Table 1).

At Marajoara, the 6-year (1997–2003) mean diameter growth rate over this period was 0.64 ± 0.02 cm year^{-1}. Juvenile trees at Marajoara grew at rates intermediate between trees in open and forested areas at Agua Azul, while adult trees at Marajoara grew slower, on average, than trees in both areas at Agua Azul (Table 1). On a year-by-year basis, mean annual diameter growth rates at Marajoara were closer to open trees at Agua Azul than to forest trees, or intermediate between the two groups (Fig. 3).

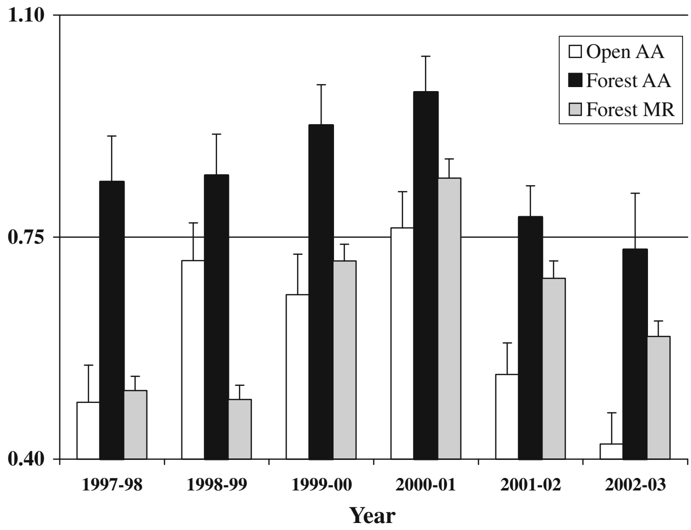

Fig. 3 Mean annual growth rates by trees 10–65 cm diameter in open clearing (*white bars*) vs. logged and thinned forest (*black*) growing conditions during 1997–2003 at Agua Azul. Error bars indicate one standard error (SE). Differences between group means were significant at $\alpha = 0.05$ (forest trees > open trees) during every year except 1998–1999. For comparative purposes, annual growth rates by trees of comparable size at Marajoara are shown (*gray*)

Table 1 Mean and maximum diameter growth rates at the Agua Azul (AA) and Marajoara (MR) study sites during 1997–2003 for trees with 5 or 6 years of data, divided by juvenile (10–30 cm diameter) and adult (30–65 cm diameter) size classes

Diam (cm)	Sample N			Mean (cm year^{-1})			Max (cm year^{-1})		
	AA Open[1]	AA Forest[2]	MR Forest[3]	AA Open (SE)	AA Forest (SE)	MR Forest (SE)	AA Open	AA Forest	MR Forest
10–30	8	5	106	0.69 (0.16)a	0.76 (0.09)a	0.72 (0.03)NA[4]	1.3	1.0	2.1
30–65	38	32	199	0.68 (0.07)b	0.87 (0.06)a	0.60 (0.03)NA	2.6	1.7	2.0

Letters beside mean values for Agua Azul trees indicate significant differences (a > b) by size class at $\alpha = 0.05$. Data from Marajoara are presented for comparative purposes only and are not tested for significant difference against Agua Azul data

[1] Open = trees in the open clearing

[2] Forest = trees in logged and thinned forest

[3] Forest = trees in logged but otherwise undisturbed forest

[4] NA = not applicable, no statistical comparison is made between MR and AA trees

Fruit production

Overall fruit production by mahogany trees >30 cm diameter at Agua Azul was high in 1997 and 2002 compared to markedly low production in 1999 and 2001. The proportion of trees in logged and thinned forest producing fruit capsules exceeded that by trees in the open clearing every year except in 1997 (annual range: forest trees 59–83%, open clearing trees 24–68%). Overall, 97% of forest trees fruited at least once during the 7-year observation period compared to 81% of open trees. Forest trees produced, on average,

