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Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil

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Summary

1. Current efforts to model population dynamics of high-value tropical timber species largely assume that individual growth history is unimportant to population dynamics, yet growth autocorrelation is known to adversely affect model predictions. In this study, we analyse a decade of annual census data from a natural population of big-leaf mahogany *Swietenia macrophylla* King to quantify the strength and duration of growth autocorrelation, and experimentally investigate the role of crown vine coverage, a major predictor of performance.

2. The sample population consisted of 358 trees >10 cm diameter. The relative contributions of predictor variables including diameter, crown vine coverage and growth history to models of growth and mortality were evaluated using Akaike's Information Criterion. Autocorrelation among trees was incorporated into growth models using generalized least squares. We experimentally removed vines from heavy-laden trees to test the strength and persistence of their impact on stem diameter growth.

3. Previous growth explained the highest amount of variation in annual diameter growth; the best-fitting model of autocorrelation was an AR(7) autoregressive model, indicating that autocorrelation persisted throughout the study period. Other factors explaining variation in growth were, in decreasing order of importance: year of measurement, crown vine coverage, diameter, crown illumination and fruit production. The best logistic regression model for mortality retained diameter growth plus crown vine coverage as predictors of risk.

4. The vine release experiment strongly supported these results. Released trees grew faster than control trees but required ≥5 years to approach growth rates of trees with minimal vine coverage. Trees with heavy vine coverage also experienced higher mortality rates.

5. *Synthesis and applications*. These results indicate that growth autocorrelation is strong, persistent, and an important predictor of future performance; demographic models for tree growth and yield projections can be improved by accounting for growth history. Our results also indicate that targeted silvicultural practices such as vine cutting can increase long-term growth and timber yield. These findings further current understanding of tropical tree growth and survival, and offer improved management tools for sustainable harvest practices for mahogany and similar species.

Key-words: Akaike's Information Criterion, Amazon, Brazil, growth autocorrelation, silvicultural treatments, sustainable forest management, tropical timber

Introduction

Sustainable production of timber from natural forests requires basic understanding of growth and mortality rates by commercial species and factors responsible for variation in those rates across the life cycle. Forest managers require detailed descriptive and predictive information about growth and mortality to evaluate impacts of current extraction practices and intensities on timber yields. This information is largely unavailable for high-value species occurring at low densities in tropical regions where forests are remote or difficult to access, logging practices

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are poorly regulated, and natural tree populations are typically high-graded or mined to supply lucrative international markets (Schulze *et al.* 2008).

Numerous studies confirm the general principles of growth and mortality for forest overstory and emergent species. Factors influencing growth are better understood than those influencing mortality. For example, trees with good crown form and full sun exposure tend to grow faster than poorly formed, suppressed trees (Finegan, Camacho & Zamora 1999; King, Davies & Noor 2006; Drobyshev, Linderson & Sonesson 2007). Stem diameter growth rates have been observed to decline as trees approach maximum size (Clark & Clark 1996). Heavy fruiting may come at the cost of lower growth rate (Terborgh *et al.* 1997; Kelly & Sork 2002).

The lack of similarly detailed information on mortality is due partly to the fact that few observations of tree death are available compared with stem diameter growth measures, considering that background mortality rates for mature forest trees in tropical forests are generally $< 2\%$ year^{-1} (Swaine, Lieberman & Putz 1987b). Mortality risk increases as diameter growth rates decline (Swaine, Hall & Alexander 1987a; Terborgh *et al.* 1997; Brienen, Zuidema & During 2006; Das *et al.* 2007).

Particularly in the tropics, crown vine coverage may depress growth, reproduction and survival (Stevens 1987; Clark & Clark 1990; Pérez-Salicrup & Barker 2000; Gerwing 2001; Grauel & Putz 2004; Kainer *et al.* 2006), and elimination of vines may improve performance by potential crop trees. However, heavy crown vine loads can have long-lasting impacts on tree performance even after removal because of previous limitations on the development of crown form and stem structure. The biological and financial efficacy of eliminating vines from the crowns of future crop trees to increase growth rates remains to be evaluated for most species and at commercial operational levels.

Another variable that is potentially strongly predictive for growth and mortality is growth history or autocorrelation (Terborgh *et al.* 1997; Landis & Peart 2005; Brienen *et al.* 2006). Growth autocorrelation describes the strong tendency for individual trees to maintain their growth rates relative to other trees in the population from one year to the next, and occurs because: (i) individual tree-level variables described above change little over time (e.g. extensive crown vine coverage remains extensive from year to year); (ii) such variables influence the development and growth of the tree, limiting its future growth; and (iii) inherent genetic and site differences such as soil fertility and water availability among trees are immutable or strongly persistent. While the phenomenon of growth autocorrelation has been widely reported (Swaine *et al.* 1987a; Kohyama & Hara 1989; Kammesheidt *et al.* 2003; Chidumayo 2007; Drobyshev *et al.* 2007), its strength, persistence, and importance relative to other explanatory variables is just beginning to be investigated. Growth autocorrelation's dramatic impact on population models (e.g. Pfister & Stevens 2003) suggests that it may be an important factor for forest managers to consider when projecting population recovery and future harvest levels (Bullock *et al.* 2004; Brienen *et al.* 2006).

