RESEARCH NOTE

Regeneration of mahogany (*Swietenia macrophylla*) in the Yucatan

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SUMMARY

Low rates of natural regeneration of big-leaf mahogany (*Swietenia macrophylla* King) were found in gaps due to felling and natural treefalls in the Yucatan. This finding is consistent with low post-logging abundances of reproductive-sized trees as well as relatively low growth rates of planted mahogany seedlings in small felling gaps. High growth rates of seedlings in large felling gaps and landings provides optimism that the extensive plantings done in the region will provide timber in the future. The long-term effects of shoot borers, which predominantly attack the fastest growing seedlings, are uncertain.

INTRODUCTION

Low rates of big-leaf mahogany regeneration in felling gaps after selective logging have been reported across the species' range (Verissimo *et al.* 1995, Gullison *et al.* 1996, Snook 1996). This problem is persistent despite long standing, though sporadic, efforts in mahogany silviculture (e.g. Stevenson 1927, Lamb 1966, Snook 1998, Brokaw *et al.* 1998).

Mahogany is a relatively shade-intolerant species widely distributed through the seasonal American tropics (see reviews in Lamb 1966, Gullison *et al.* 1996, Snook 1996, 1998, Mayhew and Newton 1998). Regeneration occurs primarily from non-dormant, wind-dispersed seeds. Logging removes reproductively valuable trees thereby reducing post-logging seed rain, a problem exacerbated in the Yucatan by early dry-season logging before seeds are shed (Snook 1996).

High rates of mahogany regeneration under natural conditions have been found to occur after intense fires (Snook 1996), on river-deposited sediments, on eroded soils (Gullison *et al.* 1996), and in areas in which floods have caused extensive mortality. In these sites, an open canopy, reduced densities of understorey vegetation, and the preparation of a seed bed appear to favour mahogany. Selective felling is thought to produce inadequate disturbance conditions for mahogany because it does not open the canopy enough and leaves too many understorey stems behind that would compete with mahogany seedings (see, e.g., Snook 1996, 1998).

In this paper, we document low rates of natural regeneration of mahogany in both felling gaps and natural treefalls (natural gaps) in a selectively-logged forest in southeastern Mexico. We then present evidence, including the results of a planting experiment, which suggest that both seed limitation and inadequate site conditions contribute to the problem.

STUDY SITE AND SAMPLING METHODS

The study was conducted in the 18,000 ha forest owned by the community of Noh Bec in Quintana Roo, Mexico. The study site is discussed in detail in Dickinson (1998) and Snook (1993). The forest is semi-deciduous (Pennington and Sarukhan 1968) and has been classified as tropical dry forest in the Holdridge system (Whigham *et al.* 1990).

Small-scale treefall gaps (natural gaps) are the prevailing natural canopy disturbance between large-scale natural disturbance events (i.e. fire and hurricanes). Logging intensities have been low, averaging 1-3 m^3 ha^{-1} (see Arguelles 1991 and Snook 1998 for discussions of management practices). Felling is done to a diameter limit (55 cm DBH for mahogany and 35 cm for smaller species) and rubber-tyred skidders are used to skid logs to landings. Portions of the study areas discussed in this paper had been logged once prior to the most recent logging event. Natural gaps are somewhat smaller than felling gaps on average (55 vs 77 m^2, see Dickinson 1988, Whigham *et al.* 1998). Large natural and felling gaps are uncommon and reach a maximum size of about 250 and 450 m^2, respectively.

Natural regeneration

To estimate rates of mahogany regeneration, felling gaps ranging in age from 4 to 11 years and natural gaps that were estimated to be within that age range were sampled over 1500 ha of logged forest along the western side of the forest (as described in Dickinson 1998). Canopy gaps were defined as vertically projected holes $\geq$20 m^2 that extended down through the canopy to the average height of the regenerating vegetation (modified from Brokaw 1982).

The natural regeneration data we present are from two samples. In the first sample, the tallest 10 stems $\geq$1.5 m in height that occurred over the entire area of each natural (n = 48) and felling gap (n = 68) were identified to species. These tall stems were assumed to be those most likely to occupy the future canopy. For this sample, a single natural and a single felling gap were selected at random along each of 68 transects. The transects were 0.5 km long and were begun at random locations along a logging road running through the sample area. The side of the road on which to run the transect was also randomly determined. Natural gaps were uncommon and were not encountered within 200 m of some of the transects.