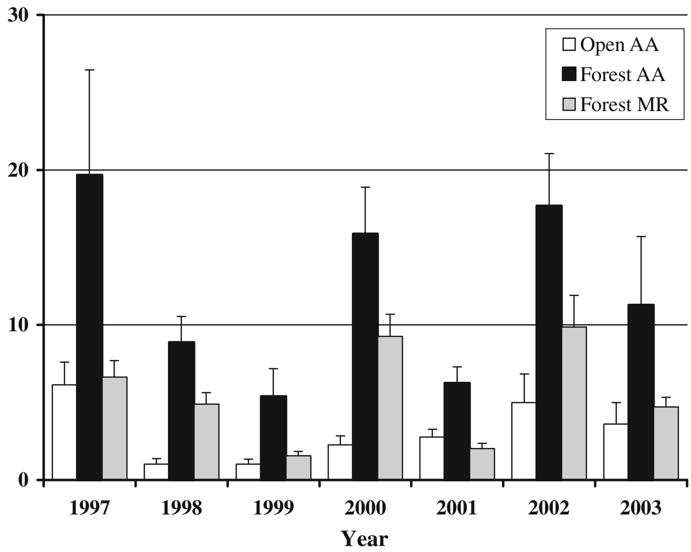

Fig. 4 Mean annual fruit production (fruit tree^{-1}) in open clearing (*white bars*) vs. logged and thinned forest (*black*) growing conditions during 1997–2003 at Agua Azul. *Error bars* indicate one standard error (SE). Differences between group means were significant at $\alpha = 0.05$ (forest trees > open trees) during every year. For comparative purposes, annual fruit production by trees of comparable size at Marajoara are shown (*gray*)

significantly more fruit capsules than open trees during every year of observation (Fig. 4). Mean long-term fruit production rates by forest trees were significantly higher than those by open trees (12.0 ± 1.9 vs. 3.6 ± 0.8 fruit year^{-1}, $P = <0.0001$).

At Marajoara, overall fruit production rates by trees 30–65 cm diameter were broadly similar to Agua Azul, with high production in 2000 and 2002 and low production in 1999 and 2001 (Fig. 4). Like diameter growth rates, mean annual fruit production by these trees was closer to production by trees growing in the open clearing at Agua Azul or intermediate between open clearing vs. logged and thinned forest trees (Fig. 4).

Flowering phenology

While estimated dates of earliest and latest flowering onset by trees in the open clearing and in logged and thinned forest were similar every dry season at Agua Azul, on average open clearing trees initiated crown leaf loss, replacement, and flowering earlier during each dry season than forest trees. The mean estimated flowering onset date for open trees during 1997–2000 was 02 August, compared to 21 August for forest trees, a difference of nearly three weeks. On an annual basis estimated mean onset dates ranged from 26 July–11 August for open trees, and from 13 August–04 September for forest trees during 4 years. Estimated mean annual and 4-year onset dates were significantly different between open and forest trees at $\alpha = 0.05$.

Discussion

Mahogany trees growing in the open clearing at Agua Azul died at higher rates, grew more slowly, produced fewer fruit, and initiated flowering earlier, on average, than trees growing in nearby logged and heavily thinned forest. Our qualitative observations indicated that open trees experienced more extensive crown die-back, crown infestation by the mahogany shootborer (*Hypsipyla grandella* Zell., Lepidoptera: Pyralidae), adventitious sprouting along the stem below the crown, and fire-damaged stem bases than trees growing in logged and thinned forest. In fact, mortality rates observed over the 6-year period likely underestimate death rates in both environments, but especially in the open clearing, that would have occurred without intervention (clearing fire-breaks around tree stems) beginning in 1997.

Though it is possible that very large mahogany trees in this region, larger than 1 m diameter, may become fire-resistant as bark thickens with age (Snook 2003), mahogany trees <65 cm diameter in this study demonstrated limited fire tolerance. Intense groundfires associated with pasture and agricultural establishment typically damage bark at the base of tree stems, partially or entirely girdling the tree. Fewer forest trees were affected in this way because fire coverage in the forest understory was less complete (Holdsworth and Uhl 1997). Rising heat from groundfires may also cause mahogany crowns to wilt and shed. If fires occur during the mid to late dry season when tree crowns are flushing or newly flushed, the loss of a year’s leaf production can cause significant crown dieback, weakening the tree and possibly killing it. We have observed this chain of events at Marajoara where groundfires killed vigorous mahogany trees over 2- to 3-year periods along the perimeter of closed-canopy forest. Reduced growth rates by trees in the open clearing at Agua Azul suggest that progressive fire damage may lead to loss of vigor.

The pattern of inter-annual variation in mean diameter growth rates by trees at Agua Azul and Marajoara was broadly synchronous over the 6-year observation period (Fig. 3). This suggests that exogenous factors such as seasonal rainfall patterns—its timing, temporal distribution, and quantity—may influence population dynamics at regional scales (Schulze 2003; Grogan and Galvão 2006a).