In this paper, we examine factors influencing growth and mortality by a natural population of big-leaf mahogany *Swietenia macrophylla* King (henceforth 'mahogany'), the premier neotropical timber species. While the role of crown vine loads and growth autocorrelation relative to other predictors of growth and mortality is poorly understood for most species, improved understanding is especially relevant for mahogany because its listing on the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) Appendix II in 2002 requires that international trade involve only legally harvested volumes deemed non-detrimental to its role in the ecosystem (Blundell 2004). The concept of non-detriment is generally understood to mean 'sustainably managed', yet the only published projections of population recovery after logging at historical and current legal extraction levels in Brazil indicate that future harvest volumes will decline and could disappear over multiple cutting cycles (Grogan *et al.* 2008). In this paper, we lay the groundwork for a more sophisticated demographic modelling approach to evaluating the sustainability of current harvest practices for mahogany and similar tropical timber species.

We measured annual stem diameter and survivorship of 358 mahogany trees at a forest management site in the Brazilian Amazon during the period 1997–2007. For each tree we quantified stem diameter, crown vine coverage, crown illumination (exposure), and annual diameter growth and fruit production. We asked: (1) Which factors influence diameter growth and mortality rates, and what are their relative importance? (2) How strong is growth autocorrelation among trees and how long does this effect persist? (3) Given the presumed negative effect of crown vine coverage on diameter growth, does release from crown vine coverage lead to increased growth rate? If so, how long does this take?

To answer the third question we eliminated vines from the crowns of heavy-laden trees known to be growing at below-average rates, and compared growth of released trees with that of a control group of unreleased trees.

Materials and methods

STUDY SPECIES

Big-leaf mahogany is the most valuable widely traded tropical timber species. It is a canopy emergent tree associated with seasonally dry tropical forests from Mexico to Bolivia. Mahogany is a fast-growing, light-demanding late successional species (Lamb 1966). In southeastern Amazonia, mahogany's local distribution commonly traces seasonal streams or rivers (Grogan, Ashton & Galvão 2003); it occurs at highly variable but consistently low density, up to *c.* 1·2 trees > 20 cm diameter ha^{-1} (Grogan *et al.* 2008). The few published studies of growth and mortality by adult mahogany trees in natural forests are summarized in Table S1, Supporting information.

STUDY SITE

Marajoara is a 4100-ha forest industry-owned management area located at 7°50′S, 50°16′W, 34 km northwest of Redenção in the southeast corner of the state of Pará. Climate is tropical dry, with

mean monthly temperatures ranging between 25 and 27 °C. Annual precipitation during 1995–2001 averaged 1859 mm (range 1636–2170 mm), with more than 90% falling between November and May; in some years no rain fell for 3–4 months during the dry season. The forest is dominated by evergreen trees intermixed with deciduous species. Marajoara was selectively logged for mahogany between 1992 and 1994, reducing landscape-scale densities from 0·65 to 0·19 mahogany trees > 20 cm diameter ha^{-1} (Grogan *et al*. 2008).

FIELD METHODS

The sample population at Marajoara consists of 358 mahogany trees > 10 cm diameter within a core research area of 2050 ha. These trees survived logging either by being designated as seed trees in fulfilment of forest management regulations or by escaping notice of loggers. Nearly half of the trees in the sample population (n = 173) were first measured as described below during the 1995–1996 rainy season, 1·5 years before the first dry season census of the full sample population in July 1997.

All trees were censused annually during the dry season (July–August) from 1997 to 2007 for survival, diameter growth and fruit production. Where discernible, primary causes of tree deaths (windthrow, vine suppression, etc.) were noted. Tree diameters were measured with steel diameter tapes at 1·3 m above-ground or at least 60 cm above the reach of the highest buttress in 1997, and again 30 cm above this height. Aluminium nails were affixed 10 cm above the second (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.

To quantify annual fruit production by mahogany trees, fruit capsules were counted by two separate observers with binoculars during annual diameter increment censuses. Mahogany's large woody fruit capsules (10–22 cm long) are readily identifiable on the tree crown from the forest floor. Fruit counts were verified by collecting dehisced capsule pericarps (five per fruit) on the forest floor beneath fruiting trees and dividing the total number by five. The final count was the larger figure yielded by the two methods.

In addition, we noted for each tree in 1997: crown vine coverage by 33%-area increments (0–4 scale, with 0 = none present and 4 = effectively 100% crown coverage); and crown illumination based on a four-point system estimating openness by projecting a four-sided box around each crown (0 = no lateral face receiving full sunlight and 4 = four sides exposed to full sunlight). This index was developed for use in a seasonally dry forest with low, highly irregular and broken canopy where the Dawkins Index and its modifications provided poor resolution among poles and trees (Dawkins & Field 1978).