In the second regeneration sample, we enumerated all stems and measured their heights in square, 10 m^2 plots established in natural gaps (n = 36), felling gaps (n = 41), and closed-canopy sites. The gaps were a subset of the ones in which tall stems were sampled. A single closed-canopy site (defined as an area without evidence of a recent gap) was randomly chosen along each of the transects on which plots were sampled in gaps. To increase replication of closed-canopy sites, eight sites sampled for another study in the same area are also included (total n = 49). Five adjacent plots were sampled in each closed-canopy site. As many adjacent plots as would fit into a given gap were sampled (except for several large gaps in which a randomly chosen portion of each gap was sampled). The number of plots in gaps ranged from one to 12.

As an indirect test of the effects of propagule limitation on natural regeneration of mahogany, we use univariate regressions to relate frequencies of occurrence of tall stems in gaps to the relative abundances of reproductive individuals. Lacking detailed data, reproductive size was somewhat arbitrarily assumed to be 30 cm DBH and over. We defined canopy species as those which reached a maximum diameter larger than the maximum diameter of the smallest logged species in a forest inventory of approximately 2500 ha of Noh Bec (Sociedad Civil de Productores Forestales de Quintana Roo, unpublished data). Thus, our canopy species are those that are either logged or, given their size, are potential logging species. For analysis, data were $\log_{10}$ transformed (after adding one) to better satisfy the homogeneity of variance assumption of parametric regression.

Planted seedlings

To determine the suitability of new felling gaps (n = 48) and landings (n = 11) as sites for mahogany seedling growth and survival, we marked and measured the heights of 10 seedlings in each site during October and November 1996 within days after they were planted. Seedlings were grown in plastic bags in the Noh Bec nursery from seed collected from trees felled in February and March of 1996. Ten seedlings were planted in each felling gap while seedlings were planted over the entire area of each landing. The spacing between plants was approximately 2 m. Canopy gap area was measured as the vertically projected hole in the canopy that extended down to an average height of $\leq$2 m above the forest floor (Brokaw 1982).

In July 1998, as part of an ongoing study, we made a census of the marked seedlings and calculated rates of growth, mortality, and shoot-borer (*Hypsipyla grandella*) attack. Using univariate regression, we relate relative height growth of the most quickly growing seedling in each site to canopy-gap area. Both variables were $\log_{10}$ transformed to better satisfy the homogeneity of variance assumption of regression. Also, using the nonparametric Spearman rank correlation method, we relate percentage of plants attacked by shoot borers in each site to the average rate of growth of the seedlings.

RESULTS AND DISCUSSION

Natural regeneration rates

Mahogany was the most heavily logged species from 1984 to 1990, accounting for 47% of felled trees, yet it did not occur among the tallest stems in any felling gap. Similarly, no tall mahogany stems occurred in the sample of natural gaps, though only one natural gap was created by the fall of a mahogany. Relatively small mahogany seedlings and saplings occurred at low densities below a closed canopy and in felling and natural gaps (Table 1). Small sizes and low densities of mahogany below a closed canopy are consistent with reduced survival and low growth rates in shaded

TABLE 1 *Natural regeneration of mahogany in closed-canopy sites and natural and felling gaps. Data refer to mahogany stem densities, the percentage of closed-canopy sites or gaps in which mahogany stems occurred, and the mean and range of stem heights.*

		Closed canopy	Natural gaps	Felling gaps
Stem density (ha^{-1})		16	51	138
Occurrence (%)		6	14	22
Stem ht. (cm):	mean	21	57	58
	range	16-30	17-178	18-300

environments for this shade-intolerant species. Densities of mahogany were too low to allow meaningful statistical comparison among sites.