Growth rates by trees in logged and thinned forest at Agua Azul not only far exceeded those by trees in the open clearing, but also were higher than by mahogany trees growing in logged but otherwise undisturbed forest at Marajoara, indicating that canopy thinning may yield higher diameter increment rates if some modicum of forest structure is retained. A contributing factor to accelerated growth rates by forest trees at Agua Azul may have been non-lethal groundfires, which enrich soils with nutrients previously bound up in litter, coarse woody debris, and understory vegetation. Recurrent groundfires eliminated essentially all vines from tree crowns by killing them at the base, a phenomenon also observed at a fire-prone fieldsite near Marajoara (‘Corral Redondo’; Grogan 2001). Mahogany trees have been shown to increase diameter growth rates in response to reduced crown vine coverage (Grogan and Landis 2009).

Similar to diameter growth rates, annual mean fruit production rates by trees 30–65 cm diameter in logged and thinned forest exceeded production by trees in the open clearing and by trees in logged forest at Marajoara (Fig. 4). Again, canopy thinning and nutrient inputs from groundfires may enhance fruit production, up to a point. Crown dieback caused by excessive exposure and wilting dry season fires may reduce the number of potential flowering and fruiting sites within a given tree crown, especially on open trees. Eliminating vines may also enhance fruit production (Kainer et al. 2007; Grogan and Landis 2009).

One consequence of flowering schedules shifting, on average, three weeks earlier under open clearing conditions at Agua Azul could be a reduction in the availability of pollen donors among both groups of trees. Small bees and butterflies thought to pollinate mahogany flowers are capable of moving across open space between forest fragments and isolated trees (White et al. 2002). However, unless these pollinators are resident in isolated tree crowns, their densities and availability for pollen transport are likely to be reduced compared to forest conditions, further contributing to lower fruit production rates.

Annual community-level fruit production at Agua Azul and Marajoara supports the possibility that mahogany population dynamics may be broadly synchronized at regional scales by inter-annual climate patterns. Peak fruit production at both sites in 2002 was mirrored by lows in 1999 and 2001. At a selectively logged but otherwise undisturbed forest management site located 35 km southeast of Agua Azul, Jennings and Baima (2005) also reported relatively high population-level mahogany fruit production in 2002 and low production in 1999 in their 3-year study.

Based on these results, small-holder agriculturists intending to cultivate remnant mahogany trees isolated in open fields after forest clearing face long odds on reaping windfall profits several decades in the future. Trees exposed to recurrent fires and the full brunt of rainy season convectional thunderstorms (Grogan and Galvão 2006b) will require constant diligence clearing firebreaks (we recommend to a minimum of 5 m radius from tree stems) and luck avoiding the most powerful winds. The mortality rate observed for trees in the open clearing, though slowing during the latter years, is unsustainable over the long term, especially in the absence of new recruits (Gibbons et al. 2008).

Mahogany trees retained after logging in forest preserves, on the other hand, promise much better returns if they can be protected from dry season groundfires. Thinning forest canopies, an example of Fredericksen and Putz's (2003) 'silvicultural intensification' for high-value, light-demanding timber species, could accelerate growth rates and open growing space for natural regeneration. Liberation experiments in other Amazon regions (Dauber et al. 2005; Wadsworth and Zweede 2006; Villegas et al. 2009) have shown a pronounced positive treatment effect on future crop tree growth with a thinning intensity well below that employed in this study. However, there is likely a threshold where greater canopy opening and isolation of residual trees results in increased crown damage, susceptibility to dry season groundfires, and rainy season windthrow that counterbalances increased population-level growth rates (Gourlet-Fleury et al. 2004; Schulze and Zweede 2006).

In the Amazonian mahogany belt, vine removal from residual trees, with or without a light canopy thinning treatment, may be an effective way to increase growth rates without dramatically altering forest structure and function (Grogan and Landis 2009). Again, in seasonal forests like those within the study region, dry season fires spotting in from nearby pastures and agricultural fields represent the most serious annual threat to mahogany and other timber species in logged or otherwise structurally disturbed forests. Absent effective regulation and control of anthropogenic fires, attempts to manage remnant mahogany trees for future profits or to restore commercially viable populations in this region may prove futile over the long term.

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