EXPERIMENTAL RELEASE FROM VINES

Following the 1998 dry season census, 36 trees > 25 cm diameter that were first measured for diameter during the 1995–1996 rainy season were selected for inclusion in the vine release experiment based on two criteria: crown vine coverage was scored as 3 or 4 (> 66% coverage), and the observed 2·5-year period (1995–1998) diameter increment rate was lower than the sample-wide average (< 0·57 cm year^{-1}). Twenty-two trees were randomly selected for vine release, leaving 14 trees as the untreated control. The full range of stem size classes was represented in both groups. In September 1998, all vines beneath the perimeters of tree crowns were cut at ground level, as well as vines visibly entering tree crowns from beyond crown perimeters.

Crown vine coverage for experiment trees was assessed in 1998, 2000 and 2006. Vines surviving the first release were cut again in 2000. Even after re-cutting, crown vine coverage on eight of 22 release trees persisted at values of 2 or higher (> 33% coverage) in 2006, possibly compromising treatment effects. Results for this group are presented as an intermediate treatment category, 'partial release'. Experiment trees were censused annually until 2007 for survival and diameter increment as described above.

DATA ANALYSIS

Growth and mortality

We used an information-theoretic approach (Anderson, Burnham & Thompson 2000; Burnham & Anderson 2002) to analyse the relative contributions of predictor variables to models of diameter growth and mortality by individual trees. Model selection was based on Akaike's Information Criterion (AIC), a measure of model fit which penalizes for model complexity. Lower values of AIC indicate better fits. Models are compared relative with the best-fitting model using AIC differences (Δ_{AIC}); the best model has a value of 0, and models with $\Delta_{AIC} \leq 2$ are considered to have strong support. Normalized Akaike weights (w_i), which sum to one for a given set of models, estimate the relative likelihood of each model given the data, and so measure the relative importance of competing models (Burnham & Anderson 2002).

To analyse variables contributing to 'growth', defined as annual diameter increment (INC, cm year^{-1}), we first fit a full model containing the following terms: year (YR), crown vine coverage index (VINES), stem diameter from the previous year (DM), ln(fruit production in the previous year + 1) (FRT) and Crown Illumination Index (CI). The YR term was treated as a categorical variable. In addition, the model included two-way interactions among all possible variables except for YR (excluded because of limitations on sample size and because variation among years was not of interest). The growth model was fit using generalized least squares with an autocorrelated error term (cf. Pinheiro & Bates 2000) to account for growth autocorrelation remaining in the residuals. The degree of autocorrelation was evaluated with 10 candidate models which included an intercept-only model and the full model described above, both with no autocorrelation. The remaining eight models consisted of the full model with an autoregressive (AR) correlation structure for the residuals (eqn 1) of order (p) from 1 to 8 years [e.g. AR(1) to AR(8); Pinheiro & Bates 2000]:

$$\varepsilon_{i,t} = \phi_1 \varepsilon_{i,t-1} + \ldots + \phi_k \varepsilon_{i,t-p} + a_{i,t} \qquad \text{eqn1}$$

This correlation structure expresses the residual growth (denoted by ε_t) for a given tree (i) and year (t) as a linear function of all previous residuals for that tree up to p years previous, and a normally distributed noise term, a_t. The estimated parameters of the covariance matrix are given by ϕ, and the order (p) indicates the number of previous years that contribute to the current observation (Pinheiro & Bates 2000).

The parameters ϕ above cannot be interpreted as correlation coefficients, so for ease of interpretation we used the empirical autocorrelation function of Pinheiro & Bates (2000, p. 227) to calculate the degree of autocorrelation. This method uses the residuals of a given model (e.g. the full model described above) and simply calculates the correlation coefficients between the residuals for all individuals at time t and the residuals at time $t - l$ where l is the lag, or number of years between observations. This represents the tendency

of fast-growing trees to remain fast growing relative to other trees in the population.

Following selection of the appropriate structure for autocorrelation using AIC, we assessed the contribution and relative importance of predictor variables included in the full model in the presence of autocorrelation. First, we refined the model with the full set of predictors and the selected autocorrelation model using backward stepwise selection based on AIC to remove unnecessary predictors (Venables & Ripley 2002). The resulting 'reduced' model was then examined to determine the relative influence of each of the remaining variables by deleting each in turn and calculating the resulting increase in Δ_{AIC}. Model fit and assumptions were assessed with plots of observed vs. predicted values and residuals vs. predicted values, as well as normal probability plots of the residuals.

Mortality was analysed using logistic regression and a comparison of 13 candidate models using AIC. The full model under consideration included the same predictor variables as for growth, with the addition of a term for diameter increment of the previous year fit as a second-order polynomial (INC + INC^2). The use of a quadratic term was suggested by visual inspection of the relationship between INC and mortality. We did not include two-way interactions between variables because of the small number of observed deaths. The remaining 12 candidate models included an intercept-only model, seven models created by deleting each of the terms from the full model (six predictors plus INC^2), and one model each defined as follows: increment as a linear term only (INC), increment plus the quadratic term (INC + INC^2), INC + INC^2 + DM and INC + INC^2 + VINES.

For both growth and mortality models, we used Nagelkerke's R^2_N (Harrell 2001) to estimate the proportion of deviance explained. This measure is analogous to R^2, but appropriate to models fit by maximum likelihood.