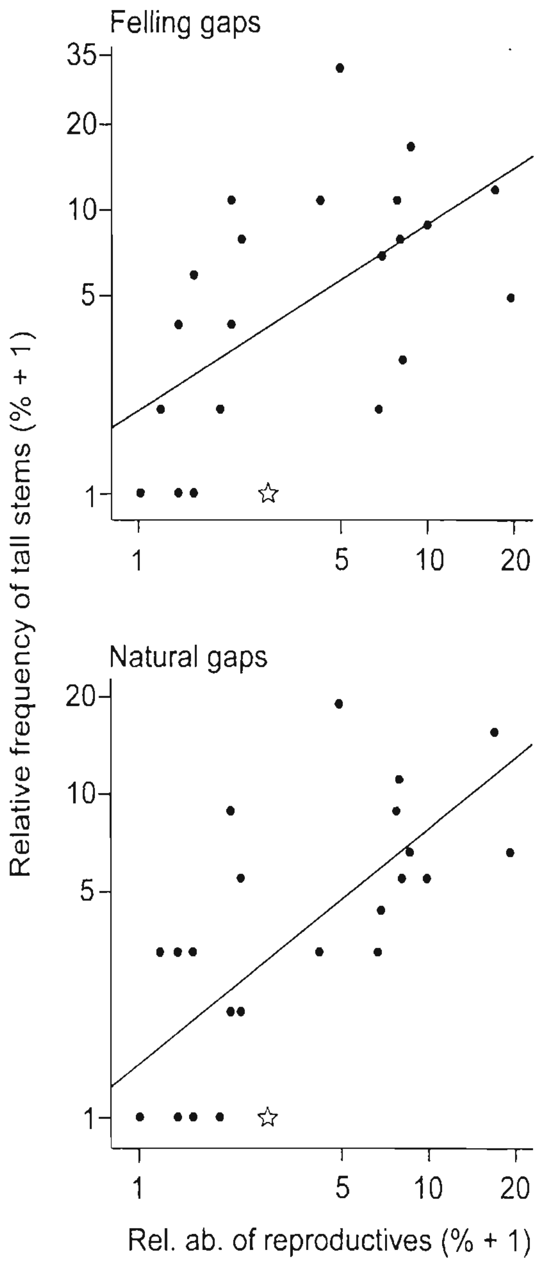

FIGURE 1 *Relative frequencies of the tallest stems in felling ($F_{(1,23)}$ = 11.93, R^2 = 0.34, P = 0.002) and natural gaps ($F_{(1,23)}$ = 24.11, R^2 = 0.51, P <0.0001) as a function of post-logging relative abundances of reproductive trees. Only canopy species are included (see text) and mahogany is indicated by a star. Relative abundance is the number of reproductive stems of each species divided by the total number of reproductive stems of all canopy species in a point-centered quarter sample of trees conducted systematically over the sample area. Relative frequency is the percentage of gaps in which a species was present among the sample of tall stems. Axes are log_{10} transformed (after adding one) as in the regressions.*

Seed limitation

A positive relationship between the frequencies of canopy species' tall stems in felling and natural gaps and the relative abundances of reproductive trees suggests that, within broad limits, mahogany regeneration is limited by seed availability (Figure 1). Mahogany and other shade-intolerant species regenerated primarily from seeds and small seedlings. A handful of species, mainly shade intolerant, sprouted adventitiously from their roots after felling disturbance. Shade-tolerant species regenerated mainly from advance growth (Dickinson 1998).

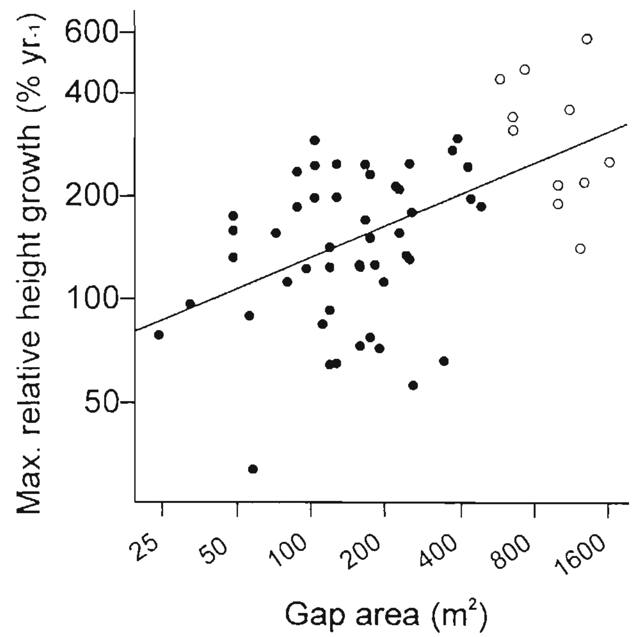

FIGURE 2 *Relative growth rates of the most rapidly growing stems in felling gaps and landings as a function of gap area ($F_{(1,57)}$ = 21.86, R^2 = 0.28, P < 0.0001). Relative growth is the percentage increase in height per year over the sample period. Felling gaps are represented by the filled symbols while the open symbols are landings. Variables are log_{10} transformed as in the regression analysis.*