Vine release experiment

Crown vine coverage scores when vines were cut (1998) and again in 2000 and 2006 were compared among three treatments (release, partial release and control) using ANOVA for group means. The effect of vine removal on diameter growth was assessed by calculating the difference between mean growth over 3-year periods at the start and end of the experiment for each tree, and evaluating effects of the three treatments using ANOVA. All data analyses were performed using the R statistical software package (version 2.7.2; R Foundation for Statistical Computing; http://www.r-project.org).

Results

POPULATION CHARACTERISTICS

The mahogany population at Marajoara was heavily weighted towards small size classes in 1997, 3–5 years after logging, with most surviving trees between 20 and 60 cm diameter (see Fig. S1a, Supporting information). Median growth rates declined slightly with increasing stem diameter (Fig. S1b, Supporting information). Fifty percent or more of crowns bore vines to some degree across size classes (Fig. S1c, Supporting information). As trees grew larger, the proportion with fully illuminated crowns increased: 9% of trees 10–30 cm diameter had crowns exposed on four sides to sunlight, while 65% of trees >70 cm diameter had fully exposed crowns (Fig. S1d, Supporting information). The sample population experienced a 1·11% annual mortality rate (*sensu* Sheil, Burslem & Alder 1995) over the period 1995–2007.

FACTORS INFLUENCING DIAMETER GROWTH

Relationships between explanatory variables and diameter growth rate can be observed from the annual diameter increment data collected over 10 years. Diameter growth during the previous year had a substantial effect on current-year growth (Fig. 1a). Growth rates declined slightly as stem diameter increased (Fig. 1c). The dampening effect on growth rates by crown vine coverage was clear (Fig. 1e), while the inverse effect of crown illumination was weakly evident (Fig. 1g). Growth rate generally increased as fruit production increased (Fig. 1i).

Annual diameter growth by mahogany trees at Marajoara demonstrated strong positive autocorrelation that persisted over a range of years, with annual correlation coefficients starting at 0·72 for lag = 1 year and declining slowly as the time lag increased to 8 years (Fig. 2). That is, relatively fast-growing trees were likely to remain so over a period of years, as were slow-growing trees. All models incorporating autocorrelation enjoyed strong support based on AIC, but the best were AR(7) and AR(8) (Table 1). These models demonstrate that, even when all individual tree-level variables (crown vine coverage, illumination, etc.) are included, substantial autocorrelation persisted in the residuals.

Based on its AIC score, we chose the AR(7) model to further investigate the effect on diameter growth of different explanatory variables (see Table S2, Supporting information for autocorrelation parameters). Backward stepwise regression based on AIC retained all main effects variables plus the VINES × FRT interaction; all other interactions were eliminated (Table 2). This reduced model was substantially improved over the full model (Δ_{AIC} = 7·64), and accounted for a large proportion of the variation in growth (R^2_N = 0·77). The relative impact of each of the retained variables in the AR(7) reduced model can be measured through Δ_{AIC} values obtained by deleting each variable in turn. Year of measurement (YR) had by far the largest effect (Δ_{AIC} = 633·14), followed in order of importance by VINES, DM, CI and FRT (see Table S3, Supporting information for estimated parameters associated with these variables). The VINES × FRT interaction contributed only marginally (Δ_{AIC} = 0·782), and the model excluding the interaction had substantial weight (w_i = 0·395). Contrasting these effects with the reduction in AIC associated with the inclusion of growth autocorrelation (Δ_{AIC} = 2138·15; Table 1), it is evident that the effect of autocorrelation on growth far exceeds even YR.

FACTORS INFLUENCING MORTALITY

From 1995 to 2007, beginning 1–3 years after selective logging at Marajoara, we observed 45 deaths by mahogany trees >10 cm diameter. Vines were directly or indirectly implicated in 36% of all cases (16 of 45). Severe wet season windstorms

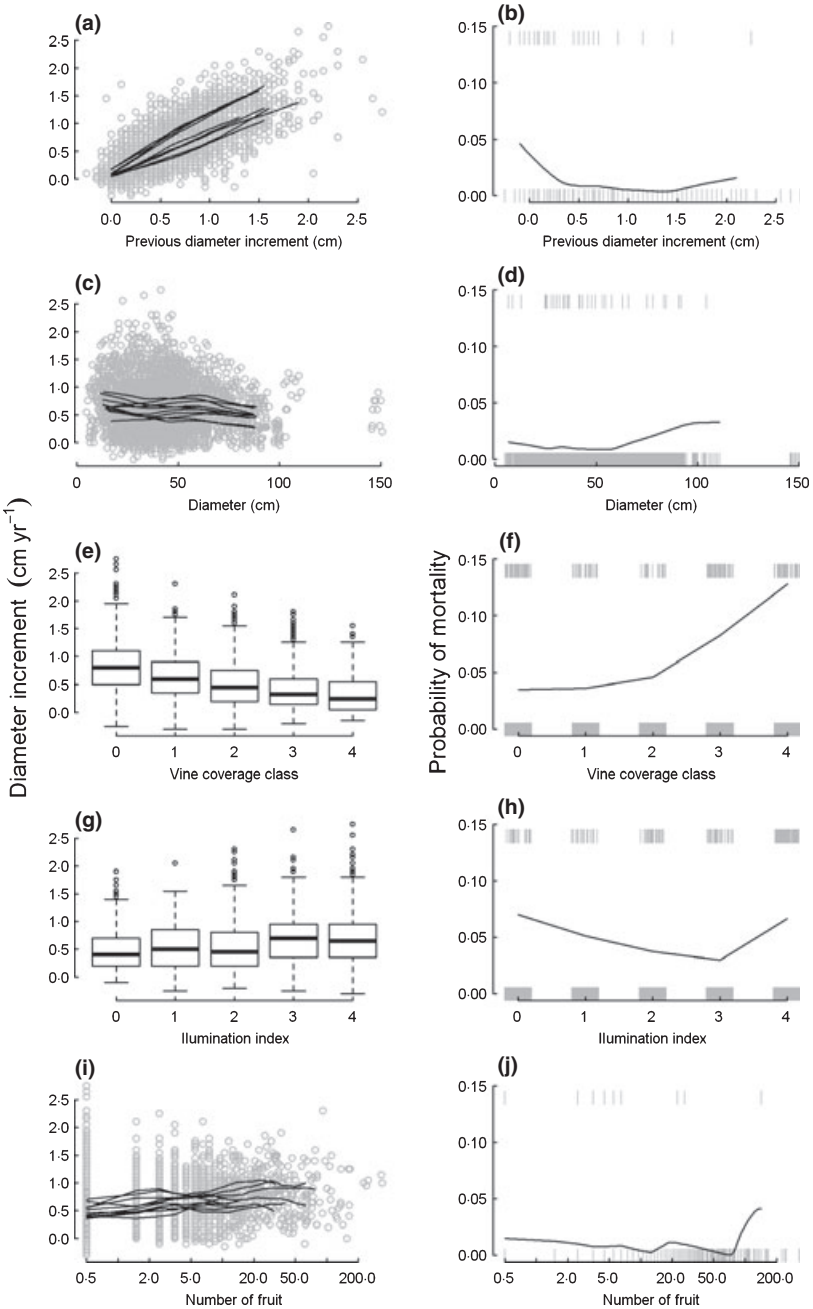

Fig. 1. Factors influencing diameter growth rates (left panels) and mortality risk (right panels) by mahogany in southeast Pará, Brazil. (a–b) Previous diameter increment (growth autocorrelation). (c–d) Stem diameter. (e–f) Crown vine coverage class. (g–h) Crown illumination class. (i–j) Mean fruit production (note log scale on *x*-axis). For growth panels, charts show all years of data combined on a single graph. Lines on scatterplots are LOWESS smoothers for each year of data. For boxplots, boxes indicate median and quartiles, whiskers indicate 10th and 90th percentiles, open points indicate extreme values. For mortality panels, a single line is shown for the full 10-year period. Survivors are shown as grey vertical bars along *x*-axes, deaths as bars across chart tops. In panels (f) and (h), locations of bars are jittered for clarity.

during 2 years (1999–2000 and 2005–2006) accounted for 39% of windthrown trees during the 12-year period.

Relationships between explanatory variables and mortality were not as clear as for growth. Increasing diameter growth rate during the previous year indicated lowered mortality risk (Fig. 1b); the upturn in probability of mortality at growth rates $>1{\cdot}5$ cm year^{-1} was because of the deaths by windthrow of two fast-growing trees with exposed crowns. The probability of mortality increased with stem diameter (Fig. 1d) and crown vine coverage (Fig. 1f). While mortality risk generally fell as crown illumination increased, trees with fully exposed crowns had an increased probability of death (Fig. 1h), suggesting trade-offs between canopy emergence and attendant risk of windthrow. These same trees were responsible for the increase in mortality risk by trees producing large numbers of fruit (Fig. 1j; see Table S4, Supporting information for estimated parameters associated with these variables).

The best logistic regression model for mortality based on AIC retained INC + INC^2 and VINES as predictors of risk (Table 3). This model was substantially improved relative to the full model ($\Delta_{AIC} = 15{\cdot}0$), but accounted for only a small proportion of the variation in risk ($R^2_N = 0{\cdot}07$). Alternative models excluding diameter increment had no support at all (combined w_i of 3×10^{-5}). In contrast to the growth analysis, YR had little effect on mortality, probably because of the small number of deaths observed in any particular year.

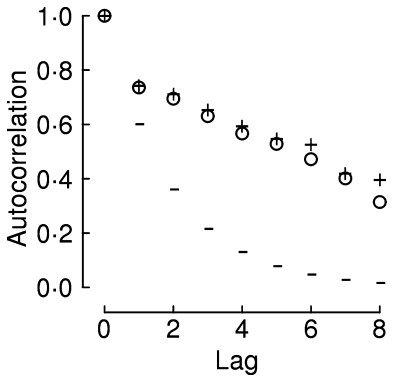

Fig. 2. Autocorrelation of residuals from the full growth model (see text and Table 1). Open circles represent the empirical autocorrelation function, indicating the correlation coefficient between the current year and successive preceding years (lag). Coefficients at all lags were significant at $\alpha = 0{\cdot}05$ level (max = 8 years). For reference, the AR(7) autoregressive model used in this paper is shown (+ symbols), as is the AR(1) model (− symbols).