Disturbance conditions

In addition to seed limitation, lack of suitable disturbance conditions has also been implicated in the poor regeneration of mahogany in selectively-logged forests (Snook 1996). Growth (Figure 2) and mortality rates of planted seedlings suggests that disturbance conditions in large felling gaps and landings are adequate for growth and survival of mahogany seedlings. Mortality rates were low, averaging 12.6 % yr^{-1}. Seedlings averaged 37 cm in height (range 11-76 cm) at planting. Planting overcomes barriers to germination and early growth and survival in felling disturbances and landings, though, the importance of these barriers are unknown at present.

Shoot borers had killed the upper meristem at least once during the sample period on 15.4 % of the planted seedlings. The rate of attack was positively correlated with the average growth rate of the seedlings in each site (see Figure 3). It is not clear whether this result is purely a function of gap area or also related to positive density-dependent attack rates stemming from higher overall abundances of planted seedlings in the landings.

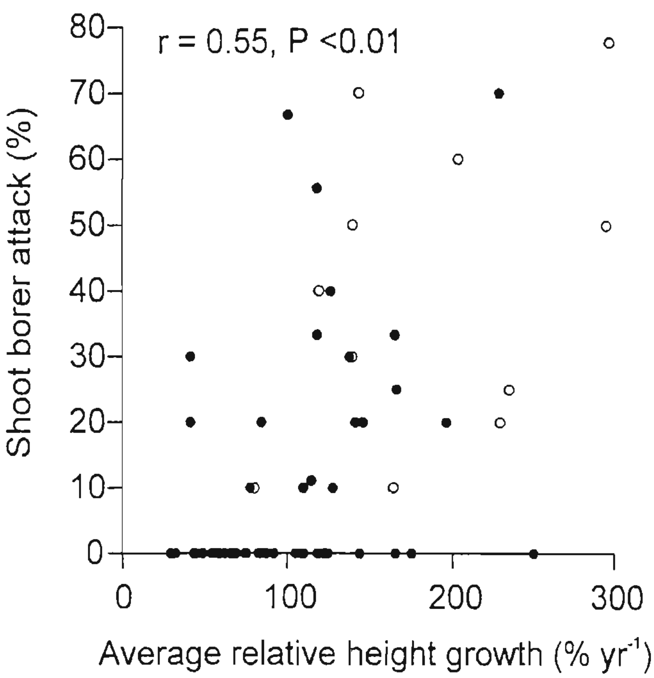

FIGURE 3 *Correlation between the percentage of planted seedlings attacked by shoot borers and relative growth rate. Felling gaps are represented by the filled symbols while the open symbols are landings. The nonparametric Spearman rank correlation coefficient is reported.*

High rates of attack on the most rapidly growing seedlings may be of greatest concern relative to the long-term success of the planting programme (see review in Mayhew and Newton 1998). Though results from a one-time sample of enrichment plantings in landings in the region suggest that saplings continue to grow rapidly after shoot-borer attack (Sanchez Rejon 1994), the more important effects of shoot borers may be on stem form. In landings, overall stem densities often remain low for many years and in consequence there is little lateral shading to inhibit the development of multiple leaders (Dickinson, personal observation).

CONCLUSIONS AND RECOMMENDATIONS

Natural regeneration rates of mahogany following highly selective logging were exceedingly low in this southeastern Mexican forest. No mahogany saplings likely to attain the canopy were found in either felling or natural gaps, although low densities of relatively small stems were found in gaps and below a closed canopy. Low rates of regeneration of mahogany appear to be related, at least in part, to low adult relative abundances after selective logging.

Early planting results provide optimism and suggest that disturbance conditions are adequate for mahogany seedling growth and survival in large felling gaps and landings. Every year, many thousands of seedlings are planted in Noh Bec and other forests in the region (Sanchez Rejon 1994, Snook 1998). Greater efficiency in these efforts could be gained by not planting in small felling gaps and along skid trails where canopy opening is minimal. Long-term effects of shoot borers on stem form require monitoring.

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