Table 1. Akaike's Information Criterion (AIC) for growth autocorrelation models with time lags from 1 to 8 years [AR(*n*)]

Model	*K*	Log(Like)	AIC	Δ_{AIC}	w_i
Intercept only	2	−1653·2	3310·4	2964·00	0
Full model, no correlation	20	−1222·3	2484·5	2138·15	0
AR(1)	21	−298·4	638·8	292·48	0
AR(2)	22	−164·8	373·6	27·26	7×10^{-07}
AR(5)	25	−151·9	353·7	7·38	0·015
AR(6)	26	−150·8	353·5	7·18	0·017
AR(4)	24	−152·0	352·1	5·74	0·035
AR(3)	23	−152·4	350·7	4·36	0·070
AR(8)	28	−146·0	348·1	1·74	0·25
AR(7)	**27**	**−146·2**	**346·4**	**0**	**0·61**

The row in bold indicates the best-fitting model with the lowest AIC value.

K, the number of parameters estimated by the model; Log(Like), the log-likelihood of the model, an indicator of fit; AIC, Akaike's Information Criterion; Δ_{AIC}, the difference in AIC between a given model and the model with the lowest AIC score; w_i, Akaike weights showing the relative support for each model; the column sums to 1; AR(*n*) = autocorrelation model for time lags of 1–8 years.

TREE RESPONSE TO RELEASE FROM VINE COVERAGE

Mean crown vine coverage scores for release trees (vines cut), partial release trees (vines cut but persisting or recolonizing) and control trees (vines uncut) were similar at the time of treatment in 1998 (Table 4). Two years later, differences in mean scores among treatments were significant at $\alpha = 0{\cdot}05$, but by 2006 vines had recolonized partial release trees to such an extent that their mean crown coverage score was similar to control trees.

Mean annual pre-release (1995–1998) diameter growth rates were similar among treatments, ranging from 0·15–0·18 cm year^{-1} (Table 4). Following release, growth rates by release trees exceeded those of partial release and control trees by a widening margin (Fig. 3), and gradually approached growth rates by sample population trees with little or no crown vine coverage. Mean growth rates by trees in all treatments, including the sample population, accelerated over the post-release period, influenced by exceptional growing conditions occurring at 2- to 3-year intervals (Fig. 3). Comparing group means of the difference in growth from the experiment's last three years (2004–2007) and the period before vine cutting

Table 2. Akaike's Information Criterion for predictors of diameter growth rate

Model	K	Log (Like)	AIC	Δ_{AIC}	w_i
Intercept only	2	−1653·2	3310·4	2971·64	0
AR(7) full	27	−146·2	346·4	7·64	0·013
AR(7) reduced	**22**	**−147·4**	**338·7**	**0**	**0·583**
AR(7) reduced – YR	14	−471·9	971·9	633·14	0
AR(7) reduced – VINES	20	−180·9	401·9	63·18	$1{\cdot}1 \times 10^{-14}$
AR(7) reduced – DM	21	−167·5	376·9	38·19	$3{\cdot}0 \times 10^{-09}$
AR(7) reduced – CI	21	−160·0	362·0	23·25	$5{\cdot}2 \times 10^{-06}$
AR(7) reduced – FRT	20	−153·5	347·0	8·27	0·0093
AR(7) reduced – VINES × FRT	21	−148·7	339·5	0·78	0·395

Annotations as in Table 1; see Materials and Methods for definitions of predictor names. The top group of three rows indicates ranks between three candidate models. 'AR(7) full' from Table 1 retains all main effects variables plus all two-way interaction terms, while 'AR(7) reduced' eliminates two-way interactions except VINES × FRT after stepwise reduction based on AIC. The bottom group of rows shows the importance in descending order of the variables remaining in the reduced model.

Table 3. Akaike's Information Criterion table for predictors of mortality

Model	K	Log (Like)	AIC	Δ_{AIC}	w_i
Full – INC^2	13	−163·8	353·5	22·07	$9{\cdot}16 \times 10^{-06}$
Full – (INC + INC^2)	14	−162·6	353·3	21·85	$1{\cdot}03 \times 10^{-05}$
Intercept only	1	−175·0	352·1	20·63	$1{\cdot}88 \times 10^{-05}$
Full – VINES	14	−160·8	349·5	18·11	$6{\cdot}63 \times 10^{-05}$
Full – DM	14	−159·2	346·5	15·05	$3{\cdot}06 \times 10^{-04}$
Full model	15	−158·2	346·4	15·00	$3{\cdot}14 \times 10^{-04}$
Full – FRT	14	−158·5	344·9	13·48	$6{\cdot}73 \times 10^{-04}$
Full – CI	14	−158·2	344·5	13·02	$8{\cdot}46 \times 10^{-04}$
INC	2	−169·3	342·6	11·15	0·00225
Full – YR	7	−160·4	334·7	3·28	0·110
(INC + INC^2) + DM	4	−163·2	334·4	2·92	0·132
(INC + INC^2)	3	−163·8	333·7	2·24	0·185
(INC + INC^2) + VINES	**4**	**−161·7**	**331·4**	**0**	**0·568**

Annotations as in Table 1; see Materials and Methods for definitions of predictor names. The full model includes main effects variables used in growth analyses except interaction terms. The row in bold indicates the best-fitting model with the lowest AIC value and $\Delta_{AIC} = 0$.

Table 4. Vine release experiment results showing sample numbers and mean values (SE) by treatment for crown vine coverage (0 = 0% coverage, 4 = effectively 100%) and diameter growth rates (cm year^{-1}) before and after vine cutting in 1998

(a) Sample *n*	1998	2007	Deaths
Release trees	14	12	2
Partial release	8	7	1
Control	14	11	3
(b) Crown vine	1998	2000	2006
P-value	0·6671	< 0·0001	< 0·0001
Release trees	3·1 (0·12)	0·4 (0·15)	0·5 (0·18)
Partial release	3·3 (0·15)	1·1 (0·20)	2·3 (0·23)
Control	3·3 (0·12)	3·2 (0·16)	2·8 (0·18)
(c) Diameter growth	1995–1998	1998–2007	End − Start
P-value	–	–	0·0644
Release trees	0·18 (0·05)	0·53 (0·08)	0·41 (0·03)
Partial release	0·16 (0·05)	0·32 (0·09)	0·12 (0·09)
Control	0·15 (0·04)	0·33 (0·07)	0·11 (0·10)
Sample (vines 0–1)	0·61 (0·03)	0·77 (0·03)	0·04 (0·03)

Pre-release values for diameter growth (1995–1998) are for 2·5 years. Post-release (1998–2007) values are 9-year averages. The one-way ANOVA *P*-value for diameter growth is for treatment comparisons by End − Start time periods as explained in the text. For comparative purposes, corresponding values are shown for sample population trees > 25 cm diameter with crown vine coverage class = 0 or 1 (< 34%) in 1998 (n = 167 vs. 157 in 2007).

(1995–1998), release trees demonstrated markedly accelerated growth rates relative to partial release and control trees (one-way ANOVA, F = 3·04, P = 0·0644; Table 4).

Discussion

Our study demonstrates that prior growth is the strongest predictor of mahogany's performance at Marajoara. This mirrors recent studies which have found evidence for strong growth autocorrelation. Kammesheidt *et al.* (2003) and Brienen *et al.* (2006) both reported lag 1 correlation coefficients ranging from 0·6 to 0·7, similar to the value of 0·72 in this study. Regarding the persistence of autocorrelation, Fox, Ades & Bi (2001) suggested that an AR(1) process (Fig. 2) sufficiently captures growth autocorrelation, and the few attempts to incorporate autocorrelation in population models have implicitly used an AR(1) structure (e.g. Pfister & Stevens 2003; Bullock *et al.* 2004; Brienen *et al.* 2006). However, our results and those of Brienen *et al.* (2006) suggest that orders substantially greater than AR(1) are necessary to fully capture the strength of autocorrelation over time. Inclusion of higher order autocorrelation would further amplify the impact of growth history on modelled population dynamics.

What accounts for the strong persistence of growth differences among trees over time? Possibilities include: (i) explanatory variables (e.g. crown vine coverage) remain constant over time; (ii) growth capacity varies among trees because of differences in crown form and size; (iii) cryptic microsite differences in soil fertility or water availability; or (iv) genetic differences. We found that the effect of autocorrelation remains strong even after accounting for other variables. The slow recovery in diameter growth rate observed in the vine release experiment suggests that explanations (i) and (ii) may both contribute substantially to persistent growth autocorrelation.

After growth history, year of observation was the strongest predictor of variation in diameter growth rates, suggesting that mahogany trees may respond to exogenous factors such as annual variation in rainfall totals or its seasonal timing (Dünisch, Montóia & Bauch 2003; Brienen & Zuidema 2005; Chidumayo 2007).

That crown vine coverage was an informative characteristic about tree performance is not surprising. Vines compete

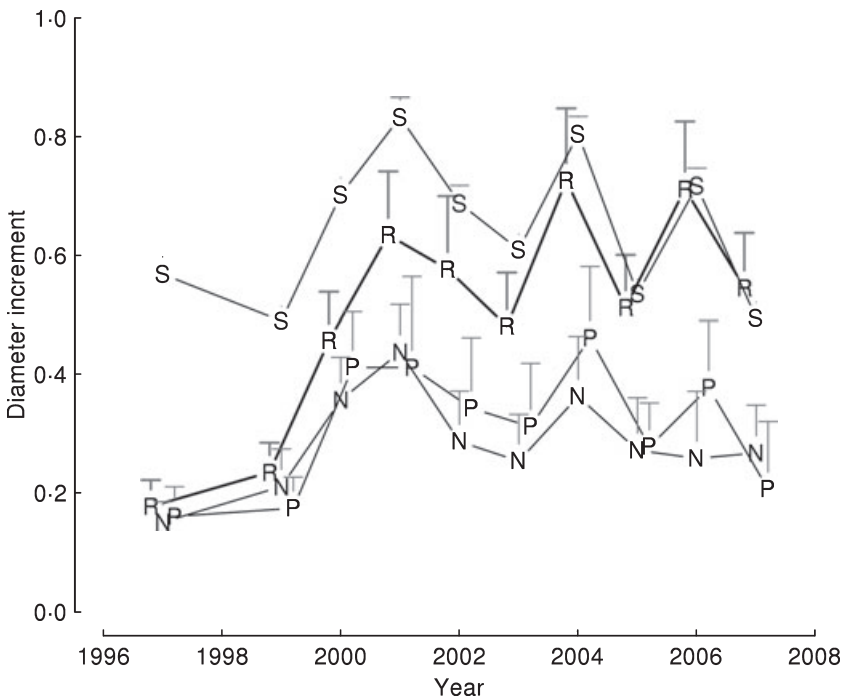

Fig. 3. Diameter growth rates (cm year^{-1}) by trees in the vine release experiment. Data for year 1997 represents annualized growth rates during 2·5 years (1995–1998) prior to vine cutting; all other intervals are for the indicated year. Groups are slightly offset from the indicated year for clarity. Letters indicate performance by treatment as follows: R, release; P, partial release; N, no release (control); S, sample population trees with minimal or zero crown vine coverage (scored 0–1). One-sided error bars show one standard error (SE).

directly with tree crowns for light without paying equivalent structural costs for arriving in the forest canopy (Putz & Mooney 1991). Mahogany tree crowns may be so heavy-laden that live leaves cannot be detected beneath solid masses of competing vegetation. In trees with lighter vine loads, flowers and fruit generally appear only on branches free of vines. Though removal of vines substantially increased diameter growth rates, the effects were not realized for several years, likely because of reduced crown size caused by previous vine coverage. We observed widespread adventitious sprouting and subsequent expansion of leaf area in released crowns during the years following vine cutting when stem growth rates gradually accelerated, indicating that crown recovery was a necessary prerequisite to diameter growth recovery. This recovery sequence is further evidence that crown form and associated growth capacity play a strong role in determining growth autocorrelation through time.

These results demonstrate that vine cutting can be an effective management tool for improving tree health and diameter growth rates. These benefits are likely to be long-lasting compared with diminishing returns over time observed in stand-level thinning and liberation treatments (De Graaf, Poels & Van Rompaey 1999). However, vine release is not without its difficulties in complex and heterogeneous tropical forests; that eight of 22 released trees 'relapsed' despite repeated vine cutting underscores how difficult this treatment can be to implement effectively (Gerwing 2001). Managing future crop trees may thus require repeated entry during prescribed cutting cycles for vine cutting by experienced field crews. Even when vines are effectively removed from tree crowns, released mahogany trees may never rival same-sized or –aged unsuppressed conspecifics in terms of overall vigour and form.

Fast-growing trees within a given diameter size class will be those, on average, with minimal crown vine coverage and high crown illumination. These individuals are likely to have achieved fast growth rates because of past access to high light and freedom from heavy vine loads and thus tend to be younger than expected based on median or mean growth rates (Terborgh *et al.* 1997; Landis & Peart 2005; Brienen *et al.* 2006). Fast-growing trees also have greater survival probabilities, so that a population's largest, most dominant trees may represent a mixed-age cohort of continually recruiting, relatively youthful, robust and lucky individuals. Slow growth rates by extremely large trees may indicate that anatomical and physiological limits on size have been reached for a given site, not that they have grown slowly over their lifetimes and are therefore very old. Given the variability in growth rates within size classes and the tendency for large trees to represent only the fastest growers, size distributions should be interpreted with care; simple relationships between size and age should not be assumed.

These findings have important implications for demographic models of mahogany and similar tropical tree species (Grogan *et al.* 2008; Schulze *et al.* 2008). Our analyses suggest that performance is, at best, weakly related to tree size, indicating that population models based on size alone, such as matrix models, poorly represent the sources of variation present within the population. Rather, we found that the single strongest predictor of future performance was previous growth, strongly emphasizing the importance of incorporating this factor as a predictor variable in population models (Pfister & Stevens 2003). As Brienen *et al.* (2006) have shown for tropical trees, models that do not incorporate growth history underestimate variability in size for a given age and overestimate the minimum number of years required to reach a given size. By correcting these deficiencies, growth and yield models could become more effective tools for evaluating long-term consequences of current logging practices and for designing sustainable harvest systems for threatened timber species like big-leaf mahogany.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Mahogany sample population characteristics during 1997–2007

Table S1. Published diameter growth and mortality rates for natural populations of big-leaf mahogany

Table S2. Estimated parameter values for the correlation structure used in the AR(7) growth model

Table S3. Estimated coefficients for variables in the reduced AR(7) growth model

Table S4. Estimated coefficients for variables in the final mortality model

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